Colin Patterson (1933 – 1998)

Colin Patterson was born in Hammersmith on 13 October 1933. He was educated at Tonbridge School and, after National Service, graduated in 1957 from Imperial College with a degree in Zoology (Parasitology). Between 1957 and 1962 he was a lecturer in Biology at Guy's Hospital Medical School during which time he was awarded a PhD by the University of London. In 1962 he joined the Palaeontology Department of the British Museum (Natural History) – now The Natural History Museum – where he remained until his retirement in 1993. He was awarded the Zoological Society of London's Scientific Medal in 1972 and the Linnean Society Gold Medal posthumously in 1998. He was elected a Fellow of the Royal Society in 1993.

Some of the participants in the Library of the Linnean Society, 17 July 1998.

Preface

On the afternoon of Friday 17th July 1998, The Linnean Society of London held a special meeting to celebrate the life of one its most respected fellows: Colin Patterson (1933–1998).

Colin had not only been a most ardent and long-serving member of the Society (Council 1970–73, 1979–85; Vice President 1980–82; Zoological Editor 1978–81; Editorial Secretary 1982–85) but also an outstanding scientist. He was a pioneering advocate of the methods of biological classification now known as cladistics, the world's leading palaeoichthyologist, a well-respected researcher in the field of molecular systematics, and an effective and original communicator of evolutionary theory.

What follows is a written transcript of that meeting. We have tried to retain the flavour of the oral communication, editing just enough to translate speech to prose, as well as to make the contents accessible to those who were not there or did not know Colin or his work as well as others. Some repetition is evident since certain events, recollections, impressions affected more than one of our contributors. We see this as emphasising the strongest points of Colin and his science. Also, the names of certain people recur throughout and we have included brief biographical details in an Appendix.

The afternoon concluded with the presentation to Colin of a posthumous award of the Linnean Gold Medal, presented by the President of the Society, Sir Ghillean Prance, and accepted by his daughter, Sarah Patterson.

The meeting was organised by Peter Forey and Brian Gardiner.

In addition to the presented talks, five additional written contributions are included here (Forey, Gardiner, Gooding, Goodwin, Grande) with justification given in the opening remarks – *How it came about.*

Peter Forey
Brian Gardiner
Christopher Humphries

30th November 1999

How it came about

BRIAN GARDINER

This special issue of *The Linnean* is devoted to the life of Colin Patterson and contains papers presented during the day held in the Society's rooms to celebrate his life. That meeting was prompted by the number of e-mails and letters which poured into the The Linnean Society and the Natural History Museum following his sudden death in March 1998. So many people wrote expressing condolences and immediate thoughts on how Colin had affected their lives, academically and socially, that it seemed to me inevitable that we organise some celebratory day to recognise the impact that Colin had on the way that systematic biology had progressed during the last quarter of this century. I am also aware that he and I grew up together in our parallel academic careers (more about this later) and saw so much happen that a record of the last 40 years may have more than a passing interest to readers. I hope that, as well as being a celebration of his life, it will be a record of changing paradigms and advances in science. During this time we have seen a revolution in systematics, the kinds of data that have been made available to systematists, the way museums work and the way that funding of taxonomy in this country is organised.

To organise this day we invited people who were particularly closely associated with Colin and his work, as well as being associated with him in the broader academic social circle. Two longer papers read by Gary Nelson and Dave Johnson recorded Colin's contribution to systematic theory and to the study of fishes, the central themes of Colin's academic life. Further papers read by Andrew Smith, Tim Littlewood, Niels Bonde and a written submission by Lance Grande described how Colin influenced so many people in various fields of palaeobiology and systematics. The remainder of the contributions touched on the many disparate but highly significant ways in which Colin, as a scientist with a remarkable presence and power of argument, instilled confidence and a sense of direction in those around him.

Of all the contributors to this issue I had known Colin the longest and although I cannot claim to have worked with him as closely as others who record their collaborations in this volume, I can recount the early years of his career through personal association.

I first met Colin in the autumn of 1954 when he joined Imperial College as a first-year student and I was in my third year. I specialised in entomology and he in parasitology. However, our careers were to assume similar pathways. In

the summer of 1954 I was awarded a vacation studentship to work in the Department of Palaeontology at the British Museum (Natural History) and two years later so was Colin. At these two separate points in time we had also decided to embrace vertebrate palaeontology because we imagined that we would be studying the very evidence of evolution. At the British Museum (Natural History) we both worked for Harry Toombs, who in turn was Errol White's assistant; consequently, our vacation training was entirely on fossil fishes.

When I graduated in 1955, I was offered a PhD position at University College, University of London, by Kenneth Kermack. On his advice I talked to Professor Emeritus D.M.S. Watson, concerning possible projects for a PhD. Watson suggested the Liassic Fish Fauna. When Colin graduated he already had a wife to support and so applied for a salaried position as Lecturer in Biology at Guy's Hospital Medical School; during his first year he decided to study part-time for his PhD. With my prompting he also went to see Kermack who agreed to act as his academic supervisor; meanwhile, White suggested that he work on Cretaceous Fishes from the English Chalk. This was very good advice because these fossils were very amenable to acetic acid preparation, a technique developed by Toombs and Arthur Rixon (a skilled preparator in the BM[NH]) which yielded a mass of new anatomical information.

From time to time during the spring and summer of 1958 our paths crossed as we worked in the BM(NH) on our respective fishes. A comradeship developed which became friendship. Later that year I joined the staff of Queen Elizabeth College as a junior lecturer. Four years later Colin joined the staff of the BM(NH) as a Scientific Officer. Our respective institutions were barely a mile apart and as our scientific interests were so close we saw a great deal of each other.

We both joined the Linnean Society, mainly as a result of Errol White (PP Linnean Society, 1964–67) who explained to Colin that it should be his scientific charity! In 1968 we both contributed to White's Festschrift, entitled 'Fossil Vertebrates' *(Zoological Journal of the Linnean Society*, **47**) which was co-edited by Colin and Humphry Greenwood. In 1973 we also contributed to the Festschrift for Professors Stensiö and Jarvik: 'Interrelationships of Fishes' (Supplement No. 1 to the *Zoological Journal of the Linnean Society,* **53**), edited by P. Humphry Greenwood, Roger S. Miles and Colin Patterson. Colin was a brilliant editor and was eventually persuaded to become first the Zoological Editor (1978–81) and then Editorial Secretary (1982–85) of the Linnean Society. During that period he read every zoological paper that passed through the Society's journals, critically correcting facts, grammar and typographical errors. By this stage of his career he had become a veritable storehouse of information and I cannot remember a month going by when I didn't ask him a question on Darwin, evolution or the relationships of some particular animal

or plant. He invariably knew the answer and always delivered it in good humour, realising that I needed the information either for teaching or maybe for a *Linnean* editorial.

I only ever wrote two papers with Colin and these were both concerned with the problem of the origin of tetrapods. The first, in conjunction with two other colleagues, Donn Rosen and Peter Forey, was entitled 'Lungfishes, tetrapods, paleontology, and plesiomorphy' *(Bulletin of the American Museum of Natural History* **167**, 159–276, 1981) and challenged a textbook scenario of the transition of vertebrate life from water to land, thereby earning us the infamous title of 'The gang of four'.

In 1996, through the auspices of Academic Press a new edition of *Interrelationships of Fishes* was produced as a Festschrift for Colin, this time under the editorship of Lynne Parenti, Dave Johnson and Melanie Stiassny. In it Bobb Schaeffer and I endeavoured to write an introductory chapter outlining Colin's academic achievements. But such an attempt was of necessity biased by its restricted authorship. Gathering many people here will, we hope, offer a broader and more rounded documentary, set in a wider academic field as well as allow his friends and colleagues to offer differing viewpoints of Colin as scientist and friend.

The Linnean Society,
Burlington House, Piccadilly, London W1

Contributions to systematics

Ancient perspectives and influence in the theoretical systematics of a bold fisherman

GARETH NELSON

I have growing sympathy with the position in which Thomas Huxley found himself in August 1894, at the meeting of the British Association at Oxford. This was 34 years after a similar meeting, when he jousted with Samuel Wilberforce, the resident Bishop. This older Thomas "hauled his faltering frame to the edge of the platform and struggled to make himself heard" (Moore, 1991:354). He spoke about his previous 30 years. He acquitted himself well. So, too, did Colin Patterson, in March 1997, at a meeting in Paris. He opened that meeting with his presentation "Molecules and Morphology, Ten Years On", in which he said (1997:1): "I suppose it's traditional to begin a meeting by putting up some old buffer to talk about the past". He spoke about the previous 30 years and the last decade in particular. He compared the meeting with a similar one that he had organized in Sussex in 1985 for the Third International Congress of Systematic and Evolutionary Biology. He (1987a) edited the proceedings which appeared as a book: *Molecules and Morphology in Evolution: Conflict or Compromise.*

I was asked to speak here about Colin's theoretical work in systematics, how it was influenced by those around him and how it influenced others. Now I play the old buffer talking about the past 30 years, in particular the development of cladistics – the cladistic revolution in paleontology, in which Colin was the major player. Those times were chronicled in a lengthy book by David Hull (1988). Colin and I had similar experiences with David, who would write a section or chapter and then send it round for comment. I remember going through a few cycles of comment, revision, request for more comment, and so on. It seemed to me that whatever comment I made, to the effect that "No, David, that was not how it happened, but rather...," caused subsequent revision to move ever further from the historical truth. Colin continued trying to help him long after I gave up. Years later Colin remarked to me that David's book,

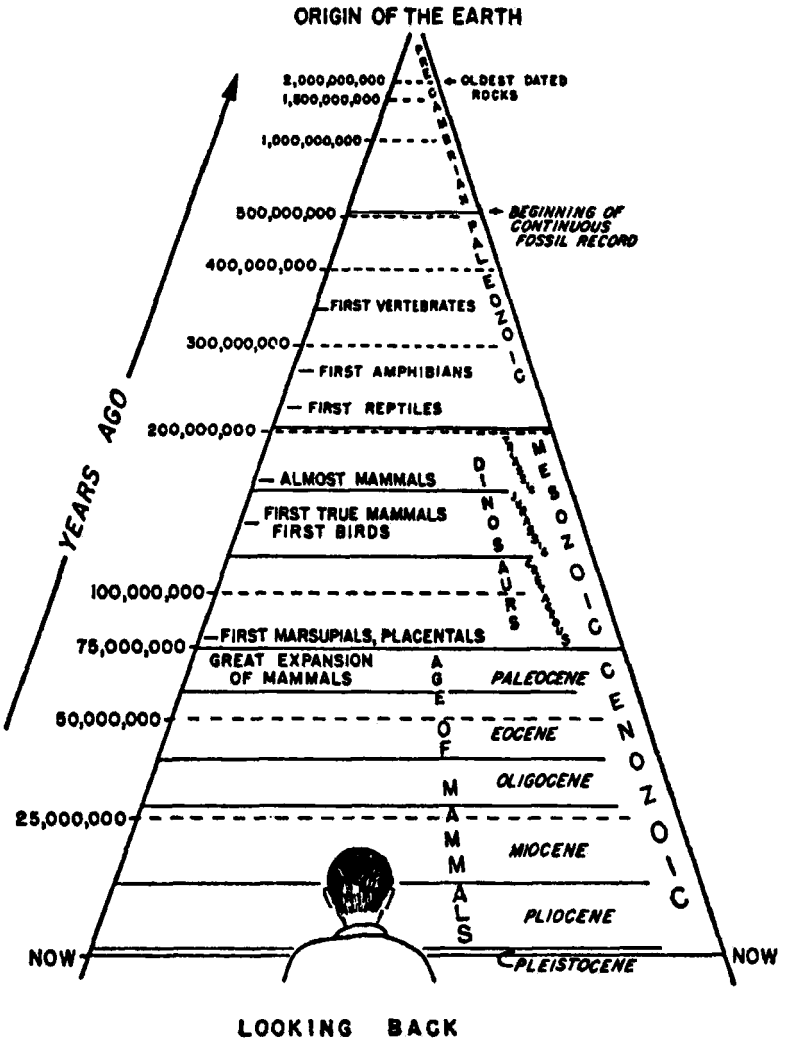
even if wrong in particulars, was not too misleading in generalities. That might be true, but I still wonder how that is possible.

Seeking some other point of reference, I re-read a different book, first published in 1974. I had read it years before because of something Colin said about it. I was surprised to discover how little I remembered of it. I had a new reprint with an Afterword, another retrospective piece – another "ten years on" – which begins (Pirsig, 1989:417):
"This book has a lot to say about ancient Greek perspectives and their meaning but there is one perspective it misses. That is their view of time. They saw the future as something that came upon them from behind their backs with the past receding away before their eyes. When you think about it, that's a more accurate metaphor than the present one. Who really can face the future? .. And who really can forget the past? What else is there to know?"

I can think of a few things, but in deference to the ancient perspectives (e.g., Simpson, 1953:fig. 2; cf., 1996:12*), I'll begin with Colin's PhD thesis, borrowing from his Annual Address to the Systematics Association of 1995. In the address, unpublished, he said (1995:2): "I rather wanted to work on early Palaeozoic vertebrates, because I'd picked up a common belief – the older the fossils, the more significant they are".

He received his PhD from University College London in 1961. During the previous three years he did the work at the British Museum (Natural History), and became employed there beginning in 1962. He said (1995:3):
"to get a PhD topic on fossils I had to go to the fountainhead, the BM(NH) and face Errol White [Patterson and Greenwood, 1967, frontispiece], Keeper of Palaeontology, expert on fossil fishes, and perhaps the most forbidding figure in London biology, with [J.B.S.] Haldane as his only competitor.... As a PhD student you didn't argue with Errol, and he put me on to Chalk fishes – the chalk is the late Cretaceous, roughly 75 to 100 million years ago. So to my disappointment, I couldn't work on the glamorous Palaeozoic fossils at the

* "That other time universe, the universe of time-dimension, might be said to consist of the past, but that is a crude way of putting the matter. The present cannot be measured [!]. It has no duration. Our familiar seconds, minutes, hours, days, and years are measurements of the past. The past is linear. It has only one dimension and only two directions: away from and toward the present. In fact, you might consider the present as the growing point of the past, much like the tip of a plant shoot that is steadily growing upward from the ground.
The past has a reality, an objective and eternal existence, even more truly than does the present. The growth of the past is conditioned and determined by the whole of that past as existent up to any given present. Even intuitively, we feel that existence and reality demand duration. Yet the world of our senses, that in which we have our subjective beings, is the present, only, and is without duration. Duration demands eternal existence in another universe, the time-dimension universe, or, so to speak very loosely, in the past. It follows, of course, that the future does not exist and has no reality in any sense of the word."



Looking back down the road of time. Geological time is seen in perspective, with approximate dates in years before the present to the left and technological geological names for subdivisions of time to the right. The dates of some important events in the history of the backboned animals (vertebrates) are indicated. (Simpson, 1953: 11).

root of the tree [of vertebrates], but had to tackle the rubbish up at the top, teleost fishes. But there was one plus point – Harry Toombs, who worked with Errol White in the Museum, had invented acid preparation of vertebrate fossils a few years before I came along, and chalk is ideal stuff for acid. For my first experiments with acid and Chalk fishes, Harry ... naturally gave me the worst specimens of the commonest things, and it happens that the commonest teleosts in the chalk are the most advanced, the spiny-finned fishes or acantho[pts], which first appear in the late Cretaceous but are the dominant fishes today. Anyway, I spent months

dunking lumps of chalk in and out of 2% acetic acid, and soon discovered that once you dissolved the chalk away you got something almost like a Recent skeleton; I could find all the details of the braincase ..., same thing with the jaws, palate, paired fin girdles.... I could describe these things in such excruciating detail that for my thesis I stuck to seven or eight genera from the chalk, the acantho[pts] and what seemed to be their immediate relatives".

Harry retired from the Museum in 1969, and died in 1987. Colin wrote (1987c:191) that Harry's "techniques of acid preparation ... revolutionised the study of vertebrate fossils". Colin was one of the first persons to benefit from that technological advance.

Thanks to Errol White, Colin's thesis (1964) was published by the Royal Society. It favourably impressed everyone. It embodied the highest standards. It extended our knowledge of these fishes beyond the distinguished accomplishment of Arthur Smith Woodward as set down in his classic monograph, of seven small volumes, published between 1902 and 1912, *The Fossil Fishes of the English Chalk* (Woodward, 1902–1912), one of the memorable titles in the history of ichthyology.

Colin's results (1964, Fig. 103) he summarized in a diagram, showing various Mesozoic beryciforms (fishes of the Chalk) and certain Recent perciforms (fishes alive today). He found that the diversity of the fossil beryciforms matched some of the diversity of the perciforms. He concluded that various fossil beryciforms are ancestral to various living perciforms – that the perciforms as a group, having more than one origin, are polyphyletic. He said (1995:5):
"I ended my thesis with this awful diagram..., using solid lines to show stratigraphic ranges and broken lines to show gaps in the fossil record and inferred relationships with Recent fishes.... I thought I'd found evidence that Recent [perciforms] are polyphyletic, with various groups originating independently from different groups of Cretaceous beryciforms. Polyphyly was the fashionable concept then, in the fifties and early sixties, and there were experts advocating polyphyly, demonstrated by fossils, for almost every major group of vertebrates."

Polyphyly – "the fashionable concept" – he afterward went beyond. He wrote (1978b:99): "I remember the period, ten to fifteen years ago, when it was fashionable to regard many vertebrate groups as polyphyletic, and I have seen those ideas die away". He came to see "the fashionable concept" not as a discovery but rather as one of a series of preconceptions, prejudices one might say, forming, in his words (1977:634) "the traditional method of phylogenetic paleontology, which produces ancestral groups or ancestor-descendant sequences". This traditional method in paleontology, the search for ancestors in ichthyology, he traced (1977:619) to Smith Woodward – back to Sir Arthur:

"During the first two-thirds of the twentieth century, it is my impression that ideas on teleostean phylogeny were profoundly influenced by Woodward's 'Catalogue [of the Fossil Fishes of the British Museum],' published from 1889–1901 [Woodward, 1889–1901]. And in the discussions of teleostean phylogeny in those works, and in others, the fossils were given pride of place and treated on the pattern laid down by Woodward."

Now why Woodward? Colin explained (1977:597):
"In preparing the four volumes of the 'Catalogue...,' Woodward reviewed all the literature, examined every specimen in the British Museum, and visited every other museum or collection of note in the world. Thus he achieved the same position of authority as Agassiz 50 years before, that of the man who has seen everything."

Colin described the consequences (1977:620):
"After Woodward had stated the claims of paleontology to lead in phylogenetic work on teleosts, ichthyologists accepted those claims, and sat back to await the answers that fossils alone could produce. But paleontologists failed to deliver the goods – specific ancestors, or any new insight on the inter- relationships of extant teleosts: when progress of that sort did come [in 1966], it was achieved, as in the nineteenth century, by comparative studies of Recent fishes."

The traditional search for ancestors and its implications are recurrent themes in Colin's publications. For him (1981a:219):
"Evolutionary relationship includes an additional type, ancestor-descendant relationship. And it is this type that fossils are expected to document. When viewed as relationship between two groups, descent means that one (the ancestral group) is paraphyletic – characterized only by lack of homologies rather than their presence. Most fossil-based theories of relationship concern such groups. The superficial attraction of these stories, apparent illumination of the history of life, has bolstered the belief that fossils determine evolutionary relationships. Yet extinct paraphyletic [ancestral] groups seem to me to obscure rather than illuminate relationships, for they exist not in nature but in the minds of evolutionists. Such groups lead to a sterile inversion of problems of relationships, which come to depend not on comparative analysis of what is accessible – the Recent biota – but on juggling what is inaccessible – uncharacterizable abstractions from the fossil record."

There are many more such accounts. In his book *Evolution* (1978a:133), published by the British Museum (Natural History), he did not mention any of these, more or less complicated, conceptions, only that "Fossils may tell us many things, but one thing they can never disclose is whether they were ancestors of anything else".

It is clear that his PhD thesis reflects the influence of Woodward and others, as it came to be embodied in "traditional method". He later (1995:5) commented rather caustically about his beginnings in ichthyology: "I had to pick up systematics like a performing monkey, trying to guess what would please the audience by imitating them." It is clear that he changed during a brief period in the late 1960s to arrive at that vantage point – of a more mature understanding – described long ago by Thomas Paine (1782, in Foner, 1945:243): "We see with other eyes; we hear with other ears; and we think with other thoughts, than those we formerly used. We can look back on our own prejudices as if they had been the prejudices of other people."

What influenced him? What helped him along? Consider an example of influence – by words printed on paper: the American Robert Aitken in 1998 writing of events of some 50 years before. He had been a civilian in Guam, the largest of the Mariana Islands in the Pacific. He was interned by the Japanese during the war. He wrote of the winter of 1942–1943 and his experience, at the age of 25, in his internment camp in Kobe, Japan (Aitken, 1998:23):
"One evening a guard came into my room, quite drunk, waving a book in the air and saying in English, "This book, my English teacher..." He had been a student of R[eginald] H[orace] Blyth ... and the book was *'Zen in English Literature and Oriental Classics*,' then just published. I was in bed but jumped up to look at the book and was immediately fascinated. I persuaded the guard to lend it to me, and weeks later he bought another copy for me so that he could have his own copy back. I suppose I read the book ten or eleven times straight through. As soon as I finished it I would start it again. I had it almost memorized and could turn immediately to any particular passage.... it set my life on the course I still maintain, and I trace my orientation to culture – to literature, rhetoric, art, and music – to that single book."

Blyth was born near London in 1898, the only child of working-class parents. He, too, was interned in Japan during the war. He died there in 1964 after a career in teaching, writing, and translating into English, much of it for the first time, the classic poetry of the Far East. Robert Aitken met Blyth when the various internment camps were combined. Robert recalled (Aitken, 1998:25) "If we had not met, I might well have spent my life mundanely, saying and doing trivial things".

This instance of influence is relevant because there was in 1966 a scientific publication that had upon Colin a similar influence, and in this respect he was not alone. The publication was a monograph on flies (midges) by the senior entomologist of the Swedish Museum of Natural History (Brundin, 1966). Colin (1995:9) spoke of events of some 30 years before:
"the week ... I got back from New York, ... I [was told] that there was something

Lars Brundin (left) and Gary Nelson, Stockholm – August 1988 [Photo CJH].

new in the Library that might interest me. It was this, ... Lars Brundin's 500-page monograph on chironomid midges, at first sight an unlikely place to find enlightenment. The Museum datestamp – 17th April 1967 – fixes the week when I first saw it. I don't know if anyone reads Brundin these days, but he was my first introduction to Hennig and phylogenetic systematics, what we now call cladistics. The first fifty pages of this are still a wonderfully clear and strong statement of Hennig's ideas. I was bowled over by it and became an instant convert."

Fifteen years later Colin was asked by the editors to write a chapter for the *Annual Reviews of Ecology and Systematics*, a book-length publication then in its twelfth year of existence. He wrote (1981a:195):
"Fifteen years ago, I think it inconceivable that editors should have offered, or a reviewer accepted, a title such as mine [*Significance of Fossils in Determining Evolutionary Relationships*]. After all, evolution is a theory about the history of life; evolutionary relationships are historical relationships; fossils

are the only concrete historical evidence of life; therefore fossils must be the arbiters of evolutionary relationships. Such an argument is implicit in most discussions of relationships during the last 120 years. As one recent example, Nash *et al.* [1976] write that 'The evolutionary origins and relationships of elasmobranchs are something of a mystery, due mostly to the lack of fossils.' These authors are biochemists, presenting their myoglobin sequence of a shark, but readers will recall similar statements in their own fields. Such beliefs epitomize the tradition in which I was educated, and influenced my decision to take up vertebrate paleontology. After ten years work in that field, I read Brundin [1966], and still recall the excitement with which I realized that there is a logical basis to evolutionary relationships which I had never seen discussed. Brundin was developing Hennig's thought [1950, 1965, 1966a], and in my view it is the dissemination and development of those ideas that have called the role of fossils into question, and necessitated this review."

He again commented (1989:472):
"The heart of Brundin's paper was one message: 'phylogenetics is the search for the sister group.' That message eventually got through, and among morphologists the cladists have won, in Hull's [1988] terms. Much of the hundreds of pages on systematic theory and method published by morphologists during the last 20 years is embroidery on and exploration of Brundin's message."

Why Brundin? His first 29 pages contain a digest of Hennig's notions, and then a criticism, original with Brundin, of vertebrate paleontology and its involvement with biogeography ("The shortcomings of the typological method"). This tradition as it developed among persons working on fossil mammals had been recently summarized by Philip Darlington (1957) of Harvard University, whom Brundin singled out for special attention. Hennig had dabbled with biogeography (Hennig, 1960, 1966b), but Brundin brought the subject into direct relation with vertebrate palaeontology and with the beginning revival of continental drift. Colin, among others, responded (1975, 1981b, 1981c, 1983a).

Do not misunderstand my focus on Brundin's 64-page introduction to the midges. Colin influenced, and was influenced by, many persons and things. Yet of the publications of the time, Brundin's had a unique significance, or quality, without which there would have been, in my opinion, a different history and, perhaps, a different Colin. Brundin's introduction did for the cladistic revolution what Thomas Paine's essay, *Common Sense*, did for the American Revolution (Keane, 1995:114): "Everyone who read and was convinced by [it] suddenly saw the world in a fundamentally different way."

Another influence on him, one which primed him for this change, was the publication in 1966 by his colleague Humphry Greenwood in the British

Museum and three Americans: Donn Rosen of the American Museum, Stanley Weitzman of the Smithsonian, George Myers of Stanford University, a publication subsequently known as Greenwood *et al.* (1966). Their conclusions they summarized in a diagram of relationships (their Fig. 1). Colin said (1995:7): "You can see from the diagram that Humphry Greenwood and his pals were still stuck in the morass of polyphyly – teleosts as a whole are polyphyletic, along three or four lines from some Jurassic fossils, and up here at the top there are other multiple origins,... with acanthopts coming along several lines from the things in my thesis, the Cretaceous ... beryciforms."

His vision is clear in retrospect. But in the mid 1960's he was struggling with teleostean polyphyly. He reported his first results at a meeting in Paris in June, 1966. He looked at some of the ancestor-descendant lineages (1967, Fig. 1) that had been proposed for the herrings and their relatives, the clupeoids, about 300 species alive today. Among the alleged ancestors were certain Mesozoic fossils. The herrings, as shown by Greenwood *et al.* (1966), have distinctive features, both in the head and the tail, which can be examined in well-prepared fossil material. He wrote (1967:99–100):
"These resemblances, many in characters which occur in no other teleost, are so detailed that it is difficult to believe that they could develop by convergence, yet according to the paleontological evidence they must have done, for none of these features is present in [the fossils]."

In herrings – all 300 species of them as we know today – certain bones in the tail, present in other fishes, are fused together. Consider Colin's drawing (1967, Fig. 7) of a Cretaceous fish tail, recognizable as that of a herring because of the fused bones (U1+H2). Consider the tail of one fossil "ancestor" (1967, Fig. 3). There are no fused bones. Consider the tail of another fossil "ancestor" (1967, Fig. 11). There is a complex of other bones that are fused together (D2+3+P1+U1). There is no evidence that the two fossils are related to herrings. If they are not related to herrings, the fossils are not ancestors of herrings. What evidence there is, is that one fossil is more primitive, a member of a group more inclusive than herrings – namely all 20,000 teleosts alive today; and the other fossil is a member of a group of teleosts other than herrings. Such is the lesson taught by cladistic analysis of an ancestral group, which disappears in the process. This is not a unique case. This, as Colin discovered, is always the case.

Here the influence is the fishes themselves, or rather what can be found out about them in the here and now – one of the possibilities for knowledge unmentioned by Pirsig in his afterword (see above). During his entire career, Colin seemed never to budge from this toilsome pit of the present. In his conclusions of 1967 he was tentative (1967:107):

"there is little evidence among fossil teleosts for polyphyletic origins of the group on any major scale. But the arbitrary nature of the line between the [ancestral group] and the teleosts and the abundant evidence of parallel evolution within the teleosts make it very probable that the line was crossed more than once."

Polyphyly: little evidence but very probable. Ten years later he noted (1977:611):
"the paleontologists chiefly responsible for the fossil lineages, are hardly to be blamed, for [before Greenwood *et al.*] no ichthyologist had previously shown how herring-like fishes were to be recognized, and the method employed by these paleontologists, the search for stratigraphic sequences of fossils which could be interpreted along ancestor-descendant lines, naturally led to assumptions of extensive parallel evolution – [polyphyly]."

Still later he noted (1981d:222):
"[Thomas] Huxley's attempt [with placoderms construed as catfishes] to extend the fossil record of teleosts into the Palaeozoic, though now virtually forgotten, initiated what later became common practice in palaeontology – driving lineages back into the past without regard to adequate characterization of the group (lineage) by comparative analysis of its living members. Hence evolutionary palaeontologists' predilection for supposed demonstrations of polyphyly."

By then he had gone through the problem of teleostean polyphyly once again with greater care, this time with Donn Rosen (Patterson and Rosen, 1977), a collaborator since 1967. Later still Colin wrote (1994a:73) "no one now doubts that the group [of teleost fishes] is monophyletic".

Teleosts once were thought polyphyletic, now they are thought monophyletic: what is the import? The ancestral group supplying the multiple origins was discovered to be an artefact of the traditional method – a group of fishes of diverse relationships. This is not an example of one "fashionable concept" replaced by another (what for Pirsig, 1989:118, is "the whole history of science, a clear story of continuously new and changing explanations of old facts"). It is an example of the demise of fashion – prerogative – and its rule. Colin wrote (1993c: 621) "The traditional ... method resulted in many extinct ... 'ancestral groups' which dissolve under cladistic analysis".

Things not so clear sometimes, thank goodness, become clear. For Pirsig they recede into the past and in perspective, as if by magic, become clarified – rather like the view of the paleontologist that a group has a polyphyletic origin. Or is the process, rather, that we see, or think we see, a pathway into the future and from evidence anticipate "what the facts, when fully known, will demonstrate to be correct" (Croizat, 1981:502)?

With Humphry Greenwood and Roger Miles in 1972, Colin organized a symposium for the Linnean Society of London. Colin said (1995:12):
"our hidden agenda was cladistics, to get as many major groups of fishes as possible worked over in the new cladistic framework. The symposium volume came out in 1973 [Greenwood *et al.*, 1973]. We didn't manage to raise a complete cast of cladists but I think this was the first multi-author volume, anywhere in biology, in which the overall message is cladistics. It has a certain historical significance."

Other multi-author volumes and, throughout the world, a flood of literature followed, and established cladistics as the 'traditional method' of today. I can't imagine that history developing in the absence of that first volume, published by the Linnean Society.

In the 1973 volume the longest paper was by Donn Rosen and dealt with the relationships of the living euteleostean fishes. This was a somewhat larger group that included the fishes of Colin's PhD thesis – the beryciforms and perciforms. He said (1995:12):
"The group covered here is the Euteleostei, first recognised by Greenwood *et al.* in 1966; it contains over 90% of living teleosts. This was Donn's theory of euteleostean relationships in 1973 [Rosen, 1973, Fig. 129], just seven years after the group was first recognised, and four years after cladistic methods were first applied to it. The actual names don't matter a scrap, but the ones I've picked out in orange are groups first recognised and named by Donn in this paper, and the ones picked out in green are groups first recognised and named in the preceding seven years, either by Greenwood *et al.*, or by ... Donn and me. As you can see, the entire higher classification was invented during those few years; it isn't that these groups were put somewhere else or called something different – none of them had been recognised before."

With this 1973 volume, it was forever clear to Colin that progress with fishes was to be achieved first by study of the ones alive today. Progress with fossils would come after. He saw this as a necessary sequence of events for knowledge of life forms in general – another recurrent theme in his many publications, leading him into theoretical studies of homology, first in morphology (1982) and then in molecular biology (1988a), and his most widely read and appreciated papers. Toward the end he was toiling, on the one hand, with DNA sequences, and on the other hand, with little fishes in pots of glycerine. The fossil fishes, true to form, followed along (1993c, 1993d).

Besides biogeography, he addressed ontogeny (1983b, 1996), pattern or non-evolutionary cladistics (1980, 1988b, 1994b), periodic extinction (Patterson and Smith, 1987, 1989; Smith and Patterson, 1988) nomenclature of fossil taxa (Patterson and Rosen, 1977; 1993a, 1993b), neutral theory of evolution and

other matters arising from molecular systematics (1987b, 1989; Patterson *et al.*, 1993). These original contributions developed from what came before. Some of them, inevitably, were seen as threatening to persons who had, it seems to me, an interest in prerogative, vested either in the old tradition or in the new. So I've learnt to see his work as a test of the character of other persons.

In aggregate, Colin's work is unique, unlike that of anyone who has gone before. He helped bring about a revolution in paleontology, systematics, and biology at large. In his view (1997:4), this revolution "began in the late 1960s, accelerated in the 1970s, and was virtually complete by the eighties". In my view the revolution continues, and his later work is part of it. In 1997 he remarked (1997:9) "we managed to get rid of one pernicious black box – evolutionary systematics – but we've replaced it with another black box – the [data] matrix". History – the Thomas Paines – seems to teach that success in one revolution means failure in the next. Better it is, maybe, but not so easy, to extend the first rather than to be on the wrong side of the second.

Colin (1992:27) once referred to Pirsig's book:
"My only previous experience with a professor of rhetoric was through the hero of ... *'Zen and the Art of Motorcycle Maintenance'*..., whose lectures led into his obsessive search for that slippery substance 'quality'."

Quality. No doubt he had this in mind, when he wrote (1991:22) of a fallen comrade, Beverly Halstead, that "He died while still in full flow, and had much more to give". No less true, that, of Colin Patterson. Quality he gave in abundance. I used to call him "Bold Fisherman", partly from an old song that Humphrey Bogart sang in the movie *The African Queen*: ("There was a Bold Fisherman, who set sail from old Pimlico"); but the sense came mainly from a fable by Robert Louis Stevenson – more words printed on paper – which I encountered in Blyth's book, when I read it for the first time in the 1950s. The fable begins (Blyth, 1942:14):
"There was a man in the islands who fished for his bare bellyful and took his life in his hands to go forth upon the sea between four planks."

One day the man encountered an apparition, the Poor Thing, and with it shared a series of adventures. The fable ends (Blyth, 1942:19):
"It came to pass in time that the Poor Thing was born; but memory of these matters slept within him, and he knew not that which he had done. But he was part of the eldest son; rejoicing manfully to launch the boat into the surf, skilful to direct the helm, and a man of might where the ring closes and the blows are going."

School of Botany, University of Melbourne,
Parkville, Victoria 3052, Australia

REFERENCES

Aitken R. 1998. Remembering R.H. Blyth. *Tricycle*, Spring 1998, **7**(3): 22-25.

Blyth RH. 1942. *Zen in English literature and oriental classics*. Tokyo: Hokuseido Press.

Brundin L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. *Kungliga Svenska Vetenskapakademiens Handlingar*, Fjärde Serien **11**(1): 1-472.

Croizat L. 1981. Biogeography: Past, present, and future. In: Nelson G, Rosen DE, eds. *Vicariance biogeography: A critique*. Symposium of the Systematics Discussion Group of the American Museum of Natural History, May 2-4, 1979, New York: Columbia University Press, 501-523.

Darlington PJ Jr. 1957. *Zoogeography: The geographical distribution of animals*. New York: John Wiley & Sons.

Foner PS, ed. 1945. *The complete writings of Thomas Paine, with a biographical essay, and notes and introductions presenting the historical background of Paine's writings, complete in two volumes*. Vol. 2. New York: The Citadel Press.

Greenwood PH, Rosen DE, Weitzman SH, Myers GS. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**(4): 339-456.

Greenwood PH, Miles RS, Patterson C, eds. 1973. *Interrelationships of fishes*. Supplement no. 1 to the *Zoological Journal of the Linnean Society*, vol. **53**. Published for the Linnean Society of London by Academic Press.

Hennig W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.

Hennig W. 1960. Die Dipteren - Fauna von Neuseeland als systematisches und tiergeographisches Problem. *Beiträge zur Entomologie* **10:** 221-329.

Hennig W. 1965. Phylogenetic systematics. *Annual Reviews of Entomology* **10:** 97-116.

Hennig W. 1966a. *Phylogenetic systematics*. Urbana: University of Illinois Press.

Hennig W. 1966b. The Diptera fauna of New Zealand as a problem in systematics and zoogeography. *Pacific Insects Monographs* **9:** 1-81.

Hull DL. 1988. *Science as a process: An evolutionary account of the social and conceptual development of science*. Chicago: University of Chicago Press.

Keane J. 1995. *Tom Paine: A political life*. London: Bloomsbury.

Moore J. 1991. Deconstructing Darwinism: The politics of evolution in the 1860s. *Journal of Historical Biology* **24:** 353-408.

Nash, AR, Fisher WK, Thompson, EOP. 1976. Haemoglobins of the shark, *Heterodontus portusjacksoni*. II. Amino acid sequence of the α-chain. *Australian Journal Biological Science* **167:** 73-97.

Patterson C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society, ser. B* **247**(739): 213-482.

Patterson C. 1967. Are the teleosts a polyphyletic group? In: Anon, ed. *Problèmes actuels de paléontologie (évolution des vertébrés). Colloque Internationaux du CRNS.* **163:** 93-109.

Patterson C. 1975. The distribution of Mesozoic freshwater fishes. *Mémoires Musée National Histoire Naturelle, Sér. A* **88:** 156-173.

Patterson C. 1977. The contribution of paleontology to teleostean phylogeny. In: Hecht MK, Goody PC, Hecht BM, eds. *Major patterns in Vertebrate Evolution*, New York: Plenum, 579-643.

Patterson C. 1978a. *Evolution*. London: British Museum (Natural History).

Patterson C. 1978b. Arthropods and ancestors. *Antenna* **2:** 99-03.

Patterson C. 1980. Cladistics. Pattern versus process in nature: A personal view of a method and a controversy. *Biologist* **5:** 234-240.

Patterson C. 1981a. Significance of fossils in determining evolutionary relationships. *Annual Reviews of Ecology and Systematics* **12:** 195-223.

Patterson C. 1981b. Methods of paleobiogeography. In: Nelson G, Rosen DE, eds. *Vicariance biogeography: A critique*. Symposium of the Systematics Discussion Group of the American Museum of Natural History, May 2-4, 1979, New York: Columbia University Press, 446-500.

Patterson C. 1981c. The development of the North American fish fauna - a problem of historical biogeography. In: Forey PL, ed. *The evolving biosphere*. London: British Museum (Natural History), 265-281.

Patterson C. 1981d. Agassiz, Darwin, Huxley, and the fossil record of teleosts. *Bulletin of the British Museum Natural History, Geology* **35**(3): 213-224.

Patterson C. 1982. Morphological characters and homology. In: Joysey KA, Friday AE, eds. *Problems of phylogenetic reconstruction*, The Systematics Association Special Volume no. 21. Published for the Systematics Association by Academic Press, London. 21-74.

Patterson C. 1983a. Aims and methods in biogeography. In: Sims RW, Price JS, Whalley PES, eds. *Evolution, time and space: The emergence of the biosphere*. The Systematics Association Special Volume no. 23. London: Published for the Systematics Association by Academic Press, 1-28.

Patterson C. 1983b. How does phylogeny differ from ontogeny? In: Goodwin BC, Holder N, Wylie CC, eds. *Development and evolution*, Cambridge: Cambridge University Press, 1-31.

Patterson C, ed. 1987a. *Molecules and morphology in evolution: Conflict or compromise?* Cambridge: Cambridge University Press.

Patterson C. 1987b. Introduction. In: Patterson C, ed. *Molecules and morphology in evolution: Conflict or compromise*? Cambridge: Cambridge University Press, 1-22.

Patterson C. 1987c. Harry Ashley Toombs, 1909–1987. *London Naturalist* **66:** 191-193.

Patterson C. 1988a. Homology in classical and molecular biology. *Molecular Biology and Evolution* **5:** 603-625.

Patterson C. 1988b. The impact of evolutionary theories on systematics. In: Hawksworth DL, ed. *Prospects in systematics*. The Systematics Association Special Volume no. 36. Oxford: Published for the Systematics Association by Oxford University Press (Clarendon), 59-91.

Patterson C. 1989. Phylogenetic relations of major groups: Conclusions and prospects. In: Fernholm B, Bremer K, Jörnvall H, eds. *The hierarchy of life: Molecules and morphology in phylogenetic analysis*. Proceedings from Nobel Symposium 70 held at Alfred Nobel's Björkborn, Karlskoga, Sweden, August 29–September 2, 1988. Amsterdam: Elsevier (Excerpta Medica), 471-488.

Patterson C. 1991. Beverly Halstead. *The Independent*, May 3, 22.

Patterson C. 1992. Bulldoggish persuasion. *Nature* **355:** 782.

Patterson C. 1993a. Bird or dinosaur? *Nature* **365**: 21-22.

Patterson C. 1993b. Naming names. *Nature* **366:** 518.

Patterson C. 1993c. Osteichthyes: Teleostei. In: Benton MJ, ed. *The fossil record* **2**, Jointly sponsored by the Palaeontological Association, the Royal Society, and the Linnean Society. London: Chapman & Hall, 619-654.

Patterson C. 1993d. An overview of the early fossil record of acanthomorph fishes. *Bulletin of Marine Science* **52:** 29-59.

Patterson C. 1994a. Bony fishes. In: Prothero DR, Schoch RM, ed. *Major features of vertebrate evolution*. Short Course in Paleontology no. 7, pp. 57-84. Knoxville: Paleontological Society.

Patterson C. 1994b. Null or minimal models. In: Scotland RW, Siebert DJ, Williams DM, eds. *Models in phylogeny reconstruction*. The Systematics Association Special Volume no 52. Oxford: Published for the Systematics Association by Oxford University Press (Clarendon), 173-192.

Patterson C. 1995. Adventures in the fish trade. Unpublished manuscript (Annual Address to the Systematics Association), 29 pp.

Patterson C. 1996. Comments on Mabee's "empirical rejection of the ontogenetic polarity criterion". *Cladistics* **12:** 147-167.

Patterson C. 1997. Molecules and morphology, ten years on. Unpublished manuscript (delivered orally to the meeting on Molecules and Morphology in Systematics, Paris, France, March 24-March 28, 1997), 21pp.

Patterson C, Greenwood PH, eds. 1967. Fossil vertebrates: Papers presented to Errol I. White C.B.E., F.R.S., President of the Linnean Society of London, 1964-67, to mark his retirement from the Keepership of the Palaeontology Department, British Museum (Natural History). *Journal of the Linnean Society of London (Zoology)*, volume **47**, number 311. London: Published for the Linnean Society of London by Academic Press.

Patterson C, Rosen DE. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158**(2): 81-172.

Patterson C, Smith AB. 1987. Is the periodicity of extinctions a taxonomic artefact? *Nature* **330:** 248-252.

Patterson C, Smith AB. 1989. Periodicity in extinction: The role of systematics. *Ecology* **70:** 802-811.

Patterson C, Williams DM, Humphries CJ. 1993. Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics* **24:** 153-188.

Pirsig R. 1989. *Zen and the art of motorcycle maintenance: An inquiry into values*. London: Vintage.

Rosen DE. 1973. Interrelationships of higher euteleostean fishes. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of fishes*. Supplement no. 1 to the *Zoological Journal of the Linnean Society*. Published for the Linnean Society of London by Academic Press, 397-513.

Simpson GG. 1953. *Evolution and geography: An essay on historical biogeography with special reference to mammals*. Oregon State System of Higher Education (Condon Lecture Publications), Eugene, Oregon.

Smith, AB, Patterson C. 1988. The influence of taxonomic method on the perception of patterns of evolution. *Evolutionary Biology* **23:** 127-216.

Woodward AS. 1889–1901. *Catalogue of the fossil fishes in the British Museum*. Parts I-IV. London: British Museum (Natural History).

Woodward, AS. 1902–1912. The fossil fishes of the English Chalk. Parts I-VII. *London: Palaeontographical Society*.

Contributions to Palaeontology

Fossils, Phylogeny, and Patterson's Rule

LANCE GRANDE

Colin Patterson had a brilliant grasp of the 'Big Picture' in comparative anatomy and phylogenetic studies. His empirical anchor was the study of fish skeletons, which he used to explore a number of theoretical and methodological concepts in natural history. His intellectual tools were logic, precision, and a desire to cut right to the heart of the matter. He was not afraid to criticize any cherished concept, belief, or individual in science; and as all people who operate in such a way, he occasionally attracted vigorous criticism and debate. But in making fields such as vertebrate paleontology more self critical, he made them better. To make a real difference in science, I believe that people have always had to be more concerned about unambiguous assessment of natural observations and theoretical concepts, than about political consequences. I will discuss some of Colin's provocative and influential work on fossils and phylogeny, part of a larger body of his work that will remain influential for generations to come.

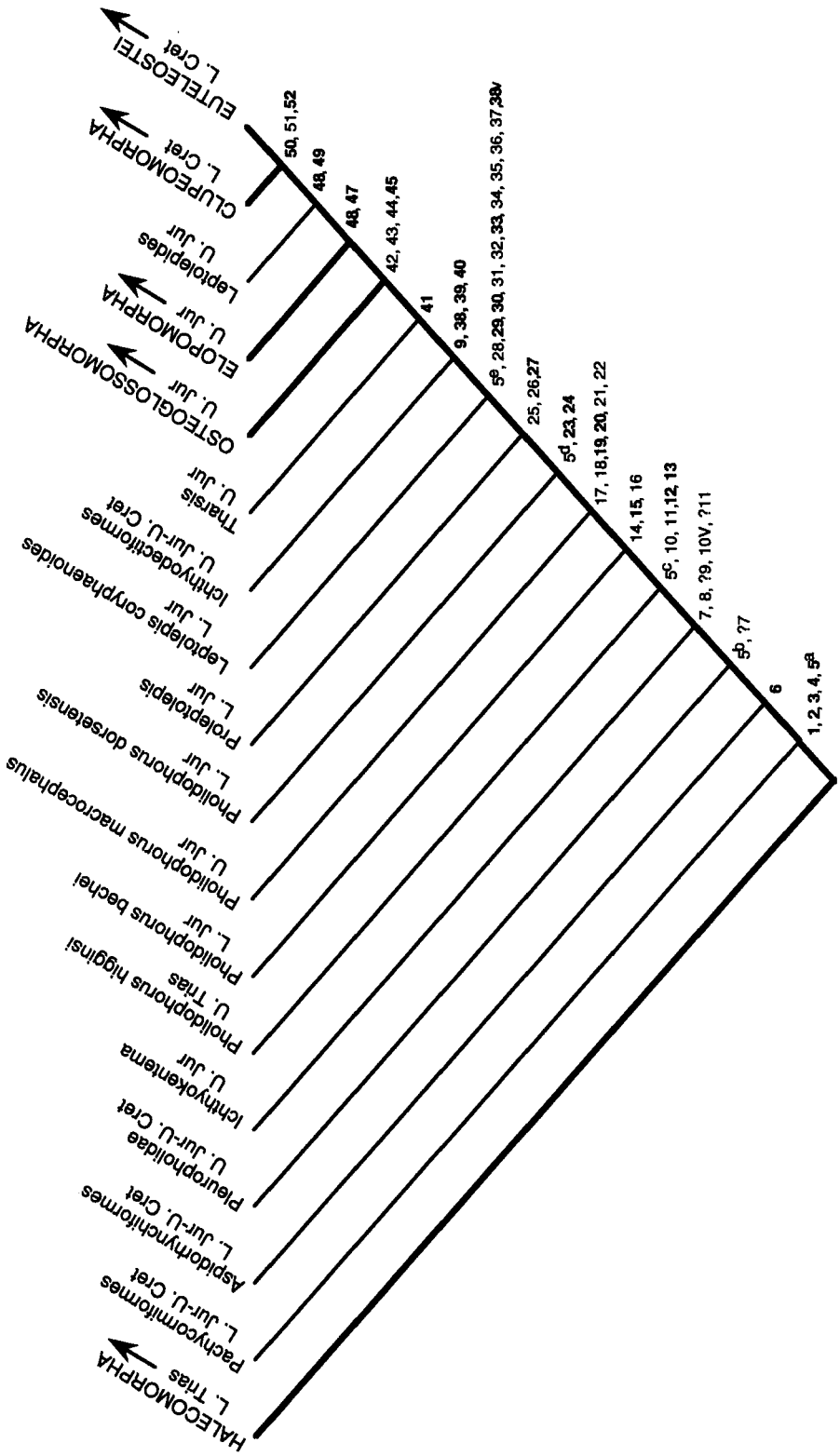
In the 1960s and 70s, Colin brought what was, at the time, a fresh approach to the study of fossil fishes. Whereas most vertebrate paleontologists were focusing primarily on stratigraphy and limiting their empirical comparisons to other fossil taxa to interpret phylogeny, Colin had a deeper appreciation for integration of fossil taxa into comparative studies of extant species. He saw this as the most effective way to fully evaluate the information content of fossils. To him, fossil fishes were more fishes than rocks. Frequently working with his friend and colleague, the late Donn Rosen, he set new standards in systematic ichthyology for a multi-disciplinary approach (e.g. Rosen and Patterson, 1969; Patterson and Rosen, 1977; Patterson, 1973, 1977a). He did not simply refer to the past literature for his data on extant taxa. Instead, he produced original empirical data on them, which gave him a deeper, phylogenetically organized understanding of comparative fish anatomy. He was one of the first paleoichthyologists to recognize the potential of the caudal skeleton to phylogenetic studies of neopterygians (e.g. Patterson,1968a,1968b).

He also wrote the most comprehensive volume to date on the comparative anatomy of the actinopterygian braincase (Patterson, 1975a). His comprehensive intellectual base and integrative approach eventually allowed him to expand his influence and contributions into other fields, such as evolutionary theory (e.g. Patterson, 1978, 1987a, 1987b, 1988a), developmental biology (e.g. Patterson, 1977b, 1983a), historical biogeography (e.g. Patterson, 1975b, 1981a, 1981b, 1983b), and even molecular biology (Patterson, 1987b, 1988b; Patterson *et. al.*, 1993).

Colin understood how to extract the maximum amount of morphological data out of fossil fishes. His first hand knowledge of extant fishes not only helped him to interpret better what he saw in the fossils, but also to more fully compare the fossil skeletons to the Recent ones. In addition he also helped develop and promote newly discovered fine preparation techniques for fossils. In particular, he was an early pioneer in applying the acid-transfer techniques developed by Toombs and Rixon (e.g. 1959) to fossil fishes (Patterson, 1964, 1972). Thus, Colin made two significant methodological contributions to the study of fossil fishes: better preparation and interpretive methods for more detailed and accurate fossil descriptions, and the early application of cladistic analytical techniques for phylogenetic evaluation of descriptive data which are intercalated with data from other fossil and Recent fishes. The integrated application of these methods led him to produce a number of original, unambiguous phylogenetic classifications of teleost fishes.

One of Colin's earliest and most significant original teleost classifications was in a paper entitled "The contribution of paleontology to teleostean phylogeny" (Patterson, 1977a). In this paper he analyzed 52 characters in 18 taxa and produced a cladogram of basal teleosts in which the first 12 teleost branches were extinct fossil taxa (see opposite page). This cladogram still serves as a highly used reference for workers on basal teleostean interrelationships who include extinct groups in their studies, and it will continue to provide a number of testable, relevant phylogenetic hypotheses for generations to come. He went on to provide several other important original cladograms of fossil and Recent fishes (e.g. Patterson and Rosen, 1977, 1989; Patterson and Johnson, 1995), some of which have generated much controversy and scientific debate (e.g. Rosen *et al.*, 1981).

Colin's interest in the utility of fossils in determining evolutionary relationships was genuine, objective, and relatively unclouded with any preconceived agenda. I find it therefore ironic that so many paleontologists mistook his stance as antievolutionary, or even antipalaeontological in spirit. Part of this misconception was the result of an oral presentation that he gave to the Systematics Discussion group at the American Museum of Natural



Cladogram of teleosts, including extinct stem-groups. Redrawn from Patterson (1977a). This was the first time a combined Recent and fossil cladogram had appeared for the origin of teleosts. The numbers along the principal axis refer to characters defining the particular nodes. The bold lines and uppercase letters denote Recent groups.

History, November 1984, in which he was openly frank about what he saw as the objective limits to evolutionary theory and the role of palaeontology within that theory. This caused discomfort among a constituency of evolutionary biologists and palaeontologists in having certain cherished concepts challenged. In a paper entitled "Significance of fossils in determining evolutionary relationships", Patterson critically reviewed the notion of some paleontologists (e.g. Simpson, 1961; Hughes, 1976; Keast, 1977; Gingerich, 1977, 1979; Chaline and Mein, 1979; Tintant and Mouterde, 1981) that fossils are the best or even the only sound basis for determining evolutionary relationships or that ancestor-descendent relationships could be recognised. After reviewing a number of examples of phylogeneticly significant fossils, he concluded (1981c: 218) that: "instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be non-existent".

He pointed out that it was not the age of fossils that was relevant to resolving phylogeny, it was the anatomy. Although Patterson's paper contained 29 pages packed with significant points, it was the above quote about fossils rarely overturning theories of relationship based on Recent organisms that ignited a long and vigorous debate. From here on, I refer to that quote as "Patterson's rule" for brevity. The ensuing controversy resulted in scientific symposia (e.g. Society of Vertebrate Paleontology, 1990), and a number of publications exploring the relevance of fossils to phylogeny construction. Some of the more visible papers included Doyle and Donoghue (1987:64); Gauthier *et al.* (1988:106); and Donoghue *et al.* (1989:432), all of which cited Patterson's rule and argued strenuously against it because it supposedly "belittled the role of fossils in phylogenetic inference" (Gauthier *et al.*, 1988:193). The arguments criticizing Patterson basically centered around possible negative effects of missing taxa (i.e. omitting certain fossils) in phylogenetic analyses. These arguments did not adequately discuss a number of counterbalancing problems (some of which were reviewed in Nixon, 1996), including the following. First, it is unlikely that any data matrix includes all extinct taxa, because many were not preserved. Consequently, phylogenetic methodology had better be able to produce meaningful results in spite of missing taxa, or it is all a waste of time anyway. Second, the missing characters in a data matrix resulting from the addition of highly incomplete fossil taxa can substantially weaken the application of parsimony to a data set (Nixon, 1996: 361; Grande and Bemis, 1998: 568–571). And third, if inclusion of a fossil in a data matrix produces a different cladogram than the one indicated without the fossil, there is no way of knowing which represents "truth". Donoghue *et al.* (1989:456) argued that "in some cases the old view that the true phylogeny cannot be obtained without fossils is correct". This suggests that in other cases we can actually "know"

a "true phylogeny". Such knowledge of absolute truth does not exist in science and especially in evolutionary studies.

Most of the authors who focused solely on Patterson's rule downplayed the context of Patterson's statement, which was to provide a word of warning about attributing special powers of phylogenetic resolution to fossils, simply because they are fossils, and that the incompleteness of many fossils is a problem worth serious consideration. The real message of Patterson's 1981c paper is given in the last paragraph of his conclusion (p. 220) where he says:
"the belief that paleontology alone should, or can, determine relationships is a myth. So too is the Haeckelian belief that ontogeny alone will do the trick, for it is negated if neoteny or other forms of secondary loss ever occur. What remains is the unity of the comparative method, in which paleontology can hold its own by acknowledging its debt to neontology, and by repaying that debt in contributing what it alone can: age of groups, paleobiogeographic data, and new character combinations that can reverse decisions on homology and polarity, so testing, and perhaps on rare occasions overthrowing, theories of relationship."

Note that the message about paleontology is a positive one, and that Patterson does not even rule out the possibility of some fossil taxa overthrowing preexisting theories of relationship. True, it is a critical look at paleontology, but it is the kind of self criticism that makes the field of paleontology stronger. To paraphrase Janvier (1984:61) Patterson defended paleontology the best way we know of in science: by defining some of its limitations.

Colin had a sharp wit, and his papers were both thought provoking and entertaining at the same time. I always appreciated the way he went right to the heart of a problem, facing controversy head on, with a keen sense of logic and ambiguity, and with a sense of humor (e.g. see Patterson, 1994). Colin's published work on fossil and living fishes was key to sparking my own interests in the phylogeny and comparative anatomy of fishes, and a big reason why I chose this field. His influence is apparent in much of what I publish. I respected him enormously as a scientist and a philosopher, and I liked him very much as a person. I will miss him greatly.

Department of Geology, Field Museum of Natural History,
Roosevelt Road at Lakeshore Drive, Chicago,
Illinois 60605, USA

REFERENCES

Chaline J, Mein P. 1979. *Les rongeur et l'evolution.* Paris: Doin.

Donoghue MJ, Doyle JA, Gauthier J, Kluge AG, Rowe T. 1989. The importance of fossils in phylogenetic reconstruction. *Annual Review of Ecology and Systematics* **20:** 431-460.

Doyle JA, Donoghue MJ. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Review of Palaeobotany and Palynology* **56:** 63-95.

Gauthier J, Kluge AG, Rowe T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* **4:** 105-209.

Gingerich PD. 1977. Patterns of evolution in the mammalian fossil record. In: Hallam A, ed. *Patterns of evolution, as illustrated by the fossil record*. Amsterdam: Elsevier Press, 469-500.

Gingerich PD. 1979. The stratophenetic approach to phylogenetic reconstruction in vertebrate paleontology. In: Cracraft J, Eldredge N, eds. *Phylogenetic analysis and paleontology*. New York: Columbia University Press, 113-163.

Grande L, Bemis WE. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Society of Vertebrate Paleontology Memoir* 4:1-690; supplement to *Journal of Vertebrate Paleontology* **18**(1).

Hughes NF. 1976. *Paleobiology of angiosperm origins*. Cambridge UK: Cambridge University Press.

Janvier P. 1984. Cladistics: theory, purpose and evolutionary implications. In: Pollard JW, ed. *Evolutionary theory: paths into the future*. New York: John Wiley and Sons, 34-75.

Keast A. 1977. Zoogeography and phylogeny: the theoretical background and methodology to the analysis of mammal and bird faunas. In: Hecht MK, Goody PC, Hecht BM, eds. *Major patterns of vertebrate evolution*. New York: Plenum Press, 249-312.

Nixon KC. 1996. Paleobotany in cladistics and cladistics in paleobotany: enlightenment and uncertainty. *Review of Palaeobotany and Palynology* **90:** 361-373.

Patterson C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Soc*iety, *ser. B*, **247**(739): 213-482.

Patterson C. 1968a. The caudal skeleton in Lower Liassic pholidophorid fishes. *Bulletin of the British Museum (Natural History), Geology* **16:** 201-239.

Patterson C. 1968b. The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History), Geology* **17:** 47-102.

Patterson C. 1972. Fossil ostracods and fishes from Brasil. In: anonymous ed. *Report on the British Museum (Natural History) 1969-1971*. London: Trustees of the British Museum (Natural History), 42-44.

Patterson C. 1973. Interrelationships of holosteans. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of Fishes*. London: Academic Press, 233-305.

Patterson C. 1975a. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London* (B) **269:** 275-579.

Patterson C. 1975b. The distribution of Mesozoic freshwater fishes. *Memoires du Museum national d'Histoire naturelle, Serie A, Zoologie* **88:** 156-174.

Patterson C. 1977a. The contribution of paleontology to teleostean phylogeny. In: Hecht MK, Goody PC, Hecht BM, eds. *Major patterns of vertebrate evolution*. New York: Plenum Press, 579-643.

Patterson C. 1977b. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In: Andrews SM, Miles RS, Walker AD, eds. *Current Problems in Lower Vertebrate Phylogeny*. London: Academic Press, 77-121.

Patterson C. 1978. *Evolution*. London: British Museum (Natural History) and Routledge & Kegan Paul.

Patterson C. 1981a. Methods of Paleobiogeography. In: Nelson G, Rosen DE, eds.. *Vicariance Bioeography: a critique*. New York: Plenum Press, 446-500.

Patterson C. 1981b. The development of the North American fish fauna – a problem of historical biogeography. In: Forey, PL, ed. *The evolving biosphere*. London: British Museum of Natural History, 265-281.

Patterson C. 1981c. The significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics* **12:** 195-223.

Patterson C. 1983a. How does ontogeny differ from phylogeny?. In: Goodwin BC, Holder N, Wylie CC, eds. *Development and evolution*. Cambridge, UK: Cambridge University Press, 1-31.

Patterson C. 1983b. Aims and Methods in Biogeography. In: Sims RW, Price J., Whalley PES, eds. *Evolution, time and space: The emergence of the biosphere*. London: Academic Press, 1-28.

Patterson C. 1987a. Evolution: neo-Darwinian theory. In: Gregory RL, ed. *The Oxford companion to the mind*. Oxford: Oxford University Press, 234-244.

Patterson C. 1987b. Introduction. In: Patterson C, ed. *Molecules and morphology in evolution: conflict or compromise?* Cambridge, UK: Cambridge University Press, 1-22

Patterson C. 1988a. The impact of evolutionary theories on systematics. In: Hawksworth DL, ed. *Prospects in Systematics*. Oxford: Oxford University Press, 59-91.

Patterson C. 1988b. Homology in classical and molecular biology. *Molecular Biology and Evolution* **5:** 603-625.

Patterson C, Johnson GD. 1995. The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* **559:** 1-85.

Patterson C, Rosen DE. 1977. A review of ichthyodectiform and other Mesozoic teleost fishes, and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158:** 81-172.

Patterson C, Rosen DE. 1989. The Paracanthopterygii revisited: order and disorder. *Science Series, Natural History Museum, Los Angeles County* **32**:5-36.

Patterson C. 1994. Bony fishes. In: Prothero DR, Schoch RM, eds. *Major Features of Vertebrate Evolution*. Knoxville: Paleontological Society, University of Tennessee, 57-84

Patterson C, Williams DM, Humphries CJ. 1993. Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics* 24:153-188.

Rosen DE, Patterson C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* **141**: 357-474.

Rosen DE, Forey PL, Gardiner BG, Patterson C. 1981. Lungfishes, tetrapod, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History* **167**: 159-276.

Simpson GG. 1961. *Principles of animal taxonomy*. New York: Columbia University Press.

Tintant H, Mouterde R. 1981. Classification et phylogenese chez les ammonites jurassiques. In: Martinell J, ed. *International symposium on a concept and method in Paleontology*. Barcelona: University of Barcelona, 85-101.

Toombs HA, Rixon AE. 1959. The use of acids in the preparation of vertebrate fossils. *Curator* **2**: 304-312.

Extinction in the fossil record

ANDREW SMITH

Colin had influences in many fields, and here I shall specifically focus on his work on extinction and how this revitalised the role of systematics in palaeobiology.

I first came to know Colin when I joined the museum in 1982. This was a time when systematic palaeontology seemed to be under considerable threat. There had recently been an N.E.R.C. review on the future funding directions for palaeontology, and the message that seemed to be coming across was that systematics was passé and that what was now needed were large-scale syntheses of the existing rich palaeontological literature.

Taxon counting was in ascendancy and papers were starting to flood out identifying this or that extinction, origination or diversity trends – based on analysis of first and last occurrence of families in the fossil record drawn from the literature. That these data contained error was acknowledged, but considered unimportant – error simply added noise and weakened original signal – it could not create pattern. What was taking place was a dramatic shift away from the analysis of specimens to the analysis of primary and particularly secondary literature sources. Systematics was being relegated to the backwaters.

In 1984 Raup & Sepkoski made their boldest claim. They claimed to have found a 26 million year periodicity in extinction in marine organisms over the past 250 million years. Almost immediately a flurry of papers was published on possible astronomical causes – with undiscovered death-stars (dubbed Nemesis) or mystery planets (Planet X) being invoked as potential causative agents. This was heralded as the first time palaeontology had provided predictive evidence that influenced one of the hard physical sciences.

There were some critics, but these questioned analytical details about the time-scale being used or the statistical approach that had been adopted. Things were getting very much out of hand and I remember Colin coming into the coffee room in the museum with yet another of these papers and asking if any of us thought there was periodicity of extinction in the groups that we knew best. From his knowledge of fossil teleost fishes he couldn't see any evidence. Nor could I from sea-urchins, so we agreed to join forces to find out what was responsible for generating the pattern that had been discovered by Raup and Sepkoski.

Colin obtained Sepkoski's original data on the ranges of families and genera and we plotted up just the fish and echinoderm last occurrences. This showed basically the same pattern of extinction peaks as the full data set. Then we checked the primary literature and often the actual specimens, on which last occurrences were based. Finally we assessed each taxon as to whether it was monophyletic, paraphyletic, polyphyletic or based on a single species or even single specimen.

The result is history. Colin and I discovered that only about one-quarter of the taxa being used were monophyletic clades correctly dated and thus in any real sense sampling extinction, and we showed that the extinction peaks appeared in the non-monophyletic data but not in the clade data. A sizeable proportion of records were based on single occurrences and thus sampled secular variation in the quality of the fossil record, not biological diversity. Periodicity of extinction appeared to be an artefact of the idiosyncratic taxonomic practices that had prevailed in the past.

I really feel that the papers that came out of Colin's initiative were turning points. They not only dealt a mortal blow to the periodicity of extinction hypothesis, but did much to raise the profile of systematics in palaeontology. Accurate interpretation of historical trends in biodiversity requires high-quality taxonomic information; systematics was thus firmly placed as an essential part of palaeobiological analysis to be ignored at one's peril.

Colin was first and foremost an excellent systematist dedicated to specimen-based research. The fact that this survives as a mainstream field of research amongst palaeontologists today is partially thanks to Colin's foresight and leadership.

Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD

REFERENCES

Raup DM, Sepkoski JJ. 1984. Periodicity of extinctions in the geological past. *Proceedings of the National Academy of Sciences (USA)* **81:** 801-805.

Colin Patterson: The greatest fish palaeobiologist of the 20th century

NIELS BONDE

Starting out in life as a parasitologist, on graduation Colin moved to palaeontology under the supervision of Kenneth Kermack, a specialist in early fossil mammals, to work on fishes of the English Chalk, specifically the spiny rayed teleosteans, the acanthopterygians.

His PhD thesis (1961, published in 1964) proved to be a major milestone in fish palaeontology. It set new standards for palaeobiology, both on the technical methodological level, in the precision and detail of the descriptions and illustrations, and in the veracity of the discussions of relationships (although pre-cladistic).

He prepared the 3-D preserved fish skulls from the chalk by using dilute acetic acid, a technique developed in the BM(NH) and used here for the first time in a major palaeontological work (the pure chalk was very well suited to this type of preparation). He demonstrated that beryciform acanthopterygians, in the traditional sense, were a polyphyletic group. He further tried to link some "beryciforms" to separate subgroups of Recent perciforms, which were also presumed to be polyphyletic. He returned to the Chalk fishes in 1987 (Patterson and Longbottom, 1987), and finally in 1993, to consider all of the Cretaceous acanthomorphs in an overview of their early fossil records (1993a).

The need for museum displays channelled his research into the phylogeny of chondrichthyans, particularly chimaeroids (1965, reviewed again in 1992) and Wealden sharks (1966). However, for the remainder of his career he concentrated mainly on the largest vertebrate group, the teleosteans, and basic theoretical and philosophical problems concerning relationships and comparative biology.

By the mid 1960s there was a growing interest in fish phylogeny and classification as manifested in the review of teleostean interrelationships by Greenwood *et al.* (1966). At that time Gary Nelson, having completed his PhD on gill arch anatomy of fishes, was visiting the Palaeozoological Department, at the Riksmuseet in Stockholm, where Stensiö and Jarvik were studying fossil fish gill arches. There he met the entomologist, Lars Brundin, and was introduced to the theory of phylogenetic systematics (later to be 'nick-named'

cladistics) following the German entomologist Willi Hennig, whose book, *Phylogenetic Systematics* (1966) had just appeared.

Nelson was immediately convinced of the efficacy of phylogenetic systematics as a result of his discussions with Brundin (whose great phylogenetic and biogeographic analysis of chironomid midges was also published in that year). Nelson brought the theory to me in Copenhagen when he visited the museum late in 1966. I too had the good fortune of discussing systematics with Brundin during January 1967. Meanwhile, Gary introduced phylogenetic systematics to Colin, Roger Miles, Humphry Greenwood and others at the British Museum (Natural History) in early 1967.

In May 1967, at the Nobel Symposium on lower vertebrates in Stockholm honouring Stensiö, several of us, including Roger Miles and Colin, met with Daniel Goujet, Bob Schaeffer, Keith S. Thomson, H-P. Schultze and many other fish palaeontologists, including Rainer Zangerl, the translator of Hennig's book (see Ørvig, 1968). The highlight of the meeting was a banquet speech by Lars Brundin on phylogenetic systematics.

From this meeting followed various crusades for cladistics – run by Colin and Roger Miles in the UK, Gary Nelson in the USA, Daniel Goujet in France and myself, to a modest degree, in Denmark. These were set up to counter a 'traditional evolutionary' (Mayr-Simpsonian) opposition, that still exists to some degree in biology and especially in micro- and invertebrate palaeontology. Not until the early 1970s had we convinced some of the emerging generation of leading cladistic systematists, including Joel Cracraft and Donn Rosen, of the importance of the Method. Donn Rosen was to become Colin's closest co-worker on teleostean classification (Rosen and Patterson, 1969). It took until the early 1970s for cladistic arguments to become embodied in the literature on fish inter-relationships, a milestone being the Linnean Society meeting of 1972 (Greenwood, Miles and Patterson, 1973 – see review by Bonde, 1974).

So, apart from some isolated corners of entomology (on the early history of cladistics see Dupuis 1979) cladistics was carried forward by fish phylogeneticists, not least of whom was Colin, who, in the 1970s and 1980s, published papers analysing several important theoretical evolutionary and classificatory problems from a cladistic perspective: the teleostean sistergroup (1973); monophyly and the role of fossils (1977); classification of fossils (Patterson and Rosen, 1977) with the introduction of the category "plesion"; teleostean biogeography (1975b, 1981a, b, 1983b); homology (1982b); the relationship between ontogeny and phylogeny (1983a); paraphyletic fossil stem groups (1981d); and the problematic relations between morphological and molecular biological analyses of relationships (Patterson, 1987).

Colin also wrote a textbook on evolution (1978a) with characteristic energy, flair and efficiency, which became widely translated (for example, the Danish edition was used within the Biology Department in Copenhagen University for several years). As an indication of his determination he had set himself the goal of writing at least 1500 words per day – and so he did. I recall staying with Colin and Rachel some days during that period, and after dinner, the pub, several discussions and a few more drinks, I went to bed. Colin, however, sat down to catch up on the word count that he had failed to reach during the day. Through this work he discovered to his surprise that evolutionary theory had no importance in classification (perhaps as a result of discussions with Nelson and Rosen) as he later specified in several publications (e.g. 1980, 1982a). This was much to the distaste of traditional neo-Darwinists, who thereafter labelled Colin a "pattern cladist" (possibly the worst swear word they could muster at the time!). During that period he also had several fights, notably with his old friend "Bev" (Tarlo/Halstead), who stirred things up at the Natural History Museum, about its exhibitions and "nests" of cladists. Halstead wrote vigorous attacks in *Nature* (see the 1978 review of the meeting at Reading University which he himself had arranged!) and in New Scientist with scurrilous accusations that Colin and his cladistic colleagues had been "...in bed with the creationists". After a particular lecture and a television presentation the creationists thought that Colin was of their opinion and even tried to capitalise on his scientific reputation to foster their anti-evolutionary ambitions. Despite Colin's chagrin, the incident was quite useful. For example, it was the first time that cladograms and some of the "awful" words of phylogenetic systematics were seen in *Nature* (a different story today!), and under Miles' management the Natural History Museum was seen to be the first major museum exhibiting cladistic theory – throwing doubt on the dogma of traditional, selectionist evolutionist arguments.

Throughout the 1970s Colin worked on his *magnum opus* (1975a), a painstaking analysis of the braincases of primitive Mesozoic teleosteans. Nothing similar had been attempted since Nielsen (1942, 1949) described in great detail the skulls of various Triassic actinopterygians from East Greenland using serial sections and wax-reconstructions. Colin used some of Nielsen's fossils housed in the Geological Museum, Copenhagen, and, in his obituary of Nielsen in *The Times* Dec. 1968, Colin showed his appreciation of this great morphologist. Colin later admitted that this work (on mostly fragmented, acid-prepared braincases) was so intellectually challenging and such a huge strenuous effort that he would never again attempt to undertake anything similar.

Nonetheless, his entire career has seemed to be exactly that: a continuous stream of critical intellectual effort, encompassing the theoretical, methodological and practical activities with analyses of both his own and numerous

other scientists' data. He advised almost everyone in the field – and everyone wanted his opinions on their ideas and manuscripts. He was precise and penetrating in his analyses and mostly friendly and constructive in his criticisms. But, first and foremost, Colin was always true to his science. See, for example, his reviews (1978b) of S. Manton and fish palaeozoologist, E. Jarvik (1981c), on the relationships among arthropods and of tetrapods among "fishes" respectively. Only on rare occasions did he resort to sharp criticism, for example of J. Blot's treatment of eels (1975) and more recently the phylogenetic analyses of Begle (Johnson and Patterson, 1996).

Colin was held in high esteem as a reviewer of cladistic contributions, and particularly papers on interrelationships of fishes papers (see, for example, Patterson 1989). Surely he was the reviewer who had the most fish manuscripts pass through his hands for comment and advice through the last 30 years. He was anti-authoritarian, but authoritative. His personality and appearance was so charismatic that he filled an entire room with his sheer presence and deep, resonant voice. The only person that my family and I can think of to compare with him is Sean Connery.

It is my great fortune to have known Colin for so many years, to have joined him in cladistic fights, to have discussed things with him and to have received his wise advice. He is an irreplaceable loss to our science now that he has gone, at such a relatively early age. To my mind never before has one person's brain stored such quantities of anatomical data on all fishes and intellectual insights of their relationships (as epitomized in his "Fossil Record" of teleosteans, 1993b). He was undoubtedly the greatest fish palaeobiologist of this century, fittingly honoured in the festschrift dedicated to him, the new *Interrelationships of fishes* (Stiassny *et al.*, 1996, which includes a bibliography). We all shall miss him a lot.

ACKNOWLEDGMENTS

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Geological Institute, University of Copenhagen,
Øster Voldgade 10, DK-1350 Copenhagen K, Denmark

REFERENCES

Blot J. 1975. A propos des téléostéens primitifs: l'ordre des Apodes. *Colloques internationaux du Centre National de la Recherche Scientifique,* Paris, **218:** 281-292.

Bonde N. 1974. Review of "Interrelationships of Fishes" by Greenwood PH, Miles RS, Patterson C, eds. *Systematic Zoology* **23:** 562-569.

Brundin L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges. *Kungliga Svenska Vetenskapsakademiens Handlingar, Series 4,* Bd. **11**(1): 1-472.

Dupuis C. 1979. La "Systematique Phylogenetique" de W. Hennig. *Cahiers Naturaliste* **34:** 1-69.

Greenwood PH, Miles R, Patterson C, eds. 1973. *Interrelationships of Fishes.* London: Academic Press.

Greenwood PH, Rosen DE, Weitzman SH, Myers G. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131:** 339-456.

Halstead LB. 1978. The cladistic revolution – can it make the grade? *Nature* **276:** 759.

Hennig W. 1966. *Phylogenetic Systematics.* University of Illinois Press, Urbana (2nd ed. 1979).

Johnson JGD, Patterson C. 1996. Relationships of lower euteleostean fishes. pp. 251-331 In: Stiassny M, Parenti L, Johnson GD, eds. *Interrelationships of Fishes.* Academic Press, London.

Nielsen E. 1942. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus. Medd. Groenland* **138:** 1-403.

Nielsen E. 1949. Studies on Triassic fishes from East Greenland. II. *Australosomus* and *Birgeria. Meddelelser om Grønland,* København, **146:** 1-309.

Ørvig T, ed. 1968. *Current Problems of Lower Vertebrate Phylogeny.* Nobel Symp. 4. Almqvist & Wiksell, Stockholm.

Patterson C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London Series B* **247:** 213-482.

Patterson C. 1965. The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London Series B* **249:** 101-219.

Patterson C. 1966. British Wealden sharks. *Bulletin of the British Museum (Natural History), Geology* **11:** 281-350.

Patterson C. 1973. Interrelationships of holosteans. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of Fishes.* Academic Press, London, 233-305.

Patterson C. 1975a. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London Series B* **269:** 275-579.

Patterson C. 1975b. The distribution of Mesozoic freshwater fishes. *Mémoires Museum National d'Histoire Naturelle, Serie A* **88:** 156-173.

Patterson C. 1977. The contribution of paleontology to teleostean phylogeny. In: Hecht MK, Goody PC, Hecht BM, eds. *Major Patterns in Vertebrate Evolution.* Plenum, New York, 579-643.

Patterson C. 1978a. *Evolution.* British Museum (Natural History) and Routledge & Kegan Paul, London; Cornell University Press; Ithaca, NY; University of Queensland Press; Brisbane (subsequent editions in Danish, Dutch and Japanese).

Patterson C. 1978b. Arthropods and ancestors. *Antenna* **2:** 99-103.

Patterson C. 1980. Cladistics. *Biologist* **27:** 234-240 [reprinted in Maynard-Smith J, ed. *Evolution Now* Macmillan. 1982. London, pp. 110-120.]

Patterson C. 1981a. Methods of paleobiogeography. In: Nelson G, Rosen DE, eds. *Vicariance Biogeography: A Critique.* Columbia University Press, New York, 446-500.

Patterson C. 1981b. The development of the North American fish fauna - a problem of historical biogeography. In: Forey PL, ed. *The Evolving Biosphere.* London: British Museum (Natural History), 265-281.

Patterson C. 1981c. Vertebrate Morphology. Review of *Basic Structure and Evolution of Vertebrates* (E. Jarvik), 1980. *Science* **214:** 431-432.

Patterson C. 1981d. Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics* **12:** 195-223.

Patterson C. 1982a. Cladistics and classification. *New Scientist* **94:** 303-306 Reprinted In: Cherfas J, ed. 1982. *Darwin up to Date.* London: New Science Publications, 35-39.

Patterson C. 1982b. Morphological characters and homology. In: Joysey KA, Friday AE, eds. *Problems of Phylogenetic Reconstruction.* London: Academic Press, 21-74.

Patterson C. 1983a. How does ontogeny differ from phylogeny? In: Goodwin BC, Holder N, Wylie CC, eds. *Development and Evolution.* Cambridge: Cambridge University Press, 1-31.

Patterson C. 1983b. Aims and methods in biogeography. In: Sims RW, Price JS, Whalley PES, eds. *Evolution, Time and Space: The Emergence of the Biosphere.* London: Academic Press, 1-28.

Patterson C. 1987. Introduction. In: Patterson C, ed. *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge: Cambridge University Press, UK, 1-22.

Patterson C. 1989. Phylogenetic relations of major groups: Conclusions and prospects. In: Fernholm B, Bremer K, Jörnvall H, eds. *The Hierarchy of Life. Nobel Symposium* **70:** 471-488.

Patterson C. 1992. Interpretations of the toothplates of chimaeroid fishes. *Zoological Journal of the Linnean Society* **106:** 33-61.

Patterson C. 1993a. An overview of the early fossil record of acanthomorph fishes. *Bulletin of Marine Science* **52:** 29-59.

Patterson C. 1993b. Teleostei. In: Benton MJ, ed. *The Fossil Record Vol.* **2.** London: Chapman & Hall, 619-654.

Patterson C, Longbottom AE. 1987. Fishes. In: Smith AB, ed. *Fossils of the Chalk.* London, Palaeontological Association, 238-265

Patterson C, Rosen DE. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158:** 81-172.

Rosen DE, Patterson C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* **41:** 357-474.

Stiassny M, Parenti L, Johnson GD, eds. 1996. *Interrelationships of Fishes.* London: Academic Press.

Contributions to the study of Recent fishes

Higher teleosts and adventures in the fish trade

DAVID JOHNSON

I thought I would start with a couple of quotes from the Systematics Association Annual Address that Colin presented in 1995. Quoting, "I called my talk Adventures in the Fish Trade as an allusion to Dylan Thomas's *Adventures in the Skin Trade* – the incident from it that stuck in my mind is Dylan Thomas's train journey from Swansea to London with no ticket and with a beer bottle stuck on his finger. The analogy – a journey with no ticket and a bottle stuck to your hand – seems close enough to my career in the fish trade." This clever analogy is exactly what one might expect from Colin, but of course, in part, it really speaks to one of his most constant and endearing qualities – basic modesty.

No ticket? As Colin would have said. "*Come on! Surely you don't believe that*!" He had the ticket, in spades. They included a strong, unwavering work ethic and one of the most brilliant and original intellects we've seen in systematics – a capacious, sharply focused mind that could rapidly absorb and retain facts from the literature and the specimens, interpret, synthesize and crystallize them, and then eloquently present the results in black in white, no waffling, both in the theoretical and the empirical work. As for the hands, sure, they had an enduring familarity with the bottle and the can, but in the fish trade what really stuck to Colin's hands for most of the time, was the fossils and the needle, the dissecting tools, the focus knob of the microscope, the literature, the writing or drawing pen or pencil, and more frequently the ever present laptop – the 'little machine' as he called it – on which he would ferociously tap away with only two fingers at an astonishing speed.

One of the most remarkable things about Colin was the breadth of his work. What was most important? Impossible to say, I think, because in each arena – paleontology, systematic theory, comparative anatomy and phylogeny of Recent fishes, his foray into molecular data and more – the impact of his work

was huge, and each had strong influences on the others. And then there is the enormous impact he had on all these areas through his personal interactions with scientists all over the world, his editorial work, and particularly, his meticulous work refereeing the papers of others – these all speak not only to his exceptional knowledge and expertise, but also to his unselfish generosity in sharing it. What I will touch on here, the work with Recent fishes, specifically teleosts, is one small part of Colin's life's work. I will emphasize our work together, because it's what I know best, and it is with this that I have a better chance of capturing Colin's "take home message" – the fun and companionship that emanates from the work.

Again quoting Colin, "But why is it such fun? Because it's inexhaustible".

That certainly could be said about trying to work out the relationships of the Teleostei, within which there are about 25,000 species – more than all the tetrapods put together – exhibiting tremendous diversity in form, anatomy and habitat, the latter ranging from high mountain streams to the abyssal depths of the oceans. At the lower or more primitive end of teleosts there are tarpon, eels, herring, cyprinids, characins, catfishes as well as some deep sea fishes. But together these comprise only about 8,500 species. That only brings us to the base of the lineage that comprises the majority of living teleosts, the Acanthomorpha, or spiny-rayed fishes – 300 families and about 15,000 species. The majority of these are in the Perciformes, a name we now apply to this whole assemblage, which includes a number of well-defined, specialized groups, such as flatfishes, scorpionfishes, puffers and triggerfishes, tunas, blennies, gobies, and many more, including the basal percoids, comprising about 70 families of mostly perch-like fishes, things like sea basses and snappers, etc. The relationships of these groups one to another remain unknown, and Colin and I were hoping eventually to work our way up into this whole perciform group and try to make sense of it. It is unarguably the outstanding problem remaining in systematic ichthyology – one that Donn Rosen had strong ambitions to tackle in his later years.

If we put that enormous diversity together with the wealth of character information that's available in one fish skeleton, combined with the additional information in the way it develops, the fact that many marine species have larval forms that differ extensively and often bizarrely from the adults, providing another suite of characters, the need to carefully gather and interpret all that character information and then to use some computer algorithm or other to find the most parsimonious solution to the way those characters are distributed among the relevant taxa, use that to propose hypotheses of relationship, cladograms and translate that into a classification, we really do have an

inexhaustible playground – again, only one of several on which Colin spent his career.

Gary Nelson spoke about Colin's dissertation on the Chalk fishes (p.10), published in 1964 and how the state of teleost classification moved from what Colin referred to as "pure chaos" at that time – with very little hierarchical structure beyond the ordinal level – to an attempt to recognise monophyletic groups, due in large part to the cladistics revolution. Donn Rosen's (1973) cladogram from his paper on euteleosts in the first *Interrelationships of Fishes* (Greenwood *et al.*, 1973) is symptomatic of this shift in which there is considerable hierarchical structure in the lower euteleosts but still not much in the acanthomorphs where the majority of teleost diversity lies. It is the acanthomorph group Paracanthopterygii [an unlikely grouping, of the freshwater percopsiforms, with the marine cods, cuskeels, toadfishes and angler fishes, first proposed by Greenwood *et al.* (1966)] that first got Donn and Colin together in 1967, and they published an extensive monograph on the group two years later (Rosen and Patterson, 1969). I believe that was Colin's first major foray into the glycerin, and they both worked on the fossils as well. You need only have a cursory glance at their correspondence from those days to see they were really having fun. And, of course, they worked together, off and on, for almost twenty years, until Donn succumbed to a brain tumor in 1986. In their last joint project Colin and Donn revisited the paracanthopts, particularly concentrating on the internal relationships, now in a cladistic framework (Patterson and Rosen, 1989). That must have been an incredibly difficult time for Colin, watching Donn's physical and eventual mental capacities decline, while he never lost his determination to continue the work.

I was just about midway through my dissertation when the first *Interrelationships of Fishes* was published (Greenwood *et al.*, 1973), and although I missed out on that fun I came on the ichthyological scene with all that hypothesized structure to test and work within. My first correspondence with Colin was a letter I wrote to him as a graduate student at Scripps in 1974 – "Dear Dr. Patterson..... Sincerely, Dave Johnson". I had discovered a foreshortened ray and a little bump on the ray above in the tail of some percoid fishes, a structure I called the 'procurrent spur', and I asked Colin to have a look at the manuscript and examine a few fossils, thinking it might be useful in placing them. True to form, he spent some time looking at the fossils, and sent me a short but encouraging response "Dear *Mr.* Johnson..... *Sincerely,* Colin Patterson" – Fifteen years later, the salutations would become "Dear Dave, Howdy, Well Dearie" etc., and he would close with "Cheers, Love to all, Yours in brotherhood", and so forth. The best part of his first letter was this: somewhere in the manuscript I had written that I had examined the

'myology' and 'osteology' of certain fishes, and Colin's only criticism of the manuscript was to provide a gentle reminder that it was the muscles and skeleton that I was examining, not the -ologies.

It would be almost ten years later that I would meet Colin. I was at the American Museum examining some of Donn Rosen's cleared and stained specimens for my chapter in the book *Ontogeny and Systematics of Fishes* (Moser *et al.*, 1984). Gary Nelson invited me to meet Colin in a local pub and introduced me, and I remember Colin turning and acknowledging the introduction in that resonant voice we all remember, "Oh, hello", he said, "procurrent spur, right? Nice to meet you". He returned to some theoretical discussion, and as I recall that was pretty much the end of our verbal interaction. I left the pub that day, very glad finally to have met Colin Patterson, and more convinced than ever that our professional or personal paths were not likely to cross in any meaningful way down the line.

So, how did we get from that day in the pub in New York, to our memorable scientific collaboration?

In 1988, I invited Colin to contribute to a symposium I was organizing for the 1990 American Society of Ichthyologists and Herpetologists meeting in Charleston, South Carolina on the phylogeny of percomorph fishes, eventually dedicated to Donn Rosen. He agreed to contribute a paper on fossil acanthomorphs (Patterson, 1993). Colin stayed with my partner Sally and me on the way to those meetings, and it was only then that I began to realize what an extraordinary, approachable and easily likeable man he was. Never mind the science – here was someone you immediately felt safe and comfortable with, imposing presence and all, someone you'd really like to get to know. He seemed to have an encyclopedic knowledge about so many things, and at the same time, an insatiable curiosity. There was also a deep, but, I thought at the time somehow understated, *joi de vivre*. When Colin arrived at out house on that first brief visit, we had Tex-Mex conjunto music playing on the stereo, and I was moving quickly to turn it off, thinking he might find it offensive or annoying. But oh no! He immediately identified the accordion player as Flaco Jimenez, who had recorded on the album *Chicken Skin Music* with Ry Cooder – one of Colin's favorites as I would soon learn.

At the symposium in Charleston, Colin, as usual, gave a superb talk, putting the fossil acanthomorphs into perspective as no one else could. I think I gave three talks in that symposium (I was younger, apparently more masochistic, and hadn't foolishly taken on the administrative responsibilities I have now). I did my usual bit, using, in rapid fire, at least three times as many slides as recommended to illustrate the characters – dissections to show gill arch muscles and mostly comparisons of cleared and stained specimens and dissected parts.

I was surprised and pleased to find that Colin took particular note of my talks, and looking back on it now, I think I can easily understand why. I suspect that what really caught Colin's attention was that I was obviously spending a lot of time with the specimens. There were already signs at that time that the emphasis in phylogenetic systematics seemed to be shifting farther away from the primary data collected carefully from the specimens to computer analysis and interpretation of the results. Also I expect all these pictures of cleared and stained specimens took Colin back to his happy days working with Donn Rosen, to whom "the glycerin dish was the crucible in which truth had to leave its residues" (Nelson, 1987).

A cleared and counterstained specimen of *Lepomis megalotis* Rafinesque, about 23mm in standard length. Bones stain red and the cartilage blue.

As he noted in his *Systematics Association Annual Address*, when Colin came into the fish trade, the study of fish skeletons was limited to dry skeletons, radiographs or a less than satisfactory wet preparation technique. Several years later, a new technique (Taylor, 1967) would change forever the comparative study of fish skeletons. A formalin-fixed, alcohol specimen is placed in the enzyme trypsin to digest the flesh, the bones are stained with alizarin red and the specimen is then placed in glycerin to clear the remaining tissue. The result is a fully articulated, flexible specimen that can be dissected to make easily accessible a world of character information that was previously unavailable. Ten years later, another technique (Dingerkus and Uhler, 1977) provided for staining cartilage blue as well. More character information, but also, because much of the fish skeleton forms initially in cartilage, it is possible to follow the actual ontogenetic development of the skeleton – more character information

and the ability to ask questions about primary homology. Do conditions that appear the same in different adults actually follow the same developmental pathway? This was the nuts and bolts of the work that Colin and I did together. Dissecting and comparing these specimens, and searching for patterns that would make sense of relationships.

Colin agreed to collaborate with me on a summary of the proceedings of the percomorph symposium, but it would be over a year before we began that. In the meantime, he had been working on another paper (Patterson and Johnson, 1995) on the intermuscular bones of some basal acanthomorph; some time after the symposium, he sent me a draft of the manuscript for comments. I want to cover this in some, hopefully not too boring, detail, because it was with this that we would recognize our shared passion to solve the giant puzzle with hard work on the specimens and the practical benefits and great pleasure of our continued collaboration. Also, it would set the standard for the way we would work together.

Intermuscular bones are those nasty little things that get in your way when you are eating something like a herring. In primitive teleosts like herrings there are three series; epineurals on the neural spines, epicentrals on the centra, and epipleurals on the pleural ribs. It had been known for some time that the spiny rayed fishes have only one series on the pleural ribs, where the epipleurals of primitive groups insert. The exception is *Polymixia* (beardfish), one of Colin's old friends from his dissertation work and the paracanthopterygian work with Donn. *Polymixia* was known to be the only acanthomorph with both epipleurals and epineurals. But Colin had been studying a large double-stained specimen and had discovered a third series on the centra between the other two series, represented not by bone but by blue stained rods – an unossified epicentral series. *Polymixia* had been shifted around quite a bit in lower acanthomorph classifications; showing that it had all three series of intermusculars, like more primitive groups, would seemingly clinch the argument that *Polymixia* is the most primitive acanthomorph, supporting Donn Rosen's (1985) hypothesis, which was subsequently corroborated by Melanie Stiassny (1986).

But, also, looking at the arrangement in another basal acanthomorph, *Holocentrus*, Colin had presented an elegant argument that the single series of intermusculars in all other acanthomorphs are not epipleurals, but descended epineurals. The so-called epipleurals of *Holocentrus*, although down on the ribs anteriorly, rise to the epineural position farther back, and Colin's surmise was that this is an intermediate step in the descent of the epineurals from the primitive dorsal position to the position they all occupy in all the more advanced acanthomorphs. This was the most stimulating paper I had read on teleost morphology and relationships in years, and I immediately started looking at

specimens to see if I agreed with Colin's observations and conclusions. What I found was also exciting and initially led me to disagree with Colin's conclusions about *Holocentrus* (in the end, not surprisingly, he was right). I saw the blue rods in my smaller specimen of *Polymixia*, but found that I could follow them back well beyond where they stained blue. I had a better microscope than Colin, a Leitz that had been discontinued in the late 70s, the 'silver bullet', as we came to call it, and found that when I got the transmitted light just right, I could see them as very well-defined glassy rods – what we would eventually call intermuscular ligaments.

When I looked at other fishes, I found that these glassy rods were actually quite common, as in the bonefish, *Albula*, where they represent the epicentral series, previously thought to be lacking there, and also continuing the epipleural series forward. So *Albula* actually has an epicentral series of intermusculars, but they are unossified, and the same would apply to many other lower teleost in all three series. This also had implications about Colin's proposal that the so-called epipleural bones in higher acanthomorphs are actually descended epineurals. I found epicentral ligaments in *Holocentrus* as well, starting just at the point where the ossified series ascends, thereby raising the possibility that the anterior bones are not epineurals but ossified epicentrals, because they could be continuous posteriorly with the epicentral ligaments. Anyway, I wrote all over the manuscript and sent it back to Colin. I could tell he was skeptical about all this – he even asked if it wasn't just nerves I was seeing. We agreed that I should bring some specimens when I came over to do the percomorph work, and we would explore it further.

In August of 1991, Colin met me at Heathrow, and with a pleasant stop at one of his favorite pubs, the "George and Devonshire" at the Hogarth roundabout – where I had my first pint with Colin and learned of his fierce loyalty to Fuller's Brewery – it all began. During that first evening spent at Colin and Rachel's house I was enjoying the very congenial company when Colin excused himself to watch something on telly. I eventually went up to join him and found him in the darkened living room watching a black and white video of Roy Orbison, another of his favorites, and singing and humming along with "Dream Baby". I was starting to feel as though I had stepped into a sort of Oz-like world, but looking back on it, the movie line that really comes to mind was Humphrey Bogart's in *Casablanca*: 'this could be the start of a beautiful friendship'. And so it was.

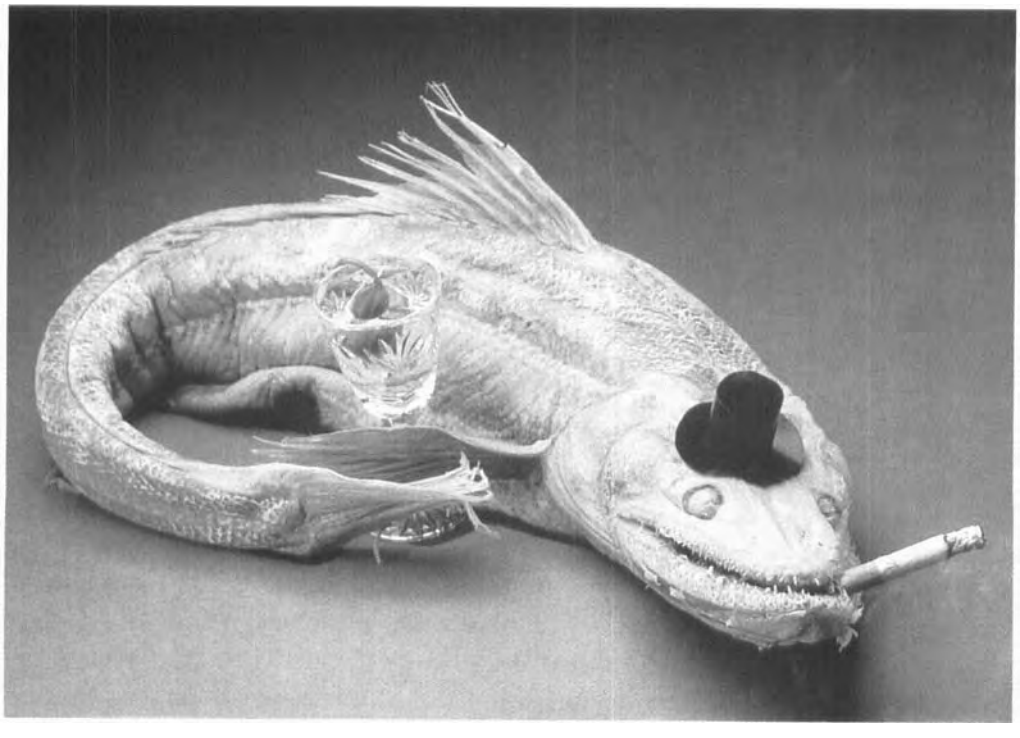
The next day we examined specimens I had brought over. Colin became convinced about what I was seeing, and we clearly established that the bones develop in the ligaments, clarifying their homology with them. As we talked, we soon realized there was a whole world of character information in the

intermusculars of teleosts that was largely unexplored. We decided to step into that world, and so it was that we set out on a fantastic voyage of discovery that would occupy us on and off for the next two years.

To find a complex morphological system in fishes that no one had tried to make sense of was phenomenal. To have a chance to explore it with Colin Patterson was like a gift from the gods. First, we would have to devise some sort of system to record all this information, and something came to me in the middle of the night during that first week. That was unusual, because it was usually Colin who had the middle of the night revelations, while I was fast asleep. We decided on a tabular format in which we could essentially map for each specimen the distribution of intermusculars along the vertebral column. Using a complex system of sub- and superscript numbers, letters and symbols, bolding, underlining, italicizing, etc. we could show for each vertebra the point of insertion of each element and its form and composition (e.g., whether it was formed in ligament, cartilage, or bone, or a combination, the presence of forking at distal or proximal ends, fusion to the attachment site and much more). In the end we did this for about 130 genera representing over 100 families of teleosts. Colin's brilliance and dogged persistence came through immediately, as he managed to figure out how to do this on a little laptop using XyWrite (a very old wordprocessing software but one used by his favourite newspaper *The Guardian*). The end result was incredibly detailed and complex (Patterson and Johnson, 1995: Tables 1–8).

The way we worked recording this information would set the pattern for the way we would work together for the remaining years. I had never experienced such intense, intimate collaboration. One of us would be at the microscope, the other recording on what we would eventually come to call the holy sheets, huge sheets of graph paper. Then we would change places to check the other's observations – the ligaments, in particular are difficult to see, and we always wanted to make sure we were seeing the same thing. It was hard work, done seriously, but always infused with humor. It had to be, otherwise, as is evident from our scribbles on the holy sheets, you'd go mad, and we often joked that maybe we had. It was tremendously exciting, because each specimen was a new adventure, and as we gradually compiled the tables we could see that there were patterns that would definitely offer insight into teleost relationships at many different levels. We gave back-to-back talks on the intermuscular work at the American Society of Ichthyologists and Herpetologists meetings in Austin in 1993. More fun – Colin bought matching Fullers rugby shirts and insisted that we wear them for those talks, and he agreed to have a slide made to acknowledge the Fullers and Carlsberg breweries for their contribution to facilitating our detection of the ligaments.

The way Colin and I worked was, in my experience, unique in many ways. For each problem we tackled we had before us more cleared and stained specimens of the pertinent groups than had ever come together in one place before, and we spent an enormous amount of time with them, combing over every aspect of the skeletons, passing them back and forth to check and recheck observations, congratulating each other on discovery of the '*synapomorphies du jour*', and, at the end of the day, rewarding or consoling ourselves in the form of liquid refreshment. Many of the specimens were revisited in subsequent work, and we began to speak of and joke about them as 'old friends'. I would be the first to admit that some of the humor that brightened our days was pretty silly, some of it bordering on schoolboy stuff. Like the day I returned from our wet collection with an old ground glass jar containing a horrible flabby specimen of a deep sea aulopiform, *Bathysaurus*, which almost certainly hadn't been out of his jar in many decades. Glancing up from the microscope, Colin said: "Look at that poor, miserable creature. He looks like he could do with a night out on the town and a couple thousand cigarettes." So it was that the Associate Director for Science, popping in to pay his respects to Colin, found two grown men in tears of laughter, standing alongside our newly liberated and fully accommodated friend – cigarette, martini, top hat and all. As Colin would have said, *"Happy times"*.



Bathysaurus ferox Günther out on the town.

During the time we were working on the intermusculars, we proceeded with the work on the percomorphs, for which the intermusculars proved to be particularly useful. In our tree of acanthomorph relationships (Johnson and Patterson, 1993: fig. 24), nine of 34 synapomorphies came from the intermusculars. Perhaps the most significant conclusions from that paper are the placement of deep-sea lampridiforms as the most primitive acanthomorphs, based on the inter-musculars, and the redefinition of the perciforms, in large part due to the creation of the smegmamorphs, a new and unlikely assemblage. The atherino-morphs (silversides, killifishes, flying fishes, and relatives) now become part of the percomorphs and are part of a new group we created based on this feature of the intermusculars. The first epineural inserts on a transverse process on the first vertebra, whereas it is right on the base of the neural arch in other fishes. We initially thought this to be present only in four taxa: *Elassoma* (the North American pigmy sunfish), gasterosteiforms (sticklebacks, seahorses and relatives), mugilids (mullets), and the atherinomorphs. So, as we drew the cladograms by hand, often on napkins in the pub, we always had these letters E-G-M-A, and needed a name for the group. Colin suggested 'egmamorpha'. My response: "Fine, but you realize if we do that we're either going to get jokes about Egg McMuffins, the McDonald's breakfast sandwich, or smegma, that substance that, in the US at least, we learn about in our first classes on health and hygiene." We decided to think on it. Colin returned to London, continued looking at fishes, and about two weeks later called me up to say he'd found two more 'egmas', and *guess* what they are – synbranchids and mastacembelids, the missing S & M. "Uh oh" we thought – *dare* we do it? My next trip to London found us in the final throes of the paper, and we had to commit to a name. The second day I was there Colin came in while I was at the scope, with lexicon in hand. He had found that aside from the well-known definition, *smegma* is Latin for soap, a *cleansing* agent. We could call the group Smegmamorpha in recognition of our attempt to "tidy up percomorph classification". We recognized that this was a once-in-a-lifetime opportunity. A long pause followed, and then Colin looked up with a twinkle in his eye, and said, "Well, ... I'm not going to lose my job, are you?" And thus was born the Smegmamorpha – progress in teleost classification and a little fun to boot.

We finished the acanthomorph and intermuscular work around the time of Colin's pending 'retirement' and he asked me what I thought about taking on a long term project to work our way through the teleosts group by group to produce, in increments, a revised classification of teleost fishes – a further example of Colin's passion for the work and how he had no intention of stepping away from it. We obtained a grant from the Smithsonian Scholarly Studies Program, largely to support the frequent travel back and forth to begin this project, which we envisaged would occupy us for years to come. It was about

at that time that the second iteration of *Interrelationships of Fishes* was planned – to be dedicated to Colin. We were planning to do the osteoglossomorphs but a student of Mark Wilson's was working on them at the time.

Douglas P. Begle, who had been asked to do salmoniforms, had dropped out of ichthyology and gone into computers. And so it fell on Colin and me to take on the salmoniforms. This, unfortunately, would prove to be the last major saga in our work together (Johnson and Patterson, 1996), one that would instill in me, even more deeply, something that had always been Colin's credo, that descriptive work is the most important and lasting thing that we do as systematists, and without it the rest is meaningless. This work again extended over a couple of years, and, while not without the usual high points of discovery and great fun, it also came with considerable agony and disappointment. This I will also discuss more extensively because it was controversial, and it goes right to the heart of something that Colin felt deeply about.

Salmoniforms comprise the northern hemisphere salmonoids (salmon and trouts), the osmeroids (northern hemisphere smelts and southern hemisphere galaxiids and retropinnids), the salangids and the argentinoids (a deep-sea group of bizarre and often ugly fishes). Colin and I had spent some time with them during the intermuscular work, which gave us cause to question hypotheses proposed by Begle in two papers based on his dissertation work at the University of Michigan (Begle, 1991, 1992).

As we began to work with Doug's two papers we soon realized that they were rife with inconsistencies between text, matrix, and character list, and obvious mistakes in the reporting of well known characters. However, it wasn't until we began to work with the specimens that we realized the magnitude of the problem. Because Begle's two papers were the most recent published hypotheses, already being incorporated into accepted classifications, we decided we had no choice but to check every character in every taxon against Doug's matrix – a total of more than 4000 observations.

The unfortunate result of this checking was that of 108 characters coded for 33 taxa in Begle's matrix we found errors in 92 (85%). Of the 16 characters that were correctly coded, six are autapomorphic, leaving only 10 correctly coded for all taxa that can actually group taxa, and those were all taken from previous cladistic analyses (Patterson and Johnson, 1997a). I say unfortunate because Begle had stated in both publications: "Every specimen was examined for every character" (1991, p.36; 1992, p.351). We had some of the very same specimens examined by Begle, and found that some hadn't been dissected adequately to detect certain characters reported in them.

In Begle's original fully resolved tree the salangids are embedded within the southern hemisphere galaxioids. When we ran Begle's matrix corrected by us, we got something quite different – over 100 equally parsimonious trees, with much less resolution, lots of homoplasy, and only five nodes in common with the original in which there were 27 nodes. Also the salangids moved to the base of the osmerids, the smelts. After two years of work, our final, fully resolved tree, based on Begle's corrected characters and many new ones of our own, produced a hypothesis that differed radically from Doug's original, including having the salangids embedded within the smelts (Johnson and Patterson, 1996).

At this point we obviously had no choice but to report Begle's errors, but should we go farther, emphasizing the magnitude of those errors, how these errors had come about and the implications for the scientific editorial system which allowed publication? Peter Forey closed his talk at Colin's funeral by saying that if you were looking for one word to describe Colin, it was 'honest' – he was honest in everything he did. It should come as no surprise then, that Colin was hugely incensed and offended that something like this could happen. A PhD dissertation approved by a committee, and two papers sailing through the peer review process and published in two highly respected scientific journals, all based on, at the very least, a cavalier and careless collection of data, and, because of the undissected specimens – there's no other way to say it – apparently an element of fraud. Colin wrote a strongly worded closing paragraph in the second iteration of *Interrelationships of Fishes*. Here is the last bit: ".....Surely at some stage between Begle's writing his papers and their publication, some ichthyologist might have cast an eye over the work and noticed absurdities like crediting *Esox*, the pike, with an adipose fin, an anteriorly placed dorsal fin, nuptial tubercles, an orbitosphenoid, and endopterygoid and maxillary teeth. To discover that *Esox* lacks these features would not need Edward Phelps Allis; a few words with an angler or someone who had glanced at a print of a pike in a pub should be enough".

I spoke about this episode on several occasions in the USA, Canada, Australia, and Japan, and except for the last location, I got mixed reactions ranging from people who said thanks for not pulling any punches to many who were obviously offended by what they saw as a personal attack.

The negative reactions from some colleagues, about a so-called personal attack that was unworthy of the authors, amazed us. We felt that we had bent over backwards in the *Interrelationships of Fishes* paper, and two short follow-up commentaries (Patterson and Johnson, 1997a,b) to make clear that this was not an attack on Doug Begle himself – we saw him as just as much a victim as the systematics community, who would use and accept his

conclusions. Our goal was to point out that the system of checks and balances that set the standards for our science had clearly failed.

Quoting again from Colin's Systematics Association Address:
"Begle's papers are prepared in the style of a lot of modern systematics – the characters are tucked away in appendix or a list at the end, and are treated briefly, a sentence or so describing the different states. The bulk of the paper isn't about characters at all, but instead about the properties of trees, different optimizations, or inferences drawn from trees about things like paedomorphosis or biogeographic history. But what matters, or matters most, in systematics is looking at specimens, as carefully and in as much detail as you can, searching for synapomorphies. If you neglect that, your primary duty, and concentrate on what is secondary, manipulating the matrix and drawing conclusions from it, you can get in a horrible mess, as Begle did, because if the matrix is rubbish, what comes out of it will be rubbish too. I really feel that in adopting this modern version of cladistics, we may be replacing one pernicious black box, evolutionary systematics, with another, the matrix."

Colin and I were both surprised and disappointed by the reactions of many in the systematics community, who apparently, would have preferred that we turn our heads away from this. However, we agreed that if we had to do it over we would do it exactly the same, recognizing also that it would put terrific pressure on our future work – we could not afford to make even a single error in our matrices, which undoubtedly would be carefully, perhaps gleefully scrutinized. And of course, as the epigraph for our *Interrelationships of Fishes* paper says, *"We all make mistakes, then we're sorry"*. We reported some of our own in the beginning of that paper concerning our work with the intermusculars.

So, what is *my* take home message? All authors in the second iteration of *Interrelationships of Fishes* were asked to write something about Colin's influence on them. To do that in a few sentences is orders of magnitude inadequate, but here was mine:
"I began collaborating with Colin Patterson in 1991, and since that time I have spent hundreds of hours working next to him at the microscope, usually surrounded by precariously stacked boxes of glycerin. Many of those hours produced exciting discoveries; even more were spent struggling to find characters, confronting our previous errors, or wallowing in what seemed like hopeless homoplasy. We have smiled and often laughed through most of those hours, and they remain memorable among all those I have spent looking at fishes over the past 25 years. Working with Colin, there is obviously much to admire and benefit from – his deep knowledge of the fishes and the literature, his facility with words on the page, the intellect, focus, and seemingly boundless

energy he brings to the work, and, of course, an *unwaivering* determination to get everything right."

I knew that Colin would be uncomfortable about this sort of thing, so I added it at final submission. He called when he got the proofs. "I saw the last bit in the paper." he said, "*very* touching, Dear, but that is *not* the way you spell *'unwavering'*."

My take home message is more specific than Colin's. The fun and companionship of working and playing with Colin Patterson is something that I will never experience again. The years I had with him enriched my life enormously and uniquely on almost every level, and his death leaves a deep hole that will never be filled. But, as Gary Nelson wrote in 1989, "Recent work has resolved the bush at the bottom, but the bush at the top persists". That bush was the golden chalice for both of us, and I was incredibly fortunate to have the opportunity to join the quest with Colin for a few years. The percomorphs, and other groups at other levels, are still there to provide the fun – and hopefully, for some, the companionship. So, as Colin would have said, *"Pull yourself together, and Get on with it!"* There's nothing more for me to say really, except that old cowboy thing – *"Happy trails....."* to Colin, and to all of us who will have to learn to live without him.

Division of Fishes, National Museum of Natural History,
Smithsonian Institution, Washington D.C. 20560, USA

REFERENCES

Begle DP. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. *Systematic Zoology* **40:** 33-53.

Begle DP. 1992. Monophyly and relationships of the argentinoid fishes. *Copeia* **1992:** 350-366.

Dingerkus G, Uhler L. 1977. Enzyme clearing of alcian blue stained small vertebrates for demonstration of cartilage. *Stain Technology* **52:** 229-232.

Greenwood PH, Rosen DE, Weitzman SH, Myers GS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131:** 339-546.

Greenwood PH, Miles RS, Patterson C, eds. 1973. *Interrelationships of Fishes*. London: Academic Press.

Johnson GD, Patterson C. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science* **52** (1): 554-626.

Johnson GD, Patterson C. 1996. Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti L, Johnson GD, eds. *Interrelationships of Fishes* New York: Academic Press. 251-332.

Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW Jr, Richardson, SL, eds. 1984. *Ontogeny and Systematics of Fishes*. Special Publication Number **1**, American Society of Ichthyologists and Herpetologists. 760 pp.

Nelson GJ. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History* **41:** 475-552.

Nelson GJ. 1987. Donn Eric Rosen (obituary). *Copeia* **1987:** 541-547.

Patterson C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English.Chalk. *Philosophical Transactions of the Royal Society, Series. B*, **247**(739): 213-482.

Patterson C. 1993. An overview of the early fossil record of acanthomorphs. *Bulletin of Marine Science* **52:** 29-59.

Patterson C, Johnson GD. 1995. The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* **559:** 1-83.

Patterson C, Johnson GD. 1997a. Comments on Begle's "Monophyly and relationships of argentinoid fishes". *Copeia* **1997:** 401-409.

Patterson C, Johnson GD. 1997b. The data, the matrix, and the message: comments on Begle's "Relationships of the osmerid fishes." *Systematic Biology* **46:** 358-365.

Patterson C, Rosen DE. 1989. The Paracanthopterygii revisited: order and disorder. In: Cohen DM, ed. Papers on the systematics of gadiform fishes. *Natural History Museum Los Angeles County Science Series* **32:** 5-36.

Rosen DE. 1973. Relationships of higher teleostean fishes. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of Fishes*. London: Academic Press, 397-513.

Rosen DE. 1985. An essay on euteleostean classification. *American Museum Novitates* **2872:** 1-57.

Rosen DE, Patterson C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* **141:** 357-474.

Stiassny MLJ. 1986. The limits and relationships of the acanthomorph teleosts. *Journal of Zoology, London* (B) **1986:** 411-460.

Taylor WR. 1967. An enzyme method of clearing and staining small vertebrates. *Proceedings of the United States National Museum* **122:** 1-17.

Colin Patterson and molecules

D.T.J. LITTLEWOOD

Colin Patterson was, like the rest of us, made of molecules, although for the most part, when we met with Colin, we would see only his morphological aspect and perceive a massive intellect. Colin was an anatomist and a palaeontologist, but he was foremost an evolutionary biologist whose pursuit of truth required that all available evidence was scrutinised with the same meticulous, methodical approach that underpinned a consistent philosophy; and for Colin it was systematics that underpinned evolutionary biology. Colin's vocabulary was as extensive in the field of molecular phylogenetics and molecular systematics as it was in any other evolutionary discipline. "What is functional genomics, Tim?" he once asked me, a few weeks, or was it days, after the term had entered the journals. He never seemed to miss an important paper or fail to recognise the power of a new technique.

This is exemplified by the speed with which Colin grasped the importance of molecular systematics. In 1983 Colin was the first to suggest a meeting where morphologists and molecular systematists would discuss whether there was conflict or compromise between molecules and morphology in phylogenetics. Molecular biology offered the opportunity to deliver a usable, seemingly endless stream of phylogenetically informative data that could at last reduce life to a strictly bifurcating tree. In July 1985 the Third International Congress of Systematic and Evolutionary Biology took place at the University of Sussex, with some of the major players in the field, including Walter Fitch, Morris Goodman and others. In 1987, four years after the original idea, a book appeared entitled *Molecules and morphology in evolution: conflict or compromise?* edited by Colin. Ten years later Colin was invited to deliver the opening talk at a meeting in Paris entitled 'Molecules and Morphology in Systematics'. Colin had actively participated in the molecular debate for over 15 years and had promised me, just 3 weeks before his death, that he and I would finally sit down and write up our own joint work on molecules, morphology and the interrelationships of the teleosts.

During those 15 or so years Colin witnessed the full gamut of emotions associated with the beginning, the rise and fall of molecular systematics whilst having to tolerate the naiveté and many wild claims from molecular systematists. Molecules provided characters for organisms with little morphology. Molecules could be used to verify and test palaeontological data, e.g. looking at divergence events employing a molecular clock. Molecules could provide additional

phylogenetic signal when combined with morphology and they could, of course, provide counter-intuitive phylogenies which were simply biologically wrong or which might on occasion allow us to view morphological evidence in a new light. For the most part, molecules provided an independent data set and yet there were and are frequent cases of conflict, or at least incongruence, between molecular and morphological phylogenies. Colin knew that the faults with molecular systematics were not faults with the molecules themselves but with the way we treated them. Just as cladistics and morphological phylogenetics continue to develop as we understand how to code and score characters, so too does molecular phylogenetics as we understand how to deal with few character states (e.g. G, A, T, and C in DNA) that not only evolve differently within and between genes, genomes and taxa, but may be selected neutrally or be influenced by their chemical makeup (e.g. GC content, hydrophobicity etc.). Furthermore, there were problems common to any data set, namely sampling (having an adequate number of characters from an adequate number of taxa) and the assessment of homology.

In terms of qualifications, Colin had all the necessary credentials to be a critic of molecular systematics. He pored over the data, dissecting it and working with them as he would and could with any character set. Certain skills, thought by some to be vital in this era of bioinformatics, were never sought. Colin appeared to have no desire to link to the 'information superhighway'. Remember, he was a cyclist and would far rather peddle independently than leap onto a train full of commuting sheep. Pulling down information from GenBank over the internet? E-mailing people to retrieve lengthy nucleotide sequences? No, no, no. Transcribing tedious lengths of G's, A's, T's and C's from the original articles onto squared paper with that famous fountain pen, or aligning sequences with overlapping sheets of paper – that was more like it. Whilst one could try and enthuse Colin as to the merits of such 'time-saving devices' as the World Wide Web or computer alignment packages, he would look on with amusement rather like a parent watching children with new toys. Colin's time was too precious to spend on learning new tricks.

Colin would rather think about the data and look for homologies. Molecular data tested Colin's systematic mind in a way that morphology did not. With four discrete character states in a string of nucleotides, ambiguous regions of alignment are commonplace. But herein lies the variability and the signal of past events and it was extremely difficult for Colin to ignore these data whilst adhering to a desire to separate homology from homoplasy. Perhaps it was the paucity of data that made him value them so much and forced him to spend so much time on these early alignments. It seemed to take years for Colin to come to terms with throwing regions of ambiguity out of our own data set.

Molecular systematics brought with it many new toys that Colin did not want to play with. It also brought ideas that Colin seemed reluctant to waste time on. Phylogenetic reconstruction based on distance measures could readily be discounted as they instantly violated notions of homology. Maximum likelihood methods required models of evolution, which in the early days were consistently generating nonsensical phylogenies and after all, the man was a cladist. Many of the fundamental arguments underlying phylogenetic systematics seemed to be constantly reinvented and more than once Colin turned to me during the Paris meeting and, shaking his head, sounding quite exasperated, said "we covered all this in 1982" (Patterson, 1982). It was Gavin Naylor's presentation which salvaged the meeting for Colin, as Gavin showed that even a mass of molecular data is quite capable of contradicting widely accepted morphologically-based schemes when we ignore the functional aspects of the genes, their chemistry and whole organism biology. Molecular systematists were taught a salutary lesson that the morphologists had long since learned, namely that we should learn to recognise features which reflect "actual historical, phylogenetic signals" (Balter, 1997; Naylor & Brown, 1997).

The intellectual 'noise' generated by a new breed of systematist was carefully dissected to reveal signal in a review published by Colin, David Williams and Chris Humphries (Patterson *et al.*, 1993). They concluded that, although there was a need for adequate sampling in terms of both sequence length and taxa, and that the day has yet to come when computers and programs are available to analyse the alignment of life, none of the authors was willing to guess whether we would have a single or 10^{*999} equally parsimonious trees. Colin's scepticism, or perhaps simply reticence, was fuelled by a relatively small data set that he and I were working with. Involving only 22 disparate teleost taxa, neither Colin's morphological data set nor the molecular data set could resolve a believable phylogeny, and by that I refer to a morphologically-based study he conducted throughout his life, and latterly with David Johnson, using many more taxa and characters. Our problems could easily be explained by poor sampling of both genes and taxa. In addition, Colin did concede that molecules were indicating relationships which were not supported by our present morphologically-based knowledge. One such relationship is the apparent connection between the herrings and the ostariophysans (characins, carp, catfishes) which, in Colin's words was "the first major change in fish systematics to be based only on molecular characters" (Patterson, 1997).

I was awed consistently by Colin's knowledge, his incredible memory, analytical mind and eye for detail, although there was one occasion very early on in our working relationship where I realised Colin had his limits. Colin brought me a couple of milkfish (*Chanos chanos*) with which to begin my

molecular work on teleost phylogeny, and he offered to help cut out the gonads for the DNA extraction (male gonads having a very high concentration of DNA). Upon opening the fish Colin was faced with soft part anatomy. No bones needed identifying, no suites of complex synapomorphies needed recognising except perhaps one: we just needed to identify some vital organs. There were lobes here and there and organs all vying for the position of paired gonads. Colin's face first dropped then broke into a characteristic smile as he breathed deeply in. He picked up the dissecting dish and said "Follow me" as we marched off to the Fish Section to solicit a qualified opinion as to "which organ is which, please?". Which brings us back to homology, a word synonymous with the man, from his morphology to his molecules.

Division of Parasitic Worms, Department of Zoology,
The Natural History Museum, Cromwell Road,
London SW7 5BD

REFERENCES

Balter M. 1997. Morphologists learn to live with molecular upstarts. *Science* **276:** 1032-1034.

Naylor GJP, Brown WM. 1997. Structural biology and phylogenetic estimation. *Nature* **388:** 527-528.

Patterson C. 1982. Morphological characters and homology. In: Joysey, KA and Friday AE, eds. *Problems of Phylogenetic Reconstruction.* London: Academic Press, 21-74.

Patterson C, ed. 1987. *Molecules and morphology in evolution: conflict or compromise?* Cambridge: Cambridge University Press.

Patterson C, Williams DM, Humphries CJ. 1993. Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics* **24:** 153-188.

Patterson C. 1997. Molecules and morphology: ten years on. Unpublished oral presentation, Molecules & Morphology in Systematics, Paris 24-28, March 1997.

Contributions to the museum service

Colin: the Museum Man

HUGH OWEN

Most of Colin's professional life was spent in researching, curating and making available to others the collection of fossil fishes in the Department of Palaeontology of the Natural History Museum. Colin always said that it was a privilege to be able to work at an institution which contains one of the finest and most comprehensive collections of fossil and Recent fishes in the World. But it was much more than that. He was totally aware of the responsibility that being a member of the staff of the Natural History Museum implies. This includes care of the national collections and their availability for research by others, together with the advisory service we must provide to both the scientific and general public. All of us are temporary custodians of the scientific heritage and data base that the collections represent. We build upon the efforts of those who went before us and hopefully, lay good foundations for the work of those who are to succeed us. Colin certainly discharged these responsibilities to the full.

Colin joined the staff of the Department of Palaeontology of what was then the British Museum (Natural History) on 2nd July 1962 to work under Errol White on the fossil fishes collection. As well as Errol White, Colin followed in the footsteps of the great Sir Arthur Smith Woodward and to a certain extent, Tate Regan who substantially built up the collection of Recent fishes in the Department of Zoology. Harry Toombs, who was our chief curator at the time, and responsible for the curation of the fossil fishes, had told us that a very promising young fish-worker was joining the staff from Guy's Hospital Medical School. It raised a few eyebrows at the time: a parasitologist joining the fossil fish section? What was the Department of Palaeontology coming to? We need not have worried. Colin's thesis on Chalk fishes, which had not then been published, was masterful and he soon made his mark in the Department and achieved a great deal of respect both as an innovative researcher and as a very good curator. He was a very modest and approachable person, rather unlike the general run of young scientific officers of the day. In those somewhat Victorian days in the Museum, there was a distinct gulf between the researchers on the one hand and the curators, preparators and conservators on the other, in spite of

An example of an acid-prepared fossil fish worked on by Colin. This individual had been secured to a glass fibre plate before the rock was dissolved away with dilute acetic acid to yield a near perfect skeleton. *Leptolepides sprattiformis* (Blainville) from the Kimmeridgian of Solnhofen, Bavaria (BMNH P.4999). The fish is about 60 mm in total length. From Patterson & Rosen (1977) *Bulletin of the American Museum of Natural History* 158:81-172, with permission.

the fact that much of the work overlapped and indeed, still overlaps. In 1970, the Fulton Report into the Scientific Civil Service was implemented and Colin, unlike others, found no difficulty whatsoever with the new unified structure.

He was very perceptive of the political changes of attitude which affected our Museum and many other public institutions from the early 1980s onward. Long before I became a Deputy Keeper in the Department, Colin and I used to talk about the mounting problems that the Department and the Museum as a whole were beginning to face. His intellect, eloquence and integrity as well as his scientific standing allowed him to make cases to visiting boards, politicians and parliamentary commissions alike. We were not defending our "ivory castle"; we were trying against the odds to preserve the heritage of this

Nation and the service that we provide internationally. Colin was always a staunch supporter of that tradition and the raison d'être for a strong natural science base in this country. Never was this more apparent than in 1990 when the Museum faced a serious financial and staffing crisis, when he and other leading scientists in the Museum showed our political masters the strength of national and international support for the work and standing of the Museum and the services that it provided. Like Colin, I fear that politicians still do not appreciate what Science is all about and the effect that it has on our lives and particularly in the education of our people.

He was deeply concerned about the decline in research on systematics in the United Kingdom in the late 1980s and the 1990s, and the effect of reduced funding on the work of the Natural History Museum during this period. He was acutely conscious of the future need for the collections to be continuously augmented, adequately curated, conserved and made available to research workers world-wide as befits a major systematic data base. His written and oral testimony to the House of Lords Select Committee on Science and Technology in 1991 was, in my view, outstanding. It not only expressed his views, his stature and sense of responsibility, but largely reflected the opinions of the scientific staff of the Museum with whom he had had prior discussion.

When I was preparing my address, I felt that Colin would have been critical of me for failing to reiterate the warnings that he made in 1991 to the Select Committee on Science and Technology. I re-read his contribution and it is in many respects as relevant today as it was in 1991; I commend it to you (Patterson, 1991). It is true that since the report of the Select Committee, the NERC initiative in taxonomy has been promulgated, which finances training courses at institutions such as Kew, Reading, Glasgow and Edinburgh. However, there still does not appear to be any fundamental improvement in the provision of career continuation for individuals to gain the necessary long-term experience and expertise vital in systematic research. There are some very good young systematists developing in this country, but short-term contract posts do not provide the essential continuity of experience and stability that they need. The upkeep of scientific collections, not only in the Natural History Museum, is still at risk owing to a shortage of experienced staff. All of this reflects politically ill-considered financial constraints, despite the recognition at the Rio summit meeting of the vital importance of systematics and the data bases provided by the various Museum collections. One day we might all pay dearly if the training and career structure is not sufficiently improved to put specialists in place who can provide meaningful answers to future environmental problems.

Colin officially retired towards the end of October 1993, but to all intents and purposes he continued to cycle into the Museum each day as if nothing had changed. He was coming to the Museum when he died. Colin was a workaholic and efforts had to be made to get him to take things more easily, particularly after his first heart attack in 1984. That was no easy task, but Colin always took exhortation patiently and in good part.

Death is always a sad loss to those loved ones and friends who are left behind, but it seemed so hard that this should have occurred while his work was still in full flow. But, in the Department, it was by no means all serious stuff. We all have a wealth of anecdotes concerning Colin and he touched all of our lives for the better. Colin had a marvellous sense of humour and fun and many were the laughs and chuckles that permeated a coffee break and a celebratory party. The group of four oldies within our coffee-circle in the Department – in which much scientific matter was discussed, I hasten to add was characterised by some as the last of the summer wine. Colin of course was the urbane Clegg and I will leave it to others to decide between Dick Jefferies, John Richardson and myself, who was Compo, Foggy and Seymour!

Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD

REFERENCES

Patterson C. Tuesday 2 July 1991. Memorandum by Dr C. Patterson .. examination of witness. In: *Great Britain. Parliament. House of Lords. Session 1990–91:* Minutes of evidence taken before The Select Committee on Science and Technology (Sub-committee II Systematic Biology Research). Pp 183-194. HMSO: London, 1991. (HL Paper 41). ISBN 0104041919.

Personal Reminiscences

Colin: Recollections of a deeply valued companionship

BRIAN GOODWIN

I knew Colin by reputation as a radical systematist long before I met him and began a stimulating, if intermittent, dialogue on the connections between ontogeny and phylogeny. The occasion that initiated our discussions was a conference at the University of Sussex on Development and Evolution in the spring of 1982. This was held under the auspices of the British Society for Developmental Biology. As one of the organisers, I invited Colin to give the first paper, setting the scene for the topic of the meeting. I was convinced that he would present an intellectually challenging position, and I was not disappointed.

Colin's brief was to discuss his views on the relationship between comparative embryology and taxonomy, presented within a historical perspective. This he did in what I regard as one of his classic papers, entitled *How does phylogeny differ from ontogeny?* (Patterson, 1983). In characterisitic style, which combined scholarship, historical depth, and conceptual elegance, Colin presented his argument for the role of developmental processes as the key to understanding evolution as transformation. I found his defence of systematics as a search for the intrinsic, real nature of taxa and their dynamic relationships inspiring, convincing, and intellectually satisfying. A quotation from the paper made clear his view of what happened to systematics after Darwin. "The change in systematic or comparative biology which accompanied the general acceptance of evolution can be summed up as a shift from an attempt to discover and represent natural order, to a world view in which life was known to be a historical continuum on which biologists must impose order". Colin was looking for this natural order, and he saw ontogeny as essential to the quest since it provides the only real empirical data on the actual transformations of organisms.

It was around this theme that our subsequent scientific discussions revolved, whether at the Open University where I went after Sussex or at the Natural History Museum. The conversations spilled over into broader subjects, since

Colin's interests extended well beyond science into literature, the arts and, of course, sport. He was always a wonderful social companion. For me he represented the best traditions of British science: intellectually exciting, empirically grounded, and socially congenial. He celebrated life well and his passing creates for me a very palpable absence.

Schumacher College,
Dartington, Devon.

REFERENCE

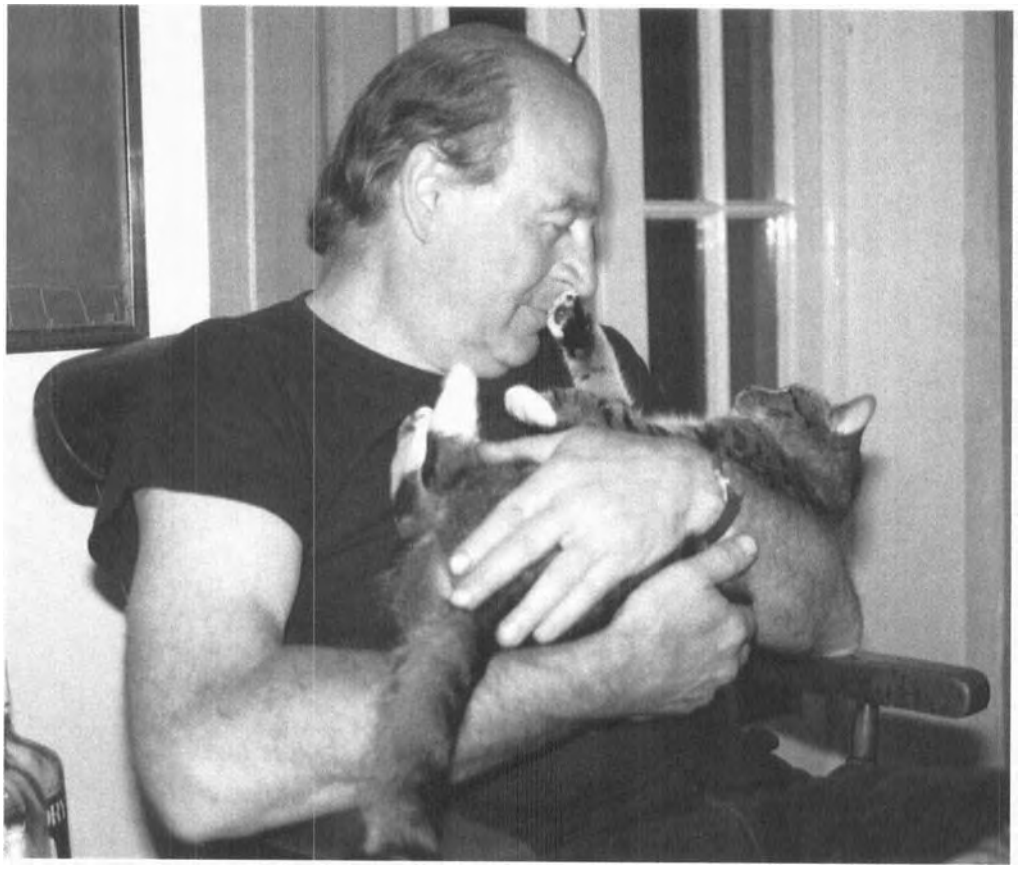
Patterson C. 1983. How does phylogeny differ from ontogeny? In: Goodwin BC, Holder N, Wylie CG, eds. *Development and Evolution.* Cambridge: University Press, 1-31.

On Influence

RICHARD VANE-WRIGHT

My favourite animal is the tiger. The essential thing about the tiger is to know that it is there. But the tiger is more than a symbol: it *defines* life in some way. I have never seen a wild tiger, and don't need or even particularly want to. But when news of the tiger's final demise comes, I will feel a terrible loss, a sense of diminishment.

Colin liked tigers too (well, cats at least). For me Colin also came to be like a tiger. Fierce and playful, and strong and purposeful, yes all those things. But in my special tiger-sense too. Weeks would go past, months sometimes, and I would not see him. But that did not matter – sufficient to know that he was out there – in the Barnes forest, the Welsh steppes, the North End Road marshes.



"Colin liked tigers too" [Colin seated at home with cat – Photo RIVW].

Then suddenly I would come across him in the General Library, or striding purposefully across the Main Hall, in that inevitable black jacket or checked shirt. "Dear boy, how are you – where have you been?", he would say.

A sense of well being flowed through me at those greetings – in some measure, I would have to admit, reflecting a vestige of that ghastly affliction of youth, the teenage crush. Colin had a natural and effortless authority, and commanded devotion without ever wishing to do so. Of course, Colin was the very opposite of an authoritarian. This gave room, on the one hand, to hold an almost reverential respect for him and his views, and at the same time disagree, or at least hold very different views on many issues. I don't think I was alone in this, a paradox that I think Richard Fortey expands upon.

Colin was much more than just a mentor or guru, of course. He was a great and generous friend, a source of wise council in times of need, and tremendous good spirits. Some of the best spirits were enjoyed at his home, thanks to Rachel and the family who, from time to time, would share the good times with Colin's professional colleagues, no doubt in the hope that their burdens in life would be lessened. At times like this, Colin seemed to define life in some way, its struggles and ups and downs, but above all the value of integrity, an unyielding concern for truth, and an overwhelming sense of loyalty.

What was Colin's influence on my own thinking and development as a scientist? My influences in biology have been various, but the three leading names have to be Ernst Mayr (even though I long ceased to believe in species in some special sense, I am ever grateful to Mayr for framing so much of the debate, and so richly exploring some of the issues), C.H. Waddington (trying to understand complex systems: biological systems *are* complex in my view, and so arrogant reductionism has always been a pet hate, and I think Waddington understood the rôle of models and analogies in the relationship between analysis and synthesis better than most), and Willi Hennig (for making plain why a principled general-reference system for biology is so essential, and giving such fantastic excitement to systematics). I became aware of Hennig's notions of phylogenetic systematics in 1965, at about much the same time as Colin and Gary Nelson and no doubt others amongst the early English-speaking converts.

So what was Colin's influence? I will give just one example. Maybe 15 years ago, in the old pub ("The Cranley") that we used to frequent on the Fulham Road, Colin made, for me at least, a key statement: "for a taxonomist it is as important to discover a new character as to discover a new species". He said this on more than one occasion, but I am not sure if he ever wrote it down. Why would that be a profound remark to an entomologist?

Entomologists are faced with a huge task: the naming, description and classification of millions of species. Most of the insects out there still have no name. But when I look back on my professional life, I might feel that I have let the side down. I doubt I have described more than a dozen new taxa, and most of those would be genera, not species. So what have I been doing? Colin made me realise, overtly rather than covertly, that I have been studying characters in order to understand taxa, rather than the reverse.

My first paper (published in 1967) was mainly about looking for synapomorphies (by a process of induction). Nowadays I look for homologies (again, a clarification due to Colin), recognised by parsimony. However, Colin's remark also made me realise something that links all three (or should I say four?) of my biological heroes. One of my major concerns has been to find a way to identify those characters that the insects use themselves, such as pheromones, bright colours or conspicuous behaviours to recognise each other. For me this is close to the real organising principle we call natural selection. I don't mean blind chance working on random variations, but the organising principle of intelligent behaviour. If an insect knows how to find a mate, and how to assess the desirability of that mate, then it really knows something. And if we can find out how it does it, and what it attends to, the signals it responds to, then I think we really know something too. So Colin's insight made me feel good: it helped to see the way in which Mayr, Waddington, Hennig and, yes, Patterson too, despite their extremely different values and interests, really did all fit together. A true synthesis, in my head at least, due to an almost off the cuff remark, a little lunch-time gift from the master.

When the tiger has gone, I shall mourn its passing. Colin has gone, and we have mourned his passing. But we can also rejoice, to have known Colin, to have shared in some part of his life. Despite the loss, the diminishment, there is a continuing and deep enrichment that comes from having known the man that was Colin Patterson. Let us celebrate his life together, his great achievements in biology – and our incredible luck and good fortune to have known him, Colin the man, Colin the tiger.

Department of Entomology, The Natural History Museum,
Cromwell Road, London SW7 5BD

Colin

RICHARD FORTEY

You cannot do justice to Colin in an afternoon. In some ways, scientists are fortunate in death because their ideas live on in those who have known them, respected them and liked them. It's not just the citation thing, rather, every time a citation is made it triggers memories and associations, controversies settled, other names of other scientists in turn. Unlike other practitioners of creative activity scientists live on in the matrix of fertile ideas, and although the trappings of personality have little to do with this endurance, published endeavour and experience handed on is a legacy that doesn't fade like ink or get spent like an inheritance.

Of course, even as I wrote these words I could hear Colin's inimitable voice saying "*Surely you don't really believe that*!"

But it *is* true that unlike the novelist or poet whose works exist as complete things in their own right – and whose achievements can be destined for an obscurity from which there is no return – scientists can alter the thought of others in ways which, even if not overtly acknowledged, are inbuilt into the whole system of reasoning thereafter. Colin's was one of those achievements.

I got to know Colin well rather later than most of the speakers today, although I have been at the NHM as long as most. To tell the truth, when I first met him I was more than a little intimidated. I think I felt that my own ideas were invariably too jejune to be taken seriously. But I too trooped along with everyone else to hear his magisterial explications of cladistics in the early days. It was like being in on progressive episodes of an unfolding serial – and for a while we had little idea of the ending. Others have shown how the ideas germinated then have born fruit in a dozen different fields. In time, I learned that Colin's forthrightness was engendered by the high standards he expected of himself rather than by judging others on their inability to reach his own exacting level. I think an observation made in error by a fellow fossil fish worker made him quite restless until it had been put right. We know how much he believed in collections as a repository for observations which could be confirmed by generations to follow. The fishes, after all, never lie – it is up to us to find out the truth.

This brings me to consider one of the paradoxical things that comes to mind regarding Colin. Several speakers have referred to his criticisms of authority in taxonomy. The word of the 'expert' serving to, as it were, fossilise taxonomy and classification into a system demanding the authority as arbitrator. To

overturn shibboleths was his particular pleasure. I recall once pooh-poohing what seemed to me a particularly bizarre published arthropod phylogeny only to have Colin remind me that nobody had done the work which might disprove it. He seemed perpetually to be able to keep an open mind. What, then, are we to make of several speakers who refer, rightly enough, to Colin's natural authority? Of voice, of thought, of presence. Some of those who exemplified the 'use of authority' in classification – A.S. Romer comes to mind – were assuredly less commanding in their personality and charisma. If you knew with Colin that observations were made from the specimens themselves – well, perhaps you could trust the authority of that work. When we had trouble at the Museum – not least in the shake-up ten years ago – it was Colin who had the authority to confront the authorities on behalf of his fellow employees. The paradox then is that one to whom authority seemed so natural should be so suspicious of authorities past and present. The resolution in this paradox is, I think, the difference between authority and authoritarianism. The former is something which can be earned, like respect, the latter can be imposed. I am certain that he despised authoritarianism. He may have had heroes but I suspect that those heroes were those who suffered in the cause of free speech.

In some ways Colin's personality was elusive; he seldom wore his heart on his sleeve, and was certainly impatient with any wallowing in self-pity. He could defuse such self indulgences painlessly with his great guffawing laugh. Maybe the 'core of character' is revealed in subtler ways; one way might be through fiction. I recalled that Colin once recommended to me a favourite novel of his, *Rogue Male* by Geoffrey Household published in 1939. It's really rather a good book and I read it recently with considerable interest. Maybe the hero strikes a chord.

The rogue male of the title seeks out a dictator (never referred to by name but obviously Hitler) – the quintessential symbol of authoritarianism – in his redoubt. This is prompted partly by philosophical objections, but also by the sheer challenge of it. It is almost a sport – the ultimate big game bag. He does not succeed, and the rest of the book is an account of his being hunted down by skilful and implacable agents whom he eventually defeats. He copes with this alone, dealing with all the problems alone. Those who aid him are themselves absolutely trustworthy, but also slightly on the outside of what might be called the 'establishment'. By the end of the book you engage absolutely with the integrity of the hero. He was incorruptible, reliant on his own resources, utterly his own man, opposed to authoritarianism, and with a liking for adventure. Maybe Colin identified with the hero – maybe not. But it is not a bad description of his own virtues.

Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD

On Friendship

CHRISTOPHER J. HUMPHRIES

Ralph Waldo Emerson once said that the qualities of friendship are so demanding that it is entirely possible that friends do not exist – rather, we only make acquaintances. To me this was such a depressing conclusion that at the time I asked Colin Patterson if he thought Ralph had got it right – he said no, but added that one does not choose friends or acquaintances, they emerge over time. To Colin, I got the feeling that most people were acquaintances because he did not take friendship lightly. To me it seemed that Colin's view on friendship was that loyalty was supreme, and in life very few friends come along. Colin went on to say, but not in these exact words, that however bad ones friends can be, personal feelings should be kept under wraps, and one should never question frailties, morals or motives. This was a little bit uncomfortable as it made me wonder what he thought about anyone at all.

Dick Vane-Wright first introduced me to Colin in 1975 after Colin had given a lecture on the principles of cladistics to interested staff and students at the Natural History Museum. Apart from hearing a superb presentation, the contents of which were similar to the paper he was later to write in the *New Scientist* (Patterson, 1982), the thing I remember most was that we all repaired down to – what was then – the Queen's Elm Pub in South Kensington. Our first conversation was about Trog (Wally Fawkes) and London Jazz bands in the 1950s. I immediately came to realise that here was a man of intense knowledge especially of fishes, cladistics, London and Life in general. I wanted to know more but at 7.00 clock sharp he hopped on his bike with a cheery "so long".

I did not see Colin very much after then until Peter Forey was editing the 1981 Museum centenary volume *The Evolving Biosphere* (affectionately known as 'The Revolving Bicycle'). Colin reviewed and edited my paper on the *Biogeography of Nothofagus* – the group of southern beech trees. The manuscript had more pencil marks on it than original text. I had not encountered anything quite like it before and it was dawning on me as to the strength of his intellect. The following year I went to Australia on sabbatical. On my return I became a frequent visitor to his lair in the museum and to the unofficial seminar room at the Cladist's Arms (The Cranley Arms) and later the Transformed Cladist (The Rose), both on the Fulham Road in South Kensington. Although I did not know it at the beginning, his office and the two Cladist's Arms were important conduits for debate with regulars and visitors alike.

Gradually, I became drawn to Colin's circle of friends and lunchtime socialites, Dick Vane-Wright, Peter Forey and Brian Gardiner. The Cladist's Arms was to become the social hub both for like-minded colleagues and for Colin's international friends, most of them in the vanguard of systematic research. Through Colin I met Norman Platnick, Søren Løvtrup, Ed Wiley, Donn Rosen, Gary Nelson, Jim Lake, Gene Gaffney and many others. It is hard to express just how important these contacts were for me at the time when cladistics and biogeography were my central interests.

In 1985 Brian Gardiner and Colin decided that an occasion was needed to celebrate Peter Forey's 40th birthday and that we needed to have a mid-week day off work and go for a walk somewhere in the countryside. It was important to Colin that it was in the middle of the week, as it would not have felt like playing truant if it were on a Saturday or Sunday.

The first trip out on 6 May 1985 was along the Pilgrim's Way to Box Hill and environs and it was the five usual suspects that went on it. We walked for about 14 miles and had a great time. Brian and Colin had decided that we should have some entertainment during the day, so they carefully had seeded the route with goodies. We stopped occasionally to peer down a rabbit hole, in the hedge, or under an old shed to extract a few cans of beer. By the end of the day I was beginning to think that Brian had recently bought some shares in the Carlsberg Brewery or was trying to indicate that there were novel uses for funds from the Carlsberg Foundation. Birthday boy, Peter, celebrated in style as not only liquid refreshments but also presents and carefully placed fossils in an old chalk pit were placed along the route to provide some academic discourse along the way.

As with almost anything in which Colin was involved, the route along the Pilgrim's Way was meticulously planned. It was such a success that we planned another walk for the following year. Our second walk took place on 16 July 1986. The route was from Colin's house to my house – Hammersmith Bridge to Teddington Lock – along the north side of the Thames, a distance of about ten miles. There was nothing particularly remarkable about this walk except that it was a beautiful, warm day and an extremely pleasant amble along the nice, flat towpath.

After this outing we thought that we should take walks on a regular basis and the ambience of the day created the pattern of future walks – we should examine as many of the waterways in the London area as possible. We went on to take 17 walks, 15 of them along some of the most important waterways in London.

The curious thing about our day trips was that the gang of five had become a cohesive group of souls that did not take easily to others. Colin turned down a couple of requests from different people when they wanted to take part. It

was almost as if five friends were enough. Ralpho Waldo Emerson made many statements about friendship and another memorable line was "The only way to have a friend is to be one", and I think this was Colin's way and perhaps why he was so wary about who he let into his life.

We all shared Colin's politics with conviction. We were, and still are, ardent socialists and our group contained at least three card-carrying members of the Labour Party. It was on the third walk that our political convictions forcefully emerged. On a warm summer day in August 1987 we decided to walk the colourful half of the Grand Union Canal, between Alperton and Limehouse proceeding in an easterly direction. As we passed the new TV-AM building at Camden Lock Mrs Thatcher's credentials on deregulation came in for serious scrutiny. Similarly, as we arrived just a whisker away from the site of the Limehouse Declaration, the new centrist politics of David Owen, Shirley Williams and their merry chums were similarly discussed and dismissed with aplomb. It was at moments like these that I realised that Colin's style was a cut and thrust approach. Things could only be in black or white and no grey views were allowed.

The sixth walk, on 2 November 1990, was a return to the Grand Union Canal, this time from Alperton in a westerly direction to Brentford Lock. For one single reason I believe this to be the best walk of all. The political machinations of the day were at the top of everybody's mind and there was no-one more pleased than Colin, apart perhaps from Brian, when Margaret Thatcher resigned as Prime Minister and Leader of the Tory Party. It transpired on this day too that Colin hated the antics of city types, barrow-boy traders and share dealers alike and preferred fair pay for a fair day's work. The Museum was dear to his heart. He hated the politics of the late 80s and many of the changes that came into the Museum after 1990, especially the divorce between research and curation. On this subject he felt that the connection between knowledge and responsibility had been lost and the importation of short-term ideas and jobs created many problems for the care of the Museum's resources.

It was along the waterways that Colin's grasp of the literature, both professional and general, came to the fore. Subjects that came in for discussion were as diverse as the books in the British Library. For example, Colin loved everything about London. On the Limehouse Grand Union Canal walk we talked about Hawksmoor churches and how they were built using Fibonacci series when determining the number of pillars for each storey of the towers.

Colin's greatest love along the waterways was bird watching. The unspoken game on every trip was "Spot the Kingfisher". I can only think of perhaps one occasion when Colin was not the first person to see one. Colin did not keep a list of all the birds we saw but it was through his enthusiasm that my own interest

Bow Locks on the River Lea, 1988.
From left to right Dick Vane-Wright (kneeling), Colin Patterson (with binoculars), Peter Forey (seated), Brian Gardiner (right hand on hip) and Chris Humphries (left hand on hip). [Photo CJH and timer.]

in bird-watching grew. Another memorable time was walking along the River Lea in 1992. It was a great sight to see a Heron colony in the reservoirs with 20 or more visible nests in view and at least 100 herons on the one small island.

George Washington once said of friendship: "Be courteous to all, but intimate with few, and let those few be well tried before you give them your confidence. True friendship is a plant of slow growth, and must undergo and withstand the shocks of adversity before it is entitled to the appellation". In the early years that I knew Colin he would often speak of his ichthyologist friend, Donn Rosen, who for Colin truly fulfilled George Washington's criterion. I met Donn through Colin, and soon realised that Colin's working style was to discuss matters with a close friend and collaborator. When Donn passed away Colin seemed clearly isolated and he mourned his old buddy deeply. It took him a long time to get close to other researchers again. Apart from some contact with Jim Lake in California, he did not really find anyone until Dave Johnson came along.

I remember just before our sixth outing that there was great debate as to whether we should invite Dave Johnson along for a walk. Colin at first wasn't so sure as he did not want to upset the established ambience, or indeed bring

in interlopers into what was rapidly becoming a clique with attitude! The rest of us, however, thought it was a good idea and Dave, our first guest walker, joined us for a soggy traipse along the Beverley Brook in 1991. I distinctly remember that the subject matter broadened into stories about Kinky Friedman and the Texas Jew Boys, the musicology of Roy Orbison songs and our most mouth-watering moments since we first noticed girls. Dave's tales of morels and truffles made us all slaver. Relatively recently, I shared a memorable collecting trip with Dave near Washington to find morels. But perhaps the most important occasion was our most recent walk in February this year. Prior to the excursion Dave, at my request, had brought over half a kilo of freshly harvested Perigord black truffles. It was on this occasion that gastroporn reached its zenith with discussions of warm smells, truffle flashbacks and fungal cuisine.

There have been only two other guests on our walks – Gary Nelson and Richard Fortey. Richard and Gary joined us on the 23 April 1997 when we walked from Shepperton to Teddington along the Thames. I remember the discussions on that day were about the author J.G. Ballard who lived in Shepperton, Richard Fortey's election to The Royal Society and Stephen Hales, perhaps the greatest botanist to live in Teddington. Richard again swelled the ranks to seven when he joined Dave and the rest of us on the last walk in Colin's presence in February this year.

For me it has been a pleasure and privilege to be a small part of Colin's rich life. Colin was a brilliant and challenging friend, who could never be ignored. He embodied our outings, and enjoyed all of the 17 walks. The important thing was that we were always a bunch of mates who did not take things too seriously.

We enjoyed walking along the Pilgrim's Way; ambling along the Thames between Hammersmith Bridge and Shepperton; strolling along the Grand Union Canal between Limehouse and Brentford, walking along the Hogsmill River into Kingston, along the River Wandle coming into Wandsworth and along the Beverley Brook. More challenging trips included the Dartford and the River Lea; an overseas trip from Deal across the channel and around Boulogne; along the River Wey, near Guildford; the Basingstoke Canal; and two outings along the River Stour. Finally, Colin had a good last look at his beloved London when we walked along the towpath from London Bridge to the Thames Barrier.

In the end, the walks became something of an institution. We went to the best pubs at lunchtime and Indian restaurants in the evening. We celebrated 40th, 50th and 60th birthdays, the politics of life, cladistics, the Natural History Museum, the ins and outs of personal relations and occasionally the importance of being earnest. We will never again be able to check the details with Colin, but what we learned over those 14 years can never be erased from our minds.

I would like to finish with one last quote from Muhammad Ali who once said: "Friendship is the hardest thing in the world to explain. It's not something you learn in school. But if you haven't learned the meaning of friendship, you really haven't learned anything". In this respect I think of Colin most days and miss him greatly. Our Thomas Paine outing, the 18th walk around Lewes, was just not the same without him.

Department of Botany, The Natural History Museum,
Cromwell Road, London SW7 5BD

REFERENCE

Patterson C. 1982. Cladistics and classification. *New Scientist* **94:** 303–306.

Australian friends

SUSAN TURNER
(with contributions from C.A. Macadie and J.M. Warren)

I first met Colin at the Natural History Museum in 1967 when I became a PhD student of Bev Halstead's at Reading University. It was then I began to visit the "BM" to study the Welsh Borderlands collections of Devonian fishes of Errol White, Bill Ball and Dave Dineley. I first saw Colin getting a book upstairs in the old library just up from the winding staircase. To me he seemed a formidable figure in a way – a BMNH man. Yet a man who wore stripey shirts and a leather jacket could not be too intimidating for a 21 year old. Harry Toombs was then my main contact in the fossil fish section along with Ian Macadie, then assistant to Toombs but now based at the Christchurch Museum in New Zealand and working on Devonian fishes. He wrote (*in litt.*, 1998):
"We had some fun during the sixties. Bergisch Gladbach in '65 looking for fossils, celebrating our finds and driving 20kms on the wrong side of the road after an excellent dinner – the following day we almost dynamited Billy Ball! In 1963 or '64, Colin narrowly avoided getting killed on the Syrian border when he crawled across a quarry floor looking for *Eurypholis,* or the like, only to be woken from his intentions by the sound of machine gun bullets whacking into the ground around him – he had come into range of a border guard. Or, the occasion we all took Harry Toombs to lunch at a fish restaurant off Leicester Square and Colin meticulously dissected his eels! He had a colourful life and it would make an excellent biography."

My first real impression was at the Geological Society of London when Bev, John (J.R.L.) Allen and I did a demonstration on the Mitcheldene locality from the Welsh Borderland (Allen *et al.*, 1968); Colin came in and looked intently at the *Turinia* specimen I had displayed, the first articulated piece of thelodont which I had attempted to describe. After the brief talks which John and Bev gave, I was waiting for some cryptic comment. But this 'bon mot' didn't really come until much later when, in 1979 at a meeting in Newcastle upon Tyne, he pronounced that the thelodonts (the group that I work on) are an 'unnatural' group and so set me the task of finding characters to use to demonstrate that this was not the case.

We met at the Annual Symposia on Vertebrate Palaeontology and Comparative Anatomy (SVPCA) meetings and especially the 1968 one at Reading which Bev and I organised and the follow-on trip to the Welsh Borders where we stayed at an amazing place, Brockhampton Court. That is where I

first came to know Colin as a person and as a friend. He eased my own first public presentation at the SVPCA in Newcastle-upon-Tyne in 1969 (with a valium before, and a brandy after). Colin was probably the first person I remember who treated me as an adult. I think he enjoyed the exchanges we had about people and it was I who sent him a first cladogram of fish cladists from Beijing in 1984.

As well as helping me learn how to deal with the Natural History Museum and its fossil fish collections – and this was during the 1960s – Colin and I both shared a love of the Rolling Stones and the Beatles, especially John Lennon. 'Hey Jude' was a favourite, but because it was played during Roger Hamilton's memorial service Colin could no longer listen to it. Instead 'Let it Be' would be Colin's song for me. And he was a great dancer; one of his little known accolades of which he was most proud was winning the Twist Competition at the Hammersmith Palais in the early 1960s.

Like many other of Colin's friends I too have happy memories of times spent in conversation with him in the Museum and up among the lakeland stone tiles having a 'fag' on the roof with Donn Rosen and others. Or at SVPCA meetings and in beloved pubs, many now sadly gone, 'The Hoop & Toy' and 'The Cranley' in South Kensington, 'The Bun Shop' in Cambridge. We shared happy and sad times. Another friend who shared those happier pub moments was Professor Jim W. Warren who writes from Kuala Lumpur, Malaysia (where he is currently Pro-Vice Chancellor of the Sunway Campus of Monash University) (*in litt.*, 1998): "Colin Patterson impacted on my academic interest and my life when I first met him in the BM in 1969. I say 'impacted' rather than 'influenced' because the latter word is too weak and rather trite. Colin was never weak and never trite.

I had gone to the BM in 1969 from Monash University in Melbourne where I had been for seven years, having gone there from UCLA. My intention in Australia was to pursue fossil reptiles, predominantly Permo-Carboniferous ones but always with the hope that Triassic therapsids would emerge. The lack of these proved so frustrating that I turned to prostitution and began fondling Paleozoic fishes, which seemed to be in abundance. However, I didn't know enough about them fully to appreciate their anatomy, so I arranged to spend several months at the BM.

It was my first visit to the old country. Colin took me in hand, offered me research materials and literally locked me in the BM basement. At the end of my first week he patiently responded to my naïve questions, correctly identified the galaxy of weaknesses in my knowledge of early fishes, and set about putting me on track. He didn't have to do this, but as all of his colleagues know, it was his way. He would help anyone in an intellectual endeavour; he would even suffer fools, at least for a while. His straightforward, no nonsense, get it

right attitude accelerated me into the world of Paleozoic fishes for which I was, and am ever grateful.

On a personal basis, Colin also tutored me in the ways of London. He introduced me to people of like mind inside and outside of academia, and with Rachel made me feel welcome in their home. He never visited Australia but we stayed in touch and enjoyed meeting at conferences or when I was using resources at the BM.

I know I am not the only one Colin touched, but his impact on me was as great as on anyone. His efforts to save the BMNH (before and after its name change) from rampant market forces and philistines, and his contributions to scholarship in general, and to our science, are internationally recognized, and I am sure will be highlighted by others."

And we shared the sad times – the sadness of visiting our friend Roger Hamilton in hospital or when we went to sign the memorial book for Eigil Nielson at the Danish Embassy in December 1968, of his relating his last visit to Barney Newman (who was dying of cancer), ever a presence in our lives. One happy memory is of a SVPCA meeting in Cambridge, rolling home from a liquid lunch with Colin and Barney flanked by N.B. 'Freddy' Marshall and Peter Purves, all slightly the worse for wear. From afar he helped me cope with the death of my mother and Beverly Halstead, who died in the same fortnight in 1991. Both Jenny Halstead and I were very appreciative of the obituary Colin wrote for Bev in *The Independent* which we agreed was closest to capturing Bev's essence. After I emigrated to Australia in 1980, we were to meet again rarely on occasions of my brief visits to the NHM or, surprisingly, as at the American Museum of Natural History in March 1983. The last time was in September 1996. However, with the wonder of email we had been in touch again in the new year (February 1998) to talk of matters historical and about our mutual interest in the life and times of Stanley Westoll.

I particularly treasured my inscribed copies of his papers "from the junior author" or "this is the last one and you can have it". Sadly they were borrowed by a member of the Queensland Museum staff and not returned but I hope are not lost forever. Also (although I have been unable to locate them) the SVPCA dinner menu cards with his alter ego signature "Roger Daltrey".

He justifiably had pride in his achievements but did not exhibit it in what might be called usual ways as typified by the *Foreword* from the first edition of *Evolution* (Patterson, 1978).

When I left Britain in 1980 to start a new life in Australia he gave me a book to help me orient myself, by biologist Professor A.J. (Jock) Marshall and artist Russell Drysdale (1966), *Journey Among Men*. I turned again to this and

another book by Marshall, *Darwin and Huxley in Australia*. I think I can do no better than to quote my the words of my now fellow Australian, Russell Drysdale, for Jock in the preface of the latter book. Marshall obviously shared many character traits with Colin – the scholarship, the wit, his devotion to a cause, his loyalty to friends, his kindliness and courage – and I presume they may have met at University College. And that fundamental part of his character which he showed not only to his friends but to the world at large was his enduring, uncompromising honesty and deep humanity.

"He challenged ideas, apathy, entrenched attitudes and lack of imaginative thinking. He disposed of sacred cows without requiem and tore to shreds the cloak of our improper conceits."

Those who knew him can never forget him for he stands too clearly in the mind.

Australian Research Fellow, Queensland Museum,
P.O. Box 3300 South Brisbane,
Queensland, Australia

REFERENCES

Allen JR, Halstead (Tarlo) LBH, Turner S. 1968. A Dittonian ostracoderm fauna from the Brownstones of Wilderness Quarry, Mitcheldean, Gloucestershire. *Proceedings of the Geological Society of London* **1649:** 141-153.

Marshall AJ. 1970. *Darwin and Huxley in Australia.* Sydney: Hodder and Stoughton [the preface is entitled "Jock Marshall" by Russell Drysdale - unnumbered pages].

Marshall J, Drysdale R. 1966. *Journey among Men.* Melbourne: Sun Books.

Patterson C. 1978. *Evolution.* London: Routledge & Kegan Paul in association with the British Museum (Natural History).

The French Connection

DANIEL GOUJET

My reasons for writing are twofold. First, I wanted to express my personal gratitude towards Colin who has for me been an impressive researcher, with his amazing capacity to integrate information from various sources and produce enlightening ideas. Secondly, I wanted to say something on behalf of my colleagues at the Paris Natural History Museum, from those who praised Colin's endeavours as well as those who criticized them with hidden admiration.

I first met Colin in 1966, during the Paris *Evolution des Vertébrés* CNRS symposium. At that time I was a new graduate student, raised in the belief that evolution was primarily a process, secondarily a pattern and that systematics was mainly a tool for identification of animals and plants. I don't blame my teachers; they were physiologists or population geneticists and they taught what they thought was right from their own point of view. Colin's intervention during the symposium was on the debate that concerned monophyly versus polyphyly of teleostean fishes. It was about fossils and pattern of phylogeny, but I must admit that I was then too far removed from what he was saying to appreciate it. Our second meeting was in 1967 in Stockholm for the '4th Nobel Symposium' on Lower Vertebrates, and after Brundin's pre-banquet lecture, it was clear that something was in the air.

In the ensuing years I paid two visits to the British Museum of Natural History and had discussions with both Colin and Roger Miles on phylogenetic issues which had started for me back in Stockholm. The best moments for discussion were whilst smoking cigarettes when on the roof of the Palaeontology department, the only place available for smoking at that time.

The cladistic revolution among French palaeontologists started with the Paris CNRS Symposium of 1973. A year earlier, the Linnean Society of London had organised the *Interrelationship of Fishes* meeting which announced the impact of cladistics on fish palaeontology. During the Paris Symposium cladistics was at last put on the menu of the Parisian academic circle of palaeontologists; Niels Bonde and Roger Miles were the speakers. The ideas of ancestor-descendent relationships that prevailed in Paris began to waver and Colin was one of the prominent activists in the revolution that was taking place in Paris among lower Vertebrate specialists. One of my colleagues, Monsieur Blot, not only suggested that teleosts were paraphyletic but also maintained that eels were the direct descendants of the amiids (the family of Recent North

American bowfins). The debate was short but very intense, and Colin stopped it quickly because of the polarised misunderstandings. It was the radical opposition of two views of science; one based on authority of experts, the other on pertinence of questions. This period was a true revolution, a process in which the French are specialists. Two different worlds were facing each other. One was a closeted science with its authoritarianism and the other an open science with an accessible methodology that allowed questions on the fundamental issue of phylogeny – how to investigate the pattern of life.

After this tense afternoon, we had a party at our house to which all ichthyological participants of the meeting were invited. Brian Gardiner, Niels Bonde and Colin arrived late. They brought with them the bottle of whisky that had been their companion on the journey. Colin presented it to my wife and with his impeccable accent said "Excusez-moi, elle n'est plus vierge" (Excuse me, it is no longer a virgin). This was a moment of triple discovery. Colin could speak French, be a great scientist and still have a positive *joie de vivre*.

Since then, Colin has been a permanent source of enlightenment. I missed the Reading meeting on Palaeontology and Comparative Anatomy in 1978 that generated the controversial correspondence in *Nature* on the pros and cons of relationships between the salmon, lungfish and cow. Later, in Cambridge, 1980, I was pleased to be present at the Systematics Association symposium 'Problems of Phylogenetic Reconstruction'. Colin addressed the audience with the 'Homology problem in morphological characters'. This paper, published in 1982, together with other theoretical contributions, provided benchmarks for systematics and phylogeny. Every time Colin and I met subsequently, he gave me his thoughts on evolution, cladistics and phylogenetics. Colin was always ready to share his knowledge and views. During visits to London and our lunch breaks with a beer and museum colleagues at the 'Cladist's Arms' (formerly The Cranley Arms) I learned a great deal and discovered even more about science.

I must say thanks to Colin, who realised early on, contrary to what many of my Parisian colleagues were saying, that to advance or support new ideas is not dangerous. It is difficult and often unpleasant to receive adverse reactions, but if you believe that it is worth doing, then do it. Colin faced many such situations. For example, I admired his response when collecting the Romer-Simpson award in Chicago in October 1997. He thanked his fellow palaeontologists for having forgiven him for them taking the brickbats over his ideas on evolution and for pointing out that it was not the age of fossils that was relevant to resolving phylogenies, but their anatomies. Through his freedom of thought and great aesthetic sense, which made his works models of prose and illustration, and his exceptional way of integrating many papers relating to systematics, Colin opened new routes of enquiry and stimulated

much new research. Thanks to him, a dialogue has opened up between morphological and molecular systematics – today, even European journals are accepting theoretical papers!

Colin was a great man with ordinary black pants and impeccable manners. He always liked big ideas, a good life, and a good drink.

Laboratoire de Paleontologie,
Museum National d'Histoire Naturelle,
8, Rue de Buffon, F-757005 Paris, France

Colin Patterson: a student's view

GORDON REID

Scanning down the programme of speakers assembled to celebrate the remarkable life and very distinguished career of Colin Patterson I feel that my inclusion may be considered to be an anomaly. While we got on well together, I was not a very close friend of Colin's and never joined in e.g. on social walks with his well known group of academic companions (see Chris Humphries' contribution, pp.69–74). Most of the other speakers were tightly bonded friends or colleagues of Colin with intensely shared scientific interests in the fields of palaeontology, comparative anatomy and phylogenetic systematics; and they all represent leading museums and universities. Colin and I never engaged in collaborative research and, curiously alone among the contributors, I come from a zoological garden – Chester Zoo in the north of England, which specialises in conserving rare and endangered animals through breeding programmes and field projects.

From this, one might wonder what possible connection could there have been between us? The short answer is that I came to know Colin through my former existence as a student, registered with the University of London but engaged in research on Recent fishes in the Zoology Department of the British Museum (Natural History) (now The Natural History Museum). As a lowly student rather than as a peer, I suppose that I will have gained a rather different perspective of Colin, who was then a Principal Scientific Officer in the Palaeontology Department and later promoted through even higher ranks.

I remember well my first meeting with Colin in the early 1970's in a curious Georgian building in London called the 'Old Coach House', which was linked to the Department of Biological Sciences, Queen Elizabeth College (now Kings, Queen Elizabeth and Chelsea). It was, under Dr Alison Jolly, also an outpost for the primate research unit of the Smithsonian Institution, Washington. On my first day as a student I travelled from Glasgow, my home town, to London, and from a telephone booth in Euston Railway Station, was instructed to first report to the Old Coach House by my new supervisor the late, great Dr Humphry Greenwood of the BMNH. "I will be responsible for your academic life at the Natural History Museum" Greenwood briskly informed me "but Dr Brian Gardiner and his friends will attend to all the rest". How right he was!

Looking rather bedraggled in a poncho, I approached the door of the Old Coach House with trepidation. It was ajar, and I could hear voices raised in

animated discussion upstairs. I gravitated towards the noise. At the head of the staircase there was a room with a light-pull to which had been affixed a baby's rattle. I paused for a moment to take this in. The rattle somehow seemed to symbolise the strange, intriguing, quirky and original environment that I was now entering. Antique desks were covered in a heaped, impossible muddle of microscopes, old leather-bound books, pickled specimens, scientific reprints, cigarette stubs, scribbled notes, incomplete data sheets and half prepared fossils. It looked and smelled just right, but who could work in such chaos I wondered? A beaming Brian Gardiner suddenly appeared, warmly clasping my shoulder: "Welcome to the philosopher's den my boy!"

I was drawn into a smoke-filled room where a lively, good natured, dispute was in progress among a singular group of young men typified by open-necked floral shirts, flared trousers, collar length hair, scuffed Chelsea boots, crumpled clothing and cigarettes dangling from their lips. They were engaged in a deep discourse on phylogenetic theory, that is to say the scientific systems used to characterise, analyse and explain the relationships or evolution of life on earth.

Strange, unfamiliar, fascinating words were being bandied around including Brundin, Hennig, synapomorphy, plesiomorphy and cladogram. I made mental notes of these words. In a dark jacket, Dr Colin Patterson stood out: a large frame, strong facial features, thinning hair with flyaway wisps above the ears and soft, intelligent brown eyes. He had an extraordinary aura and spoke carefully in deep, rich, cultured tones. When he did so, the others fell silent and listened intently and there was no mistaking his easy air of authority – he seemed to see further than the rest. Brian introduced me to everyone and Colin offered a cigarette, which I accepted even though I did not smoke! Trying not to cough, I aped the others in flicking my cigarette ash into the fossilised vertebral disc of a dinosaur and imagined this to be the height of sophistication.

Among others in the debating circle were the palaeontologists Dr Alan Bartram (a colleague of Brian's who later mysteriously disappeared without trace, following a visit to Paris) and Dr Gavin Young (an Australian researcher from the Bureau of Mineral Resources, Canberra working with Dr Roger Miles of the BMNH). The discussion resumed and, believing that I was rather well read, I started chipping in with memorised quotations from the books of the famous evolutionists George Gaylord Simpson, Ernst Mayr and Beverley Halstead. They exchanged glances and there were some awkward silences. My enthusiastic interjections seemed not to hit the spot; but somehow I was tolerated, rather like a harmless puppy chewing at the ankles of adult dogs. Soon we were off to the pub for a lunch break and I discovered that one major benefit of being a student in the company of seniors is that all drinks are paid for! Weaving my way back to the college, with raw throat and spinning head,

I remember Colin telling me that I was in dire need of training. I cannot be sure whether he was referring to phylogenetic systematics or to reliably finding my way back from the pub to the Old Coach House!

Late in the afternoon Brian and Colin kindly strolled with me from West to South Kensington and the neo-gothic splendour of my new home, the Natural History Museum. Humphry Greenwood was not available but Colin left me in the 'Spirit Building' with the fine ichthyologist Gordon Howes who allocated work space and equipment ("New eh? You can have the *Russian* microscope"). I soon settled down to the task of investigating *Labeo*: a fairly obscure group of tropical, carp-like fishes sometimes called 'warty mud suckers' ("New eh? You can sort out the warty mud suckers ... now *there's* a challenge").

One strange aspect of embarking on a research programme under the aegis of great men like Colin, Brian and Humphry is that no one actually tells you how to *do* research. There seemed to be the general expectation that I should know exactly what I was about and quietly get on with it. This caused deepening furrows in my brow because I barely knew how or where to begin and did not want to be a bother to anyone. In fairness, I got tremendous support from all three when I plucked up the courage to ask for it and Colin was especially marvellous at rattling off bibliographic details of the key literature to be covered. Sometimes he did this rather in the manner of a wine connoisseur, cautioning me against imbibing certain authors outside of a particular time frame ("Allis is far better after 1909").

Beyond reading, I soon recognised that direct examination of the specimens was an essential task. I polished up my Russian microscope and toiled for three years, performing dissections, examining skeletons and gathering copious morphological data on *Labeo*; until I realised, belatedly and rather uncomfortably, that it was time for analysis, interpretation and the submission of my thesis for examination! Confusion and anxiety reigned on phylogenetic aspects until Dr Richard Vari (a visiting North American post-doctoral student who now works in the Division of Fishes, Smithsonian Institution, Washington) strongly advised me to "consult with the oracle". By this he meant, of course, Colin Patterson.

Colin was easily located on 'smokers alley' outside the Spirit Building and readily agreed to assist. Our session turned out to be a rather humbling experience for me. It emerged from the discussion that Colin had once taken a 'casual look' at my *Labeo* and from this had gained a clearer perspective than I had on where they might fit in the scheme of things. To explain the idea of cladistic relationships more simply he used the analogy of the salmon, the lungfish and the cow – central players in a phylogenetic debate which was then raging and which is now a famous landmark in the evolution of knowledge in

this area. After only about an hour of schooling from my helpful mentor, everything suddenly clicked into place. I now knew how to best interpret my findings. An immense feeling of relief flooded over me. Sometimes I think that at least a part of my doctorate should have been awarded to Colin!

I left the Natural History Museum to work for a few years as a lecturer and researcher in a northern Nigerian university. There was little contact between us during that time, apart from the occasional request for assistance in locating references in the scientific literature that were difficult for me to get hold of. Colin always faithfully responded to such enquiries and (as any fieldworker in a remote outpost will tell you) it is tremendously reassuring to have dependable contacts back at home. While retaining a strong interest in systematics, phylogeny and evolution, there were also exciting opportunities in Africa for me to become involved in ecological and zoogeographical fieldwork. This, in turn, sparked an increasing concern in conservation biology, mainly from observing aquatic habitats and the fishes being frequently obliterated by human activity.

I became convinced that *ex situ* breeding programmes should be organised for threatened species of fish in much the same way as they were being organised for rare terrestrial vertebrates such as Black Rhino, Scimitar-horned Oryx and West African Crowned Crane. Fishes, too, needed this kind of protection and management off-site to help ensure their long-term survival, ideally in nature. The evidence then emerging for the mass extinction of cichlid fishes in Lake Victoria, East Africa (the taxonomic speciality of Humphry Greenwood) confirmed me in this view and I returned to Britain with a bit of a 'bee in my bonnet' on this topic. Back for a spell at the Natural History Museum, the timeless atmosphere and apparent lack of urgency on issues of species survival was starting to get to me.

I met up with Colin and the rest of the museum and university gang in a pub in Fulham on a warm summer afternoon. The others drifted back to work but we hung on, debating conservation matters. He argued that, while he had a particular soft spot for birds, he found it difficult to argue for conserving any particular recent species if one considered patterns of extinction over geological time. Normally deferring to Colin in discussion, I took the bait. I charged that there was insufficient concern in the museum community over the conservation of recent organisms which were being lost at an unprecedented rate and that there should be far more emphasis on the documentation and mapping of threatened biodiversity. With impeccable logic he carefully picked off my points one by one, suggesting that meaningful conservation priorities for species and higher level taxa could only be set within a rigorously tested phylogenetic framework. I countered that museum taxonomists, in their preoccupation with arcane phylogenetic analyses, were perhaps abdicating their responsibilities for

the real world and were in my view 'fiddling while Rome burns'. The thrust and parry of the argument went on for a long time. "Colin I absolutely and profoundly disagree with you!" I finally blurted out, heart pounding. He started to chuckle, shoulders heaving in that distinctive way of his. "Good!" he said "Good!". We met several times after that but, sadly, this was to be our last in-depth conversation. He was a lovely man and I owe him grateful thanks for sowing some of the seeds which have happily altered the course of my life.

North of England Zoological Society,
Zoological Gardens, Chester CH2 2LH

On Remembrance

(Address given to the congregation at the committal service.)

MEL GOODING

I don't think anyone who met Colin did not know immediately that he was a most extraordinary person. He had a natural and unforced authority of presence. He was, of course, physically imposing, handsome of aspect, and he had a beautiful speaking voice, expressive, resonant and musical. Being utterly without vanity or pretension himself, without pretence of any kind, Colin could be alarmingly direct and honest in his address to others. His amazement that you might take a particular view – "surely you can't believe that" he would say, incredulously – was unfeigned and genuine. But there was nothing overbearing in this manner, and that powerful presence of which I spoke had a marvellous simplicity to it; the simplicity of an absolute candour. This found perfect expression in his distinctive manner of dress; in my experience his only concession to formality was an ordinary black jacket. Indifferent to fashion and impatient of convention, he made out of habit a kind of insouciant all-weather elegance.

It is impossible to think of Colin without remembering his apparent indifference to the elements. I never once saw him in an overcoat, however wintry the weather. This was more than an idiosyncrasy; it was the sign of a characteristic discipline, a visible aspect of his stubborn self-sufficiency; and it was, in this respect, a function of something deep in him, something intrinsic to his personality. He was unmoved by common expectations or by social convention, being governed in his own behaviour by a profound moral decency that came from within, and which manifested itself in all his dealings. Its sources were private and unspoken, though I refer to something in his nature that might properly be called philosophical, having to do with a love of truth, and a concern for a proper way of behaving, in the sense of what belongs as appropriate to a situation. He was, as we say, a proper person; his own person.

Colin laughed easily and often, until the tears ran down his cheeks, to be brushed away, in an inimitable way, with the back of his hand. He brought to the things that made him laugh the sense of complete engagement that marked everything he did; mixing a champagne cocktail or a Margarita, carving the Sunday joint, collecting Staffordshire figures, listening to music, buying second hand books, making wine, watching birds. Continuously alert and perpetually curious, he brought to everything a wonderful vitality.

His professional life was rich in achievement; it was embedded in a personal and family life rich in texture; a full life, fully lived. And at its heart was

"A natural and unforced authority of presence" [Colin in hat with binoculars - Photo CJH].

Rachel, and Sarah and Jane. With Rachel he shared over forty years of marriage, and the love and the comradeship that comes of a world created together. A generous and convivial world, with space for other people, a world of many friendships. And many are the friends for whom Colin will come to mind, above all, as one who brought to their times of difficulty a reserved and diffident tact, a quality of temperament that enabled him to help without intrusion. Colin was devoid of sentimentality but capable of great affection; he was kind, and he was very wise.

Colin knew, with a knowledge as capacious and profound as that of anyone on earth, of the fundamental kinships and intricate relations of all things in creation. But his joy in the quiddities of the natural world, the world as given, was utterly immediate and unaffected, and imbued with a typical quickness and exactitude of attention to the characteristic distinctiveness of things; the taste of a fungus, the look of an insect, what W.H. Hudson first called 'the jizz' of a bird. It pleases me to mention Hudson, who wrote the first

birdwatcher's book on London, for Colin loved London's birds, and had a sharp eye for them. One of my enduring memories will be of the cold day this January when Rhiannon and I, called by Colin, hurried round to see a great winter rarity, a bird with a special London history*, as Colin would have known. For many minutes together we were enchanted by a male black redstart, smart in full Spring plumage, on the plots directly behind the new house.

Thomas Hardy's *Afterwards* has a realism and an unsentimental emotional truth that Colin would have appreciated: I can think of no poem that better conveys how we will so often remember him.

Afterwards

When the Present has latched its postern behind my tremulous stay,
And the May month flaps its glad green leaves like wings,
Delicate-filmed as new-spun silk, will the neighbours say,
'He was a man who used to notice such things'?

If it be in the dusk when, like an eyelid's soundless blink,
The dewfall-hawk comes crossing the shades to alight
Upon the wind-warped upland thorn, a gazer may think,
'To him this must have been a familiar sight.'

If I pass during some nocturnal blackness, mothy and warm,
When the hedgehog travels furtively over the lawn,
One may say, 'He strove that such innocent creatures should come to no harm,
But he could do little for them; and now he is gone.'

If, when hearing that I have been stilled at last, they stand at the door,
Watching the full-starred heavens that winter sees,
Will this thought rise on those who will meet my face no more,
'He was one who had an eye for such mysteries'?

And will any say when my bell of quittance is heard in the gloom,
And a crossing breeze cuts a pause in its outrollings,
Till they rise again, as they were a new bell's boom,
'He hears it not now, but used to notice such things'?

Castelnau, London SW13

* For several years post-war remarkable numbers of black redstarts bred in Inner London, the bombsites providing favourable nesting and feeding conditions. Cripplegate, near St Pauls, was a specially favoured site. The London Natural History Society's *Birds of the London Area* (1964) records that between April and August 1927, a singing male took up territory on the Natural History Museum, South Kensington.

Summary

PETER FOREY

Sue Turner ended her contribution with the words "Those who knew him can never forget him for he stands too clearly in the mind". How true! As I sit in the fish library in The Natural History Museum writing this summary I can see Colin in my mind's eye; sitting at the microscope saying "haven't you got anything better to do with your time?" Well no – not on this day and nor had 150 people who gathered together 16 months ago in the rooms of the *Linnean Society*. Colin had influenced so many of our lives in so many different ways that some kind of celebration was inevitable. It was also an occasion with another purpose: namely, to record developments in science during the life of one central person. Colin lived through one of the most exciting and refreshing times in the natural sciences and within systematics in particular. The last 50 years have witnessed times of great upheaval and re-evaluation of many cherished scientific beliefs.

Pause to think what has happened since Colin enrolled as an undergraduate in the early 1950s. The structure of DNA, the genetic code and translation to proteins have all been revealed. Molecular biology, in turn, has had a significant impact on evolutionary theory by suggesting that much of the variation in genetic material is selectively neutral. Also, in the early 1950s people began to take seriously the idea that the continents were not fixed and immutable but could move about, split up and come together again. Plate tectonics had profound implications for the way in which we explain the distributions of animals and plants. In systematics the ideas of Willi Hennig led to a fresh way of looking at the relationships between animals and plants and offered guidance about how those relationships may be discovered. In all of these disciplines Colin quickly appreciated the significance of paradigm shifts on the way we did science, the kinds of questions that should now be asked. He made many contributions in asking those questions and articulating the answers in persuasive prose.

The timing was perfect. In the 1960s, as Brian Gardiner records, Colin was a young researcher setting out on his career, gathering a wealth of new data on fossil fishes which needed interpretation. Lance Grande and Niels Bonde both record Colin's appreciation of the elegance of cladistics to understanding the origin of teleosts and this was one of his many innovative contributions which now form the starting point and the backbone for modern studies.

For most of our contributors Colin had the greatest impact on their systematic work. Gary Nelson records that Colin got the tip-off that something in the library, buried in a rather obscure publication on the systematics and biogeography of midges, was of considerable theoretical import. Gary modestly omitted to mention that it was he who gave the tip. However, Colin grasped the essentials of cladistics – the new paradigm in systematics – and quickly made his individual theoretical contributions to debates and arguments which inevitably blossom when new ideas come head-to-head with traditional beliefs. And Colin certainly had his runs in with 'authority'.

In 1982 Colin published a paper questioning the role of palaeontology in understanding relationships between organisms. His doubts arose as a result of his own work with fossil fishes and his adoption of cladistics. He questioned whether ancestors could be recognised based on the distribution of characters. At that time fossils were considered to hold the key to life's history. They were the only tangible record of past life and only palaeontology had the authority to pronounce opinions on ancestry. But, as Lance Grande points out, Colin questioned whether palaeontology was capable of supplying these answers. In effect, he suggested that palaeontologists often stepped over the boundary from what can be legitimately deduced from the fossil record to 'just so' stories which had to be accepted without question. Colin's paper and the subsequent talks he gave on the subject created considerable disquiet within the palaeontological community on the one hand and personal anguish on another. The palaeontologists were understandably upset by what they saw as a challenge to their science and their perceived role. But his critique provoked many papers which considerably clarified the way in which palaeontologists' work and the contributions they can make. As a result, cladistics is now firmly in the mainstream of palaeontological studies and much of this is due to his plea for transparency in systematic endeavour. Truth be known, others, including Gary Nelson, had questioned the authority of palaeontology, but it was Colin's eloquence and power of argument that identified him as the 'enfant terrible'. Despite many years of suspicion it is to palaeontologists' credit and his ability to maintain respect even amongst his opponents that he earned the highest award from The Society of Vertebrate Palaeontology (Grande).

But in another direction his arguments ended less cheerfully. His criticisms of the role of palaeontologists were mutilated by advocates of creation science. They quoted him out of context, and distorted and contorted his ideas. This caused him a great deal of extra work replying to the masses of mail and requests for information and opinion relating to US state tribunals examining the role that evolution theory should or should not play in public education. I

believe this to have been the extra burden adding to a punishing workload which led to his first heart attack late in 1984.

Colin had an international view of the Museum as do all of us who have worked there. Colin clung to the name *British Museum (Natural History)* as long as he could, even using traditional headed notepaper for his familiar correspondents long after it was deemed 'illegal'. For him the title raised the status of the institution of which he was so proud, above the generic and parochial *The Natural History Museum* by which it is now formally known. The name change emerged in the early 1990s as an attempt to avoid confusion with the *British Museum* at Bloomsbury in the public mind and to recognise the fact that most local people had been calling it *The Natural History Museum* for decades. The spin doctors were in. For Colin, this name change was one of many revisions within the Museum which he and many other scientists saw as a downward spiral. Most significantly, research and curation were formally separated, such that it was no longer clear who had responsibility for work on the collections. Furthermore, the exhibition policy started in the mid-1970s had marched on with exhibits relying less on specimens and more on plastic. The tensions had already started in the '80s when we were asked to dismantle the Fossil Fish Hall and move all the specimens out of public display into hidden storage. The Hall had particular significance for Colin. The cases containing the specimens were laid out in systematic order in agreement with what was currently regarded as the most informative classification, beginning with the jawless fishes and progressing through to the most specialised of teleosts and sarcopterygian fishes. When Colin started at the Museum Errol White had told him that one of his first tasks would be to revise the cases of cartilaginous fishes and actinopterygian fishes (ray-finned fishes which form 99% of the modern fish fauna). This involved original specimen- based research and threw him into parts of the collection previously unvisited. Through this experience he came to know the collection very thoroughly and could usually recall how many specimens we had of a particular taxon, on what grounds the species were diagnosed and which of our specimens were of particular importance and why. This mine of information was borne out of direct work with the collection and used on numerous occasions to answer queries, drive acquisition policy, to justify the importance of the National collection and the Museum scientists to administrators and politicians (see contribution by Hugh Owen, p.58).

It was Colin's affinity for detail and raw data that led to many of his most colourful confrontations and most significant contributions. Andrew Smith records his collaboration with Colin over extinction patterns. In the early '80s a string of papers appeared purporting to show that extinction in the fossil

record followed a regular periodicity and this, in turn, led to wild claims of astronomical causes. These claims had been based on literature surveys, i.e. on secondary sources taken at face value in the hope that any errors in these sources would be outweighed by reliable data. Colin and Andrew questioned this, at least for the groups they knew first hand, and their reanalyses showed the alleged patterns to be spurious artifacts.

It is quite usual that the more a particular a line of enquiry grows, the more it also accumulates and magnifies errors drawn from previous works. One very dominant trait of Colin's work was his recurring question – "how do we know that?". Nowhere was this more clearly demonstrated than with the 'Begle episode' as recorded by Dave Johnson (see pp. 49–51) who worked with Colin on this project. Doug Begle had published his PhD thesis suggesting a theory of relationships of a group of primitive teleost fishes, stating that the results were gained by analysing raw data. As Johnson records this was patently not the case and both he and Colin set about correcting the original observations by examining specimens, both those used by Begle and others. They found a plethora of mistakes which, when corrected, suggested a completely different theory. The papers and talks presented on this subject seemed to some to be a pernicious and almost vindictive attack on this research student. But, it was nothing of the kind. They were just as critical of the review process which had allowed the publication of so many errors which, as Colin knew only too well, may have added to the errors of future work. This was their way of putting things right, to correct mistakes made in ignorance or in this case perhaps knowingly through disregarding specimens. It was this lack of concern for specimens – the raw data – which stirred Colin and Dave to spend two years of joint research on this remedial work.

Attention to all of the data was another of Colin's credos. This, of course, is something reputedly inherent to science but sadly not always manifest in the current environment of 'publish or perish', especially in the field of molecular systematics. Colin had worked here too as Tim Littlewood records, (see pp. 54–57). For most comparative analyses of molecules the first and most crucial stage is to align DNA. For most genes parts of the sequence are readily aligned while other parts seem to defy any attempts to match one particular nucleotide position across the taxa. Faced with this difficulty, many molecular systematists disregard the diffcult, hypervariable bits by deleting them from their analyses. But, as Tim records, Colin would have none of this: after all, the data are there and they have to be explained, no matter how long it takes to arrive at the most sensible aligment.

Several of the contributors reflect the internationalism of Colin's influence. Daniel Goujet records the impact on French systematists, a notoriously discerning audience, and Niels Bonde recalls Colin's influence on him and

Danish systematics. Niels was in on the ground floor of the cladistics revolution and echoes, from a personal perspective, the larger picture painted by Gary Nelson. Colin's reputation across many areas of systematics – palaeontological, molecular, neontological and theoretical – led to separate invitations from both French and Swedish science policy makers to advise on future direction of systematics in those countries. And Sue Turner sees his influence from an Australian perspective, although Colin never went to that continent.

His attitude to students was somewhat ambivalent. Although he examined several PhD theses he never sought graduate students and indeed was only an official supervisor to one. As Gordon Reid writes, students found him a somewhat daunting person on first meeting. But he did help and influence a great number in his own way, myself included. His advice was always pertinent and thought provoking. I recall approaching him in the late '60s with a question about some detailed anatomy of a fish braincase. Without looking up from what he was doing he suggested that if I looked at Allis 1897, plate 22 I would find enlightenment. I did not find the answer but the clue that led to the answer. And this was very characteristic of Colin. He gave the hint but expected you to do the work. He certainly had the pastoral ability to encourage (see Susan Turner's contribution, p.75) and provided a great deal of constructive criticism (although I did not immediately appreciate this as he handed me back an astonishingly heavily annotated thesis at the end of my viva). I think that, in part, his reticence to formally take on students was part of the ethos of the contemporary Museum for it is only in the last ten years that close associations between the Museum and universities have been encouraged.

Colin's personality is most accurately and sensitively sketched by his brother-in-law, Mel Gooding, and I'm sure that anyone who knew Colin will find their own impressions rekindled by Mel's words. Others have recorded their own impression and particular landmarks of influence. Dick Vane-Wright speaks of Colin's generosity with advice, often given as incidental remarks. And Chris Humphries records the most intimate of some of our associations with Colin – the river and canal walks around London. At one level these walks were, as Chris relates, congenial days of 'truancy'. But, as with all of Colin's endeavours, they were carefully planned, making sure we arrived at a suitable hostelry at the right time of day, ensuring that we passed significant landmarks and persevering until we completed the route to end at some significant point where canal tips into river.

Here, in enjoyable microcosm, were some of the most obvious traits of a good scientist – enthusiam and thoroughness in every endeavour and a constant desire for knowledge and understanding. Dave Johnson certainly experienced and appreciated this during their productive and enjoyable association both

professional and social. Dave and Colin had so much planned in specimen-based research – the core of Colin's output from which sprang so much theoretical contribution (Nelson, Grande, Smith) – that his death seems to have robbed us of greater insight. However, we must remember that few scientists had already contributed so much in so many fields. And significant contributions inevitably lead to demands for more information and explanation. Perhaps there is an inherent limit to what we might expect from our scientific leaders such as Colin. As Richard Fortey says "..scientists are fortunate in death because their ideas live on in those who have known them, respected them and liked them".

Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD