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Editorial

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Adventures in the fish trade*

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*** deceased March 1998*
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Introduction

The Systematics Association (SA), a London based organisation dedicated to the promotion of systematic (comparative) biology in all its various aspects, was founded in May 1937. It is based on objectives set out for its earlier incarnation, the “Committee on Systematics in Relation to General Biology” (some relevant history can be found in Winsor 2000). That group’s remit was, and the SA’s still is, “to provide a forum for the discussion of the general theoretical and practical problems of taxonomy” (http://www.systass.org ; see also *Nature* 140:163, 1938).

Early in December of each year the SA hold its AGM. To attract an audience to an otherwise potentially stuffy business meeting a noted speaker is invited to talk on a subject dear to his or her heart (the outgoing president delivers a parting lecture on retirement, so every third year, by default, the president speaks).

On December 6th 1995 Colin Patterson FRS, celebrated palaeo-ichthyologist of the Natural History Museum, London, and instigator of the cladistic revolution in systematic biology (Forey 1999, Nelson 1998, 2007, Bonde 1999 and essays in Forey *et al.* 2000), gave the 29th lecture with a presentation entitled ‘Adventures in the Fish Trade’, a summary of his career, in fishes and cladistics. At one time the SA lectures were published, usually by the Linnean Society in one of its journals. Patterson’s lecture never was published, nor was it intended for publication, although it has since been widely circulated. As it has attracted some attention, we thought it wise to organise its publication in an appropriate venue. Here we offer his account in a slightly edited form.

Patterson meticulously prepared all his talks and lectures, writing out a full script, which he would learn by heart and then deliver the lecture almost verbatim. The text before you is derived from Patterson’s notes, which will be archived at the Natural History Museum, London. For the most part, we have stayed as close as possible to the written words in his notes. We have had to remove a few passages that only make sense in the context of a talk, where transparencies depicting old friends and old specimens convey more than words ever can. We have added (and, in some cases, corrected) references and include a selection of illustrations, those that are necessary to make sense of the text.

As a history of ichthyology in the second decade of the 20th century and a history of the development of cladistics, *Adventures in the Fish Trade* offers some useful, if not crucial, insights into the past—and, if the words are considered carefully—precautions for the future. We have endeavoured to remain true to the spirit in which the presentation was delivered, captured by Patterson’s closing words, which included a phrase from a book review we were unable to trace: “Fish systematists take their work seriously, but they seem to have an awful lot of fun. There was a phrase in a book review in *Nature* last month that caught my eye—‘Scientists, the good ones at least, do it only because they enjoy it’.”

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Adventures in the Fish Trade

COLIN PATTERSON

Back in the 1970s I came to this room[1] at this time of year to hear my first Systematics Association Annual Address. It was given by a senior and eminent systematist who talked about principles, various theoretical and philosophical aspects of the business. The talk was so awful that I felt I had to do something – the only response I could think of was to join the Systematics Association, so I did. Now here we are, a quarter of a century later, and the tables are turned. I've become the old buffer, and I can't hope to do more than my eminent predecessor, give a talk awful enough to fire up one or two younger people into joining the Association.

I shan't talk about the theory or philosophy of systematics: I'm naïve enough to believe that the days when that were necessary are past. I think we know what we're doing today in terms of theory and philosophy. The arguments are now on a practical level, things like what algorithm to use, whether to combine molecular and morphological data or keep them apart, or on an even more practical level, how to raise funds and what uses systematics can be put to. I don't want to talk about any of those things, so I'll try to provide some light entertainment until the bar opens upstairs; I'll do what old buffers are best at, and reminisce. I call my talk "Adventures in the Fish Trade" as an allusion to Dylan Thomas's "Adventures in the Skin Trade" (Thomas [1938] 1969), 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.

I got into the fish trade by sheer accident. I came out of the army in 1954 knowing nothing except how to use explosives economically—how to blow things up. Completely ignorant of universities, I chose Imperial College (IC) because I happened to have access to a flat within walking distance of it. When I got there, I discovered that Imperial offered zoology degrees in only two subjects, entomology and parasitology. Having no interest in either, I chose parasitology as the lesser of two evils. But much of my final year's work turned out to be delving in little pots of human faeces, delivered fresh daily from the London hospitals, looking for *Entamoeba histolytica* and other nasty things that you need an oil immersion lens to see. When we weren't delving in little pots of faeces, we were delving in warm entrails, looking for worms. I got sick of the abattoir and resolved that I needed to work on something that didn't smell, so to be completely safe I decided to go into vertebrate palaeontology. I was lucky because Brian Gardiner, not yet President of the Linnean and two years before me at IC, had already blazed the trail, going from entomology at IC to fossil vertebrates at University College, where Kenneth Kermack (Patterson 1984) had taken him on for a Ph.D. I followed Brian, but didn't need to put in time at University College because I was lucky enough to get a job, as an assistant lecturer at Guy's Hospital Medical School. Very probably I got that job because of my degree in parasitology.

Meanwhile, I had to find a Ph.D. topic. 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. That belief is still around—look at the mileage there is in the Burgess Shale. But to get a Ph.D. topic on fossils I had to go to the fountainhead, the Natural History Museum, London (NHM)[2], and face Errol White (portrait in Patterson & Greenwood 1967, see Stubblefield 1985), 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—it's a close contest. In fact, hidden behind Errol's forbidding exterior was a sweet nature, as I was lucky enough to learn later. But as a Ph.D. 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 root of the tree, but had to tackle the rubbish up at the top, teleost fishes. But there was one plus point—Harry Toombs (Patterson 1987), 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 Toombs 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 acanthomorphs, which first appear in the late Cretaceous but are the dominant fishes today—there's about 15,000 living species, out of a total of about 25,000 Recent teleosts. In fact, there are more living acanthomorphs than birds and mammals put together—birds and mammals add up to about 14,000 species, and there are more teleost fishes than tetrapods—all tetrapods add up to about 23,000 species. With teleosts we're talking big groups.

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—the jaws, palate, and 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 acanthomorphs and what seemed to be their immediate relatives. My only comparative material came from the Recent skeleton collection at the NHM, at that time the best in the world. Luckily it included about a dozen skeletons of the things I was working on, beryciform fishes. I want to choose one of them as the theme of my talk, *Polymixia* (Figure 1). *Polymixia* is called the beardfish, because of the barbels below the chin; it's a marine genus found from about 200 metres to 600 metres down, in all the tropical and subtropical oceans. The beard, the barbels under the chin, is supported by modified bits of the skeleton of the hyoid arch, and I was able to find the same modified bits in one of my Chalk fishes, and to find other characters showing that at least four Cretaceous genera are close relatives of *Polymixia*, so that polymixiids were more diverse in the Cretaceous than they are now. At that time, *Polymixia* had a family of its own, but was lumped with about ten other marine families in the order Beryciformes. Beryciformes were supposed to be ancestral to all other spiny-finned teleosts, that huge group of about 15,000 Recent species. All my Cretaceous acanthomorphs seemed to belong in this group, so as part of my thesis I tried to revise beryciform systematics.

FIGURE 1. *Polymixia berndti* (Hawaii, USA, Oahu; original by J.E. Randall, 2007. *Reef and shore fishes of the Hawaiian Islands*, Honolulu: Sea Grant College Program, University of Hawai‘i. (http://fishbase.sinica.edu.tw/photos/HI_Reef_Shore_Fishes.pdf)

Some of you may remember that Simpson begins his 1961 book, *Principles of Animal Taxonomy* (Simpson 1961), with a quote from a talk by Arthur Cain given in this room in July 1958, as part of the Darwin-Wallace centenary celebrations, when that plaque was unveiled: "Is it not extraordinary that young taxonomists are trained like performing monkeys, almost wholly by imitation, and that in only the rarest cases are they given any instruction in taxonomic theory?" (Cain 1959, p. 243, and quoted in Simpson 1961, p. vii and, much later, Felsenstein 1982, p. 379)[3]. That was certainly true in my case; I had to pick up systematics like a performing monkey, trying to guess what would please the audience by imitating them. In my thesis I named only two new species and two new genera, but I made six new families, three new suborders and a new order, all without the slightest training in systematics. One of my new suborders was for *Polymixia*, starting its journey up the ranks. I ended my thesis with this diagram (Figure 2, from Patterson 1964, fig. 103), 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 acanthomorphs 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. Perhaps the ultimate example is Erik Jarvik's view of vertebrate evolution, first published in 1960, where all is polyphyly back into the primordial slime (Figure 3, after Jarvik 1968: 510, fig. 3; Jarvik 1960). That's an extreme version of a view of evolution that was fashionable among palaeontologists—actually this is a denial of evolution.

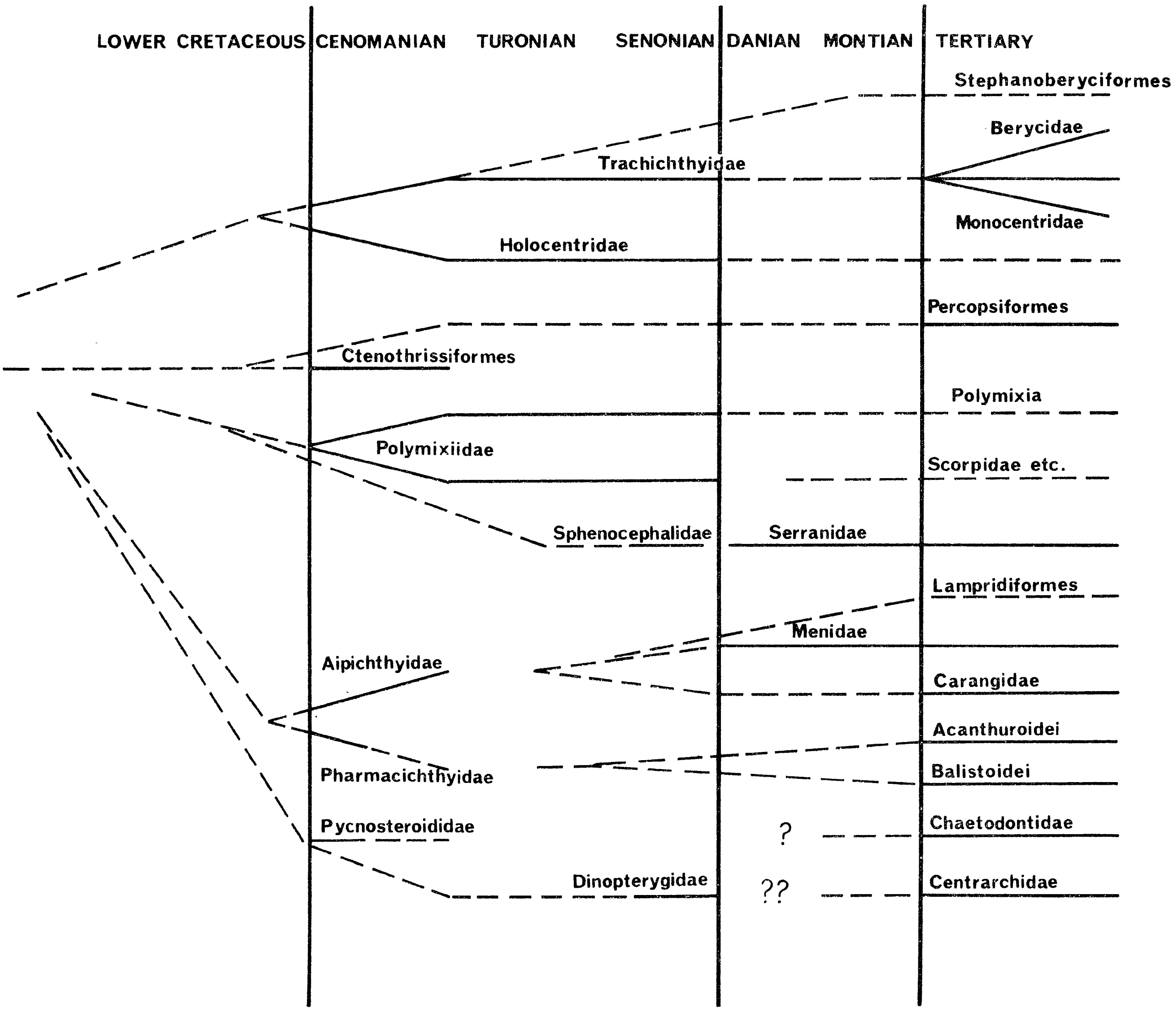
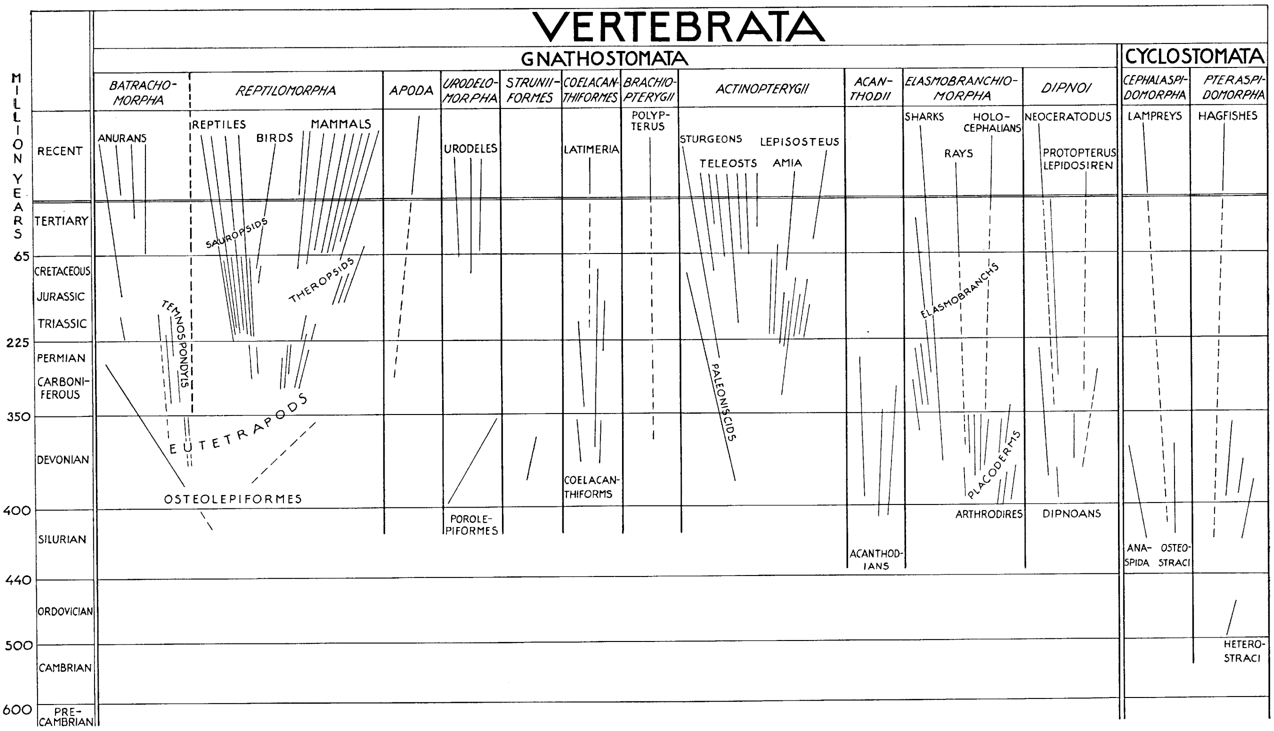


Figure 103. Diagram showing the suggested relationships of the Mesozoic acanthopterygians and Ctenothrissiformes with each other and with Tertiary groups. Solid lines indicate groups known by fossils.

FIGURE 2. After Patterson (1964), figure 103.

Anyway, in systematics I felt free to make new higher taxa ad lib – families, suborders and orders. My free hand was just part of the performing monkey syndrome, imitating the others, because at that time, in the 50s and early 60s, fish classification was pure chaos. There were two teleost classifications in use. One by Leo Berg, first published in Russian in 1940 (second edition in 1955), and in German in 1958—it had a long shelf life (Berg 1940, 1955, 1958). And another by Bertin and Arambourg, which came out in the French *Traité de Zoologie* in 1958 (Bertin and Arambourg 1958). In both of these, the only theoretical principle seemed still to be the *scala naturae,* hanging on from the eighteenth century. Berg had 41 orders of teleosts, arranged roughly in sequence from primitive to advanced, but with no hierarchical structure above the order, and the French *Traité* was much the same. Each classification had a basal order called Clupeiformes, after *Clupea*, the herring, and that order was treated in just the same way in both classifications, with 19 suborders arranged in sequence but with no other structure. It was as bad at the base of higher teleosts, the acanthomorphs, where there was an order Perciformes, named after *Perca*, the perch, and in the French classification it contained 27 suborders, with no hierarchical structure whatever. It was pure chaos, so for me to add a few more suborders and orders was a drop in the ocean.



Diagrammatic representation of the evolution of the vertebrates. Modified from Jarvik, 1960; 1964.

FIGURE 3. After Jarvik (1968), p. 510, fig. 3

My thesis was published in 1964 (Patterson 1964), and things began to change two years later when Greenwood, Rosen, Weitzman and Myers was published (1966). They summarised that classification in a famous diagram (Figure 4 after Greenwood *et al.* 1966, fig. 1). Their real innovation was to break up the old basal group, the Clupeiformes, and distribute it among four new higher taxa, Elopomorpha, Clupeomorpha, Osteoglossomorpha and the rest, called Division III but named Euteleostei the following year (Greenwood *et al.* 1967). The analogy I always use is that it's as if the distinction between monotremes, marsupial and placental mammals were not noticed until 1966—no wonder we had chaos before.

Despite that information, from the diagram there remains a morass of polyphyly – teleosts as a whole are polyphyletic, along three or four lines from some Jurassic fossils, and other multiple origins. But Greenwood *et al.* had another major innovation – they split the spiny finned fishes into three major groups: Paracanthopterygii for cod and their relatives, about a 1,000 species; and Atherinomorpha for killifishes and their relatives, about another 1,000 species; and Acanthopterygii for all the rest, about 12,000 species. As you see, they thought that both paracanthopts and acanthopts were polyphyletic, with acanthopts coming along several lines from the things in my thesis, the Cretaceous ctenothrissiformes and beryciforms.

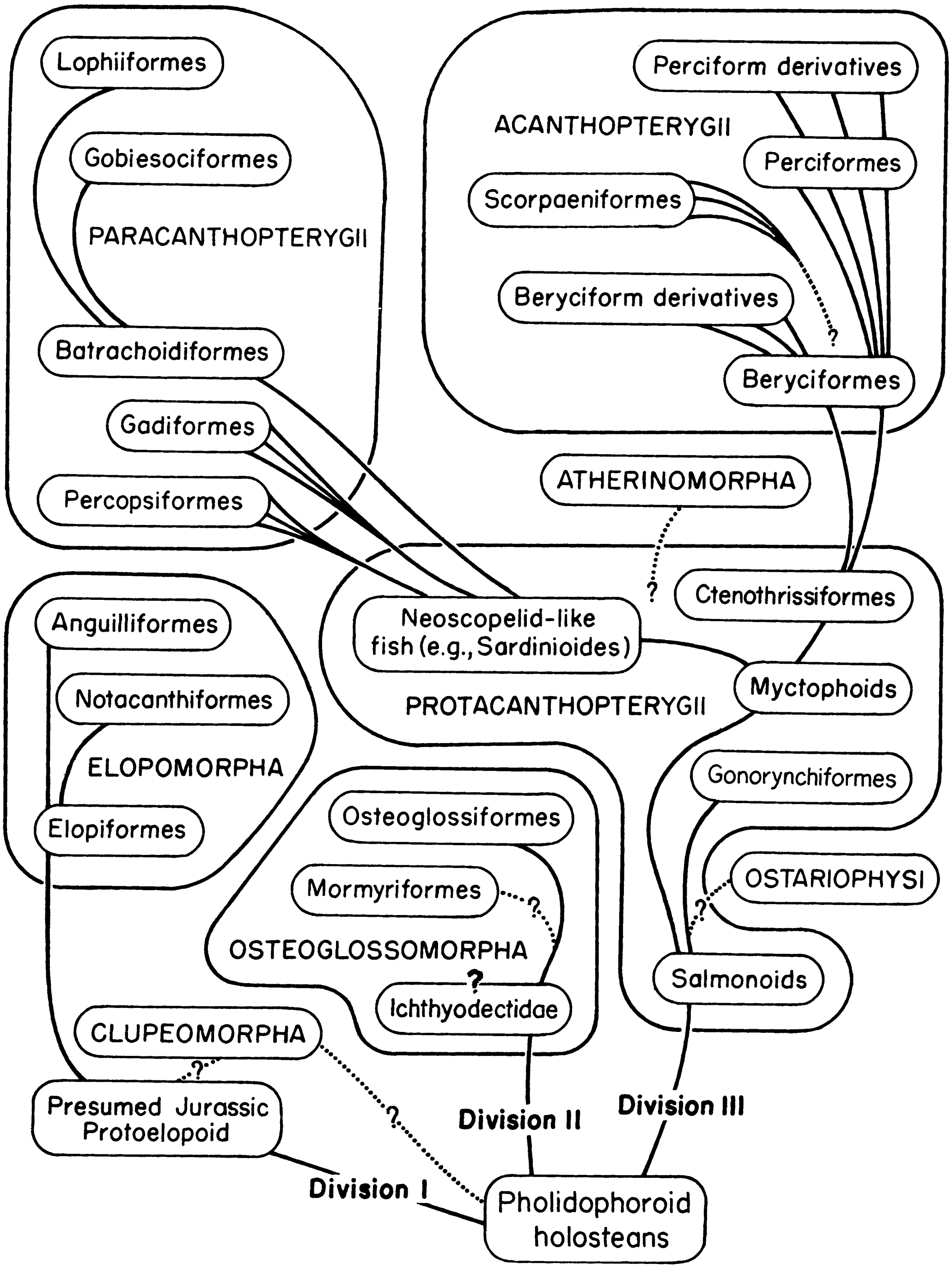


FIGURE 4. After Greenwood *et al.* (1966), p. 349, figure 1, “Diagram showing our conception of the evolutionary relationships of the principal groups of teleostean fishes. Uncertain relationships are shown by a broken line and question mark”.

Among the four authors of this paper, Humphry Greenwood in the NHM, Donn Rosen in the American Museum, Stan Weitzman in the Smithsonian, and George Myers at Stanford, the prime movers were certainly Greenwood and Rosen. They were the two who had the new ideas, whereas Weitzman and Myers had just tidied up some corners.

Humphry Greenwood died of a stroke in March 1995 (Patterson 1997) and Donn Rosen died of a brain tumour in 1986 (Nelson *et al.* 1987). But in the 1960s we were all full of beans, and Donn asked me to collaborate with him in an attack on the paracanthopterygians. We started work at the beginning of 1967, when I made my first trip to New York, on the same plane as Twiggy and her minder, Justin De Villeneuve, then at the peak of their fame as symbols of swinging London.

Donn Rosen had a job going in the fish department of the American Museum at that time, and during this trip to London he'd interviewed a likely candidate who was on a post-doc at the Museum in Stockholm – the young Gary Nelson. Some of you may have been lucky enough to hear him at Imperial College, 17th March, 1995, when he recreated Alfred Russel Wallace (Nelson 1995). Gary came to London to be interviewed by Donn Rosen and got the job—no search committees or managers in those days. Gary was splitting his year's post-doc, six months in Stockholm and then six months in London with us in the Museum. He arrived in London in April 1967, the week before I got back from New York, and when I saw him he told me that there was something new in the library that might interest me. It was Lars Brundin's 500-page monograph on chironomid midges, at first sight an unlikely place to find enlightenment (Brundin 1966). The Museum date-stamp – 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. I learned that Hennig's book, published in German in 1950 (Hennig 1950), had come out in a new English version in the States in 1966 (Hennig 1966), but I couldn't find a copy anywhere in London in the summer of 1967 so I asked Donn Rosen to bring me one when he came over in September to work with me. Donn brought the book, but read it first and scribbled all over it in pencil – things like "nonsense" and "a gross misunderstanding of well-known principles." He thought the book was rubbish; I read it and thought the opposite. So while Donn and I spent a couple of years working on paracanthopts, I was a committed Hennigian and he wasn't.

But Gary Nelson joined Donn Rosen in New York in October 1967, and began the campaign of argument and persuasion that eventually turned the American Museum of Natural History into the world's leading institute of systematics, or a hotbed of crazy cladists, depending on your point of view. You can find the detail of Gary's campaign in David Hull's book *Science as a Process* (Hull 1988). Donn Rosen soon came round, to become one of the leaders in cladistics, particularly in developing vicariance biogeography during the late 1970s.

What we all learned from Hennig back in those early days boiled down to just one thing, what relationship means. No one had put it plainly before. Once you agreed what relationship meant, how to recognise it became obvious—synapomorphy—and then it was also obvious what was wrong with systematics as we'd been practising it in the 50s and early 60s, when everyone was preoccupied with polyphyly. Our mistake was thinking in terms of origins rather than relationships—Darwin may well be to blame for that preoccupation. Anyway, 'origins' has been a dirty word to me ever since, a symptom either of ignorance or of creationism. We were so fond of polyphyly because we lacked a vital concept—paraphyly, a word that Hennig invented. For example, when Greenwood *et al.* believed that teleosts originated by polyphyly from Jurassic pholidophoroids, all they really meant was that pholidophoroids are paraphyletic, held together by nothing but primitive characters. It's the same with the beryciforms, the group I'd been working on, an assortment of Recent and fossil fishes held together by nothing but primitive characters.

Donn Rosen and I finished our paracanthopt monograph in the summer of 1968, and it came out in 1969 (Rosen & Patterson 1969). By the time it came out, Gary had worked Donn over and turned him into a committed cladist, but in the paper Donn wouldn't allow any cladist jargon or references to Hennig and Brundin. Yet he did agree that our classification should by phylogenetic and on evidence that seemed weak even at the time, we moved *Polymixia* into the paracanthopts, as the sister-group to everything else (Rosen & Patterson 1969). So whereas I'd bumped *Polymixia* up from a family to a suborder in my thesis, five years later Donn and I bumped it up first to an order, and then to a supraordinal category that we called Series (Table 1). But this arrangement didn't last long. In 1972, Humphry Greenwood, Roger Miles and I organised a Linnean Society symposium called 'Interrelationships of Fishes'. Our excuse was to produce a Festschrift for two honorary Foreign members of the Linnean, two Swedish heroes: Erik Stensiö (Patterson 1990) and his colleague Erik Jarvik (Janvier 1998). A Festschrift for those two was our excuse, but 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.

TABLE 1. After Rosen & Patterson (1969, p. 460–461): “The three main groupings, representing parallel radiations into a “neoteleostean” grade, may be arranged as follows, with the equivalents given in Greenwood, Rosen, Weitzman, and Myers (1966) in brackets and parentheses…”

- Superorder Scopelomorpha, new name
    - Order Myctophiformes
- Superorder Paracanthopterygii
    - Series Polymixiomorpha, new
        - Order Polymixiiformes, new (= Polymixioidei)
    - Series Salmopercomorpha, new
        - Order Percopsiformes
        - Order Gadiiformes
        - Order Batrachoidiformes
        - Order Lophiiformes
        - Order Gobiesociformes
- Superorder Acanthopterygii
    - Series Atherinomorpha
        - Order Atheriniformes
    - Series Percomorpha
        - Order Lampridiformes [= Lampridiformes + Ateleopodoidei + Miriapinnatoidei, in part (Mirapinnidae + Eutaeniophoridae) + Megalomycteroidei
        - Order Beryciformes [= Stephanoberycoidei + Berycoidei + Cetomimoidei + Mirapinnatoidei, in part (Kasidoroidae)]
- Order Perciformes and related groups

For this symposium, we asked Donn Rosen to tackle the acanthopterygians, the huge group of about twelve thousand species that he and I had put as the sister-group of paracanthopts. Although Donn’s paper was by far the longest in the book, he didn’t really get to grips with the acanthopts because he had to devote most of his effort to clearing away the shrubbery or the swamps surrounding them. He ended his paper with the diagram in Figure 5 (Rosen 1973, fig. 129). The group covered is the Euteleostei, first recognised by Greenwood *et al.* (1966). In 1966, it contains over 90% of living teleosts. The diagram in Figure 5 was Donn’s theory of euteleostean relationships in 1973, just seven years after the group was first recognised, and four years after cladistic methods were first applied in it. The actual names don’t matter a scrap, but the ones indicated by arrows are groups first recognised and named by Donn in this paper, and the ones indicted by chevrons are groups first recognised and named in the preceding seven years, either by Greenwood *et al.* in 1966, or by Gary Nelson and Donn and me. The actual names don't matter a scrap, but many of the groups were first recognised by Donn in this paper (Neognathi, Stenopterygii, Cyclosquamata, Aulopiformes, Aulopoidei, Europterygii, Ctenosquamata, Acanthomorpha), and many others were named in the previous seven years by Greenwood et al. in 1966, or by Gary Nelson and Donn and me (Protacanthoptergyii, Euteleostei, Neoteleostei, Paracanthopterygii, Atherinomorpha). 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. Things were fun in those days. Of course, you see here one of the disadvantages of cladistics – naming every node in a dichotomous tree needs an awful lot of ranks—above the orders there are series, super-order, sub-section, section, sub-division, division, and finally cohort. There are ways around this kind of thing, but maybe its better just to admit that nature isn’t simple. On a more mundane level, in this paper Donn changed his mind about our interpretation of *Polymixia*, and moved it from where we’d had it, at the base of the paracanthopts, and put it back with the other beryciforms, at the base of this group, Percomorpha. It stayed there for another ten years of so. As for myself, by this time I’d got my own *Polymixia* to play with. When Dan Cohen went back to Washington as Director of the National Fisheries laboratory he had access to the output from the Smithsonian Sorting Centre, which worked over the collections brought back by the American research ships—they still had them then. Over the years Dan sent me all sorts of rare fishes that we were short of in London, mostly nasty black things from the depths, but including a good collection of *Polymixia*. In the fifties and sixties, the only Recent comparative material I’d had was dried skeletons. The only other ways of studying fish skeletons were by X-rays, or by staining the bones with alizarin, and clearing the flesh with potassium hydroxide and glycerine, a method that sometimes gave reasonable results but was far from perfect. In 1967 a method was published that used the enzyme trypsin instead of potassium hydroxide; the flesh is digested rather than eaten away (Taylor 1967). The trypsin method gives pretty good results. But ten years later, in 1977, a wonderful new method was developed—you stain the bone with alizarin and the cartilage with alcian blue (Dingerkus & Uhler 1977) This technique has revolutionised fish osteology; you can study ontogeny direct, without the laborious business of serial sectioning and reconstruction that used to be necessary. Double staining with alcian and alizarin came into the NHM at the end of the 70s, and a few years later I asked Mandy Holloway, then of the NHM fish section, if she'd prepare one of my *Polymixia*. My specimens were rather big, almost 20cm long, so it took a long time and didn't clear perfectly, but the result wasn't bad. About then, in the middle 80s, Donn Rosen took yet another look at *Polymixia*. Donn and I had continued to work together, with almost annual trips back and forth across the Atlantic. We'd published a big paper on fossils and classification in 1977 (Patterson & Rosen 1977), and in the early 80s we started on the paracanthopts again. But in the spring of 1983 Donn's brain tumour surfaced, and he had his first bout of surgery. He recovered from that, but never regained full use of his left hand so that he couldn't do the minute dissections that had been his lifeblood. In 1985 (Rosen 1985) he published an essay on teleost classification in which he concluded that *Polymixia* didn't belong where we'd put it in 1969, with the paracanthopts, or where he'd put it in 1973, with the acanthopts. Instead it was the sister of both put together, the group he'd named Acanthomorpha. Donn's evidence was pretty tenuous, but in 1986, the year Donn died, Melanie Stiassny reached the same conclusion (Figure 6, after Stiassny 1986, fig. 27). Melanie had been a Ph.D. student with Brian Gardiner and Humphry Greenwood in London, and in 1983 she got a job in the Museum of Comparative Zoology (MCZ) at Harvard. Her two characters separating *Polymixia* from other acanthomorphs are in the jaw ligaments and by the middle 80s *Polymixia* was the sister-group of about 15 thousand species, another promotion through the ranks. The year after Donn died, Melanie Stiassny took over his job at the American Museum in New York. Melanie Stiassny, Lynne Parenti and Dave Johnson are the editors of the new *Interrelationships of Fishes* book (Stiassny *et al.* 1996).

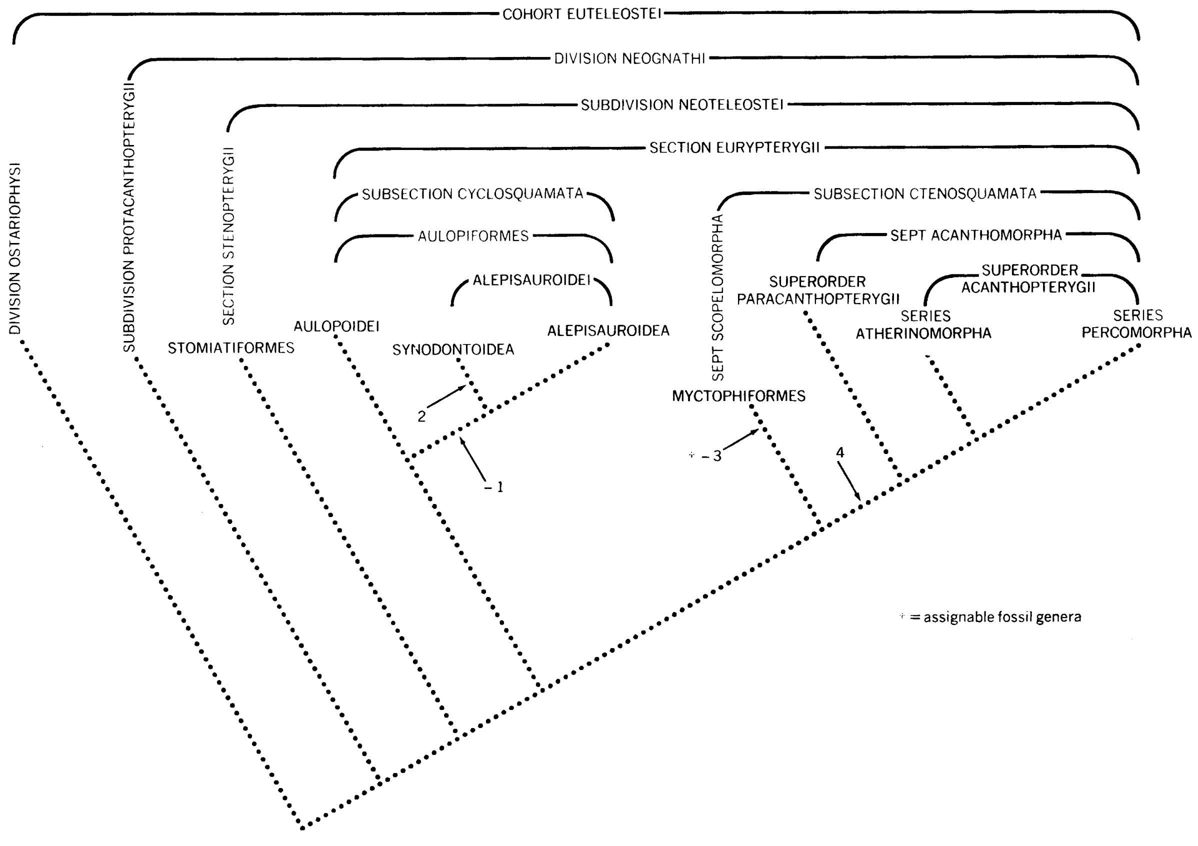


FIGURE 5. After Rosen (1973), figure 129.

I first met Dave Johnson in London in 1988. He was planning a symposium as a memorial to Donn Rosen—the meeting was to cover the percomorphs, the most derived major group of teleosts, and the point where Donn had stopped short in his paper in 1973. For his percomorph meeting, Dave asked me to tackle the fossils, which meant revisiting creatures that I'd hardly touched since the sixties. In working towards that meeting, I got down to the cleared and stained *Polymixia* that Mandy Holloway had done for me, and soon found that I didn't understand it.

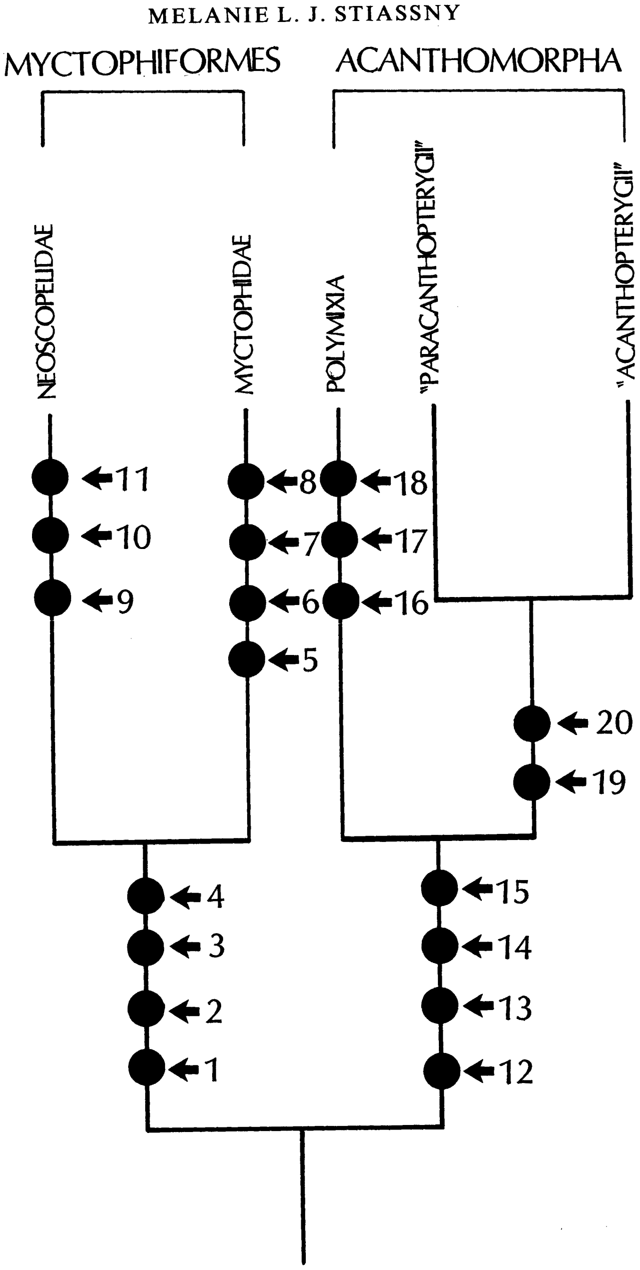


FIGURE 6. After Stiassny (1986), p. 448, figure 27, "Cladogram of ctenosquamate relationships, summarizing the results of the present study"

This was the problem. I already know that *Polymixia* differs from other acanthomorphs in having an extra set of intermuscular bones, but there is an extra set that has nothing to do with these. In *Polymixia* there is the ordinary set of intermuscular bones, and below them there are a series of cartilage rods. I'd never seen anything like this before, and in trying to understand it I went back into the literature. I found a German paper from 1895 (Göppert 1895, p. 15, figure 7) saying that there were bits of cartilage in this position in herrings, but when I checked the herrings in double-stained specimens the cartilages were there sure enough, but they were something quite different, little superficial chevrons, arranged at the tips of a series of bones coming out from the vertebrae—this pattern turned out to be autapomorphous for herrings and their relatives. Going further back into the literature, I came to Richard Owen, who first described and named teleost intermuscular bones in 1866 (Figure 7, after Owen 1866, fig 37). Figure 7 is Owen's drawing of a herring vertebra seen from in front, with the bone names added. Owen said that there were three series of bones in herrings – there are, epineurals above, epicentrals in the horizontal septum, and epipleurals below it – and that other fishes had only two series, or one, or none. In particular, he said the salmon has the upper series, and what he called "gristly representatives of the epipleurals" (Owen 1866, p. 44). Gristle is cartilage, so I thought perhaps salmon would have something like my blue rods in *Polymixia*. Luckily, there was a Ph.D. student in the NHM in the middle 80s, Chris Sanford, who'd worked on salmon and their relatives, and had made lots of double-stained preparations. When I checked a small salmon, sure enough, there were the blue rods, and just like *Polymixia*, they were in the horizontal septum, not below it, where the epipleurals would be. The blue rods turned out to be there in lots of things that were supposed to be somewhere near salmonin galaxiids, a group with an austral distribution, Australia, New Zealand, South Africa and South America, unlike the boreal distribution of salmonids. And even more conspicuous in a Japanese fish called *Plecoglossus*. Chris Sanford had made these preparations for his Ph.D., but there was no mention of the blue rods in his thesis, and by the time I found them he'd gone to a job in the States, so I couldn't ask him what he thought of them. But in 1987 Chris Sanford had published a paper on *Plecoglossus*, with Gordon Howes, who was still in the NHM (Howes & Sanford 1987a, 1987b), so I took the specimen to Gordon to ask him what he and Chris had made of the blue rods. He said, more or less, that they hadn't noticed them—how could you fail to notice them?—they're the most conspicuous things in the specimen. What he meant was that they'd seen them but hadn't known what they were, and so neglected them—you only notice what you expect to see.

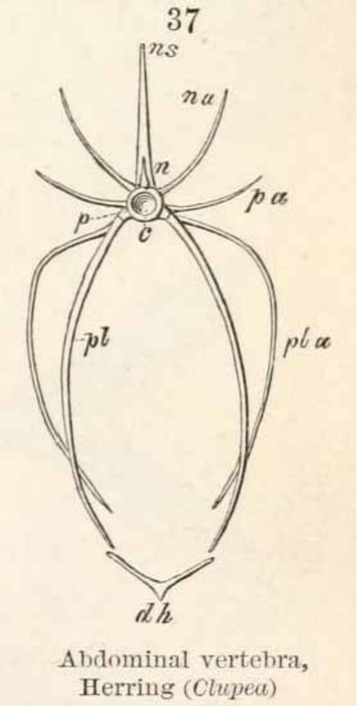


FIGURE 7. After Owen (1866), p. 43, figure 37, "Abdominal vertebra, Herring (*Clupea*)…These 'scleral' spines are termed, according to the vertebral element they may adhere to, 'epineurals,' 'epicentrals,' and 'epipleurals'; though each may shift its place, rising or falling gradually along the series of vertebrae. All three kinds are present in the herring, fig. 37, in which *n a* is the 'epineural,' *p a* the 'epicentral,' *pl a* the epipleural spines".

Anyway, I wrote a manuscript on the intermuscular bones and the blue rods, illustrating them in *Polymixia* and beryciforms, trying to explain the differences between these two patterns, and commenting on the different patterns in herrings and in salmon and their relatives, which have the blue rods. I sent that manuscript out for review to a few people, including Dave Johnson in Washington. As I've discovered, when Dave meets a problem in morphology his first response is to go the microscope and the specimens, whereas my first response is to go the library and the literature. Dave had access to more cleared-and-stained specimens than me, and more important, he had a better microscope: he has a Leitz whereas I only have a Wild. It makes a hell of difference, as I've learned. Dave started looking at specimens, and soon found that the strands of connective tissue in which my blue rods were sitting are very widely distributed in teleosts. They are ligaments, and we already knew that intermuscular bones are usually ossifications in ligament. What Dave noticed was the ligaments are there whether or not there are bones in them. *Holocentrus* has two series of ligaments with no bones in them at all, and in *Polymixia* the blue rods are developed in about the first fifteen of a series of ligaments that extends back into the tail. I met Dave Johnson in June 1990, at the Rosen memorial percomorph symposium, in Charleston, South Carolina. We agreed that we should collaborate on the intermuscular bones and ligaments, and he proposed that we should also collaborate on a paper to summarise and conclude the percomorph symposium volume. So we started a series of pilgrimages; once or twice a year Dave came to London for three weeks or so, and once or twice a year I went to the Smithsonian. On the intermusculars, we developed a system on shorthand, a sort of algebra to map the distribution and structure of the bones and ligaments in a fish. We mapped the intermuscular system in 130 genera of teleosts, representing about 100 families. We found that we could make sense of the system throughout teleosts: we could identify a basic pattern and find all sorts of variations on it—we'd discovered a new world of morphological characters that no one had touched before.

The intermusculars turned out to be particularly useful in sorting things out around the *Polymixia* level, and we used them in revising the lower acanthomorphs for the percomorph volume. After a lot of work, we discovered that the Percomorpha, the subject of the symposium we were summarising, had no characters at all and had never had any—the emperor was naked. We felt we had to salvage the name—you can hardly publish a symposium on a group when the conclusion is that it doesn't exist. But the only way we could salvage the name was by excluding a lot of things that were supposed to belong in it, and including a lot more things that weren't supposed to be there. In particular, we had to include the atherinomorphs, the large group that Donn Rosen had placed as the sister-group of percomorphs, which is a fairly fundamental change. Figure 8 is our tree of acanthomorphs (after Johnson & Patterson 1993, p. 617, fig. 24), finally published in 1993 along with the rest of the percomorph symposium (Johnson & Anderson 1993). The numbers at the nodes are our synapomorphies – the intermusculars provided almost a third of the characters we used within the group. The Percomorpha has expanded to include the atherinomorphs, which are hidden in a new group we called Smegmamorpha—something of a private joke, but the name comes from the initials of the included groups, atherinomorphs and five other things that had previously been put in eight different orders of unknown relationships. As for *Polymixia*, the intermusculars convinced us that at last we knew exactly

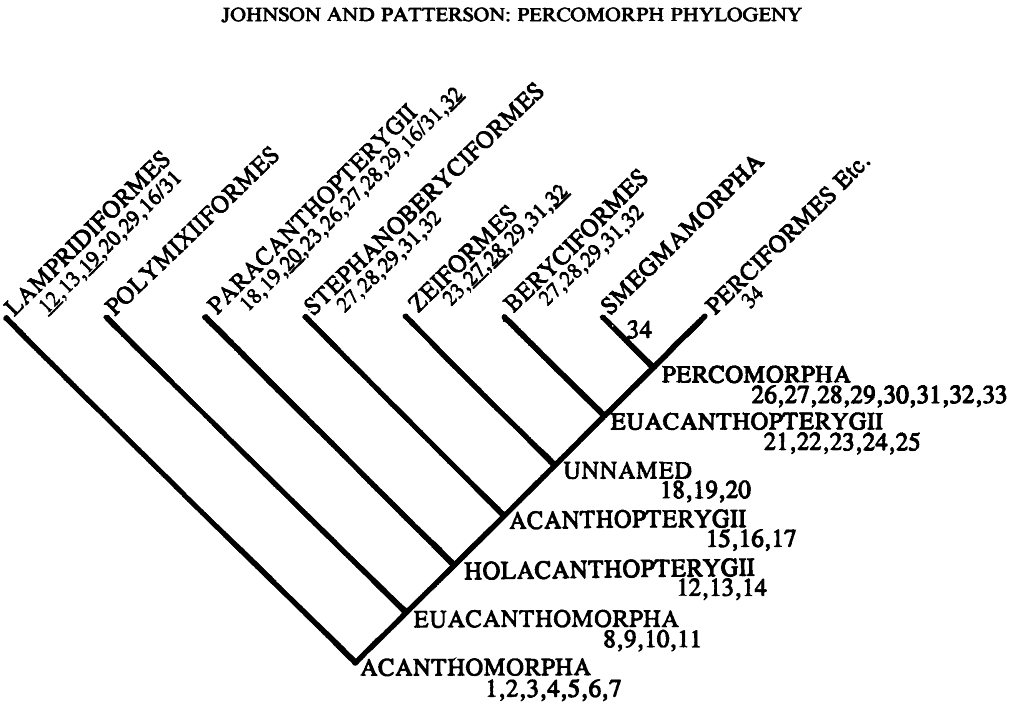


FIGURE 8. After Johnson & Patterson (1993), p. 617, figure 24, "C1adogram summarizing our views on acanthomorph interrelationships. The names on the axis of the c1adogram are those that we propose for major groups, and the numbers beneath those names refer to the characters listed in the text. Numbers beneath the names of terminal taxa indicate characters from that list that must be assumed to have originated independently in all (underlined numbers) or some members of those groups. Reversals that must also be assumed to have occurred within terminal taxa are not entered in the c1adogram but summarized in the text".

where it went. It's sister-group not of all the acanthomorphs, but of all of them except one group, the lampridiforms, an assortment of rare and mostly bizarre oceanic fishes that have been a problem ever since the group was first recognised in 1907 (Olney *et al.* 1993). The type genus is *Lampris* which gets up to about six feet long and 600 pounds in weight; *Regalecus* gets up to almost sixty feet long and is the source of a lot of the sea serpent legends. So by 1993 Dave and I felt that with help from the intermusculars we'd sorted out the acanthomorphs and percomorphs as best as we could. As for our intermuscular monograph, it was held up by funding problems in the Smithsonian and wasn't published until April 1995 (Patterson & Johnson 1995); and as for the blue rods in *Polymixia*, which first got me into the intermusculars seven years ago, ironically, they turn out to be autapomorphous for *Polymixia*—we found them nowhere else among acanthomorphs. The only other place we did find blue rods was in salmon and their relatives, where they seemed to be a good character for a large group. That was a discovery that did eventually pay off, in a roundabout and rather unpleasant way. I'll have to tell you the story.

Salmon and their supposed relatives are mostly freshwater fishes with a bipolar distribution, salmon, smelts and so on in the boreal zone, and galaxiids and so on in the austral zone, at the southern end of the world. Because of the commercial importance of the northern fishes, and the biogeographic problem of their distribution, lots of people have worked on salmoniforms. Donn Rosen had a go in 1974, in a big paper that includes the diagram in Figure 9, which I think is the first area cladogram, plate tectonics put into the cladistic framework (Rosen 1974, p. 317, fig. 44). Anyway, over the last 25 years there have been endless disputes about what belongs in salmoniforms and how the groups are related. But things seemed settled by 1992, because of two papers by a chap named Doug Begle, who'd done a Ph.D. at Michigan. His first paper came out in *Systematic Zoology* in 1991, *Relationships of the osmeroid fishes and reductive characters in phylogenetics* (Begle 1991); and the second came out in *Copeia* in

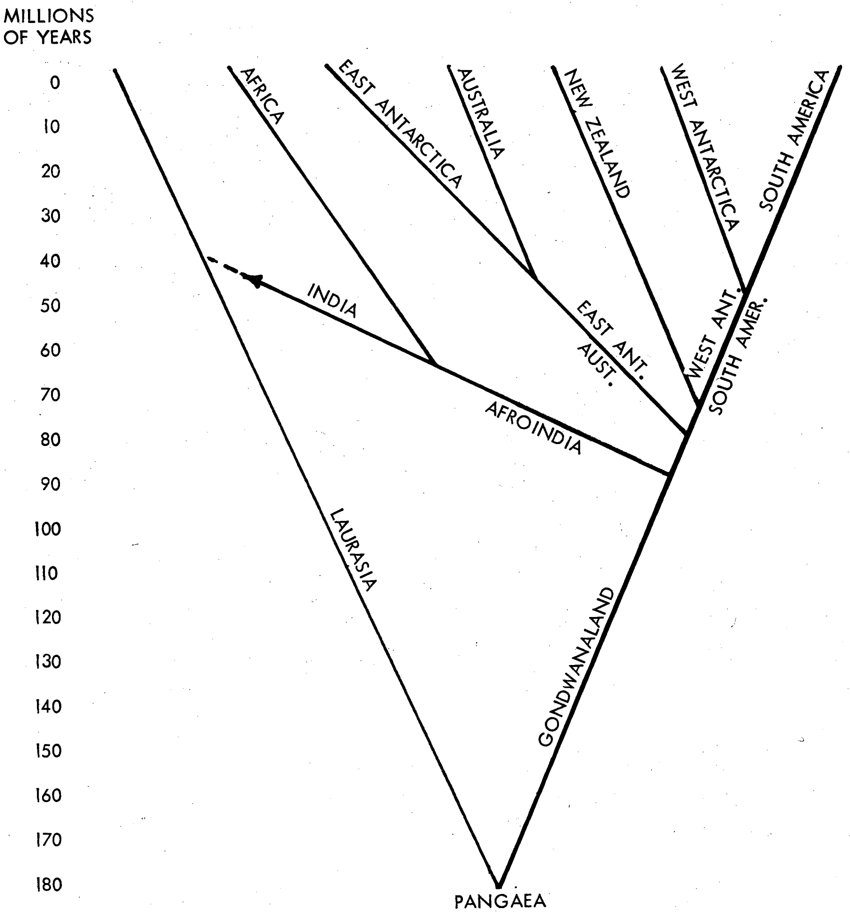


FIGURE 9. After Rosen (1974), p. 316, fig. 44, "Diagrammatic representation of the sequential disruptions of the supercontinent Pangaea through time, according to data from McKenna (1973, and personal commun.). The beginning of disruption of the Gondwanaland fragment is located at minus 90 million years".

1992, *Monophyly and relationships of argentinoids* (Begle 1992). You don't need to know what these fishes are to understand what follows. By this time, 1992 or so, the new *Interrelationships of Fishes* volume was planned, and Doug Begle was asked to tackle the salmoniforms for it, because he'd covered the ground in these two papers. But in 1993 Doug had left the fish trade to go into computer programming, so he dropped out of the *Interrelationships* project. To fill the gap, Dave Johnson and I said we'd take on the salmoniforms, feeling that we had a new angle on them from our work on the intermusculars. Doug Begle's two papers are in the style of modern systematics – a big matrix, computer-generated trees, discussions of alternative optimisations. Doug had 108 characters coded in 33 taxa, of which 26 were genera and seven were collective, families or higher taxa. Dave and I started work on them in London, in September 1994. As soon as we got into Doug Begle's matrix, we got a sinking feeling, because there seemed to be an awful lot of mistakes, some of them very obvious or well known characters. In fact, we found so many mistakes that we decided we had to check every character in every taxon against specimens; with 108 characters and 33 terminal taxa, seven of them collective, that means a minimum of 3564 observations, actually many more. But when we were working on the intermusculars I remember Dave saying that he was amazed to have found someone who was as anal as him when it comes to collecting data. So we went ahead gathering specimens and beginning our thousands of observations. To cut a long and boring story short, here's what we found: out of 108 characters in Begle's matrix, there were errors of fact in 81 and errors of interpretation in three, a total error rate of 78%. Of the 24 characters that were correctly coded, eight are autapomorphous, so that leaves just 16 characters, or 15% of the total, that can be used to group taxa.

That's the situation, with someone who has included this statement in two publications: "Every specimen was examined for every character…" (Begle 1991, p. 36; Begle 1992, p. 351). I haven't spoken on this stuff before; Dave has, at a couple of meetings, and people have grumbled afterwards usually not directly to him, about how wrong it is to destroy someone's reputation in public. Dave and I don't see it like that. There's much more at stake here than the personal reputation of one scientist—effectively we're accusing him of fraud. But fraud needs victims and accomplices. Doug Begle produced this work as a Ph.D. thesis in a top-class institution, the Museum of Zoology at the University of Michigan. And his work went through all the processes that we're familiar with as systematists—submission of drafts to supervisors, giving seminars to colleagues and talks at meetings, examination of the thesis, refereeing of papers submitted to top-class journals like *Systematic Zoology,* and so on. Through all of that, it seems that no one—no colleague, no examiner, no referee, no editor – thought it necessary to glance at the data to see if they made sense. So I feel that what's at fault here is not just one individual, but the whole system, or this chunk of the system, as represented by Begle's colleagues, committee, referees and editors. But it doesn't stop there. I think we have to spread the blame even wider. Begle's papers are prepared in the style of a great deal of modern systematics—the characters are tucked away in an appendix or a list at the end, and are treated very briefly, a sentence or so describing the different states. The bulk of the paper isn't about characters at all, but about the properties of trees, or inferences drawn from trees about things like paedomorphosis or biogeographic history. But what matters in systematics, or matters most, is looking at and comparing 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 it 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. In Begle's case the rubbish in rubbish out maxim was certainly true. Figure 10 is his original tree, beautifully resolved, and with lots of synapomorphies (after Begle 1991, p. 40, fig. 3). But when we ran his corrected data we got the tree in Figure 11 (after Patterson & Johnson 1997, p. 359, fig. 1), over a hundred equally parsimonious trees, homoplasy everywhere, and only five nodes in common between his tree and our one. Dave and I had to do the whole job again, starting more or less from scratch.

Begle's papers are an example of modern morphological systematics, the matrix fed through a parsimony program. Well, I've yet to work through a published matrix covering animals that I know well where I haven't found any obvious mistakes. That crusty remark reminds me of a similar remark about the other half of modern systematics, the molecular half, where the matrix is strings of A's, C's, G's, T's and dashes. A few years ago I was in a bar in Woods Hole with Walter Fitch, who invented large parts of molecular phylogenetics, starting in the middle 1960s, and who edited *Molecular Biology and Evolution* for its first ten years (1983–1993). Walter said that he'd never seen a molecular alignment that he couldn't improve. What Walter meant was that he had never seen an alignment that he couldn't improve by fiddling with the gaps. Of course, you can't do that with a morphological matrix, or if you do you're in even worse trouble than Doug Begle, because in morphology primary homology comes in the columns, the characters, whereas in molecular systematics primary homology comes from maximising matches between the rows. So Walter Fitch didn't mean what I mean about mistakes in matrices, that characters are wrongly scored. In this alignment, who knows whether two C's in *Polymixia* are a mistake or not? Does it really differ from all its neighbours at those two positions? It would take an awful lot of effort and money to find out; it isn't really a sensible question. So the mistakes in molecular alignments are different, you correct them by massaging the rows rather than the columns.

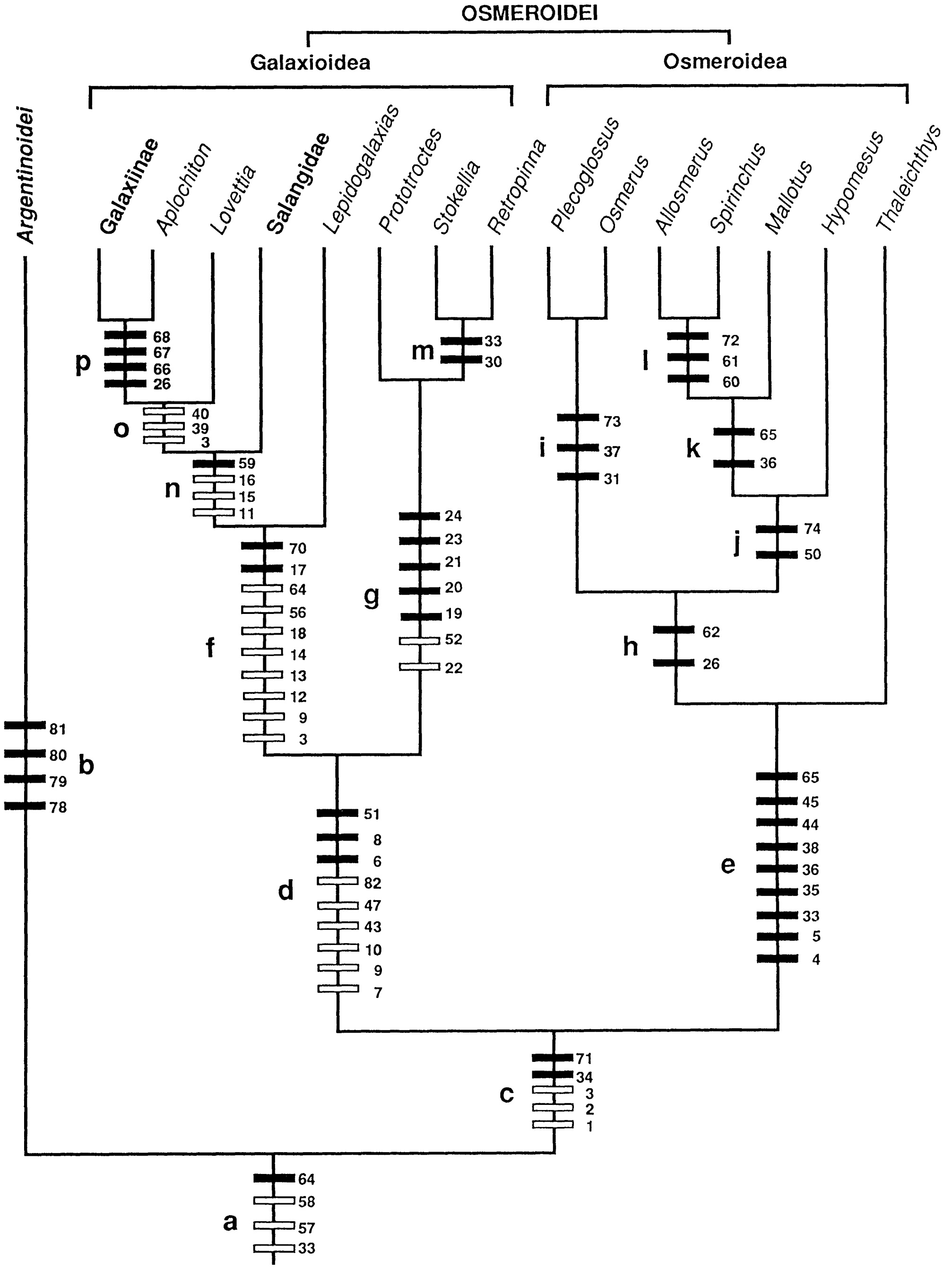


FIGURE 10. After Begle (1991, p. 40, figure 3), "Relationships of osmeroid taxa. Autapomorphies of terminal taxa are not shown on the cladogram…Reductive characters are indicated by open bars, other characters by closed bars. Reversals of characters 1 and 33 shown as closed bars. Reversal of character 64 shown as open bar".

This business of alignments and possible mistakes in them is one that concerns me at the moment. Five years ago, Andrew Smith (NHM) and I got a grant to compare patterns of molecular and morphological evolution in sea urchins and in teleost fishes, two groups with respectable cladistic phylogenies and a good fossil record. Our plan was to get ribosomal RNA sequences from a range of sea urchins and fishes, to collect morphological data from the same sample of animals, and to compare the trees from the two sets of data with each other, with trees from the combined data, and with the fossil record. The sequencing was done by Tim Littlewood (NHM), who spent three years with us as a post-doc, slaving at the gels. Our sample of teleosts was designed to catch the major clades, so we included *Lampris*, type genus of the lampridiforms, and *Polymixia*, because I believed that these two are successive sisters of everything beyond them. But when we ran Tim's sequences through a parsimony program, we found a very different story. The tree makes good enough sense overall, but there are two notably long internal branches. The first is linking *Clupea*, the herring, with *Chanos*, which is a primitive ostariophysan (Figure 12). That branch didn't surprise us, because a French group published just the same strong signal in 1993, using a different molecule and a different sample of fishes (Lê *et al.* 1993). The other long internal branch is linking *Polymixia* and *Lampris* (Figure 12), which is completely unexpected from morphology, yet we had a very strong signal. Using an alignment that's more conservative, because it leaves out some questionable bits, the *Lampris/Polymixia* branch is even more striking, 54 steps, almost as long as the herring/*Chanos* branch, at 59 steps. Notice that the terminal branch to *Polymixia* is also very long—that's because the *Polymixia* sequence contains a huge deletion of almost 50 bases that the parsimony program treats as 50 separate characters; we haven't found such a big deletion in any other small subunit ribosomal RNA. So of course the question comes up–is this artefact? Are *Polymixia* and *Lampris* linked because we're looking at two corrupt versions of the same sequence? Has PCR, the magic of modern science, let us down or deceived us? We've no way of knowing until we get more money and fresh material. And both *Lampris* and *Polymixia* are very hard to come by.

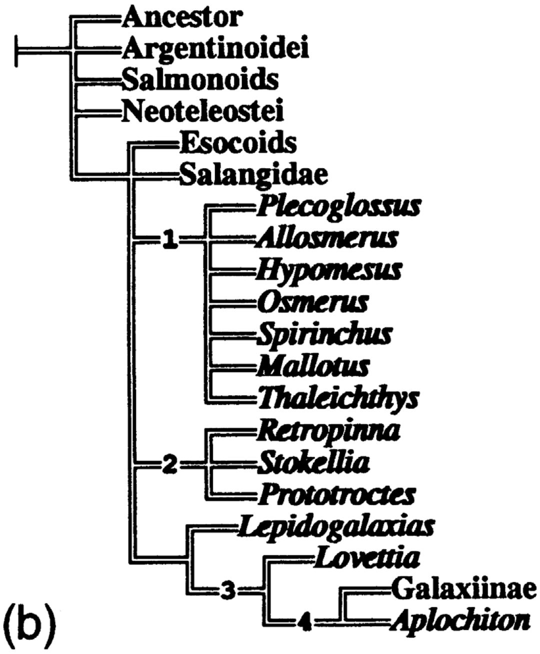


FIGURE 11. After Patterson & Johnson (1997), p. 359, figure 1b, "Reanalysis of Begle's (1991) characters for teleost fishes,…(b) Strict consensus of 225 shortest trees found by Hennig86 after our corrections when polymorphisms in terminals…are treated as missing data (?)".

I've used *Polymixia* as the theme of my talk, and I can't sum up better than providing a passage from the latest edition of Joe Nelson's book *Fishes of the World*: "Few groups have been shifted back and forth as frequently as this one " (Nelson 1994, p. 230), and off he goes summarising the last thirty years. I've used *Polymixia* as a theme in reminiscing about almost forty years in systematics. I could have used something else, perhaps one of my fossils, but in terms of theory, *Polymixia* has kept me occupied from my time as a performing monkey in evolutionary systematics, through the cladistic revolution of the late sixties and early seventies, and on through the later revolution-sthe coming of parsimony programs and molecular sequences in the eighties. During that time, I've seen *Polymixia* climb up the tree or the hierarchy, first just a family, then a suborder, then an order, then a series, and at present a superorder. *Polymixia* has also been with me through all the changes in technique, from my early days with dried skeletons prepared in the nineteenth century, on through the alizarin preparations that I used with Donn Rosen in the sixties, and then the staining for cartilage that revealed the blue rods in the eighties, and all the ramifications that those blue rods led me into in the last seven years, and most recently to the problems that molecular sequences from *Polymixia* are just beginning to bring to the surface.

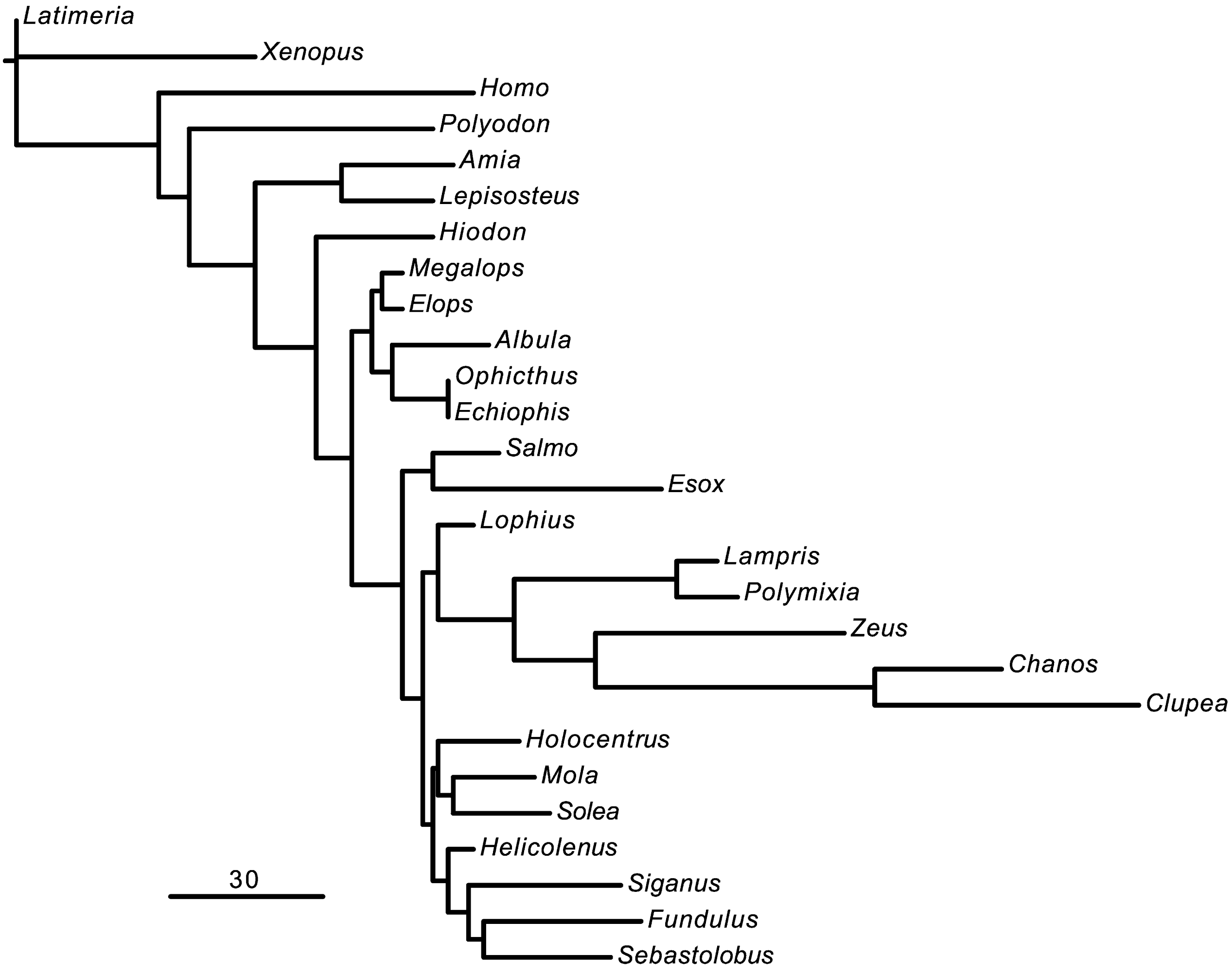


FIGURE 12. After Littlewood & Patterson (unpublished), Parsimony tree derived from analysis of 1755 aligned 18s RNA bases (189 parsimony informative), outgroups omitted from diagram (Littlewood, pers. comm.).

Are there any conclusions to draw from my ramblings? Well, here's one possible message. Fish systematists take their work seriously, but they seem to have an awful lot of fun. There was a phrase in a book review in *Nature* last month that caught my eye – "Scientists, the good ones at least, do it only because they enjoy it." How true. If fishes and systematics ever stopped being fun that would be the day to give it up. But why is it such fun? – because it's inexhaustible. You never have enough specimens or enough characters, and that sampling problems becomes really acute once you get into molecular systematics. And of course, you never know enough about anything, and if for a few months or years you should ever believe that you do, you are either past it or in for a surprise, like the surprises I got from the blue rods and the molecular sequences in *Polymixia*. Yesterday's secure knowledge is tomorrow's laughing matter. And so often the changes, the surprises, come about entirely by chance. I could describe all sorts of examples, but the chain of events that included me asking Mandy Holloway to clear and stain a big *Polymixia* will do – I only had big ones because Dan Cohen had sent me specimens big enough to dissect. Because they were big, the blue rods were much too obvious to miss, and through that Dave Johnson and I got into sorting out the intermusculars, sorting out the acanthomorphs, finding out poor Doug Begle and so coming to distrust the basis of much contemporary systematics, and sorting out the salmoniforms. I couldn't have done any of that on my own, so perhaps the last thing to mention is the companionship that goes with the fun of systematics. Apart from the people in one's own institution, I worked with Donn Rosen for almost twenty years, and felt like I'd lost a brother when he died. I'm lucky to have found Dave Johnson to take his place. And I can't talk about fun and companionship without bringing in the excursions of the Temperance Five, the systematics walking club Peter Forey, Brian Gardiner, Chris Humphries, Dick Vane-Wright and me. Dave Johnson is greatly honoured, as the only outsider who's ever been allowed to come on these excursions. Our most recent outing was on a beautiful day to the river Stort, September, 1995. Like science in general, systematists do it only because they enjoy it. Dave Johnson and I now have a cosy grant to write a new classification of teleosts. I look forward to our further adventures in the glycerin and the fish trade. Thank you.

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FOOTNOTES

[1] Patterson is referring to the Linnean Society rooms, Burlington House, Piccadilly, London, the venue for the Systematics Association Annual General Meeting presentation lecture.

[2] Formerly abbreviated as BM(NH), sometimes as BM, now simply as NHM. Patterson used both BM(NH) and BM. We have substituted NHM for BM(NH) or BM throughout the text.

[3] Cain's paper was given on 15th July as part of the Linnean Society's 'Linnaeus' *Systema Naturae* bi-centenary and Darwin-Wallace centenary celebrations' (*Proceedings of the Linnean Society of London* 170, p. 226, 1959). As part of those celebrations 20 silver Darwin-Wallace medals were awarded to British and Foreign Biologists "in recognition of their outstanding contributions to our knowledge of Evolution…" (*Proceedings of the Linnean Society of London* 170, p. 226, 1959). One recipient was Erik Anderrson Stensiö, a significant influence on Patterson (Patterson 1990).