JENNIFER A. CLACK
3 November 1947 — 26 March 2020
Jennifer A. Clack (née Agnew) dedicated her entire research career of more than 40 years to the fish-tetrapod transition, the evolutionary process during the Devonian and Carboniferous periods that transformed a lineage of lobe-finned fishes into the earliest land vertebrates. She was widely regarded as the world leader in this field. During an expedition in the summer of 1987 to the Late Devonian vertebrate localities of East Greenland, Clack collected numerous fossils of two of the earliest tetrapods, *Acanthostega* and *Ichthyostega*, which revolutionized the understanding of these animals and created a surge of renewed interest in what had previously been a small and somnolent research area. However, much of her work focused on the Carboniferous, the time when the group underwent its first major diversification and the amphibian and amniote lineages first appeared. Here too she produced a stream of groundbreaking discoveries. She published close to 100 primary research papers, many in flagship journals, as well as numerous popular articles and the influential textbook *Gaining Ground*. Modest and unassuming in person, and unfailingly supportive towards young scientists, Jennifer Clack was enormously respected and helped to make the entire research field into a more open, collaborative, and welcoming environment.

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Biographical Memoirs

Early Years: The Influence of Alec Panchen

Jennifer Alice Agnew (known as ‘Jenny’) was born on 3 November 1947 in Manchester, the only child of Ernest and Alice (née Winsom), and attended Bolton School. Early in life she learned to play the piano, which kindled an interest in music that she kept all her life. She also developed a deep love of natural history and fossils. Hers was not an academic household, her parents were poorly educated and there were almost no books in the house apart from the ones Jenny borrowed from the local library, but its location had one great advantage: across the road was a pond full of sticklebacks, tadpoles and other wonderful things. As an only child, Jenny would go there regularly by herself to marvel at its strange denizens, and would bring home sticklebacks and newts which her mother hated but let her keep anyway. Later, when she read about 19th century fossil collector Mary Anning and her extraordinary discoveries of ichthyosaurs at Lyme Regis, Jenny realized that she had found her life-goal; a family holiday to Lyme Regis failed to produce any ichthyosaurs, but Jenny was thrilled by the ammonites she found and was hooked on palaeontology for good. In due course her interests led her to pursue a four-year degree course (1966–1970) in zoology, with botany and geology as subsidiary subjects, at Newcastle University. Natural history never lost its fascination for her, and from time to time she would take the opportunity to engage actively with it. For example, during her time at Birmingham City Museum and Art Gallery in the mid-1970s (see below), she set up a moth trap on the roof of the building and recorded the catches; these records are now being used as a research resource to chart changes in the local insect fauna over the past five decades.

During her final year at Newcastle she attended the popular lectures on vertebrate palaeontology and evolution given by Alec Panchen, Reader in Vertebrate Palaeontology (1930–2013), an inspiring teacher and researcher who was to have a huge influence on her career trajectory, and indeed on British vertebrate palaeontology as a whole. At this time, Panchen was engaged on a project that he had begun in the early 1960s, and which proved to be pivotal in the revival of interest in the origin of tetrapods: the revision of the Coal Measures (Late Carboniferous) ‘amphibians’ in the Hancock Museum, Newcastle-upon-Tyne. These had last been the subject of serious study in the 1920s. Using modern techniques of fossil preparation, Panchen was able to draw out a wealth of new information, which not only gave a much clearer picture of the animals but began to hint that long-established ideas of their interrelationships and evolution would need to be fundamentally revised.

Jenny wanted to join Panchen’s research group as a PhD student, but to her disappointment he was unable to offer her a place at that time. Instead she went on to study for a Graduate Certificate in Museum Studies at the University of Leicester, after which she found work as an Assistant Curator at the City of Birmingham Museum and Art Gallery. Later in life she would occasionally refer to this period as her ‘wilderness years’, but in 1976, while working in Birmingham, she met fellow motorbike enthusiast Rob Clack and discovered that they shared a passion for palaeontology. They married in January 1980, shortly after a serious bike crash on an icy road that left them both bandaged and plastered-up. Bikes, fossil collecting, choral singing, gardening and cats were to be some of the constant themes of a long and happy marriage (figure 1). Rob was unfailingly supportive of Jenny’s work throughout her career, participating in fieldwork and conferences whenever possible, and taking on other supporting roles such as editing the newsletter of the TW:eed project (see below).
With characteristic tenacity, Jenny eventually managed to create an opening for herself back into the Panchen research group. During the late 1960s, Panchen had attempted to borrow the unique specimen of the Carboniferous tetrapod *Pholiderpeton scutigerum* from Keighley Museum, for preparation and study, but had been rebuffed. This was a source of considerable frustration, given the obvious importance of the specimen, which had not been investigated in earnest since its original description by T. H. Huxley in 1867. The loans policy had changed at Keighley in the intervening years, and Jenny managed to obtain the specimen on loan in 1977. She took three weeks of study leave to work in Panchen’s lab, preparing part of the specimen with a so-called airbrasive machine – a miniature sand blaster that removes the softer sediment from the fossil bones by shooting abrasive powder at the specimen with compressed air. The initial results were promising enough to form the basis of a successful application for a Natural Environment Research Council (NERC) studentship, and she began her PhD research under Panchen’s supervision in October 1978.

The impact of the Panchen research group on the development of British vertebrate palaeontology in the last third of the 20th century and beyond is a reflection both of his skill at choosing PhD students and of the intellectual atmosphere of vigorous argumentation and critical thinking, that he created in his lab. In addition to Jenny, his alumni include, *inter alia*, Andrew and Angela Milner, Tim Smithson and Michael Coates, all of whom were to make
important contributions to the study of early tetrapods, and would collaborate with Jenny in various combinations over the years. However, one of the key figures to enter her orbit during these years was not an academic, but a former merchant seaman from Edinburgh turned professional fossil collector, Stan Wood (1939–2012).

Wood had started collecting Carboniferous fish fossils at Wardie on the Firth of Forth in 1969 and quickly demonstrated an almost preternatural ability to find world-class material at seemingly unpromising fossil localities (‘by the sewage outflow pipe’ in the case of Wardie). After his Wardie collection was purchased by the Royal Scottish Museum in the early 1970s, and Panchen used this material as the basis of a PhD project, Wood and Panchen developed a close working relationship. Under Panchen’s tutelage, Wood began to prospect for Early Carboniferous vertebrate localities in southern Scotland, and soon scored spectacular successes at Dora near Cowdenbeath in Fife (1974), Foulden near Berwick-on-Tweed (1978), Bearsden near Glasgow (1980) and East Kirkton Quarry near Bathgate, West Lothian (1984) (Smithson & Rolfe 2018). As a result, the Panchen Lab developed into a scientific ‘perfect storm’ of gifted researchers and world-class material that led an international renaissance of Carboniferous tetrapod studies. East Kirkton, in particular, would play a central part in Jenny’s later research, as would Stan Wood himself.

Further impetus was provided, somewhat surprisingly, by a savage review article by Rosen et al. (1981) that systematically and with ferocious glee set about trying to demolish the entire conceptual framework around the origin of tetrapods. The ‘Gang of Four’, as Rosen and his colleagues became known because of their revolutionary fervour, espoused a particularly rigorous (or dogmatic, according to its opponents) version of cladistic analysis, which replaced the previous somewhat intuitive approach to phylogeny reconstruction – often based heavily on ‘key characters’ identified as especially informative by the author – with a mathematical search for the phylogenetic tree topology that required the smallest number of character changes. They were also somewhat disparaging of fossils, taking the view that living organisms were far more informative about phylogenetic relationships because they offer more extensive data sets. The members of the Panchen Lab were simultaneously scandalized and energized by this paper; they regarded its principal conclusions as wrong-headed, but could see that some of its methodological criticisms were justified, and this realization brought a new openness as well as a hunger for new information to their research.

Panchen was in some respects a relaxed supervisor, not overly concerned with deadlines, and most of his PhD projects over-ran. Jenny’s was no exception; her NERC funding ended in 1981 but she did not defend her thesis until 1984. However, he had high expectations of his students, who were expected to become intimately familiar with their specimens through a process of preparation (often with the airbrasive) and detailed drawing before moving on to the descriptive and analytical parts of their projects. Draft sections of the monographic thesis would be critically reviewed in depth, with focus on clarity, brevity and insight. The approach to science that Jenny imbibed during her PhD years stood her in good stead throughout her life. Her entire body of work is characterized by meticulously careful description and interpretation of the specimens, paired with analyses of contextual topics such as functional morphology and phylogenetics that stick close to the material and never degenerate into speculative arm-waving. Far from resulting in pedestrian output, this carefully grounded but open-minded approach allowed Jenny to arrive, when warranted, at startlingly novel conclusions.

The first of these emerged into the daylight as the airbrasive jet stripped the coal shale from the skull region of *Pholiderpeton*. One of the most puzzling aspects of the fish-tetrapod
transition is the transformation of part of the gill apparatus into a middle ear capable of amplifying airborne sounds. Ears with eardrums are widely distributed among tetrapods, but not universal, and the stapes ossicle can either be the sole connection between eardrum and inner ear (in amphibians, reptiles and birds) or form part of a three-bone chain with the malleus and incus (in mammals). Such structural disparity hints at a complex evolutionary history. Nevertheless, when Jenny began her research, it was almost universally agreed that the primitive tetrapod condition was a frog-like ear with an eardrum and a slender rod-like stapes. What Jenny found in *Pholiderpeton* was a curious butterfly-shaped bone, clearly a stapes on account of its characteristic footplate and piercing canal, but equally obviously not associated with an eardrum.

Her discovery came at a serendipitous time. Even while she was working on the specimen, two American colleagues published a ground-breaking paper (Lombard & Bolt 1979) arguing from a comprehensive review of the known fossil material that the earliest tetrapods lacked eardrums. Shortly afterwards, a third colleague from Canada described a large and heavy stapes from another Carboniferous tetrapod, *Greererpeton* (Carroll 1980). When Carroll showed the as-yet-undescribed stapes of *Greererpeton* to Jenny and Panchen at a conference in Newcastle in 1979 and floated the idea that the earliest tetrapod ‘middle ear’ had actually been an open spiracle, a vestigial gill slit used for breathing air, the strange butterfly-shaped bone of *Pholiderpeton* suddenly made sense.

This discovery became the subject of Jenny’s first paper (1), published in *Zoological Journal of the Linnean Society* shortly before she was elected FLS. The hypothesis that the earliest tetrapods lacked a tympanic ear has stood the test of time and been repeatedly supported by later discoveries. Jenny’s interest in middle ear evolution would continue for the rest of her career, with a series of influential papers culminating in co-editorship of a Springer Handbook on Auditory Research, *Evolution of the vertebrate ear: evidence from the fossil record* (20).

**CAMBRIDGE, EAST KIRKTON AND EAST GREENLAND**

In 1981, while still working on her PhD, Jenny secured a non-tenured position as Assistant Curator at the University Museum of Zoology, Cambridge. At this time the Director of the museum was Ken Joysey (1928–2012), who became a long-term supporter, encouraging her and providing funding for her purchases of fossils for the museum.

Jenny would stay at the museum for the rest of her career, eventually rising to the rank of Professor, but her initial appointment rested as much on her curatorial experience from Birmingham as on her status as a nascent, still-unpublished researcher. Alongside her curatorial duties she began teaching second-year and third-year vertebrate palaeontology courses for the Department of Zoology. In 1984 this brought her into contact with an undergraduate, Per Ahlberg, who would become her first PhD student and eventually a long-term collaborator. The same year saw her successfully defend her PhD thesis, which was eventually converted into a monographic description of *Pholiderpeton* published in *Philosophical Transactions of the Royal Society* (2).

Two pivotal events during these years set the direction for much of Jenny’s research career. The first was the initiation in 1985 of a broad collaborative project to study the extraordinary fossil material that Stan Wood had started unearthng at East Kirkton, and to continue the
excavation of that site. Jenny was a founder member of this project. East Kirkton held out the promise of helping to close two vexing lacunae in the early tetrapod fossil record: ‘Romer’s Gap’, a barren hiatus of some 20 million years between the earliest tetrapods of the Late Devonian and their much more advanced successors of the mid-Carboniferous; and the preservational bias in favour of aquatic environments that leaves us with few glimpses of the terrestrial tetrapods that may have existed during this time. Temporally, East Kirkton falls at the end of ‘Romer’s Gap’. Environmentally, it is a strange lake deposit from a Yellowstone-like volcanic landscape, almost devoid of aquatic fauna but containing beautifully preserved fossils of the eurypterids, scorpions, harvestmen and small terrestrial tetrapods that lived around its shores (figure 2). In the coming decades, Jenny would play a central role in the description of this tetrapod material.

The second event had even more profound effects, in that it led not only to dramatic new discoveries but to a reshaping of the entire research landscape around the origin of tetrapods. It began with Jenny stumbling on some Devonian tetrapod remains in a neglected
collection from East Greenland at the Department of Earth Sciences in Cambridge. This was a momentous discovery. While the tetrapods of the Carboniferous had long been within the purview of what could be called the Anglo-American research community, comprising not only British workers such as Panchen and D.M.S. Watson (1886–1973) before him, but also North Americans such as Robert (‘Bob’) Carroll in Montreal and John Bolt in Chicago, all of the few known Devonian tetrapods were thought to be in the hands of two people, one in Stockholm and one in Moscow.

The first, and by far the largest, body of Devonian tetrapod fossils to have been discovered was the material of *Ichthyostega* and *Acanthostega* from East Greenland, collected by a series of Swedish-Danish expeditions in the 1930s to 1950s. Apart from an initial paper by Gunnar Säve-Söderbergh in 1932, this material had been studied exclusively by Erik Jarvik at the Swedish Museum of Natural History in Stockholm. The rate of publication had been slow, with just one substantive paper in 1952 and a book chapter in 1980. Jarvik and his colleagues in what was known as the ‘Stockholm School’ worked within a distinctive scientific tradition, influenced by the German concept of ‘Idealmorphologie’, and substantially at odds with the more empirical perspectives of the Anglo-American community; relations between the two communities were polite but rather frosty, although Jenny herself had been made welcome during a visit to Stockholm in 1985, and it did not extend to collaborations. Jarvik’s publications were illustrated with retouched photographs and reconstruction drawings, but not with the kind of detailed specimen drawings central to the work of the Panchen lab.

The result of all this was that the East Greenland tetrapods, while universally accepted as such, played almost no part in the discussion about tetrapod evolution except as placeholders for the origin of the group. *Ichthyostega*, which was represented by extensive material including partial skeletons, had been reconstructed by Jarvik but several aspects of the morphology seemed problematic; *Acanthostega*, clearly a very different animal, was known only from a single semi-complete skull. A third Devonian tetrapod genus, *Tulerpeton*, was described from central Russia in 1984, by Oleg Lebedev of the Palaeontological Institute in Moscow. It was represented by a partial skeleton with well-preserved limbs but was not illustrated in detail and could not easily be accessed because of the political situation.

At a stroke, Jenny’s discovery in the Department of Earth Sciences broke open this frustrating scientific impasse. The collection she had discovered had been made by a PhD student, John Nicholson, who had visited Greenland around 1970 as a participant in a series of expeditions run by Cambridge geologist Peter Friend. Nicholson was principally interested in the Late Devonian siltstones and sandstones of Greenland, but he also collected vertebrate fossils that he came across. In one drawer, Jenny found a series of *Acanthostega* skulls. Not only did they, on their own, greatly expand the known material of this animal; they fitted together tightly into a single block, and the broken surfaces at their rear ends showed short sections of vertebral columns. Nicholson, it seemed, had picked up a single piece of rock from a locality where *Acanthostega* bodies lay stacked like sardines in a tin. At last one of the enigmatic Devonian tetrapods could be examined with fresh eyes and compared in detail with Carboniferous forms.

Jenny set about describing the new material, publishing a first account in the journal *Palaeontology* (3), but she also sought out Nicholson, borrowed his field notebooks, and set about planning an expedition to Greenland. A funding application to NERC was rejected on the strength of an anonymous review which asserted that such an expedition “was unlikely
to contribute significantly to our understanding of the origin of tetrapods” – a misjudgement of historic proportions, as the future would show. Jenny, furious but undeterred, managed to secure alternative funding from sources in Cambridge and Denmark.

On a June morning in 1987 she left Cambridge on a northbound train in the company of her husband Rob and PhD student Per Ahlberg. In Glasgow they met with the two other expedition members, Svend Bendix-Almgreen and Birger Jørgensen from Copenhagen University, before flying to Reykjavik in Iceland. A series of ever smaller and more rugged aircraft carried them towards their goal: a domestic airliner to Akureyri on the north coast, then a chartered six-seater plane across the vast expanse of the North Atlantic to the mining-settlement airstrip at Mestersvig on the east coast of Greenland; onwards by de Havilland Twin Otter to the tent encampment at Stordal, base camp of that year’s field programme of the Greenland Geological Survey; and finally over the mountains in a tiny bubble-nosed red helicopter that deposited them at their first field site on Gauss Peninsula, at the foot of Mount Stensiö, overlooking Kaiser Franz Josephs Fjord (figure 3).

So began six summer weeks of extraordinary discoveries. At first the task ahead seemed daunting. The fossil-bearing strata on Gauss Peninsula comprise two units, the Aina Dal and
Britta Dal Formations, separated by the barren Wiman’s Bjerg Formation. The expedition set up camp on the only level ground, which was a wide ‘bench’ formed by the top of the Aina Dal Formation. To the south-west, this bench ended in a sea cliff and scree slope tumbling down to the fiord a hundred metres below; to the north-east, the ground leaped up and up, turning into the scree slopes and sandstone ledges of the kilometre-high flank of Mount Stensiö. Somewhere up there, towards the top of the Britta Dal Formation, at a recorded height of more than 800 metres, was Nicholson’s locality.

After a couple of false starts, when the team struggled to find a safe route up the treacherous slopes, they finally gained the south ridge of the mountain at an altitude of about 700 metres and proceeded to work upwards, following the line that Nicholson described in his notebook. It was Jenny herself who found the first Acanthostega fossil, a piece of skull roof bearing the unmistakable curved spine that gives the genus its name. The team realized that the scree on which they were walking was covered in Acanthostega fragments, which must be weathering out of the bedrock higher up. Following the trail of fossils up slope, they discovered a small grey sandstone ridge with a whitish-purple Acanthostega jaw exposed on the surface; here indeed was Nicholson’s locality, as would be proved conclusively back in Cambridge when some of the blocks were found to fit against Nicholson’s specimens.

Excavating the Acanthostega locality was gruelling work. Each excavation session, when blocks would be prised out of the sandstone ridge with hammers and chisels, was bookended by a four-hour climb from the camp and an even more exhausting descent with rucksacks full of rocks. The constant daylight far above the Arctic Circle allowed for flexible working arrangements, with the team sometimes trudging back to camp in the small hours of the morning, but it was still too much to attempt on a daily basis. The team thus decided to spend every other day exploring the more easily accessible Aina Dal formation in the sea-cliff below the camp. This decision proved serendipitous, as it led to the discovery of a second rich tetrapod locality with a different faunal composition, dominated by the other Greenland tetrapod, Ichthyostega. The discoveries from this site included a complete hindlimb of Ichthyostega, split into two pieces. The first piece to be found showed two toes in a v-shaped formation, suggesting either a Churchillian ‘victory’ sign or something much ruder; Jenny, delighted, held it aloft and proclaimed it a message to the hostile NERC reviewer.

After a few weeks, the expedition split into two, with Jenny, Rob Clack and Per Ahlberg moving across the fiord to the classic Ichthyostega localities of Mount Celsius on Ymer Island while the Danes went on to explore Permian localities elsewhere. On Mount Celsius, pickings were leaner, but nevertheless some important additional specimens were collected before it was time to pack up and go home. The 1987 expedition had yielded by far the largest single-season haul of Devonian tetrapod material ever collected from Greenland. Svend Bendix-Almgreen, himself a veteran of the 1950s expeditions led by Jarvik, could only shake his head with a smile and mutter “This is grotesque . . . just grotesque!” as he surveyed the row of packing boxes.

**THE Acanthostega PROJECT: EIGHT LITTLE PIGGIES**

Back in Cambridge, Jenny set about raising funding to describe the Greenland material, and this time NERC came good, providing sufficient support for a full-time preparator and a postdoc. Jenny offered the postdoctoral position to Michael Coates, one of Alec Panchen’s
last two PhD students. As preparator she employed an archaeologist, the extraordinarily skillful Sarah Finney (now Sarah Wallace-Johnson). Coates had previously worked mainly on Carboniferous ray-finned fishes; their combined expertise areas were to prove ideally suited to making sense of Devonian tetrapod anatomy.

At this time, the only way to study such fossil material was to extract it physically from the rock. If the rock was limestone, this could be done with dilute acetic acid, but the hard, silty sandstone of East Greenland proved completely insoluble and had to be removed laboriously from the bones, chip by tiny chip, using modified dentists’ drills that worked like miniature jackhammers. An alternative approach, favoured by Jarvik and colleagues in Stockholm (though never used on their Ichthyostega material), was to carry out a method termed serial grinding, analogous to microtome sectioning of biological specimens and equally destructive. The process involved grinding away the specimen, one 0.25 mm thick layer at a time, and using enlarged drawings of the ground surfaces as templates for wax sheets that could be built up into a physical tomographic model of the fossil. Although informative, this technique was extremely time-consuming and resulted in the complete destruction of the fossil, so Jenny (like almost all researchers in the English-speaking world) chose not to use it. She did however purchase a diamond-wire saw, nicknamed ‘Hubble’ by Coates because of its repeated breakdowns. This became a key piece of equipment for the team; it could make very thin and precisely positioned cuts, allowing articulated remains to be cut up into ‘jigsaws’ of manageable units for preparation, with little data loss (figure 2).

Much later, during the first two decades of the 21st century, the development of powerful techniques for x-ray tomography – initially conventional CT (Computed Tomography) (13) and later synchrotron microtomography – would open up startling new possibilities for studying the Greenland tetrapod material. Tomographic investigation of limb bones from the Acanthostega locality would suggest that the animals are juveniles (22), while an isolated tiny lower jaw from the same site, which was noticed already in 1987 but could not be prepared, would prove to represent a new genus Brittagnathus (26). However, at the end of the 1980s all this lay in the future, as a tangle of semi-complete Acanthostega skeletons slowly began to emerge from the encasing rock (figure 2).

The defining discovery of the Acanthostega project came quite early on, during the preparation of a near-complete individual known as ‘Boris’. (Jenny was in the habit of giving nicknames to her specimens, not just for whimsical reasons but because it provided an informal nomenclature for fragments with different field numbers that proved to belong to the same individual. A near-perfect Acanthostega skull was called ‘Grace’ because its flat-topped head recalled the haircut sported at the time by singer and actress Grace Jones; ‘Boris’ combined a topical reference to Russian President Boris Yeltsin with a pun on ‘boreal’.) Until that time, all known living and fossil tetrapods had either five toes on each foot, or fewer; it had been universally assumed that a five-toed foot was ancestral for tetrapods, and much energy had been expended over the course of almost a century in arguing exactly how this pattern related to the various kinds of fin skeletons found in different groups of lobe-finned fishes. However, what emerged during the preparation of ‘Boris’ put all such speculation to shame: a beautifully preserved forelimb with no fewer than eight digits arranged in a perfect fan shape (figure 2). Not long afterwards, preparation of the Ichthyostega hindlimb that Jenny had brandished so defiantly on a Greenland scree slope revealed that this foot had seven digits.
Mike Coates and Jenny published the two discoveries together in a paper in *Nature* (4) that caused a huge stir, not only for the novelty of the conclusions but because of the way it demonstrated that data from palaeontology – at that time a research area that was seen by many biologists as a pedestrian descriptive science that had little to contribute to our understanding of evolution – could overturn a well-established interpretation based on living organisms.

At a stroke, this paper catapulted not only the authors but their entire research area to star status. *Acanthostega* became a palaeontological poster child that started appearing in all kinds of popular contexts. The ultimate accolade came when the immensely popular and influential palaeontologist-author Stephen Jay Gould featured the feet of *Acanthostega* in his sixth volume of collected essays, and named the entire volume *Eight little piggies* in their honour (Gould 1993). His reference was the classic nursery rhyme, ‘This Little Piggy’, often recited to young children as they count their (usually five) toes. Jenny, herself a fan of Gould’s writings, was immensely proud of this recognition.

Over the next decade, the work by Jenny and Mike Coates step by step documented the entire preserved morphology of *Acanthostega*, turning it into by far the best understood of the Devonian tetrapods. It proved to possess a remarkable mélange of tetrapod-like and fish-like characteristics, obvious pieces of tetrapod anatomy such as limbs with digits and a sacrum linking the pelvis to the backbone jostling with leftover pieces of the fish body plan such as a leaf-shaped tail fin and a full set of gill arches in the head. This led them to develop a new framing scenario for the fish-tetrapod transition, where tetrapod characteristics were seen as having evolved initially in wholly aquatic animals to facilitate behaviours such as underwater walking, especially in spatially complex environments such as flooded forests, before later becoming coopted for terrestrial life (7, 11). This scenario quickly superseded previous models such as the “drying pond scenario”, which had posited that tetrapod morphology evolved to allow overland travel in times of drought, enabling the animals to escape from ephemeral water bodies. The ‘underwater walking scenario’ has dominated research on the origin of tetrapods during the first two decades of the 21st century, although is now starting to be challenged by other perspectives that emphasize the adaptations for terrestrial locomotion in these animals.

In addition to the flood of new information, the *Acanthostega* project also heralded a dramatic and decisive break with past research on Devonian tetrapods. Where Jarvik’s work on *Ichthyostega* had been glacially slow, with no major publications between 1952 and 1980, Clack and Coates published their work promptly in a series of mostly short- to medium-length papers. They also maintained a fundamental openness towards the wider research community. Although none of the early descriptive papers on *Acanthostega* involved external collaborators, they were not secretive about their work; they were happy to talk about it at conferences and show the material to other researchers, including the elderly Jarvik, who took a friendly and somewhat paternalistic interest in the project even though he disparaged their short papers as ‘Penny Dreadfuls’.

This approach not only raised the awareness of Devonian tetrapod research in the palaeontological community and beyond, but also allowed the research field to move forward much faster than before because information was shared quickly and freely. A key example can be seen in the interaction with Jenny’s former PhD student Per Ahlberg. Shortly after leaving Cambridge for a postdoctoral position in Oxford, Ahlberg discovered previously unrecognized Devonian tetrapod material from Scotland and Latvia, which would later be described under the names *Elginerpeton* and *Ventastega*. These forms were both far more fragmentary than
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Acanthostega, making them difficult to interpret, especially as little was known at the time about the skull, jaws and limb girdles of Devonian tetrapods. Indeed, there was a lively debate about whether such tetrapods could even be distinguished from contemporary lobe-finned fishes if the fossil material lacked articulated limbs.

By giving Ahlberg unrestricted access to the unpublished Acanthostega material, Jenny created a comparative context that allowed the Elginerpeton and Ventastega material to be correctly interpreted, even as these tetrapods in turn contextualized Acanthostega. Out of this exchange developed a shared understanding of the numerous but subtle differences between Devonian tetrapod and lobe-finned fish anatomy. Similar interactions with other researchers led to the identification of the first Devonian tetrapod from North America (Daeschler et al. 1994) and to the collaborative redescription of the Russian genus Tulerpeton (5) (Lebedev & Coates 1995). Thus, within a few years, the understanding of Devonian tetrapod anatomy advanced from rudimentary beginnings to a point where even very fragmentary new remains could be readily identified. The following decades saw an explosion of new Devonian tetrapod discoveries around the globe, almost all based on fragmentary material that would previously have gone unrecognized.

In 1996 Jarvik published his last paper, a monographic atlas of Ichthyostega, which documented the material in extensive detail but still left many questions unanswered. Notably, the reconstructed ear region of the skull – of great interest to Jenny – bore no resemblance to those of other early tetrapods. Jarvik had in fact allowed Jenny to examine the material a few years earlier, and she had started to form her own ideas about its interpretation, but the unwritten rules of conduct in the palaeontological community prevented her from publishing these thoughts. However, soon afterwards, two events opened the door to a comprehensive re-evaluation of Ichthyostega. As part of a large collaborative field programme with National Geographic support, Jenny led a second expedition to Greenland in the summer of 1998, fielding an all-female team that became known as the ‘Girls in Greenland’ (Ruta et al. 2019). The material they collected included a partial skull of Ichthyostega with a complete ear region on one side, untouched by mechanical preparation (unlike Jarvik’s material) and suitable for investigation with the novel Computed Tomography technique.

Around the same time, Jarvik finally relinquished his material, which had been held on long-term loan in Stockholm since the time of collection in the 1930s–50s, but which was now returned to the Geological Museum of Copenhagen University. This at last made it freely available to other scholars, and Jenny (this time in collaboration with Ahlberg) wasted no time borrowing some of the key specimens. During the next few years they were able to show that Ichthyostega had a specialized but now-comprehensible middle ear (13) and a highly distinctive body skeleton with locomotory adaptations hinting at terrestriality (14, 17, 19). A new tetrapod, Ymeria, was also identified in material collected by Jarvik and the ‘Girls in Greenland’ Expedition (16).

Back to the Carboniferous I: the east Kirkton Project

Although Jenny’s name will always be associated with her momentous discoveries in the Devonian of Greenland, it is fair to say that this was not the research area closest to her heart. She remained loyal to her first scientific love, the mysterious and diverse tetrapods of the Carboniferous that she had first encountered in the Panchen Lab. Central to this area
of interest was the tantalizing hidden history of tetrapods during ‘Romer’s Gap’, the first 20 million years of the Carboniferous, from which hardly any tetrapod fossils were known.

The gap had first been recognized by American palaeontologist A. S. Romer (1894–1973; F.M.R.S. 1969) in 1956, but it was Coates and Clack (7) who coined the name ‘Romer’s Gap’ and drew attention to this strange lacuna in the tetrapod record. The tetrapods after the Gap are very different from Devonian forms like *Ichthyostega* and *Acanthostega*, more advanced and more diverse; clearly, important things had been happening during the intervening years, but researchers could only speculate about the details, especially as the immediate post-gap fossil record was also quite meagre. There was also a good deal of speculation about why the gap existed, with factors such as an end-Devonian mass extinction and a supposed subsequent drop in global oxygen levels being invoked; all of it proceeded from an assumption that the gap was a real biological event, but Jenny herself was not entirely convinced, and she nurtured an ambition to explore the sedimentary strata of the Early Carboniferous in search of undiscovered tetrapods.

The discovery of the East Kirkton fossil assemblage by Stan Wood, which revealed a high-diversity terrestrial tetrapod fauna from the end of Romer’s Gap, promised at last to shine a spotlight on the immediate aftermath of this obscure period in tetrapod evolution. Jenny, who developed a close working relationship with Wood and bought numerous specimens from him for the University Museum of Zoology, Cambridge, responded enthusiastically and was one of the founding members in 1985 of the collaborative East Kirkton Project, which addressed all aspects of this fossil biota and its environment. She continued to fly the flag for the locality and its fossils to the end of her life.

Thus, even as the Devonian work was propelling her to fame, Jenny was methodically investigating the East Kirkton tetrapod fauna, attending the concluding Project Conference at the Royal Society of Edinburgh in 1992 and presenting her description of one of the tetrapods, *Silvanerpeton* (figure 2), in the conference volume (6). Other descriptions followed. One of these, for *Eucritta melanolimnetes* (9), showed Jenny in one of her occasional playful moods; the binomial of this innocuous little tetrapod translates (if allowance is made for the dog-Latin of the generic name) as ‘The Creature from the Black Lagoon’, referencing an origin-of-tetrapods themed horror movie from 1954.

In addition to the East Kirkton tetrapods, these years saw Jenny addressing herself to describing or redescribing other Carboniferous forms such the small reptile-like *Casineria* and the much larger *Crassigyrinus* – a bizarre aquatic predator, like a tetrapod version of a moray eel, with tiny legs. She ventured into novel areas such as the fossil tetrapod trackway record (8) and the evolutionary developmental biology of the tetrapod skull (10), which she would never explore fully but which would prove to be of great significance in the later development of the research field. Jenny also began working on a textbook on the origin of tetrapods, the aptly named *Gaining ground* (11) (second edition 2012), which became the standard text in the field and brought her work to a wider audience. At this point, once again, a serendipitous discovery intervened to open up a new direction for her research.

**BACK TO THE CARBONIFEROUS II: CLOSING ROMER’S GAP**

One of Jenny’s PhD students during the late 1990s was Jonathan Jeffery, who studied rhizodonts, a group of large to gigantic lobe-finned fishes known chiefly from Carboniferous
strata. Rhizodonts have a particularly impressive fossil record from the British Isles, and, as is usual with this kind of research, Jeffery borrowed many specimens from museums across the country. One of these was GLAHMS 100815 from the Hunterian Museum in Glasgow, collected in 1971 from a geological unit known as the Ballagan Formation, which lies at the base of the Carboniferous and corresponds to a substantial part of Romer’s Gap. Although well known to be fossiliferous, the Ballagan Formation had never yielded tetrapods. However, when Jeffery saw the supposed ‘rhizodont’ he immediately became suspicious and brought the large limestone block back to Cambridge, where Jenny confirmed that it was something extraordinary: an articulated, near-complete tetrapod skeleton. The fossil was approximately 15 million years older than the East Kirkton tetrapods, placing it right in the middle of Romer’s Gap. No articulated tetrapod material of any kind had ever been found from this time period, anywhere in the world.

The immediate priority was the preparation and description of the specimen, which was given the name Pederpes finneyae in honour of Jenny’s longstanding preparator Sarah Finney (12, 15). Pederpes proved to be a slightly more advanced tetrapod than Acanthostega, similar in some respects to the later Carboniferous genus Whatcheeria from the United States and possibly related to it. More importantly, it flagged the Ballagan Formation as a potential source of articulated tetrapod material. By contrast, the only other reasonably productive Romer’s Gap tetrapod locality, Horton Bluff on the east coast of Canada, had yielded only isolated – and thus much less informative – bones. Jenny visited the Pederpes locality near Dumbarton with her husband Rob but found nothing apart from a single lungfish rib.

There things might have rested, had it not been for Stan Wood and Tim Smithson. Smithson, another dedicated Early Carboniferous enthusiast, had spent more than 20 years hunting for tetrapods in the small Ballagan Formation outcrops along the rivers and streams of the Tweed Basin, as well as the coastal cliffs at Burnmouth, just north of Berwick-upon-Tweed. While the results were not overwhelming, they were certainly promising, and in 2006 he decided to invite Wood to begin exploring these localities with him. Success came in 2008, when, at Willie’s Hole on the Whiteadder Water, Wood found three richly productive fossil horizons. Further productive horizons were discovered by Smithson and Wood at Burnmouth. Crucially, these localities were yielding not just isolated bones but a diversity of articulated tetrapods.

Smithson and Wood presented their first findings in 2009, and in 2010 Jenny joined the project. She saw the potential for a multidisciplinary team-based approach to investigating, not just the tetrapods and other vertebrates of the Ballagan Formation, but the entire biota and its environmental setting. To that end she assembled a team comprising experts in fossil vertebrates, land plant spores, sedimentology and stratigraphy, and put together a large NERC grant proposal titled The Mid-Palaeozoic biotic crisis: setting the trajectory of tetrapod evolution. This application was successful, helped in part by the timely publication of the first major paper on new Ballagan Formation tetrapods in PNAS (18), and in August 2012 the TW:eed Project – Tetrapod World: early evolution and diversification – was launched.

Over the next four years, with good humour, tact and quiet authority, through a series of biannual team meetings, Jenny ensured that the scientific objectives of the multimillion-pound project were far exceeded. Jenny was lead author on three papers (21, 23, 25) and co-author on a further nine. The full significance of these results will take many years to become apparent, as they impact future research on early tetrapod evolution, but Romer’s Gap is beginning to look like a sampling artefact.
The Ballagan Formation and Horton Bluff together reveal an Early Carboniferous world teeming with tetrapods and other vertebrates, in the immediate aftermath of the supposedly devastating end-Devonian mass extinction. For the Ballagan Formation it has proved possible to reconstruct a map of the Early Carboniferous landscape of southern Scotland and Northumberland (then part of the equatorial landmass of Laurussia), complete with rivers, forests and lakes; a true birds-eye view of a lost world. Sadly, the beginning of this triumphantly successful project coincided with the death of Stan Wood who, after playing a major part in the planning phase, fell ill and passed away in 2012. Jenny was one of the editors of a celebratory volume in his honour, published in *Earth and Environmental Science Transactions of The Royal Society of Edinburgh* (24).

**RECOGNITION**

By the late 1990s, even as the results from the Greenland and East Kirkton projects kept coming and her scientific star was firmly in the ascendant, Jenny had begun to grow restive about her career development and professional position. She had originally been appointed as Assistant Curator at the University Museum of Zoology; although she had been promoted to Senior Assistant Curator in 1995 (and elected a Fellow of Darwin College, Cambridge in 1997), this was still an anomalous position for a successful researcher, without tenure and with no obvious career path ahead. For advice, Jenny turned to her old mentor Alec Panchen, who suggested that she submit her collected published work to the University of Cambridge for consideration for a Doctor of Science degree. This proved to be a successful gambit. She was awarded the ScD in 2000, and shortly afterwards she was promoted, first to Reader (2000) – which finally gave her tenure – and then to Professor (2006).

Other honours followed. In 2008 she was awarded the Daniel Giraud Elliot Medal of the National Academy of Sciences of the USA, the first woman to receive that honour. She was also awarded the T. Neville George Medal of the Geological Society of Glasgow in 2013, and the Lapworth Medal of the Palaeontological Association – the highest award of that society – in 2018. She received honorary Doctor of Science degrees from the University of Chicago (2013) and the University of Leicester (2014), was elected a Fellow of the Royal Society (2009), and was made a Foreign Member of the American Academy of Arts and Sciences (2009) and the Royal Swedish Academy of Sciences (2014). In April 2012, she was the subject of one of the six one-hour episodes of the BBC4 television series *Beautiful Minds*, which showcased the lifetime achievements and ideas of some of Britain’s greatest contemporary scientific thinkers (the others being Jocelyn Bell Burnell, James Lovelock, Tim Hunt, Andre Geim and Richard Dawkins). In 2015, Jenny retired, but she continued working actively at the Cambridge University Museum of Zoology.

In 2015, not long after retirement, Jenny began to experience the first symptoms of the endometrial cancer that would eventually end her life. Her friends and colleagues had time to organize a Festschrift Symposium in her honour at the University of Cambridge in December 2017, which she and Rob attended with evident enjoyment. The resulting volume, which not surprisingly focuses heavily on early tetrapods but ranges from Devonian fishes to developmental biology and macroevolution, was published in *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* in 2019 (Ruta et al. 2019). Mindful of the limited available time and driven to complete as much of her research as possible,
Jenny continued working energetically until her final days. Several papers were in press or nearing completion at the time of her death (26). As a final honour, in 2020, she was posthumously awarded the Romer-Simpson Medal – the lifetime achievement award of the Society of Vertebrate Paleontology.

A LIFE IN SCIENCE

Jenny will be remembered above all for having transformed the study of the origin of tetrapods from a small niche subject, almost unknown outside the immediate circle of active researchers, to a high-profile discipline with a broad popular audience. Of course, she was not the sole driving force behind this transformation, but the combination of her personal qualities and the strategic decisions she took in launching the Greenland, East Kirkton and TW:eed projects enabled her to achieve a lifetime impact equalled by few other scientists.

She did so almost entirely through her research: ambitious for scientific recognition, but not for authority, she consistently eschewed organizational leadership roles. Rather than shape things through organizational change, she sought to transform the discipline through research and publications. She also supervised a number of PhD and M.Phil. students, of whom Per Ahlberg (Uppsala University), Paul Upchurch (University College London), Michael Lee (Flinders University) and Matt Friedman (University of Michigan) have gone on to found research groups of their own.

Given the importance of the origin of tetrapods as an evolutionary event, and the attendant theoretical questions that have swirled around it for decades – different palaeobiological scenarios, intractable homology problems, the question of tetrapod mono- or diphyly, and so on – it is interesting to note that Jenny was not overly invested in the theoretical framework. She was not really enthusiastic about phylogenetics or taxonomy, although she was a competent practitioner of both, and she did not enter the subject with a view to proving or disproving some grand overarching theory of the origin of tetrapods. It was the fossils themselves that attracted her, the possibility of understanding them as once-living organisms in a living world. They also appealed to her aesthetic sense. Jenny was a skilled silversmith and frequently used vertebrate fossils as inspiration for her jewellery; her first major discovery, the stapes of *Pholiderpeton*, reappeared as a pair of silver earrings that she often wore at conferences (see this Memoir’s frontispiece).

Although she will be remembered by the wider community as a researcher, Jenny was also a dedicated curator, working constantly to enhance the collections of the Cambridge University Museum of Zoology. She purchased numerous important fossils, especially from Stan Wood, and oversaw a complete rearrangement of the lower vertebrate displays. Here too, her aesthetic side found expression, both in the layout and in the form of some illustrative paintings that she incorporated into the displays. There were also some wilder flights of fancy. The first author has happy memories of a playschool-like day spent turning the base of a cast of the Permian amniote *Limnoscelis* into a mock riverbed using copious amounts of red pigment, sand, pebbles and resin.

The transformation of the subject during the four decades of Jenny’s scientific career was not just a matter of astonishing discoveries that advanced our knowledge and attracted public attention. It also involved a radical change in the way the science was done. Jenny began her research in the era of competing ‘schools’, characterized by incompatible
theoretical frameworks (especially between the Stockholm School and the Anglo-American research community), single author publications, and a good deal of secrecy. By the time she retired, this had been replaced by a global research community united by a shared theoretical framework, spawning collaborative networks in response to the need for particular combinations of expertise.

Jenny was an early adopter of the new approach. For example, she visited Oleg Lebedev in Moscow at the earliest opportunity after the fall of the Iron Curtain, in the summer of 1990, and initiated a collaboration that yielded a two-paper redescription of the Russian Devonian tetrapod *Tulerpeton* (5) (Lebedev & Coates 1995). This ‘collaborative revolution’, which in fact affected the entire field of vertebrate palaeontology, clearly suited Jenny’s personality. Although justly proud of her achievements and confident in her argumentation, she was fundamentally modest, never inclined to pull rank or use her standing to browbeat anyone. She was not secretive about her research, and she projected a quiet generosity of spirit that did not begrudge the successes of others. As a result, she was universally respected in the research community and had many loyal friends, even though people who did not know her well could sometimes mistake her slight shyness for standoffishness.

For us, who were her friends and colleagues, Jenny leaves an enduring memory as a positive and inspiring influence. Working indefatigably until the end, still sharing her thoughts and discussing ideas over email just a few days before she died, Jenny Clack made the field of early tetrapod research a happier place. She leaves a void that will not be easy to fill.

**Honours, degrees and awards**

*Degrees*

1970 BSc Zoology, Newcastle University
1984 PhD, Newcastle University
1989 MA, University of Cambridge
2000 ScD, University of Cambridge

*Fellowships*

1984 Linnean Society of London
2009 Royal Society

*Honorary Degrees*

2013 DSc, University of Chicago
2014 DSc, University of Leicester

*Other Distinctions*

2008 Daniel Giraud Elliot Medal, National Academy of Sciences, USA
2009 Foreign Honorary Member of American Academy of Arts and Sciences
2013 T. Neville George Medal, Geological Society of Glasgow
2014 Foreign Member of Royal Swedish Academy of Sciences
2015 Lapworth Medal, Palaeontological Association
2020 Romer-Simpson Medal, Society of Vertebrate Paleontology
Appointments

1971 Display Technician, City of Birmingham Museum and Art Gallery
1974 Education Officer, City of Birmingham Museum and Art Gallery
1981 Assistant Curator, University Museum of Zoology Cambridge
1995 Senior Assistant Curator, University Museum of Zoology Cambridge
1997 Fellow of Darwin College, Cambridge
2000 Reader in Vertebrate Palaeontology, University of Cambridge
2005 Curator of Vertebrate Palaeontology, University Museum of Zoology Cambridge
2006 Professor and Curator of Vertebrate Palaeontology, University of Cambridge
2010 Research Associate, National Museums Scotland
2013 Research Associate, Natural History Museum, London
2015 Emeritus Professor and Curator of Vertebrate Palaeontology, University of Cambridge
2015 Emeritus Fellow of Darwin College, Cambridge

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The portrait photograph is by Chris Green, and is used with permission from the Department of Biochemistry, University of Cambridge.

Author profiles

Per Erik Ahlberg FLS

Born in Stockholm, Sweden, Per Ahlberg moved to Britain in his teens and graduated with a BA in Zoology from University of Cambridge in 1985. Ever since childhood he had dreamt of becoming a palaeontologist. During his undergraduate years he got to know Jenny Clack, who offered him the opportunity to try his hand at an undergraduate research project describing a Devonian fossil fish from the collections of the University Museum of Zoology. This led directly on to a PhD under Jenny’s supervision (1985-1989), continuing to work on the same poorly known group of lobe-finned fishes (the so-called porolepiforms) and attempting to put them in an evolutionary and phylogenetic context. As part of this project, Jenny invited Per to participate in the 1987 expedition to Greenland. At the end of his PhD, having in the meantime made the acquaintance of Alec Panchen, Tim Smithson, Stan Wood, Mike Coates and other members of Jenny’s circle, Per moved to University of Oxford to take up a postdoctoral position under the mentorship of Tom Kemp (1989-1994). During this time, his experience with Devonian tetrapod material from the Greenland expedition enabled him to identify the first
Devonian tetrapod fossils from Britain, in a 19th century collection from a Scottish locality. In 1994 he was appointed as a Researcher in the Department of Palaeontology at the Natural History Museum in London, and remained there until 2003 when he returned to Sweden to take up a newly created Professorship in Evolutionary Organismal Biology at Uppsala University. Per’s research touches on a range of areas from the origin of jawed vertebrates to the early evolution of hominins and the relationship between morphological evolution and developmental biology, but the fish-tetrapod transition has remained one of his major themes and he continued to work intermittently with Jenny Clack until the final weeks of her life. In 2012, he was elected to the Royal Swedish Academy of Sciences, and in 2017 to Academia Europea.

Tim Smithson graduated with a BSc in Zoology from Newcastle University in 1975. He stayed on to undertake a PhD in vertebrate palaeontology with Alec Panchen, defending his thesis in 1983. Tim first met Jenny Clack during her study leave in Panchen’s lab in 1977 and they overlapped as research students for a year between 1978 and 1979. In 1979 Tim joined Bob Carroll’s lab at McGill University and later returned to Newcastle University in 1982 as Sir James Knott Fellow. In 1985 he changed direction to pursue a career in further education. He was appointed Lecturer in Biology at Northumberland College in 1986 and Senior Lecturer at Cambridge Regional College in 1989. In 1995 he was promoted to Head of School before moving to Aylesbury College in 2000 as Vice Principal. In 2006 he joined the Learning and Skills Council (LSC) first as Director for Wiltshire and then in 2007 as Director for Gloucestershire. Reorganization of the LSC saw him relocate to offices in Bristol and a regional commissioning role for post-16 education and training. He continued to pursue his academic interests, largely through fieldwork in the Scottish Borders conducted over a period of 35 years. After some success at Coldstream, he began exploring the early Carboniferous rocks exposed on the coast at Burnmouth, north of Berwick on Tweed, and discovered a number of fossil bearing beds. He was joined in 2007 by his old friend Stan Wood and together they built up a sizeable collection of early Carboniferous tetrapods. Tim encouraged Stan to explore the inland outcrops in the banks of Whiteadder Water, a tributary of the River Tweed, and in spring 2008 he was rewarded with spectacular success at Willie’s Hole. Their discoveries formed the basis of the TW:eed Project led by Jenny. Tim joined her in Cambridge as a Research Associate in 2012 and they worked together describing the vertebrate fauna until his retirement in 2017.

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