Early Vertebrate Evolution

Fossils, function and phylogeny: Papers on early vertebrate evolution in honour of Professor Jennifer A. Clack – Introduction

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This special issue of the *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* (*EESTRSE*) celebrates the career and scientific achievements of Professor Jennifer (Jenny) Alice Clack FRS, FLS, Professor Emeritus and Curator of Vertebrate Palaeontology at the University Museum of Zoology, Cambridge (UMZC). In recognition of Jenny's professional services and outstanding accomplishments in vertebrate palaeontology, and to mark her official retirement in 2015, we have assembled 21 original research papers from 55 international scientists. The breadth of topics reflects Jenny's wide-ranging interests. Beside vertebrate palaeontology, these include (but are not limited to) comparative anatomy, development, phylogeny, macroevolution, biomechanics, palaeoecology, palaeobiogeography, geology, and stratigraphy. The contributors to this volume include many of Jenny's colleagues, collaborators, former students, and long-time friends. We are especially delighted to see the scientific endeavours of several young scientists at early stages of their careers alongside those of established professionals – a solid testament to Jenny's scholarly influence.

The planning of this volume started in the late spring of 2017, when we submitted a formal proposal to the Editorial Board of *EESTRSE*. Key contributions to the study of early vertebrates, many authored by Jenny herself, have featured in the pages of *EESTRSE*. Two and a half decades ago, a seminal volume on the Scottish fossil site of East Kirkton, published in what was then known as the *Transactions of the Royal Society of Edinburgh: Earth Sciences*, opened a new era in the study of Palaeozoic vertebrates, particularly Carboniferous tetrapods. As recently as the summer of 2018, *EESTRSE* issued a special volume dedicated to the life and work of the late Stan Wood, whose painstaking fossil-collecting efforts greatly expanded our knowledge of the Carboniferous world. For these reasons, *EESTRSE* appeared to us to represent an excellent venue for a *Festschrift* in honour of Jenny, and an appropriate vehicle for consolidating the UK's long-standing tradition of research on early vertebrates.

Alongside the planning of the volume, we also organised a one-day conference in Jenny's honour. This was held at the University of Cambridge on 13th December 2017 (Dunne & Armfield 2018) and proved to be immensely successful. It was hosted by the Department of Zoology and the University Museum of Zoology and received generous sponsorship from The Linnean Society, The Palaeontological Association, and Dunedin Academic Press. Many of the volume contributors took part in the conference and we thank all our colleagues for their prompt and enthusiastic responses to our invitation to contribute research papers, for attending to manuscript revisions in a timely fashion, and for providing intellectually stimulating outputs. We acknowledge the demanding task of all our referees, who acted with courtesy and professionalism in reviewing the original manuscripts and, often, their revised versions. Special thanks go to some of our contributors for their generous offer to referee colleagues' manuscripts when we experienced difficulties with reviewer selection. We also thank Rob Clack and Sarah Wallace-Johnson for their very helpful comments, corrections, and additions to the biographical section, and for providing many of the photographs we have used to illustrate it. We are grateful to the Royal Society of Edinburgh for making this volume possible, and to our Editor-in-Chief, Stig Walsh, for coordinating various stages of its production. We would like to take this opportunity to thank Vicki Hammond, former Journals and Archive Officer at the Royal Society of Edinburgh, for providing unwavering support, strong encouragement, and prompt technical assistance with countless aspects of manuscript handling, and for attending to our numerous queries with competence and kindness. Vicki has been a driving force behind *EESTRSE* for many years, until her retirement in 2018, and greatly facilitated our editorial efforts during the initial stages of this *Festschrift* production. After Vicki's retirement, we were delighted to receive equally strong support and invaluable help from Susie Bloor, Technical Editor at Cambridge University Press, who guided us through all final stages of volume editing, ensuring a steady and fast delivery of the revised manuscripts to her production team. Last but not least, our thanks go to Amy Woolf (Cambridge University Press) and Sharon Nickels (Sunrise Setting Ltd.) for their painstaking work with last-minute queries concerning proof corrections, typographic and iconographic glitches, and paper layouts.

1. Volume synopsis

Although early tetrapods feature prominently in Jenny's work, several other vertebrate groups have captured her interest throughout her career. Five palaeoichthyological papers – two on actinopterygians and three on sarcopterygians – discuss various aspects of osteichthyan biology. **Coates and Tietjen** describe a new genus of stem-group ray-finned fish and examine the structural and functional variety of pectoral fins in early members of this clade. **Friedman *et al.*** present

 doi:10.1017/S1755691019000057

evidence for durophagy in their study of *Eurynotus crenatus* and discuss the diversification of feeding ecologies in ray-finned fish following the end-Devonian mass extinction. **Smithson *et al.*** address dipnoan diversity in the latest early Carboniferous through a re-examination of historically important fossil material collected by Ramsay Traquair and present new data on the ontogeny of lungfish tooth plates. **Lebedev and Clément** introduce us to new tetrapodomorph taxa from the Middle–Late Devonian of northwestern Russia. **Kamska *et al.*** discuss the morphology and ontogeny of the humerus of the large Devonian tetrapodomorph *Hyneria lindae* and present palaeohistological evidence in support of the slow skeletal development, large genome size, and possible neotenic nature of this near-tetrapod relative.

Evolutionary developmental biology is an ever-expanding and rapidly changing field that Jenny has embraced with enthusiasm since its inception, through her work on vertebrates' paired appendages and ears. Aptly, two papers focus on these two anatomical regions in light of embryological data from two new model organisms. **Dickson and Pierce** give novel insights into the origin and evolution of paired limbs through their analysis of pectoral fin development and musculoskeletal anatomy in anglerfish. **Pfaff *et al.*** produce a detailed account of the ontogeny of the ear region in the skate *Leucoraja erinacea* and discuss the relevance of cartilaginous fish in comparative evolutionary and developmental studies of vertebrate neuroanatomy.

Eight papers are devoted to early tetrapods, including two general and six taxonomic contributions. **Ahlberg** presents an in-depth review of the origin and diversification of tetrapods, summarises research milestones in this area, and offers new evidence in support of alternative scenarios to the aquatic origin of limbed vertebrates. **Long *et al.*** review the body of evidence for the origin and diversification of tetrapod faunas in Gondwana. **Herbst and Hutchinson** use advanced methods in fossil image analysis to cast a fresh look at the osteology of one of the most problematic of all Carboniferous stem-group tetrapods, the aquatic moray eel-like predator *Crassigyrinus scoticus*, and describe important new details of its axial and appendicular skeleton. **Bolt and Lombard** investigate the complex morphology of the palate and braincase of *Whatcheeria deltae* from the Mississippian of North America, a key stem-group tetrapod with a mosaic of primitive and derived features. **Andrew Milner** discusses two trematopid temnospondyl amphibians from the Pennsylvanian of the Czech Republic, describes a new taxon, and reviews the morphology and ontogeny of trematopids alongside a detailed account of character distribution within the family. **Klembara and Mikudíková** offer a new account of the cranial anatomy of the Lower Permian discosauriscid seymouriamorph *Discosauriscus pulcherrimus* from the Czech Republic and detail major ontogenetic changes in its skull roof, palate, and braincase. Two additional tetrapod contributions concern representatives of the problematic 'lepospondyls', a collection of early tetrapod groups long suspected to form a polyphyletic assemblage rather than a distinct clade. **Angela Milner** gives us a captivating narrative of the history of discovery and research on the Pennsylvanian genus *Keraterpeton*, a representative of a group of 'lepospondyls' known as the nectrideans, several of which were characterised by elongate and backward-pointing horns projecting from the skull. A detailed description of the skeletal anatomy of *Keraterpeton* is accompanied by a discussion of the group's affinities. Lastly, **Pardo *et al.*** reveal the intricate morphology of an isolated aïstopod braincase from the middle Pennsylvanian of North America. The snake-like and limbless aïstopods are perhaps the most challenging of all early tetrapod groups in terms of their affinities, but the new braincase data lend support to their placement in the tetrapod stem-group.

Jenny's approach to the study of extinct vertebrates reveals attention to the wider physical context – geological, stratigraphic, environmental – accompanying fossil data. Two papers focus on the stratigraphic and palaeoenvironmental settings for tetrapod origins. **Marshall *et al.*** provide crucial new information on the age of the uppermost part of the Old Red Sandstone – an all-time favourite in geological studies – and on the position of the Devonian–Carboniferous boundary through their detailed analysis of palynological and palaeoichthyological data from recently discovered stratigraphic sequences in central Scotland and the Scottish Borders. **Millward *et al.*** supply a detailed palaeogeographic, paleoclimatic, and palaeoenvironmental analysis of the coastal wetland habitats of northern Great Britain where some of the earliest known Carboniferous tetrapods lived.

Four macroevolutionary papers fall under the broad umbrellas of theory and practice of phylogenetic analysis, patterns and processes of phenotypic change in deep time, and tempo and mode of evolution. **Tschopp and Upchurch** review specimen-based approaches to the construction of cladograms from morphological data using maximum parsimony as an optimality criterion, highlighting potential and limitations intrinsic to these methodological protocols. **Lee *et al.*** address the complex question of a Laurasian vs Gondwanan origin for dinosaurs using a new Bayesian method that simultaneously accounts for phylogeny, fossil age and location, and changes in the interconnections among geographic areas through time. **Witzmann and Ruta** examine the complex relationships between orbital and palatal openings in early tetrapods, especially temnospondyls, quantifying patterns of covariance between their shape and size and discussing the possible functional implications of their varying proportions. **Ruta *et al.*** tackle the morphological diversity of early tetrapod humeri, the temporal and clade-wise distribution of increases and decreases in rates of evolutionary change in this structure, and the correlation between evolutionary rates and major morphological, ecological, and functional transitions in early tetrapod history.

2. Jenny Clack: a biography

Jenny was born in 1947 in Manchester, and attended Bolton School. During these early years she developed a keen interest in natural history and a passion for fossil collecting. Jenny graduated from the University of Newcastle upon Tyne with a degree in Zoology in 1970. In her final year she attended Alec Panchen's popular lectures in Vertebrate Palaeontology, which kindled her lifelong interest in vertebrate evolution. She had hoped to undertake postgraduate research in Panchen's lab but missed out because Alec was unwilling to take on another student and add to his current class including Andrew Milner, Angela Milner, and David Brown. Undaunted, Jenny chose to stay close to natural history and obtained a Graduate Certificate in Museum Studies at the University of Leicester. She secured her first job at the City of Birmingham Museum and Art Gallery. In 1976, while working there, she met Rob Clack, with whom she shared her interests in cooking, motorcycling, music, natural history, and especially fossil collecting. Jenny and Rob got married in 1980. While in Birmingham, Jenny was able to use her position within the network of local authority museums to access the type specimen of the anthracosaur *Pholiderpeton scutigerum* at Keighley Museum. This specimen, recovered from a deep mine at Toftshaw near Bradford, was first described by Huxley in 1867 but had not been studied since then. Alec had tried to borrow it in the late 1960s, whilst preparing his *Handbook of Palaeoherpetology* (Panchen 1970), but his request was refused. Jenny was much more successful and in 1977 she took a three

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Figure 1 Jenny in the galleries of the UMZC, 2009. Photograph credit: departmental photographer Neil Maskell.

week's study leave to work in Alec's lab preparing part of the specimen with an airbrasive machine. This revealed a beautiful braincase and the promise of much more to come. It was the catalyst for a successful application for a NERC studentship, and Jenny began her PhD on *Pholiderpeton* in October 1978, sharing the lab with Angela Kirton and Tim Smithson.

And so began Jenny's lifelong interest in early tetrapods. The Toftshaw specimen is the most complete Pennsylvanian anthracosaur and Jenny's research yielded much new information on its skull and skeleton. But what particularly attracted Jenny's interest was the braincase, otic region, and stapes. The stapes had been lying unrecognised in plain sight in two anthracosaurs for more than 100 years. However, it was not until Robert Carroll first described the stapes of the colosteid *Greererpeton* at a conference organised by Alec in Newcastle upon Tyne in 1979 (Carroll 1980) that all became clear. Jenny published her first paper in 1983 on the anthracosaur stapes (Clack 1983). This was the earliest of a series of influential papers on the evolution of the tetrapod ear (Clack 1994, 1997, 1998; Clack *et al*. 2003) that eventually led to Jenny being invited to co-edit the recent Springer Handbook of Auditory Research on the *Evolution of the Vertebrate Ear: Evidence from the Fossil Record* (Clack *et al*. 2016). This authoritative volume provides a comprehensive review of the structure and function of the ear in bony fishes, early tetrapods, amphibians, and amniotes.

In 1981 Jenny secured a permanent position as Assistant Curator at the UMZC, where she remained for the rest of her career (Fig. 1). She successfully defended her PhD thesis in 1984 and the resulting monograph on *Pholiderpeton* was published three years later (Clack 1987). In the three intervening years, Jenny became a founding member of the East Kirkton Project, attending its first meeting at the East Kirkton Quarry in the summer of 1985 (Fig. 2). This eventually led to an international conference held in Edinburgh in 1992. Jenny's paper on a new anthracosaur from the site, *Silvanerpeton miripedes*, was published in the conference proceedings (Clack 1994). This was the first of her three papers on new tetrapods from East Kirkton (Clack 1994, 1998, 2011), and recently she has provided a comprehensive review of the entire fauna from the site (Clack 2017) in a volume dedicated to the description of fossil lagerstätten from around the world (Fraser & Sues 2017). While beginning work on the East Kirkton fauna, Jenny made a discovery in the collections of the Earth Sciences Department in Cambridge that was to shape the rest of her career. Among material collected from the Upper Devonian of East Greenland by a field party from Cambridge in 1970, she found several specimens of the early tetrapod *Acanthostega gunnari* alongside accompanying field notes by geologist Peter Friend and his students, who had visited Greenland over a number of years. These were the first new Devonian tetrapod specimens to have been found since the original discoveries during the 1930s to 1950s. It is perhaps an indication of how the academic world has changed that, at the time, Jenny chose to publish a full description of the new material in the journal *Palaeontology* (Clack 1988) rather than a brief announcement in a much higher profile journal like *Nature*. However, the significance of Jenny's new material was not underestimated, and eventually led to a paradigm shift in our understanding of the evolution of early tetrapods.

Following the discovery of the *Acanthostega* specimens, Jenny borrowed the field notebook kept by John Nicholson, who had collected the material in 1970, and was able to obtain precise locality information from him. On the strength of this, she applied for a NERC grant to finance an expedition to East Greenland, only to be turned down because one of the referees doubted whether such a collecting trip would 'contribute significantly to our understanding of the origin of higher vertebrates.' Annoyed but undeterred, Jenny managed to secure alternative funding from the Crotch Fund of the UMZC, the Hans Gadow Fund of the Department of Zoology, University of Cambridge, and the Carlsberg Foundation in Denmark, and in late June 1987 she set off from Cambridge accompanied by her husband Rob and her first PhD student, Per Ahlberg. The fieldwork was to be carried out as part of a seven-week summer field programme organised by Grønlands Geologiske Undersøgelse (the Greenland Geological Survey), with the Cambridge team initially working in collaboration with two colleagues from Copenhagen, Svend Bendix-Almgreen and his student Birger Jørgensen (Fig. 3).

Work began on Stensiö Bjerg on the north shore of Kaiser Franz Josef's Fjord, where Nicholson had stumbled on his tetrapod locality at an altitude of about 800 m. The expedition camped on a plateau at the foot of the mountain, with a daunting climb up scree slopes and crumbling sandstone ledges, which brought them to the vicinity of Nicholson's locality. After nearly a week of prospecting, they located a dense scatter of *Acanthostega* fragments that proved to be the talus of a small outcrop packed full of partly articulated tetrapods. Some of the specimens collected in 1987 were later found to fit against Nicholson's blocks, demonstrating that this was indeed the same locality. Over the next few weeks, the expedition collected extensive material of *Acanthostega*. They also discovered a second, stratigraphically older tetrapod locality just below the camp. This locality, which was inspected on alternate days to allow the team to recover from the gruelling climbs to the *Acanthostega* site, principally

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Figure 2 East Kirkton Quarry, 1985. Left to right: Stan Wood; unknown; John Cater; Andrew Milner (squatting); Tim Smithson; Euan Clarkson (sitting); Maggie Rowlands (squatting); Mahala Andrews; Ian Rolfe; Jenny; Norman Butcher. Photograph credit: Hunterian Museum.

Figure 3 East Greenland, 1987. Left to right: Per Ahlberg; Jenny; Svend Bendix-Almgreen; Birger Jørgensen (squatting); Rob Clack. Photograph credit: Birger Jørgensen.

yielded the other classic Devonian tetrapod, *Ichthyostega*. The most important find from this site was an articulated hind limb of *Ichthyostega* showing seven toes. During the second part of the expedition, Jenny, Rob, and Per parted company with Svend and Birger, and were helicoptered south across the fiord to Celsius Bjerg on Ymer Ø, where they continued to collect *Ichthyostega* material.

This summer expedition was in many respects the watershed of Jenny's research career. The material revolutionised our understanding of Devonian tetrapods and has substantially continued to shape the research agenda in this field, right up to the present.

Back in Cambridge, preparation of the new tetrapod material began. On the strength of the discoveries in East

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Figure 4 East Greenland, 1998. Left to right: Becky Hitchin; Sally Thomas; Jenny; Sarah Wallace-Johnson. Photograph credit: Denmark and Greenland Geological Survey.

Figure 5 East Greenland, 1998. Jenny (left) and Sarah Wallace-Johnson (right) collecting a specimen of *Acanthostega*. Photograph credit: Sally Thomas.

Greenland, Jenny once again applied to NERC for funding to support a postdoctoral research associate and a preparator. This time she was successful and hired Sarah Finney as preparator and Mike Coates as a postdoctoral researcher. Over the following decade Sarah, who has recently reverted back to her maiden name of Sarah Wallace-Johnson, was a stalwart in Jenny's lab, preparing meticulously many of the specimens described by Jenny. Among these was a small skull of *Acanthostega*, informally named 'Grace' because of a fancied resemblance of its flat-topped skull to the haircut of supermodel Grace Jones, which adorns the front cover of this *Festschrift* volume. Sarah eventually secured a permanent position in the Sedgwick Museum in Cambridge, and her enormous contribution was recognised by Jenny when she named a new Early

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Figure 6 Jenny elected Fellow of the Royal Society, 2009. Photograph credit: Angela Milner.

Carboniferous tetrapod *Pederpes finneyae* (Clack, 2002) after her.

The four years Mike Coates spent at the UMZC proved to be a very productive time. Together, Jenny and Mike showed that *Acanthostega* retained internal gills (Coates & Clack 1991) and that polydactyly was probably the plesiomorphic condition for the earliest tetrapods (Coates & Clack 1990). They also coined the term Romer's Gap to describe the apparent hiatus in the fossil record of early tetrapods at the beginning of the Carboniferous (Coates & Clack 1995). During this time Jenny also described the stapes of *Acanthostega* (Clack 1989), which turned out to be remarkably similar to that of *Pholiderpeton* she had described six years previously. Papers on the *Acanthostega* skull (Clack 2002, 2003), lower jaw (Ahlberg & Clack 1998), and braincase (Clack 1994, 1998) followed, and with Mike's description of the postcranial skeleton (Coates 1996), *Acanthostega* became, and remains, the most completely known of all Devonian early tetrapods. But by no means did this resolve all the problems of early tetrapod evolution and relationships. This could only come with the discovery of more Devonian fossils. And so a new expedition to East Greenland was planned.

In collaboration with De Nationale Geologiske Undersøgelser for Danmark og Grønland (GEUS: Denmark and Greenland Geological Survey) and the Geological Museum in Copenhagen, a party of four from Cambridge undertook a six-week expedition in 1998, funded by National Geographic and a Gibbs Fellowship from Newnham College, University of Cambridge. Led by Jenny, the party included Becky Hitchin, a graduate student from the University of Bristol, Jenny's PhD student Sally Thomas (née Neininger), and Sarah Wallace-Johnson. Rob Clack was due to go with them but slipped a disc a few weeks before departure and had to retire hurt. So the 'Girls in Greenland' set off (Fig. 4). Once there they travelled to the sites by helicopter and received weekly food drops, weather permitting. During the first three weeks they explored the Aina Dal Formation on Gauss Halvø, logging the exposure to gain a better picture of the distribution of vertebrates. They covered the area from central Smith Woodward's Bjerg to the southeastern corner of Wiman Bjerg, where they collected juvenile tetrapod specimens, possibly belonging to *Acanthostega* (Fig. 5). In the following three weeks they explored the S side of Celsius Berg with the aid of Jarvik's 1947 and 1954 field note books, which had been translated from Swedish by Per Ahlberg. They found good tetrapod material from the talus on the SW face of the mountain, including two ichthyostegid skulls with postcranial material. At a new site on the mountain they also found new tetrapod material which, together with one of Jarvik's original specimens, was subsequently described and named *Ymeria* (Clack *et al.* 2012).

The second Greenland trip coincided broadly with the end of Erik Jarvik's research career (he published his last paper in 1996) and the return of his Greenland tetrapod material to the Geological Museum of the University of Copenhagen. This opened up new possibilities for research on *Ichthyostega*: although Jenny had always maintained cordial relations with Jarvik, and had been a welcome guest at the Swedish Museum of Natural History, he had never made his tetrapod material available to others for publication purposes. Together with Per and Sarah, Jenny visited the collections in Copenhagen and began systematically re-examining the *Ichthyostega* specimens. One of these specimens was later nicknamed 'Mr Magic', as it provided significant new insights into the structure of the vertebral column and forelimb of *Ichthyostega*. The combination of new and old *Ichthyostega* material allowed a thorough revision of this enigmatic tetrapod that cast new light on its braincase and stapes (Clack *et al.* 2003), axial skeleton (Ahlberg *et al.* 2005), and limbs (Callier *et al.* 2009).

In 2000 Jenny was awarded the degree of Doctor of Science by the University of Cambridge in recognition of the transforming impact of her published work. In the same year she was promoted to Reader. Meanwhile, her extraordinary output continued. She worked on the introductory chapter of the Heatwole & Carroll (2000) volume in the *Amphibian Biology* series. Dedicated to the early tetrapod fossil record, the volume included Jenny's preliminary account of the new tetrapod *Pederpes finneyae* from the Early Carboniferous of western Scotland (Clack 2002). This was the first articulated specimen described from Romer's Gap. It was collected in the 1970s by Peder Aspen but at the time was thought to be a rhizodont fish. It was housed in the Hunterian Museum, Glasgow, where one of Jenny's former PhD students, Jonathan Jeffery, spotted it, realising it was not a rhizodont and alerting Jenny. A full description of *P. finneyae* was published a few years later (Clack & Finney 2005). But by far Jenny's most significant publication at the beginning of the new millennium was *Gaining Ground: The Origin and Evolution of Tetrapods* (Clack 2002). In this important and transforming book, she summarised the results of work on early tetrapods and tetrapodomorph fishes over the previous 25 years, including Stan Wood's discoveries at Dora and East Kirkton, the finds at Delta in Illinois, USA, and at Duckabrook in Australia, and the increasing number of Late Devonian tetrapods from East Greenland, Latvia, and Russia. The volume stands out as an example of scholarly enterprise and accessibility, coupled with fine scientific artwork mostly produced by Jenny herself.

During the early 2000s new techniques were being developed which opened up new ways to study fossils. Micro-computed

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Figure 7 Members of the TW:eed Project Team at the opening of the Fossil Hunters exhibition, National Museums Scotland, 2015. Left to right: John Marshall; Stig Walsh; Janet Sherwin; Emma Reeves; Tim Kearsey (kneeling); Ket Smithson; Sarah Wallace-Johnson; Maggie Wood; Tim Smithson (kneeling); Tom Challands; Andy Ross; Dave Millward; Jenny; Carys Bennett (kneeling); Nick Fraser; Mike Brown; Rob Clack (kneeling); Sarah Davies. Photograph credit: British Geological Survey.

tomography (μCT) scanning enabled high-resolution approaches to analyses of fossils, revealing their intricate anatomy in the round without the need for complete removal from the surrounding rock. It also allowed internal parts of the skull, such as the braincase and palate, to be studied without resorting to destructive techniques, including the serial grinding employed by Jarvik in the study of *Eusthenopteron* (Jarvik 1980) or serial sectioning which had helped Jenny describe the braincase of *Acanthostega* (Clack 1998). With John Hutchinson at the Royal Veterinary College, she successfully applied for beamtime at the European Synchrotron Radiation Facility (ESRF) in 2010 to investigate the postcranial skeleton of *Ichthyostega* using propagation phase-contrast synchrotron microtomography (PPC-SRμCT). Based largely on Jarvik's specimen, Mr Magic, and with the expertise of postdoctoral researcher Stephanie Pierce, they revealed that the vertebral column of this animal was not rhachitomous, as previously described by Jarvik (1980), but was a reverse rhachitomous arrangement whereby the pleurocentrum of a vertebra (the posterior of the two main elements forming the body of a vertebra) is sutured or fused with the intercentrum (the anterior of the two main elements forming the body of a vertebra) of the following posterior vertebra (Pierce *et al*. 2013). They also investigated the morphology of the forelimb and shoulder girdle using conventional μCT, concluding that limb movement was more restricted than previously thought and that walking would have been improbable (Pierce *et al*. 2012). This, in part, built on a previous investigation of the humeri of *Acanthostega* and *Ichthyostega* using μCT by Jenny's former student Viviane Callier (Callier *et al*. 2009).

In recognition of her considerable achievements, Jenny was promoted to a personal chair in 2006 and took the title of Professor and Curator of Vertebrate Palaeontology. In 2008 she was awarded the Daniel Giraud Elliot medal by the National Academy of Sciences, USA, and in the following year she was made a Foreign Honorary Member of the American Academy of Arts and Sciences and was elected Fellow of the Royal Society (Fig. 6).

Around the time that Jenny began her groundbreaking research on Devonian tetrapods, Tim Smithson started to explore the Early Carboniferous of the Scottish Borders for new vertebrate localities. After some success at Coldstream and Burnmouth, he joined forces with Stan Wood in 2006 and, together, they discovered a further seven tetrapod horizons in Romer's Gap. Following their announcement at the Society of Vertebrate Paleontology meeting in Bristol (Smithson & Wood 2009), Jenny worked with them to publish their discoveries (Smithson *et al*. 2012). Together with colleagues from the Universities of Leicester and Southampton, the British Geological Survey, and National Museums Scotland, Jenny prepared a successful large consortium grant proposal to NERC. This funded a four-year multi-institutional and cross-disciplinary

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

study led by Jenny of the fauna, flora, stratigraphy, and sedimentology of the new sites. The TW:eed Project (Tetrapod World: early evolution and diversification) began in 2012 and has produced a series of important multi-authored papers (e.g., Smithson *et al*. 2015; Clack *et al*. 2016, 2018; Otoo *et al*. 2018; Richards *et al*. 2018; Smithson & Clack 2018), which have shown that, far from being an impoverished hiatus in the fossil record, Romer's Gap had a rich and diverse fauna that quickly recovered from the end-Devonian extinction event and contained the foundations of the modern vertebrate fauna (Fig. 7).

Exactly ten years after the publication of *Gaining Ground*, the second edition of Jenny's book was released, rapidly topping the success of its predecessor (Clack 2012). Lavishly illustrated and entirely revised, this impressive 544-page tome (an increase of 175 pages relative to its first edition) exudes excitement for palaeontological research, narrating the beautiful journey through time back to our own ancestral roots and presenting all the new discoveries that had accrued between the two book editions. The style of the second edition remains engaging and captivating, providing the reader with a clear and comprehensive picture of tetrapod origin and diversification in ten chapters. Many of the new ideas that Jenny expounds in her book have provided strong foundations for new research programmes and new collaborative enterprises in which Jenny continues to be involved up to the present.

Six decades of paradigm-shifting research on early tetrapods, initiated by Alec Panchen at the University of Newcastle and continued and perfected by his research students, crystallised in a series of volumes in the prestigious *Handbook of Paleoherpetology* series, which has featured work on 'lepospondyls' (Carroll *et al*. 1998), stereospondyls (Schoch & Milner 2000), and non-stereospondyl temnospondyls (Schoch & Milner 2014). In the most recent instalment of the *Handbook* series, Jenny and her long-time friend and colleague, Andrew Milner, teamed up to produce a much-needed synthesis of Devonian and Carboniferous stem-group tetrapods (Clack & Milner 2015). In the best German tradition of palaeontographical monographs, the volume includes revised taxonomic diagnoses, succinct redescriptions, up-to-date palaeobiogeographical and stratigraphic information, in-depth scrutiny of current theories of tetrapod origin, discussions of phylogenetic hypotheses, and a chronology of research. For anyone interested in the intricacies of vertebrate morphology and current issues in early tetrapod palaeobiology, this work provides a goldmine of data in a user-friendly format, attaining greater immediacy than specialist journal publications.

Jenny continues to publish. She has described new lungfish from the Famennian of East Greenland, including specimens she collected in 1998 (Clack *et al*. 2018). This has shown that the Devonian/Carboniferous boundary did not really mark any evolutionary division between faunas of lungfish with tooth plates, given that taxa showing characters normally associated with Early Carboniferous forms are found in the Late Devonian and *vice versa*. Most recently, taking advantage of the wonders of micro-CT scanning, she has redescribed the skull of the Late Mississippian limbless tetrapod *Acherontiscus* (Carroll 1969) and shown it to be the earliest known tetrapod with a heterodont dentition (Clack *et al*. 2019).

3. Legacy

Jenny's mentoring activity is extraordinary. Beginning in 1985, she has guided several young researchers, many of whom have become international leading figures in various fields of evolutionary biology. In 1985, Per Ahlberg (now Professor of Evolutionary Organismal Biology, Uppsala University, and Fellow of the Royal Swedish Academy of Sciences) embarked on a PhD project on the anatomy and phylogeny of porolepiforms, a group of lobe-finned fish widely recognised as being closely related to lungfish. In 1989, Paul Upchurch (now Professor of Palaeobiology, University College London) began his PhD research on the anatomy, biomechanics, and phylogeny of sauropods, one of the most speciose and most iconic dinosaur groups. In 1991, PhD student Mike Lee (now Matthew Flinders Fellow, Flinders University, Adelaide) delved into the morphology and relationships of pareiasaurs, an extinct group of herbivorous tetrapods with robust skeletons, leaf-shaped teeth, and often heavily ornamented skulls. In 1992, PhD student Elizabeth Pringle reviewed the morphology, life-style, and interrelationships of Carboniferous anthracosaurs. In 1994, Jonathan Jeffery (now Research Fellow, University of Bristol) tackled the anatomy and phylogeny of rhizodonts, a clade of lobe-finned fish that sits in a basal position on the tetrapod stem, for his PhD project. In 1996, Sally Thomas (née Neininger; now Publications Officer for the *Palaeontological Association*) examined the palaeohistology of dermal skull bones in early tetrapods, with a focus on *Acanthostega*, for her PhD. The year 2002 saw three additions to Jenny's lab, with PhD students Esther Sharp (now Curator at the Science Museum's stores, Wroughton) and Roz Wade (now Education and Outreach Officer, University of Cambridge) and Masters student Matt Friedman (now Director and Associate Curator, Museum of Paleontology, and Associate Professor, University of Michigan) all involved in morphological, phylogenetic, and systematic projects on lobe-finned fish, with Esther working on British Carboniferous lungfish, Roz on Scottish osteolepidids, and Matt on Devonian lungfish from Greenland. Masters student Brian Swartz (now Integrative Biologist at Moorpark College and at The Millennium Alliance for Humanity and the Biosphere, Stanford University) joined the lab in 2004, working on Devonian ray-finned fish interrelationships. In 2006, Viviane Callier (now a San Antonio-based Freelance Science Writer whose articles have appeared in *Nature*, *Science*, and *Scientific American*) researched on the ontogeny of the appendicular skeleton of Devonian tetrapods, with emphasis on the forelimb. In 2009, Kelly Richards (now Exhibition Officer at the Oxford University Museum of Natural History) began her PhD project on the skeletal anatomy, interrelationships, and palaeoecology of cartilaginous fish from the Early Carboniferous of the Peak District in Derbyshire. In 2014, Masters student Benjamin Otoo (now a PhD student at the University of Chicago) examined the taxonomy and palaeoecology of fossil faunas from Burnmouth.

4. Conclusion

Jenny has had a remarkable career. She was elected a Fellow of Darwin College, Cambridge, in 1997. She was the first Professor of Vertebrate Palaeontology at the University of Cambridge (2006), the first woman to be awarded the Daniel Giraud Elliot medal by the National Academy of Sciences, USA (2008), the first woman vertebrate palaeontologist to be elected a Fellow of the Royal Society (2009), and the first vertebrate palaeontologist to receive the Lapworth Medal from the Palaeontological Association (2015). She is a Foreign Honorary Member of the American Academy of Arts and Sciences (2009) and the Royal Swedish Academy of Sciences (2014), and has been awarded honorary degrees by the Universities of Chicago (2013) and Leicester (2014). In 2013, she

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

was awarded the T. Neville George Medal by the Geological Society of Glasgow. Her achievements were brought before a much wider audience when she was the subject of the BBC Four programme *Beautiful Minds*. Perhaps nothing can capture the essence of a beautiful mind better than a few excerpts from Jenny's own narration, presented with modesty and grace: the new discoveries of *Acanthostega* were 'probably the most exciting thing after falling in love'; and the realisation humans are but a recent twig on the big tree of life, with hundreds of millions of years of evolution occurring before the emergence of that twig, 'really makes you feel quite insignificant'.

5. References (excluding Jenny's own contributions)

BBC. 2012. *Beautiful minds*. https://www.bbc.co.uk/programmes/b01fq4yh.

Carroll, R. L. 1969. A new family of Carboniferous amphibians. *Palaeontology* **43**, 151–70.

Carroll, R. L. 1980. The hyomandibular as a supporting element in the skull of primitive tetrapods. *In* Panchen, A. L. (ed.) *The terrestrial environment and the origin of land vertebrates*, 293–318. Systematics Association Special Volume 15. London: Academic Press.

Carroll, R. L., Bossy, K. A., Milner, A. C., Andrews, S. M. & Wellstead, C. F. 1998. *Lepospondyli. encyclopedia of paleoherpetology*, 1–219. München: Verlag Dr. Friedrich Pfeil.

Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **87**, 363–421.

Dunne, E. & Armfield, R. 2018. The early tetrapod world: laying the foundations of the modern vertebrate fauna. *The Palaeontology Newsletter* **97**, 65–67.

Fraser, N. C. & Sues, H.-D. (eds) 2017. *Terrestrial conservation lagerstätten: windows into the evolution of life on land*. Edinburgh: Dunedin Academic Press.

Heatwole, H. & Carroll, R. L. (eds) 2000. *Amphibian biology, 4: palaeontology*. Chipping Norton: Surrey Beatty & Sons.

Jarvik, E. 1980. *Basic structure and evolution of vertebrates*. London and New York: Academic Press.

Panchen, A. L. 1970. *Handbuch der paläoherpetologie, teil 5a, anthracosauria*, 1–83. Stuttgart: Gustav Fischer Verlag.

Schoch, R. R. & Milner, A. R. 2000. Stereospondyli. *In* Wellnhofer, P. (ed.) *Handbuch der paläoherpetologie, part 3: stereospondyli*, 1–220. München: Verlag Dr. Friedrich Pfeil.

Schoch, R. R. & Milner, A. R. 2014. *Handbook of paleoherpetology, part 3A2: temnospondyli I*, 1–150. München: Verlag Dr. Friedrich Pfeil.

Smithson, T. R. & Wood, S. P. 2009. Bridging Romer's Gap: new tetrapods from the basal Carboniferous of the Scottish Borders. *Journal of Vertebrate Paleontology* **29**, 183A.

6. Jenny Clack: a bibliography

6.1. Peer-reviewed papers

Ahlberg, P. E., Clack, J. A. & Luksevics, E. 1996. Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* **381**, 61–4.

Ahlberg, P. E., Clack, J. A. & Blom, H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. *Nature* **437**, 137–40.

Ahlberg, P. E., Clack, J. A., Luksevics, E., Blom, H. & Zupins, I. 2008. *Ventastega curonica* and the origin of tetrapod morphology. *Nature* **453**, 1199–204.

Ahlberg, P. E. & Clack, J. A. 1998. Lower jaws, lower tetrapods: a review based on the Devonian tetrapod *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **89**, 11–46.

Anderson, J. S., Smithson, T. R., Mansky, C., Meyer, T., Carroll, R. L. & Clack, J. A. 2015. A diverse tetrapod fauna at the base of Romer's Gap. *PloS ONE* **10**, e0125446.

Bendix-Almgreen, S. E., Clack, J. A. & Olsen, H. 1988. Upper Devonian and Upper Permian vertebrates collected in 1987 around Kejser Frans Joseph Fjord, central East Greenland. *Rapp. Grønlands geol. Unders.* **40**, 95–102.

Bendix-Almgreen, S. E., Clack, J. A. & Olsen, H. 1990. Upper Devonian tetrapod palaeoecology in the light of new discoveries in East Greenland. *Terra Nova* **2**, 131–137.

Bennett, C. E., Kearsey, T. I., Davies, S. J., Millward, D., Clack, J. A., Smithson, T. R. & Marshall, J. E. A. 2016. Early Carboniferous sandy siltstones deposited in seasonal flooding episodes preserve rare non-marine fossils. *Sedimentology* **63**, 1677–700.

Blom, H., Clack, J. A. & Ahlberg, P. E. 2005. Localities, distribution and stratigraphical context of the Late Devonian tetrapods of East Greenland. – Meddelelser om Grønland. *Geosciences* **43**, 1–50.

Blom, H., Clack, J. A., Ahlberg P. E. & Friedman, M. 2007. Devonian vertebrates from East Greenland: a review of faunal composition and distribution. *Geodiversitas* **29**, 119–41.

Callier, V., Clack, J. A. & Ahlberg, P. E. 2009. Contrasting ontogenetic trajectories in the earliest known tetrapod forelimbs. *Science* **324**, 364–7.

Clack, J. A. 1983. The stapes of the Coal Measures embolomere *Pholiderpeton scutigerum* Huxley and otic evolution in early tetrapods. *Zoological Journal of the Linnean Society* **79**, 121–48.

Clack, J. A. 1987. *Pholiderpeton scutigerum*, an amphibian from the Yorkshire Coal Measures. *Philosophical Transaction of the Royal Society of London B* **318**, 1–107.

Clack, J. A. 1987. Two new specimens of *Anthracosaurus* (Amphibia: Anthracosauria) from the Northumberland Coal Measures. *Palaeontology* **10**, 15–26.

Clack, J. A. 1988. New material of the early tetrapod *Acanthostega* from the Upper Devonian of East Greenland. *Palaeontology* **31**, 699–724.

Clack, J. A. 1989. Discovery of the earliest-known tetrapod stapes. *Nature* **342**, 425–7.

Clack, J. A. 1992. The stapes of *Acanthostega gunnari* and the role of the stapes in early tetrapods. In Webster, D., Fay, R. & Popper, A. N. (eds) The evolutionary biology of hearing, 405–20. New York: Springer-Verlag.

Clack, J. A. 1994. *Acanthostega gunnari*, a Devonian tetrapod from Greenland; the snout, palate and ventral parts of the braincase, with a discussion of their significance. Meddelelser om Grønland. *Geoscience* **31**, 1–24.

Clack, J. A. 1994. Homologies in the fossil record – the middle ear as a test case. In Dubbeldam, J. L., Goodwin, B. C. and & Kortmulder, K. (Eds) Evolution and Development – generative and stability principles of biological form. *Acta Biotheoretica* **41**, 391–409.

Clack, J. A. 1994. *Silvanerpeton miripedes*, a new anthracosauroid from the Viséan of East Kirkton, West Lothian, Scotland. In Rolfe, W. D. I., Clarkson, E. N. K. &and Panchen, A. L. (Eds) Volcanism and Early Terrestrial Biotas. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**, 369–76.

Clack, J. A. 1994. The earliest tetrapod braincase and the early evolution of the stapes and fenestra ovalis. *Nature* **369**, 392–4.

Clack, J. A. 1996. Otoliths in Fossil Coelacanths. *Journal of Vertebrate Paleontology* **16**, 168–71.

Clack, J. A. 1996. The palate of *Crassigyrinus scoticus* from the Viséan of Scotland. In Milner A. R. (ed.) Studies on Carboniferous and Permian *vertebrates*. *Special Papers in Palaeontology* **52**, 55–64.

Clack, J. A. 1997. Devonian tetrapod trackways and trackmakers; a review of the fossils and footprints. *Palaeogeography, Palaeoclimatology, Palaeoecology* **130**, 227–50.

Clack, J. A. 1997. The evolution of tetrapod ears and the fossil record. *Brain, Behavior and Evolution* **50**, 198–212.

Clack, J. A. 1998. A new Early Carboniferous tetrapod with a mélange of crown group characters. *Nature* **394**, 66–9.

Clack, J. A. 1998. The neurocranium of *Acanthostega gunnari* and the evolution of the otic region in tetrapods. In A study of fossil vertebrates. Norman, D. B., Milner, A. R., & Milner, A. C. (Eds) *Zoological Journal of the Linnean Society of London* Volume **122**, 61–97. Academic Press.

Clack, J. A. 1998. The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker) – cranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 127–42.

Clack, J. A. 2001. *Eucritta melanolimnetes* from the Early Carboniferous of Scotland, a stem tetrapod showing a mosaic of characteristics. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **92**, 75–95.

Clack, J. A. 2001. The otoccipital region – origin, ontogeny and the fish-tetrapod transition. In: Major events in early vertebrate evolution. In Ahlberg, P. E. (ed.) Systematics Association Special. Volume **61**, 392–405. London: Taylor and Francis. Chapter 23.

Clack, J. A. 2002. An early tetrapod from 'Romers Gap'. *Nature* **418**, 72–6.

Clack, J. A. 2002. Patterns and processes in the early evolution of the tetrapod ear. *Journal of Neurobiology* **53**, 251–64.

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

Clack, J. A. 2002. The dermal skull roof of *Acanthostega*, an early tetrapod from the Late Devonian. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **93**, 17–33.

Clack, J. A. 2003. A new baphetid (stem tetrapod) from the Upper Carboniferous of Tyne and Wear, UK, and the evolution of the tetrapod occiput. *Canadian Journal of Earth Sciences* **40**, 483–98.

Clack, J. A. 2003. A revised reconstruction of the dermal skull roof of *Acanthostega*, an early tetrapod from the Late Devonian. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **93**, 163–5.

Clack, J. A. 2005. Making headway and finding a foothold: tetrapods come ashore. In Briggs, D. E. G. (ed.) Evolving form and function: fossils and development. Peabody Museum of Natural History Special Publications, Yale University 223–44.

Clack, J. A. 2006. The emergence of early tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**, 167–89.

Clack, J. A. 2007. Devonian climate change, breathing, and the origin of the tetrapod stem group. *Integrative and Comparative Biology* **47**, 510–23.

Clack, J. A. 2009. The fin to limb transition: new data, interpretations, and hypotheses from paleontology and developmental biology. *Annual Review of Earth and Planetary Sciences* **37**, 163–79.

Clack, J. A. 2009. The fish – tetrapod transition: new fossils and interpretations. *Evolution: Education and Outreach* **2**, 213–23.

Clack, J. A. 2011. A Carboniferous embolomere tail with supraneural radials. *Journal of Vertebrate Paleontology* **31**, 1150–3.

Clack, J. A 2011. A new microsaur from the Early Carboniferous (Viséan) of East Kirkton, Scotland, showing soft tissue evidence. *Special Papers in Palaeontology* **86**, 45–56.

Clack, J. A., Ahlberg, P. E., Finney, S. M, Dominguez Alonso, P., Robinson, J. & Ketcham, R. A. 2003. A uniquely specialised ear in a very early tetrapod. *Nature* **425**, 65–9.

Clack, J. A., Ahlberg, P. E., Blom, H. & Finney, S. M. 2012. A new genus of Devonian tetrapod from East Greenland with new information on the lower jaw of *Ichthyostega*. *Palaeontology* **55**, 73–86.

Clack, J. A., Witzmann, F., Snyder, D. & Müller, J. 2012. A colosteid-like early tetrapod from the St. Louis Limestone (Early Carboniferous, Meramecian), St. Louis, Missouri, USA. *Fieldiana Life and Earth Sciences* **5**, 17–39.

Clack, J. A., Bennett, C. E., Carpenter, D. K., Davies, S. J., Fraser, N. C., Kearsey, T. I, Marshall, J. E. A., Millward, D., Otoo, B. K. A., Reeves, E. J., Ross, A. J., Ruta, M., Smithson, K. Z., Smithson, T. R. & Walsh, S. 2017. Phylogenetic and environmental context of a Tournaisian tetrapod fauna. *Nature Ecology and Evolution.* doi: 10.1038/s41559-016-0002.

Clack, J. A., Challands, T. J., Smithson, T. R. & Smithson, K. Z. 2018. Newly recognized Famennian lungfishes from East Greenland reveal dental diversity and blur the Devonian-Carboniferous boundary. *Papers in Palaeontology.* doi: 10.1002/spp2.1242.

Clack, J. A., Porro, L. B. & Bennett, C. E. 2018. A *Crassigyrinus*-like jaw from the Tournaisian (Early Mississippian) of Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 37–46.

Clack, J. A., Bennett, C. E., Davies, S. J., Scott A. C., Sherwin, J. E. & Smithson, T. R. 2019. A Tournaisian (earliest Carboniferous) conglomerate-preserved non-marine faunal assemblage and its environmental and sedimentological context. *PeerJ.* doi: 10.7717/peerj.5972.

Clack, J. A., Ruta, M., Milner, A. R., Marshall, J. E. A., Smithson, T. R. & Smithson, K. Z. 2019. *Acherontiscus caledoniae*, the earliest heterodont and durophagous tetrapod. *Royal Society Open Science*.

Clack, J. A. & Ahlberg, P. E. 2004. A new stem tetrapod from the Early Carboniferous of Northern Ireland. In Arratia, G., Cloutier, R. & Wilson, M. V. H. (eds) Recent advances in the origin and early radiation of vertebrates, 309–20. Verlag Friedrich Pfeil.

Clack, J. A. & Coates, M. I. 1993. *Acanthostega gunnari* – our present connection. In Hoch, E. & Brantsen, A. K. (eds) Deciphering the natural world and the role of museums and collections, 39–42. Copenhagen: Geological Museum.

Clack, J. A. & Coates, M. I. 1995. *Acanthostega* – a primitive aquatic tetrapod? In Arsenault, M., Lelièvre & Janvier, P. (eds) Proceedings of the 7th International Symposium on Lower Vertebrates, Miguasha: Studies on Early Vertebrates. Bulletin de la Muséum national d'Histoire naturelle, Paris. 17, 359–72.

Clack, J. A. & Finney, S. M. 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. *Journal of Systematic Palaeontology* **2**, 311–46.

Clack, J. A. & Holmes, R. 1988. The braincase of the anthracosaur *Archeria crassidisca* with comments on the interrelationships of primitive tetrapods. *Palaeontology* **31**, 85–107.

Clack, J. A. & Klembara, J. 2009 An articulated specimen of a chroniosuchid from the Late Permian of Russia. *Special Papers in Palaeontology* **81**, 15–42.

Clack, J. A. & Milner, A. R. 1994. *Platyrhinops* from the Upper Carboniferous of Linton and Nýřany and the family Peliontidae (Amphibia; Temnospondyli). In Schweiss, D. & Heidtke, U. (eds) New results on permo-carboniferous fauna, Pollichia-buch No. 29, 185–92, Bad-Durkheim.

Clack, J. A. & Milner, A. R. 2010. The morphology and systematics of the Pennsylvanian amphibian *Platyrhinops lyelli* (Amphibia: Temnospondyli). *Transactions of the Royal Society of Edinburgh, Earth Sciences* **100**, 275–95.

Clack, J. A. & Milner, A. R. 2015. *Basal tetrapods*. Handbook of *paleoherpetology*. Part 3A1. Friedrich Pfeil, Munich.

Clack, J. A & Neininger, S. L. 2000. Fossils from the Celsius Bjerg Group, Upper Devonian sequence, East Greenland: significance and sedimentological distribution. In Friend P. F. & Williams, B. (eds) New perspectives on the old red sandstone, Volume 180, 557–66. Geological Society, London Special Publication.

Clément, G., Ahlberg, P. E., Blieck, A., Blom, H., Clack, J. A., Poty, E., Thorez, J. & Janvier, P. 2004. Devonian tetrapod from western Europe. *Nature* **427**, 412–3.

Coates, M. I. & Clack, J. A. 1990. Polydactyly in the earliest known tetrapod limbs. *Nature* **347**, 66–9.

Coates, M. I. & Clack, J. A. 1991. Fish-like gills and breathing in the earliest known tetrapod. *Nature* **352**, 234–6.

Coates, M. I. & Clack, J. A. 1995. Romer's Gap – tetrapod origins and terrestriality. In Arsenault, M. Lelièvre & Janvier, P. (eds) Proceedings of the 7th International Symposium on Lower Vertebrates, Miguasha: Studies on Early Vertebrates. Bulletin de la Muséum national d'Histoire naturelle, Paris.17, 373–88.

Daeschler, E. B, Clack, J. A. & Shubin, N. H. 2009. Late Devonian tetrapod remains from Red Hill Pennsylvania, USA: how much diversity? In Ahlberg, P. E., Blom, H. & Boisvert, C. A. (eds.) Forty Years of early vertebrates: papers from the 11th International Symposium on Early and Lower Vertebrates. *Acta Zoologica Special Issue, Supplement* **90**, 306–17.

Kimmel, C, Sidlauskas, B. & Clack, J. A. 2009. Linked morphological changes during palate evolution in early tetrapods. *Journal of Anatomy* **215**, 91–109.

Klembara, J., Clack, J. A. & Cernansky, A. 2010. The anatomy of the palate of *Chroniosaurus dongusensis* (Chroniosuchia, Chroniosuchidae) from the Upper Permian of Russia. *Palaeontology* **53**, 1147–53.

Klembara, J., Clack, J. A., Milner, A. R. & Ruta, M. 2014. Cranial anatomy, ontogeny, and relationships of the Late Carboniferous tetrapod *Gephyrostegus bohemicus* Jaekel, 1902. *Journal of Vertebrate Paleontology* **34**, 774–92.

Larsen, H., Olsen, P. & Clack, J. A. 2008. The Devonian Basin in East Greenland – Review of basin evolution and vertebrate assemblages. In Higgins, A. K., Gilotti, J. A. & Smith, M. P. (eds) The Greenland Caledonides: evolution of the Northeast Margin of Laurentia. *Geological Society of America Memoir* **202**, 273–92.

Lebedev, O. A. & Clack, J. A. 1993. Upper Devonian tetrapods from Andreyevka, Tula Region, Russia. *Palaeontology* **36**, 721–34.

Marshall, J. E. A., Astin, T. R. & Clack, J. A. 1999. East Greenland tetrapods are Devonian in age. *Geology* **27**, 637–40.

Molnar, J. L., Pierce, S. E., Clack, J. A. & Hutchinson, J. R. 2012. Idealized landmark-based geometric reconstructions of poorly preserved fossil material: a case study of an early tetrapod vertebra. *Paleontologica Electronica* **15**, 1–18.

Otoo, B. K. A., Clack, J. A., Smithson, T. R., Bennett, C. E., Kearsey, T. I. & Coates, M. I. 2018. A fish and tetrapod fauna from Romer's Gap preserved in Scottish Tournaisian floodplain deposits. *Palaeontology.* doi: 10.1111/pala.12395.

Paton, R. L., Smithson, T. R. & Clack, J. A. 1999. An amniote-like skeleton from the Early Carboniferous of Scotland. *Nature* **398**, 508–13.

Pierce, S. E., Clack, J. A. & Hutchinson, J. R. 2011. Comparative axial morphology in pinnipeds and its correlation with aquatic locomotory behaviour. *Journal of Anatomy* **219**, 502–14.

Pierce, S. E., Clack, J. A. & Hutchinson, J. R. 2012. Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. *Nature* **486**, 523–6.

Pierce, S. E, Hutchinson, J. R. & Clack, J. A. 2013. Historical perspectives on the evolution of tetrapodomorph movement. *Integrative and Comparative Biology* **53**, 209–23.

Pierce, S. E., Ahlberg, P. E., Hutchinson, J. R., Molnar, J. L., Sanchez, S., Tafforeau, P. & Clack, J. A. 2013. Vertebral architecture in the earliest stem tetrapods. *Nature* **494**, 226–30.

Polgar, G., Malavasi, S., Cipolato, G., Georgalas, V., Clack, J. A. & Torricelli, P. 2011. Acoustic communication at the water's edge: Evolutionary insights from a mudskipper. *PLoS ONE* **6**, e21434.
Porro, L. B., Rayfield, E. M. & Clack, J. A. 2015. Computed tomography, anatomical description and three-dimensional reconstruction of the lower jaw of *Eusthenopteron foordi* Whiteaves, 1881 from the Upper Devonian of Canada. *Palaeontology* **58**, 1031–47.
Porro, L. B., Rayfield, E. J. & Clack, J. A. 2015. Descriptive anatomy and three-dimensional reconstruction of the skull of the early tetrapod *Acanthostega gunnari* Jarvik, 1952. *PloS ONE* **10**, e0118882.
Richards, K. R., Sherwin, J. E., Smithson, T. R., Bennion, R. F., Davies, S. J., Marshall, J. E. A. & Clack, J. A. 2018. Diverse and durophagous: Early Carboniferous chondrichthyans from the Scottish Borders. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 1–21.
Ruta, M. & Clack, J. A. 2006. A review of *Silvanerpeton miripedes*, a stem amniote from the Lower Carboniferous of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **97**, 31–63.
Sanchez, S., Tafforeau, P., Clack, J. A. & Ahlberg, P. E. 2016. Life history of the stem tetrapod *Acanthostega* revealed by synchrotron microtomography. *Nature* **537**, 408–11.
Sharp, E. L. & Clack, J. A. 2012. Redescription of the lungfish *Straitonia waterstoni* from the Viséan of Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **102**, 179–89.
Sharp, E. L. & Clack, J. A. 2013. A review of the Carboniferous lungfish genus *Ctenodus* Agassiz, 1838 from the United Kingdom, with new data from an articulated specimen of *Ctenodus interruptus*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **104**, 169–204.
Smithson, T. R., Wood, S. P., Marshall, J. E. A. & Clack, J. A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. *Proceedings of the National Academy of Sciences, USA* **109**, 4532–7.
Smithson, T. R. & Clack, J. A. 2013. Tetrapod appendicular skeletal elements from the Early Carboniferous of Scotland. *Comptes Rendus Palevol* **12**, 405–17.
Smithson, T. R., Richards, K. R. & Clack, J. A. 2015. Lungfish diversity in Romer's Gap: reaction to the end-Devonian extinction. *Palaeontology* **59**, 29–44.
Smithson, T. R., Browne, A. E., Davies, S. J., Marshall, J. E. A., Millward, D., Walsh, S. A. & Clack, J. A. 2017. A new Mississippian tetrapod from Fife, Scotland, and its environmental context. *Papers in Palaeontology* **3**, 1–11.
Smithson, T. R. & Clack, J. A. 2018. A new tetrapod from Romer's Gap reveals an early adaptation for walking. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 89–97.
Sookias, R. B, Böhmer, C. & Clack, J. A. 2014. Redescription and phylogenetic analysis of the mandible of an enigmatic Late Carboniferous tetrapod from Nova Scotia and the lability of Meckelian jaw ossification. *PloS ONE* **9**, e109717.

6.2. Accepted for publication

Challands, T. J., Smithson, T. R., Clack, J. A., Bennett, C. E., Marshall, J. E. A., Finney, S. M. & Hill, H. A Lungfish survivor of the end-Devonian extinction and an Early Carboniferous dipnoan radiation. *Journal of Systematic Palaeontology*.
Clack, J. A. Fossil vertebrates – Palaeozoic non-amniote tetrapods. Encyclopaedia of Geology. Update for 2019 Elsevier, Oxford 2.

6.3. Submitted manuscripts in revision

Clack, J. A., Milner, A. R., Ruta, M., Marshall, J. E. A., Smithson, T. R. & Smithson, K. Z. The earliest heterodont and durophagous tetrapod. *Royal Society Open Science*.

6.4. Books, book chapters and web pages

Clack, J. A. 1997. World Wide Web pages for University of Arizona 'Tree of Life' describing the taxa *Acanthostega*, *Ichthyostega*, *Crassigyrinus* and the baphetid tetrapods. Updated 2006.
Clack, J. A. 2000. Gaining ground – the water to land adventure (in Japanese). Kodansha, Japan. (A commissioned semi-popular book on the emergence of tetrapods.)
Clack, J. A. 2000. The origin of tetrapods. Amphibian Biology Volume 4, Paleontology; Chapter 2. In Heatwole, H. & Carroll, R. L. (eds) Surrey Beatty. pp. 973–1029.
Clack, J. A. 2002. Gaining ground: the origin and evolution of tetrapods. Bloomington, Indiana, USA: Indiana University Press. 369 pp.
Clack, J. A. 2005. Fossil vertebrates – Palaeozoic non-amniote tetrapods. Encyclopaedia of Geology. Elsevier, Oxford 2, 468–497.
Clack, J. A. 2012. Gaining Ground second edition. Indiana University Press. ISBN 978-0-253-35675-8. 523 pp.
Clack, J. A. 2014. Fossil vertebrates – Palaeozoic non-amniote tetrapods. Reference Module in Earth Systems and Environmental Science. Elsevier. (Online update of Encyclopaedia of Geology 2005. Elsevier, Oxford 2, 468–97).
Clack, J. A. 2016. Land vertebrates, the origin and evolution of. In Kilman, R.M. (ed.) *Encyclopedia of evolutionary biology*, Volume 2, 296–304. Oxford: Academic Press.
Clack, J. A. 2016. Vertebrate diversity in a sensory system: the fossil record of otic evolution. In Clack, J. A., Fay R. & Popper, A. N. (eds) *Evolution of the vertebrate ear: evidence from the fossil record*, Volume 59, 1–16. Springer Handbook of Acoustical Research.
Clack, J. A. 2017. The East Kirkton Lagerstätte: A window onto Early Carboniferous land ecosystems. In Fraser, N. C & Sues, H. D. (eds) *Terrestrial lagerstätten*. Dunedin. Chapter 2, 39–64.
Clack, J. A., Sharp, E. L. & Long, J. A. 2011. The fossil record of lungfishes. In Jørgensen, J. M. & Joss, J. (eds) The biology of lungfishes, 1–42. Enfield, New Hampshire, USA: Science Publishers Inc.
Clack, J. A. & Allin, E. 2004. The evolution of single- and multiple-ossicle ears in fishes and tetrapods. In Manley, G. A., Popper, A. & Fay, R. R. (eds) *Evolution of the vertebrate auditory system*, 128–63. New York: Springer-Verlag.
Clack, J. A. & Ahlberg, P. E. 2016. Sarcopterygians: from lobe-finned fishes to the tetrapod stem group. In Clack, J. A., Fay R. & Popper, A. N. (eds) *Evolution of the vertebrate ear: evidence from the fossil record*, Volume 59, 51–70. Springer Handbook of Acoustical Research.
Clack, J. A. & Anderson, J. S. 2016. Early tetrapods: experimenting with form and function. In Clack, J. A., Fay R. & Popper, A. N. (eds) *Evolution of the vertebrate ear: evidence from the fossil record*, Volume 59, 71–106. Springer Handbook of Acoustical Research.
Clack, J. A & Carroll, R. L. 2000. Early Carboniferous tetrapods. In Heatwole, H. & Carroll, R. L. (eds) *Amphibian biology*, Volume 4, Paleontology; Chapter 3 Surrey Beatty. pp. 1030–1043.
Fraser, N. C., Smithson, T. R. & Clack, J. A. 2018. A legacy in fossils: a tribute to Stan Wood – preface. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 1–5.
Manley, G. A. & Clack, J. A. 2004. An outline of the evolution of vertebrate hearing organs. In Manley, G. A., Popper, A. & Fay, R. R. (eds) Evolution of the vertebrate auditory system, 1–26. New York: Springer-Verlag.

6.5. Published abstracts

Ahlberg, P. E. & Clack, J. A. 1997. The lower jaws of early tetrapods: morphology and evolution. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 17, suppl 3, p. 28A.
Ahlberg, P. E., Clack, J. A. & Blom, H. 2003. The axial skeleton of the Devonian Tetrapod *Ichthyostega*. In Schultze, H.-P., Luksevics, E. & Unwin, D. (eds) The Gross Symposium 2. Advances in *palaeoichthyology*, Ichthyolith Issues Special Publication Volume 7, pp. 7–8.
Ahlberg, P. E., Besnosov, P., Luksevics, E., & Clack, J. A. 2010. A primitive Devonian tetrapod from the Lower Famennian of South Timan. Third International Palaeontological Congress, London. Abstracts. p. 66.
Ahlberg, P. E., Beznosov, P., Lukševičs, E. & Clack, J. A. 2011. A very primitive tetrapod from the earliest Famennian of South Timan, Russia. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 31, suppl 2, p. 60A.
Anderson, J. S., Brazeau, M., Carroll, R. L. & Clack, J. A. 2009. A diverse tetrapod fauna at the base of Romer's Gap. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 29, suppl, p. 54A.
Bennet, C. E., Clack, J. A., Kearsey, T., Davies, S. J., Millward, D., Smithson, T.R., Ruta, M., Otoo, B. K. A., Marshall, J. E. A., Reeves, E. & Ross, R. 2015. Five new Tournaisian tetrapods: their sedimentology and palaeoenvironments. Palaeontological Association annual meeting, Abstracts volume. p. 18.
Bennett, C. E., Davies, S. J., Kearsey, T. I., Millward, D., Smithson, T. R., Clack, J. A., Brand, M., Ross, A. J., Clark, N. & Ruta, M.

2016. Emergence of the modern freshwater food web in the early Carboniferous. (poster) Palaeontological Association annual meeting Abstracts. p. 57.

Blom, H., Clack, J. A., Ahlberg, P. E. & Friedman, M. 2003. Devonian vertebrates from East Greenland: a review of faunal composition and distribution. In Schultze, H.-P., Luksevics, E. & Unwin, D. (eds) The Gross Symposium 2. Advances in *palaeoichthyology*, Ichthyolith Issues Special Publication Volume 7, 13.

Blom, H., Ahlberg, P. E. & Clack, J. A. 2005. The postcranial skeleton of the Devonian tetrapod *Ichthyostega* from East Greenland. GFF 127, 44–45.

Bolt, J. R., Clack, J. A. & Lombard, R. E. 1994. The origin and early evolution of tetrapods: new fossil data and their interpretation. 4th International Congress of Vertebrate Morphology, Chicago, Abstracts. Journal of Morphology 220, 327–28.

Callier, V. & Clack, J. A. 2007. Comparative ontogeny of the humerus of *Ichthyostega* and *Acanthostega*. Ichthyolith Issues Special Publication 10, 23.

Challands, T., Bennett, C. E., Clack, J. A., Fraser, N. C., Kearsey, T., Marshall, J. E. A., Smithson, T. R. & Walsh, S. 2015. The Tournaisian: a sarcopterygian incubator? Palaeontological Association annual meeting, Abstracts volume. p. 57.

Challands, T. J., Smithson, T. R., Clack, J. A., Marshall, J. E. A. & Bennett, C. E. 2016. Earliest Carboniferous Dipnoi: post-Hangenberg recovery and the dawn of a new era of lungfish EAVP programme and abstracts volume. p. 89.

Clack, J. A. 1989. Affinities of *Acanthostega*. Published Abstracts, First World Congress of Herpetology, Canterbury, Kent.

Clack, J. A. 1993. Hard evidence and terrestriality in Devonian tetrapods – an assessment. Invited abstract in 'Paleoecology of Terrestrial Ecosystems'; Geological Society of America Annual Meeting Abstracts with Programs p. A–81.

Clack, J. A. 1993. How to tell a stapes from a hyomandibula, and homologies of the stapedial footplate; new evidence from *Acanthostega*. Journal of Vertebrate Paleontology. SVP Annual Symposium Published Abstracts. Volume 13, suppl 3. p. 30A.

Clack, J. A. 1993. The evolution of the fenestra ovalis and stapes in early tetrapods. 2nd World Congress of Herpetology, Adelaide – Abstracts. p. 57.

Clack, J. A. 1994. Otoliths in fossil coelacanths. 4th International Congress of Vertebrate Morphology, Chicago, Abstracts. Journal of Morphology 220, 333–34.

Clack, J. A. 1997. A new tetrapod taxon from the Viséan of East Kirkton, Scotland. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 17, suppl 3, p. 38A.

Clack, J. A. 1997. Head and shoulders knees and toes – the song of the earliest tetrapods? Plenary lecture. 5th International Congress of Vertebrate Morphology Bristol, Abstracts Journal of Morphology 232, 221–23.

Clack, J. A. 1997. The snout and external naris of *Crassigyrinus scoticus*, a primitive tetrapod from the Carboniferous of Scotland 3rd World Congress of Herpetology, Prague. Abstracts. pp. 42–43.

Clack, J. A. 1999. New fossils from the Famennian of East Greenland. In Luksevics, E., Stinkulis, G. & Wilson, M. V. H. (eds) Lower-Middle Palaeozoic *events* across the Circum-Arctic. Ichthyolith Issues Special Publication Volume 5, 15–17.

Clack, J. A. 2000. Head first: the skull roof in early tetrapods. Palaeontological Association Newsletter 45 Conference Abstracts. p. 10.

Clack, J. A. 2001. Patterns and processes in the early evolution of the tetrapod middle ear. ICVM-6 abstracts. J. Morph. 248–18.

Clack, J. A. 2001. Stepping into the Tournaisian: five toes and two fingers for early tetrapods. Palaeontological Association Newsletter 48 Conference Abstracts. p. 6.

Clack, J. A. 2002. A new whatcheeriid from the Tournaisian of western Scotland. IPC 2002, Geological Society of Australia Abstracts 68, 34.

Clack, J. A. 2008. The emergence of tetrapods: how far have we come in the last 20 years, and where can we go in the next? Annual Address, 52nd Palaeontological Association Annual Meeting, Palaeontological Society Newsletter 69, Abstracts p. 12.

Clack, J. A. 2009. A probable microsaur from the Early Carboniferous of East Kirkton, Scotland, showing soft-tissue evidence. Journal of Vertebrate Paleontology 29, 79A.

Clack, J. A. 2009. On the 'imperfection of the geological record': recent palaeontological discoveries to delight Darwin. Comparative Biochemistry and Physiology A 153, S545.

Clack, J. A., Lombard, R. E. & Bolt, J. R. 1995. The Paleozoic Preserve Project. An interactive world wide web site for systematic data. Journal of Vertebrate Paleontology. SVP Annual Symposium Published Abstracts. Volume 15, p. 24A.

Clack J. A., Ahlberg, P. E., Ketcham, R. A. & Dominguez Alonso, P. 2002. The braincase and ear region of *Ichthyostega*: a uniquely specialised ear in an exceptionally primitive tetrapod braincase IPC 2002, Geological Society of Australia Abstracts 68, 34.

Clack, J. A., Ahlberg, P. E. & Blom, H. 2003. *Ichthyostega*: the makeover. Palaeontological Association 47rd Annual Meeting. Palaeontological Association Newsletter 54, 166.

Clack, J. A., Blom, H. & Ahlberg, P. E. 2003. New insights into the forelimb skeleton of *Ichthyostega*. In Schultze, H.-P., Luksevics, E. & Unwin, D. (eds) The Gross Symposium 2. Advances in Palaeoichthyology, Riga, Latvia, Ichthyolith Issues Special Publication Volume 7, 17.

Clack, J. A., Blom, H. & Ahlberg, P. E. 2003. New insights into the postcranial skeleton of *Ichthyostega*. Journal of Vertebrate Paleontology 23, suppl 3, 41A.

Clack, J. A., Ahlberg, P. E. & Blom, H. 2004. A new genus of tetrapod from the Devonian of East Greenland. Palaeontological Association Newsletter 57, 116–17.

Clack, J. A., Ahlberg, P. E. & Blom, H. 2004. *Ichthyostega*: innovative, but not intermediate. ICVM Abstracts, Journal of Morphology 260, 283.

Clack, J. A., Ahlberg, P. E. & Blom, H. 2005. Ontogeny of the humerus in *Ichthyostega*. North American Palaeontological Convention abstracts. PaleoBios, 25, suppl 2, 30.

Clack, J. A., Smithson, T. R. & Anderson, J. 2014. Evolution of the tetrapod appendicular skeleton: new evidence from Romer's Gap. 74th SVP Annual Meeting, Berlin Journal of Vertebrate Palaeontology abstract volume. p. 109A.

Clack, J. A., Ruta, M. & Smithson, T. R. 2016. Phylogenetic analysis (and additional specimens) imply early diversification of tetrapods in the Tournaisian. Palaeontological Association annual meeting Abstracts. p. 25.

Clack, J. A., Ruta, M. & Smithson, T. R. 2016. Phylogenetic analysis implies early diversification of tetrapods in the Tournaisian. Symposium of Vertebrate Palaeontology and Comparative Anatomy Abstracts. p. 17.

Clack, J. A., Smithson, T. R. & Challands, T. J. 2017. New Late Devonian lungfishes from Greenland morphologically and phylogenetically blur the D-C boundary. Symposium of Vertebrate Palaeontology and Comparative Anatomy Abstracts. p. 41.

Clack, J. A., Ruta, M., Milner, A. R., Marshall, J. E. A., Smithson, T. R. & Smithson, K. Z. 2018. *Acherontiscus*, the earliest durophagous tetrapod redux. Symposium of Vertebrate Palaeontology and Comparative Anatomy Abstracts. p.36.

Clack, J. A. & Ahlberg, P. E. 1998. A reinterpretation of the braincase of *Ichthyostega stensioei*. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. 18, suppl 3, 34A.

Clack, J. A. & Ahlberg, P. E. 2002. A new stem tetrapod from the mid-Carboniferous of Northern Ireland. Journal of Vertebrate Paleontology 22, 44A.

Clack, J. A. & Finney, S. M. 1997. An articulated tetrapod specimen from the Tournaisian of Western Scotland. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 17, suppl 3, 38A.

Clack, J. A. & Milner, A. R. 2007. The amphibamid *Platyrhinops*, morphology and metamorphosis. Journal of Vertebrate Paleontology, 27, 59A.

Clack, J. A. & Smithson, T. R. 2013. Diversity among new Tournaisian tetrapods from Scotland. Palaeontological Association annual meeting, Abstract volume. p. 29.

Clack, J. A. & Smithson, T. R. 2015. Tetrapod diversity in the Tournaisian IGCP Strata. **16**, 33–34.

Clack, J. A. & Smithson, T. R. 2016. Morphological innovations in the earliest post-Devonian tetrapods: adaptations for terrestriality? European Association of Vertebrate Palaeontology programme and abstracts volume. p. 91.

Daeschler, E. B., Clack, J. A. & Shubin, N. H. 2007. Early tetrapod remains from the Red Hill site in Pennsylvania (Catskill Formation; Upper Devonian): how much diversity: Ichthyolith Issues Special Publication. 10, 30.

Davies, S. J., Bennett, C. E., Kearsey, T. I., Millward, D., Clack, J. A., Smithson, T. R., Marshall, J. E. A., Reeves, E., Fraser, N. A., Walsh, S. A., Ross, A. & Sherwin, J. 2016. Early Mississippian palaeoenvironments and their significance for tetrapod preservation. British Sedimentological Research Group. Abstracts volume. p. 31.

Edge, M., Clack, J. A. & Beck, J. 2006. New skeletal and dental material of Mississippian chondrichthyans from Derbyshire, UK Palaeontological Association Newsletter 63, 53.

Klembara, J., Clack, J. A., Milner, A. R. & Ruta, M. 2011. The Late Carboniferous tetrapod *Gephyrostegus bohemicus* Jaekel, 1902: the anatomy of the skull and relationships. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 31, suppl, p. 22A.

Long J., Graham J., Clack J. A. & Ahlberg P. 2011. The origins of air-breathing in tetrapodomorph vertebrates. Early Vertebrates, Lower Vertebrates, Texas, 7.

Luksevics, E., Ahlberg, P. E. & Clack, J. A. 2003. The dermal skull roof and braincase of the early tetrapod *Ventastega curonica* from the Late Devonian of Latvia. In Schultze, H.-P., Luksevics, E. & Unwin, D. (eds) The Gross Symposium 2. Advances in Palaeoichthyology, Ichthyolith Issues Special Publication. Volume 7, 36–37.

Malavasi, S., Polgar, G., Cipolato G., Georgalas, V., Clack, J. & Torricelli, P. 2010. Sound production in a mudskipper (*Periophthalmodon septemradiatus*): Implications for the study of evolutionary convergence related to the vertebrate water-land transition. Joint meeting of Ichthyologists and Herpetologists. Program Book. Providence Rhode Island, p. 26.

Marshall, J. E. A., Reeves, E., Bennett, C. E., Davies, S. J., Kearsey, T. I., Millward, D., Smithson, T. R. & Clack, J. A. 2016. The Ballagan Formation, the CM spore zone and the Tournaisian of Scotland. XIV International Palynological Congress X International Organisation of Palaeobotany Conference, *Boletín de la Asociacíon Latinoamericana de Paleobotánica y Palinología* 16, 102.

Marshall, J. E. A., Reeve, E., Bennett, C. E., Davies, S. J., Kearsey, T. I., Millward, D., Smithson, T. R., Browne, M. E. A. & Clack, J. A. 2018. The first palynological assemblage from the Famennian of Scotland and its significance for understanding early tetrapod relationships. https://ipc5.sciencesconf.org/user/submissions?docid=194273.

Molnar, J., Pierce, S. E., Clack, J. A. & Hutchinson, J. 2011. New features and biomechanics of the axial skeleton of the early tetrapod *Pederpes finneyae*. Journal of Vertebrate Paleontology abstract volume 160A.

Pierce, S. E., Molnar, J., Hutchinson, J. R. & Clack, J. A. 2010. Comparative biomechanics of the axial skeleton in potential extant analogues for early tetrapod locomotor function. 9th International Congress of Vertebrate Morphology, Uruguay.

Pierce, S. E., Molnar, J., Hutchinson, J. R. & Clack, J. A. 2010. Regional variation of intervertebral joint stiffness: importance for the water-land transition. Journal of Vertebrate Paleontology 30, 146A.

Pierce, S. E., Clack, J. A. & Hutchinson, J. 2011. Comparative limb range of movement in the Devonian tetrapod *Ichthyostega* and the evolution of terrestrial locomotion. Journal of Vertebrate Paleontology abstracts 174A.

Pierce, S. E., Hutchinson, J. R. & Clack, J. A. 2013. Historical evolution of early tetrapod movement. Society of Integrative and Comparative Biology.

Platt, C. & Clack, J. A. 1997. A proposed evolutionary derivation of hair cell patterns in the lagena of the inner ear. 5th International Congress of Vertebrate Morphology, Bristol, Abstracts Journal of Morphology 232, p. 308.

Porro, L., Rayfield, E. & Clack, J. 2013. 3-D reconstruction and analysis of the early tetrapod lower jaw. ICVM 10 Barcelona, Programme and Abstract volume.

Porro, L., Rayfield, E. & Clack, J. 2013. Computed tomography, digital preparation and three-dimensional reconstruction of the early tetrapod lower jaw. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 33, suppl, p. 70A.

Porro, L. B., Rayfield, E. J., & Clack, J. A. 2014. Tetrapods rising: 3D reconstruction and finite element analysis of the lower jaw across the water-land transition. Abstract Volume: 4th International Palaeontological Congress, Mendoza, Argentina, p. 597.

Reeves, E., Marshall, J. E. A., Bennett, C. E., Davies, S. J., Kearsey, T. I., Millward, D., Smithson, T. R. & Clack, J. A. 2016. Tournaisian (early Carboniferous) palynology of the West Mains Farm Borehole, UK. XIV International Palynological Congress X International Organisation of Palaeobotany Conference, *Boletín de la Asociacíon Latinoamericana de Paleobotánica y Palinología* 16, 103–04.

Richards, K. R., Sherwin, J. E., Smithson, T. R., Bennion, R. F., Davies, S. J., Marshall, J. E. A. & Clack, J. A. 2015. A new fauna of early Carboniferous chondrichthyans from the Scottish Borders. Palaeontological Association annual meeting, Abstracts volume. p. 75.

Richards, K. R. & Clack, J. A. 2011. A mid-Carboniferous chondrichthyan braincase from the Peak District of Derbyshire, UK. Journal of Vertebrate Paleontology SVP Annual Symposium Published Abstracts. Volume 31, suppl, p. 178A.

Richards, K. R. & Clack, J. A. 2014. A new Carboniferous chondrichthyan from the Derbyshire Limestone, UK. 74th SVP Annual Meeting, Berlin Journal of Vertebrate Palaeontology abstract volume. p. 214A.

Sanchez, S., Tafforeau, P., Clack, J. A., Daeschler, E. B & Ahlberg, P. E. 2009. Limb bone histology across the fish – tetrapod transition. Journal of Vertebrate Paleontology 29, 175A.

Smithson, T. R., Richards, K., Bennion, R. & Clack, J. A. 2014. Chondrichthyan diversity in the Early Carboniferous: new evidence from the Tournaisian of northern Britain. 74th SVP Annual Meeting, Berlin Journal of Vertebrate Palaeontology abstract volume. p. 232A.

Smithson, T. R., Richards, K. R. & Clack, J. A. 2015. Romer's Gap, the beginning of the modern fish fauna. IGCP Strata **16**, 132–33.

Smithson, T. R., Anderson, J. S., Mansky, C. F. & Clack, J. A. 2015. Tetrapods from the Tournasian of Nova Scotia and northern Britain: new evidence of tetrapod diversity in the Early Carboniferous. Atlantic Geosciences Colloquium and Annual Meeting abstract volume. p. 39.

Smithson, T. R., Clack, J. A., Anderson, J. S. & Mansky, C. 2015. Tournaisian tetrapods of Nova Scotia and northern Britain: diversity, associated fauna and environmental setting. Palaeontological Association annual meeting, Abstracts volume. p 76.

Smithson, T. R., Bennett, C. E., Clack, J. A., Davies, S. J., Kearsey, T. I., Marshall, J. E. A., Millward, D. & Sherwin, J. 2016. Predicting the likely location of new early tetrapod sites: lessons from recent discoveries in Romer's Gap. European Association of Vertebrate Palaeontology programme and abstracts volume. p. 90.

Smithson, T. R., Challands, T., Hill, H., Richards, K. R., Smithson, K. & Clack, J. A. 2016. The diverse dentition of Early Carboniferous lungfish: an adaptive response to the end-Devonian extinction? Symposium of Vertebrate Palaeontology and Comparative Anatomy Abstracts. p. 29.

Smithson, T. R., Bennett, C. E., Clack, J. A., Clark, N., Davies, S. J., Edgecombe, G. D., Kearsey, T. I., Marshall, J. E. A., Millward, D., Ross, A. J. & Sherwin, J. E. 2016. Where to find the Carboniferous terrestrial fauna: recent discoveries in Romer's Gap point the way. Palaeontological Association annual meeting Abstracts. p. 50.

Smithson, T. R. & Clack, J. A. 2013. New tetrapod and fish faunas from the Earliest Carboniferous of Scotland. ICVM 10 Barcelona, Programme and Abstract volume.

Smithson, T. R. & Clack, J. A. 2013. Romer's Gap: a surprisingly productive period in vertebrate evolution. Palaeontological Association annual meeting, Abstract volume. p. 56.

Smithson, T. R. & Clack, J. A. 2013. Tetrapod and fish faunas from the earliest Carboniferous of Scotland. 73rd SVP Annual Meeting, Los Angeles Journal of Vertebrate Paleontology abstract volume. p. 215A.

Smithson, T. R. & Clack, J. A. 2016. Morphological innovations in the earliest post-Devonian tetrapods: adaptations for terrestriality? International Congress on Vertebrate Morphology 11 Anatomical Record 299 special feature. p. 189.

6.6. Solicited reviews

Ahlberg, P. E. & Clack, J. A. 2006. A firm step from water to land. News and Views Nature 440, 747–49.

Benton, M. J., Briggs, D. E. G., Clack, J. A., Edwards, D., Galway-Witham, J., Stringer, C. B. & Turvey, S. T. 2017. Russia-UK collaboration in palaeontology: past, present, and future. *Paleontological Journal* 51, 576–99.

Clack, J. A. 2004. From Fins to Fingers, Perspectives. *Science* 304, 57–58.

Clack, J. A. 2015. The origin of terrestrial hearing. News and Views. *Nature* 519, 168–69.

6.7. Edited volumes

Clack, J. A., Fay, R. & Popper, A. N. (eds) 2016. Evolution of the Vertebrate Ear: Evidence from the Fossil Record. Springer Handbook of Acoustical Research. Volume 59.

Ruta, M., Clack, J. A. & Milner, A. C. (eds) 2009. Patterns and processes in early vertebrate evolution. Special Papers in Palaeontology 81, 1–173.

Sánchez-Villagra M. R. & Clack, J. A. (eds) 2004. Fossils of the Miocene Castillo Formation, Venezuela: Contributions in Neotropical Palaeontology. Special Papers in Palaeontology 71, 1–112.

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press

6.8. Popular, semi-popular and non-refereed articles

Clack, J. A. 1987. Museum File 10: University Museum of Zoology, Cambridge. *Geology Today* 3, 70–71.
Clack, J. A. 1988. Pioneers of the land in East Greenland. *Geology Today* 4, 6, 407.
Clack, J. A. 1990. Early tetrapod hearing. Sci. Corresp. *Nature* 344, 6269.
Clack, J. A. 1990. Nos ancêtres, respiraient-ils par les oreilles? *La Recherche* 21, 770–71. (Invited article.)
Clack, J. A. 1995. Tetrapoda. Invited piece for McGraw-Hill *Yearbook of Science and Technology for 1996*. pp. 339–41.
Clack, J. A. 1997. Les premiers tétrapodes vivaient dans l'eau. *La Recherche* (Invited article) 296, 58–61. (Also published in Spanish, in Mundo Cientifico.)
Clack, J. A. 1998. Vertebrate Evolution. McGraw-Hill *Yearbook of Science and Technology for 1999.* pp. 389–92.
Clack, J. A. 2004. Finding our Feet. In 'Miracle Planet: part 3' NHK publications. pp. 78–105 (translated into Japanese).
Clack, J. A. 2005. Getting a leg up on land. Invited article. *Scientific American* 293, 100–07.
Clack, J. A. 2006. From fins to limbs. *Natural History Magazine* 115, 36–41.
Clack, J. A. 2006. Le premier pied à terre. *Pour la Science*. 340, 30–36.
Clack, J. A. 2006. Tetrapod origins. McGraw-Hill *Yearbook of Science and Technology.* pp. 325–27.
Clack, J. A. 2007. Anthracosauria, *In* McGraw-Hill Encyclopedia of Science & Technology, Volume 2, pp. 30–31. McGraw-Hill, New York.
Clack, J. A. 2008. Devonian Missing Link: *Tiktaalik roseae*. *McGraw-Hill Yearbook of Science & Technology*, 10th edn. McGraw-Hill, New York, 2008, pp. 91–93.
Clack, J. A. 2008. Overview from the chair: Sea to Sand. Proceedings of the 2007 Moray Society. Conference. Moray Society, Elgin Museum, Elgin, Moray, Scotland. pp. 7–10.
Clack, J. A. 2010. What is a tetrapod? Grzimek's Animal Life. Gale Web 17 May.
Clack, J. A. 2015. BBC Focus Magazine.

6.9. Book reviews

Clack, J. A. 1987. Evolution of Vertebrate Design by L. B. Radinsky, Chicago Univ. Press. *Palaeontological Association Newsletter*.
Clack, J. A. 1990. The Dicynodonts by G.M. King, Chapman and Hall. *Trends in Ecology and Evolution* **5**, 376–77.
Clack, J. A. 1994. Palaeozoic Vertebrate Biostratigraphy and Biogeography. In Long, J. A. (ed.) *Historical biology*, Volume 9, 237–42. Belhaven Press.
Clack, J. A. 1997. The Devonian tetrapod *Ichthyostega*. E. Jarvik. Fossils and Strata 40, 1–213. *Palaeogeography, Palaeoclimatology, Palaeoecology* **128**, 365–74.
Clack, J. A. 1998. History of the Coelacanth Fishes P. L Forey. Chapman & Hall – Natural History Museum TREE.
Clack, J. A. 2005. Digging for clues. Review of 'Discovering Dorothea: the life of the pioneering fossil-hunter Dorothea Bate', by Karolyn Schindler. *Nature* 438, 163–64.
Clack, J. A. 2007. Fins into Limbs: evolution, development and transformation. In Hall, B. K. (ed.) Chicago University Press. *Palaeontological Association Newsletter* 65, 111–15.
Clack, J. A. 2008. 'Your Inner Fish', by N. H Shubin. *Journal of Clinical Investigation* 118, 2370.
Clack, J. A. 2011. 'How vertebrates left the water' by M. Laurin. *Copeia* 2011, 615–17.
Clack, J. A. 2015. 'When the invasion of the land failed' by G. McGhee. *Quarterly Review of Biology*. March. 81.

6.10. Miscellaneous publications

Hanney, P. W. 1975. Rodents: their lives and habits. David and Charles. Produced the illustrations (as Jenny Agnew).

6.11. Work for commercial publishers

Supply of text and photographs for Dorling Kindersley 2009: 'Prehistoric'.

https://doi.org/10.1017/S1755691019000057 Published online by Cambridge University Press