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Novel approaches to the environments and ecosystems of the fish-tetrapod transition

HANNAH BYRNE



ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2022

ISSN 1651-6214
ISBN 978-91-513-1581-2
URN urn:nbn:se:uu:diva-482647

Dissertation presented at Uppsala University to be publicly examined in Ekmansalen, Evolutionsbiologiskt centrum,, Norbyvägen 14, Uppsala, Thursday, 13 October 2022 at 13:25 for the degree of Doctor of Philosophy. The examination will be conducted in English. Faculty examiner: Associate Professor, Director Museum of Paleontology Matt Friedman.

Abstract

Byrne, H. 2022. Novel approaches to the environments and ecosystems of the fish-tetrapod transition. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 2182. 57 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-513-1581-2.

The fish-tetrapod transition is one of the most important evolutionary events in Earth's history, giving rise to terrestrial vertebrates around 390 million years ago. It set the stage for a series of evolutionary events that ultimately resulted in modern-day terrestrial vertebrates including ourselves. The fish-tetrapod transition occurred during the Middle Palaeozoic and although it has been the subject of intense study over the last century, many questions remain unanswered. In this thesis, novel techniques were used to help elucidate certain aspects of the fish-tetrapod transition. The first project sought to use numerical tidal simulations to test the premise of a hypothesis that large tides occurred during the Middle Palaeozoic and acted as a driver for the evolution of lungs and limbs. The simulations produced for the Late Silurian-Late Devonian revealed unusually large tides during the Late Silurian, thus the origin of lungs, supporting the hypothesis that deoxygenated tidal pools could have been the setting for this evolutionary step. The following three projects used propagation phase-contrast synchrotron microtomography (PPC-SR μ CT) to analyse new tetrapod material from the terminal Famennian (latest Devonian) and coprolite material from the earliest Tournaisian of Greenland (earliest Carboniferous), spanning a mass extinction event (the Hangenberg crisis) believed to have impacted early tetrapod diversity. Spectacular data sets were generated using this technique, with analysis of the tetrapod material revealing the presence of new taxa, making East Greenland home to the greatest known diversity of tetrapods in the world during the Devonian. Synchrotron scanning allowed for the accurate determination of coprolite morphotypes from a post-Hangenberg crisis lake deposit, revealing greater diversity among the coprolites compared with vertebrate body fossil taxa and thus demonstrating that the fauna contained additional taxa not captured by the body fossil record. Most of the large coprolites are non-spiral and were probably produced by a large aquatic tetrapod. One large coprolite is spiral and is postulated to have been produced by a chondrichthyan. Virtual reconstructions of several coprolites were generated using the scan data. The largest coprolites were full of actinopterygian and acanthodian remains, showing that the probable tetrapod was a proficient aquatic predator. Another large coprolite contained remains of two new body fossil taxa; an actinopterygian and small tetrapod. The coprolite data challenge our initial interpretation of a low-diversity lake fauna, revealing instead a complex ecosystem immediately after a major mass extinction event. Tetrapods and chondrichthyans appear to have been the apex predators in this ecosystem. This thesis demonstrates the capabilities of two novel analytical techniques, tidal simulation and synchrotron microtomography, to uncover previously inaccessible information about the fish-tetrapod transition and its environmental-ecological context.

Keywords: fish-tetrapod transition, synchrotron scanning, tides, coprolites, Carboniferous

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ISSN 1651-6214

ISBN 978-91-513-1581-2

URN urn:nbn:se:uu:diva-482647 (<http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-482647>)

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The front cover image is of the East Greenland Devonian Basin, taken by Grzegorz Niedzwiedzki during fieldwork in 2022

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. **Byrne, H. M.**, Green, J. A. M., Balbus, S. A., Ahlberg, P. E. (2020) Tides: A key environmental driver of osteichthyan evolution and the fish-tetrapod transition? *Proceedings of the Royal Society A*, 476(2242), 202003554
- II. **Byrne, H. M.**, Niedźwiedzki, G., Blom, H., Kear, B. P., Ahlberg, P. E. Coprolite diversity reveals a cryptic ecosystem from the Devonian-Carboniferous boundary in East Greenland. *Accepted in Palaeogeography, Palaeoclimatology, Palaeoecology*.
- III. **Byrne, H.M.**, During, M. A. D., Niedźwiedzki, G., Blom, H., Kear, B. P., Ahlberg, P. E. The implications of coprolites from the Devonian-Carboniferous boundary in East Greenland. *Manuscript*.
- IV. **Byrne, H.M.**, Niedźwiedzki, G., Blom, H., Kear, B. P., Ahlberg, P. E. New tetrapod material from the terminal Famennian of East Greenland. *Manuscript*.

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The following manuscripts were worked on during my PhD but have not been included in this thesis:

- I. Ahlberg, P. E., Niedźwiedzki, G., Long, J., Stössel, I., Marugán-Lobón, J., Dupret, V., **Byrne, H. M.**, Qvarnström, M., Clement, A., Lewenstam, W. Terrestrial tetrapods and giant arthropods in a Middle Devonian ecosystem *Manuscript*.
- II. Dupret, V.; **Byrne, H. M.**, Castro, N., Hammer, Ø., Higgs, K., Long, J., Niedźwiedzki, G., Qvarnström, M., Stössel, I., Ahlberg, P. E. The *Bothriolepis* (Placodermi, Antiarcha) material from the Valentia Slate Formation of the Iveragh Peninsula (middle Givetian, Ireland): morphology, evolutionary and systematic considerations, phylogenetic and palaeogeographic implications. *Manuscript*.

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Abbreviations

AFS	Anal fin spine
Bc	Braincase
D-C	Devonian-Carboniferous
DFS	Dorsal Fin Spine
F-t	Fish-tetrapod
FS	Fin Spine
Ma	Million years ago
MCF	Missing Caudal Fin part
OBF	Obrutschew Bjerg Formation
PPC-SR μ CT	Propagation Phase-Contrast Synchrotron Microtomography
SBF	Stensiö Bjerg Formation
SR	Sclerotic Ring
VFS	Ventral Fin Spine

Introduction

Vertebrates, both terrestrial and aquatic, are one of the most successful animal groups occurring globally in a diverse range of environments. The origin of vertebrates (including ourselves) can be traced back to the Cambrian explosion with the appearance of various soft-bodied taxa like *Haikouichthys* and *Metaspriggina* in China and Canada in the Early to Middle Cambrian (542-499 Million years ago (Ma)) (Friedman and Sallan, 2012). These organisms have been attributed to belonging to the vertebrate total or crown group (Shu et al., 2003, 1996). The Middle Palaeozoic era (Late Silurian-Early Carboniferous; 420 Ma – 355 Ma; **Figure 1**) encompassed a fundamental period in early vertebrate evolution. By the Late Silurian, the four major gnathostome (jawed fish) groups had emerged. These are the extant Chondrichthyes (cartilaginous fish) and Osteichthyes (bony fish), and the extinct groups of Placodermi (armoured fish) and Acanthodii (spiny sharks) (Friedman and Sallan, 2012).

These four groups went through a period of rapid diversification during the Devonian period, dubbed the “Age of fishes”, with Placoderms reaching their peak diversity (Sallan and Coates, 2010). The earliest crown-group members of Actinopterygii (ray-finned fish) and Sarcopterygii (lobed-finned fish) occur in the Early Devonian, which are both osteichthyan sub-groups (Lu et al., 2016; Zhu and Schultze, 1997). By the Middle Devonian (390 Ma), the emergence of the first terrestrial vertebrates occurred as documented by trackway data from Poland and Ireland (Niedźwiedzki et al., 2010; Stössel et al., 2016) (**Figure 1**). This period of diversification is contrastingly followed by one of the six major mass extinctions in Earth’s history, the Late Devonian extinction event. It consisted of two extinction events: The Kellwasser extinction at the Frasnian-Famennian (F-F; 370 Ma) boundary and the Hangenberg extinction event at the Devonian-Carboniferous (D-C; 360 Ma) boundary (**Figure 1**). The Kellwasser event predominantly impacted marine fauna in near-shore environments, resulting in a 50-60% loss of marine genera (Carmichael et al., 2019). The Hangenberg extinction event affected both terrestrial and marine ecosystems and led to a 50% loss of all vertebrate taxa including the extinction of all placoderms, and is deemed by Sallan and Coates (2010) to be a “bottleneck in vertebrate evolution” (Sallan and Coates, 2010). The Late Devonian extinction episode consequently resulted in a major restructuring of vertebrate

ecosystems during the Early Carboniferous, which shaped the beginning of modern biodiversity (Sallan and Coates, 2010).

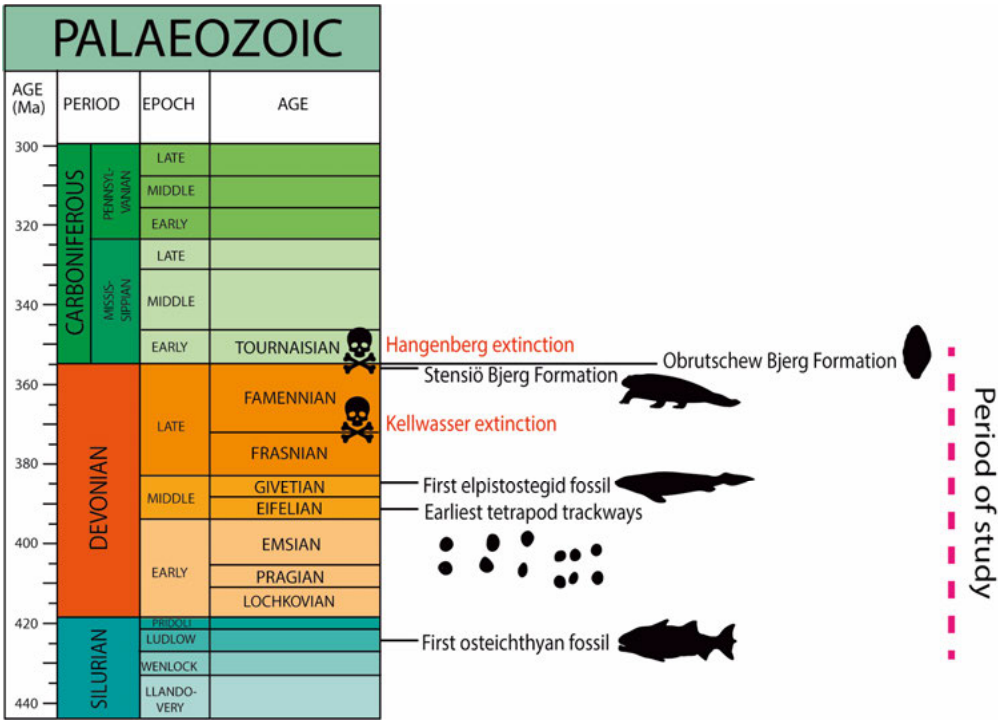


Figure 1. Geological timeline for part of the Palaeozoic era, with significant events and formations, highlighted within the period of study (Late Silurian- Early Carboniferous).

Arguably one of the most important evolutionary events to occur in Earth's history is the origin and evolution of tetrapods from the sarcopterygian group during the Middle Palaeozoic, known commonly as the fish–tetrapod transition. The fish-tetrapod transition encompasses the first and only complete transition of vertebrates from an aquatic to terrestrial setting. The emergence of tetrapods set in motion a long sequence of evolutionary events, including the rise and fall of dinosaurs, that has resulted in the terrestrial vertebrate assemblage of present-day, including ourselves (Clack, 2012). This transition has been the subject of intensive research over the last two centuries, with a central focus on body fossil remains and deducing what the animals may have looked like (Clack, 2002; Coates, 1996; Jarvik, 1955). However, less focus has been placed on the environments and ecosystems during the transition. It is a more straightforward process to describe a body fossil specimen than to contextualise the environment and the ecosystem in which a fossil is found.

This is especially true if the right tools are not available to fully extract information from surrounding material like ichnofossils (trace fossils) and sedimentological data.

New technologies now allow us to investigate aspects of the environmental and ecological context in a capacity which could not be achieved prior to a decade ago (Ahlberg and Clack, 2020; Green et al., 2017; Qvarnström et al., 2017; Sanchez et al., 2012). Two of these technologies will be exhibited in this thesis, which are used to explore two environmental and ecosystem topics directly related to the fish-tetrapod transition during the Middle Palaeozoic: numerical tidal simulations to investigate tidal regimes during the fish-tetrapod transition in the Late Silurian to Middle Devonian (**Paper I**), and synchrotron microtomography as a tool to investigate tetrapod body fossils and ecosystems across the Devonian-Carboniferous boundary in a unique section of East Greenland (**Papers II-IV**).

Drivers of the fish-tetrapod transition

Drivers behind the fish-tetrapod transition are poorly understood, right from the emergence of the sarcopterygian group in the Late Silurian up to the occurrence of the first terrestrial tetrapods (Ahlberg, 2018; Clack, 2012)(**Figure 1**). The transition consists of a series of important adaptations to a terrestrial lifestyle, two of the most notable being the development of lungs for air-breathing and limbs for terrestrial locomotion (Ahlberg, 2018; Clack, 2012).

Several hypotheses have been put forward as to why the transition took place. The earliest came from Barrell in 1916, who proposed that the Old Red Sandstone (ORS) from the Devonian represented an arid climate and so an air-breathing organ (which originated in the osteichthyan group) emerged in response to hypoxic/anoxic condition in shrinking pools (Barrell, 1916; Perry et al., 2001). This hypothesis was adapted by Romer in 1933 to suggest that shrinking pools in an arid climate were also a driver in the development of limbs for animals to manoeuvre to replenished water bodies (Romer, 1933). We now know that the ORS actually represent fluvial environments e.g., distributive fluvial systems (McKellar and Hartley, 2021; Trewin et al., 2012). Contemporary hypotheses, therefore, place a focus on marginal aquatic environments as the central evolutionary setting for the fish-tetrapod transition (Balbus, 2014; Colbert, 1955; Niedzwiedzki et al., 2010; Retallack, 2011; Schultze, 1999). An example is the woodland hypothesis which proposes that limbs were selected to competently manoeuvre and hunt in shallow-flooded woodlands (Retallack, 2011).

Another hypothesis pertains to the impact of tides (Balbus, 2014; Niedźwiedzki et al., 2010; Schultze, 1999). The role of tides on the fish-tetrapod transition has been the subject of numerous studies by both palaeontologists and developmental biologists, with a primary example pertaining to observations of analogous adaptations seen in the intertidal mudskipper (which are capable of exploiting supratidal and semi-terrestrial habitats) and tetrapod-like fish named elpistostegids, suggesting similar environmental pressures (Schultze, 1999; You et al., 2014). There are only a few studies aimed at quantifying tidal regimes during the fish-tetrapod transition, the majority of which have been done on a local scale using sedimentological features (Cloutier et al., 2011; Pontén and Plink-Björklund, 2007; Slingerland, 1986; Tanavsuu-Milkeviciene and Plink-Björklund, 2009; Tovmasjana, 2013). The most comprehensive intertidal hypothesis and study came from Balbus in 2014; large tides during the fish-tetrapod transition may have acted as a driver for the acquisition of lungs and limbs in response to repetitive stranding in warm stagnant tidal pools. In particular, if there was a large tidal range difference between spring tides and neap tides (i.e. spring-neap variation) individuals could be trapped in the upper intertidal zone for a prolonged time – possibly weeks. Balbus supported the hypothesis through a theoretical tidal model forced with the equilibrium tide which resulted in large tidal ranges near the equator for a palaeogeographic setting similar to that for the Devonian (Balbus, 2014).

As tides are a major component of the interaction between the marine and terrestrial environments, they likely played an important role in shaping the environmental context of the fish-tetrapod transition. Many of the earliest fossils of tetrapods and elpistostegids (e.g., *Panderichthys*, *Elpistostege*) are found in sediments identified as deltaic or estuarine, and isotopic evidence supports a euryhaline lifestyle (i.e., adapted to a wide range of salinities) (Ahlberg, 2018; Gess and Ahlberg, 2018; Goedert et al., 2018; Luksevics and Zupins, 2004). Furthermore, a study on ancestral vertebrate habitats suggested that many early vertebrate clades originated in shallow intertidal-subtidal environments (Sallan et al., 2018).

The generation of numerical tidal simulations using the Oregon State Tidal Inversion Software (OTIS), a dedicated numerical tidal model, is an approach which has been used to investigate deep-time tides as far back as the Cryogenian (Egbert et al., 2004; Green et al., 2020). OTIS will be used here to investigate whether large tidal ranges were present during key evolutionary events along the fish-tetrapod transition and if these large tidal regimes persist in areas of evolutionary interest.

Tetrapod ecosystems across the Devonian-Carboniferous boundary

As aforementioned, the Devonian-Carboniferous boundary was a tumultuous period for both faunal and floral assemblages, with the magnitude of extinction among jawed vertebrates comparable to that of the End Cretaceous and End Permian extinction events (Kaiser et al., 2016; Sallan and Coates, 2010). *Archaeopteris* forests completely disappeared as a result of the Hangenberg crisis, coral reefs disappeared and did not fully recover until the end of the Tournaisian (Kaiser et al., 2016).

The Hangenberg extinction event at the D-C boundary heavily impacted both marine and non-marine ecosystems, but at slightly different times over a span of around 100-300 thousand years (Kaiser et al., 2016; Marshall et al., 2020). The Hangenberg extinction event is a phased crisis consisting of three intervals; the lower crisis occurring in the upper Famennian, the middle crisis occurring right below the D-C boundary and the upper crisis occurring immediately at the boundary (Kaiser et al., 2016). The early and main phase of the Hangenberg crisis occurred in marine environments with black shale deposits associated with anoxic conditions, with the later phase impacting terrestrial ecosystems (Marshall et al., 2020; Sallan and Coates, 2010). The drivers behind the Hangenberg crisis have not been fully resolved, with many scenarios suggested including volcanic activity, anoxia, glaciation, asteroid impact, and supernovas (Caplan and Bustin, 1999; Fields et al., 2020; Glikson et al., 2005; Rakociński et al., 2020). It is therefore highly likely a combination of factors that drove the crisis throughout the different phases.

Fossil-bearing deposits across the D-C boundary are few, thus limiting our understanding of important faunal turnovers at this time. One of the poorest understood is that of tetrapods. There is a paucity in the tetrapod body fossil record beginning at the start of the Hangenberg crisis and persisting some 20 million years into the Carboniferous, colloquially referred to as Romer's gap (Clack, 2002). Although this gap is likely a result of sampling bias and has begun to fill in from body fossil findings from the Early Tournaisian of Canada and Scotland, the small sample of tetrapod body fossils, particularly at the D-C boundary, severely limits our understanding of the evolution of early tetrapods across the D-C boundary (Anderson et al., 2015; Clack, 2002; Smithson et al., 2012). It is of vital importance that any new fossil-bearing deposits from this period are studied in great detail. This will also aid in our understanding of ecosystem recovery after the Hangenberg crisis.

The Late Devonian-Early Carboniferous Celsius Bjerg Group of East Greenland is world-renowned as it yields the tetrapods *Ichthyostega* and *Acanthostega* (Astin et al., 2010)(**Figure 2 B-C**). These tetrapods remain the best

understood of all Devonian forms due to their completeness, preservation and number of specimens available, which is over 500 (Astin et al., 2010; Blom et al., 2007). Although the sediments and fossils of the Celsius Bjerg Group have been the focus of intense study for over a century, limited attention has been paid to the upper two formations; The Stensiö Bjerg Formation (SBF) and Obrutschew Bjerg Formation (OBF) (Ahlberg and Clack, 2020; Astin et al., 2010; Blom et al., 2007; Clack et al., 2012; Coates, 1996; Friedman and Blom, 2006; Jarvik, 1996; Marshall, 2020) (**Figure 1** and **2**). These two formations constitute what is probably the only known truly terrestrial sequence to span the D-C boundary with an ancient location in central Laurussia; the sequences analysed regarding the Hangenberg crisis are marine (Kaiser et al., 2016; Marshall, 2020) (**Figure 2A**). Expeditions to Greenland from 2009-2016 have yielded tetrapod body and ichnofossil remains from the Stensiö Bjerg Formation and fish body fossils and coprolites from the Obrutschew Bjerg Formation. The vertebrate fossils from the Stensiö Bjerg Formation represent the youngest Devonian tetrapod fossils (contemporaneous with *Tulerpeton* from Russia) and have not been previously described (Lebedev and Coates, 1995). The fossiliferous Obrutschew Bjerg Formation represents a deep permanent lake which occurs immediately above the D-C boundary, representing the earliest Carboniferous fossil assemblage to date (Marshall, 2020). One study has been carried out on the vertebrate assemblage of the OBF, with a preliminary survey of the body fossil record suggesting the lake contains a low-diversity fish fauna of three taxa (Friedman and Blom, 2006). There is a large assemblage of coprolites (fossilised faeces) from the OBF, with large coprolites suggested to have been produced by tetrapods.

Analysis of fossil material using propagation phase-contrast synchrotron microtomography (PPC-SR μ CT) is a novel tool that has been used in the last decade to extract sub-millimetre details yielding spectacular results informing evolutionary patterns and ecosystem dynamics (Chen et al., 2016; Dupret et al., 2014; Qvarnström et al., 2017; Sanchez et al., 2012; Vaškaninová et al., 2020). This tool has been used here to examine tetrapod body fossil material from the SBF to identify whether they can add to our understanding of early tetrapod evolution. The tool was also used to examine coprolite specimens from the OBF to quantify the coprolite diversity, determine if tetrapods could be inferred from the large coprolites and to enable the virtual reconstruction of coprolites and their inclusions to explore the trophic levels of this post-extinction lake deposit.

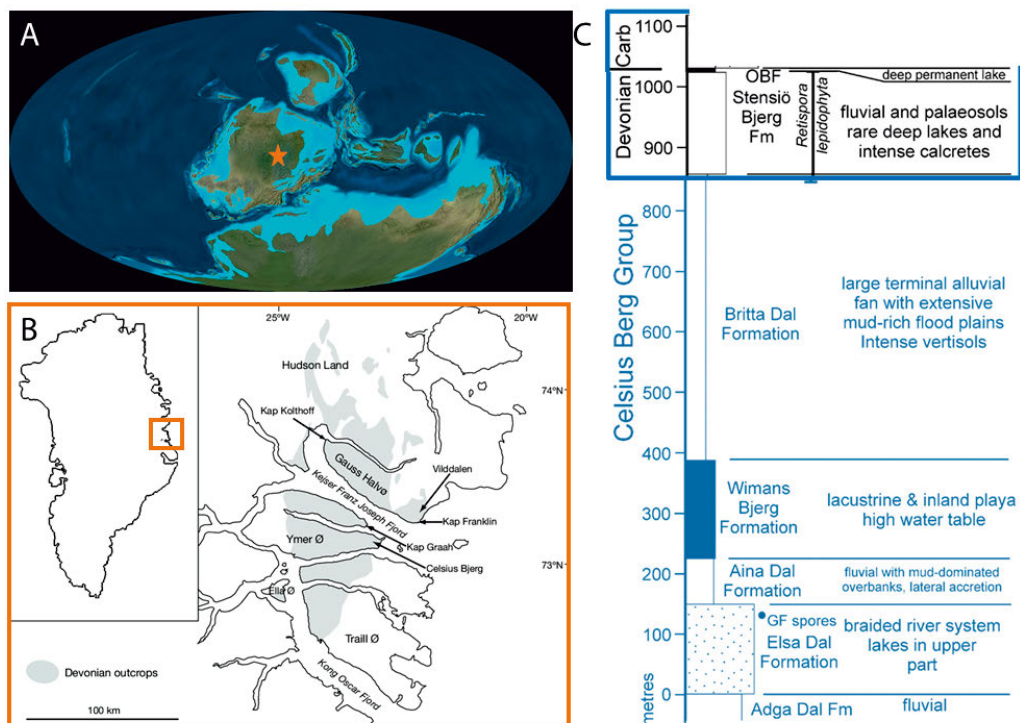


Figure 2. Ancient location of East Greenland on a palaeogeographic map from the D-C boundary (359 Ma) (A) along with the present-day locality of the East Greenland Basin (B). A sedimentary log of the Celsius Bjerg group is shown in (C) with all seven formations and their respective depositional environments, with the formations at the D-C boundary, highlighted, with the OBF and SBF examined as part of my PhD studies. Modified from Blom et al., 2007 and Astin et al., 2010.

Aims of the Thesis

The aims of this thesis are to explore the environment and ecosystems during the fish-tetrapod transition using novel techniques. The first is to investigate, using numerical tidal simulations, whether there is a detailed hydrodynamic basis for inferring that large tides occurred during key evolutionary events of the fish-tetrapod transition (**Paper I**). This is work that was started as a four-month project during my Master's degree at Bangor University, UK and has been greatly expanded upon during my PhD. The second aim is to use propagation phase-contrast synchrotron microtomography to describe new tetrapod body fossils from the terminal Famennian of East Greenland and determine whether they represent a new taxon (or taxa) and if the material can further elucidate the evolution of early tetrapods across the D-C boundary (**Paper IV**). The last project uses propagation phase-contrast synchrotron microtomography on coprolites from a lacustrine deposit from the earliest Tournaisian of East Greenland to explore the ecosystem dynamics of a post-extinction faunal assemblage and assess if there is an inferred presence of tetrapods (**Papers II and III**).

Material and Methods

Tides

Tidal modelling

Tides play a significant role on earth. On a global scale, tides serve an important function in regulating climates through the Atlantic meridional overturning circulation contributing to vertical mixing (Johnson et al., 2019; Wilmes et al., 2021). Tidal dissipation in the oceans induces tidal breaking which slows the rotation rate of the earth and causes the recession of the moon (Daher et al., 2021). Tides are a primary physical driver in nutrient production and mixing in the oceans and also generate temporary thermal refugia during periods of high ocean temperatures, especially along reefs and atolls (Guillaume-Castel et al., 2021; Sharples et al., 2007; Tuerena et al., 2019). In the marginal marine environment, tides introduce rapid but predictable sea-level variations which are of great importance when considering storm surges, marine navigation and marine renewable energy (Byrne et al., 2017; Rulent et al., 2021; Slingsby et al., 2021). They are also fundamental in shaping and maintaining marginal marine environments like estuaries and deltas (Longhitano et al., 2012). The ability to simulate tides can therefore be of great importance and benefit to scientists across multiple disciplines. Tidal modelling, certainly on a local scale, has been around since the time of Laplace in the 18th Century and basic equations on tidal dynamics can allow for the deduction of tidal dynamics, even for ancient tidal regimes (Egbert and Erofeeva, 2002; Slingerland, 1986). Research on ancient tides has been limited due to a paucity of tidal proxy data, and this data only reveals a localised insight into tidal regimes. Numerical tidal modelling has been used over the last 14 years to provide global simulations of ancient tidal regimes (Green, 2010; Green et al., 2020, 2017; Green and Huber, 2013).

OTIS is a portable numerical tidal model which solves the linearised shallow-water equations with energy sinks from bed friction and tidal conversion. It has been used for global and regional modelling of present-day tides, but it is more commonly used to investigate tidal regimes of the ancient and future tides on earth and even other planets (Blackledge et al., 2020; Davies et al., 2018; Green et al., 2020, 2019, 2017; Zaron and Egbert, 2006). The model has been used to investigate ancient tides as far back as the Cryogenian (720-635

Ma), where weak tides may have contributed to the onset of prolonged “Snow-ball Earth” glaciations (Green et al., 2020). Based on the success of this model in simulating deep-time tides, the model is ideal to be used to investigate tidal regimes during the fish-tetrapod transition.

Numerical tidal simulations result from a dynamic tidal model, which differs from an equilibrium tidal model (which was used in Balbus’ study on tides during the Devonian). A dynamic tidal model encompasses the multiple tidal waves which result from various forcing exerted by the Moon, Sun, and Earth (these waves are referred to as tidal constituents) and the ocean bathymetry determines which of these constituents becomes amplified (Kvale, 2012). In the context of global tidal regimes, two of the main tidal constituents are the principal semi-diurnal lunar constituent M_2 (which is the largest constituent in terms of forcing) and the principal semi-diurnal solar constituent S_2 (which is around half the size of M_2). Apart from often dominating the tidal signal, they were selected to be simulated as they produce the spring-neap tidal cycle. The spring-neap cycle is a result of the close, but crucially slightly different, frequencies of the M_2 tide and the S_2 tide. When both constituents are in phase with one another, they produce spring tides where there is a large range difference between high water and low water. When the two constituents are out of phase with one another, they result in neap tides where there is a small range difference between high water and low water. This cycle occurs on a 14.7-day period presently, and the extent of the difference between spring tides and neap tides depends on the size of the S_2 tide, meaning the S_2 tidal range is synonymous with the difference in tidal range between springs and neaps (henceforth the spring-neap range). The impact this modulation has on the intertidal environment is that fauna in the upper intertidal zone will not be submerged for the duration of a spring-neap cycle resulting in almost certain warm and stagnant pools acting as a driver for air-breathing. This environment would be similar to modern-day oxygen-poor swamps where air-breathing fish frequent (Kramer et al., 1978). There have been studies that argue that the relatively short duration of a tidal cycle would not allow for prolonged stranding and hypoxic conditions to occur in the intertidal zone, thus it could not create an evolutionary pressure for the development of air-breathing (Graham, 1997; Graham and Lee, 2004). It is important therefore to investigate the potential for a large upper intertidal zone through the spring-neap range. Tidal range equates to the vertical height difference between high water and low water.

Three time periods were chosen to be studied based on key evolutionary events in the fish-tetrapod transition. The first is the Late Silurian when the first osteichthyans appear in the geological record through the finding of the stem-sarcopterygian *Guiyu oneiros* from South China (Zhu et al., 2009) (**Figure 1**). The origin of the lungs occurs during the origin of this group, a key

adaptation allowing air-breathing (Perry et al., 2001). The second is the early Middle Devonian when the earliest evidence of terrestrial tetrapods appear in the fossil record in the form of fossil footprints (Niedźwiedzki et al., 2010; Stössel et al., 2016) (**Figure 1**). The last time period chosen is the early Late Devonian when the first elpistostegids occur in the fossil record with *Panderichthys* from the Baltic Delta Basin (present-day Estonia, Latvia, and Lithuania), (Vorobyeva, 1995) (**Figure 1**). The elpistostegids are tetrapod-like fish which are the earliest in the body fossil record to possess adaptations for weight bearing and substrate locomotion (Ahlberg, 2018).

OTIS needs to be altered when producing ancient tidal simulations as the tidal forcing parameters would have differed during the past e.g the moon would have been closer to Earth and the earth's rotation rate would have been faster. The main parameters that need to be altered are the day length, the M_2 period and the S_2 period. The day length and S_2 period were derived from palaeontological data in a study where the daily growth accretions and monthly patterns of corals and brachiopods from the Silurian and Devonian were analysed to deduce the number of days in a year (Mazzullo, 1971). The M_2 period values were derived from a study using numerical ocean models and tidal laminae (Bills and Ray, 1999). More details on the values used can be seen in the methods section of **Paper I**.

To state whether the tides were large during the fish-tetrapod transition, there needs to be something to compare it to. It is postulated that there is a tectonically driven supertidal cycle, with periods in between supercontinents suggested to be tidal maxima periods i.e., times of exceptionally large tidal ranges due to the potential of multiple ocean basins reaching tidal resonance (Green et al., 2018). Presently, it is postulated that we are in a tidal maxima period, and so comparing the tidal ranges to present-day will provide validity in stating whether a tidal range value is large or not.

Palaeogeographic reconstructions

Palaeogeographic reconstructions are maps of the earth displaying different continental configurations throughout geological time (Domeier and Torsvik, 2014) (see **Figure 2A** for an example). These maps have been synthesised by several researchers, who use parameters such as palaeomagnetic, sedimentary and paleontological data to reconstruct what the world may have looked like at a given geological time period (Blakey, 2016; Domeier and Torsvik, 2014; Golonka et al., 1994; Matthews et al., 2016; Scotese, 2009).

Palaeogeographical reconstructions display a vast amount of data at one time and can be very useful for many deep time-researchers, for example for pal-

aeontologists exploring biogeographical links between fossil groups and palaeoclimatologists who want to simulate ancient climate systems (Brazeau and Friedman, 2015; de Vleeschouwer et al., 2014; Ladant and Donnadieu, 2016; Zhao and Zhu, 2010). These maps are also needed for tidal models to simulate ancient tides. For our study, we decided to use the latest products from Deep Time MapsTM produced by Ron Blakey (Blakey, 2016). The reconstructions available for the three stages of interest in the fish-tetrapod transition are 420 Ma representing the Late Silurian, 400 Ma representing the early Middle Devonian and 380 Ma representing the early Late Devonian.

The bathymetry data from the reconstructions is qualitative and this needs to be quantified in order to be inputted into the tidal model. As the vast majority of present-day oceanic crust is no older than 280 Ma, it makes it difficult to accurately depict what the true bathymetry was at a particular time period prior to this time point (Müller et al., 2008). We have used a numerical bathymetry set based on present-day values using step-changes in depths of 150 m, 300 m, and 800 m for the continental shelf, and a 4200 m deep abyssal plain, referred to as the control bathymetry set. We have used this bathymetry set based on the assumption that the oceanic crust would have been of similar age and therefore depth due to both the period of study and present-day being at similar stages in the supercontinental cycle (Davies et al., 2018; Matthews et al., 2016). To test the sensitivity of the tidal simulations to depth, a ‘shallow’ and ‘deep’ bathymetry was also used for each time period. Additional simulations were conducted to test sensitivity to coastline locations, involving altering the shelf sea values (for more details on the sensitivity simulations, please see the methods section in **Paper I**).

Tidal proxies

Tidal sedimentology involves the study of tidal deposits in a wide range of settings, from marginal marine to the deep ocean (Davis and Dalrymple, 2012). The focus of tidal sedimentology can be seen as two-pronged; to better understand tidal environments on the coast to predict how climate change and sea level will impact these areas, and to provide information and context to ancient environments impacted by tides (Davis and Dalrymple, 2012). Tidal sedimentology can also be very useful as a proxy in which to constrain tidal simulations. Ancient tidal deposits can provide tidal regime information either directly or indirectly. Direct information comes in the form of tidalites, which are sedimentary structures consisting of thinly layered sediments deposited cyclically, with the thickness of layers varying due to lunar or solar cycles (Davis and Dalrymple, 2012). These tidalites can offer very precise information on the tidal range values, and also the duration of the spring-neap cycle (Longhitano et al., 2012). Indirect information comes in the form of tidal de-

posits that depict a particular environment, such as an estuary or wave-dominated delta, and these tidal depositional systems can be correlated with relative tidal ranges (Longhitano et al., 2012). For example, an estuary is associated with macro-mega-tidal ranges (4-8m) and a wave-dominated delta is associated with micro-meso-tidal ranges (0-4m) (Longhitano et al., 2012). For our study, three tidal proxies were selected for the three time periods (420 Ma, 400 Ma and 380 Ma) to help constrain our simulations and to test whether the simulation using the control bathymetry fitted best (for more details on the proxies, please see the methods section of **Paper I**).

Devonian-Carboniferous of East Greenland

The East Greenland Devonian basin was located in the centre of the Laurusian supercontinent and exhibits a high sedimentation rate with around 7 km of sediments deposited from the Givetian to Tournaisian (Larsen et al., 2008; Marshall, 2020) (**Figure 2A**). The basin extends laterally some 150 km across the islands of Traill Ø, Geographical Society Ø, Ymer Ø and the peninsula Gauss Halvø in East Greenland (Astin et al., 2010) (**Figure 2B**). The Celsius Bjerg group belongs to the upper part of the basin and is composed of seven formations ranging in age from the Late Famennian to Early Tournaisian (Larsen et al., 2008) (**Figure 2C**).

Stensiö Bjerg Formation

The Stensiö Bjerg Formation is a 160 m deposit from the Celsius Bjerg Group (Astin et al., 2010; Marshall et al., 2020) (**Figure 2C**). It has been dated using palynological evidence, with an abundant presence of the spore *Retispora lepidophyta* pointing to an age of latest Famennian (Maziane et al., 2002). The deposit is made up of several layers including palaeosols, calcrete beds and sandstones indicating cyclical arid and wetter intervals (Astin et al., 2010). Dark mudstone layers become more abundant closer to the Obrutschew Bjerg Formation layer, which signifies the presence of permanent lakes and flooding of the system (Astin et al., 2010). Fossil material from the SBF has been collected during expeditions in 2016 and 2022, with only part of the material from 2016 being studied in this thesis.

Tetrapod body fossils

The body fossil material collected in 2016 consists of a lower jaw ramus, a shoulder girdle and a suspensorium along with numerous fragmentary remains from the same lens, also tetrapod in origin. Higher in the formation, an ichno-assemblage consisting of a resting trace and short trackway were discovered along with a lower jaw ramus. This higher assemblage will be studied as part of future work.

Obrutschew Bjerg Formation

The Obrutschew Bjerg Formation is the second-last member of the Celsius Bjerg Group in which the D-C boundary lies and it is also the thinnest deposit of the group (Astin et al., 2010) (**Figure 2C**). The black shales from the deposit represent an anaerobic lacustrine environment, with the formation beginning concurrently with the Hangenberg extinction event. The deposit is laterally very extensive, covering most of the basin and has been estimated to be around 50,000 km² in size (Marshall, 2020). A detailed log of the OBF reveals two primary sections, termed the lower lake and the upper lake. The lower lake begins at the beginning of the OBF, and thus is latest Famennian in age, with the first half containing malformed spores referred to as the LN* spore zone. The transition into the VI spore zone, consisting of a different spore assemblage, marks the Devonian-Carboniferous boundary (Marshall, 2020). The spores from the LN* zone are postulated to have been malformed as a result of UV-B radiation, which could have been responsible for the terrestrial biotic crisis during the Hangenberg extinction event (Marshall, 2020; Marshall et al., 2020). Immediately after the spore zone transition, there is a 20 cm decollement layer (detachment), which is followed by the last third of the lower lake deposit where the OBF fossils have been collected from. Fossil material from this formation studied as part of this thesis has been collected over the course of four field excursions in 2006, 2009, 2015 and 2016 with the majority of material coming from the latter two trips. More material has been collected in an expedition in 2022.

Fish body fossils

Among the vertebrate specimens collected from the OBF, three fish taxa have been identified. The most abundant is an actinopterygian (ray-finned fish) named *Cuneognathus gardineri* which is a small rover fish which was originally described from material collected in 1954 by H. Butler, and based on this original material was believed to be around 5 cm in length, though additional specimens now suggest a length of 10 cm (Friedman and Blom, 2006). *Cuneognathus* bears a strong resemblance to *Limnomis delaneyi* (an actinopterygian from the Late Devonian Catskill Formation), and based on this it is postulated that *Cuneognathus* preyed on small soft-bodied invertebrates (Daeschler et al., 2006). An updated description is needed of the species based on the numerous new specimens collected by the aforementioned field excursions, which will be done in future work.

The next most abundant taxon is an acanthodian (spiny shark), which has not been formally described. Preliminary results suggest that the specimens belong to the genus *Acanthodes* based on the fusiform shape of the fish, the absence of teeth on the jaws and the absence of paired ventral spines (Beznosov, 2009). There are only two almost complete specimens collected, consisting of

a part and counterpart, and they are both of similar lengths around 9 cm (**Figure 3**). Based on the length and positioning of the ventral, anal and pectoral fin spines, along with similarities in the sensory line positioning and orbital bone count, the specimens from the OBF most closely resemble the species *Acanthodes lopatini*, from the Early Tournaisian Os'kin formation in Siberia, Russia (Beznosov, 2017, 2009) (**Figure 3**). We cannot determine if the OBF *Acanthodes* is a new species as the dorsal spine is missing in both specimens, which is a crucial diagnostic feature. The most posterior part of the caudal fin is absent, meaning the presence of an axial lobe cannot be observed which is also very characteristic of *Acanthodes lopatini* (Beznosov, 2009) (**Figure 3C**). An ontogenic series for *Acanthodes lopatini* is available thanks to a high number of specimens (>100) and based on length, the number of orbital bones and scale squamation, we postulate the OBF *Acanthodes* specimens are likely adults (Beznosov, 2017). Based on the large gape, large gill rakers and lack of teeth in *Acanthodes*, it is postulated that they are filter feeders (Brazeau and de Winter, 2015).

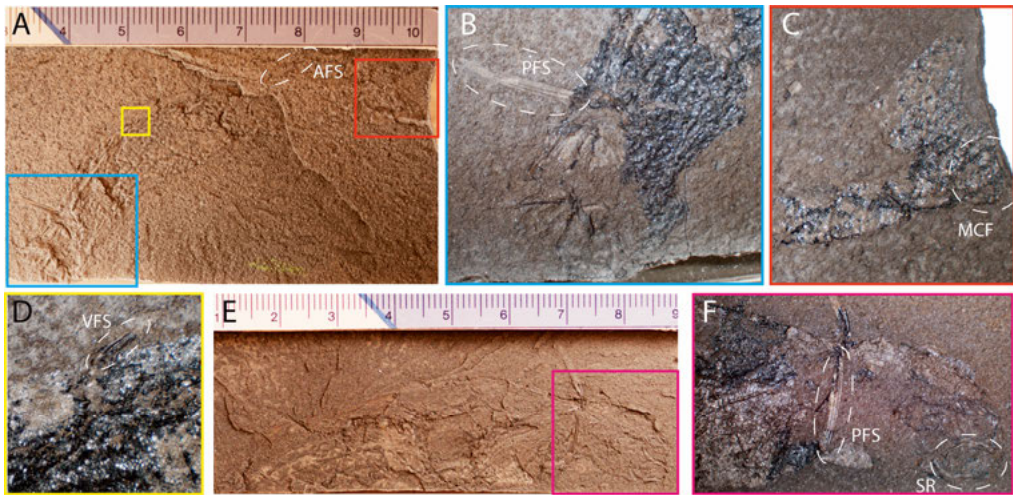


Figure 3. Images of three acanthodian specimens from the OBF. (A) shows a complete view of PMU 31350b covered in ammonium chloride with Anal Fin Spine (AFS) highlighted. (B) shows the head of the same specimen covered in alcohol with the Pectoral Fin Spine (DFS). (C) shows the tail of the same specimen covered in alcohol highlighting the Missing part of the Caudal Fin (MCF) and (D) shows the short Ventral Fin Spine (VFS). (E) shows a complete view of PMU 33845a covered in ammonium chloride, (F) shows the head from the same specimen covered in alcohol with the pectoral fin spine and Sclerotic Ring highlighted (SR).

The last taxon, represented by a single partly articulated specimen and isolated teeth, is a chondrichthyan (**Figure 4**). It is represented by the anterior half of the animal, and it is definitively a chondrichthyan based on the appearance of tessellated calcified cartilage and other attributes such as teeth, scale and fin spine morphology (Cuny et al., 2015; Maisey et al., 2021) (**Figure 4B-E**). The specimen is in the process of being fully described by other researchers, but the shape of the visible portion of the braincase and the teeth morphology suggests an affinity with the genus *Cladodoides* (Cuny et al., 2015; Maisey, 2005) (**Figure 4B and E**).

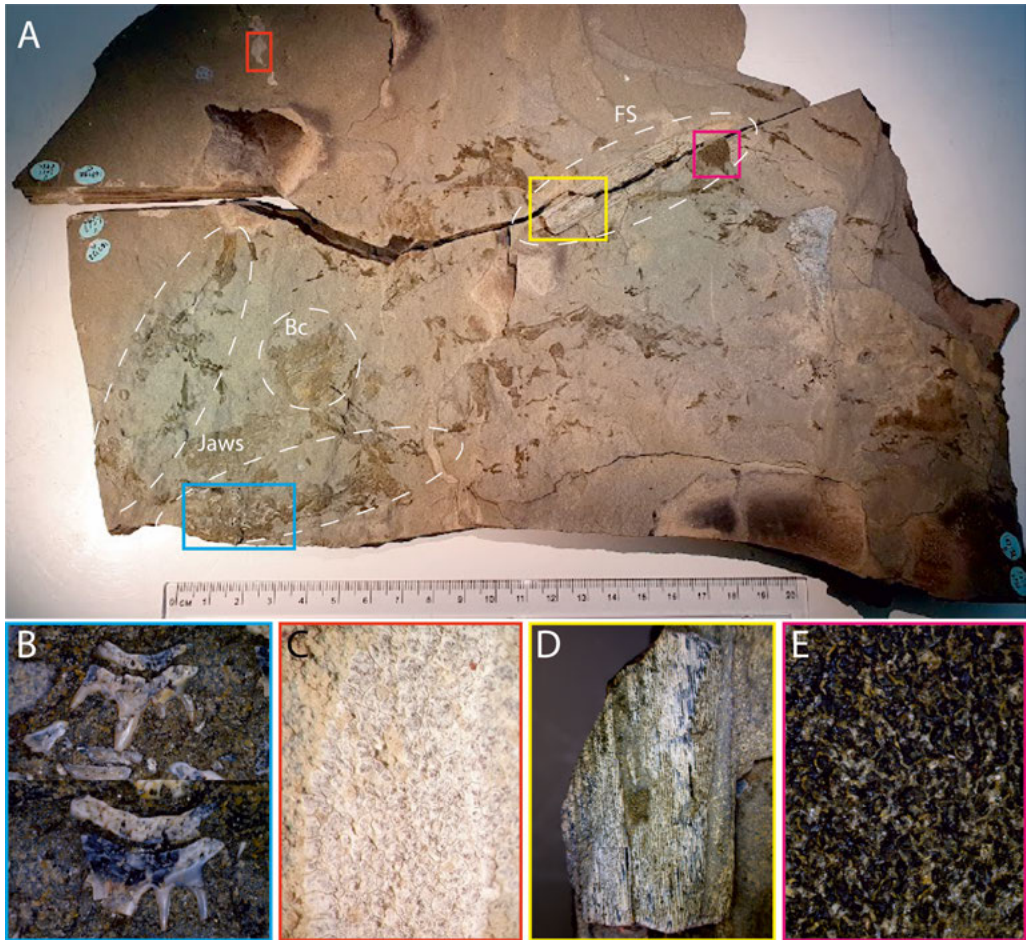


Figure 4. Images of the chondrichthyan specimen from the OBF. (A) shows the complete specimen with the jaws, Braincase (Bc) and Fin Spine (FS) highlighted. (B) shows magnified images of two isolated teeth near the jaw region. (C) shows a magnified example of tessellated calcified cartilage. (D) shows a magnified image of the basal portion of the fin spine. (E) shows a magnified patch of scales.

Coprolites

Coprolites are the most well-known type of bromalite, which is a term for any fossilised material that has originated from the digestive system of an organism, other examples include cololites which are fossilised remains from within the colon and regurgitalites which are fossilised regurgitated material (Hunt and Lucas, 2012). Coprolites are also a type of ichnofossil, which are fossil recordings of the biological activity of an animal (Turner, 2003). The origins of coprolite research occurred in the early 19th Century in the UK, where compound evidence of faecal remains from a Quaternary cave deposit and from Jurassic ichthyosaurs (presented by Mary Anning) led to William Buckland coining the term coprolite, which means dung-stone (O'Connor and Ford, 2001). Coprolites, although largely over-looked by many palaeontologists, offer a vast amount of information such as direct evidence of an animal foraging in an environment, indicative of trophic dynamics within an ecosystem (Chin, 2002; Chin and Gill, 1996; Eriksson et al., 2011; Qvarnström et al., 2019a; Zatoń et al., 2017). Coprolites have been referred to as miniature *Konservat-Lagerstätte* as the rapid lithification of a coprolite induced by bacteria and high-phosphate content (in carnivore coprolites) result in minimal compression of the coprolite and its inclusions (Qvarnström, 2020). This leads to a high-preservation potential, with the occurrence of hair, parasite eggs, feathers and soft-tissue being recorded (Chin, 2002; Dentzien-Dias et al., 2013; Qvarnström et al., 2016). Coprolites are usually categorised into morphotypes based on their physical characteristics, shape and size. Shape can be of particular importance, as it can indicate whether it came from an animal possessing a spiral gut valve (thus the coprolite will be spiral) or lacking a gut valve (thus it will be non-spiral in shape). Traditional methods used to observe the internal morphology and contents of a coprolite involve cutting the specimen to acquire thin sections to be viewed under a compound microscope. Fortunately, advances in technology enable us to avoid this destructive method and instead scan the coprolites to produce a stack of virtual thin sections which can be used to virtually reconstruct the coprolite and its contents (Qvarnström et al., 2021, 2019a, 2019b).

There is a large collection of coprolites and regurgitalites from the OBF, with over 200 specimens, and they come from coprolite-bearing beds which are approximately 1 to 2 m thick from black claystone and sandy mudstone layers. Among the vast coprolite assemblage, two groups are clear to distinguish from external observations, these are the large coprolites and small coprolites (**Figure 4 A-D**). The large coprolites are characterised by their large size (<2.5 cm in length) and are generally oblong shaped, the smallest in the collection is 2.6cm in length and the longest is 7cm (**Figure 4 A and D**). The smaller coprolites have a diverse set of shapes, from very slender and long to bullet-shaped (**Figure 4 B-C**). Fifty-five specimens were synchrotron scanned; these were selected to enable the full diversity of the assemblage to be studied.

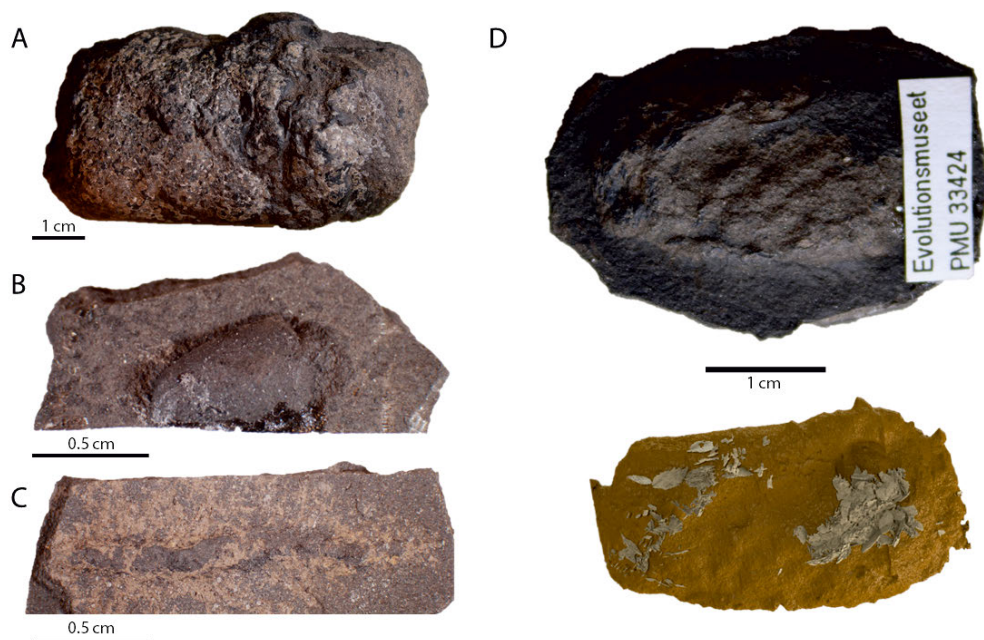


Figure 5. External images of three coprolites from the assemblage display the diversity of coprolite morphology (A-C). (A) shows PMU 313519, which is a large coprolite, with (B) and (C) showing PMU 33443 and 33487 respectively, which are small coprolites. (D) shows an external image of PMU 33424 (top) and a rendered image of the virtual reconstruction of coprolite PMU 33424 (bottom), with the outline of the coprolite in brown and inclusions in cream.

Propagation Phase Contrast Synchrotron Microtomography

Propagation phase-contrast synchrotron microtomography (PPC-SR μ CT) is a powerful imaging technique which is a non-invasive and non-destructive way to obtain high-resolution three-dimensional data from fossil specimens (Pereau and Tafforeau, 2011). Synchrotron microtomography results in very high spatial resolutions of the specimen and internal structures (Tafforeau et al., 2006). The additional measurement of phase contrast utilises the phase shifting of the beam emerging from the specimen, rather than just measuring the decrease in beam intensities that emerge from the specimen which is traditionally done with x-ray absorption (Qvarnström, 2020; Tafforeau et al., 2006). This generates images which have very high contrast, which is fundamental in palaeontology as many fossils exhibit low absorption contrasts, and especially important in the case of coprolites to distinguish between matrix and inclusions (Qvarnström et al., 2017; Tafforeau et al., 2006).

The use of this technique on fossils from the fish-tetrapod transition has yielded spectacular results informing evolutionary patterns and obtaining details which would never have been achievable through traditional methods (Ahlberg and Clack, 2020; Sanchez et al., 2016, 2014, 2012). PPC-SR μ CT has been used in one previous body fossil study similar to the tetrapod study in this thesis, by Per Ahlberg and Jenny Clack (Ahlberg and Clack, 2020). They scanned a small tetrapod jaw ramus from the Britta Dal Formation of East Greenland and found surprisingly derived features for a Devonian tetrapod, like a step in the prearticular and the presence of a surangular crest (Ahlberg and Clack, 2020). The study of tetrapod body fossils from the Stensiö Bjerg Formation is the second study using PPC-SR μ CT to investigate a new Devonian tetrapod material and is the most comprehensive study with three elements scanned. The use of PPC-SR μ CT on coprolites was pioneered by Martin Qvarnström and colleagues in 2017 and proved to be a great success in analysing coprolites and acquiring their palaeoecological implications (Qvarnström et al., 2019a, 2019b, 2019c). The coprolites studied were Triassic-Jurassic in age, and so this is the first time this technique has been used on Carboniferous coprolites.

The tetrapod body fossils and coprolites were scanned at the European Synchrotron Radiation Facility in Grenoble, France. One large coprolite (PMU 31517) was scanned as a pilot study and was part of Experiment ES-505 which was awarded to Valéria Vaškaninová in 2016. The voxel size of the scans was 13.49 μ m. The rest of the specimens were scanned during Experiment LS-2821 which was awarded to Per Ahlberg in 2018. The tetrapod material was scanned individually at a voxel size of 23.3 μ m, the large coprolites were scanned at a voxel size of 13.22 μ m and the small coprolites were scanned at a voxel size of 6.66 μ m. Reconstructions of the scanned data were based on a phase-retrieval approach (Paganin et al., 2002; Sanchez et al., 2012).

For the tetrapod data described in **Paper IV**, the reconstructed volumes were converted into a stack of 16-bit TIFF files and were imported and segmented in the 3D imaging software Materialise Mimics Research 19.0. STL files of the segmented structures were rendered using Blender 2.79b. For the coprolite data described in **Paper II**, the reconstructed volumes were converted into a stack of 16-bit TIFF files, and these images were imported into ImageJ and compiled as a virtual stack to enable visualisation and thus the description of the internal morphology of the entirety of each coprolite. For the coprolites described in **Paper III**, the image stacks for 18 coprolites were imported and segmented in two 3D imaging software programmes; three large coprolites and two small coprolites were segmented using Materialise Mimics Research 19.0 and rendering performed in Dassault Systèmes' SOLIDWORKS 2022

and the remaining small coprolites were segmented using VGStudio Max version 3.0. A comparison of a coprolite in real-life and a corresponding virtually constructed model can be seen in **Figure 4D**.

Summary of Results

Large tides in areas of key evolutionary interest in Late Silurian-Early Devonian (**Paper I**)

The fish-tetrapod transition is a very important evolutionary event in earth's history, giving rise to terrestrial vertebrates, with the drivers behind the transition poorly understood. One hypothesis states that large tides occurred during the transitions, resulting in the repetitive stranding of fish in the intertidal zone which would face drying and hypoxic conditions thus acting as a driver to evolve lungs and limbs to survive (Balbus, 2014). It was the aim of this project to test the premise of this hypothesis that large tides occurred during the fish-tetrapod transition using numerical tidal simulations. The portable tidal inversion software OTIS was used along with three palaeogeographic reconstructions for three key time points in the fish-tetrapod transition - the Late Silurian (420 Ma) with the emergence of the osteichthyan group and origin of lungs, early Middle Devonian (400 Ma) with the earliest evidence of terrestrial tetrapods in the form of trackways and the early Late Devonian (380 Ma) with the earliest elpistostegid body fossils (Niedźwiedzki et al., 2010; Vorobyeva, 1995; Zhu et al., 2009). Two key areas were focused upon; the South China region as this is where the osteichthyan group originates and diversifies and Laurussia as this is where the earliest tetrapod trackways and elpistostegid body fossils occur. The two main tidal continents M_2 and S_2 were simulated to gauge tidal ranges and also the spring-neap range, as a large value would signify a large upper intertidal zone and fish stranded here would experience much longer aerial exposure lasting a full spring-neap cycle. The bathymetric values used were based on present-day, referred to as the control set, with a shallow and deep bathymetry set used for sensitivity purposes. Three tidal proxies for each time period were selected to constrain the output of our model.

The control simulation output for the Late Silurian (420 Ma) shows globally that there are several large M_2 and spring-neap range regions. Many occur in the South China region, demonstrating a large tidal variability occurring in the region and at the time of the origin and diversification of osteichthyans, thus the origin of lungs. The control simulation output for the late Early Devonian

(400 Ma) shows that the tide is less energetic globally compared with the previous time period. There are a small number of localised large M_2 and spring-neap range areas along the North coast of Laurussia with the South coast showing smaller tidal ranges. The control simulation output for the early Late Devonian (380 Ma) shows that the tide is again less energetic globally compared with the other two periods, with no large M_2 or spring-neap range areas occurring around Laurussia. The proxies fit best with the control bathymetry simulations, and the sensitivity simulations do not vary unexpectedly meaning we can have confidence in the control simulation results. This study demonstrates that large tides occurred during the origin of the lungs with the emergence of the osteichthyans in the Late Silurian. Given that the tidal range values are comparable to the present day, which is postulated to be in a tidal maxima period, the tides of the Late Silurian were therefore exceptionally large relative to other periods in Earth's history (Green et al., 2018).

New tetrapod material from the terminal Famennian with some unexpected derived characters (**Paper IV**)

The depauperate tetrapod body fossil record across the Devonian-Carboniferous, referred to as Romer's Gap hampers our understanding of the evolution of early tetrapods across the boundary (Clack, 2012). Here we present new tetrapod material from the terminal Famennian of East Greenland. Only one other tetrapod is contemporary, that of *Tulerpeton* from Russia (Lebedev and Coates, 1995). The aim of this study was to examine this new tetrapod material and determine if it belonged to a new taxon or taxa and to see whether it could inform us about tetrapod evolution across the D-C boundary. The three body fossil specimens; lower jaw ramus, suspensorium and shoulder girdle were scanned using PPC-SR μ CT and the image stacks were imported and segmented in a 3D imaging software. This technique has yielded spectacular results when studying other fossils from the fish-tetrapod transition and it has been used to describe the lower jaw of a slightly older Greenland tetrapod, *Brittagnathus*, with the high-resolution data revealing surprisingly derived characteristics for a Devonian tetrapod (Ahlberg and Clack, 2020). The first results from the analysis of the three SBF tetrapod specimens are presented here, with future work planned to include new tetrapod material from the SBF in 2022.

The shoulder girdle has a short cleithrum and large robust scapulocoracoid, which is a derived characteristic shared with *Tulerpeton* and later tetrapods but not present in older tetrapods like *Ichthyostega* and *Acanthostega*, which have rather long cleithra (Coates, 1996; Jarvik, 1996; Lebedev and Coates, 1995). The coracoid plate is large and flared, with a post-glenoid coracoid

extension which is an unusually derived characteristic seen in the likes of *Dimetrodon*, a non-mammalian synapsid from the Early Permian which was a highly capable terrestrial animal (Laurin and de Buffr  nil, 2016). A large robust scapulocoracoid and extension to the coracoid plate may indicate competent terrestrial locomotory capabilities. The contact between the cleithrum and scapulocoracoid is also unusual, with a socket-like connection with the base of the cleithrum forming the socket with the top of the scapulocoracoid forming the head. This arrangement has not been observed in any other tetrapod.

The suspensorium captures the cheek area of the skull and is quite flat and elongated in overall shape with a low angle between the cheek and skull roof indicating that this animal had a quite dorsally-ventrally flattened head. The suspensorium bears a striking resemblance with a slightly younger tetrapod, *Ossinodus* from Australia (Warren and Turner, 2004). There is a temporal fenestra present (hole in the cheek) which is a surprisingly derived feature not seen in tetrapods until the Late Carboniferous with *Anthracosaurus* from the UK (Panchen, 1977). This fenestra is associated with the expansion of the jaw musculature and the rise of reptiles (Frey et al., 2001).

The jaw has been partially eroded on the external surface, but the natural mould has been captured for most of this surface. The jaw is quite slender and curved along the bottom margin, similar to *Acanthostega* and *Brithynodus*, different from the boxy shapes of *Ichthyostega* and *Ymeria* and not as deep as *Whatcheeria* (Ahlberg and Clack, 2020, 1998; Clack et al., 2012; Rawson et al., 2021). A very unique characteristic of this jaw is that the anterior margin of the surangular does not extend very far on the jaw, meaning there is no overlap of this element with the dentary. The jaw also possesses a modest surangular crest, slightly larger than the surangular crest of *Brithynodus* (Ahlberg and Clack, 2020). There is a strong denticulate field on the front half of the prearticular, similar to *Ymeria* and *Whatcheeria* (Clack et al., 2012; Rawson et al., 2021).

There is also material in the cavity of the suspensorium; a displaced paired skull bone and an acanthodian spine. The paired skull bone has been interpreted as the left and right exoccipitals. This is based on curved arches surrounding the notochord at the bottom, with flared ends to the arches likely representing the contact to the basioccipital which is absent (Johanson et al., 2003). The extensions pointing upwards likely form the margins of the foramen magnum (Johanson et al., 2003). The acanthodian spine would need to be scanned at a higher resolution to determine what type of acanthodian it is from, but preliminary analysis rules out that it is from *Acanthodes* based on the broad c-shape of the spine when viewed in cross-section.

All three elements possess characters which are unique and therefore cannot be attributed to any of the already established Greenland taxa. The character complement of both the suspensorium and lower jaw suggests they are more crown-ward than the shoulder girdle, due to a lack of scapular blade and features shared with *Ichthyostega*. A full study on new tetrapod material collected in 2022 will aid in our understanding of the specimens discussed and also tetrapods as a whole across the D-C boundary.

Large coprolite diversity reveals cryptic fauna in a post-Hangenberg lake ecosystem (**Paper II**)

The Obrutschew Bjerg Formation is a black shale lacustrine deposit from East Greenland and the earliest fossil-bearing Carboniferous deposit to date occurring just after the Hangenberg extinction event. There are only three fish taxa represented in the deposit, indicating a low diversity fauna. There is a large coprolite assemblage from this deposit, with some large-sized coprolites postulated to have been produced by tetrapods. The aim of this study was to quantify the diversity of coprolites in this assemblage using the traditional method of external observations in conjunction with the novel approach of making internal observations using virtual thin sections from PPC-SR μ CT. Fifty-five specimens were selected for analysis, with external morphology groups produced based on the shape and size of the coprolites and then internal morphology groups based on internal data from virtual thin sections.

Our results reveal that the groupings based on the two different analysis techniques were vastly different, with external observations performing poorly in deducing accurate morphotypes. External observations were most inaccurate at deducing whether a coprolite was spiral or non-spiral. This was primarily a result of the obscuring of many of the coprolites by shale (referred to as host rock). The internal observations of coprolites using virtual-thin sections resulted in a wealth of data including levels of deformation, internal structuring i.e spiral or non-spiral and visualisation of inclusions. The virtual thin sections displayed an additional ten coprolites which were not visible externally. The internal observations were used to inform the morphotype groups among the coprolites, with a total of eight groups. Coprolites in morphotype A are large and non-spiral in structure, indicating they came from an animal that lacks a spiral gut valve. Tetrapods are probably the only vertebrates to lack a spiral gut valve during this period, inferring the presence of tetrapods in this post-extinction ecosystem. This is significant as there is no body fossil record of tetrapods immediately after the Hangenberg event, adding further evidence that Romer's Gap is likely a sampling bias effect (Mansky and Lucas, 2013; Smithson et al., 2017). Morphotype B is postulated to have been produced by

the chondrichthyan taxon recorded from the lake due to the large size of the coprolites and spiral structure. The diversity of coprolites exceeds the fish body fossil diversity, suggesting the presence of a cryptic fauna not captured by the body fossil record, and may suggest the lake was part of an open system.

Coprolite inclusions introduce two new taxa and reveal trophic levels in a post-Hangenberg lake ecosystem (Paper III)

The Obrutschew Bjerg Formation of East Greenland is the earliest insight we have into ecosystem recovery after the Hangenberg event. It is also unique in being one of the very few terrestrial deposits from the early Tournaisian (Marshall, 2020). The large coprolite assemblage has the potential to be highly informative on the ecosystem dynamics of this post-extinction lake ecosystem. Bromalites (including coprolites) provide direct evidence of feeding and give a more accurate interpretation of trophic levels than from taxonomic of trophic information alone (Chevrinais et al., 2017; Qvarnström, 2020; Robin et al., 2022). Coprolites have been largely neglected in the past due to the lack of data obtained from traditional analysis methods. The application of PPC-SR μ CT to coprolites allows for the virtual reconstruction of coprolites and their content. This technique results in high-quality inclusion data from the coprolites which have revealed fascinating trophic dynamics into ecosystems from the Triassic-Jurassic (Qvarnström et al., 2021, 2019b, 2019a). The aim of this study is to apply this technique to the OBF coprolite assemblage to examine the ecosystem dynamics of this lake fauna, thus gathering insight into faunal recovery after the Hangenberg crisis.

Fifteen coprolites were virtually reconstructed using 3D imaging software. The coprolites analysed are representative of seven morphotype groups from the assemblage. The results are still to be expanded upon using more coprolites, but the data thus far reveal a plethora of exceptionally well-preserved inclusions both in three-dimensionality and in detail. The true external surface of the coprolites could be visualised for the first time, with the identification of three different spiral coprolite morphologies among the small coprolites; amphipolar, heteropolar and 'knot' (Dentzien-Dias et al., 2012). The majority of inclusions are better preserved than the body fossils from the deposit, likely due to the early lithification that coprolites experience resulting in reduced compression of the inclusions (Qvarnström et al., 2016). Many of the inclusions possess complete ornamentation and other details meaning they can be accurately attributed to a genus. One large coprolite (PMU 31370) has a particularly remarkable inclusion set. The inclusion set of this coprolite differs greatly from the other coprolites segmented from morphotype A which mainly

consists of remains of *Cuneognathus*. PMU 31370 contains large cranial elements belonging to an actinopterygian that is not *Cuneognathus*. The inclusions indicate that they belong to a larger species, with the teeth morphology of the premaxilla indicating it is a predatory fish. Additionally, there are two small lower jaw fragments, a premaxilla and ectopterygoid, attributable to a small tetrapod. This is based on the lack of ganoine ornamentation on both elements, with the premaxilla possessing a single row of tooth sockets, which get progressively bigger from anterior towards the posterior and the flatness of the palatal lamina of the ectopterygoid. More analysis is planned to compare the size of inclusions with body fossil elements to deduce the size range of animals represented in the coprolites. It is hoped this information will lead to more informed interpretations of the producers of certain coprolite morphotypes.

Using our data to infer trophic levels, we are mindful that the producers of many of the coprolites are unknown but we can deduce that tetrapods and chondrichthyans were the apex predators of the lake based on their coprolites containing inclusions from more than one taxa. *Cuneognathus* appeared to be the primary prey item of the tetrapods, with the occasional acanthodian and the chondrichthyan appearing to feed primarily on *Acanthodes*. The small coprolite data shows two feeding strategies; animals feeding on *Acanthodes* appear to avoid large elements like spines and scapulocoracoids and producers of coprolites with actinopterygian inclusions appear to target the fin regions of *Cuneognathus*, possibly the caudal fin. The disclosure of two new taxa in the ecosystem echoes the inferences from **Paper II** that the lake is part of an open system. A large amount of coprolites and inclusion sets indicates a stable and productive ecosystem dominated by active predation, with the inferred presence of at least eight taxa including two tetrapod taxa. This challenges our initial perception that the lake hosted a low-diversity recovery fauna and points to a rapid recovery of a terrestrial ecosystem in East Greenland.

Conclusions and Future Directions

The use of novel analysis techniques has proven greatly successful in furthering our understanding of certain aspects of the ecosystems and environments of the fish-tetrapod transition.

Our numerical tidal simulations during the fish-tetrapod transition have produced robust results constrained by tidal proxy data demonstrating that large tides occurred during the Late Silurian, notably in the region of the earliest osteichthyans and thus the origin of lungs. There is a notable reduction in tidal energy from the Late Silurian to early Late Devonian, and it would be of interest to expand the production of tidal simulations to include later reconstructions in the Devonian to investigate whether low tidal ranges could have been a contributing factor to anoxic conditions in marginal marine environments during the Kellwasser and Hangenberg extinction events. The premise is that low tidal ranges result in weak tidal mixing leading to stratified water columns leading to stagnant anoxic conditions, and it has been suggested that palaeo-oceanographic factors have played a role during the Hangenberg extinction event (Kaiser et al., 2016). Marginal marine environments were not only an important part of the fish-tetrapod transition but also played a key role in the origins of other early vertebrate clades, with a study demonstrating that these clades originated in shallow intertidal-subtidal environments (Sallan et al., 2018). Numerical tidal simulations during the timing of these clade origins could be highly informative on these vastly important ecosystems. The study on tides during the fish-tetrapod transition can also be expanded upon; analysis of different palaeogeographic reconstructions at higher temporal and spatial resolution would result in a more comprehensive picture of tidal regimes during this period. There is a wealth of tidal proxy data from the deposits of the Baltic Delta Basin in present-day Estonia, Latvia and Lithuania (also home to the elpistostegid *Panderichthys* and stem-tetrapods *Ventastega* and *Livoniana*), as well as tidalites from the Escuminac formation in Canada (also home to the elpistostegid, *Elpistostege*), so high-resolution simulations of these areas would be ideal (Ahlberg et al., 2008, 2000; Cloutier et al., 2011; Luksevics and Zupins, 2004; Schultze and Arsenault, 1985; Vorobyeva, 1995).

Analysis of tetrapod body fossils from the SBF using synchrotron microtomography has provided exceptionally detailed data on well-preserved body

fossil material which likely represents more than one new tetrapod taxa. This technique has allowed for the visualisation of minute details such as muscle attachment scars and tooth reabsorption which would not have been achievable through conventional study methods. Our study highlights the need to perform this analysis technique on more taxa from the Devonian and Carboniferous, particularly with abundant material from *Acanthostega* and *Ichthyostega*, in order to resolve early tetrapod evolution. This technique will be applied to new material collected from the SBF and it is hoped this information will help in further informing on the SBF tetrapod material presented in **Paper IV** and also tetrapod evolution across the D-C boundary.

Analysis of coprolites using synchrotron microtomography from the OBF has produced spectacular results, redefining our prior perception of the OBF as a low-diversity post-extinction recovery fauna. The coprolite data demonstrate that at least eight taxa are part of a stable and productive ecosystem dominated by active predation with tetrapods and chondrichthyans as the likely apex predators. This new interpretation of the OBF lake ecosystem demonstrates a rapid recovery of a terrestrial ecosystem in East Greenland immediately after the Hangenberg crisis. The presence of a cryptic fauna strongly suggests that the lake ecosystem was part of an open system, and future work is planned to perform isotopic analysis of hard tissues from the OBF body fossils to investigate whether there is a euryhaline signal which would demonstrate a marine link to the lake. We have also demonstrated that the classic technique of quantifying coprolite morphotypes based on external morphology can be highly misleading and inadequate, especially when the coprolites are enclosed in host rock (Dentzien-Dias et al., 2021). This highlights the importance of having internal observations whether it is physical or virtual thin sections in accurately determining coprolite morphotypes. Synchrotron microtomography and segmentation should be applied to other coprolite assemblages from around the D-C boundary to better our understanding of the major faunal restructuring that occurs across the boundary and ecosystem recovery after the Hangenberg extinction. Coprolite assemblages that come to mind are the Late Devonian Escuminac deposits and Early Carboniferous Horton Bluff and Blue Beach deposits in Canada and the abundant coprolite assemblages from the Early Carboniferous Strathclyde group in Scotland (Mansky et al., 2012; McAllister, 1996; Sumner, 1993).

Svensk sammanfattning

Många viktiga evolutionära händelser har inträffat under livets historia på jorden. Berömda exempel är dinosauriernas uppkomst under triasperioden samt däggdjurens övergång från land till vatten under eocenperioden, vilket skedde inom två separata däggdjursgrupper och som i sin tur gav upphov till bland annat sälar respektive valar. Dessa exempel hade inte inträffat om det inte varit för en av de allra viktigaste evolutionära händelserna, nämligen den första och enda övergången av ryggradsdjur från vatten till land, även kallad fisk-tetrapod-övergången. Denna övergång innebar att vissa så kallade kvastfeniga fiskar utvecklade flera anpassningar till liv på land, inklusive lungor för att kunna andas luft med samt extremiteter med kapacitet att bära upp kroppsvikten. Resultatet blev de första landryggradsjuren, eller tetrapoderna. Processen började med de kvastfeniga fiskarnas uppkomst i den senare delen av silur, men de äldsta beskrivna lämningarna av tetrapoder finns i form av fossila fotspår, med spår från stenbrottet i Zachełmie i Polen som är omkring 390 miljoner år gamla, samt något yngre spår från Valentia Island, Irland, som är daterade till 387 miljoner år sedan.

Ryggradsjurens övergång från vatten till land har studerats utförligt under de senaste 200 åren, men många frågor kvarstår. En sådan fråga är vad det var som orsakade övergången – vilken var den drivande faktorn som låg bakom att några kvastfeniga fiskar utvecklade lungor och ben och blev de första tetrapoderna? Ett annat exempel är frågan om hur tetrapodernas utveckling såg ut under övergången mellan devon och karbon. Vid den här tiden inträffade ett stort massutdöende, kallat Hangenberg-episoden. Tillsammans med det något yngre Kellwasser-massutdöendet bildar Hangenberg ett av de fem stora massutdöendena under jordens historia, det devonska utdöendet. I samband med Hangenberg och vidare en bit in i karbon finns det en avsaknad av bevarade kroppsfossil från tetrapoder, vilket fått namnet ”Romer’s Gap”. Även om den här bristen på bevarade tetrapoder börjat fyllas genom fynd från Skottlands och Kanadas tidiga karbon så återstår många frågor om vad som hände med tetrapoderna under det här tidsintervallet, hur de såg ut och hur deras ekosystem påverkades.

Syftet med det här doktorandprojektet var att försöka besvara några av dessa högintressanta frågor med hjälp av nya analysmetoder. Teknikutvecklingen

inom naturvetenskapen har varit mycket snabb de senaste tjugo åren, med exempel som datormodellering och synkrotrontomografi som nått framkanten. I den här studien har vi använt dessa tekniker för att bättre förstå tre aspekter hos fisk-tetrapod-övergången.

Den första aspekten (Artikel I), som utgör en fortsättning på min masteruppsats, var att undersöka om tidvatten kan ha varit en drivande faktor under övergången från vatten till land. En tidigare formulerad hypotes har varit att det förekom stora tidvattenrörelser under perioden för de tidiga tetrapodernas evolution, och att detta ledde till stora tidvattenzoner där kvastfeniga fiskar kunde bli fångade i mindre, isolerade vattensamlingar vid lågvatten. Dessa vattensamlingar blev sedan syrefattiga eller dunstade bort, och om detta förlopp inträffade kontinuerligt skulle det kunna driva utvecklingen av lungor och extremiteter bland kvastfeniga fiskar vilket i sin tur ökade chansen för överlevnad. För att testa denna hypotes användes en numerisk tidvattenmodell för att simulera tidvattenrörelser vid tre viktiga tidpunkter under övergången från vatten till land. Den första är den sena delen av silur, dvs under den period där de äldsta fossilen från kvastfeniga fiskar har hittats. Den andra är mellandevon, där de första spåren av ryggradsdjur på land hittats, i form av de tidigare nämnda fotspåren. Den tredje är tidiga sendevon, när de äldsta fossilen från elpistostegider – stamtetrapoder med vissa tecken på förmåga till att kunna hålla uppe sin egen vikt och vandra på ett substrat – har identifierats. Jämfört med idag såg världen väldigt annorlunda ut under perioden sensilur till sendevon, med tre superkontinenter (Gondwana, Laurussia och Sibirien) och ett antal mindre mikrokontinentalblock. Paleogeografiska rekonstruktioner är kartor över hur landmassorna sett ut genom jordens historia, och tre av dessa användes i modellen för tidvattenrörelser – en för 420 miljoner år sedan (sensilur), en vid 400 miljoner år (mellandevon) och en vid 380 miljoner år (sendevon). Havsdjupet är inte känt i detalj så långt bakåt i tiden. Därför baserade vi havsdjupet i modellen på moderna värden, och lade till ett dataset med djupare och ett med grundare värden för att testa hur detta påverkade simuleringarna.

Två tidvattenkomponenter genererades med hjälp av modellen, en måndriven (M_2) och en soldriven (S_2), eftersom dessa två är de huvudsakligen drivande tidvattenkomponenterna globalt idag. För att testa om de producerade simuleringarna gav rimliga resultat användes proxydata för tidvattennivåer från de tre nämnda perioderna för att sätta gränser för de simulerade nivåerna. Simuleringarna för perioden för 420 miljoner år sedan visade att det fanns flera områden där både M_2 och S_2 bidrog till stora tidvattenrörelser, med de största svängningarna i östra Gondwana. Detta är signifikant eftersom det sydkinesiska kontinentalblocket fanns i det här området, och det är här de äldsta fossilen från både kvastfeniga fiskar och stamtetrapoder har hittats. Simuleringarna för perioden för 400 miljoner år sedan gav inte lika stora nivåskillnader i

tidvattnet, och den största skillnaden identifierades fortfarande i östra Gondwana. För den yngsta perioden, 380 miljoner år sedan, verkade nivåskillnaderna vara ännu mindre, med de största svängningarna för både M₂ och S₂ fortfarande lokaliserade till östra Gondwana. Dessa resultat reflekterades också i en känslighetsanalys, och tillsammans med proxydata för historiskt tidvatten drogs slutsatsen att simuleringarna som använde dagens havsdjup var de mest korrekta, vilket gör resultatet mera robust.

Den andra aspekten (Artikel IV) var att undersöka nytt fossilt tetrapodmaterial från den allra sista delen av östra Grönlands devon. Det nya materialet består av en underkäke, en skuldergördel och ett suspensorium (del av kinden). Målet med den här studien var att avgöra om materialet kommer från en och samma individ, samt ifall det är en ny art. Detta skulle i så fall förbättra vår förståelse för de tidiga tetrapodernas evolution genom sendevon och in i tidiga karbon. För att undersöka proverna så utförligt som möjligt skiktröntgades de i en synkrotronfacilitet (ESRF) i Frankrike, vilket producerade serier av virtuella tvärsnitt som sedan importerades till ett 3D-visualiseringsprogram där fossilen kunde återskapas i digital form. Den här metoden ger oerhört detaljerade och informativa resultat, med visualisering av tredimensionella detaljer under milimeterskala. Rekonstruktionerna av de tre exemplaren visar att de tillhör åtminstone en ny tetrapodart, kanske fler, vilket ökar det totala antalet tetrapodarter från östra Grönlands devon. Det innebär att östra Grönland är den mest artrika regionen i världen vad gäller devontetrapoder. Skuldergördeln är den mest kompletta som hittats för en devontetrapod, och har en stor och expanderad coracoidregion vilket skulle kunna indikera god gångförmåga. Suspensoriet liknar starkt det hos en tetrapod från tidiga karbon i Australien, *Ossinodus*, och har en temporalöppning (ett hål i kindbenen) som är ovanligt i devontetrapoder och inte ses i andra tetrapoder förrän senkarbon. Sammanfattningsvis visar de tre elementen en blandning av primitiva, härledda och unika karaktärer och det finns hopp om att framtida studier, inklusive en fylogenetisk analys, kan klargöra mer detaljer kring tetrapodernas evolution vid övergången mellan devon och karbon.

Den tredje aspekten (Artiklar II och III) var att undersöka fossil avföring (koproliter) från avlagringar från botten av en sjö som fanns i östra Grönland precis efter Hangenberg-episoden. Baserat på förekomsten av stora koproliter antas tetrapoder ha funnits i det här ekosystemet. Målet var att först sortera koproliterna i olika typer, eftersom detta kan ge en indikation om hur många olika koprolitproducenter som fanns och därmed hur djurlivets diversitet i sjön såg ut (Artikel II). Det andra målet var att analysera innehållet i alla typerna av koproliter för att rekonstruera en näringsväv för ekosystemet (Artikel III). Studien av koproliternas innehåll utfördes med hjälp av synkrotronmikrotomografi, där de virtuella tvärsnitten först användes för att underlätta sorte-

ringen av koproliterna i olika typer, och sedan användes för att göra tredimensionella rekonstruktioner av deras innehåll. Den här tekniken har använts i tidigare koprolitstudier med fantastiska resultat, men det här är första gången tekniken används för att undersöka koproliter från slutet av devon.

Resultat från den första delen av koprolitstudien (Artikel II) avslöjade att sortering av koproliterna enbart baserat på yttre utseende inte ger helt tillförlitliga resultat, och belyser vikten av att studera koproliternas interna struktur. Koproliterna kan sorteras in i åtta olika grupper, vilket är intressant eftersom det bara finns kroppsossil från tre ryggradsdjur i sjöavlagringarna (en strålfenig fisk, en taggpansarhaj (acanthod) och en broskfisk). Koproliterna indikerar därför en större mångfald där flera av producenterna därmed är okända. En av koprolitgrupperna består av stora koproliter utan spiralförmig struktur. Det här är en viktig observation eftersom den absoluta majoriteten vertebrater vid den här tidpunkten hade en spiraltarm, vilket ger spiralförmad avföring. Tetrapoder har dock inte en spiraltarm. Därför pekar den här koprolittypen på att en stor tetrapod fanns närvarande i det här ekosystemet som existerade direkt efter massutdöendet under Hangenberg-episoden. Resultatet från den andra delen av koprolitstudien (Artikel III) avslöjade en intressant samling exceptionellt välbevarade benfragment, med mycket bättre bevaring än kroppsossil funna i samma avlagringar. Det intressantaste innehållet kommer från en enskild stor koprolit, med benfragment från en stor strålfenig fisk samt även från en liten tetrapod. Ingen av dessa finns representerad i den stora samlingen kroppsossil. Den här informationen, sammantaget med det stora antalet olika koprolittyper, indikerar att sjön kan ha varit del av ett större, öppet vattensystem, kanske även med en marin kontakt. Framtida arbete med analyser av storleken på fragmenten i koproliterna och jämförelser mellan dessa och kroppsossilerna från sjön kan ge möjlighet att rekonstruera en heltäckande näringsväv. I förlängningen kommer denna studie att vara ett mycket informativt bidrag till förståelsen för sendevonska ekosystem och även ekosystems återhämtning efter ett massutdöende.

Sammantaget kan användandet av moderna metoder inom datamodellering och synkrotron mikrotomografi ge möjlighet till stora framsteg för förståelsen vad gäller fisk-tetrapod-övergången.

Acknowledgements

There are so many people I would like to thank for their support and guidance along this immense journey that has been my PhD Studies!

Firstly, to **Per Ahlberg** my main supervisor, I am immensely grateful to you for giving me the opportunity and for believing that I could make the jump into the world of Palaeontology and for enthusiastically supporting me throughout. Thank you also very much for supporting me to go to conferences and field trips and for making me a core team member on the Valentia Island Slate Formation study, not just because of the great seafood platters!

To **Grzegorz Niedźwiedzki**, one of my co-supervisors, I am very grateful for your enthusiastic input to my work and for collecting the material studied as part of my PhD. I will be forever grateful for the fieldwork in Skåne and Vättern you have invited me on, I have learnt a lot from you and had a lot of fun along the way.

To **Henning Blom**, one of my co-supervisors, I am thankful for the actinopterygian knowledge you have passed on to me and for collecting the material studied during my PhD. Despite your busy schedule as head of teaching, you have always made time for my queries and made time to assist me with photographing and analysis of specimens, thank you.

To **Ben Kear**, one of my co-supervisors, I am very grateful for your ecosystem dynamics insights and for collecting the material that I have studied during my PhD. You have a great knack for eeking out as much information from data and how to best present it which I hope I have managed to learn from!

To **Mattias Green**, Master's supervisor and co-author on Paper I, words cannot express my gratitude to you for your support over the last 9 years. You have been an immense support during my university studies and I am very fortunate to have you as a mentor in this scary world of Academia!

To **Steve Balbus**, founder of the Devonian tides project and co-author on Paper I, and to others who have been involved in the project, thank you for including me in such an exciting project and enthusiastic team.

Many thanks to my opponent **Matt Friedman** and members of my defense committee for kindly accepting to review my thesis. Thanks also to Jake, Sifra, Mattias and my supervisors for their comments on my kappa and to Daniel and Henning for their translation work on my Svensk sammanfattning.

To my work colleagues of present and past (**Sophie, Vincent, Elena, Dennis, Marie, Tatjana, Zivile, Dong-Lei, Matthew, Jordi, Valeria, Laura, Joss, Johan, Chrysa, Mohammad, Francois, Philipp, Bianca, Manolis, Gizem, Adriane, Alessia, Eleonora, GP, James, Cecile, Mikael**), it has been a pleasure meeting you all and getting to know you. Special thanks to a few members of my department: To **Daniel**, I am very grateful for your help with image importation, Mimics drama and many more tech related issues! To **Melanie**, thank you for your enthusiastic support and segmentation work on some of the small coprolites presented in my thesis. To Jake, aka **Jakey boi**, who has been my PhD brother, thank you for the great banter and discussions over the years. To **Martin Q**, the rockstar palaeontologist who I have learnt from a lot (not just about poop!), thank you for being great company on many conferences and field excursions. To **Sifra**, my wonderful office mate, thank you for your support and great discussions on Sharpey's fibres to Formula one drama.

Thanks to everyone I have met at conferences and fieldwork over the years, it has been an incredible privilege being part of the early vertebrate research community. Big thanks to **Richard Dearden** for his wisdom and knowledge in helping with the chondrichthyan identification. Thanks also to **Luke** for helping me when I needed it most.

To my climbing friends, thank you for the great craic and adventures over the years! A mighty special thanks are in order to **Imke**, my wee bestie, you are a wee ball of positive energy and I am very thankful for the wonderful times and climbing adventures we have shared.

To **Anna** and **Oskar**, thanks for being great work companions and also great friends, thank you for the wonderful food, craic and support you have provided me and thanks also to their cats **Aoife, Oonagh** and **Vega** for lovely cuddles and relaxation. I promise the cardigan will be finished one day!

To my beloved family, **Joseph, Rita** and **Joanna**, your love and support over the years have made it possible to achieve this incredible milestone and I hope I have been able to make you proud. Go méadaí Dia thú.

Lastly, but certainly not least, to my incredible partner **Neddy**, thank you so much, my love. I have been incredibly lucky to have you by my side supporting me through thick and thin. Grá Geal Mo Chroí.

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