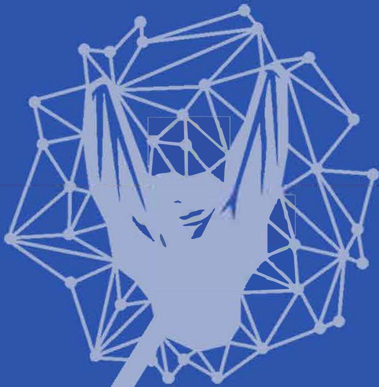
June 2022

Ichthyolith Issues
Special Publication 15



16th International Symposium on Early and Lower Vertebrates

Valencia, Spain, 2022

Edited by M. Victoria Paredes-Aliaga, Esther Manzanares, Jorge Mondéjar Fernández, Sonia Ros-Franch, Héctor Botella & Carlos Martínez-Pérez

ISSN 1302-1314

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16th International Symposium on Early and Lower Vertebrates

Honoring Tiiu Märss
&
Philippe Janvier

Conference programme and abstracts

Valencia, Spain, 2022

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ISSN 1302-1314

Special Publication 15 of Ichthyolith Issues

ISSN 1302-1314

Published by

University of Valencia

Conference logo: Designed by Hugo Salais

Copies and pdf available from Héctor Botella

Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia,

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16th International Symposium on Early and Lower Vertebrates

Valencia, Spain, 20-28.06.2022

Organised by

Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia

Department of Botany and Geology, University of Valencia

&

Botanical Garden of the University of Valencia

Co-funders

Valencian Regional Government,
Cavanilles Institute of Biodiversity and Evolutionary Biology,
Faculty of Biological Sciences
Spanish Society of Palaeontology

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Ayuntamiento de Cuenca

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16TH ISELV PROGRAMME

June 20th, Monday

16:00-19:00. **Registration** at the entrance of the Botanical Garden of the University of Valencia (entrance from st. Quart nº 80). During the rest of the congress, the registration point will be at the secondary entrance (st. Beato Gaspar Bono) of the Botanical Garden.

19:00-22:00. **Ice Break Party** in the "Umbracle" of the Botanical Garden of the University of Valencia.

June 21st, Tuesday

9:00-9:20. **Opening ceremony**.

9:20-10:30. **Invited talk: Tiiu Märss.** *Endolymphatic structures in headshields of the osteostracan genus* Tremataspis *(Agnatha) from the Silurian of Estonia*. Introduced by Henning Bloom.

10:30-11:10. **Coffee Break** at the "Osteomeles" square and **Poster sessions** in the "Hort de Tramoieres" hall.

Thematic session: Jawless wonders – the earliest vertebrates (Chair: Per Ahlberg)

11:10-11:30. **Olive, S. et al.** *Enigmatic early chordates and vertebrates from the Lower Devonian of Belgium.*

11:30-11:50. **Reeves, J. et al.** *Reviving* Lasanius*, an enigmatic Silurian jawless vertebrate at the split of cyclostomes and gnathostomes.*

11:50-12:10. **Keating, P. et al.** *Development of the pteraspid cranial dermal skeleton and the evolution of vertebrate skeletal remodelling.*

12:10-12:30. **Dearden, R. et al.** *Anatomy and function in the mouth of the Early Devonian heterostracan* Rhinopteraspis*.*

12:30-12:50. **Randle, E. et al.** *A Phylogeny for Heterostraci.*

12:50-13:10. **Vaškaninová, V. & Alhberg, P.** *Unexpected hypophyseal morphology in basal stem gnathostomes challenges the consensus phylogeny of vertebrates.*

13:10-14:30. **Lunch**.

Thematic session: Origin, diversity and development of the jawed vertebrates (Chairs: Valeria Vaškaninová, Piotr Szrek, Donglei Chen & Joseph Keating)

14:30-15:10. **Keynote: Lauren Sallan** (online). *The conquest of the oceans by jawed vertebrates.*

15:10-15:30. **Brazeau, M. et al.** *Early Devonian placoderms from Mongolia and new anatomical details of* Minjinia turgenensis.

15:30-15:50. **Dupret, V. et al.** *Vertebrate bone remains from the Givetian (Middle Devonian) of Valentia Island (Ireland) – focus on* Bothriolepis *(Placodermi, Antiarcha) and palaeobiogeographic implications.*

15:50-16:10. **Jobbins, M. et al.** *Description and ecomorphological reconstruction of a new selenosteid placoderm from the Late Devonian of the eastern Anti-Atlas (Morocco) with preserved body outline.*

16:10-16:50. **Coffee Break** at the “Osteomeles” square and **Poster sessions** in the “Hort de Tramoieres” hall.

16:50-17:10. **Trinajstic, K. et al.** *New insights into assignment of the largest Gogo arthrodire to the genus* Eastmanostues *and implications for arthrodire phylogeny.*

17:10-17:30. **Lukševičs, E.** *Rare faunal elements from the Baltic Late Devonian: antiarchan placoderm* Walterilepis speciosa.

17:30-17:50. **Grygorczyk, K. et al.** *A large Late Devonian (uppermost Frasnian) ptyctodont (Placodermi) from Poland.*

18:00-20:00. Social drinks at the terrace of the “Estefua Freda”

June 22nd, Wednesday

9:00-9:40. **Keynote: Tetsuto Miyashita**. *The Head, Heart, and Fins of* Norselaspis *– a glimpse into the origin of jawed vertebrates.*

9:40-10:00. **Brazeau, M.** *The origin of the pectoral girdle.*

10:00-10:20. **Long, J. et al.** *The evolution of the innear ear in basal gnathostomes.*

10:20-11:00. **Coffee Break** at the "Osteomeles" square and **Poster sessions** in the "Hort de Tramoieres" hall.

11:00-11:20. **Sansom, R. & Randle, E.** *Fossil bite marks in heterostracans support predation by jawed vertebrates as a factor in the demise of ostracoderms.*

11:20-11:40. **Andreev, P. et al.** *Timing the origins and early diversification of jawed vertebrates, evidence from the lower Silurian of South China.*

Thematic session: Cartilaginous vertebrates – chondrichthyan diversity and evolution (Chairs: Richard Dearden & Mike Coates)

11:40-12:00. **Itano, W.** *Psephodus and the transition from teeth to tooth plates in holocephalians.*

12:00-12:20. **Ginter, M.** *The interrelationships of Devonian omalodontiform sharks.*

12:20-12:40. **Luccisano, V. et al.** *Systematics, ontogeny and palaeobiogeography of the large xenacanth Orthacanthus from the lower Permian of France.*

12:40-13:00. **Leyhr, J. et al.** *A 3D histological survey of the vertebrate jaw cartilage with implications for chondrichthyan skeletal evolution.*

13:00-14:30. **Lunch**.

14:30-15:10. **Keynote: Christian Klug.** *New early vertebrate-treasures from the Late Devonian of the Moroccan Anti-Atlas.*

15:10-15:30. **Greif, M. et al.** *A minute chondrichthyan Meckel's cartilage from the Hangenberg Black Shale in Morocco and its position in chondrichthyan jaw morphospace.*

15:30-15:50. (Online) **Schentz, L.** *Diversity patterns of early chondrichthyans*.

15:50-16:10. **Flament, R. et al.** *Developmental pattern of fin spines and scales of the Early Devonian shark* Wellerodus priscus *from the Cairo Lagerstätte (New York, USA).*

16:10-16:50. **Coffee Break** at the “Osteomeles” square and **Poster sessions** in the “Hort de Tramoieres” hall.

16:50-17:10. **Venkataraman, V. et al.** *Evolution and development of the anterior lateral line - new insights from Elasmobranchs.*

Thematic session: Ray-finned fishes – a history of extinction and diversification (Chairs: Donald Davesne, Martin Brazeau & Sébastien Olive)

17:10-17:30. **Chen, D. et al.** *'Natural experiments' reveal patterning logic of the dental development in the most primitive osteichthyan* Lophosteus.

17:30-17:50. (Online) **Mickle, K.** *The dermosphenotic, intertemporal and supratemporal in lower actinopterygian fishes.*

19:00-20:30. **Guided Tour to Valencia’s old town**. The meeting point is at the main entrance of the Botanical Garden (St. Quart, 80).

June 23rd, Thursday

9:00-9:40. **Keynote: Sam Giles.** *Revisiting the rise of the ray-finned fishes.*

9:40-10:00. **Henderson, S. et al.** *Diversity estimates and paleogeographical patterns for Palaeozoic ray-finned fishes (Actinopterygii).*

10:00-10:20. **Vanhaesebroucke, O. & Cloutier, R.** *Early actinopterygian diversification or how to “get in shape” after a crisis.*

10:20-11:00. **Coffee Break** at the “Osteomeles” square and **Poster sessions** in the “Hort de Tramoieres” hall.

11:00-11:20. **Burrow, C. et al.** *Dermal skeleton of the stem osteichthyan* Ligulalepis *from the Lower Devonian of New South Wales.*

11:20-11:40. **Caron, A. et al.** *Rethinking actinopterygian roots: new estimates using endoskeletal data from* Trawdenia planti*.*

11:40-12:00. **During, M. & Ahlberg, P.E.** *A Terminal Mesozoic Paddlefish from Tanis (ND, USA) – unique preservation of a K-Pg impact victim.*

12:00-12:20. **Johanson, Z. et al.** *Mechanisms of dermal bone repair after predatory attack in the giant stem-group teleost Leedsichthys problematicus Smith Woodward, 1889 (Pachycormiformes).*

12:20-12:40. **Davesne, D.** *The evolution of canalicles of Williamson in actinopterygian bone*.

12:40-13:00. **Houle, L. et al.** *Morphometric variation of cranial nerve foramina in a model fish, the zebrafish (*Danio rerio*): phylogenetic implications.*

13:00-14:50. **Lunch**.

Thematic session: Lobe-finned vertebrates – from the Devonian and beyond (Chairs: Zerina Johanson & John Long)

14:50-15:10. **Long, J. et al.** *Observations on a new sarcopterygian fish from the Late Devonian (Frasnian) of the Gogo Formation, Western Australia.*

15:10-15:30. **Cloutier, R. et al.** *History of the coelacanth fishes: phylogeny, disparity and diversification.*

15:30-15:50. **Mondéjar Fernández, J. et al.** *The exceptionally preserved branchial skeleton of a new coelacanth from the Late Carboniferous of Texas (USA).*

15:50-16:10. **Cuidad Real, M. et al.** *3D reconstruction and phylogenetic relationships of* Grossius aragonensis *(Osteichthyes, Sarcopterygii).*

16:10-16:50. **Coffee Break** at the “Osteomeles” square and **Poster sessions** in the “Hort de Tramoieres” hall.

16:50-17:10. **Szrek, P. et al.** *A new fossil record of the Early Devonian dipnoans behaviour from the Holy Cross Mountains, Poland.*

17:10-17:30. **Gess, R. & Ahlberg, P.E.** *A new Famennian species of* Hyneria *from the terra incognita of southern Gondwana – evidence from the Waterloo Farm Lagerstätte in South Africa.*

17:30-18:00. **Online Poster Session**

At this session the online posters must be defended by their authors, but the rest of the in-person poster authors must be present to answer the possible questions about their works by part of the online attendees.

June 24th, Friday

Thematic session: Tetrapods and the transition to land (Chair: Richard Cloutier)

9:00-9:40. **Keynote: Sophie Sanchez**. *Early limb-bone evolution.*

9:40-10:00. **Ahlberg, P. E. et al.** *Trackways of a terrestrially competent tetrapod from the Middle Devonian of Ireland.*

10:00-10:20. **Byrne, H. et al.** *A new tetrapod from the terminal Famennian of East Greenland.*

10:20-11:00. 10:20-11:00. **Coffee Break** at the "Osteomeles" square and **Poster sessions** in the "Hort de Tramoieres" hall.

11:00-11:20. **Coates, M. et al.** *Testing phylogenetic signal consistency in the early tetrapod record.*

11:20-11:40. **Otoo, B. et al.** *The shape of things to come: reexamining early tetrapod evolution after the end-Devonian mass extinction.*

11:40-12:50. **Invited talk: Philippe Janvier.** *Early vertebrates: on the importance of reputedly insignificant specimens*. Introduced by Alan Pradel.

12:50-13:30. **Closing Business.** Next Symposium.

13:30. **Lunch**.

20:30. Conference dinner at "Masía Santa Rita" restaurant at the Albufera's Natural Park. The bus will depart from the main entrance of the Botanical Garden (St. Quart, 80) at 19:00 pm.

INTRODUCTION

To our Honoured colleagues

I first met Tiiu Märss and Philippe Janvier at the 1st Middle Palaeozoic Fish conference in Tallinn in September 1976, nearly half-a-century ago but had already been influenced by their respective scientific papers. Since, we have worked together, co-operated on projects small to major, discussed, exchanged information, met at conferences and in our homes, all to good effect and in the friendly and inspirational spirit of our discipline, palaeoichthyology. We have wrangled on occasion, as good scientists should. Now we celebrate their achievements, over five decades, admire their outputs and energy, and wish them long life to continue adding to scientific knowledge and mentoring.

From Tiiu, we have excellent and numerous works on early vertebrates to Recent fish showing the quality of this great Estonian's life's output. These are constantly on my desk as I attempt to identity specimens down my microscope, currently dealing with Arctic Canadian, Scottish and Irish Silurian remains. Despite the vagaries of political change over the decades, Tiiu has maintained an honoured career in her homeland and now is helping a new cohort in Sweden. We came together in 1989 to forge one of the most important developments in the late 20th century for our community, the proposal of a UNESCO: IUGS IGCP project on Palaeozoic microvertebrates (1991-1996) that then spawned several more, the next of which (IGCP 406), she co-led and that took her to new realms in the Arctic. Her expertise in microvertebrates has revolutionised our understanding of early vertebrates (Wiki shows 171 taxa, at least(!) to her name).

Through his diverse and classic body of work, including his 'Early Vertebrates', Professor 'Phil' has achieved one of France's highest accolades as a member of the Académie des Sciences in Paris. But for me he will always be the mercurial 'Aramis' of my Three Musketeers (along with Daniel Goujet and our dear late friend Alain Blieck). I thank him for all his help over the years and have enjoyed all our conversations since the heady days of '76, and in introduction to and traverses of Paris. As the only western woman at that gathering, it was a delight to meet up with young and enthusiastic fellow workers on Palaeozoic fossil fish (then in short supply in the UK). We have not always agreed (notably on conodonts) but this is the nature of science and has spurred scientific effort and new perspectives for us both.

Susan Turner

Southern Hemisphere Microvertebrate Lab, 69 Kilkivan Avenue, Kenmore, Queensland, 4069, Australia.

Dr. Tiiu Märss

Fish studies by Tiiu Märss in Estonia started due to two needs. One was to give to an undergraduate student topic for two term papers to be presented in 1967 and 1969, and later on for the diploma work, which she defended in 1970. Her first steps in paleoichthyology were taken at Tartu University, supervised by prof. Arvo Rõõmusoks, to make acquaintance with Estonian osteostracans, with their morphology and publications about them. The second need arose because the correlation difficulties between the Estonian Silurian sections with the international British standard as in Britain the upper part of the sequence did not contain shelly fauna such as ostracodes or brachiopods neither graptolites or conodonts but did contain fish scales.

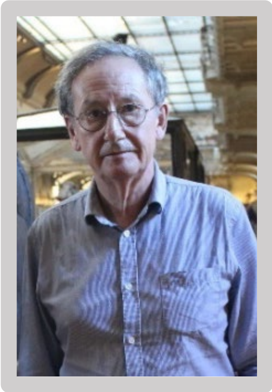
Logania ludlowiensis Gross (now called as *Paralogania ludlowiensis*) was the taxon which was needed to be found in Estonian Silurian. Dr Dimitri Kaljo, director of the Institute of Geology at that time, and the leading Silurian biostratigrapher, was behind that idea. T. Märss agreed with the task and in 1970 became a permanent member of the Institute of Geology working in palaeontology, with an emphasis on morphology-based taxonomy and biostratigraphy of Silurian vertebrates. To say beforehand, during her career she did find one scale of *P. ludlowiensis* in the Ohesaare core, Saaremaa, basal beds of Kuressaare Regional Stage, Ludlow.

During her scientific career a high number (about 3800) of rock samples from up to 70 drill cores of East Baltic and many outcrops from Estonia, Russia, Bohemia, British Isles, Canadian Arctic and elsewhere have been treated by T. Märss to obtain fish microremains. Scales and fragments that have been used for taxonomic as well as for biostratigraphic and palaeoecological studies, supporting posterior phylogenetic constructions. A big part of these material (but far from all) has been already published in numerous contributions authored or co-authorer by her.

Tiiu's work has been deeply developed under the umbrella of international projects. In this sense, since 1970's fish studies have been tightly tied with the studies of the other Silurian fauna carried out in the Institute of Geology. These works in turn were linked with the International Geological Correlation Programme (IGCP) projects, highlighting the importance of the Estonian fish fossil record in the Project Ecostratigraphy' and 'Global Events and Event Stratigraphy in the Phanerozoic', led by A. Boucot and O. Walliser, respectively. Highly valuable for Palaeozoic fish researches were two specific international projects, the IGCP project 328 'Mirovertebrates' (leaders S. Turner and A. Blieck), and the IGCP project 406 'Circum-Arctic Palaeozoic Vertebrates' (led by M. Wilson, T. Märss and P. Männik), the second one continued the vertebrate microremain studies but included also invertebrates and focused on the sections of modern Arctic regions. In addition, very important was the project on the remote Russian and Canadian Arctic, revealing new and diverse fossils as well as new data about the biostratigraphy of these regions, where T. Märss participated in both. T. Märss was the first among the international geologists' team investigating the Canadian Arctic islands (Baillie-Hamilton and Cornwallis) to simultaneously use the distribution data of several faunal groups (fishes, conodonts, ostracodes) to solve stratigraphical problems.

Among her main scientific results, T. Märss proved that most of the known Silurian agnathans and fishes dwelled in marine environments, some, maybe were migratory fishes refuting the widespread opinion of their freshwater habitats. She has devoted great attention to the use of agnathans and fish scales in the subdivision and correlation of sedimentary rocks of the Silurian Sea basins. She proved that new vertebrate taxa appeared during the transgressive phases of the development of the Palaeobaltic Sea and identified the levels of bioevents in the distribution of Silurian vertebrates. As the author of the Regional Vertebrate Biozonal Scheme, she initiated the creation of the Global Silurian Vertebrate Biozonal Scheme. She mapped the squamation of thelodont *Phlebolepis elegans* Pander and reconstructed its sensory-line canal system from Estonia, and lateron continued similar work on thelodonts from Scotland, and Cornwallis and Baillie-Hamilton islands, Arctic Canada. She discovered a second pair of ventral fins in the thelodont *Shielia taiti* Stetson from Scotland, which can be used in elucidating the formation and phylogeny of fins of early vertebrates. Osteostracans were treated in the monographic paper, and also this 16th ISELV conference talk is about a taxon of that group, *Tremataspis*, about their tiniest external endolymphatic structures. As a result of her individual or co-authored studies, T. Märss has established 167 new vertebrate and 4 invertebrate taxa with the focus on the Silurian agnathan thelodonts, anaspids, osteostracans, heterostracans, and less on the gnathostome acanthodians, chondrichthyans and osteichthyans. All that resulted over 190 publications including three monographs and four monographic papers.

Dr. Philippe Janvier



Dr. Philippe Janvier, born in 1948, is Emeritus Director of Research at the Centre National de la Recherche Scientifique (CNRS) and currently working in the 'Centre de Recherche en Paléontologie – Paris' (CR2P) at the Department 'Origines et 'Evolution' at the Muséum national d'Histoire naturelle, Paris, which he chaired from 1996 to 2002 and from 2009 to 2013. During his scientific career, Dr. Janvier has been essentially dealing with questions of early vertebrate phylogeny and evolution. As early as 1972, he was trained in this field by Prof. Jean-Pierre Lehman in Paris, then by Profs. Erik Stensiö and Erik Jarvik in Stockholm. His first research works were on the anatomy and relationships of osteostracans (also known as "cephalaspids"), a 430 to 360-million-year-old group of armoured, jawless fishes, which was hitherto regarded as closely related or ancestral to modern lampreys.

Thanks to the outstanding preservation of the braincase in some of these fossils, he managed to provide a new interpretation of their brain cavity, cranial nerves and vascular canals, in the light of the anatomy of early jawed vertebrates (or gnathostomes), namely the Silurian and Devonian placoderms. This has led him to study all the other groups of Palaeozoic, armoured jawless vertebrates (often referred to as "ostracoderms") and reconsider the entire large-scale phylogeny of the major living and extinct vertebrate groups. Through a cladistic analysis of the major fossil and living piscine vertebrate groups, he showed that the "ostracoderms" are not ancestral to the living cyclostomes (hagfishes and lampreys), as it was then believed, but rather more closely related to the jawed vertebrates, although they have no jaws. Among them, osteostracans, in particular, appear to be the closest known fossil relatives of the jawed vertebrates. In other words, the "ostracoderm" grade straddles the vast morphological and adaptive gap that separates cyclostomes from jawed vertebrates. In sum, 'ostracoderms' are jawless stem gnathostomes.

Dr. Janvier then tried to feature out the timing of the rise of the major anatomical characters that are common to all living jawed vertebrates but already appeared successively among "ostracoderms": scleral ossifications, open endolymphatic ducts, developed cerebellum, dorsal jugular vein, cellular bone, perichondral bone, paired fins, epicercal tail, etc. Certain of these characters display a series of progressive evolutionary states that can be followed throughout the various "ostracoderm" groups, whereas others seem to arise quite suddenly in the phylogenetic pattern.

The consequence of Dr. Janvier's theory is thus that the living jawless vertebrates, hagfishes and lampreys (i.e., cyclostomes) do not have a highly reversed (or "degenerate") morphology and physiology, as it was long believed, but rather display a primitive vertebrate or craniate condition and have diverged from all other vertebrates before the rise of a calcified skeleton in vertebrates; that is, no later than ca. 470 million years ago.

Beside his research activities on early vertebrate phylogeny, Dr. Janvier has been doing extensive field work all over the world (e.g., Spitsbergen, Middle-East, South America, Vietnam), in the search for new Palaeozoic vertebrate taxa. In the wake of his field research in Bolivia, for example, occurred the discovery of the earliest known articulated vertebrate with a bony dermal skeleton, the Ordovician arandaspid *Sacabambaspis janvieri*, described by his former student Dr. P.Y. Gagnier.

During these field expeditions, Dr. Janvier has incidentally contributed to the knowledge of various Palaeozoic jawed fish, some of which are now raising large-scale questions about gnathostome phylogeny. This was for instance the case for the still enigmatic genus *Andreolepis*, from the Silurian of Sweden, which is the earliest known osteichthyan ("bony fish"), and *Pucapampella*, a peculiar chondrichthyan ("cartilaginous fish") from the Lower Devonian of Bolivia, which allies unambiguous chondrichthyan characters and a somewhat osteichthyan-like braincase anatomy. These and other discoveries, such as the presumed Silurian and Devonian sarcoptergyian *Psarolepis*, from China and Vietnam, have now led Dr. Janvier to tackle the question of jawed vertebrate phylogeny, with particular reference to the question of the hypothetical ancestral morphotype of this vast group. Since the late 19th century, chondrichthyan morphology was generally regarded as quite close to that of the hypothetical ancestor of all jawed vertebrates. In contrast, the new palaeontological data mentioned above suggest that either the placoderm or the osteichthyan skeletal patterns may well be primitive for the gnathostomes, and this would better accord with the theory that the massively ossified osteostracan "ostracoderms" are their closest fossil relative. More recently, Dr. Janvier has also been involved in the study of the earliest known vertebrate, from the Lower Cambrian of China, in the framework of a collaboration with Dr. S. Conway-Morris (Cambridge) and Chinese scientists. Currently, Dr. Janvier's research focuses on exceptional soft tissue preservations in early fossil vertebrates, as means for providing new kinds of characters that can complement classical skeletal characters in phylogeny reconstructions. Dr. Janvier, in collaboration with J. Maisey (New York) provided the first evidence for the origin of chondrichthyans among 'acanthodians' an extinct group of Palaozoic fishes, thereby pushing the emergence of the chondrichthyan lineage back to the Late Ordovician, 445 Million years ago.

INVITED TALKS

Species-specific morphology of the endolymphatic openings in the headshields of the osteostracan genus *Tremataspis* (Agnatha), from the Silurian of Estonia

Märss, T.[1*]; Wilson, M. V. H.[2] & Viljus, M.[3]

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2. Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.
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Keywords: Endolymphatic openings, *Tremataspis*, Osteostraci, Silurian, Estonia

Osteostracan headshields from the Wenlock and Ludlow, Silurian, of Saaremaa Island, Estonia, vary in the detailed morphology of their paired, endolymphatic duct openings. Well-preserved specimens reveal each of the duct openings to be surrounded by tiny, characteristic plates, here termed covering plates, which are arranged in one or two (vertical) layers within a slightly larger fossa. The covering plates are pierced by pores that are usually larger than those in the headshield of the same specimen. The fossa often extends posteriorly, also with covering plates. The fossa, openings, and covering plates are species specific and located on elevations in the shield above the otic capsules. *Tremataspis schmidti* Rohon has covering plates on one level and in one or two wreath-like rings, formed of one longer and several shorter plates, around the opening. *Tremataspis milleri* Patten has variable patterns. Larger plates are on one or two levels, with a few large, deep pores per plate, or sometimes marginal notches and hooks rather than pores. Posterior extensions of the fossae are common. Some covering plates give the impression of moveability. Specimens of *Tremataspis rohoni* Robertson are very rare. Three large, smooth, and flat covering plates occur, with 1–2 pores per plate, or a notch at the margin close to the opening. In *Tremataspis mammillata* Patten, the roundish fossa has one large, flat, smooth, and inclined plate, plus a tiny cap-like plate; posterolateral extensions of the fossa are common. Each species-specific morphology characterizes a stratigraphic interval during the East Baltic Silurian.

Early vertebrates: on the importance of reputedly insignificant specimens

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Keywords: Doubtful vertebrate remains, History, Published data, Interpretations

During the last 30 years a number of fossil taxa could become "shoehorned" in the general tree of the vertebrates. Some of these taxa were first known only by enigmatic specimens that many years later turned out to be the first evidence of a key taxon that revolutionized vertebrate phylogeny. Such supposedly 'insignificant' specimens are still numerous in the back of collection drawers, and I suggest that our community should pay a particular attention to them. Current analytic and imaging techniques are a great asset for providing a systematic position to these orphan taxa.

KEYNOTES

Revisiting the rise of the ray-finned fishes

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Ray-finned fishes (actinopterygians) are a phenomenally successful group, comprising over half of all living vertebrates. With evolutionary roots stretching back nearly half a billion years, the fossil record of actinopterygians is as vital to understanding its vast modern diversity as the living members, but this also presents challenges to understanding their evolution. Unequivocal ray-finned fishes do not appear until the mid-Devonian, with the group seeming to remain depauperate throughout the rest of the Devonian and radiate explosively in the early Carboniferous. In recent years, a combination of CT scanning, mixed phylogenetic methods, and macroevolutionary analyses have revolutionised our understanding of the rise of the ray-finned fishes. In particular, CT-based windows into the braincase and other hard-to-access internal anatomy have filled in (some of) the conspicuous gaps in the group's early history. Identification of extinct relatives of early-diverging living groups has caused a fundamental shift in our understanding of when living ray-finned fishes evolved, and targeted re-investigation of key taxa hints at cryptic but extensive diversification in actinopterygians before the End-Devonian Mass Extinction. Restudy of well-known Carboniferous taxa also reveals unprecedented soft tissue preservation, with major implications for the timing and acquisition of key actinopterygian characters. Together, these findings prompt a re-evaluation of the early history of ray-finned fishes, with knock-on effects for how ray-finned fish evolution was shaped by mass extinctions and their rise to dominance through the Palaeozoic.

New early vertebrate-treasures from the Late Devonian of the Moroccan Anti-Atlas

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Keywords: Chondrichthyes, Placodermi, ecomorphology, evolution, Famennian

The Tafilalt and Maïder region in the Moroccan Anti-Atlas has become a classical region for research on Devonian vertebrates. While some placoderm plates and chondrichthyan teeth are well documented, other skeletal materials are still poorly known. We give an overview over the diversity of gnathostome remains with a focus on Famennian occurrences. Chondrichthyan teeth, dermal denticles and fin spines are reasonably well documented from Morocco. Almost complete skeletons of most of these genera were found including soft tissue-remains. Additionally, three-dimensionally preserved crania with mandibular and hyoid arches of five species of the genera *Ctenacanthus*, *Ferromirum*, *Phoebodus*, *Symmorium,* and Cladoselachidae gen. et sp. nov. are available. Morphological information is extracted using computed tomography-scanning. Although the X-ray density is high and the contrast is low, the anatomy of the cartilages and the endocast can be visualized. This information improves our understanding of the holocephalan-elasmobranch split with a range extension of the elasmobranchs and a new minimum date for the origin of the chondrichthyan crown-group. Remains of mostly arthrodires are frequently found in the Famennian. While the iconic genera *Dunkleosteus* and *Titanichthys* as well as some less-known ones like *Tafilalichthys* and *Driscollaspis* were described many years ago, two new forms are currently being described. Some taxa are occasionally found within large nodules in the shape of their body outlines, revealing information on body proportions and fins, enabling interpretations of their ecomorphology. Bony fish are mostly represented by incomplete remains of onychodontids (fragmentary actinistian and tristichopterid remains were already described). One partially disarticulated actinopterygian was found in the digestive tract of a cladoselachian, suggesting that small actinopterygians might be underrepresented for taphonomic reasons. One tooth plate of a dipnoan is available. Overall, the new materials provide a rare glimpse into a Late Devonian ecosystem, helping to reconstruct food webs and other ecological aspects of these epicontinental basins.

The head, heart, and fins of *Norselaspis* – a glimpse into the origin of jawed vertebrates

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Keywords: Gnathostomata, Osteostraci, brain, heart, Devonian

A conventional sister group to jawed vertebrates, osteostracans anchor synapomorphies and symplesiomorphies of the clade. This canonical view sets osteostracans in a mosaic of derived gnathostome traits (such as cellular bone) against the background of lamprey-like overall morphology (such as a blind nasohypophyseal canal). Extensive studies of their perichondrally ossified endoskeletons have provided support for this interpretation. However, few CT scans have been undertaken for osteostracan internal anatomy. Here we present preliminary results from a synchrotron X-ray tomography scan of a new specimen of *Norselaspis*, and reveal surprisingly derived gnathostome traits in this osteostracan exemplar. Contrary to the earlier interpretations, the vestibular *sinus superiorsus* is as tall in *Norselaspis* as those in jawed vertebrates. The pericardial chamber is closed dorsally, which precludes the lamprey-like single midline Cuvierian duct. There is no articular facet in the pectoral cavity, which suggests an entirely fleshy base of the pectoral fin. Our three-dimensional model also enhances key findings from the previous reconstruction, including: configurations of the extraocular muscles and associated motor nerves, exogenous infillings in the labyrinth, and brachial plexus derived from the most anterior spinal projections. These findings both refine and revise the stem-to-crown continuum of gnathostome characters. *Norselaspis* has derived gnathostome conditions in the inner ear and circulatory system. However, we present evidence that endoskeletal joints emerge with the evolutionary origin of jaws; in this respect, *Norselapis* remains resolutely plesiomorphic. Interestingly, an apparent lack of the crown-like hypobranchial system in *Norselaspis* implies its independent and divergent evolution in cyclostomes and gnathostomes.

The conquest of the oceans by jawed vertebrates

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Keywords: Gnathostomes, Macroevolution, Paleoecology, Habitats, Dispersal

In modern oceans, jawed vertebrates are colorful, diverse, and ubiquitous, occupying key niches and dominating food webs from the abyssal plain to Arctic shallows. This same ecological and biogeographic breath is observable in marine sites dating back to at least the mid-Paleozoic. Yet in the early Paleozoic, jawed vertebrates and their jawless relatives were vanishingly rare and mostly homogeneous, outdone by ammonoids, arthropods, and perhaps even conodonts. Until recently, there had been little investigation into when and how jawed vertebrate ecological diversity was achieved, particularly from macroevolutionary and paleontological perspectives. Here I show how the application of analytical and phylogenetic comparative methods to new databases of early vertebrate occurrences, habitats, traits and phylogenies is being used to flesh out the origins and assembly of modern jawed vertebrate communities. These approaches have revealed key roles for ancestral waters, extinction and post-extinction refugia, as well as convergence in traits that both enabled and constrained dispersal and habitat shifts, in jawed fish diversification and the establishment of early communities. These approaches have also revealed that much of modern ecological diversity was already established by the mid-Paleozoic, suggesting that competitive and sudden turnover within fish communities, rather than widespread ecological innovation, is responsible for the gross characteristics of modern marine vertebrate communities.

Early limb-bone evolution

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Keywords: bone microstructure, bone marrow, 3D virtual histology, stem tetrapods, fin-to-limb transition

The appearance of the limb is a crucial event in the evolutionary history of tetrapods. Transforming a fin into a limb profoundly affects the 3D architecture of the appendage at both morphological and histological levels. Biologists have demonstrated the diversity of developmental patterns in modern vertebrate appendages (e.g., zebrafish, mouse), assuming that they are representative of the group they belong to (respectively, ray-finned fishes and tetrapods). However, it is likely that long-bone microstructures in these models are highly derived and may not reflect their original function. Very few studies were conducted on stem-tetrapod bone microstructure to investigate the histological changes occurring over the fin-to-limb transition. The use of high-resolution phase-contrast imaging at the European Synchrotron Radiation Facility permitted to access the three-dimensional arrangement of skeletal tissues in basal ray- and lobe-finned fishes (including *Mimipiscis*, *Glyptolepis*, *Gogonasus*, *Hyneria*, and *Eusthenopteron*). This revealed that endochondral ossification produced a complex spongiosa in the marrow cavity of appendage elements before they start elongating. The elongation of long bones seemed to relate to the appearance of marrow processes, thereby suggesting that bone marrow played a major role in initiating a directional endochondral ossification. In parallel, long bones have evolved from a strictly locomotion-related organ to a multifunctional element also involved in the production of blood cells (called haematopoiesis). The fossil record of stem-tetrapod limbs brings evidence for the first migration of haematopoiesis in long bones after the water-to-land transition. These discoveries will bring new perspectives on the early evolution of the tetrapod limb.

ABSTRACTS OF CONFERENCE PRESENTATIONS AND POSTERS

Trackways of a terrestrially competent tetrapod from the Middle Devonian of Ireland

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Keywords: Devonian, Givetian, tetrapod trackway, Ireland

The Givetian tetrapod trackway mega-locality of Valentia Island, south-west Ireland, is no younger than 384.9 Ma and thus the second oldest in the world after Zachełmie in Poland (Eifelian, 391 Ma). Twenty-four trackways, some exceeding 10 m in length, are known from sediments representing streams traversing vegetated floodplains. The footprints lack toe impressions, showing instead a mitten-like morphology with a single cleft between a 'hallux region' and the rest of the foot. In other respects, they are wholly tetrapod-like: the pes is larger than the manus and the movement pattern is indistinguishable from undisputed tetrapods of the Carboniferous and Permian. The tracks show a range of locomotory styles from 'skipping' in quite deep water (Dohilla 4) to walking on land (Beennakryraka Head). The most informative is Dohilla 3, which transitions from underwater walking to 'belly-skating' on emergent mud - a behaviour documented in extant alligators. Because this track combines footprints, body drag and tail drag, we are able to reconstruct the morphology of the track maker: it is a typical tetrapod with large limbs, similar in proportions to much later forms such as the Permian *Orobates*. The narrower Beennakryraka Head track shows the same taxon doing a terrestrial 'high walk'. Tetrapods fully capable of terrestrial walking locomotion had thus evolved by the Middle Devonian, before the earliest known elpistostegalians, and established a body morphology that persisted for at least 100 million years. The Valentia Island tetrapods coexisted with a gigantic chelicerate, probably a scorpion, that may have preyed on them.

Acknowledgements: This presentation forms part of ERC Advanced Grant project ERC-2020-ADG 10101963 "Tetrapod Origin".

Timing the origins and early diversification of jawed vertebrates, evidence from the lower Silurian of South China

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Keywords: Silurian, evolutionary radiation, chondrichthyans, osteichthyans, teeth

Time-scaled phylogenies of vertebrates reflect a growing consensus in morphological and molecular data for a deep evolutionary split of jawed vertebrates from their agnathan ancestors in the Middle to Upper Ordovician. The fossil evidence for this predicted initial radiation is scant and comes from enigmatic dermal scales and fin spines that predate the widespread appearance of 'placoderm', osteichthyan and chondrichthyan body fossils in the late Silurian/Lower Devonian. Here we provide direct support for early diversification models of jawed vertebrates by reporting the disarticulated remains of the oldest toothed chondrichthyans and osteichthyans from lower Silurian (Aeronian) strata of the Rongxi Formation at Leijiatun, Guizhou province, China. This assemblage contains isolated tooth whorls, individual teeth, dermal plates, scales and fin spines of stem chondrichthyans represented by a new climatiid genus, a potential ischnacanthid and a sinacanthid. Also occurring in the samples are conical teeth and tooth-bearing plates akin to the tooth 'cushions' previously reported in the stem osteichthyans *Lophosteus* and *Andreolepis*. These discoveries allow us to produce a revised timeline for branching events within early crown gnathostomes that places the origins of established stem chondrichthyan groups and the actinopterygian-crossopterygian split in the Upper Ordovician (Katian) to lower Silurian. Our results offer the strongest support yet for an initial evolutionary radiation of jawed vertebrates as part of the Great Ordovician Biodiversification Event. Moreover, the data from the Rongxi indicate that the absence of undisputed tooth remains in coeval and older vertebrate assemblages is, at least in part, a consequence of limited bulk sampling.

Acknowledgements: We thank Y.-M. Hou for the acquisition of the micro-CT X-ray data, Y. Hwu (Academia Sinica) and Y.-T. Weng (NSRRC) for performing and assisting with the synchtrotron X-ray imaging. We also want to acknowledge Dr Martin Rücklin (Naturalis) for providing beamtime at the Swiss Light Source (SLS) synchrotron facility, as well as carrying out together with Dr Federica Marone (SLS) synchrotron X-ray analyses of fossil specimens.

New Late Devonian vertebrate locality in the Sosnogorsk Formation (South Timan, NE Europe)

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Keywords: vertebrates, Famennian

The Upper Devonian Sosnogorsk Formation consists of shallow-water deposits formed in a coastal-plain water body, which alternated over time between a saline lagoon and a fresh-water lake. It contains the most complete sequence of Frasnian-Famennian boundary beds in the East European Platform, and the upper part of the formation exposed in the type section on the Izhma River yields abundant well-preserved vertebrate remains including the tetrapod *Parmastega*. Until recently this was the only known fossil site of the Sosnogorsk Formation. A new locality was discovered on the Pon'yu River (right tributary of the Izhma River) in 2012 and excavated in 2021. The exposed sequence also belongs to the upper part of the Sosnogorsk Formation but differs from the type section in less bed thicknesses and less variable C and O isotopic compositions. The bone-bearing limestone bed lies somewhat higher in the section and does not resemble the 'fish dolomite' layer of the Izhma site. Compared to the type section, no remains of *Parmastega*, *Duffichthys* or *Bothriolepis leptocheira* were found at the new locality. In addition to taxa common for both sites (*Holoptychius*, onychodontid and lungfishes), a new bothriolepid, the acanthodian *Cheiracanthus*, tetrapodomorph fish, and a probable new tetrapod are present in the Pon'yu River assemblage. In contrast to the previously known vertebrate assemblage of the Sosnogorsk Formation, lithological and geochemical peculiarities of the bone-bearing bed as well as an associated find of a scolecodont element indicate that the newly discovered community inhabited a shallow-water environment of rather normal salinity.

The origin of the pectoral girdle

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Keywords: Pectoral girdle, gnathostomes, paired appendages, evolution

The origin of a distinct pectoral girdle in jawed vertebrates is one of the most persistent mysteries in the evolution of the vertebrate body plan. This remains problematic due to the highly divergent morphology of the earliest jawed vertebrates (i.e., placoderms) and their nearest, well-studied jawless outgroup, the osteostracans. Two classical hypotheses based in ideal morphology continue to be widely discussed: the ventrolateral fin-fold and the archipterygium. The fin-fold hypothesis explains similarities between pelvic and pectoral appendages and some fossil stem-group gnathostomes appear to exhibit ventrolateral fin-folds. However, it provides no explanation for the origin of the girdle or a distinct head-shoulder separation, or the apparent earlier origin of pectoral fins relative to pelvic fins. The archipterygium provides an explanation for the origin of the girdle but lacks any apparent palaeontological support. I will present an integrated palaeontological, comparative anatomical, and developmental case for a partial return to the archipterygium. New and long-overlooked evidence in early gnathostomes and osteostracans provides evidence of a pharyngeal origin of the pectoral girdle. This new hypothesis resolves the problem of the location of the head-trunk interface in jawless fishes simultaneously with other vexing comparative anatomical problems. Furthermore, it reconciles diverse lines of evidence from comparative anatomy and developmental genetics. This hypothesis is testable on the basis of existing evidence, but will require more satisfactory resolution of early gnathostome interrelationships.

Early Devonian placoderms from Mongolia and new anatomical details of *Minjinia turgenensis*

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Keywords: Devonian, Placoderm, *Minjinia*, Mongolia, Acanthothoraci

Discoveries of new vertebrate faunas from previously undersampled geographic regions yield transformational insights on the phylogeny and palaeobiogeography of the earliest vertebrates. This is most striking in the Silurian and Early Devonian, where continental fragmentation may have promoted high faunal provinciality. Mongolia is thought to have formed part of the Siberian palaeocontinent and remains a very poorly sampled region for early vertebrates. We describe a placoderm fauna from the Early Devonian (Pragian) Yamaat Gol locality in western Mongolia. The site contains at least five distinct placoderm morphologies. These include three acanthothoracid morphologies, a rare arthrodire, and the recently described *Minjinia turgenensis*. Although fragmentary and disarticulated, the fossils from Yamaat Gol are often remarkably well-preserved, maintaining much of their original three-dimensional shape and histology. We present new details of a completely preserved *Radotina*-like upper jaw complex that clarifies issues about the unusual dentitions of acanthothoracid placoderms. Additionally, we will report on the first postcranial and additional cranial material of *Minjinia*. The shoulder girdle of *Minjinia* exhibits a combination of traits resembling acanthothoracids, arthrodires, and osteichthyans. As in the braincase, the scapulocoracoid is endochondrally ossified. New cranial material provides additional information on the overall outline of the skull and sensory line distribution. Together, the new data highlight phylogenetically valuable traits of the pectoral girdle. Unequivocal evidence of jawless fishes remains absent from the Devonian of Mongolia, and the gnathostome-enriched fauna of Yamaat Gol demonstrates some peculiar resemblances to Early Devonian faunas of East Gondwana.

Dermal skeleton of the stem osteichthyan *Ligulalepis* from the Lower Devonian of the Lachlan Fold Belt, New South Wales, Australia

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Keywords: Osteichthyes, Gleninga Formation, Troffs Formation, Taemas Formation, palaeohistology

When first described based on isolated scales, *Ligulalepis* was assigned to the Palaeoniscoidea, a basal group of actinopterygians. Most recent cladistic analyses, in the main based on skull and neurocranial characters, have recovered the taxon (or '*Ligulalepis*') as a stem osteichthyan. Here we present information on *Ligulalepis* dermal elements other than scales and the skulls from the Taemas Formation, including a skull fragment, premaxilla, other marginal jaw elements and teeth, a partial shoulder girdle, and incomplete spine-like elements from central New South Wales (NSW) localities in the Gleninga and Troffs formations of centralNSW, and jaw elements and a ?median gular/interclavicle/ventral plate from the Taemas Formation, Wee Jasper. The shoulder girdle and premaxilla compare closely with those of basal actinopterygians. The spine-like element is compared with the distal end of the spines on medial dorsal plates of the Chinese late Silurian stem osteichthyans *Guiyu* and *Sparalepis*, as well as dermal fin rays on the ?basalmost stem osteichthyan *Dialipina*, and dorsal fulcra of *Cheirolepis*. A phylogenetic analysis incorporating post-cranial characters is proposed.

A new tetrapod from the terminal Famennian of East Greenland

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Keywords: Late Devonian, Greenland, Tetrapod, Romer's Gap

The Hangenberg extinction at the end of the Devonian marks the beginning of a hiatus in tetrapod body fossils for around 20 million years into the Carboniferous, colloquially referred to as “Romer’s gap”. Although it is now suspected that this gap is due to sampling bias, the paucity of body fossils has resulted in a poor understanding of the evolution of early tetrapods across the Devonian-Carboniferous boundary. Here we present a new tetrapod taxon from the Stensiö Bjerg Formation (latest Famennian) of East Greenland, represented by a lower jaw ramus, shoulder girdle, and suspensorium. These specimens have been scanned using propagation phase-contrast synchrotron microtomography (PPC-SRµCT) at ESRF in France, and have been segmented using the 3D modelling software Materialise Mimics 19.0. Analysis of the three elements suggests that they may belong to a single individual. They share broad similarities with other Greenland tetrapods, for example the absence of a scapular blade, but nevertheless are clearly distinct and represent a new taxon. Notably, the cleithrum is much shorter compared with the other Greenland taxa, the suspensorium possesses a small temporal fenestra similar to that of *Anthracosaurus*, and the cheek lateral line canal is represented as a groove and not as pores as seen in *Acanthostega* and *Ichthyostega*. This will be the fifth taxon among the Devonian tetrapods of Greenland, and, together with *Brittagnathus*, also the most crownward tetrapod of the group. Preliminary comparison with other early tetrapod taxa suggests that the new taxon is slightly less crownward than *Tulerpeton*.

Rethinking actinopterygian roots: new estimates using endoskeletal data from *Trawdenia planti*

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Keywords: actinopterygian, phylogenetics, Palaeozoic, Carboniferous

Though the actinopterygian crown group is estimated to originate near the Devonian-Carboniferous boundary, phylogenetic analyses have persistently failed to recover stem-members of extant clades, obscuring our understanding of early ray-finned fish evolution. We present new endoskeletal data of the Early Pennsylvanian *Trawdenia planti* from Lancashire, UK, and explore its systematic implications. Advances in microcomputed tomography (µCT) have revealed in exquisite detail undistorted anatomical structures of specimens NHMUK P7989 and NHMUK P11656 including the jaws, hyoid and gill arches, pectoral, axial, and dermal skeleton, and an incongruous neurocranium. While *Trawdenia planti* appears externally an archetypal "palaeonisciod" actinopterygian, newly-revealed morphologies of the braincase and visceral skeleton demand revision of current phylogenetic hypotheses. We created a new dataset comprised of primarily endoskeletal morphological characters designed to be inclusive of both fossil and extant actinopterygians. Using both Bayesian and Maximum Parsimony phylogenetic methods, we recover *Trawdenia planti* as a stem-chondrostean. Furthermore, including *Trawdenia planti* in systematic analysis changes character state optimizations across the tree, resulting in many late Palaeozoic species also attaching to the chondrostean stem. This radical departure from prevailing hypotheses may have significant implications regarding the evolutionary trajectory of endoskeletal systems, the timing and pattern of divergence and diversification of the actinopterygian crown group, and estimates of survivorship through the end-Devonian mass extinction events. Exceptionally well-preserved specimens such as *Trawdenia planti* are information dense, yielding new comparative data that might resolve the deep Palaeozoic roots of the extant actinopterygian divisions.

'Natural experiments' reveal patterning logic of the dental development in the most primitive osteichthyan *Lophosteus*

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Keywords: synchrotron scan, hard-tissue resorption, dental patterning

Developmental regulation of dental pattern has come under recent scrutiny, but only in extant vertebrates, whose dentitions have been reduced in various degrees. Although many signal pathways have been identified, understanding of the origin and early evolution of teeth has been hindered by the distinctions between the oral and dermal odontode systems, and between the osteichthyan shedding tooth rows and the chondrichthyan conveyor-belt-like tooth files. 3D reconstruction of the entire dental ontogeny of the Silurian stem osteichthyan *Lophosteus* presents a key to this conundrum. *Lophosteus* teeth are organized in chondrichthyan-like tooth files, but are replaced by osteichthyan-style resorption. The resorption removes both bone and dentine within a tooth file, but only bone if spilling over onto the territory of adjacent files, illustrating a spatial regulation of odontoclast and osteoclast activity. First-generation tooth files show fan-shaped radiation from the ossification center along with the appositional bone growth, while the replacement files become parallel, demonstrating a change in polarity signals as the bone changes to mainly increasing in width. The marginal teeth are conical and the dermal ornament is stellate, but mixed morphologies emerge when the two sets are in proximity, indicating 'cross-contamination' of patterning signals. The ornament can invade the tooth field and disturb the tooth replacement. The mineralized tip of a rudimentary tooth bud is observed. Each tooth file shows different domino effects due to the tempo-spatial difference in the ornament overgrowth. Thus, each ornament is like an experimental treatment, and the tooth files are like control and experimental groups.

History of the coelacanth fishes: phylogeny, disparity and diversification

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Keywords: sarcopterygians, actinistians, phylogeny, disparity, geometric morphometrics

More than 30 years ago, the first phylogenetic analyses of coelacanths suggested an early burst of evolution followed by a slow and conservative evolution over a period of 380 million years. In 1998, Peter Forey published “History of the Coelacanth Fishes”, a landmark in coelacanth morphology and phylogeny. Subsequently, 19 phylogenetic analyses addressed partial or complete phylogeny of this clade, 16 of which were strictly built on minor modifications of Forey’s matrix (30 genera, 108 characters). Over a period of 23 years, 18 genera and 2 new characters have been added without major revision of the original coding. To assess the phylogeny, disparity and diversification of coelacanths, we designed three new phylogenetic matrices for 87 species: 268 discrete, 40 morphometric and 14 meristic characters. Bayesian and maximum parsimony analyses were used to present a new phylogeny of the group. In addition, 2D geometric morphometrics of the body shape and skull on a reduced sample was used to describe evolutionary changes over the history of the group. As expected, the Carboniferous *Allenypterus* and the Triassic *Foreyia* differ from a more classical coelacanth body shape accounting for approximately 40% of the total variation. The second source of variation (ca. 20%) considers the discrepancies associated with the heterocercal and triphycercal caudal fins. Bayesian and principal component analyses for incomplete data on the morphometric and meristic matrices permitted to recognize conservative and disparate anatomical traits responsible for evolutionary shape variation. Time-binned disparity and diversification are interpreted in the light of the morphometric trends.

3D reconstruction and phylogenetic relationships of *Grossius aragonensis* (Osteichthyes, Sarcopterygii)

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Keywords: Sarcopterygii, Devonian, computed microtomography, phylogeny, osteology

Onychodonts (Osteichthyes, Sarcopterygii) are an extinct group of predatory marine fishes from the Devonian period with putative "intermediate" characteristics between early branching osteichthyans and coelacanths. Due to their limited fossil record, there is a lack of consensus regarding their relationships within sarcopterygians and whether onychodonts are actually a monophyletic group. The partial remains of the holotype and the only specimen of *Grossius aragonensis* from the Moyuela Formation (Eifelian, Middle Devonian) of Aragón province (Spain) is one of the most complete onychodont skulls known. Despite this, it has a high percentage of missing data in phylogenetic analyses. In this work, *Grossius* osteology and internal cavities were restudied by applying computed microtomography and 3D post-processing techniques to access previously unknown anatomical information. In particular, the morphology of the dermal bones of the snout, neurocranium, mandibular arch, and most teeth has been determined for the first time. Including this new information from *Grossius* has improved the resolution of strict consensus trees in previously published datasets for phylogenetic analyses. The strict consensus retrieves a monophyletic Onychodontida. This has allowed to determine that *Grossius* is an onychodont that differs from the rest by several autapomorphies, enabling to establish a new emended diagnosis of the genus *Grossius*.

Testing phylogenetic signal consistency in the early tetrapod record

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Keywords: phylogeny, tetrapods, completeness, macroevolution

Ongoing searches for the earliest limbed tetrapods have greatly enriched the record. However, this newly evident diversity remains underrepresented in phylogenetic hypotheses because many taxa are fragment-based, and thus unlikely to contribute to well-resolved trees. To explore signal in this patchy, representationally biased data set, we constructed a maximally inclusive matrix. Despite presence of *Tiktaalik*, *Acanthostega*, *Ichthyostega*, and Carboniferous tetrapods including the revised *Whatcheeria*, a mere 36% of cells were filled. To test for anticipated deleterious effects of inclusivity and replicate our research protocol on successive dataset variants, we developed a tool for serial searches using standard software, to sequentially exclude least complete OTUs, evaluate changes in phylogenetic signal strength, and calculate deviation in output consensus tree shapes. As expected, although some consistency is evident, phylogenetic signal attenuation correlates with taxon incompleteness. But we also found that erosion patterns, stepped or gradual decline, vary with search method. Subjecting our results to tip-dating methods enabled maximum and minimum estimates of Devonian lineages persisting into 'Romer's Gap'. Similarly, inclusion/exclusion of least complete taxa, although having limited influence on tree shape, exposed large effects on node-date estimates. Macroevolutionary hypotheses of stem-tetrapod radiations are especially sensitive to these tests; nevertheless, Famennian tetrapod diversity appears consistently higher than in previous estimates, prompting a greater appreciation of pre-Hangenberg (and likely pre-terrestrial) tetrapods yet to be discovered.

The evolution of canalicles of Williamson in actinopterygian bone

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Keywords: bone histology, Actinopterygii, Holostei, Teleostei, canalicles of Williamson

Canalicles of Williamson (CW) are peculiar histological structures, cellular expansions into mineralised tissues that are found in the dermal bone and scales of modern holosteans (gars and bowfins). These structures have also been observed in Palaeozoic and Mesozoic extinct lineages of actinopterygians, and they seem to follow a phylogenetic distribution. Where exactly in the phylogeny the canalicles of Williamson occur is unclear, however. In addition, they have been mostly surveyed in scales, but not much in endoskeletal elements. Using a 3D histological dataset previously collected in a synchrotron-based palaeogenomic study, I was able to track the presence of CW in the dentaries (lower jaws) of a range of fossil and extant actinopterygians. The distribution of the CW in dentary bone seems to be the same as in scales. Holosteans s*ensu stricto* all have CW, as well as early diverging stem-teleosts (e.g., aspidorhynchids, pachycormids, pholidophorids). In the teleost lineage, the loss of CW corresponds to that of ganoid scales, and ganoine covering of dermal bone in general. However, non-neopterygian actinopterygians with ganoine (e.g., polypterids) do not possess CW. This calls into question the physiological role of this histological structure. Early-diverging neopterygians with debated phylogenetic positions, such as dapediids or pycnodontiforms possess CW but this is not the case in several Triassic stem-neopterygians. Canalicles of Williamson thus appear to have potential as a phylogenetic character to decipher phylogenetic relationships within neopterygians and stem-teleosts.

Anatomy and function in the mouth of the Early Devonian heterostracan *Rhinopteraspis*

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Keywords: stem-gnathostome, feeding, heterostracan, Devonian, pteraspid

Heterostracans are a morphologically diverse group of heavily armoured, jawless stem-gnathostomes that were a major component of Laurussian ecosystems in the Silurian and Devonian. The functionality of heterostracan feeding systems, and the role of jawless stem-gnathostomes in these ecosystems, is however poorly understood, obscured by a lack of data on the anatomy of heterostracan oral regions in articulation. Here, we use computed tomography to describe the articulated oral region of the Early Devonian pteraspid heterostracan *Rhinopteraspis dunensis*, from Odenspiel Quarry, Germany. The mouth of *Rhinopteraspis* is bordered ventrally by a postoral cover, and laterally by the anterior orbital plates. Dorsally it is bounded by a plate comprising the ascending lamella and pre-oral field, but which is separate from the rostrum, the oral boundary of this plate is marked by a row of tubercles. The oral apparatus comprises 13 imbricated oral plates which articulate with a sulcus in the postoral cover; these plates are varied in form and characterised by marked hooked processes at their distal tips. By retrodeforming and reconstructing this model, we show that the oral plates would have met the anterodorsal plate, suggesting that it was functionally the upper boundary of the mouth. This observation appears to rule out previous interpretations that it was the roof of a prenasal sinus and supports the idea that the nasohypophyseal duct opened inside the mouth. These new data provide an anatomical framework on which future inferences for the functionality of feeding in heterostracans can be based.

Vertebrate bone remains from the Givetian (Middle Devonian) of Valentia Island (Ireland) – focus on Bothriolepis (Placodermi, Antiarcha) and palaeobiogeographic implications

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Keywords: Middle Devonian, phylogeny, Placodermi, palaeogeography

The Middle Devonian deposits of Valentia Island (South-Western Ireland) are renowned for their tetrapod tracks, but also yield lower green schist facies metamorphosed vertebrate bone remains. In his seminal review of the fossil bone material of the Valentia Slate Formation in 1978, Kenneth J. Russell identified two taxa: a *Bothriolepis* species (Placodermi, Antiarcha) and an indeterminate acanthodian. Revision of this material and study of newly collected specimens, especially using CT-scanning, allows an update of the previous faunal list. The vertebrate fauna of the Valentia Slate Formation now consists of one new species of *Bothriolepis*, one rhizodont (Sarcopterygii, previously misinterpreted as acanthodian), one lungfish, and of course tetrapod(s) (as ichnofossils). A new phylogenetic analysis of the genus *Bothriolepis* is proposed and resolves the new form as sister species to the Frasnian Scottish form *B. gigantea*, but confirms the difficulty of investigating the relationships within such a speciose genus. The reliability of the shape of the preorbital recess, hitherto used as a systematic marker for the genus *Bothriolepis*, is questioned. Comparisons between Givetian vertebrate faunas reveal the strong Gondwanan affinities of the Laurussian Valentia Slate Formation deposits, and a northward dispersal episode as early as the Givetian is proposed for *Bothriolepis* and Rhizodontida.

A Terminal Mesozoic Paddlefish from Tanis (ND, USA) – unique preservation of a K-Pg impact victim

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Keywords: Acipenseriformes, paddlefish, synchrotron tomography, KPg, anatomy

The terminal Maastrichtian Tanis event deposit yields undescribed acipenseriform fish that perished on the last day of the Mesozoic. Propagation Phase-Contrast Micro-Computed Tomography was used to investigate a partial paddlefish from this assemblage. Comparison with the two extant paddlefishes *Polyodon* and *Psephurus*, and with fossil forms including the Maastrichtian *Paleopsephurus* shows that the Tanis paddlefish represents a new taxon. The elongate cranial roof appears intermediate between the more robust *Polyodon* skull and the slenderer *Psephurus* skull. It is distinctly curved anteroposteriorly, as is the parasphenoid, which trends parallel with the cranial roof up to its anterior margin. This differs from the condition in the extant forms, especially *Polyodon*, in which the parasphenoid is straight and converges on the skull roof anteriorly. The postorbital foramen features a unique interfenestral strut. The posttemporal widens posteriorly, whereas it narrows in both *Polyodon* and *Psephurus*. The parietal is significantly longer and intermediate in width relative to both extant genera. Its centre of ossification is positioned much further forward than in *Polyodon*. The gill rakers appear comparatively short and unlike those of the modern paddlefishes. The cause of death was likely burial in the massive seiche wave and/or suffocation with impact spherules. The spherules are almost exclusively encountered between the second and the third gill arch, possibly indicating the main respiratory water flow path, since the gill arches are obscured by a gill cover that cannot be removed without damaging the specimen, such details would remain invisible without the use of synchrotron microtomography.

Developmental pattern of fin spines and scales of the Early Devonian shark *Wellerodus priscus* from the Cairo Lagerstätte (New York, USA)

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Keywords: histology, primitive chondrichthyan, ontogeny, Devonian

Teeth, fin spines and scales of Siluro-Devonian chondrichthyans are a great source of anatomical, developmental and phylogenetic information. However, little attention has been given to the developmental patterns of fin spines and scales while it is a crucial feature towards the understanding of their primitive morphology, which is still a matter of debate. In order to investigate developmental patterns in basal chondrichthyans, we studied the growth of the fin spines and scales of the Givetian chondrichthyan *Wellerodus priscus* using micro-CT scanning, scanning electronic microscopy and paleohistology. The external morphology of the pectoral and dorsal fin spines reveals subparallel longitudinal ridges of aligned pectinated triangular odontodes with lateral projection. The apex exposes two rows of curved thorn-like denticules. The histological differences between the proximal and the distal part suppose a proximo-distal growth with a lateral expansion along the leading edge. With regard to body scales, three different morphotypes are associated with different regions of the body of *W. priscus*. Differences in the overlapping of odontodes suppose that the deposition and growth of the scales are made by successive rows of odontodes with an exponential increase in the number of odontodes for each newly formed row of odontodes. Spines and scales developmental patterns are compared with putative chondrichthyans from Man On The Hill (MOTH, Canada) which share similar shapes but also some fundamental differences in the ornamentation.

A new Famennian species of *Hyneria* from the terra incognita of southern Gondwana – evidence from the Waterloo Farm Lagerstätte in South Africa

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Keywords: Devonian, Sarcopterygii, Tristichopteridae, Hyneria, Gondwana

Hyneria lindae is a tristichopterid described in 1968 from the Famennian Catskill Formation of Pennsylvania. Daeschler and Downs greatly expanded and emended its description in 2018, following more systematic collecting. This has permitted comparative analysis of material from Waterloo Farm preliminarily identified by Gess and Hiller, in 1995, as a ‘probable eusthenopterid’, and subsequently considered ‘similar to *Hyneria*‘ by Gess and Coates in 2008 or *Hyneria*-like by Gess in 2009 and Gess and Whitfield in 2020. Assignment to *Hyneria* is confirmed, though slight proportional differences justify erection of a novel species. In 2020 Olive and colleagues hypothesised a western European (Laurussian) origin for tristichopterids, suggesting migration from Western Europe to Australia during the Famennian. Thereafter they suggest that a clade of giant Famennian tristichopterids, represented by *Cabonnichthys burnsi*, *Mandageria fairfaxi*, *Eusthenodon wangsjoi*, *Edenopteron keithcrooki*, and *Hyneria lindae* likely differentiated in Australia. Of these *Cabonnichthys, Mandageria* and *Edenopteron* are known from single localities in eastern, Australia. *Eusthenodon wangsjoi* from Greenland and Western Europe, and *Hyneria lindae* from Pennsylvania are hypothesised to have migrated to Laurussia from an Australian centre of origination. Evidence from Waterloo Farm strongly supports a Gondwanan origin for this clade, whilst casting doubt on an Australian centre of origination. An almost entire lack of evidence from Late Devonian southern Gondwana has frequently misled biogeographical analyses, resulting in concluded tropical distribution of, for example, *Archaeopteris* trees and digitate tetrapods. Waterloo Farm’s unique provision of a window into high latitude Gondwanan diversity, continues to supply some remedy to this challenge.

Acknowledgements: R.G. acknowledges funding from the South African Millennium Trust, GENUS (the South African DST-NRF Centre of Excellence in Palaeosciences) and the South African NRF. Attendance at the 16th ISELV was funded by Rhodes University.

The interrelationships of Devonian omalodontiform sharks

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Keywords: Chondrichthyes, Omalodontiformes, dentition, taxonomy, Devonian

The representatives of the Devonian chondrichthyan order Omalodontiformes are generally characterised by the teeth whose basal extensions are directed not lingually, as in the most of Palaeozoic sharks with a primitive dentition, but labially or there is no extension at all. Several genera based on differences in tooth morphology were erected, viz. *Omalodus*, *Portalodus* (with two species, *P. bradshawae* and *P. manoliniae*), *Aztecodus*, *Anareodus*, *Doliodus*, *Siberiodus* and *Manberodus*. It was previously suggested that *Aztecodu*s and *Anareodus* were in fact congeneric and the subdivision of the order in two families was proposed: Aztecodontidae for those with no basal extension (*Aztecodus* and *Manberodus*) and Omalodontidae for those with the extension directed labially (*Omalodus*, *Portalodus* and *Doliodus*). However, the single articulated specimen of *Doliodus* from the Lower Devonian of New Brunswick, the dentition of which was described in detail a decade ago based on CT-scan, shows considerable heterodonty, with *Portalodus*-like teeth anteriorly and *Aztecodus*-like teeth in the postero-lateral region. Therefore, the proposed subdivision appears to be untenable and it is highly probable that the teeth found in the Aztec Siltstone in Antarctica and originally described as *Portalodus* and *Aztecodus* actually belong to the same genus (*Portalodus*, by priority) or even the same species. Also, the great similarity of teeth of *Portalodus* and *Doliodus* casts doubt on the sense of taxonomic separation of the latter two genera.

A minute chondrichthyan Meckel's cartilage from the Hangenberg Black Shale in Morocco and its position in chondrichthyan jaw morphospace

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Keywords: chondrichthyans, jaw morphospace, jaw disparity, Hangenberg black shale, Anti-Atlas

Extinct chondrichthyans are mostly known from their teeth and fin spines, while their poorly calcified cartilages require exceptional conditions to become fossilized. During the Famennian (Late Devonian), the taphonomic conditions were suitable repeatedly to preserve cartilage and even complete skeletons of chondrichthyans in the Maïder and Tafilalt regions of Morocco. While most skeletal remains of chondrichthyans were found in the middle and the older parts of the late Famennian, such remains were unknown from the Hangenberg Black Shale and only a few chondrichthyan teeth had been found in these layers previously. During a field trip to the Moroccan Anti-Atlas, a new minute chondrichthyan lower jaw was found in the Hangenberg Black Shale. Jaws are known as key innovation in early vertebrate evolution and therefore of extreme importance. We describe this new jaw and compare it morphologically to 41 other chondrichthyan taxa from the literature. Elliptical Fourier and Principal Component Analyses were employed to illustrate the disparity of jaw shapes among stem (acanthodians) and crown chondrichthyans (elasmobranchs and holocephalans) and to identify the position of the new specimen therein. The PCA revealed a large overlap between the fields occupied by acanthodians, holocephalans and elasmobranchs. The overlap between the fields containing the two modern clades is less extensive, while these fields overlap strongly with the acanthodian field, because the latter group comprises some extreme shapes.

Testing hypotheses on heterostracan feeding using Computational Fluid Dynamics (CFD) and Finite Element Analysis (FEA)

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Keywords: heterostracans, suspension feeding, computational fluid dynamics, mechanical feeding, finite element analysis

Teeth constitute a key innovation underpinning the evolutionary and ecological development of jawed vertebrates. As the earliest jawed vertebrates already possess teeth, we must study tooth-like structures in stem gnathostomes to learn more about the evolutionary origin of teeth. Heterostracans are a group of extinct, jawless vertebrates, that possess tooth-like structures (oral plates). The heterostracan oral plates have been hypothesised to perform a diversity of functions, from filter-feeding to predation. We tested the suspension-feeding hypothesis using computational fluid dynamics. In our analyses we compared flow patterns of different models with forward-facing denticles to alternative models with rear-facing denticles. Independent of denticle orientation, similar velocity and turbulence patterns develop in the spaces between the denticles and on their upper surface. Formally rejecting the suspension-feeding hypothesis is challenging, but we can at least reject the hypothesis that the forward-facing heterostracan oral plate denticles are an adaption to suspension-feeding. To test the predation hypothesis, we used finite element analysis and microstructural analysis to test whether the plates are adapted to a mechanical feeding function. FEA stresses in the shaft of the oral plate are negatively correlated with bone volume fraction, the smaller the compressive or tensile stress, the higher the bone volume fraction. The anterior part of the oral plate shows the highest bone volume fractions. This points towards a specific adaptation of the microstructure to a mechanical function. Thus, we reject a filter-feeding function for heterostracan oral plates, instead concluding that they performed a mechanical feeding function.

A large Late Devonian (uppermost Frasnian) ptyctodont (Placodermi) from Poland

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Keywords: ptyctodont, Upper Devonian, Holy Cross Mountains, Poland

The specimen was found in the slump-origin uppermost Frasnian Płucki section in the central part of the Holy Cross Mountains, Poland among the diversified vertebrate assemblage. The part of a head shield has been identified as a large ptyctodont. The entire preserved specimen is 23 cm long and 17.5 cm wide. The remain consists of the right posterior portion of the head shield with nuchal, central, paranuchal, postorbital and part of preorbital plates and is high crested. Based on general proportions the estimated sizes of the head were about 40 cm wide and 20-25 cm long. Considering the ptyctodonts were usually relatively small, the specimen from the Holy Cross Mountains is the largest and comparable to the *Eczematolepis*. Due to the cranial portion of the *Eczematolepis* is not attested as a ptyctodont, the affinity of the described specimen to this taxon based on size only is highly speculative and it most probably represents a new genus. Its presence supplements an important large durophagous fish into the Late Devonian ecosystem. Those aspects are under detail studies together with the general revision of Polish ptyctodonts.

Diversity estimates and paleogeographical patterns for Palaeozoic ray-finned fishes (Actinopterygii)

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Keywords: diversity, Actinopterygii, fossil record bias, Palaeozoic

Actinopterygians (ray-finned fishes) are the most diverse living group of vertebrates and dominate present-day aquatic environments. However, their early patterns of diversity and evolutionary dynamics are far from understood. Importantly, there have been limited quantitative attempts to understand the fossil record biases that may be influencing interpretations of changes in actinopterygian diversity through the Palaeozoic. Here, we present patterns of local richness of Palaeozoic actinopterygians, alongside sampling standardised and extrapolated estimates of 'global' diversity. We identify significant geographic bias, with the majority of occurrences from Europe and North America. Furthermore, diversity estimates essentially track evenness in the abundance distributions of occurrences, which is determined by biases. Taxonomic issues with Palaeozoic actinopterygians and historical biases in sampling have a major influence on abundance distributions and therefore diversity estimates. Identifying these issues also allows for the prescription of avenues of research that will rectify the biases: increased sampling of underrepresented regions and inclusion of museum collection data in occurrence datasets will be key to increasing the accuracy of Palaeozoic actinopterygian diversity estimates. In tandem, analysing extensively sampled regional subsets of the 'global' fossil record will help with the identification of local diversity patterns.

Morphometric variation of cranial nerve foramina in a model fish, the zebrafish (*Danio rerio*): phylogenetic implications

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Keywords: geometric morphometrics, zebrafish, morphological variation, cranial nerve foramina, phylogeny

For the past twenty years, neurocranial characters have been increasingly used in phylogenetic analyses of lower vertebrates (e.g., acanthodians, actinopterygians, dipnoans) although the preservation of neurocrania is considerably rarer than the dermatocrania. Frequently, the coding of neurocranial characters relies on a reduced sample and therefore does not take into account potential intraspecific variation. Among these characters, position, relative position, and size of cranial nerve foramina are commonly used as phylogenetic characters under the premise that they are less variable in their relative position and thus are more stable and informative than osteological characters. Furthermore, the increasing usage of micro CT-scan and synchrotron in neuropaleontology has provided non-destructive and reliable methods of investigation. Here we investigate the degree of morphological variation of cranial nerve foramina in the zebrafish (*Danio rerio*) to verify if cranial foramina are suitable characters for phylogenetic analyses. We used 3D geometric morphometrics from micro-CT imaging of more than 100 skulls of adult *D. rerio*. Based on our preliminary results, a low level of variation was found in the position of cranial foramina, associated with a low level of fluctuating asymmetry. However, we found a higher degree of variation in the shape of cranial foramina. Our results seem to confirm that cranial nerve foramina represent suitable characters for phylogenetic investigations, however, this type of investigation would benefit from being carried out on fossil taxa in order to validate the robustness of our findings.

An enigmatic chondrichthyan rostral cartilage from the Carboniferous of North America that resembles that of *Squaloraja*

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Keywords: Carboniferous, Chondrichthyes, Holocephali, Chimaeriformes, Squalorajidae

Squaloraja is a genus of chimaeriform fishes known from the Early Jurassic of England, Belgium, and Italy. *Squaloraja* has a flattened body and a long, median rostral cartilage. Males have a lance-like tenaculum (frontal clasper) that articulates with a central groove on the dorsal face of the median rostral cartilage. The genus is remarkably isolated, being the only member of the family Squalorajidae, itself the only family in the suborder Squalorajoidei of the order Chimaeriformes. Phylogenetic analyses indicate a divergence of the Squalorajoidei from other Chimaeriformes in the Mississippian, implying the existence of a `ghost lineage' of more than 130 Ma. Absent rare preservation of soft tissue, the only evidence of taxa comprising the ghost lineage would be isolated hard parts. *Squaloraja* lacks dorsal fin spines; similar tooth plates are unknown. A locality in the Viséan St. Louis Formation of Indiana, USA, preserves a diverse chondrichthyan assemblage including teeth, tooth plates, dorsal fin spines, and several undescribed holocephalian tenaculae. A structure that resembles a median rostral cartilage of a male *Squaloraja polyspondyla* was found at the Indiana locality. As in *Squaloraja*, the dorsal face has a long narrow groove that would have articulated with a long narrow tenaculum. The main difference between this rostral cartilage and that of *Squaloraja* is the extension of the groove nearly to the anterior tip. Whether the similarity between the median rostral cartilage from the St. Louis Formation and that of *Squaloraja* indicates a phylogenetic affinity or represents convergence is not possible to determine at present.

Acknowledgements: We thank Robert Schacht for collecting the rostral cartilage and Emma Bernard (NHMUK) for access to collections.

Psephodus and the transition from teeth to tooth plates in holocephalian chondrichthyans

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Keywords: Chondrichthyes, Holocephali, Cochliodontiformes, Carboniferous, dentition

Extant chondrichthyans comprise two clades: the Elasmobranchii and the Holocephali. The dentition of the former consists of mesiodistally separated, linguolabially-oriented files of individual teeth. Extant Holocephali (chimaeroids) have a dentition consisting only of tooth plates. The elasmobranch arrangement is believed to be the ancestral condition. How and when the transition from individual teeth to tooth plates took place in the lineage leading to the chimaeroids is poorly understood. *Helodus simplex*, a stem holocephalian from the Pennsylvanian, is the most commonly cited example of a transitional form. Its dentition includes files of teeth as well as tooth plates that consist of fused teeth from a single file. The stem holocephalian *Psephodus* has a range from Late Devonian to Late Mississippian. Remains of *Psephodus* consist of tooth plates as well as of individual teeth having *Helodus*-like and *Lophodus*-like form. *Psephodus* is possibly more informative than *H. simplex* with regard to the transition from teeth to tooth plates. As in *H. simplex*, some specimens of *Psephodus* display fusion of teeth from the same file into tooth plates. Unlike in *H. simplex*, some specimens of *Psephodus* display fusion of mesiodistally separated tooth plates, each representing a fused tooth file, into a larger tooth plate. *Psephodus*, which crosses the Devonian-Carboniferous boundary, is better placed chronologically to be a transitional taxon connecting basal holocephalians having individual teeth to Mississippian holocephalians that have dentitions consisting mainly of tooth plates, such as *Cochliodus* or *Chondrenchelys*, and to the poorly known lineage leading to the chimaeroids.

Acknolwedgements: I thank L. White and R. Schacht for collection of specimens, T. Culver (University of Colorado Museum of Natural History) and A. Gishlick (American Museum of Natural History) for help with repositing of specimens, J. Maisey and A. Gishlick (American Museum of Natural History), S. Walsh (National Museum of Scotland), and E. Bernard (Natural History Museum, London) for access to collections, and W. Simpson (Field Museum of Natural History) and M. Brett-Surman (National Museum of Natural History, Washington, DC) for photographs of specimens.

Description and ecomorphological reconstruction of a new selenosteid placoderm from the Late Devonian of the eastern Anti-Atlas (Morocco) with preserved body outline

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Keywords: Arthrodire, selenosteid, body outline, morphometrics

Placoderms are an extinct group of early jawed vertebrates that play an important part in understanding the evolution of the vertebrate body plan, including the origin of jaws, teeth and pelvic fins. The predominantly cartilaginous post thoracic skeleton with sparse perichondral ossifications renders axial and fin elements extremely rare, unlike that of the heavily mineralised dermal skeleton forming the skull and thoracic armour. Therefore, the gross anatomy of these animals and their body shape are only known for very few taxa, particularly within the arthrodire group, and reconstructions of the swimming function and ecology remain speculative. Here, we describe articulated skull roofs and shoulder girdles as well as the body outline of a new derived arthrodire. This new selenosteid reveals a reticular ornamentation and raised sensory lines on the dermal armour like that of *Driscollaspis*, a median dorsal plate with a unique sharp posterior depression, the presence of a pelvic girdle, the proportions and shape of the pectoral, dorsal and caudal fins as well as a laterally enlarged region apparent to some modern sharks and bony fish' lateral keel. A new phylogenetic analysis supports the monophyly of the Selenosteidae and places the new taxon in a clade with *Melanosteus*, *Enseosteus*, *Walterosteus* and *Draconichthys*. The shape of its heterocercal caudal fin in combination with the pronounced laterally enlarged region suggest this animal was an active macropelagic swimmer capable of maintaining high swimming speeds.

Mechanisms of dermal bone repair after predatory attack in the giant stem-group teleost *Leedsichthys problematicus* Smith Woodward, 1889 (Pachycormiformes)

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Keywords: *Leedsichthys*, bone repair, dermal bone, lepidotrichia, stem-teleost

Bony calluses in the caudal fin lepidotrichia of the pachycormid suspension-feeder *Leedsichthys problematicus* (stem-group Teleostei) are the result of macroscopic processes of dermal bone repair in response to damage. Distinctive tissue changes occur, including the initial deposition of woven bone onto bone fragments and onto the surface of the lepidotrichium, after resorption of these has occurred. Later to form is a more organized circumvascular bone around intrinsic blood vessels, as osteons, identified as part of the primary structure, all evidence of a vital response through survival of a predatory attack by a large marine reptile, coeval with *Leedsichthys*. The vasculature (represented by canal spaces) is prominent within the broken remains and repair tissue would have been an integral part of the mechanism, from the soft tissue haematoma, unpreserved in fossil specimens. Within the woven bone are many clear elongate spaces, consistent with their interpretation as bundles of unmineralized collagen (Sharpey’s fibres). These normally provide attachment within dermal bones, and here attach new bone to old, particularly to resorbed surfaces. These surfaces are identified by scalloped reversal lines, where resorption has stopped before new bone is added. Both new repair bone and undamaged bone have numerous embedded osteocyte spaces. Haversian systems are retained in the old bone, from which initially vessels possibly invaded the callus, bringing stem cells committed to forming bone onto the surfaces of the damaged area.

Development of the pteraspid cranial dermal skeleton and the evolution of vertebrate skeletal remodelling

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Keywords: heterostracans, pteraspids, dermoskeleton, remodelling, resorption, growth ontogeny

Jawless pteraspid heterostracans are among the most primitive vertebrates that exhibit evidence of skeletal ontogeny. Pteraspid cranial dermal plates frequently exhibit size variation compatible with an ontogenetic series, as well as concentric invaginations, previously interpreted as lines of arrested growth. Yet, internally these plates show no evidence of incremental development. This apparent paradox has inspired several competing growth hypotheses, which have yet to withstand rigorous testing. To this end, we undertook a comparative histological study on the pteraspid dermal skeleton based on specimens representative of different developmental stages from the same population. These data inform a new model of skeletal mineralisation in pteraspids: mineralisation initiates with a superficial sheet of dentine tubercles, which is subsequently thickened via mineralisation of vertical trabeculae. Dermal plates grow laterally via marginal mineralisation of the superficial layer, followed by delayed mineralisation of the middle layer. The basal layer is the last to mineralise, allowing initially independent plates to fuse together. Ancestral state estimation using parsimony and likelihood-based approaches reveal that dynamic remodelling evolved in a stepwise manner along the gnathostome-stem. Extensive resorption is identified as a synapomorphy of osteostracans + jawed vertebrates, whilst secondary osteon formation evolved later, prior to the divergence of jawed vertebrates. Our data suggest that the skeletons of early vertebrates were constrained by the limitations of appositional growth, which may explain the diversity of dermal plate organisations in fossil jawless vertebrates.

Biomechanics of the head–neck boundary in early tetrapods

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Keywords: tetrapod, motion, CT, atlas, neck

The transition to land by some lobe-finned fishes was accompanied by anatomical innovations that imply biomechanical innovation. Head motion in aquatic fish is accompanied by considerable movement in the trunk. Tetrapods display a capacity for independent motion of the head from the trunk by way of a specialized cervical vertebra or region of vertebrae. This independent head–neck motion may have arisen early in tetrapod evolution and facilitated life and feeding out of the water. Anatomical markers of increased head–neck boundary mobility across the transition include reduction of opercular series bones, loss of these and cleithral series bones, and specialization of the anterior-most vertebrae. Two taxa on the tetrapod stem, *Acanthostega* and *Ichthyostega*, are both represented by many specimens, including at least a few that preserve enough of the head–neck boundary bones for three-dimensional (3D) reconstruction with computerized tomography (CT) scans. By similar means to previous work that modelled limb mobility in these taxa based on CT models of their limbs and measurements of joint motion in modern analogues, we aim to re-construct the head–neck boundary and model its mobility in these taxa. This work will test previously suggested impacts of anatomical changes on neck function and demonstrate the changes to range of motion at the head–neck boundary within early tetrapods. Improved knowledge of the biomechanics of this system will better inform our interpretations of each of these taxa as well as the path to terrestrial life.

Acknolwedgements: This work was planned on the traditional unceded territory of the Anishinaabe Algonquin First Nation. Specimens used in this study come from north-eastern Kalaallit Nunaat – traditional land of the Kalaallit people that is managed in part by the Inuit Circumpolar Council.

Feeding in the Devonian antiarch placoderm fishes: a study based upon morpho-functional analysis of jaws

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Keywords: Antiarchi, Placodermi, jaw apparatus, feeding, trophic webs

Antiarch placoderms were an abundant component of the Middle Palaeozoic vertebrate assemblages. Despite a large number of known taxa and specimens, the morphology and function of the skeletal elements of their jaws is inadequately known. Because of this, questions regarding their feeding modes and their roles in trophic webs remain open. We present a skeleto-muscular model of the antiarch jaw apparatus with an attempt to reconstruct its potential biomechanical function. The position of the upper jaw suborbital bones within the plane of the ventral side of the fish armour is suggested to represent the natural 'mouth closed' position. During mouth opening the suborbitals rotated antero-ventrally with simultaneous depression and inward rotation of the infragnathals, facilitated by the ball-and-socket jaw articulation. Earlier described lower jaw elements of *Livnolepis zadonica* and *Bothriolepis* sp. from the Upper Devonian (Lower Famennian) of Central Russia demonstrate very deep and porous blades of the oral division of the infragnathals. This porosity reflects intense vascularization to supply blood to connective tissue underlying a proposed keratinous sheath, which protected and strengthened the jaws, and made possible the scraping tough food objects from the substrate, such as thallus algae. Although expressed to a smaller degree, this kind of porosity is also present in numerous other antiarchs. Supposedly, antiarchs became the first macrophytophagous vertebrates occupying the trophic level of primary consumers during the late Silurian – Early Devonian, diversifying the only previously existing predator-prey interrelationships between filter-feeding agnathans and predatory gnathostomes.

A 3D histological survey of vertebrate jaw cartilage with implications for chondrichthyan skeletal evolution

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Keywords: cartilage, jaw, acanthodian, chondrichthyan

Cartilage is a fundamental tissue in the vertebrate endoskeleton. It serves as the scaffold for the development of many bones in osteichthyans and a cortical layer is directly mineralised in chondrichthyans, leaving most of the internal cartilage unmineralised. Fossil evidence suggests that the modern chondrichthyan endoskeleton is derived from an ancestor possessing a more osteichthyan-like state: able to produce hypertrophic chondrocytes and replace globular cartilage with bone via endochondral ossification. We performed high-resolution propagation phase contrast synchrotron microtomography (PPC-SRμCT) scans of a diverse range of fossil and iodine-stained extant vertebrate lower jaw cartilages at different developmental stages to provide an overview of evolutionary trends in vertebrate cartilage histology. We interpreted general histology through virtual thin sections and segmented chondrocyte lacunae in 3D to analyse trends in their volume and distribution in the cartilage matrix. We find that while extant chondrichthyans display a relatively consistent cartilage histology, stem-chondrichthyans are far more variable in their modes and locations of mineralisation, suggestive of a period of evolutionary experimentation following the divergence with osteichthyans. As we expand our dataset by sampling more diverse stem- and crown-chondrichthyan fossils, we aim to provide a greatly resolved view of chondrichthyan cartilage evolution from the Devonian to the present day.

The evolution of the inner ear in basal gnathostomes

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Keywords: placoderm, brain, evolution, inner ear, phylogeny

The appearance of the modern inner ear with its 3 distinct semicircular canals is part of a novel suite of characters appearing with the first jawed fishes. We know much about the brain shape and inner ear morphology for some placoderms (e.g., arthrodires, petalichthyids, acanthothoracids) but nothing for the other groups. Micro-CT scans of 2 complete ptyctodontid braincases from the late Devonian of Russia were analysed using Mimics and Drishti software. One is the Holotype of *Chelyphorus vernueli*, the other an undescribed taxon. Both confirm that the braincase is segmented into several units, as seen in specimens from the Gogo Formation. The anterior and posterior semicircular canals are present but are short and chunky, akin to the condition in osteostracans and galeaspids. The lateral semicircular canal is located ventral to the saccular cavity and aligned at a very acute angle, conforming to the steeply sloping front of the skull in life restoration. We propose that these features represent a basal condition for placoderms in lacking the more extensive development of canals that extend further away from the sacculus that characterises arthrodires, osteichthyans and chondrichthyans.

Observations on a new sarcopterygian fish from the Late Devonian (Frasnian) of the Gogo Formation, Western Australia

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Keywords: Sarcopterygyii, evolution, Gogo Formation, Devonian

A skull roof, oticco-occipital unit and hyomandibular bone were found associated in a single nodule from Gogo representing a new basal sarcoterygian fish of unknown affinity. The specimen has a skull roof showing the regular bone pattern as seen in many basal sarcopterygians: a pair of long tapering postparietals with equidimensional but narrow tabular and supratemporal bones. The dermal bones are ornamented with rounded coarse tubercles of differing sizes. The oticco-occipital unit has a large ventral fossa with two anazygals present (as in coelacanths). Two large hyomandibular facets are continuous with the jugular canal running mesial to them. This specimen shows two unusual features: the presence of a pair of large posteroventral-facing processes coming off the dorsal part of the otic region, and a large, anteriorly-directed process coming off the anterolateral face of the basioccipital area, as seen otherwise only in certain porolepiform fishes. The hyomandibula is short and broad as in actinistians. The CT-scan of the braincase revealed only parts of the saccular cavity and semicircular canals. In summary, this specimen presents a unique combination of features: different characters suggest an affinity with coelacanths, but the two processes present on the lateral wall of the oticco-occiptal, and the presence of separate supratemporals, are at odds with this interpretation. Our preliminary analyses do not support a close phylogenetic relationship between our specimen and coelacanths. Further work is required to expand the matrix with more sarcopterygian taxa to clarify its relationships.

Acknowledgements: Funded by ARC DP200103398.

Systematics, ontogeny and palaeobiogeography of the large xenacanth *Orthacanthus* from the lower Permian of France

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Keywords: *Orthacanthus*, Buxières-les-Mines, Muse, lower Permian, palaeobiogeography

The xenacanthid shark *Orthacanthus* was a major top predator of European freshwater ecosystems in the late Palaeozoic (Carboniferous and Permian). It diversified in the upper Carboniferous and almost completely disappeared in the transition from the Carboniferous to the Permian. Only a few representatives survived into the lower Permian. However, the study of its evolutionary and palaeobiogeographic history is limited by some disputed systematic attributions. The species *O. buxieri* from the French lower Permian is controversial: some authors advocate synonymy with the species *O. kounoviensis* known from Germany and the Czech Republic. Furthermore, *Orthacanthus* from French Carboniferous sites is so far unknown, whereas it is relatively common in comparable other European freshwater basins. In order to decipher the palaeogeographical distribution of this genus, we described isolated tooth material of *O. buxieri* from the type locality Buxieres-les-Mines (Asselian-Sakmarian, Bourbon l'Archambault Basin) and compared it with material from the Muse locality (lowermost Permian) in the nearby Autun Basin. The investigations revealed that the teeth from Buxières-les-Mines can indeed be placed with *O. kounoviensis* and the finds from Muse were identified as a closely related form. Buxières-les-Mines can be considered a refuge for the last large xenacanthids in the European Permian. However, until a complete reassessment is made, *O. buxieri* should be restricted to its holotype for the time being.

Rare faunal elements from the Baltic Late Devonian: the antiarchan placoderm *Walterilepis speciosa*

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Keywords: Frasnian, biostratigraphy, morphology, placoderm

The Frasnian (Upper Devonian) antiarch *Walterilepis speciosa* was first described by Walter Gross in 1933 (as *Taeniolepis*) on the basis of a single specimen (jointed Nu and Pp plates), from the outcrop of the Ogre Formation along the Daugava River close to Bramberģe (central part of Latvia). Later a partly preserved AMD of antiarch from the Langsēde site (western part of Latvia) along the Imula River, from the same formation was demonstrated. In 1981 a new species was established, *Asterolepis*? *amulensis*, from the Ogre Formation cropping out along the Amula River in a distance of about 2 km east from the Langsēde site. The newly collected material of a small antiarch from the Gurova ravine (eastern part of Latvia) has allowed to synonymise Antiarcha gen. indet. by Gross and *Asterolepis*? *amulensis* with *Walterilepis speciosa.* The head can be described in more detail. Other newly found elements include bones of the pectoral appendages and trunk armour, demonstrating a rather high and short trunk armour. The shape and proportions of the head and trunk armour suggest the attribution of *Walterilepis* to the family Pterichthyodidae; it is most probably closely related to *Lepadolepis* from the late Frasnian of Germany. Whilst *W. speciosa* is endemic to the Latvian part of the Baltic Devonian Basin, the connection to the Rheinisches Schiefergebirge is probably closer than previously presumed. *Walterilepis* fits into the biostratigraphical column at the same level as *Bothriolepis maxima* and *B. evaldi*, indicating the high diversity of antiarchs during Pamūšis time.

The dermosphenotic, intertemporal and supratemporal in lower actinopterygian fishes

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Keywords: lower actinopterygian, dermosphenotic, intertemporal, supratemporal

A review of lower actinopterygian literature shows that there are numerous naming conventions for the bone in the posterodorsal corner of the orbit that bears the upper extremity of the infraorbital canal and its angle with the otic canal as well as the bones bearing the otic canal. Some of the terms used to describe these bones include dermosphenotic and dermopterotic; dorsal and ventral dermosphenotic (which themselves have variations in shapes and conditions) and dermopterotic; dermosphenotic, supratemporal, and intertemporal; and a variety of names that suggest fusions of different bones. The lack of a standardized nomenclature scheme for these bones is problematic because it makes comparisons amongst different taxa difficult, may hide morphological diversity, and can potentially make building and coding character matrices for phylogenetic analyses difficult. Here, a review of previously published nomenclatural schemes is presented and a preferred method for identifying and naming these bones is discussed. It is proposed that the terms dermosphenotic, intertemporal, and supratemporal be used to identify the bones in this region and that landmarks such as bone position and presence of sensory canals be used as identifying criteria. Complex bone names such as intertemporo-dermosphenotic and intertemporo-supratemporal are also suggested. Applying these standardized terms to a variety of lower actinopterygian fishes has revealed a great deal of morphological diversity. A review of the morphological diversity is presented and the importance of clear standardized criteria for identifying and naming bones in lower actinopterygian fishes is discussed.

The exceptionally preserved branchial skeleton of a new coelacanth from the Late Carboniferous of Texas (USA)

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Keywords: Actinistia, computed tomography, cranial skeleton, Palaeozoic, Sarcopterygii

The hyobranchial or visceral skeleton of gnathostomes (jawed vertebrates) plays a fundamental role in breathing and feeding. Nevertheless, despite a relatively good fossil record, our knowledge on the anatomy and evolution of the hyoid and branchial arches of coelacanths is extremely limited. This is caused by the poor preservation of many small and delicate elements forming the arches due to their mainly cartilaginous nature. As such, the bones easily disarticulate after death and, when preserved, are found scattered and displaced from their original position. Comparative data are mainly available from the extant *Latimeria* which represents a crucial landmark for all morphological descriptions of fossil taxa. Here we describe a new coelacanth from the late Carboniferous (Pennsylvanian) of Texas, USA, preserved inside a phosphatic nodule, using micro-computed tomography. It exquisitely preserves the complete series of the hyoid and branchial arches as well as part of the braincase, dermal skull roof and cheek. The uniquely preserved complete gill arches shed light on the organization of the hyobranchial skeleton in coelacanths and comparisons with other fossil and extant actinistians reveal that the establishment of the anatomical organization of the branchial skeleton of coelacanths as displayed in *Latimeria* dates at least back to the Carboniferous.

Enigmatic early chordates and vertebrates from the Lower Devonian of Belgium

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Keywords: Belgium, early chordate, euphaneropid, Lower Devonian

The evolutionary history of vertebrates began, at the latest, during the early Cambrian with the first occurrence of elongated and laterally flattened soft-bodied organisms known as chordates, possessing a notochord but devoid of backbones and jaws. Vertebrates subsequently underwent major anatomical changes, such as the acquisition of a vertebral column, development of jaws, and adaptations to terrestrial life. Early chordate and early vertebrate fossils provide the only direct evidence of the origin of vertebrates and on how their distinctive body plan evolved. Unfortunately, the fossil record of early chordates and part of the early vertebrates is extremely scarce as these organisms mostly consist of decay-prone soft parts that are usually degraded and lost prior to fossilisation, making the interpretation of their anatomy highly challenging. Recently, new mysterious soft-bodied fossils have been discovered in the Lower Devonian of southern Belgium. We studied their visible and hidden anatomy, as well as their chemistry, using state-of-the-art imaging and spectroscopy techniques. We undoubtedly identify some specimens as euphaneropids, a group of early jawless vertebrates. The other fossils display a mosaic of characters that make their identification between early chordates and early vertebrates difficult.

The shape of things to come: reexamining tetrapod evolution after the end-Devonian mass extinction

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Keywords: tetrapod, Carboniferous, paleobiology, phylogenetics, paleoecology

With the accretion of an increasingly robust consensus around the Devonian origin of limbed tetrapods, uncertainties concerning the origin of the crown group are ever more apparent. The end-Devonian mass extinction and Romer’s Gap have persistently stymied attempts to explore connections between Devonian and Carboniferous tetrapod lineages. Here, incorporating new discoveries from the earliest Carboniferous and new data from Mississippian taxa such as *Whatcheeria*, we constructed a new phylogenetic matrix to analyze early tetrapod relationships. *Whatcheeria* remains an early-diverging plesion and exhibits a bodyplan unique among Devonian-Mississippian taxa. *Aytonerpeton*, a new discovery from Romer’s Gap, extends the range of the aquatic colosteids from the Visean into the Tournaisian, but colosteid oscillation between stem and crown locations implies crown-date uncertainty, switching between Visean and Tournaisian estimates. Nevertheless, despite multiple Carboniferous lineages now seeming to have diverged within the Devonian, the crown group remains a post-Devonian phenomenon. Furthermore, analyses consistently suggest that crown groups diverged within an aquatic, rather than terrestrial context. Thus, total group lissamphibians and amniotes had independently moved onto land by the time of the Visean East Kirkton biota, the oldest known terrestrial tetrapod assemblage. This scenario accords well with the increasing paleobiological diversity found among the earliest Carboniferous tetrapods, and raises exciting new questions about the evolution of post-Devonian tetrapods and the deep-time origins of the modern biosphere.

A phylogeny for Heterostraci

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Keywords: Heterostraci, phylogeny, Pteraspidimorphi, stem-gnathostome

The armoured jawless fishes (ostracoderms) are major and widespread components of middle Palaeozoic ecosystems. As successive plesia on the gnathostome lineage, they reveal the early sequences of vertebrate evolution, including the assembly of the vertebrate skeleton. This is predicated, however, on understanding of their diversity and interrelationships. The largest ostracoderm clade, the Pteraspidimorphi, is often reconstructed as sister taxon to other bony vertebrates, yet they lack a phylogenetic framework, in particular the heterostracans. Problematic heterostracans with a tessellate headshield ('tessellate-basal' model) are often reconstructed as the plesiomorphic condition for the clade but no phylogenetic analysis has included these taxa. Here we review the Heterostraci and present their first comprehensive phylogenetic analysis (131 heterostracan taxa and 12 outgroup taxa). Heterostraci and Ordovician Pteraspidimorphi are recovered as sister-group to all other bony jawless vertebrates in parsimony analyses, however, in no instances do we recover a monophyletic Pteraspidimorphi. Tree visualisation reveals lack of resolution results from two conflicting solutions for the heterostracan 'root'. Stratigraphic congruences provides support for the macromeric Ctenaspididae as sister taxon to all other Heterostraci rather than the "tesselate-basal" model. The results presented here are the first phylogenetic hypotheses of heterostracan relationships and will provide a foundation for future interpretation of character evolution and polarity in this crucial episode of vertebrate evolution.

Reviving *Lasanius*, an enigmatic Silurian jawless vertebrate at the split of cyclostomes and gnathostomes

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Keywords: Gnathostomata, Cyclostomata, Anaspida, exceptional preservation, EDS-SEM

The split between cyclostomes (modern jawless vertebrates) and gnathostomes (modern jawed vertebrates) is difficult to characterise in terms of its timing and evolutionary dynamics due to its conflation with the origin of biomineralized tissues, and the difficulties inherent to the interpretation of soft-bodied fossil taxa. A key player in this story is the previously enigmatic taxon, *Lasanius*. This exceptionally preserved jawless vertebrate from the Silurian of Scotland exhibits a curious melange of ostensibly biomineralized and soft-bodied characteristics. The unique mix hints that *Lasanius* may be an important transitional form. However, its anatomy and affinity are poorly understood, plagued by ambiguous taphonomy and conflicting interpretations. Here we use an array of modern techniques to reassess the anatomy of *Lasanius*. A new reconstruction clarifies the identity and position of preserved features, including paired sensory organs, a notochord, and digestive tract, supporting the vertebrate affinities of this genus. EDS-SEM trace element mapping suggests a bone-like composition of mineralized parts, but finds no evidence for mineralized dermal armour. Phylogenetic analysis recovers *Lasanius* as an early stem-cyclostome, but the alternative placement (stem-gnathostome) cannot be eliminated on the basis of current data. We highlight that while distinguishing between the early cyclostome and gnathostome condition is problematic, increasing confidence in the anatomy of key taxa, such as *Lasanius*, is vital for increased stability throughout the early vertebrate tree.

Fossil bite marks in heterostracans support predation by jawed vertebrates as a factor in the demise of ostracoderms

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Keywords: heterostracan, predation, ostracoderm

Although modern vertebrate diversity is dominated by jawed vertebrates, early vertebrate assemblages were predominantly composed of jawless fishes. Hypotheses for this faunal shift and the Devonian decline of jawless vertebrates include predation and competitive replacement. The nature and prevalence of ecological interactions between jawed and jawless vertebrates are highly relevant to both hypotheses, but direct evidence is limited. Here, we use the occurrence and distribution of bite mark type traces in fossil jawless armoured heterostracans to infer predation interactions. A total of 41 predated specimens are recorded, their prevalence increases through time, reaching a maximum towards the end of the Devonian. The bite mark type traces significantly co-occur with jawed vertebrates, and their distribution through time is correlated with jawed vertebrate diversity patterns, particularly placoderms and sarcopterygians. Environmental and ecological turnover in the Devonian, especially relating to the nekton revolution, have been inferred as causes of the faunal shift from jawless to jawed vertebrates. Here, we provide direct evidence of escalating predation from jawed vertebrates as a potential contributing factor to the demise and extinction of ostracoderms.

Diversity patterns of early chondrichthyans

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Keywords: Chondrichthyes, diversity, sampling bias, origination, extinction

The Palaeozoic is considered the key interval in time for the origin and early diversification of chondrichthyans (cartilaginous fishes), yet much of their early diversity and macroevolutionary patterns remain unresolved because of the limitations of their fossil record. This is predominantly due to heterogenous spatial and temporal sampling of chondrichthyan fossils. Here, we use sampling standardisation and a newly compiled, comprehensive genus-level dataset to analyse global total-chondrichthyan diversity and speciation-extinction dynamics from the Ordovician to the end-Permian. We found that subsampled chondrichthyan genus richness was initially low in the Ordovician and Silurian and increased substantially in the early Devonian. Richness reached its maximum in the middle to late Carboniferous before dropping across the Carboniferous/Permian boundary and gradually decreasing throughout the Permian. The rise in Carboniferous diversity is dominated by euchondrocephalans (stem holocephalans) which increase greatly in richness across the Devonian/Carboniferous boundary. Our results indicate two pronounced events of origination in the Lochkovian (Early Devonian) and Tournaisian (early Carboniferous) and three extinction events in the Famennian (Late Devonian), Gzhelian (late Carboniferous) and Kungurian (late early Permian). Our results also suggest two radiations in Palaeozoic chondrichthyan diversity in the earliest Devonian, led by acanthodian chondrichthyans, and earliest Carboniferous, led by euchondrocephalans. Reduced diversity in the Permian may indicate poor sampling but also could suggest a response to changes in environment and unstable climatic periods.

Acknowledgements: This research is funded by the Natural Environmental Research Council (NERC) CENTA DTP.

Triassic times and the early radiation of ‘flying’ fishes (Neopterygii, †Thoracopteroidea)

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Keywords: ‘flying’ fishes, anatomy, taxonomy, phylogeny, Xingyi Lagerstätte

After the end-Permian mass extinction, the Triassic was an important time in fish evolution, especially for neopterygians, when many taxa appeared and diversified, mainly in Europe and Asia. Recent research in southern China, especially the Guizhou province (Xingyi Lagerstätte), has changed our understanding of early neopterygians with the discovery of new fishes belonging to colobodontids, luganoids, thoracopteroids, the oldest holosteans and teleosts, and others. The present study is a revision of the morphology, taxonomy and phylogenetic relationships of Triassic gliding or ‘flying’ fishes, the thoracopterids (with enlarged pectoral, pelvic and anal fins and enlarged hypaxial lobe of the caudal fin or hypocercal tail), which appear to have an important radiation in Austria, Italy, and China during the Ladinian to Norian, with the oldest member (†*Potanichthys wushaensis*) living in China. Additionally, †*Wushaichthys exquisitus* and members of †*Peripeltopleurus* were included in the study. We interpret these fishes as ‘subholostean’ neopterygians placed within †Peltopleuriformes. The results suggest that †*Wushaichthys* is a member of a clade, the new superfamily †Thoracopteroidea, which contains the families †Wushaichthyidae (†*Wushaichthys* + †*Peripeltopleurus*) and †Thoracopteridae and is the sister taxon of the non-monophyletic †Peltopleuridae within †Peltopleuriformes. The †Thoracopteridae now includes the European genera †*Thoracopterus* (one species), †*Gigantopterus* (one species), and †*Italopterus* (two species), and the Chinese †*Potanichthys* (one species). Although the record for ‘flying’ fishes is incomplete, convergent ‘flying’ fishes are known from the Cretaceous of Madagascar (†*Kradimus*; one species) and one extant teleostean family (Exocoetidae) of about 70 species.

A new fossil record of the Early Devonian dipnoans behaviour from the Holy Cross Mountains, Poland

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Keywords: dipnoans, locomotion traces, Lower Devonian, Holy Cross Mountains, Poland

The Early Devonian (middle-upper Emsian) ichnoassemblage from the Ujazd locality in the Holy Cross Mountains, Poland which was preliminary characterized revealed new data on the dipnoans live-behaviour and locomotion abilities at the early stage of their evolution. Already described ichnospecies *Osculichnus tarnowskae*, documents hunting trace of a fish and was assigned to a short-snouted dipnoan fish with a head morphology similar to *Dipnorhynchus* or '*Chirodipterus' australis*. This assumption was recently confirmed by finds of *'Dipnorhynchus'*-like form described based on fragments of the jaw and skull. Now we interpreted other traces preserved among those described previously. They probably were left by crawling fish and are represented by imprints of trunk and attributed to tail, whole body drag marks and pectoral fins as well. Moreover, some of low-angle Osculichnus may be attributed as involved in movement traces. Generally, the traces documented refer the trackways produced by extant lungfish during terrestrial locomotion. However, employing pectoral fins in Ujazd's fish movement suggests sub-aquatic locomotion and/or terrestrial behaviour which, in that way, precedes other vertebrate's locomotion record on land.

Acknowledgements: Our researches were financed by the Polish National Science Center (project number 2019/35/B/ST10/01505 granted to Michał Ginter)

A new Late Devonian *Dunkleosteus* from Lompret, southern Belgium

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Keywords: *Dunkleosteus,* Upper Devonian, Dinant Synclinorium, Belgium

Several elements of the large arthrodire *Dunkleosteus* are reported for the first time from the upper Frasnian of southern Belgium. They were collected at the ‘Carrière de Lompret’ Quarry (Lompret village, Chimay municipality, Hainaut province), ex-situ, from within a sequence of dark coloured shales of the Matagne Formation (upper rhenana - linguiformis conodont Zones). The association comprises parts of the skull (nuchal, paranuchals, centrals and suborbital plates) and thoracic (median dorsal and anterolateral plate) armours. Characters that are available for investigation on the nuchal plate reveal large ellipsoidal levator pits separated by a wide and elongated backwardly median septum. The paranuchal processes are ellipsoidal and have a shallow lateral articular fossa, as well as a prominent para-articular process. The median dorsal plate is relatively short, wide, and low, with a well-expressed keel present along the entire plate. The carinal process is wide at the base, relatively short, and massive, with a characteristic spoon-like depression in the posterior part. The morphology of all these elements corresponds generally to that of the less well preserved *Dunkleosteus* material from Poland previously described. Even although the Lompret material seems to be significantly larger, we interpreted the Polish and Belgian material as conspecific. The new material also preserves characters which were not preserved in the Polish material, thus supplementing the description of the species.

Acknolwedgements: We gratefully acknowledge the owners, operators and staff of the ‘Carrière de Lompret’ for granting access to their quarry. We also greatly acknowledge all those helping us in the field, collecting specimens and revealing their finds, in particular Natalie Tolisz (Zulte, Belgium) and Tom Vercammen (Antwerp, Belgium).

New insights into assignment of the largest Gogo arthrodire to the genus *Eastmanosteus* and implications for arthrodire phylogeny

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Keywords: *Easmanosteus calliaspis*, Gogo Formation, ontogeny, phylogeny

The vertebrate fauna from the Late Devonian Gogo Formation comprises around 50 species of fish, primarily placed within monospecific genera. The arthrodires comprise the dominant taxa and, with the exception of *Eastmanosteus* and *Holonema* are endemic to the region. The previous assignment of a ptyctodont from the Gogo Formation to the European genera *Ctenurella* was revised to *Austroptyctodus.* The largest placoderm from the Gogo Formation was assigned to the genus *Easmanosteus*; however, the genus was amended to accommodate this. The exceptional preservation and completeness of the Gogo specimens meant that *Easmanosteus calliaspi*s became the preferred taxon to represent the eastmanosteids within taxonomic analyses (with *E. pustulosus* and *E. lundarensis* Hanke et al. 1996 rarely being considered. The most recent phylogenetic analysis that included *E. calliaspis* and *E. pustulosu*s resulted in *E. calliaspi*s nesting with the Chinese taxon *X. wui* to form a monophyletic clade, separate from *E. pustulosus*, however this analysis did not include *E. lundarensis*. Based on these results it was suggested that the Australian species may represent a new genus. New material has resulted in an ontogenetic series being represented which shows several features, particularly in the dentary, that change with growth. In addition, a second species has been determined to be present. However, it now appears that neither can be assigned to *Easmanosteus*.

Acknolwedgements: The authors acknowledge the Gooniyandi peoples, the traditional custodians of the lands where we conducted this research. We pay our respects to ancestors and Elders, past and present and to honour the Gooniyandi peoples' unique cultural and spiritual relationships to the land, waters and seas and their rich contribution to society. The authors also thank The WA Museum for access to specimens and recognise the support of ARC- Discovery Projects DP200103219, DP140104161 and DP110101127.

To Shed or Not to Shed, THAT is the Question

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Keywords: Thelodonti, scales, bases, aspidin, retention

Members of the Late Ordovician (at least) to Late Devonian ‘agnathan’ Thelodonti show the oldest dermal system. Possession of a complete placoid squamation of ‘non-growing’ dentine crown and neck and a base of growing aspidin, and a large range of scale types are characteristic of the clade. Not “only the peculiar handle” (or basal root/’prong’/process of aspidin), noted by Janvier, but also basal shape separates thelodonts from other monoodontode scale-bearing vertebrates. The nature of the thelodont scale bases will be reviewed, with thoughts on the shedding of scales, lifestyles and monophyly of thelodonts. The most bizarre and deepest occur in different families and the so-called “aspidin pegs” of Märss et al. seem to offer functional strength. Review and comparison of thelodont bases of with those of other fish, e.g., shark ‘placoid’ scales and earliest known gnathostomes/‘sharks’, shows that thelodonts possessed unique growing bases that allowed the scales to be retained in the epidermis much longer than other clades; we can speculate on the reasons for this. Phylogenetically their scales with growing bases are a synapomorphy of the clade. Functionally the various taxa developed different strategies to enhance the ability of scale retention. Ultimately, however, thicker bases meant heavier scales. Through time, thelodont taxa tended to reduce basal height and weight but still most seem to have basal adaptions.

Early actinopterygian diversification or how to “get in shape” after a crisis

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Keywords: ray-finned fishes, morphological disparity, Palaeozoic, evolutionary radiation

“Placoderm” and sarcopterygian fishes dominated Devonian waters. However, vertebrate biodiversity completely changed after the Kellwasser and Hangenberg events at the end of the Devonian. Actinopterygians played a key role in these changes by rapidly becoming major contributors to the vertebrate diversity in the early Carboniferous. This transition constitutes the first major diversification event in actinopterygian history. The colonization of new ecological spaces could have driven this diversification with the extinction of potential competitors represented by the dominant Devonian vertebrates. The increase of actinopterygian morphological disparity has been previously studied to understand radiation events in their evolution closely linked to modification of ecological habits. Here, we focused on the morphological diversification of actinopterygians from the Early Devonian to the late Carboniferous to better understand their first diversification. Morphological disparity of early actinopterygians was measured using 2D geometric morphometrics on body shape and skull morphology. Thirteen landmarks and 136 semi-landmarks were digitalized on revised reconstructions of 75 early actinopterygian species to represent the complete body shape, while 23 landmarks were digitalized on lateral cranium reconstructions of 62 species. A similar pattern of disparity was detected in the two morphospaces. Devonian species were more closely packed. The early Carboniferous was characterized by new extreme forms such as deeper and shorter shapes, while the late Carboniferous shapes seemed to return to original Devonian forms. These shifts could suggest that an ecological diversification of actinopterygians occurred right after the Devonian with the exploration of highly disparate body shapes.

Unexpected hypophyseal morphology in basal stem gnathostomes challenges the consensus phylogeny of vertebrates

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Keywords: acanthothoracids, synchrotron, cranial morphology, pituitary, evolution

The phylogenetic consensus divides the living gnathostomes into two clades –Chondrichthyes and Osteichthyes. The only concern seems to be in placing the fossil early gnathostomes relative to the osteichthyan-chondrichthyan node. The current majority view is that all ‘placoderms’ are stem gnathostomes arranged in a paraphyletic series with acanthothoracids near the bottom and maxillate placoderms at the top. All acanthothoracids share an extended precerebral trabecular region –so-called ‘upper lip’– a feature in some respects intermediate between the jawless and jawed conditions, which strongly confirms their position on the tree. Our research on the dentition of acanthothoracids shows, that they differ fundamentally from the ‘placoderm’ dentitions that had been thought to characterise stem gnathostomes and instead resemble the dentitions of crown gnathostomes. The character distributions suggest that osteichthyans could be rooted close to the acanthothoracids, but in the consensus phylogeny they are widely separated. Recently, we made an important anatomical discovery concerning the hypophyseal area of the acanthothoracid genus *Radotina* –paired adenohypophyseal cavities are widely separated from the neurohypophysis and open directly onto the palate. The subsequent comparative study of hypophyseal cavities from tomographic data of selected early vertebrate fossils already shows a completely unexpected pattern. The hypophyseal cavities of the stem chondrichthyan *Gydoselache* are almost indistinguishable from the morphology observed in most studied acanthothoracids, whereas the acanthothoracid *Kosoraspis* (which has the most osteichthyan-like dentition and upper jaw morphology among acanthothoracids) resembles the condition in the stem osteichthyan *Ligulalepis* –implying a major convergence between crown osteichthyans and chondrichthyans.

Evolution and development of the anterior lateral line: new insights from Elasmobranchs

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Keywords: lateral line, evo-devo, sensory canal, sharks

The lateral line is a specialized network of mechanosensory hair cells plesiomorphic to all major lineages of vertebrates and is crucial for predation, escape and schooling. The patterns of connectivity of this network vary characteristically in different clades, affording an opportunity to investigate the evolution of a sensory system in the context of changing craniofacial morphologies like shifts in nostril position and number or the advent of jaws. Prior comparative histological studies have produced conflicting hypotheses of homology between different components of the network. However, modern molecular methods affording high spatiotemporal resolution have been restricted to a few model systems like the zebrafish. Data regarding the developmental morphology of lateral lines in elasmobranchs are particularly sparse. Using a combination of micro-CT and immunohistochemistry, we describe the development of lateral line canals in two elasmobranchs: *Leucoraja* and *Scyliorhinus*. Expression of the conserved pro-neural marker Sox-2 reveals that, unlike teleosts, elasmobranch lateral lines develop as elongating sensory ridges that subsequently fragment and coalesce to individual hair cells on both the head and trunk. Our analyses also shed new light on the development of pleural lines in skates, which are cranial lines migrating on to a pectoral appendage; and reveal that the anterior pleural line is a recurrent branch of the infraorbital canal, showcasing the first known example of an infraorbital line drastically reversing direction during development. Our data highlight the importance of using molecular assays in ‘non-model’ systems and suggest that vertebrate mechanosensory systems develop through divergent trajectories in cartilaginous and bony vertebrates.

General look on the sarcopterygians from the Placoderm Sandstone from the Holy Cross Mountains, Poland with special reference to the porolepiforms

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Keywords: Lower Devonian, Holy Cross Mountains (Poland), Porolepiformes

The presence of sarcopterygians from Lower Devonian (Emsian) storm-origin bone-bearing breccia (so-called Placoderm Sandstone) was previously reported before the present work. The presence of *Porolepis* ex g. *P. posnaniensis* was ascertained based on scales, skull and shoulder-girdle elements. Previous analyses suggested the presence of *Heimenia* apart from *Porolepis*. Said previous works additionally suggested the presence of dipnoans, what was later a matter of debate. Recent studies based on more than 300 specimens, using both CT-scans and silicon casts indicate not two, but at least three different representatives of porolepiformes in the "Placoderm Sandstone". Two already confirmed genera, *Porolepis* and *Heimenia*, as well as a third genus, currently being studied, which is only represented by one element. Its jugal shows relatively large eyes and is proportionally short, which differentiates this element from *Porolepis* and *Heimenia*. Recent studies result in a picture of a more diversified assemblage of sarcopterygians in the marginal-marine environment of the Lower Devonian of the Holy Cross Mountains, Poland and shed a new light on sarcopterygians diversity along the shelves of the Old-Red continent.

Acknowledgements: The research was financed by the Polish National Science Center (project number 2019/35/B/ST10/01505 granted to Michał Ginter).

Lower Devonian porolepiformes from the Canadian Arctic

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Keywords: Lower Devonian, Emsian, Porolepiformes, Canadian Arctic

Situated in the Western Canadian Arctic, the Anderson River locality has yielded a diverse fish fauna from the Early Devonian (Emsian), which include exceptionally preserved skeletons of placoderms, acanthodians, actinopterygians, and sarcopterygians. Often a prominent component of Devonian fish faunas elsewhere, there were a number of loose scales and a few isolated elements identified as porolepiforms in this locality. *Nasogaluakus chorni* was the only representative based on a single articulated specimen, described in 2000. However, a subsequent expedition in 2008 collected many additional porolepiform materials. We present a preliminary inventory of the approximately 50 specimens pertaining to this group and new information on the anatomy of *Nasogaluakus*. The newly identified specimens include diagnostic skull elements, which are associated with scales, unknown at the time of the original description. These dermal elements unambiguously feature cosmine –previously posited absent in the holotype. We also identified lower jaws and scales referable to *Heimenia* sp. and *Porolepis* sp. from this locality. The increase in species richness implies that porolepiforms are more common and diverse in the Anderson River fauna than previously assessed.

Environmental differentiation reflected in vertebrate fauna diversity in the Lower Devonian of the Holy Cross Mountains, Poland

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Keywords: vertebrates, Lower Devonian, environments, Emsian, Holy Cross Mountains, Poland

The Lower Devonian of the Holy Cross Mountains is fairly well known in the field of vertebrate palaeontology but remains unrecognized in paleoenvironmental considerations. Our research followed previously developed and tested methodology in order to understand their spatial and amount distribution. The vertebrate fauna from the Early Devonian (Emsian) siliciclastic bone-bearing breccia exposed in four sections of the Łysogóry Region and five sections of the Kielce Region were subjected to quantitative and qualitative analyses. Relative abundances of agnathans, acanthodians, placoderms, osteichthyans and chondrichthyans suggest more open marine conditions in the Łysogóry Region and terrestrial-influenced in the Kielce Region during the Emsian. The results show that the average agnathan content of the Łysogóry Region is significantly larger than that in the Kielce Region. A similar difference in faunal content concerns acanthodians. On the other hand, there are relatively fewer osteichthyans in the Łysogóry Region, and a significantly higher proportion of bony fishes was recorded in the fauna of the Kielce Region. Placoderms are characterized by the generally similar frequency in both regions and from site to site in of each of them. However, the slightly greater abundance was noted from the Kielce Region. Also differences in proportion of particular groups in the Kielce Region suggest a big variety of marginal-marine environments under an influence of certain unidentified factors such as, perhaps, sea currents or complicated conditions of a river mouth.

Acknowledgements: Our research was financed by the Polish National Science Center (project number 2019/35/B/ST10/01505 granted to Michał Ginter).

First chondrichthyan and actinopterygian remains from the Upper Pennsylvanian of Perú

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Keywords: Fish, Pennsylvanian, Perú, teeth, scales

Ongoing works on Paleozoic outcrops from Perú are showing that the relatively scarcity (or until recently, absence) of fossil vertebrate can be more related with a low sampling effort than to other aspects. Thus, the finding of a rich vertebrate locality from the middle Devonian of Puno was recently documented by the authors, reporting the first occurrence of palaeozoic vertebrates in the country (see the special volume of the meeting). Here we describe a new -chondrichtyan dominated- fish assemblage from the Upper Pennsylvanian (Carboniferous) of Perú. The material consist on microremains, recovered after the disolution of carbonate rocks, from outcrops of the Copacabana Formation close to the locality of Puerto Arturo (Puno), Oriental Andes of the South East of Perú. The assemblage comprises typical teeth, pharyngeal and dermal denticles of Synmmoriiforms, Ctenacanthiforms, Euselachians, Neoselachians, and isolated teeth and scales of Actynopterigians. Although the systematic study is still in progress, the assemblage suggests a shallow water fauna similar to those described in nearby carboniferous localities of Brazil, Mexico or North America. Those remains represent the first record of the carboniferous vertebrates from Perú and the Central Andes, showing an important taxonomy diversity with palaeogeographic and palaeoecolgical implications.

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