Deciphering early stages of VERTebrate evolution: insights from long IGnored Belgian Devonian fossil Organisms

Context

The evolutionary history of vertebrates began, at the latest, during the early Cambrian (c. 520 Myr) with the first occurrence of elongated and laterally flattened soft-bodied organisms known as chordates, possessing a notochord (the forerunner of the vertebral column) but devoid of backbone and jaw. Vertebrates subsequently underwent major anatomical changes, such as the acquisition of a vertebral column, development of a skull, formation of jaws, and adaptations to terrestrial life. Early chordate and early vertebrate fossils provide our only direct information on 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 (e.g. muscles) that are usually degraded and lost prior to fossilisation, making the interpretation of their anatomy highly challenging. As a result, the affinities of soft-bodied fossils of purported chordates, such as *Metaspriggina* or *Pikaia*, remain highly debated. Although early stages of vertebrate evolution are regularly clarified by new finds of fossils, serious gaps remain in our understanding of the modalities and the timing of the character acquisitions.

Objectives

The VERTIGO project proposed to focus on the study of new findings of putative early chordates and early vertebrates (euphaneropids) from the Early Devonian siliciclastic succession of the southernmost part of Belgium, in the Neufchâteau Synclinorium. It was crucial to retrieve as much anatomical details as possible from these unique specimens for systematic, phylogenetic and evolutionary purposes. In this aim, we used state-of-the-art imaging and spectroscopy techniques in the search for new sources of morphological contrasts and for resolving at high spatial resolution their (bio)chemistry: band-pass emission macroscopy and synchrotron-based micro X-ray fluorescence (μXRF) elemental mapping. In addition to those two techniques, we also used surface scanning, X-ray radiographies, CT scanning to further investigate the anatomy of the fossils, and scanning electron microscopy coupled to energy-dispersive X-ray spectroscopy (EDS), and Raman microspectroscopy to study the elemental and mineralogical composition of the fossils and sediment.

Other important objectives of the VERTIGO project were to (i) find more of these interesting specimens by prospecting public and private collections from Belgium and by organising new excavations in Belgian historical localities as well as to prospect for new coeval localities, (ii) identify the rest of the non-bio and biomineralized fossil fauna from the historical collections and newly collected material and study the diversity of organisms that lived in Belgium during the Early Devonian, (iii) understand the taphonomy — i.e. the mode(s) of preservation — of the fossils

and identify potential preservation biases that could affect their interpretation, and (iv) highlight the historical and geological importance of slate mining in Belgium.

Conclusions

Thanks notably to µXRF fluorescence elemental mapping and band-pass emission macroscopy, the putative chordate material from the Lower Devonian locality of Warmifontaine has been confirmed in its assignment. The study of this material is still in progress, but we hope to publish the results soon. On the contrary, the presumed material of euphaneropids from the Lower Devonian locality of La Roche has been disproved. Actually, the material was more likely parts of an arthropod.

By visiting numerous palaeontological collections in Belgium, important discoveries have been made: 1) the first occurrence of a shark in the Upper Devonian of the Liège Province, Belgium, has been highlighted, 2) numerous chondrichthyan egg capsules from the Carboniferous of Belgium have been inventoried, and 3) the first occurrence of oviparity in the fossil record of chondrichthyan has been disproved.

Thanks to extensive excavations in Warmifontaine organised in 2021 and 2022 in the scope of the VERTIGO project, hundreds of additional fossils have been discovered. They include cephalochordates and various invertebrate taxa too, mainly cephalopods and arthropods, but also many enigmatic specimens. Amongst them, fossils of a selkirkid worm that represents one of the latest occurrences in the fossil record of the group and that constitutes a remarkable testament to their persistent ecological and evolutionary success well beyond the Cambrian. Amongst them also, fossils attributed to two classes of echinoderm that are reported for the first time in the Lower Devonian of Belgium. A new methodology has been established using fossil elemental composition as a complement to anatomy to help identifying specimens otherwise difficult to classify. Regarding the taphonomy of the Warmifontaine locality, the data show that the fossils are preserved as pyritized and carbonaceous compression fossils, decaying organic matter having participated to the trace elemental composition of the pyrite crystals. Preservation of the Warmifontaine fossils therefore closely resembles that of the coeval Hunsrück Slate fossils, Germany.

The Belgian locality of Warmifontaine constitutes a new Lower Devonian *Konservat-Lagerstätte*, with the preservation of both bio- and non-biomineralized organisms. Future identification of problematic taxa should shed more light on the biodiversity of that new fossil locality.

Keywords

Belgium, Devonian, early chordates, soft-bodied fossils, Synchrotron µXRF elemental mapping