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„Branchiopoda from the Late Triassic Polzberg Konservat-
Lagerstätte in the glance of the Carnian Pluvial Episode –
implications on palaeoecology and palaeobiology“

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ABSTRACT

English

In this study samples from the Polzberg locality (Northern Calcareous Alps, Lower Austria) were gathered of distinctly laminated Reingraben Shales and analysed. Polzberg is a known Konservat-Lagerstätte, with fauna dating from the late Triassic period, and has recently gained increased popularity. These samples stem from the Carnian (lower Carnian, Julian 2/Ib), which has been investigated intensely to explain the changes that occurred during that time. One significant event was the Carnian Pluvial Episode (CPE), which drastically increased the global temperature and rainfall, which led to the almost perfect conservation of fossils found in Polzberg. A dysoxic bottom with little to no bioturbation led to the sedimentation of the dark and finely laminated Reingraben Shales, in which the samples were found. The aim of this study was to look into the fauna of Polzberg, in particular the conchostracan *Euestheria*. *Euestheria* occurs today as well and lives mainly in freshwater environment, but the samples from Polzberg, which was a normal marine environment might suggest otherwise. We aim to explain and answer questions about how these little organisms ended in a habitat, that they are normally not living in and how they may have adapted to it. *Euestheria* lay drought-resistant eggs which could be transported by wind, which is one explanation of how they got into the Polzberg Konservat-Lagerstätte. Another possibility is a sporadic influx of freshwater into the otherwise marine Reifling basin during the lower Carnian (*Austrotrachyceras austriacum* Zone).

Deutsch

In dieser Studie wurden Proben vom Polzberg (Nördliche Kalkalpen, Niederösterreich) aus den laminierten Reingrabenschiefern schichtweise gesammelt und analysiert. Der Polzberg ist eine bekannte Konservat-Lagerstätte, deren Fauna aus der späten Trias stammt und in letzter Zeit an Popularität gewonnen hat. Diese Proben stammen aus dem Karn (frühes Karn, Julian 2/Ib), das intensiv untersucht wurde, um die Veränderungen zu erklären, die in dieser Zeit stattfanden. Ein bedeutendes Ereignis war die Karnische Pluvialepisode (CPE), die zu einem drastischen Anstieg der globalen Temperatur und der Niederschläge führte, was wahrscheinlich zu der fast perfekten Erhaltung der in Polzberg gefundenen Fossilien führte. Ein dysoxisches Milieu mit wenig bis gar keiner Bioturbation führte zur Ablagerung der dunklen und fein geschichteten Reingrabner Schiefer, in denen die Proben gefunden wurden. Ziel dieser Studie war es, die Fauna des Polzbergs zu untersuchen, insbesondere den conchostracen *Euestheria*. *Euestheria* kommt auch heute noch vor und lebt hauptsächlich in Süßwasser, aber unsere Proben vom Polzberg, der ein marines Milieu war, lassen etwas anderes vermuten. Wir wollen erklären und Fragen dazu beantworten, wie diese kleinen Organismen in einem Lebensraum gelandet sind, in dem sie normalerweise nicht leben, und wie sie sich an diesen angepasst haben könnten. *Euestheria* legen trockenheitsresistente Eier, die durch den Wind transportiert werden könnten, was eine Erklärung dafür ist, wie sie nach Polzberg gelangt sind. Eine andere Möglichkeit ist ein sporadischer Zufluss von Süßwasser in das ansonsten marine Reifling-Becken im frühen Karn (*Austrotrachyceras austriacum* Zone).

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1. Introduction

1.1. General introduction

Euestheria represents a group of branchiopod crustaceans (Olesen, 2007) classified under the Spinicaudata class, commonly referred to as clam shrimps. These diminutive, bivalve creatures can be found today in various freshwater habitats such as lakes, ponds, and temporary pools (Kozur et al., 2010). The extensive fossil record of *Euestheria* dates back to the Early Triassic period, approximately 250 million years ago, and the genus still flourishes in present-day freshwater ecosystems (Dzik et al., 2008).

Encased within a two-valved carapace, the body of *Euestheria* is safeguarded by a shield made of chitin. Unlike ostracods, spinicaudatans do not lose the cuticle of their carapace. Instead, after each molt a typical concentric line, growth line, is formed on the surface of their valves (Vannier et al., 2003). The carapace often features diverse structures like the aforementioned growth lines and nodes, which are valuable for categorizing species and studying the evolutionary trajectory of this genus (Warrington, 2007). The unique shape of the carapace and the patterns of its adornments serve as key elements that researchers employ to distinguish between various species within the *Euestheria* genus (Warrington, 2007). The morphology of the carapace is also dependent on the environmental factors such as salinity, temperature and oxygen level (Horne, 1971). The use of conchostracans as a biostratigraphical tool may be problematic, when the species cannot be readily distinguished from others (Morton, 2017).

Species belonging to the *Euestheria* genus are filter feeders (Eder et al., 1996), leveraging their unique thoracic appendages, known as phyllopodia, to generate water currents (Vannier et al., 2003) that aid in seizing and conveying food particles to their mouths. They further suggest that spinicaudatans are deposit-feeding omnivores and only few feed on plankton (Vannier et al., 2003). On the other hand, Felgenhauer et al. (1989) claim *Euestheria*' primary dietary components are small organic matter particles, algae, and microorganisms.

Euestheria employs a distinct reproductive approach, which includes generating drought-tolerant resting eggs or cysts. These eggs can even be frost-resistant (Kozur et al., 2010). These cysts can withstand extreme conditions for prolonged durations, enabling the population to endure adverse environmental circumstances, like droughts. As favorable conditions reemerge, the cysts hatch, releasing juveniles and guaranteeing the species' continued existence (Brendonck & Riddoch, 1999). Eggs hatched in the mud are controlled by osmotic reactions

and an alternation of wet and dry bottom conditions is necessary for these reactions (Thierry, 1987).

Another study by Astrop et al. (2020) show evidence of clam shrimps that reproduce through both androdioecy (a mix of males and hermaphrodites) and dioecy (distinct male and female individuals). They further go into detail that groups with many androdioecious species tend to have fewer species (less speciose) but survive for longer periods (persist longer) compared to groups that are mostly dioecious.

The fossil evidence of *Euestheria* offers crucial understanding of the evolutionary timeline and prehistoric environmental circumstances. A research study conducted by Gallego & Shen (2010) scrutinized the morphological diversity and variations of *Euestheria* from the Mesozoic period in Argentina and China, unveiling fresh perspectives about the genus's palaeobiogeography and palaeoecology during that era. The researchers discovered that *Euestheria* was a prominent part of freshwater ecosystems in both regions. The similarity in morphological trends between the two locations indicates a strong palaeobiogeographic link. Vannier et al. (2003) conducted a separate study that explored the functional morphology of the thoracic limbs in *Euestheria*, paying particular attention to the function of the phyllopodia in filter feeding. The researchers discovered that the unique structure of the phyllopodia, along with their associated setae, enables *Euestheria* to effectively seize and process food particles. This functional design likely plays a significant role in the enduring success and persistence of the genus over time.

1.2. Geographical setting

The Reifling Basin is a geologically complex area influenced by Alpine nappe tectonics. It forms part of a larger geological framework that includes the Reifling/Partnach basins and the Hallstatt deeper shelf, which is significant for its proximity to the open Tethys ocean (Mandl et al., 2000). Middle Triassic carbonate platforms are thick and had two main growth phases - in the Anisian period and from the Ladinian to Early Carnian. The second phase was much longer lasting. The carbonate platforms find themselves in two long belts on the north and south sides of the Northern Calcareous Alps. In between the belts the Reifling Basin is situated, a deep basin named after its limestone composition (Lein et al., 2012). Figure 1 shows a reconstruction of the palaeoenvironment and the location of the Polzberg locality within the Reifling Basin.



Figure 1. Palaeogeography of the Reifling Basin and Polzberg locality marked by white star with the name POLZ. Artwork by Mathias Harzhauser, NHMW. Figure modified after Lukeneder et al., 2023.

1.3 Geological setting

1.3.1 Tectonic overview

The samples were collected from the Polzberg locality in Lower Austria, a notable palaeontological site dating back to the Upper Triassic (around 233 Ma) in the Northern Calcareous Alps. This site, located in the Reifling Basin of the Bajuvaric Lunz Nappe System, is distinguished by its Carnian Reingraben Shales, which are fossiliferous in the lowermost parts. Due to the exceptional fossil preservation, the site is classified as a Konservat-Lagerstätte (Seilacher, 1970). The exact location is 4.5 km northeast of Lunz am See on the western-facing slope of Mount Schindelberg (Lukeneder et al., 2021).

Historically, the Polzberg locality has been known and examined since the late 19th century and was first mentioned by Dionýs Stur (Stur, 1874). It was initially a black coal mining area. Subsequent fossil recovery efforts were made by geologists in 1885 and later by Joseph Haberfelner in 1909 (Lukeneder & Lukeneder, 2022).

The samples, aged approximately 237 – 227 Ma, originate from the Carnian Pluvial Episode (CPE). This period, lasting 1-3 Ma, is noted for significant global climate changes. Terrestrial

climates transitioned to a warmer and more humid state with increased precipitation and runoff. Concurrently, oceans saw a decrease in the deposition of carbonate minerals, potentially caused by the extinction of carbonate-forming organisms or a rise in the carbon compensation depth (CCD).

Figure 2 shows the location of the Polzberg locality and the Northern Calcareous Alps and the units in which they are divided.

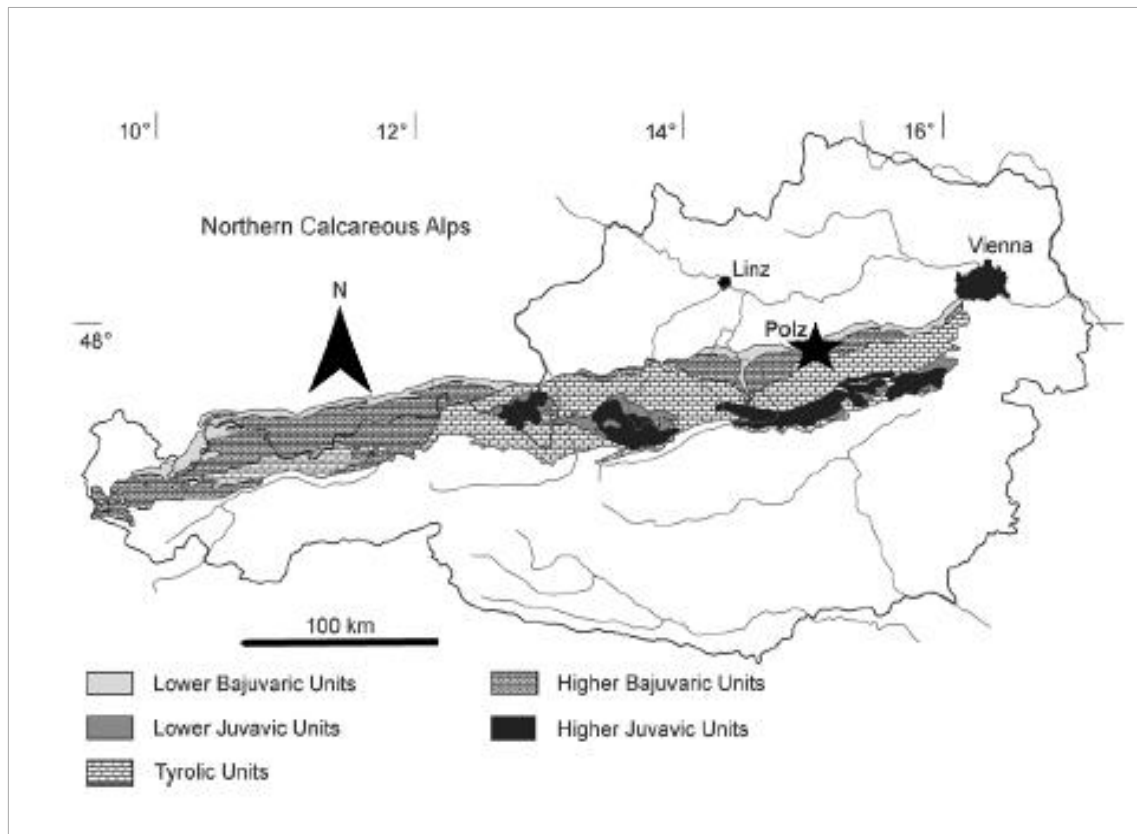


Figure 2. A map of Austria with marked position of the Polzberg locality as well as the main tectonic units of the Northern Calcareous Alps (NCA). Modified after Lukeneder et al. (2021).

It is theorized that the global climate shift may have been driven by volcanic activity related to the early rifting of Pangea, potentially including the formation of the Wrangellia Large Igneous Province (LIP; Dal Corso et al., 2020).

Located near Gaming and Lunz am See in Lower Austria, the Polzberg site is a Konservat-Lagerstätte. This term refers to a sedimentary deposit that showcases entire and extraordinarily preserved fossil content, capturing even fragile structures and soft tissues typically lost in fossil records. The Polzberg site is highly recognized for its Late Triassic (lower Carnian) fossil collections. These assemblages provide a distinctive glimpse into the palaeoenvironments and ecosystems prevalent in the region during that era (Krystyn et al., 2009).

The main tectonic elements of the Northern Calcareous Alps (NCA) in Lower Austria are the Frankenfels Nappe and to the south the Lunz Nappe and within the Lunz Nappe lies the Reifling Basin, located between Polzberg and Großreifling (Krystyn et al., 1991; Lukeneder & Lukeneder, 2021). The Reifling Basin was an intraplateau basin during the Upper Triassic (Lukeneder & Lukeneder, 2021). Festa et al. (2018) mention that the occurrence of an intraplateau basin is a rare feature, when it happens to be in a carbonate platform and is interpreted as a signal of syndepositional tectonics. Intraplateau basins such as the Reifling Basin were filled completely with clay and sand amounting to a thickness of over 200 m (Hornung et al., 2005).

Polzberg sits south of the Lunz Nappe, which is part of the Upper Bajuvaric Unit in the NCA, whose northern and southern borders are next to the Lower Bajuvaric Unit of the Frankenfels Nappe and the lake of Lunzer See, close to the Tyrolic Ötztal Nappe, respectively (Lukeneder et al., 2020). The Lunz Nappe is one of the Bajuvaric tectonic units of the NCA and has many steep synclines and anticlines (Lukeneder et al., 2005). The stacks of the Lunz Nappe could have developed by a syndepositional normal fault that was reactivated, which is evidenced by an extreme change in thickness of Carnian rocks (Linzer et al., 1995).

The Frankenfels Nappe, which is in a Bajuvaric setting at the northern edge of the NCA, is understood to be the tectonically relocated and thus unmetamorphosed original overlay of the Middle Austroalpine region (Häusler et al., 1993).

During a movement of tectonic plates, the Cimmerian Micro-Continent collided with the Eurasian plate, during the formation of the Neotethys and Atlantic Ocean (Hornung et al., 2005). Close to the Ladinian-Carnian boundary, the Tethys split close to its northwestern part into the Palaeo-Tethys and Hallstatt-Meliata Ocean (Stampfli et al., 2002). During the Early to Late Carnian, due to rifting, the Keuper facies belt, Bajuvaric and Tyrolic units developed, where the Reifling Basin is located. High amounts of siliciclastics were moved by large rivers from the Baltic Craton towards Hallstatt-Meliata Ocean (Aigner et al., 1992). This stunted the development of reefs and the carbonate factory was turned off in shallow water during the Tuvalian (Hornung et al., 2005).

1.3.2 Geological Setting and lithology

The Polzberg locality or "Polzberggraben", is a significant palaeontological site located in Lower Austria west of Mount Schindelberg, approximately 4 km NE of Lunz am See. This site is part of the Southern Lunz Nappe within the Reifling Basin of the Northern Calcareous Alps (Lukeneder & Lukeneder, 2021).

Historically, the area has been known for fossil excavation, with significant fossil retrieval campaigns performed in the past. More recent explorations have been conducted by private collectors in the same fossil-rich layers (Lukeneder & Lukeneder, 2022).

The site features deposits from the lower Upper Triassic period, specifically the lower Carnian, (*Austrotrachyceras austriacum* Zone, Julian 2), dating back approximately 233 million years (Lukeneder & Lukeneder., 2021). These deposits are composed of Reingraben Shales, also known as " Göstling Member" among other names. These shales include dark grey to black claystones, marlstones and occasional sandstone layers (Lukeneder & Lukeneder, 2021).

The Reingraben Shales are approximately 50m thick and are overlain by the Lunz Formation, worldwide known for its Upper Triassic Lunz flora. The shales are rich in pyrite and vary in calcium carbonate content from 86.9% in marly limestone to 2.9% in claystone/mudstone. The total organic carbon (TOC) amounts within the *Austrotrachyceras* abundance zone oscillate between 1.4 and 0.3% (Lukeneder & Lukeneder, 2021).

The shales are characterized by laminations of dark organic material and light-coloured laminae composed of loads of halobiid shells (Lukeneder & Lukeneder, 2021). Abundant phosphatic debris, mainly actinopterygian fish scales, and other hard structures, as well as bivalves living in the benthos, forming congregations of shells from young to adult organisms of the dominating species *Halobia rugosa*, are also present (Lukeneder & Lukeneder, 2021).

Figure 3 shows the location of the Reingraben Shales in the stratigraphic sequence as well as the layers that make up the Upper Triassic (Lower Carnian) Polzberg palaeobiota.

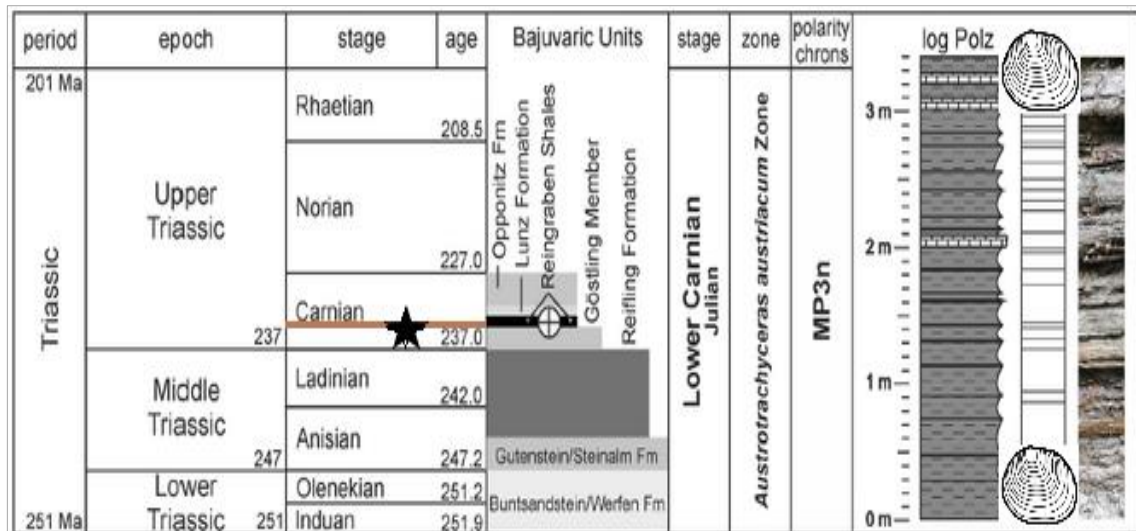


Figure 3. Stratigraphic position of the Polzberg deposits. Brown bar and black star mark the stratigraphic age. Also portrayed in this figure are the two layers, marked by *Euestheria*, with the highest amount of specimen found (Layer 1 [Po -50 – 0cm] and Layer 4 [Po 300 - 320cm]). Modified after Lukeneder & Lukeneder (2021).

1.3.3 Reingraben Shales

The Reingraben Shales („Reingrabner Schiefer“; Piller et al., 2004) are found within a zone of the Reifling Basin between Großreifling (Styria), to Polzberg (Lower Austria) and the easternmost edge of the Northern Calcareous Alps in Hinterbrühl (Lower Austria). They consist of finely laminated, dark grey and brownish marls that are slightly bituminous. The layers show a distinct contrast between bright and dark strata (Ildefonso type), and there are no signs of bioturbation (Krystyn, 1991). The fauna found in the Reingraben Shales are mainly nektonic organisms such as fish (actinopterygiids) and cephalopods (ammonoids, coleoids). Samples obtained from there are usually in a great condition and were well preserved (Forchielli et al., 2013). The researchers further noted that due to the organic content in the sediment, a lack of bioturbation and no sessile organisms all point to a dysoxic to anoxic environment. This makes the Reingraben Shales excellent conservation deposits.

The thickness of the Reingraben Shales is ca. 50 m and on the top, layers of the Lunz Formation are found at the top, replacing the shales (Lukeneder & Lukeneder, 2021).

1.4 Konservat-Lagerstätte

The Polzberg site comprises a Konservat-Lagerstätte with exceptional preservation of fossils, which provides valuable information about the Upper Triassic (lower Carnian) species interactions of the Polzberg organisms. The preservation of fossils at Polzberg is a result of the unique environmental and geological conditions during the Late Triassic period.

According to a study by Lukeneder & Lukeneder (2021), the finely laminated sediments of the Reingraben Shales created anoxic conditions that were conducive to the preservation of fossils. The rock's layered look is due to thin, intermittent, ribbon-like layers of dark, shapeless organic matter, and light-colored layers made up of clusters of halobiid shell fragments, which are formed from a light grey to white calcite (Lukeneder & Lukeneder, 2021). These anoxic conditions prevented scavengers and decay, allowing for the exceptional preservation of a wide variety of organisms.

Additionally, the study explains that the Carnian Pluvial Episode (CPE) played a role in the formation of the Konservat-Lagerstätte in Polzberg. The CPE was a global phase of increased humidity that led to changes in the lithology and facies in the area, promoting the deposition of organic-rich mudstones and terrigenous siliciclastic deposits in the Reingraben Formation: "The humidification is reflected by a change in lithology and facies. The basal Julian sequence in the Polzberg area is characterized by nodular limestones of the Reifling Formation deposited on the palaeoslope. At the base of the Julian 2 *Austrotrachyceras austriacum* Zone (*A. austriacum* Subzone, biohorizon of *A. triadicum*), the Reifling Formation is replaced by the limestone deposits with organic-rich mudstones of the Göstling Member to terrigenous siliciclastic deposits of the Reingraben Formation", citation from (Lukeneder & Lukeneder, 2021).

1.5 Carnian Pluvial Episode (CPE)

The Carnian Pluvial Episode (CPE) was a notable weather phase in the Late Triassic period, triggering a global increase in temperature and humidity that caused heavier rainfall and a distinct crisis in carbonate platforms (Simms et al., 1990). This international event profoundly influenced life in the Triassic seas, including organisms in the Mediterranean Reifling Basin (Lukeneder & Lukeneder, 2021), prompting alterations in the environmental conditions of that era.

Throughout the CPE, the Polzberg region was positioned at the northwestern edge of the Tethys, within the latitude range of 15°N to 30°N (Lukeneder et al., 2012). This period triggered marine

life forms to adapt to the unique environmental conditions of the time, an adaptation that can be seen in the make-up of the ammonoid community and the noticeable changes in shell shape and/or size reduction visible in the fossil record (Zhang et al., 2018). The scientists also note that the size reduction and adaptation of marine life coincides with the global ocean euxinia/anoxia and temperature fluctuations.

The CPE occurred during the Carnian Age of the Late Triassic Period, approximately 232 to 228 million years ago. This episode is characterized by a series of intense and prolonged rainfall events, which led to profound environmental changes that played a crucial role in the evolution of life on Earth. The CPE had a global impact, with evidence found in various regions, including the Tethys Ocean, Europe, and South America (Dal Corso et al., 2020).

The CPE is often associated with the diversification and flourishing of several groups of organisms, such as dinosaurs, early mammals, and modern plant groups like conifers and ferns. The increased humidity and rainfall during this period created a more favorable environment for these organisms to thrive, leading to a significant evolutionary radiation (Simms & Ruffell, 1989).

One of the main factors that contributed to the CPE was a massive volcanic activity phase, known as the Wrangellia Large Igneous Province (LIP), which took place in what is now the western coast of North America. The release of large amounts of volcanic gases, such as sulfur dioxide and carbon dioxide, led to a sharp increase in atmospheric greenhouse gas concentrations, resulting in global warming (Dal Corso et al., 2020).

The warming climate caused a change in global atmospheric circulation patterns, leading to an increase in humidity and intense precipitation events. These events caused widespread flooding and the formation of extensive lakes and inland seas, which in turn led to an increase in organic productivity and the expansion of coastal ecosystems (Ruffell et al., 2016).

Several studies have been conducted to understand the CPE better, including an examination of the sedimentary record. For example, one study by Hornung et al. (2007) used sedimentary facies, palynology, and stable isotope analyses to reveal that during the CPE, a significant change in sedimentation rates and increased organic matter accumulation occurred in the Tethys Ocean.

In another study, Mueller et al. (2015) analyzed geochemical and palaeontological data from various sections of the European and South American regions. They found a clear correlation

between the CPE and the diversification of dinosaurs, which supports the hypothesis that the CPE played a crucial role in shaping the course of life on Earth.

1.6 Triassic Branchiopoda

The Permian-Triassic boundary marks the biggest extinction event in Earth's history (Scholze et al., 2019). Many genera died out during that mass extinction, but some also survived. Stanley et al. (2016) report that 81% of all marine life went extinct during this catastrophic event, whose causing mechanisms are still debated today.

Branchiopods have been alive for many years during Earth's history and have a long evolutionary history, which is supported by the extensive fossil record (Fryer, 1985). Representatives of the order Notostraca, *Lepidurus* and *Triops*, which still exist today, have been known since the Triassic (Fryer, 1985) and have gone through, assumed as a period of stasis.

Clam shrimps, our branchiopod crustaceans, have been known since the Devonian (Leather, 2017) and are still existing today. Scholze et al. (2019) mentions that during Early Triassic the following conchostracans have been studied for the first time: *Cornia germari*, *Euestheria gutta*, *Magnietheria mangaliensis* and some others. Conchostracans can be used in biostratigraphy and are an important tool for fine-scale biostratigraphy of continental sedimentary deposits (Scholze et al., 2018).

2. Background

The CPE is a significant climatic phase that occurred during the Late Triassic Period and had a profound impact on the evolution of life on Earth, including the diversification of various groups of organisms such as dinosaurs and early mammals (Simms & Ruffell, 1989; Dal Corso et al., 2020). *Euestheria*, a genus of branchiopod crustaceans, has a fossil record spanning from the Early Triassic to the present day and provides valuable insights into the ecology and evolution of branchiopod crustaceans (Gallego & Shen, 2010). A study investigating the relationship between the CPE and *Euestheria* would enhance our understanding of how the CPE affected freshwater ecosystems and the organisms inhabiting them, including *Euestheria*.

Despite the importance of the CPE and *Euestheria* in understanding the evolution of life on Earth, the relationship between the CPE and the diversification, distribution, and ecological dynamics of *Euestheria* remains poorly understood. This knowledge gap hinders our

understanding of how the CPE influenced the evolution of freshwater ecosystems and the organisms that inhabit them.

Investigating the relationship between the CPE and *Euestheria* is crucial for several reasons:

- Filling knowledge gaps: Understanding the impact of the CPE on *Euestheria* and other freshwater organisms provide valuable insights into how climatic and environmental changes shaped the distribution and diversification of these organisms during the Late Triassic
- Palaeoecological implications: Examining the relationship between the CPE and *Euestheria* shed light on how the CPE influenced the ecological dynamics of freshwater ecosystems, such as changes in species interactions, food web structures, and resource availability
- Broader applications: Studying the impact of the CPE on *Euestheria* help researchers better understand the responses of freshwater ecosystems to climatic and environmental changes, providing valuable information for predicting and managing the impacts of ongoing and future environmental changes on modern ecosystems

Given the limited research on the relationship between the CPE and *Euestheria*, further studies are needed to address this knowledge gap and enhance our understanding of the palaeoecological and evolutionary implications of the CPE for freshwater ecosystems and their inhabitants.

3. Methods

3.1. Sampling

The study concentrated on 78 *Euestheria* specimens sourced from the Polzberggraben ravine (i.e. Polzberg site). No soft parts (e.g. appendages, internal organs) were preserved during the fossilization process and thus only imprints were analyzed. The fossils were analyzed by the use of various analytical tools and electronic instruments to gain insights into their structure and composition. The exact location of the fossil-rich locality was found with the help of GPS (global positioning system): N47°53'4.98" and E15°4'28.15" (Lukeneder & Lukeneder, 2022).

Sampling began through excavation campaigns organized by the Geological Survey of Austria (GBA) in 1885 and the Natural History Museum Vienna (NHMW) in 1909. More recently, researchers sampled near the historical mine tunnels in the same fossil-rich layers, collecting

samples bed-by-bed. The fossil-rich part of the Reingraben Shales contains abundant ammonoids, from the lowermost sample/layer number 1 (Po -50 cm) up to the topmost layer 5 (Po 320 cm) in the section. (Lukeneder & Lukeneder, 2022).

3.2. Analytical Methods

In the Natural History Museum Vienna (NHMW), digital high-quality photographs of the samples were obtained using a Discovery.V20 Stereo Zeiss microscope, with magnifications of $\times 4.7$, $\times 20$, and a layered photo with up to 35 layers were taken in incident light mode. The data from the AxioCam MRc5 Zeiss was documented and processed using the AxioVision SE64 Rel. 4.9 imaging system at the NHMW.

Energy dispersive x-ray (EDX) analyses of the Polzberg samples were conducted in the NHMW using JSM-6610LV (brand Jeol) Secondary Electrons Microscope in a low vacuum setting. The 5 samples were uncoated and unpolished and were analyzed using 15kV voltages.

4. Results

4.1 Taxonomy – Branchiopoda – Euestheria

The exact classification of the genus *Euestheria* has been a matter of change in the last decades and will probably change in the future again when more data has been acquired. The current systematic palaeontology of *Euestheria* is as follows:

Phylum *Arthropoda* VON SIEBOLD, 1848

Subphylum *Crustacea* PENNANT, 1777

Class *Branchiopoda* LATREILLE, 1817

Superorder *Diplostraca* GERSTÄCKER, 1866

Order *Conchostraca* SARS, 1867

Suborder *Spinicaudata* LINDER, 1945

Superfamily *Cyzicoidea* STEBBING, 1910

Family *Euestheriidae* DEFRETIN-LEFRANC, 1965

Genus *Euestheria* DEPÉRET & MAZERAN, 1912

Type species *Euestheria minuta* (ALBERTI in VON ZIETEN, 1833)

78 specimens were sampled in this study and belong to the type species *Euestheria minuta*. The most common method of identification for these conchostraca is their carapace and their

symmetry. Size, shape, and ornamentation differ between different *Euestheria* species. The morphology of *Euestheria* appears to be stable over time and has changed little during the evolutionary history of these animals (Hethke, 2014). Figure 4 provides a schematic look at the ornamentation of *E. minuta* and its growth lines.

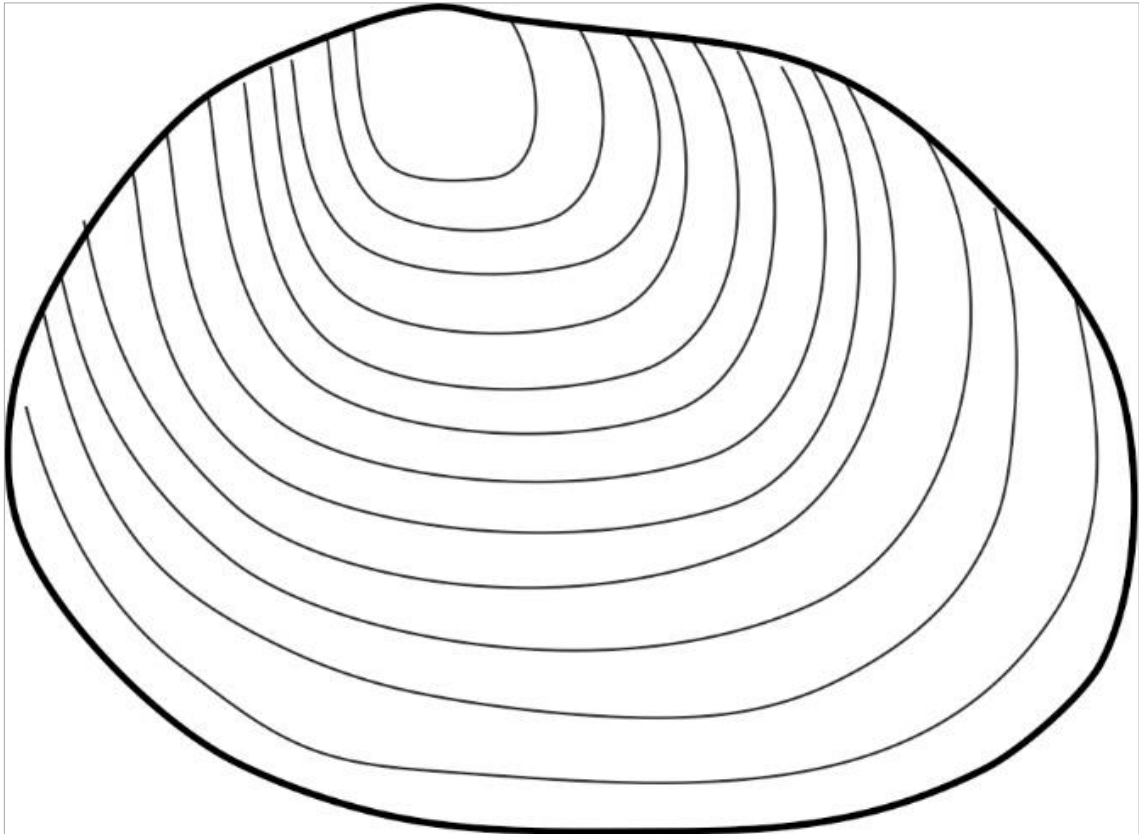


Figure 4. Ornamentational rings of *Euestheria minuta*; made with the software CorelDraw based on a specimen (NHMW 2021/0123/0456) from the samples. The moulting lines are artistically displayed here.

4.2 Branchiopoda in the Polzberg section

In total, 78 specimens were collected, photographed and measured using the Discovery.V20 Stereo Zeiss microscope and its software. Figure 5 shows the mean shell size distribution of *Euestheria* along the layers. Each layer has a thickness of 20 cm, except layer 1, which has 50 cm thickness. What is clearly noticeable is that the x-axis of the shell is bigger than the y-axis. The biggest mean size of shells was found in layer 2. This is mostly probably due to the low amount of specimens (n=1) found there. The specimen with the largest carapace in the x-axis direction, measured 5.18 mm and the largest carapace in the y-axis direction was 4.33 mm. No general pattern can be seen in Figure 5 regarding size increase/decrease with depth. Layers 1 and layer 4 had the highest number of specimens, n=29 and n=43 respectively. These layers are the most statistically significant regarding the mean shell size distribution. It should be noted

that the highest amount of *Euestheria* fossils (n= 29) found in our study were in layer 1 (Po -50 – 0 cm), and in layer 4 (Po 300 – 320 cm), 43 specimens were detected. These layers are predominantly calcareous.

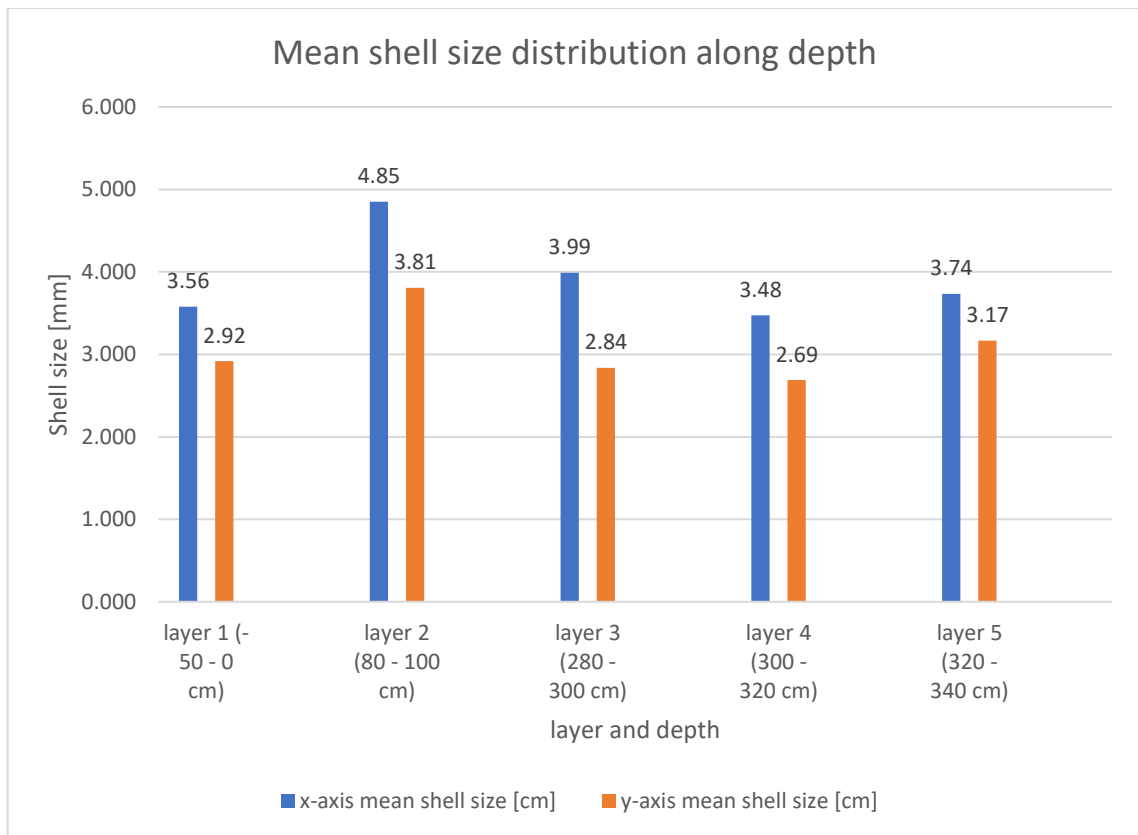


Figure 5A. Mean shell size distribution along log. The biggest specimen was found in layer 2 with 4.85 mm, the smallest in layer 4 with 2.69 mm.

Figure 5B shows a scatter plot with the carapace length on the x-axis and carapace width on the y-axis. The samples are somewhat scattered around, but a high number of them are located in the space between 2.8 mm – 4.5 mm length and 2 mm – 3.8 mm width. Furthermore, the coefficient of determination (R^2) in this graph is 0.28, indicating a not very strong predictive power in our model.

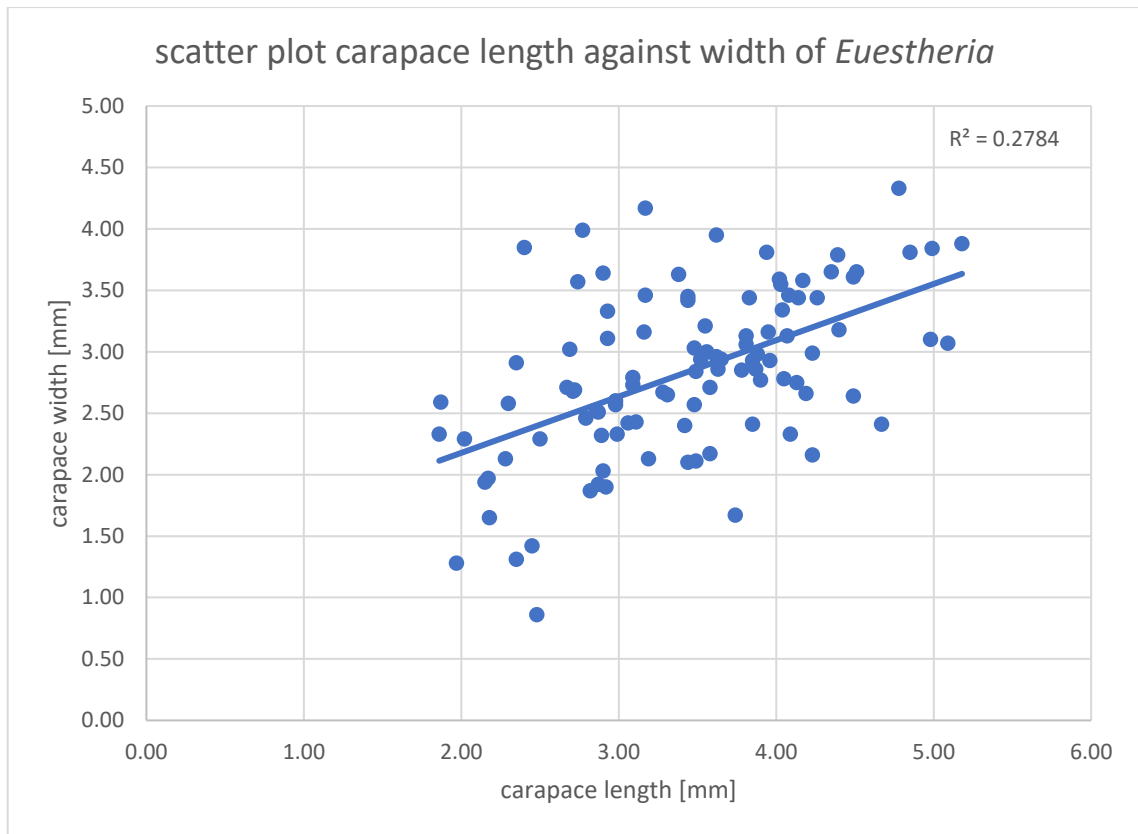


Figure 5B: Scatter plot displaying *Euestheria* carapace length on the x-axis and carapace width on the y-axis. Most of the samples are in the 3 – 4 mm length and 2.50 – 3.00 mm width rectangle.

As Figure 6 shows, the highest amount of specimen found in a layer is layer 4 (Po 300 – 320 cm) followed by layer 1 (Po -50 – 0 cm). Layer 2 (Po 80 – 100 cm), layer 3 (Po 280 – 300 cm) and layer 5 (Po 320 – 340 cm) show 1, 2 and 3 specimens respectively. Thus, only layer 1 and layer 4 are of statistical relevance.

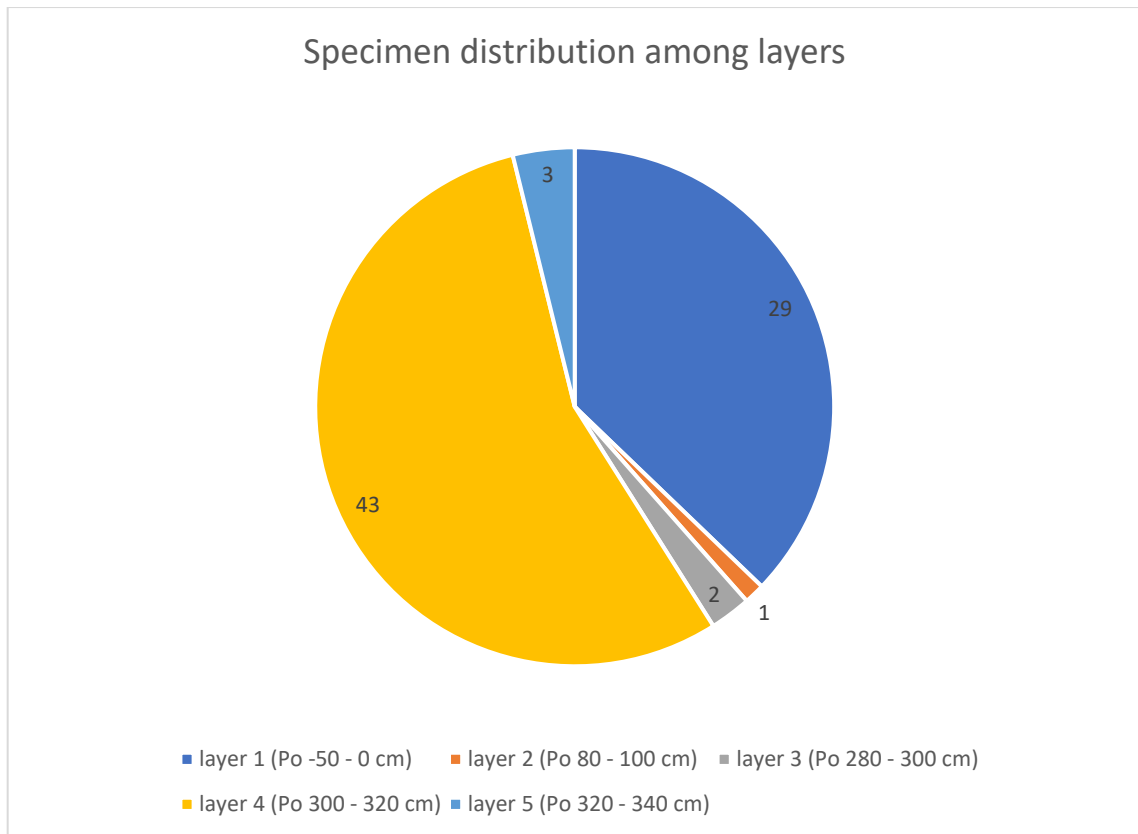


Figure 6. Distribution of specimens among different layers. Layer 1 appears with 29 specimens, whereas layer 4 with 43. Layers 2, 3 and 5 shows 1, 2 and 3 specimens collected from them, respectively.

Figure 7 shows a bell curve with the normal distribution of shell size across all specimens. The mean shell size of all samples is 3,18 cm. This curve shows a high standard deviation as it is wide and covers a lot of area. This indicates that the values in the dataset used, are spread out and vary significantly from the mean value. The numbers in our dataset are not closely bunched around the average value. Instead, they spread out over a wider range. This shows that the shell size in our samples is highly variable.

In our case, 78 samples were analyzed. A higher number of samples usually means a more accurate and even size distribution.

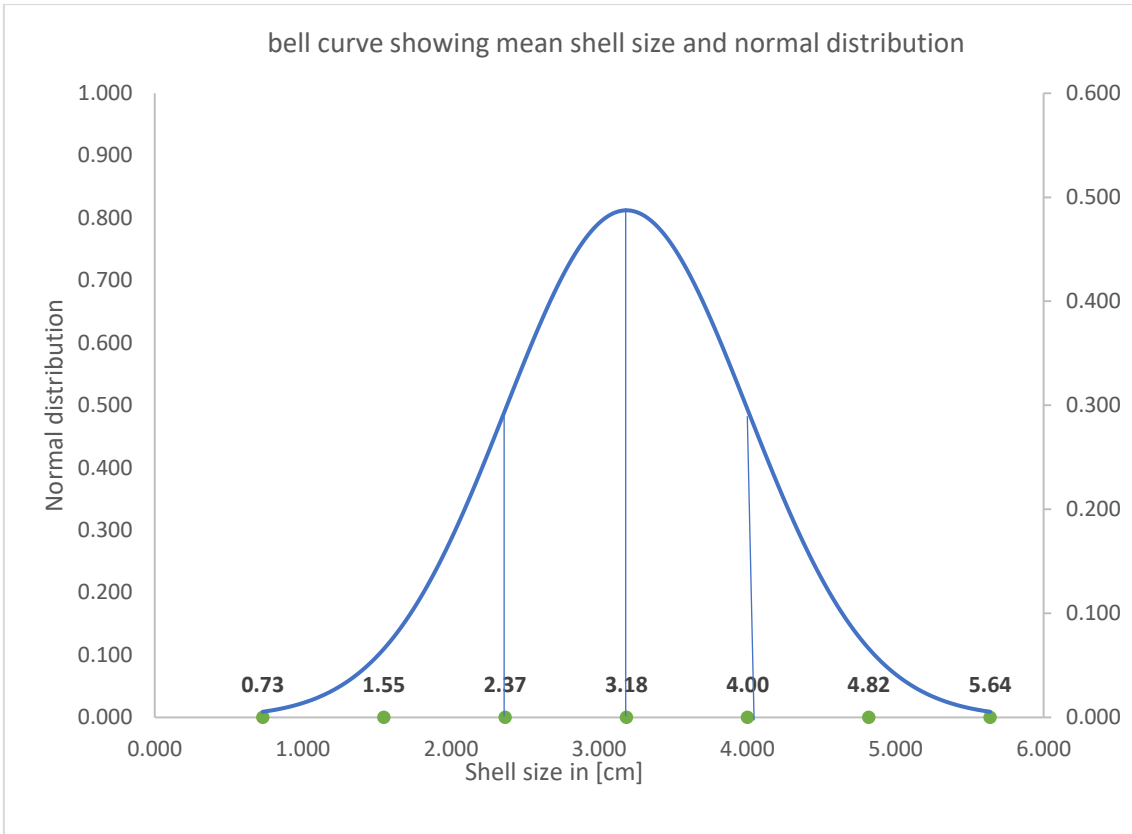


Figure 7. Normal distribution and shell size. Note a high standard deviation, indicating spread-out data set.

4.2.1 Incident Light Mode images of *Euestheria*

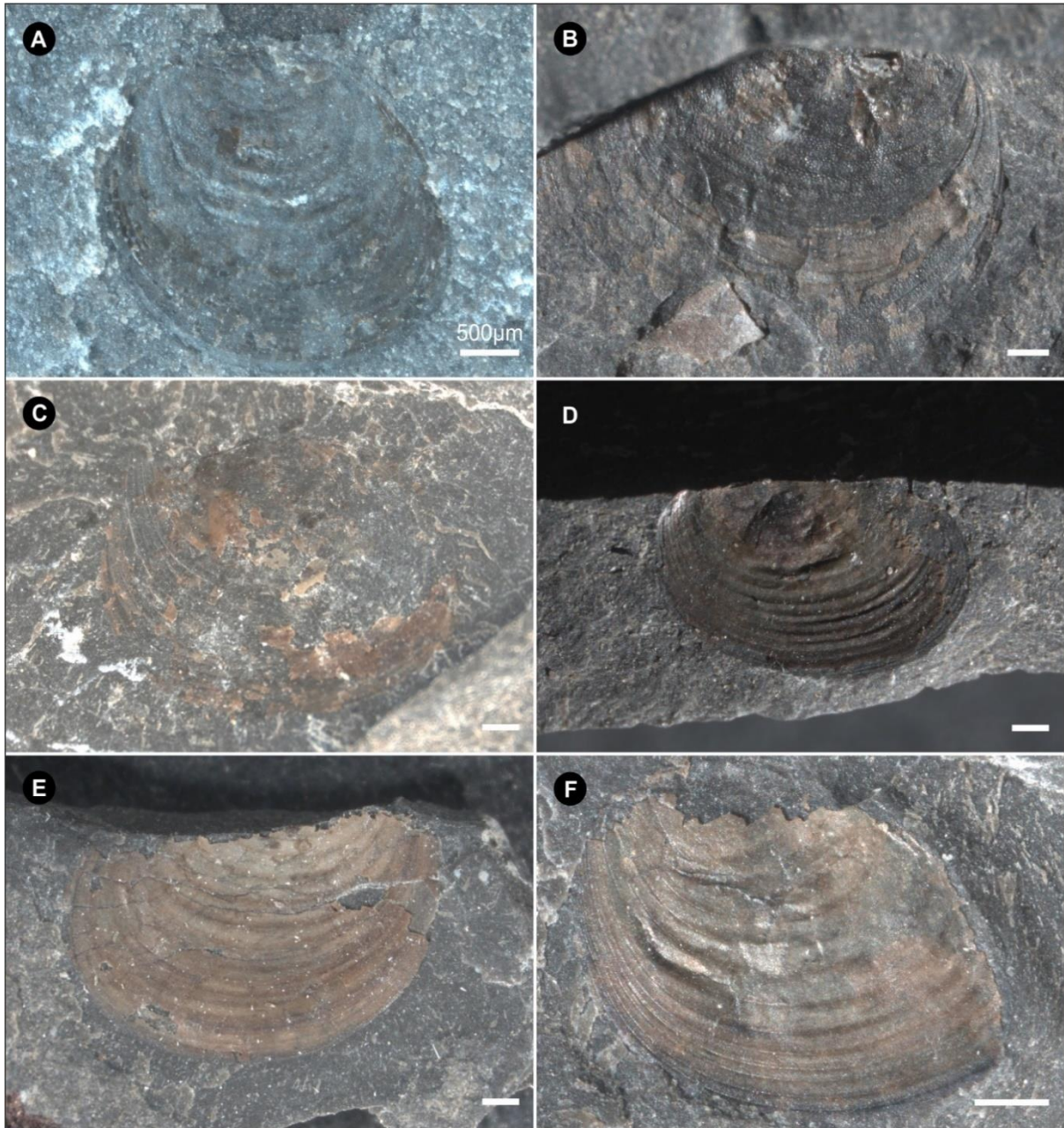


Figure 8. **A** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0437. **B** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0489. **C** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0463. **D** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0490. **E** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0464. **F** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0465. Scale bar 500 µm

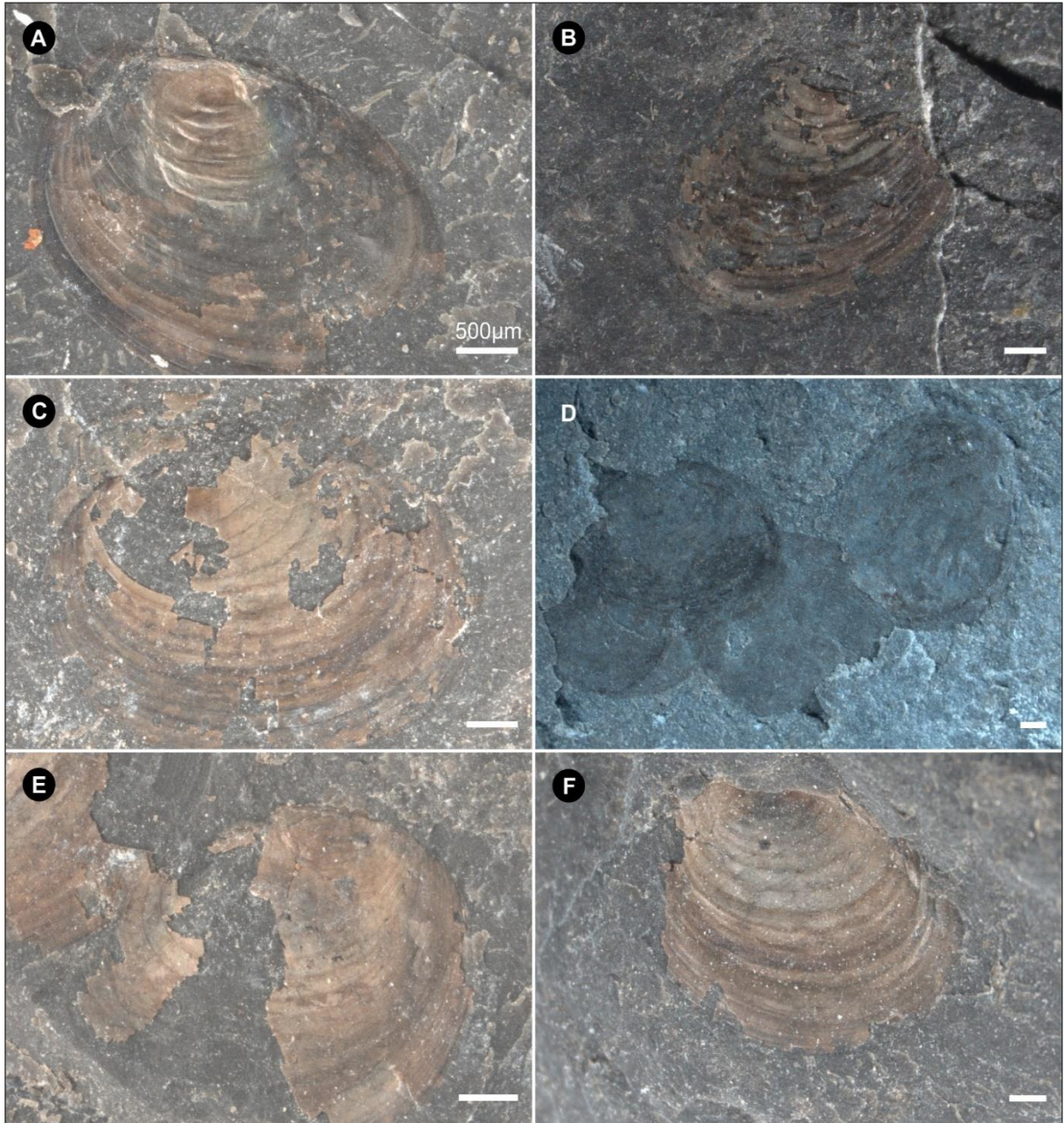


Figure 9. **A** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0466. **B** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0493. **C** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0468. **D** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0442. **E** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0494. **F** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0471. Scale bar 500 μ m

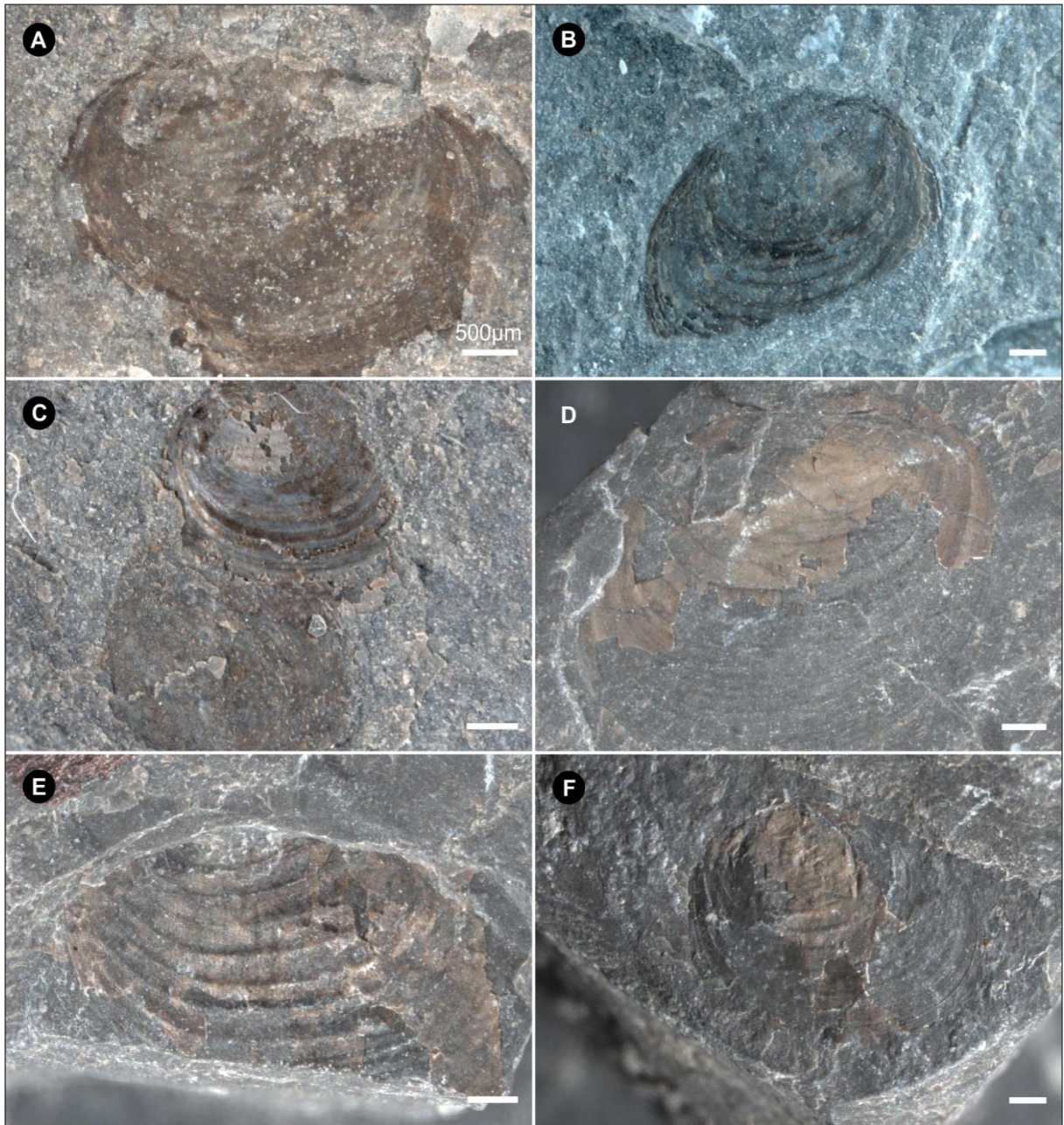


Figure 10. **A** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0435. **B** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0443. **C** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0444. **D** *Euestheria minuta*, positive, lateral view, layer 4 (300 - 320 cm), NHMW 2021/0123/ 0485. **E** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0508. **F** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 - 320 cm), NHMW 2021/0123/0510. Scale bar 500 µm

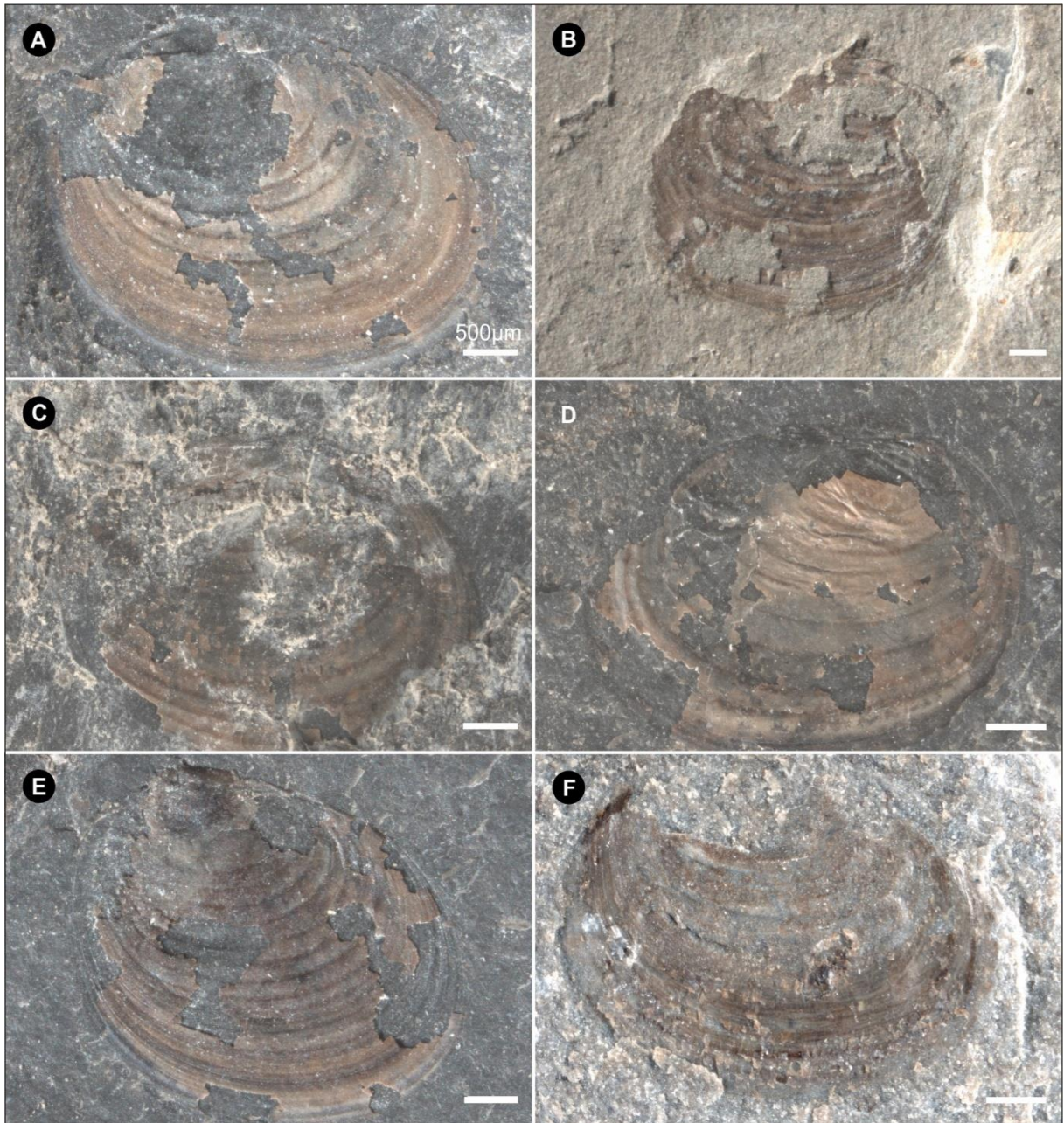


Figure 11. **A** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0511. **B** *Euestheria minuta*, positive, lateral view, layer 5 (Po 320 - 340 cm), NHMW 2021/0123/0513. **C** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0486. **D** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0497. **E** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0478. **F** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 - 0 cm), NHMW 2021/0123/0040. Scale bar 500 µm

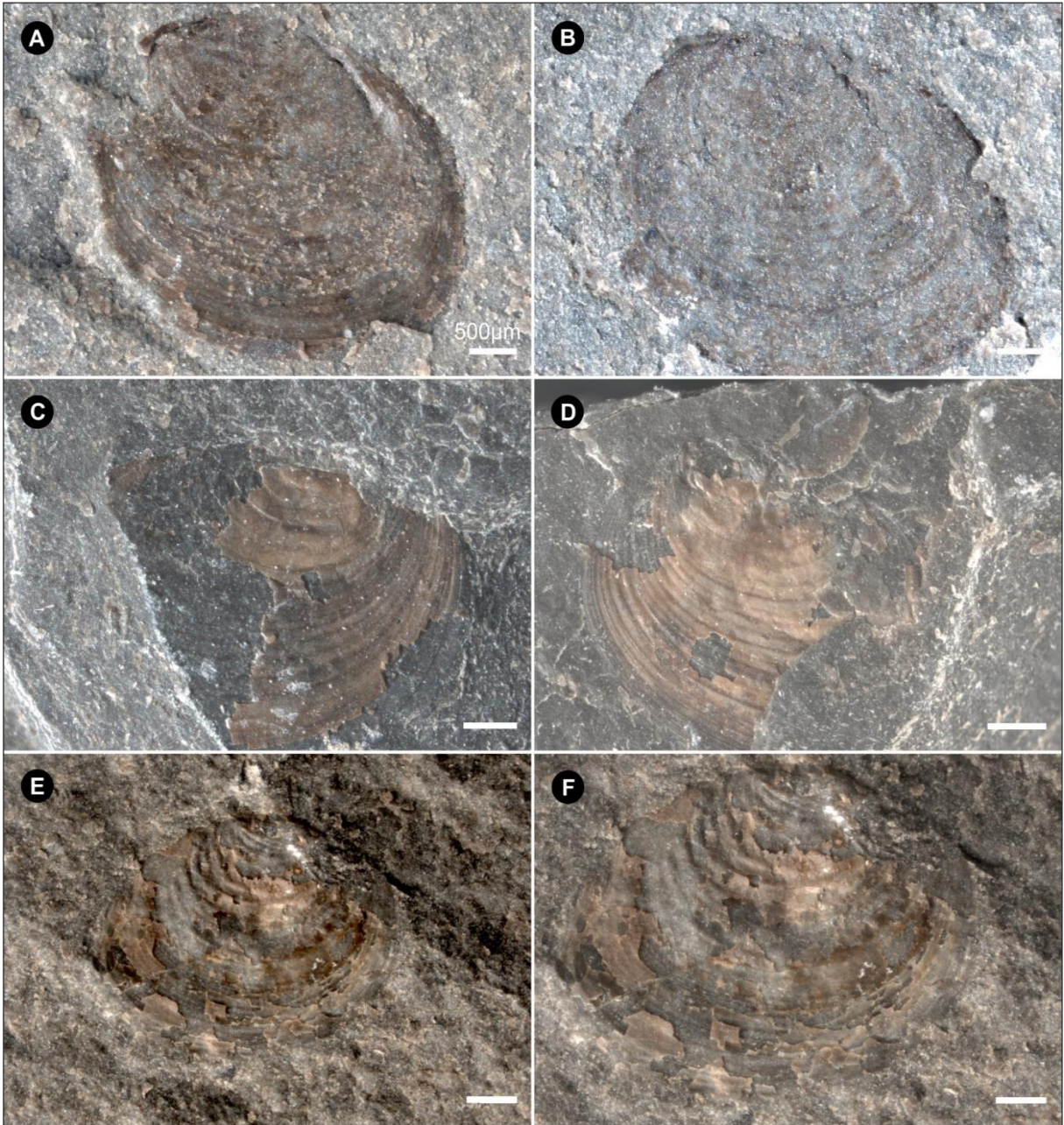


Figure 12. **A** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0041. **B** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0037. **C** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0476. **D** *Euestheria minuta*, positive, lateral view, layer 4 (Po 300 – 320 cm), NHMW 2021/0123/0483. **E** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0455. **F** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0455. Scale bar 500 μ m

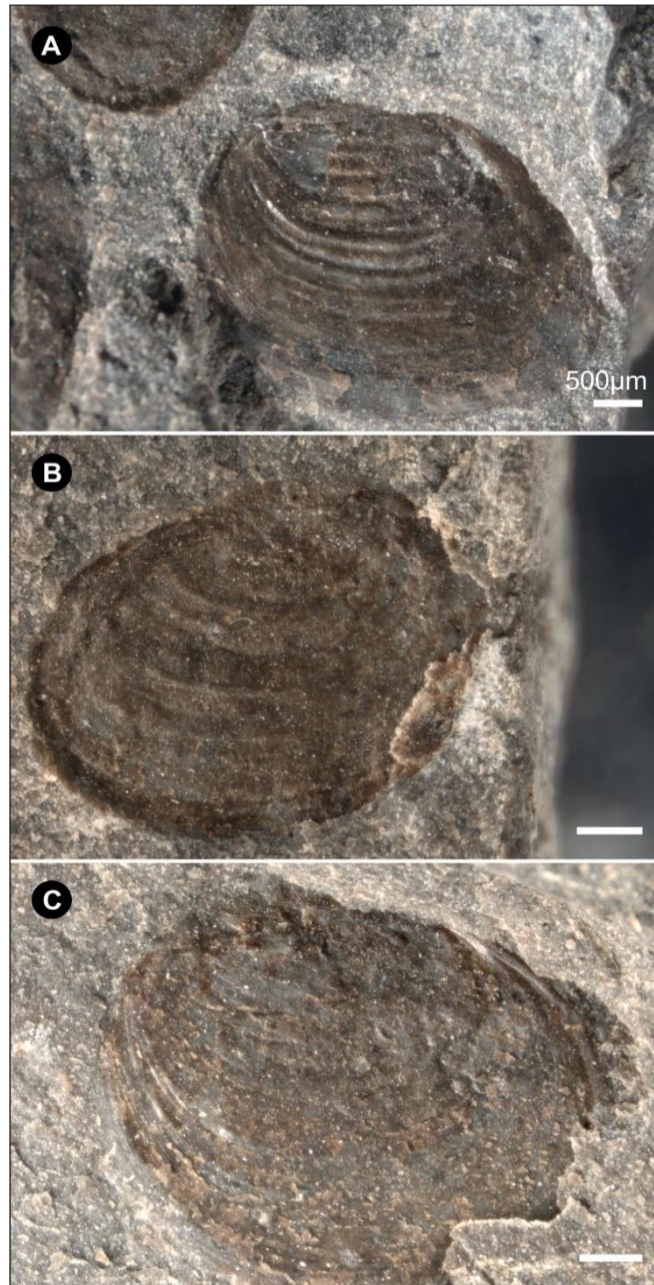


Figure 13. **A** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0456. **B** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0456. **C** *Euestheria minuta*, positive, lateral view, layer 1 (Po -50 – 0 cm), NHMW 2021/0123/0457. Scale bar 500 µm

4.2.2 Chemical analysis of the samples with EDX and Secondary Electron Microscope (SEM)

Energy Dispersive X-ray (EDX) was performed on 5 selected samples (NHMW 2021/0123/0507, NHMW 2021/0123/0464, NHMW 2021/0123/0465, NHMW 2021/0123/0466 and NHMW 2021/0123/0471) to find out the chemical composition of the shells (carapace). The areas selected for analyses had parts of the shells still intact. Analysis was not performed on the imprints in the sediment. Some samples were analyzed not only once,

but twice on different areas. EDX can provide us with insights about the mineralization process that occurred during fossilization as well as the environmental conditions at the time of preservation.

As seen in the figures below, the main composition of the *Euestheria* fossils is silicium (Si), phosphate (P) and calcium (Ca). The spikes of the other elements come from the rock matrix and are to be neglected. The chemical composition also differs depending on analyzed points. This indicates that the elements of which the original carapace of *Euestheria* primarily is made of are calcium, phosphate and chitin.

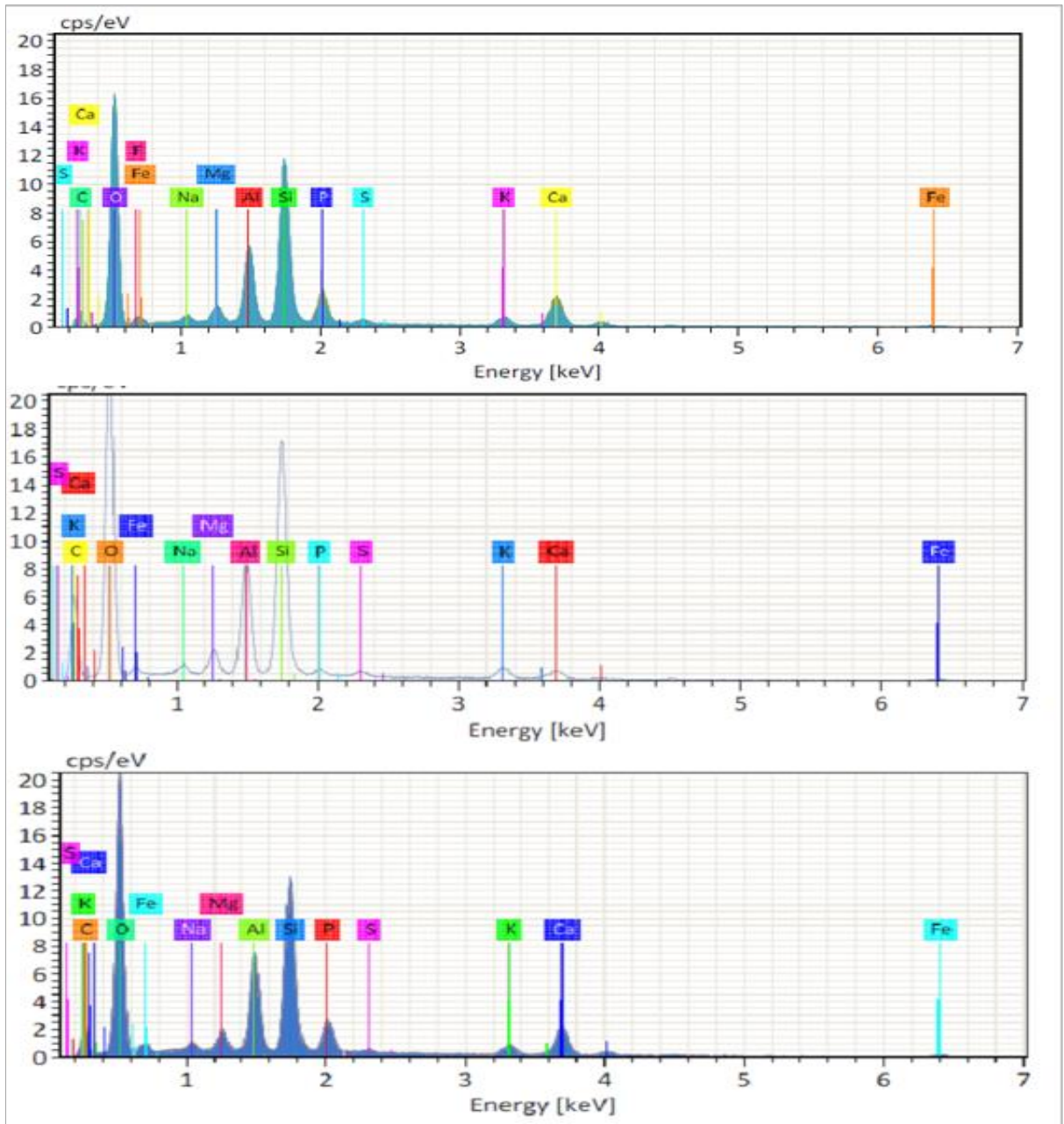


Figure 14. Chemical composition of the valves of *Euestheria*. The main chemical elements seen here are calcium (Ca), silicium (Si), oxygen (O) and sulfur (S).

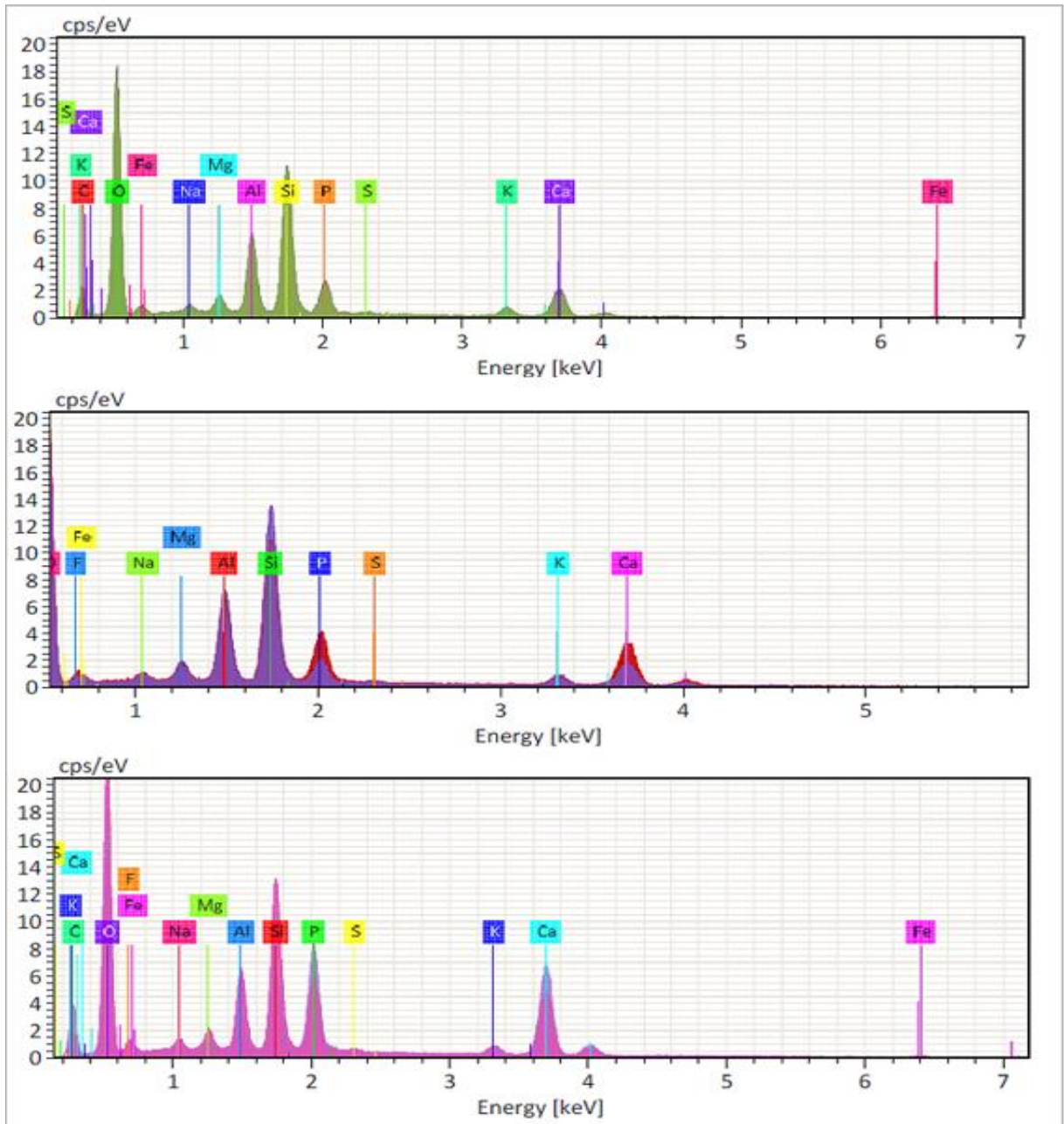


Figure 15. Chemical composition of the valves of *Euestheria*. Main elements seen here, displayed by the peaks, are sulfur (S), calcium (Ca), silicium (Si) and oxygen (O).

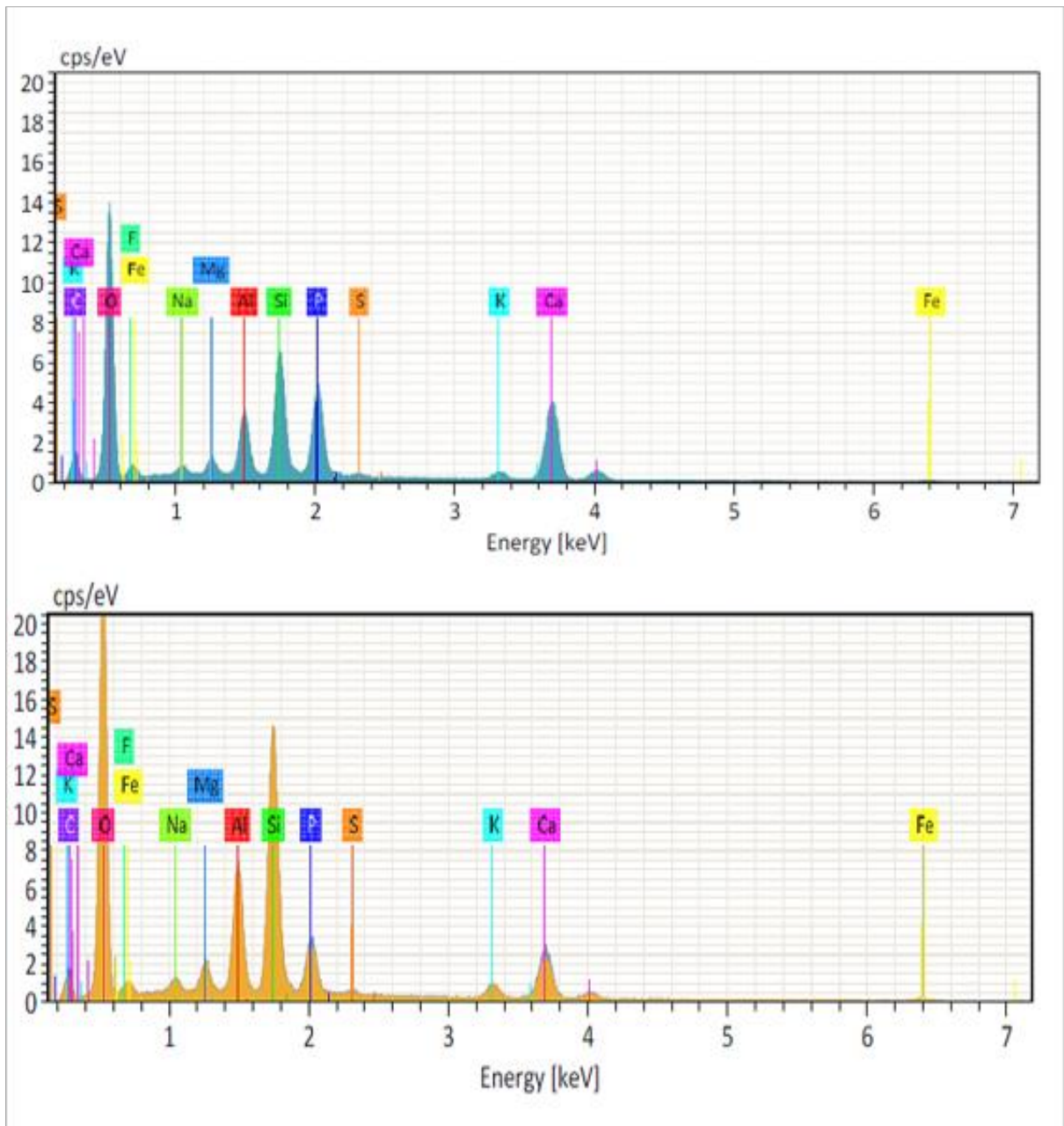


Figure 16. Chemical composition of the valves of *Euestheria*. The main chemical elements seen here are sulfur (S), calcium (Ca), oxygen (O) and silicium (Si).

Spectrum	C	O	F	Na	Mg	Al	Si	P	S	K	Ca	Fe
Euestherien 4309 1	9,22	38,64	1,73	0,57	0,61	2,59	7,73	9,68	0,29	0,75	26,46	1,73
Euestherien 4309 2	4,20	44,07	0,86	0,68	1,09	4,94	15,45	6,56	0,32	1,63	17,49	2,72
Mean	6,71	41,35	1,30	0,62	0,85	3,76	11,59	8,12	0,30	1,19	21,98	2,22
Sigma	3,55	3,84	0,62	0,08	0,34	1,66	5,46	2,21	0,02	0,62	6,35	0,70
SigmaMean	2,51	2,71	0,44	0,06	0,24	1,18	3,86	1,56	0,01	0,44	4,49	0,50

Figure 17. Chemical analyses of the valves with the elements in weight percentage [wt. %]

4.2.2.1 Secondary Electron Microscope

The samples used for EDX were also used for creating Secondary Electron Microscope photos. Figure 18 and Figure 19 show 12 pictures of selected samples that have been viewed through and photographed with a secondary electron microscope. Samples NHMW 2021/0123/0507, NHMW 2021/0123/0464, NHMW 2021/0123/0465, NHMW 2021/0123/0466 and NHMW 2021/0123/0471 were used to obtain the pictures below.

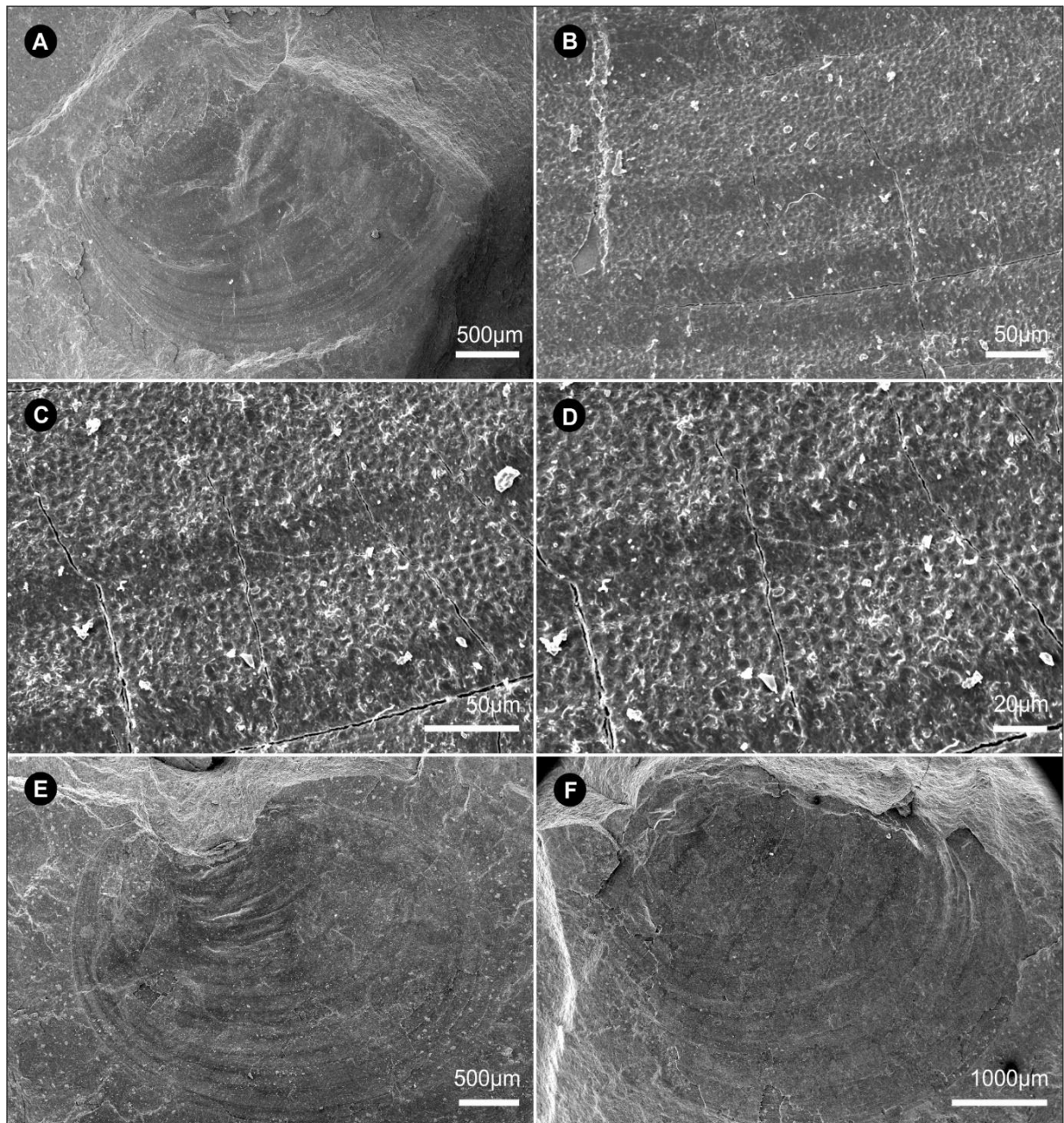


Figure 18. A full size *Euestheria minuta*. NHMW 2021/0123/0465, B magnification of A with growth lines C magnification of B with small sized reticulations on growth bands in the anterior part of the carapace of the specimen NHMW 2021/0123/0465, D displays small tubercles which appear to be radially aligned, NHMW 2021/0123/0465 E sample NHMW 2021/0123/0466 showing clearly visible growth bands, F sample NHMW 2021/0123/0471 also displaying the growth lines, Scale bars in distinct images.

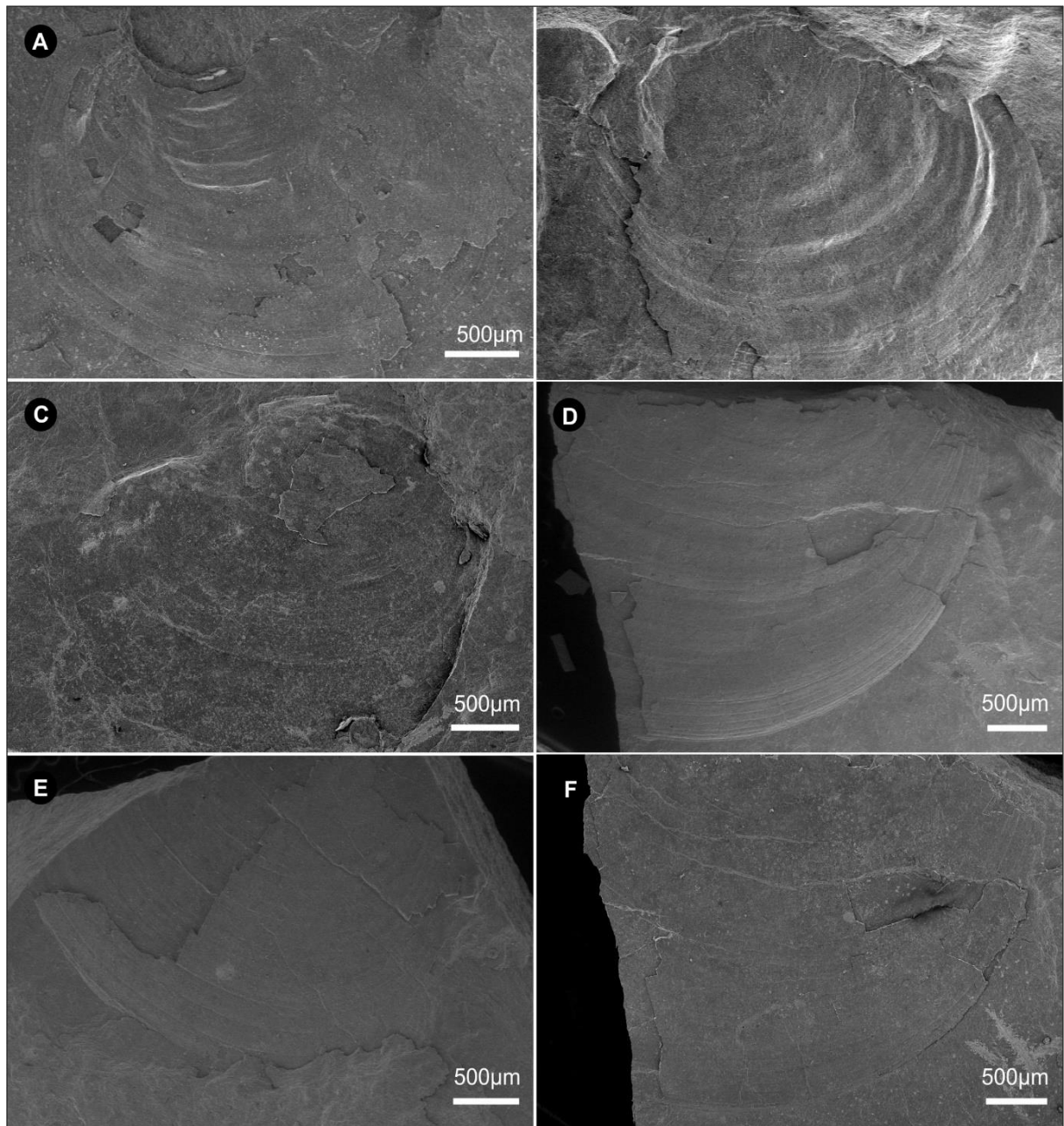


Figure 19. **A** *Euestheria minuta*., partially broken carapace showing growth bands, NHMW 2021/0123/0466, **B** *Euestheria minuta*., a more complete carapace with growth bands, NHMW 2021/0123/0471 **C** *Euestheria minuta*., posterior view of the carapace where growth bands are not so clearly visible, NHMW 2021/0123/0507, **D** *Euestheria minuta*., displays a smoother growth over time, thus more growth bands, NHMW 2021/0123/0464, **E** *Euestheria minuta*., NHMW 2021/0123/0464, **F** *Euestheria minuta*. NHMW 2021/0123/0464, scale bar is 500 µm

What we hoped to achieve with these SEM pictographs is to make the reticulation patterns and the growth bands more visible, which are very important for taxonomy and identification of *Euestheria*. Small tubercles are visible on Figure 18 B, C and D. They occur only on the uplifted growth lines of the carapace and not in the constrictions. Figure 19 D shows a specimen whose growth lines are smoother and not clearly ridged like the specimen from the other figure. The growth-rings represent the ontogenetic stage of each individual since it is not shed during

ecdysis (moulting). A wider ring could indicate that the environmental conditions were favourable (i.e., plenty of food, enough oxygen), whereas many rings, closer together indicate the opposite – stressful conditions like scarce food availability and a changing temperature. Analyzing these growth bands is important for understanding how *Euestheria* lived during the Triassic and not only that, but also how it adapted and evolved to fit in its environment. With this information an accurate reconstruction of this palaeoenvironment can be created.

5. Discussion

5.1 Palaeoecology of the Reingraben Shales

The Reingraben Shales are relatively dark and laminated deposits, which formed in a normal marine environment of the Reifling Basin (Forchielli et al., 2013; Lukeneder et al., 2020). During deposition of the shales, the bottom conditions were inhospitable with little oxygen content or even lack of oxygen (Tintori et al., 1992; Forchielli et al., 2013; Lukeneder & Lukeneder, 2023). In the Polzberg sub-basin, from where the samples were collected, an excellent preservation of fossils occurred, due to anoxic/dysoxic conditions near sea-floor and a lack of bioturbation in the sediment. Euxinic bottom water conditions limited and restricted the predator presence and allowed the fossils to be unaffected (Lukeneder & Lukeneder, 2021). This led to the formation of the fossiliferous Reingraben Shales, comprising the Polzberg Konservat-Lagerstätte, which are rich in organic material and well laminated due to the lack of bioturbation (Savrda et al., 1991; Lukeneder & Lukeneder, 2021, 2023).

The Reingraben Shales together with the siliciclastic dominated deposits from the Lunz Formation interrupted the carbonate factory in the Tethys Ocean (Mueller et al., 2015). The study suggests that the climate was wetter and warmer, thus the Reingraben Shales were deposited. This in turn supports the assumption of a global Carnian Pluvial Episode. Roghi et al. (2010) reported the demise of the carbonate platforms during the CPE. A decline in carbonate production led to new environmental conditions in marine shelf and basinal environments. Reduced biodiversity, changes in the sediment deposition and type as well as altered ecosystem dynamics are some examples for a declining carbonate factory (Weidlich et al., 2007).

Forchielli et al. (2013) studied the Polzberg fauna and reported the predominance of nektonic organisms. Marine nektonic taxa as cephalopods and fish dominate the soft bodied fauna in Polzberg (Lukeneder et al., 2021; Lukeneder & Lukeneder, 2022) and the scientists also suggest a dysoxic to anoxic environment in the Reingraben Shales.

The Reingraben Shales were also detected in the Indian Himalaya of Spiti (and also indicate a carbonate production collapse coupled with an increase in siliciclastic output (Hornung et al., 2007). Laminated shales discovered in a remote section of the Spiti basin indicate the beginning of anoxic conditions in the deeper shelf, occurring simultaneously with the 'Reingraben Event' in Austria, according to the study.

5.2 Palaeobiology of *Euestheria*

The main habitat of extant and fossil conchostracans is fresh to brackish water (Yanbin et al., 2002). These organisms are predominantly found in ponds, small pools, coastline, or edges of big lakes is where (Tasch et al., 1969; Chen et al., 1985). *Euestheria* from the Polzberg Konservat-Lagerstätte might be an exception to the assumption. A study on Early Triassic conchostracans reports, a new environment for these little organisms. The samples were found in brackish, deltaic to shallow-marine deposits (Scholze et al., 2019). The evidence is not enough to predict a marine or freshwater lifestyle of the Polzberg specimens, adapted to live in marine environments or if they were transported from their original habitat and deposited in the Reifling Basin within the Reingraben Shales. Another speculative hypothesis for the presence of conchostracans within the basinal Polzberg area is the transport and redeposition caused by aeolian mechanisms (Scholze et al., 2016). As mentioned at the beginning, these tiny (2 – 5 mm) organisms produce drought-resistant and freeze-resistant (Kozur et al., 2010) eggs, which can survive for a long time without water. These eggs can be easily transported from one area to another by the sheer force of the wind. In modern species, conchostracans' life cycle from hatching to sexual maturation is very short (5-23 days; Webb, 1979) and this allows them to occupy small (isolated) lakes and ponds, which may not be there all year around (Kozur et al., 2010). Further investigations would be needed to determine the original habitat of *euestheriids* in the Polzberg locality.

Microsculptures are important for distinguishing different species of conchostracans. The most frequent feature is a net-like pattern on the carapace's outer surface, where polygons in different sizes, from small to large, can be seen (Kozur et al., 2010). The configuration of these polygons can vary - aligned vertically or obliquely or parallel to the growth lines, more often than not, the microsculpture forms radial lines that are closely spaced (Kozur et al., 2010), which can be seen in Figure 18D. Further magnification might have been needed, to clearly see additional microsculptures such as, a pitted surface or small, closely spaced nodules along the growth lines.

Branchiopods are also known for laying dormant eggs which can either be transported by water currents, either marine or fresh water, or by wind (Havel et al., 2000; Graham & Wirth, 2008; Vanschoenwinkel et al., 2009; Kozur et al., 2010). Eggs of these branchiopods were constituents of the sediment and sand- or wind-storms can have transported them over thousands of kilometers distance.

Stur (1886), Teller (1891) and Lukeneder & Lukeneder (2022) described remains of a lungfish *Tellerodus*, which is assumed to be a freshwater taxon, and other conchostracan shells indicating at least a sporadic and temporary influx of brackish water or freshwater into the otherwise isolated Reifling Basin (Polzberg subbasin). Recent studies (Lukeneder & Lukeneder 2022; 2023) also found additional evidence confirming freshwater or terrestrial influx in area of investigation – plant remains of a member of the family *Coniferophyta*, with the genus *Voltzia*, was found alongside the conchostracans and other fossil remains.

As mentioned in the introduction, *Euestheria* have different interesting reproduction strategies. They can have asexual, sexual reproduction and lay eggs, which are drought-resistant (Frank et al., 1988). This could mean that *Euestheria* eggs can be transported by freshwater currents and be brought to an otherwise marine environment or that wind currents can raise dust comprising such eggs and relocate them (Tasch et al., 1987; Graham et al., 2008; Scholze et al., 2019). This might explain how the specimens ended up finally in a marine environment.

Figure 20 shows an animation of how the environment during the late Triassic in Polzberg could have looked like. Number 19 on the left and right sides of the picture displays *Euestheria* in a freshwater to brackish water environment. Many different species have been found in the

Polzberg Konservat-Lagerstätte and show again how important it is to continue excavation work and scientific research there.

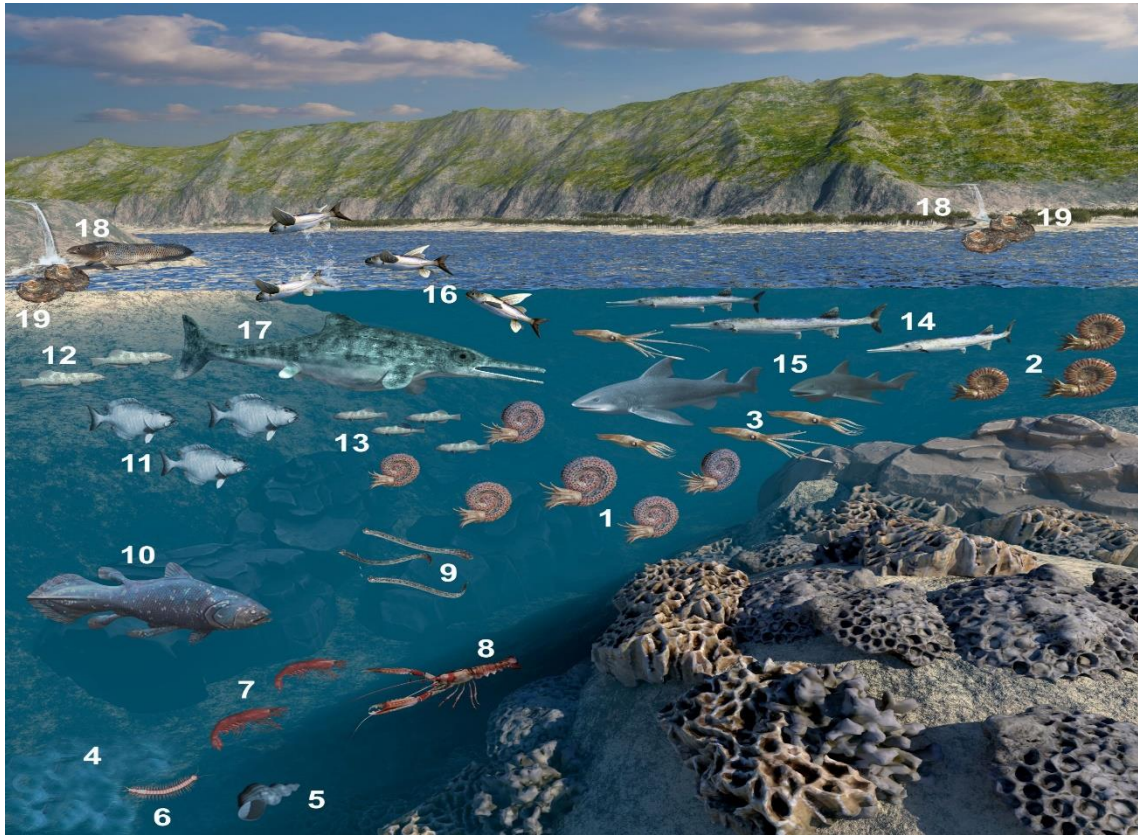


Figure 20. A reconstruction of the palaeoenvironment during the late Triassic in the Polzberg locality. 1 *Austrotrachyceras minor*, 2 *Austrotrachyceras haberfellneri*, 3 *Phragmoteuthis bisinuata*, 4 *Halobia rugosa*, 5 *caenogastropod*, 6 *Palaeoaphrodite*, 7 *Antrimpos*, 8 *Platychela trauthi*, 9 *conodonts*, 10 "*Coelacanthus*" *lunzensis*, 11 *Polzbergia brochatus*, 12 *Habroichthys gregarius*, 13 *Nannolepis elegans*, 14 *Saurichthys calcaratus*, 15 *Acrodus*, 16 *Thoracopterus niederristi*, 17 potential *Sauropterygia*, 18 *Tellerodus sturii*, 19 *Euestheria*. Modified after Lukeneder et al., 2023.

Figure 21, on the other hand, shows what the trophic network ("who fed on whom"; diet) might have been like. The arrow coming from *Euestheria*, for example, and pointing towards *Phragmoteuthis* means that *Phragmoteuthis* consumed *Euestheria*. *Euestheria* specimens were most likely been devoured by *Phragmoteuthis*, an extinct coleoid cephalopod, with strong beaks enough to crack open the carapace of *Euestheria*, by ammonoids and larger crustaceans. This might also support the theory that *Euestheria* were mainly freshwater organisms and have been moved to the marine Polzberg deposits.

Other predators found in the Polzberg locality, such as fish, ammonoids, squids but also coelacanths and lungfish, were also most likely feeding on *Euestheria* (Lukeneder & Lukeneder, 2021).

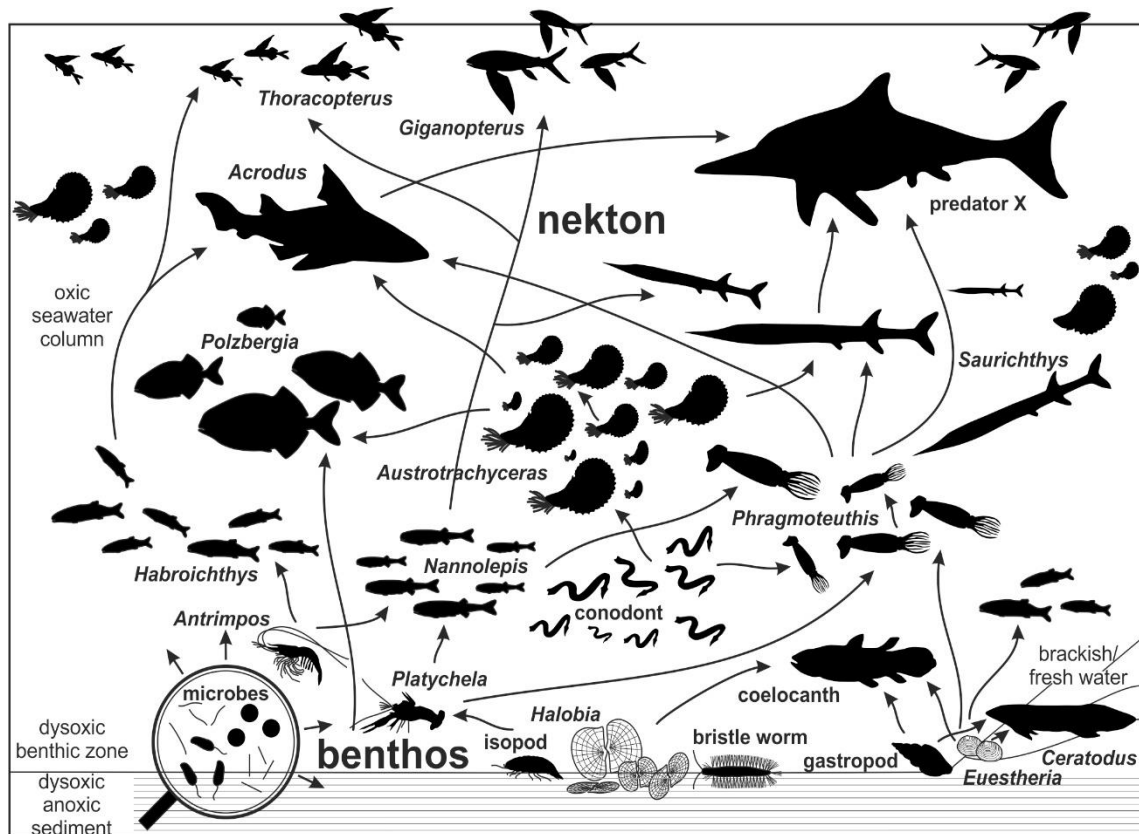


Figure 21. Trophic network of the organisms found in Polzberg. The organisms with arrow pointed at means that they fed on the organisms where the arrow is coming from. For example, Predator X fed on *Phragmoteuthis*; *coelocanth* fed on *Halobia*; *Ceratodus* fed on *Euestheria* etc. Modified after Lukeneder et al., 2023.

Extant and fossil *Euestheria* have been found all over the world. Scholze et al. (2019) published a study from the Permian-Triassic transition in Southwest China and noted that their *Euestheria* sp. were gathered from yellow- to green-grey clay and siltstones, which they interpreted as coastal plain deposits, with freshwater.

Another study from Southwest China determined *Euestheria gutta* as markers of the Permian-Triassic transitional beds, which were in a marine siliciclastic setting (Chu et al., 2016). They found *Euestheria* in brownish-yellow siltstone and mudstone, which they think hint to marine environment.

From the Central United Kingdom, another study reports Middle Triassic (Ladianian) deposits of the Cotham Member in which *Euestheria minuta* are found. Morton et al. (2017) investigated Cromhall Quarry and described the deposits as grey-green calcareous mudstones, shales, and laminated siltstones. The authors assume that the conchostracans lived in brackish to freshwater intervals and that adult *Euestheria* died in shallow ponds, leaving their eggs in the dried sediment to hatch once new rains arrived. This provides additional confirmation that *E. minuta* is also found in our samples. Further confirmation that our samples are in fact *Euestheria*

minuta, provides Kozur et al. (2010), where they mention that *Euestheria minuta* is distinguishable by its consistent range of 10-20 growth lines, setting it apart from the slightly younger *Euestheria winterpockensis* of the early Carnian period (Northern hemisphere), which exhibits a wider range of 19-46 growth lines. *Euestheria winterpockensis* developed from *Euestheria minuta* through a significant increase in the number of growth lines (Kozur & Weems, 2007). This evolutionary process is evidenced by transitional forms, which show a minor stratigraphic overlap in the occurrences of these two species (Kozur et al., 2010). Morton et al. (2017) mentions samples from the German Keuper deposits, which is dated to the Carnian, where *E. minuta* was also detected. Kozur et al. (2010) reports that conchostracans are commonly found in sediments that formed in terrestrial and brackish environments. The study analyzed continental Triassic in the northern hemisphere with the help of samples from all around the world (Morocco, England, Central and Southern Germany, Italy, Hungary, Southeastern Poland, Northwestern China, Eastern and Southwestern USA, Southeastern Canada, Argentina). They also noted that the best sediments for studying *Euestheria* are claystones, shales or limestones, because of the remarkable preservation of the carapace in these sediments.

A study from Madagascar reported conchostracan found in sandy marls, with concretions rich in iron oxide (Yanbin et al., 2002). They also confirm the main habitat of *Euestheria* being freshwater to brackish. *Limnesteria* from Ireland was found in very dark carboniferous shales (Yanbin et al., 2002). The authors mention that *Euestheria mangaliensis* found in Hungary is common in brackish intercalations of marine Werfen Beds.

Tassi et al. (2015) studied a section in Argentina comprising *Euestheria* specimens consisting of fine-grained sandstones and interbedded mudstones, which the authors interpret as playa lake or ephemeral rivers or streams. The lacustrine environment has been characterized by interbedded siltstones. The authors confirm a drastic increase in volcanic activity during the Middle Triassic time period, as they found a high amount of pyroclastic deposits. Zharinova et al. (2020) published a study about conchostracans, like *Sphaeresteria*, *Lioesteria*, *Wetlugites*, *Pseudesteria*, *Euestheria* in the Republic of Sakha (Yakutia). They studied samples from Early Triassic (Induan) deposits, which are composed of siltstone with sparse interlayering of fine- to medium-grained sandstones.

Conchostraca from the Middle Keuper, Carnian (Upper Triassic) have also been studied. Geyer et al. (2017) did their study in the southern Germanic Basin, where one of the formations, the

Coburg Sandstone Member, has been found to include *Euestheria kozuri*. The lithology of the Coburg Sandstone is predominantly sandstone, which is interstratified with minor grey very fine-grained sandstone, mudstone and siltstone, and interpreted as a brackish environment.

Olempska (2004) investigate Late Triassic conchostracans in southwestern Poland. The author describes the assemblage of *Euestheria* as being from lacustrine late Carnian claystones. They mention that occasionally, these animals occur in more saline environments such as playa lakes and coastal salt flats, but they die if the salinity of the water goes above 5‰. As for the development of the growth lines of *Euestheria*, Olempska (2004) notes that low temperature and food scarcity stunt the number of growth lines, leading to less than normal amount.

Euestheria has been found in the claystones of the Krížna Unit in Slovakia. Sykora et al. (2011) studied the Tržinovo Formation in the Fatric Basin and found the little conchostracans there. What is more interesting, the occurrence of freshwater to brackish *Euestheria* in the Tržinovo Formation reflects the carbonate productivity crisis during the Carnian, in the northern Tethyan realm, which in turn corresponds to the Reingraben Event during the Early Carnian.

A study from Central England is known to have investigated the late Triassic (Carnian) Arden Sandstone Formation. Burley et al. (2023) reports finding lacustrine lithofacies, such as finely interlaminated fine-grained sandstones and silty mudstones in which *Euestheria* have been found.

Chen et al. (2006) published a study about the geological ages of rock formations in China and on findings of *Euestheria minuta* among other fossils, in the Xujiahe Formation, which is dated to the Upper Triassic (Carnian) This formation consisted of thick-bedded sandstone and black shale. Furthermore, they say the Xujiahe Formation is not marine and appears with dark colored mud- and siltstone, which is again, evidence for freshwater to brackish water habitat for *Euestheria*.

Jenisch et al. (2017) investigated the stratigraphic distribution of spinacaudatans during the Triassic and Jurassic in Paraná Basin, which is located in central-eastern South America. There they investigated the lithofacies and found among other fossils, *Euestheria minuta* in laminated mudstone beds, which were deposited in floodplains. The study reports finding conchostracans from the Lower to Upper Triassic period. Jenisch et al. (2017) notes the importance of conchostracans as biostratigraphic markers, due to their geographical distribution and high reproduction rates.

Scholze et al. (2016) mentions that conchostracans have adapted to small inland water bodies where a freshwater environment was present, during the Early Triassic in Central Germany, representing good indicators for such environments. But the study also suggests that conchostracans could also have lived in brackish water, as the species *Magniestheria mangaliensis*, which had adapted to increased salinity. The researchers interpret the depositional environment as a low energy, shallow inland body of water.

6. Conclusions

In this study we report findings of *Euestheria* a conchostracan taxon from the Polzberg Konservat-Lagerstätte. We would like to increase the understanding and knowledge of this crucial faunal element. The Upper Triassic Polzberg locality, which is dated to the lower Carnian, situated in the Lunz Nappe as part of the Northern Calcareous Alps, has been known for a long time by private collectors, scientists, and researchers. The excellent preservation of fossils here is most likely due to special environmental conditions formed during the Carnian Pluvial Episode (CPE). This episode increased the temperature and humidity globally and caused dysoxic to anoxic bottom water conditions, hence the formation of black and laminated deposits, like the argillaceous Reingraben Shales, on the seafloor in the Reifling Basin (Polzberg Subbasin). The normal marine and well oxygenated environment of the Reifling Basin in the Carnian depicts the favourable habitat for numerous planktic and nektic taxa (e.g. ammonoids, coleoids, actinopterygian fish), however *Euestheria* is meant to be a freshwater to brackish water taxon, which specimens were probably redeposited or transported sporadically from surrounding land masses with their fresh water sources. One assumption is that the increased humidity with heavy rainfall during the CPE intensified the influx of freshwater into the otherwise isolated marine Reifling Basin, thus washed the conchostracan shells in the final depositional environment of the Polzberg Subbasin. Another hypothesis for their occurrence in the Polzberg Konservat-Lagerstätte focuses on the eggs and the resilience against dehydration and freezing, which eggs of *Euestheria* appear to have. This could mean that adults laid eggs in the sediment which subsequently was transported by water currents or wind over hundreds to thousands of kilometers away from their original habitat. An additional possible explanation could be an adaptation to higher salinities, allowing them to populate and inhabit new environments in marine ecosystems. All of these assumptions could be taken into account, hence further research on the conchostracan community at the Polzberg locality and the documented *euestheriids* is highly needed. Studying different fossil groups from the Polzberg

Konservat-Lagerstätte also provides new information about the Late Triassic Carnian time-period, the prevailing environmental conditions, and species interactions. The Polzberg site with the numerous fossil members and their unique preservation, with the potential for exciting future findings is yet one of the worlds most famous Konservat-Lagerstätten.

7. References

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8. Appendix

8.1 Images of all specimens



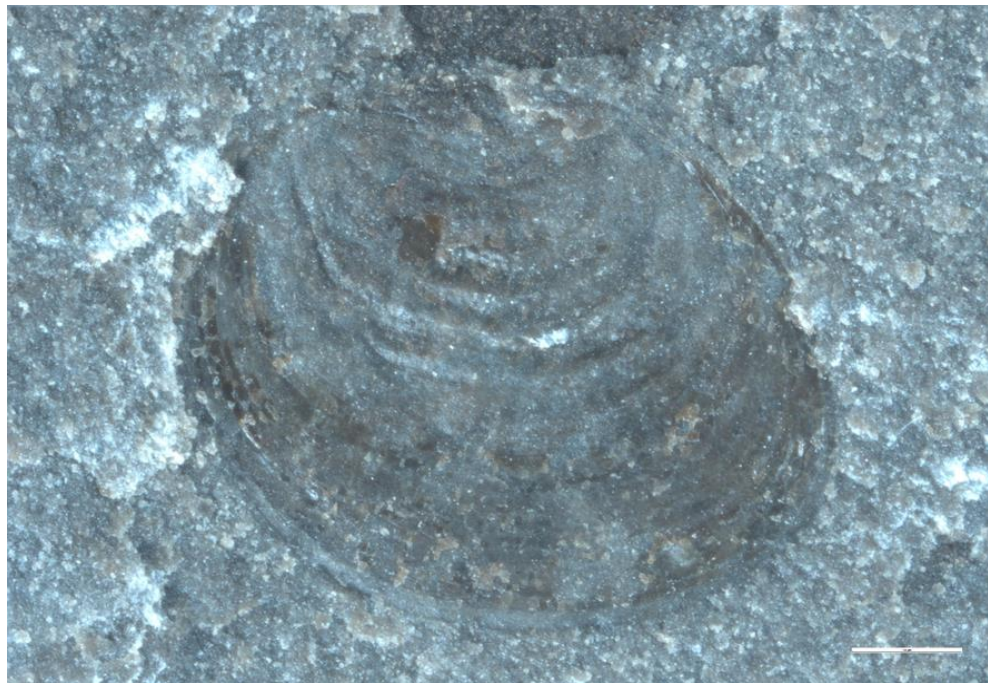
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NHMW 2021/0123/0436; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0437; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0438; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0439; layer 1 (Po -50 - 0 cm)



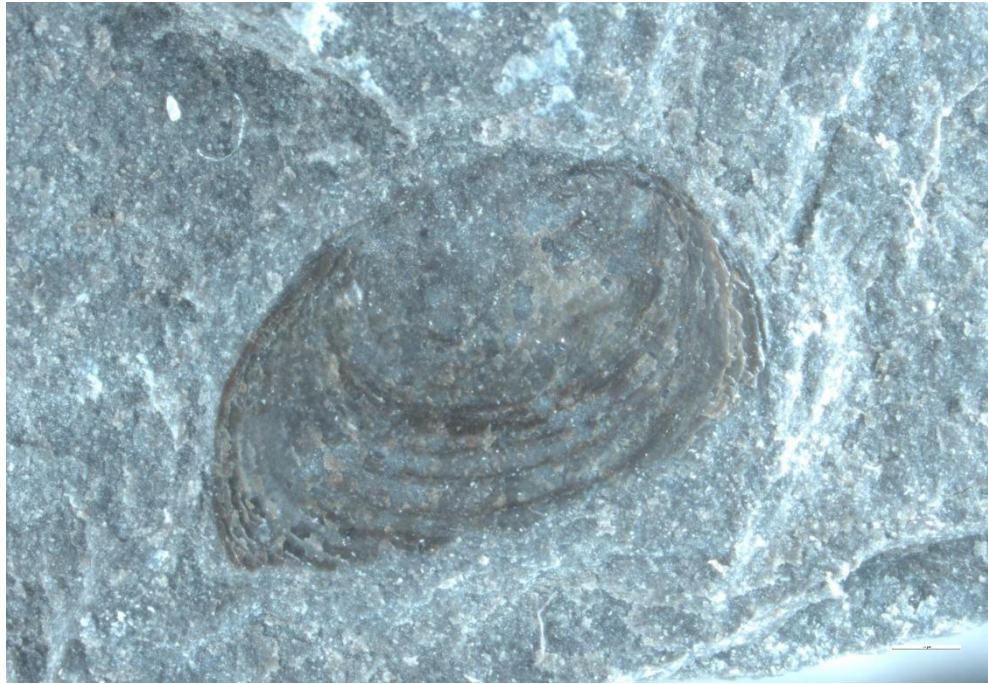
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NHMW 2021/0123/0442; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0443; layer 1 (Po -50 - 0 cm)



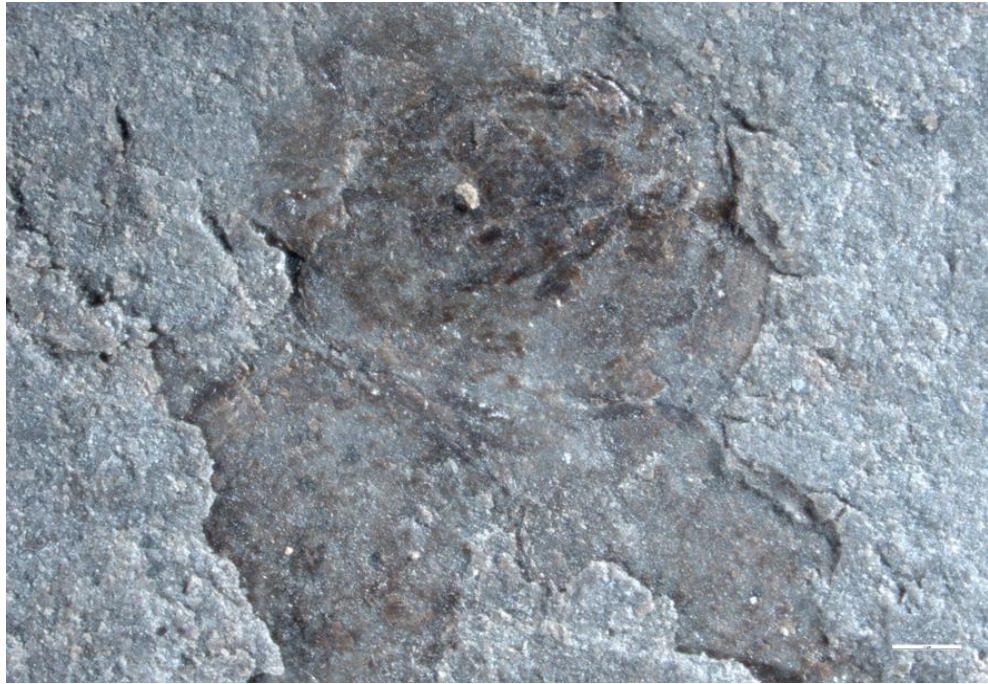
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NHMW 2021/0123/0446; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0447; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0448; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0450; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0039; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0040; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0041; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0042; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0451; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0452; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0453; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0454; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0455; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0456; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0457; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0458; layer 1 (Po -50 - 0 cm)



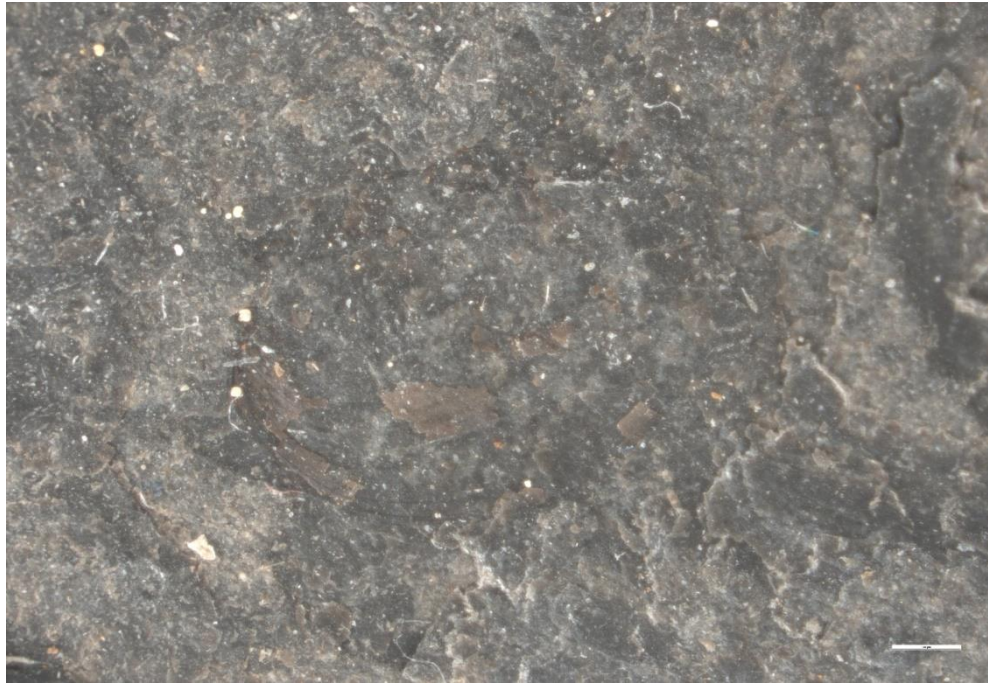
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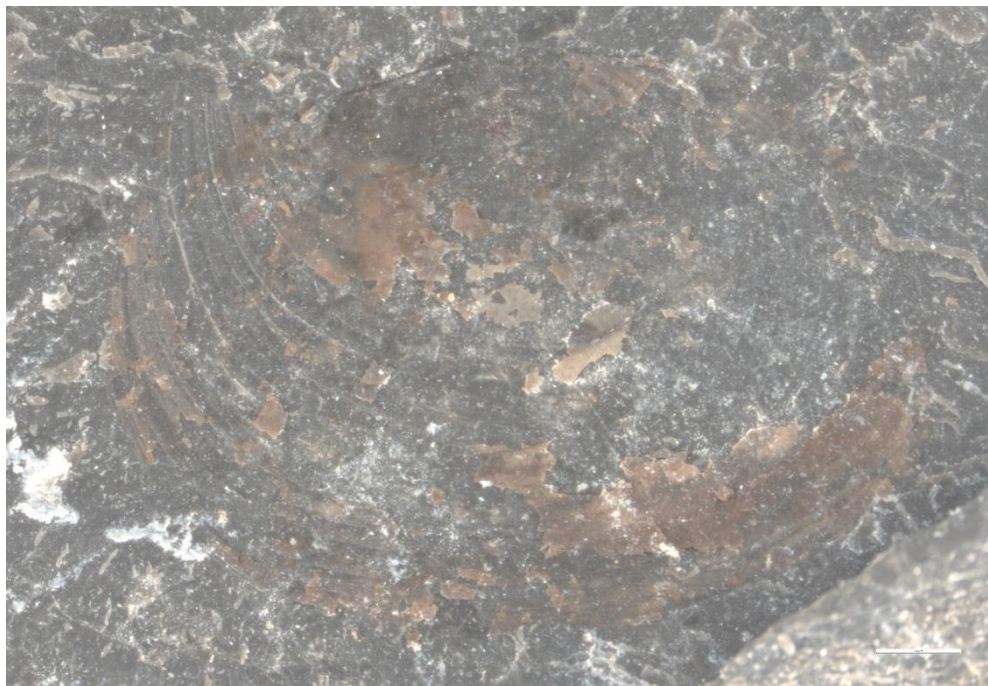
NHMW 2021/0123/0460; layer 2 (Po 80 - 100 cm)



NHMW 2021/0123/0461; layer 3 (Po 280 - 300 cm)



NHMW 2021/0123/0462; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0463; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0464; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0465; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0466; layer 4 (Po 300 - 320 cm)



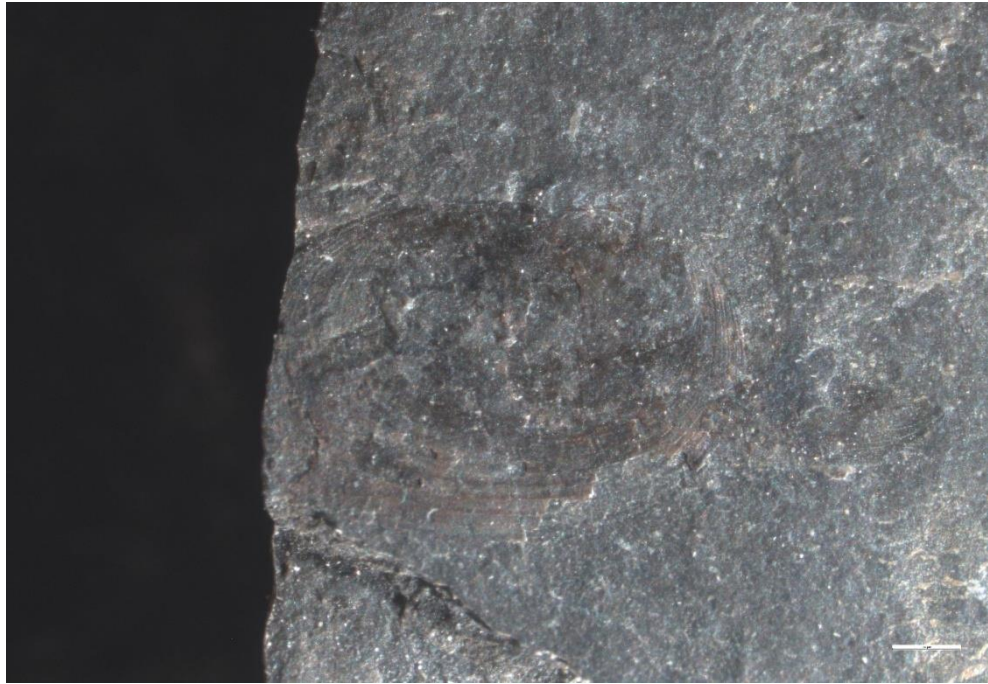
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NHMW 2021/0123/0471; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0472; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0473; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0474; layer 4 (Po 300 - 320 cm)



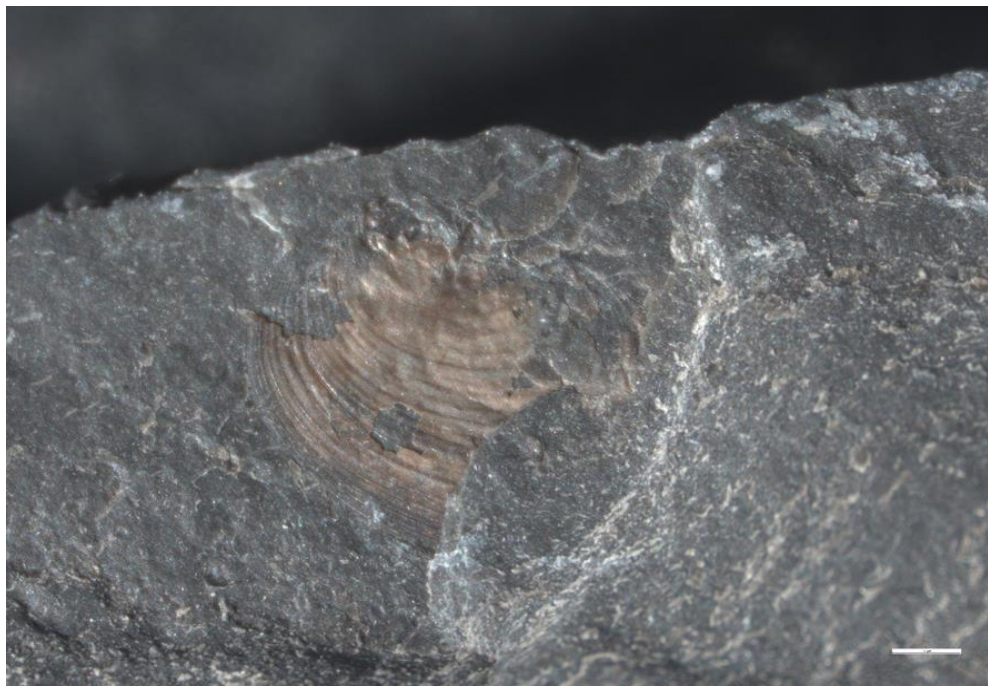
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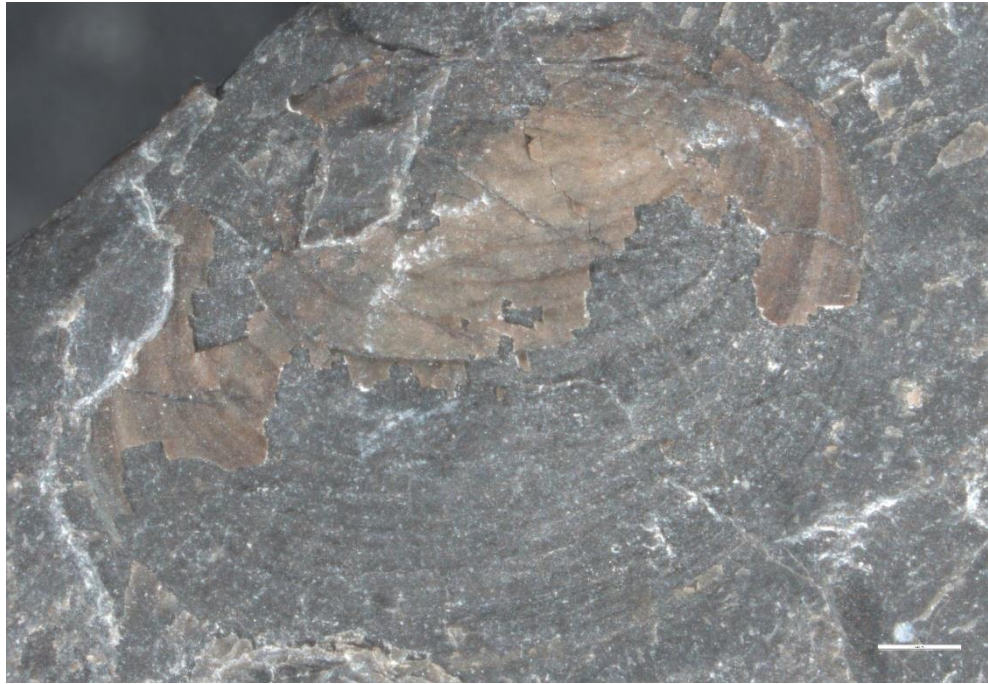
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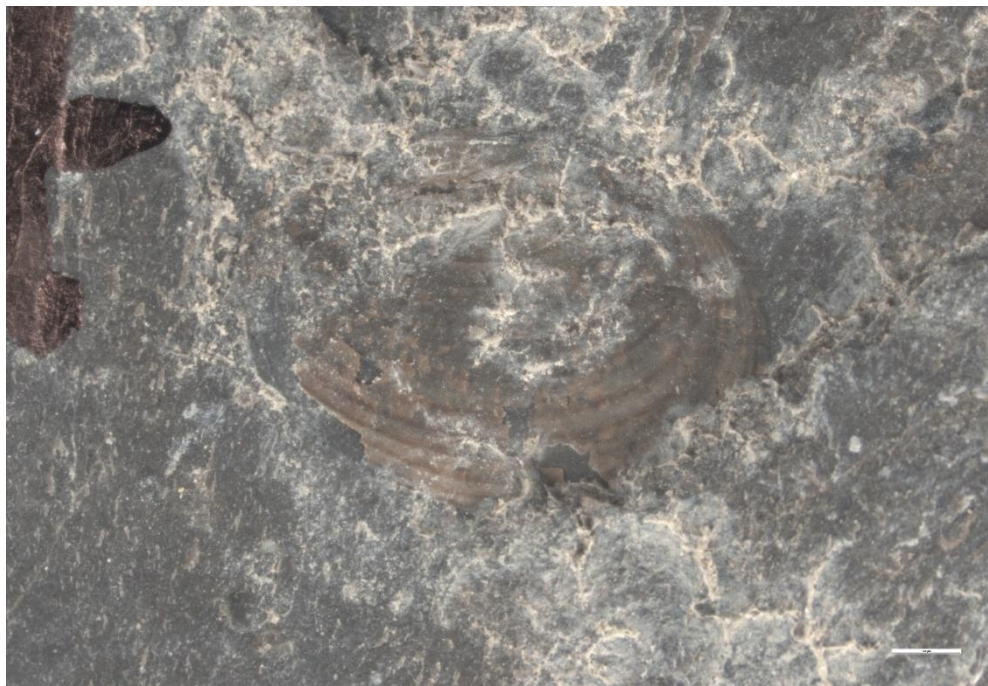
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NHMW 2021/0123/0483; layer 4 (Po 300 - 320 cm)



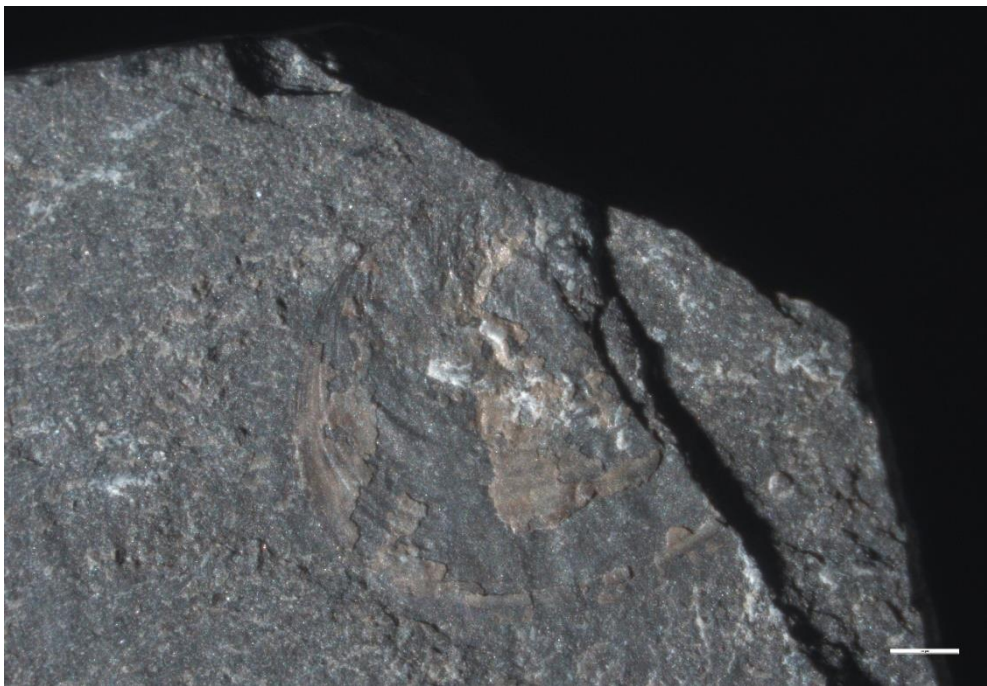
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NHMW 2021/0123/0487; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0488; layer 4 (Po 300 - 320 cm)



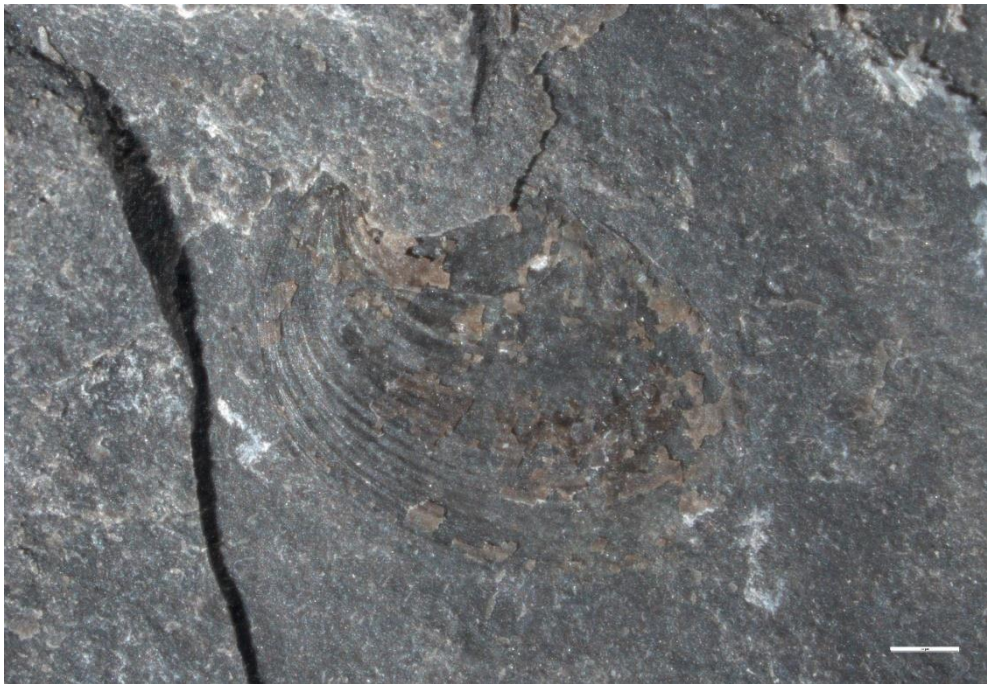
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NHMW 2021/0123/0490; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0491; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0492; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0493; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0494; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0495; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0496; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0497; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0498; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0499; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0501; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0502; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0503; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0504; layer 4 (Po 300 - 320 cm)



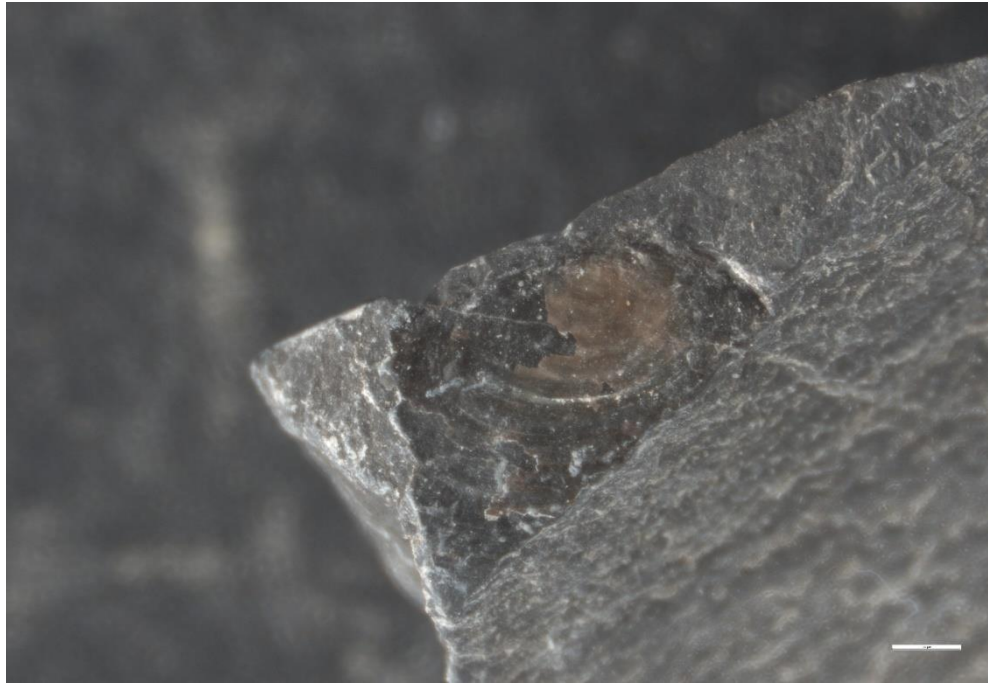
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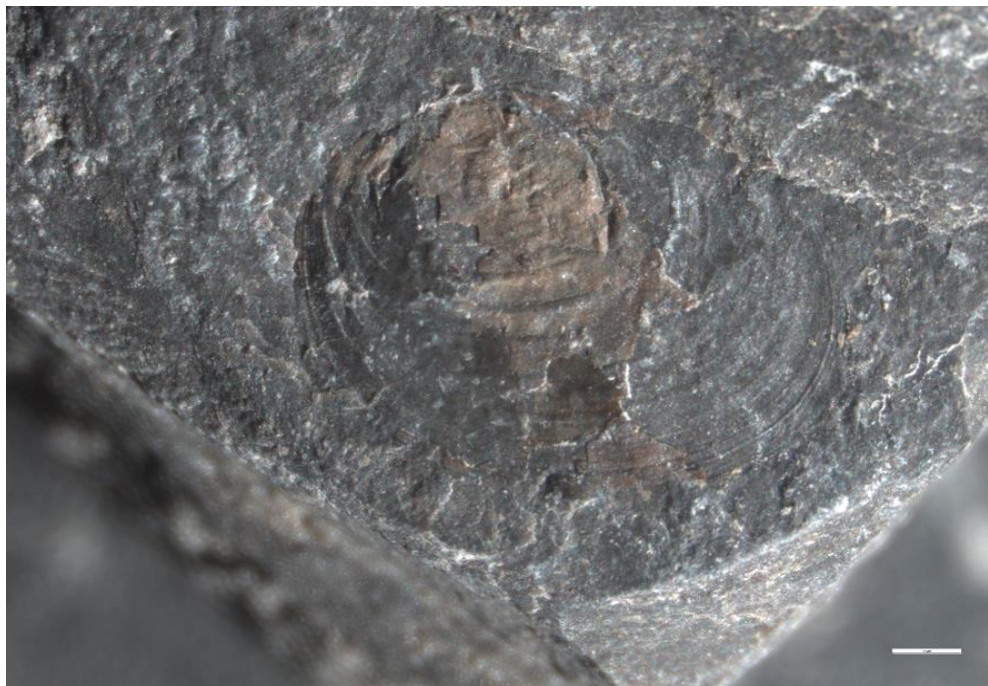
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NHMW 2021/0123/0508; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0509; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0510; layer 4 (Po 300 - 320 cm)



NHMW 2021/0123/0511; layer 4 (Po 300 - 320 cm)

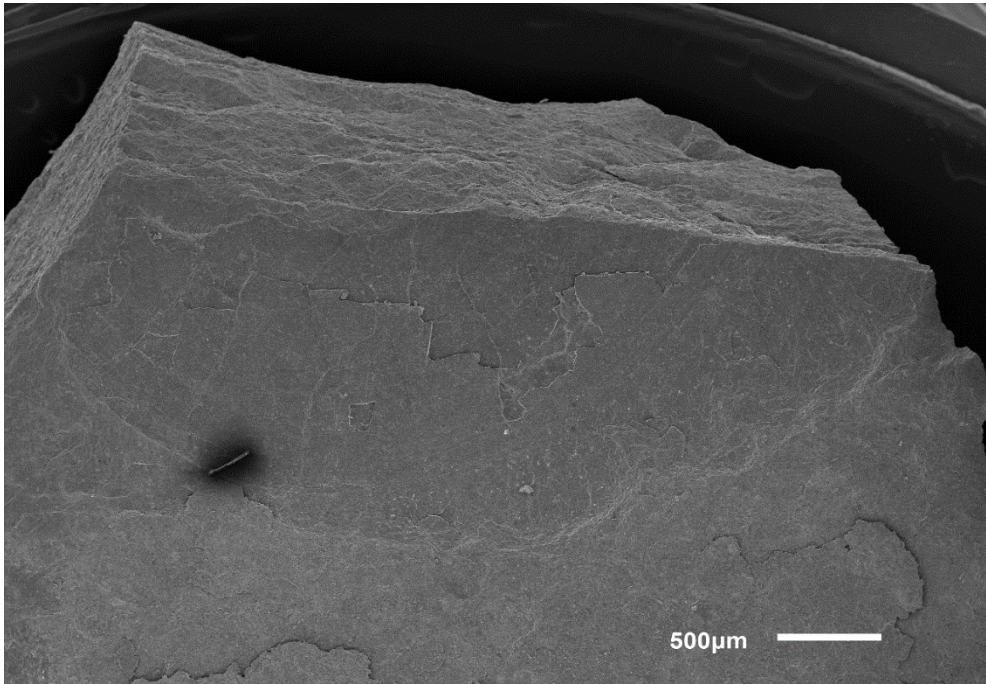


NHMW 2021/0123/0512; layer 5 (Po 320 - 340 cm)

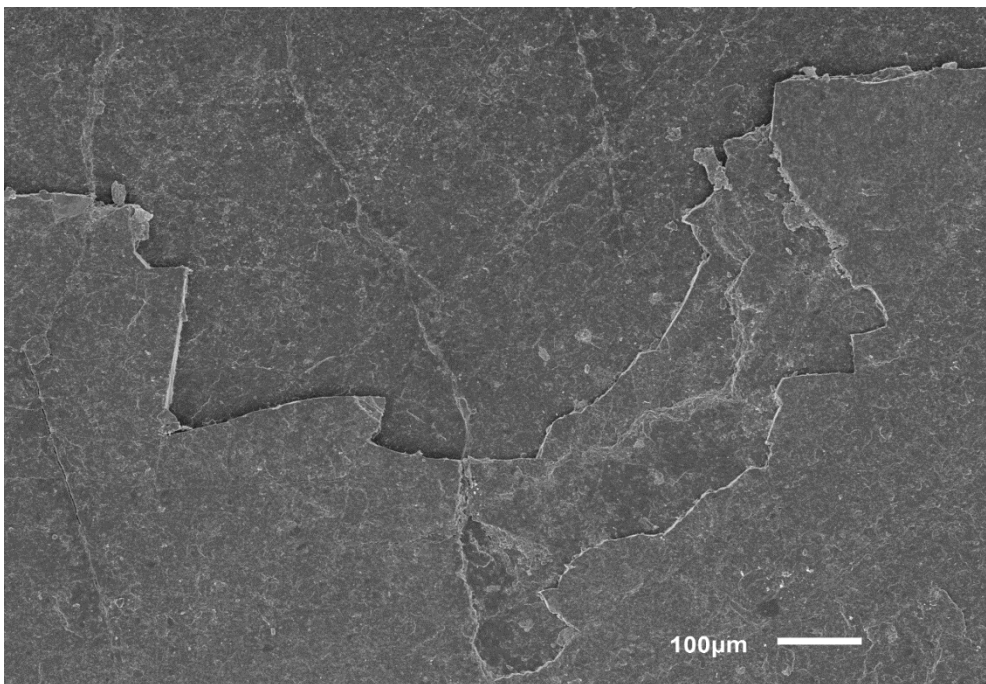


NHMW 2021/0123/0513; layer 5 (Po 320 - 340 cm)

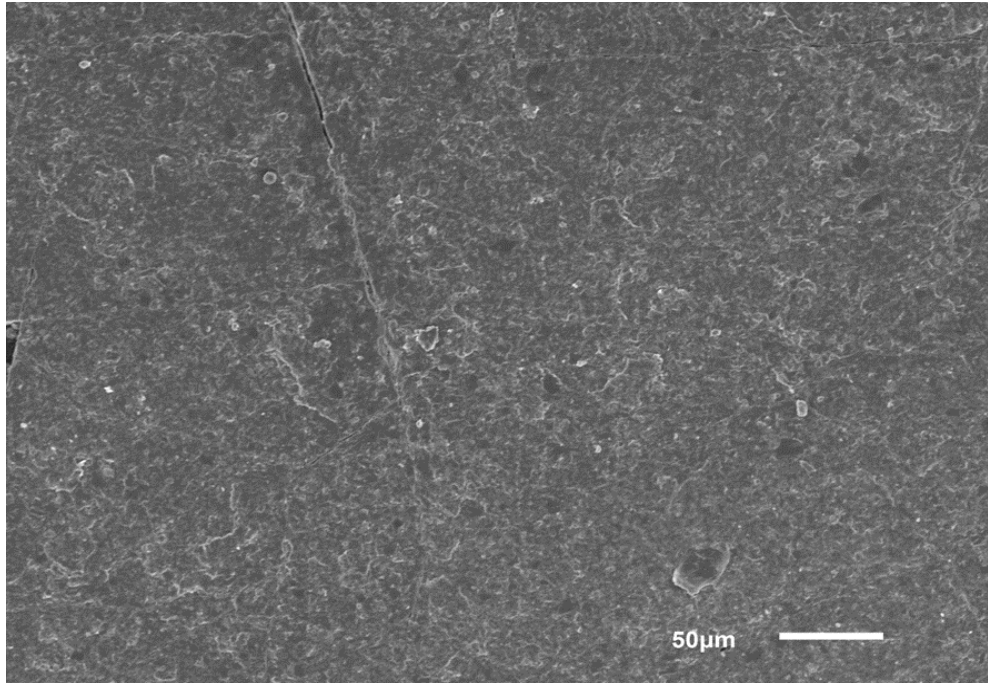
8.2 SEM data



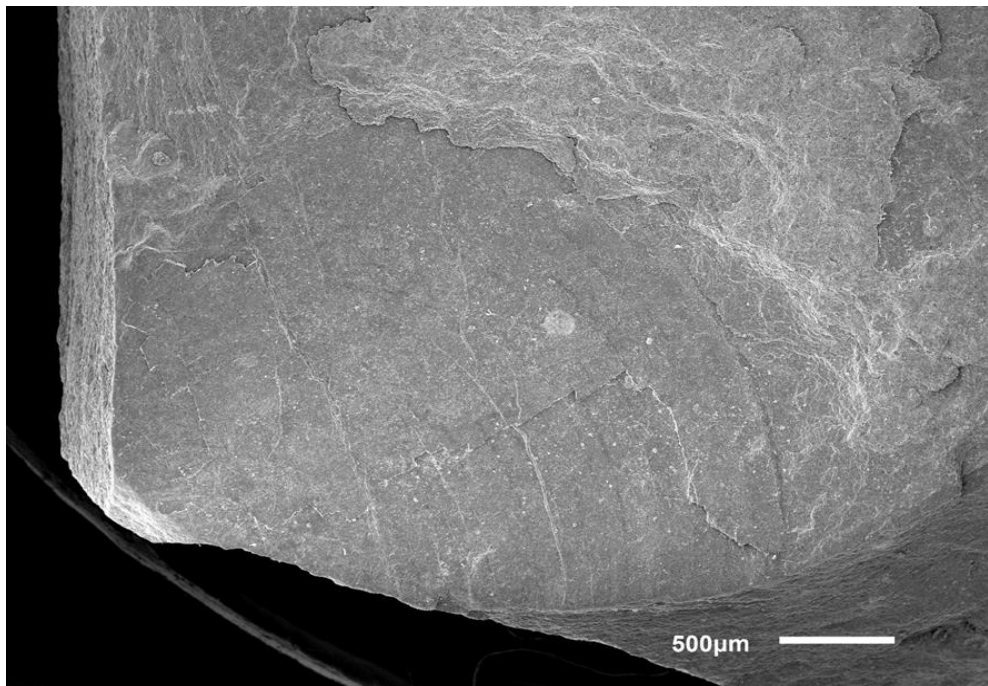
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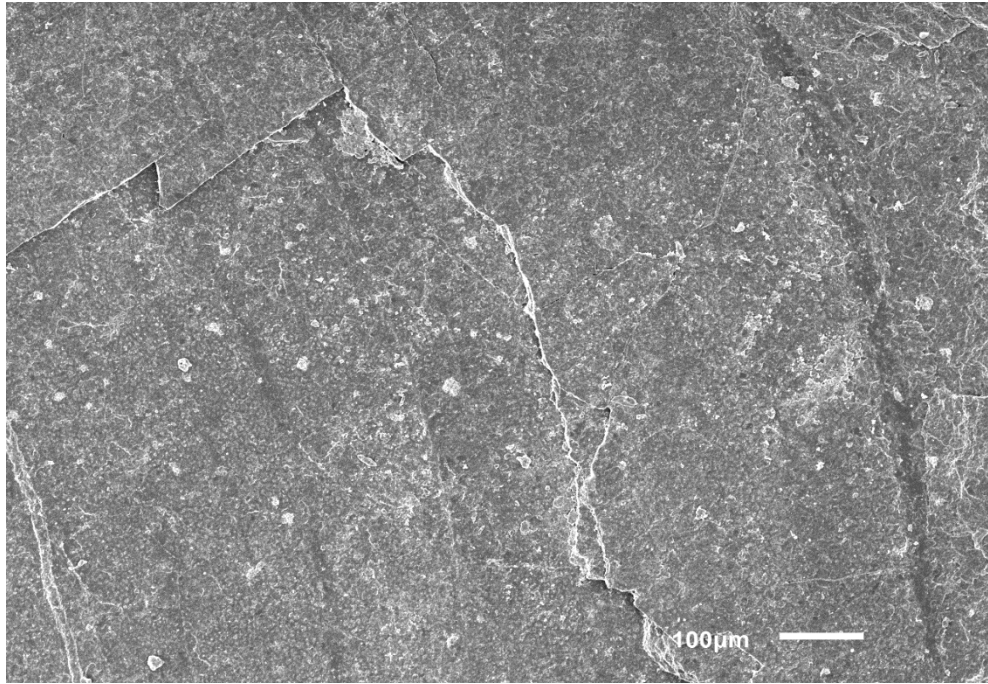
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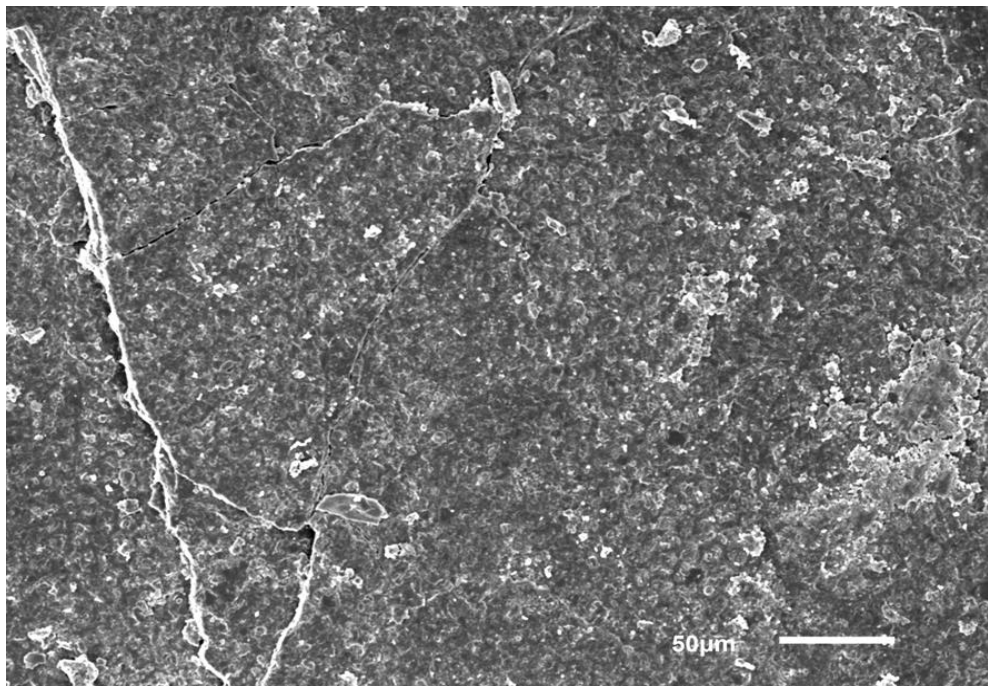
NHMW 2021/0123/0464; layer 4 (Po 300 - 320 cm)



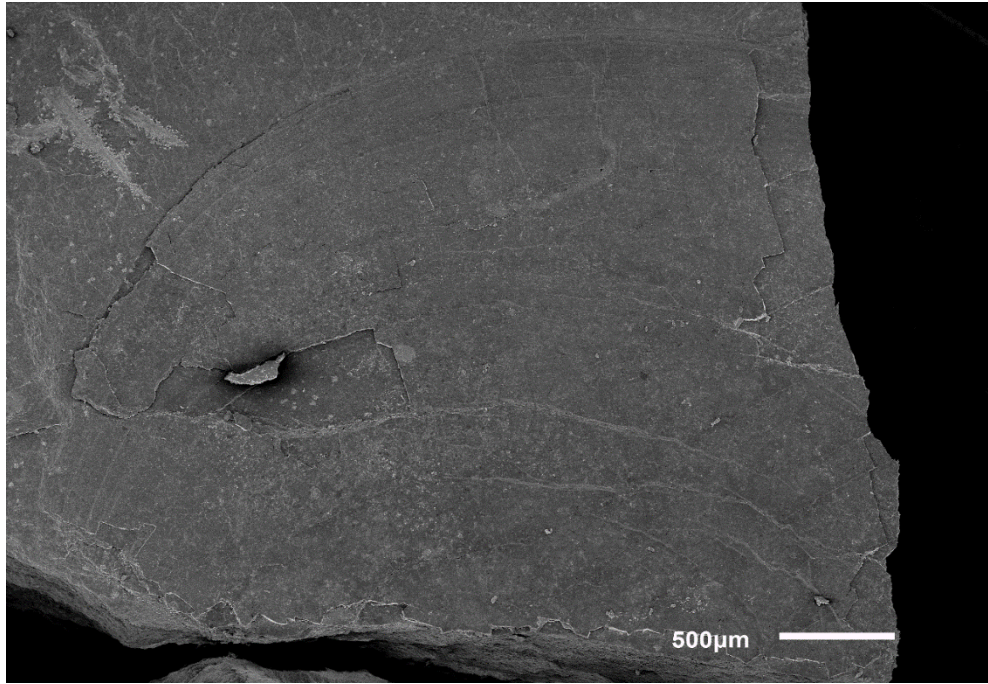
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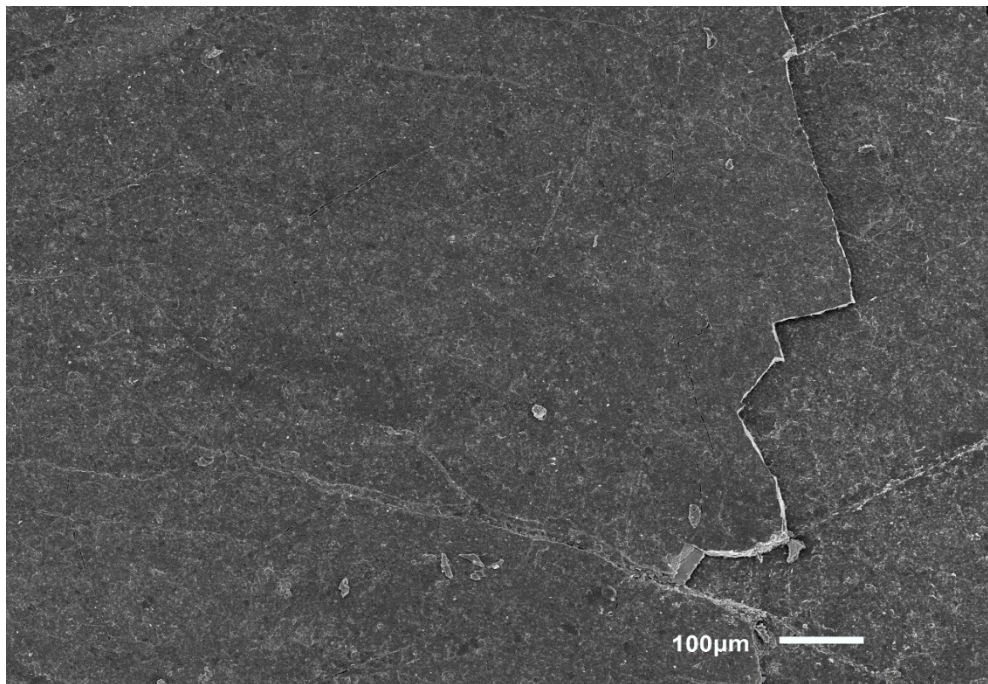
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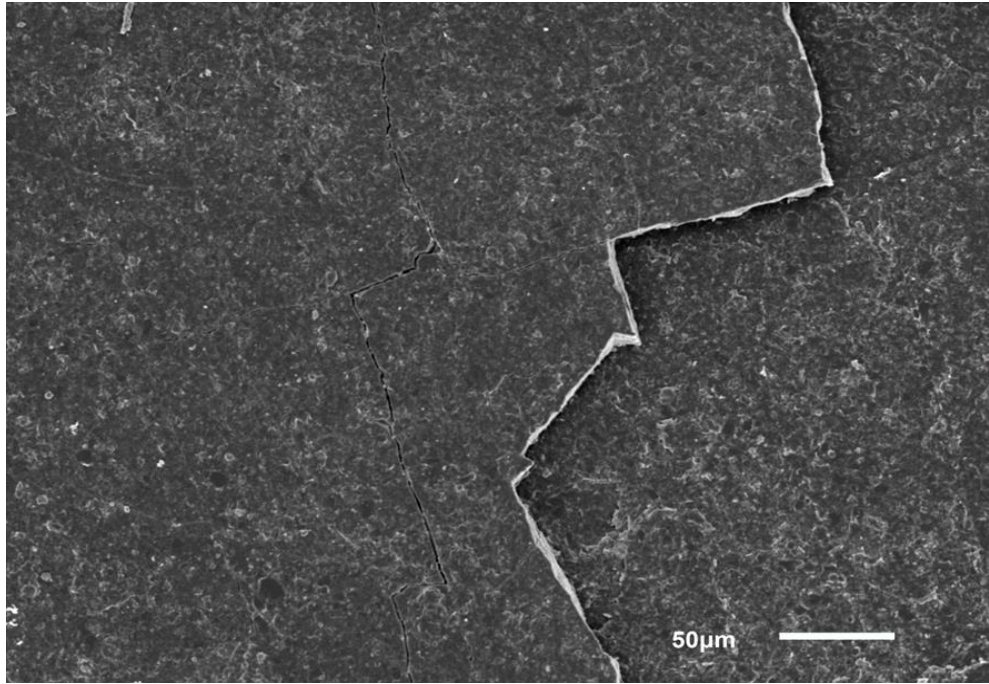
NHMW 2021/0123/0465; layer 4 (Po 300 - 320 cm)



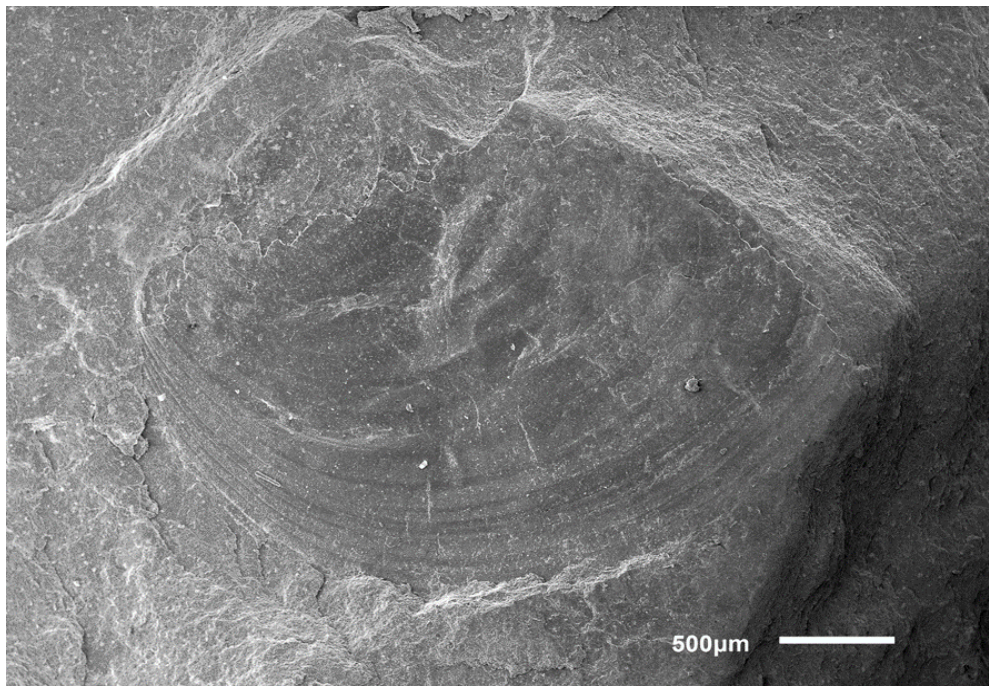
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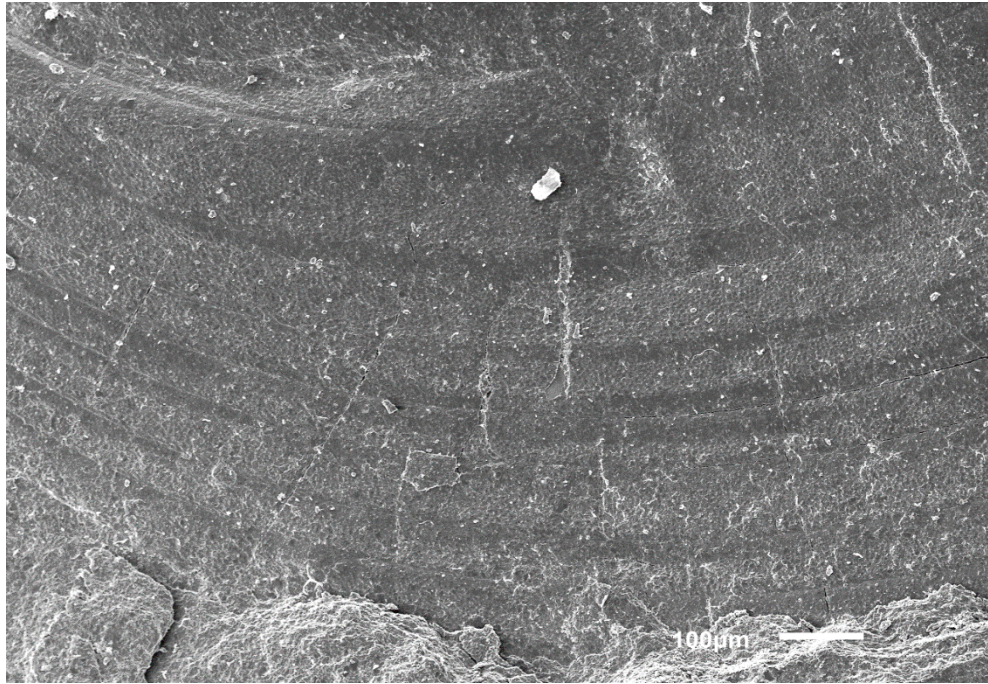
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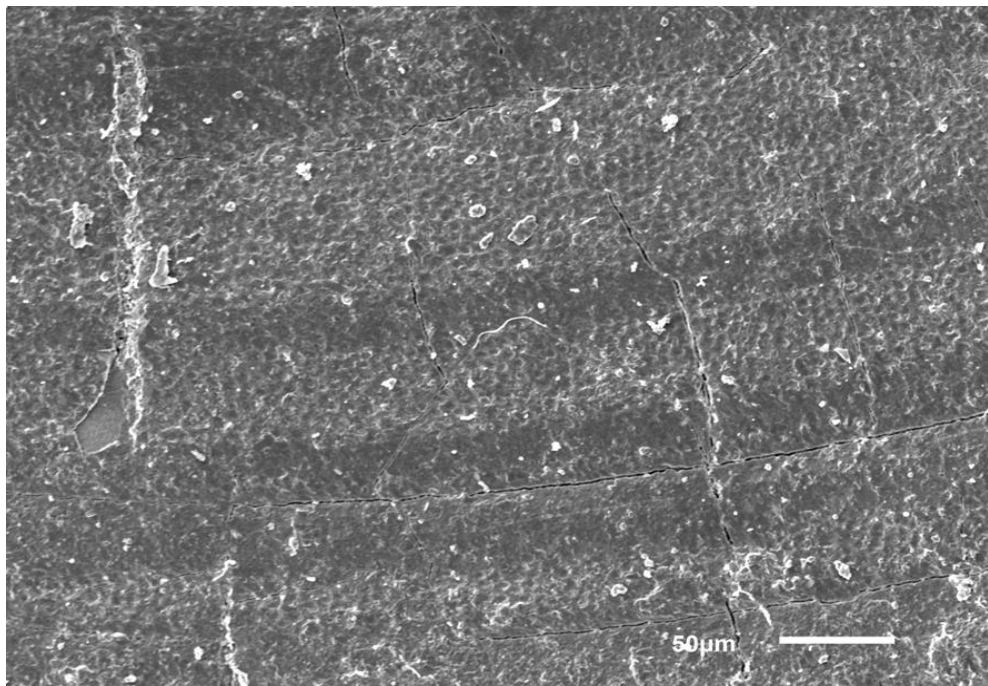
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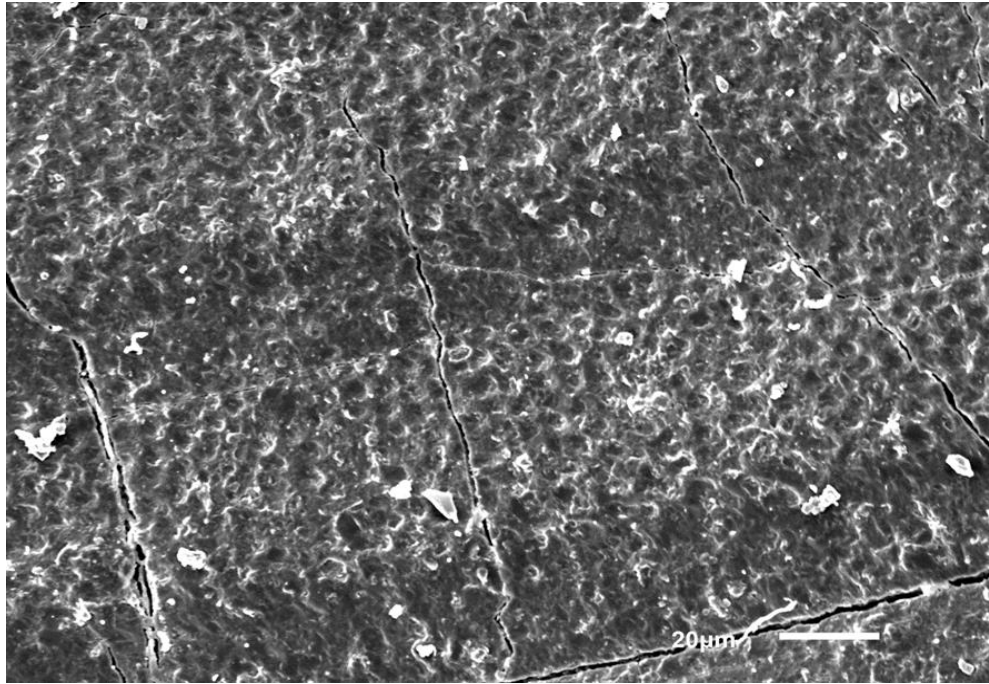
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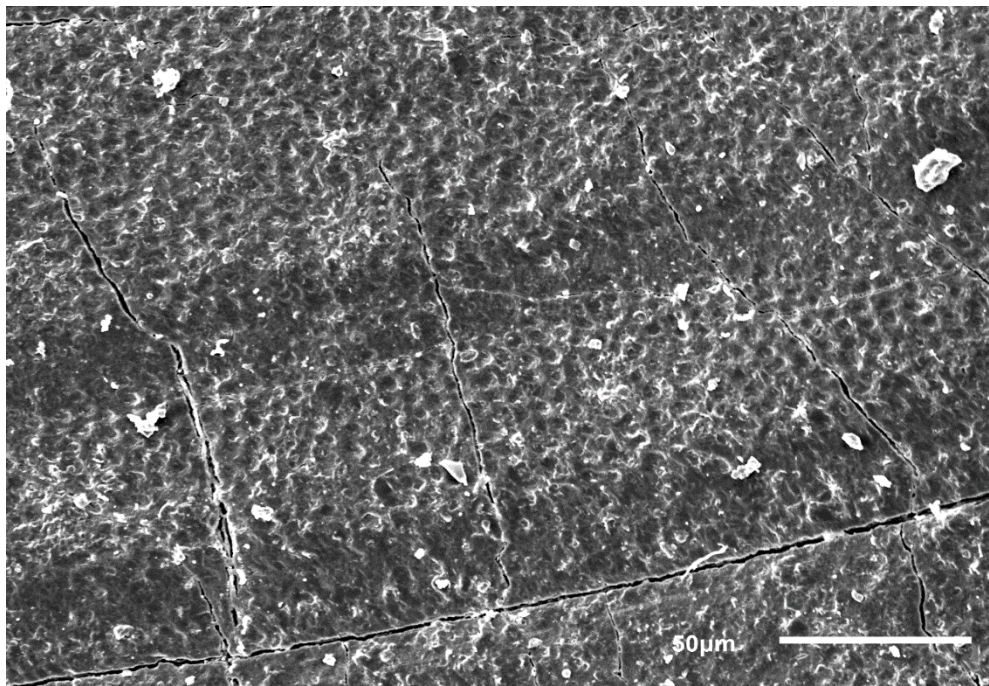
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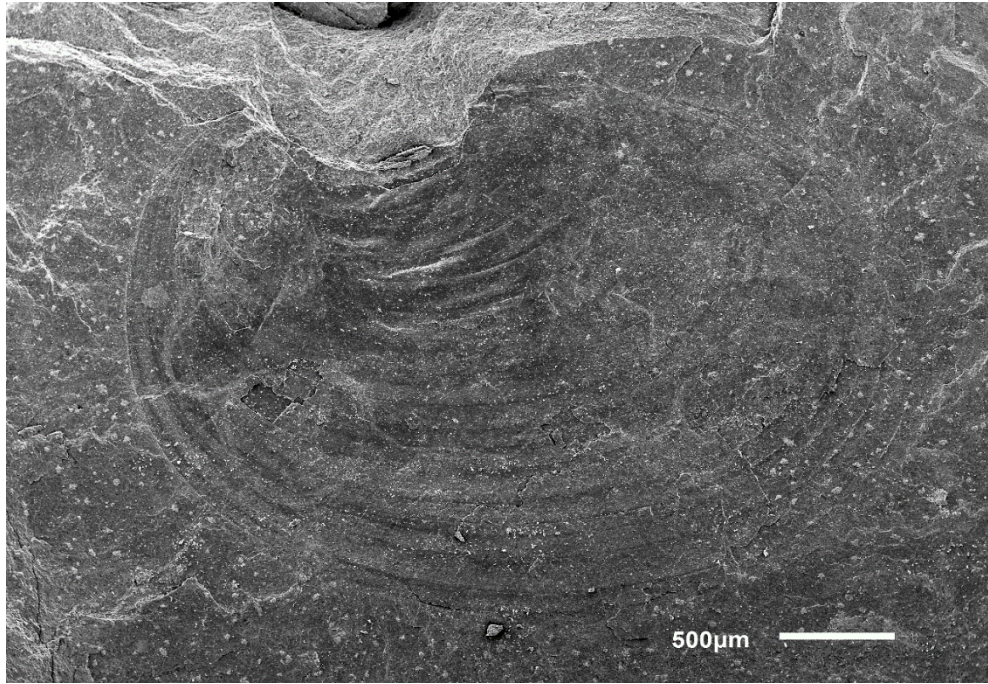
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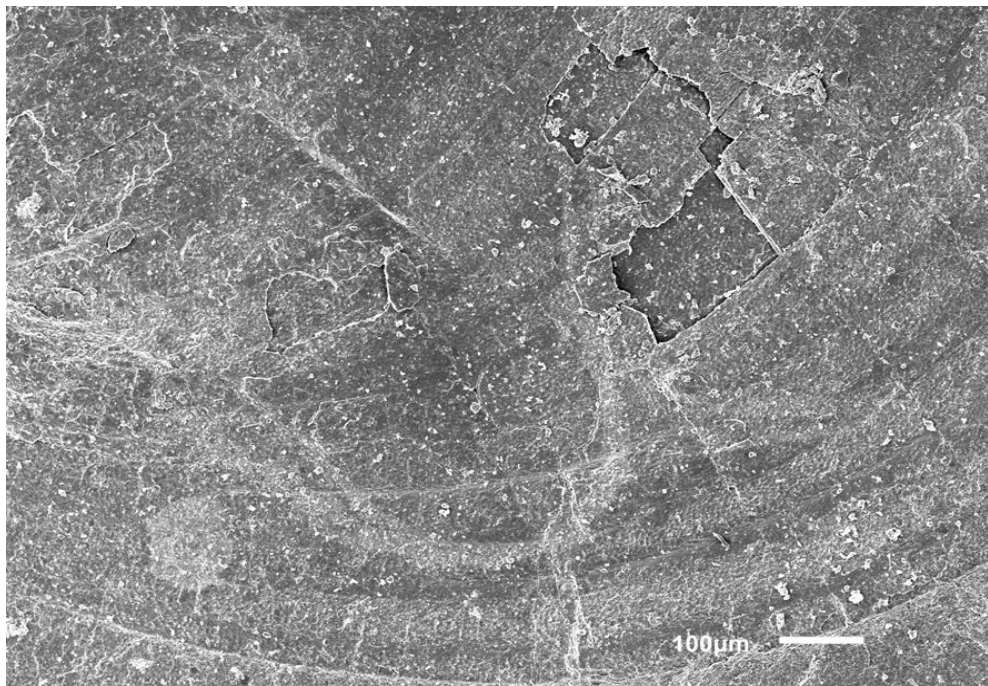
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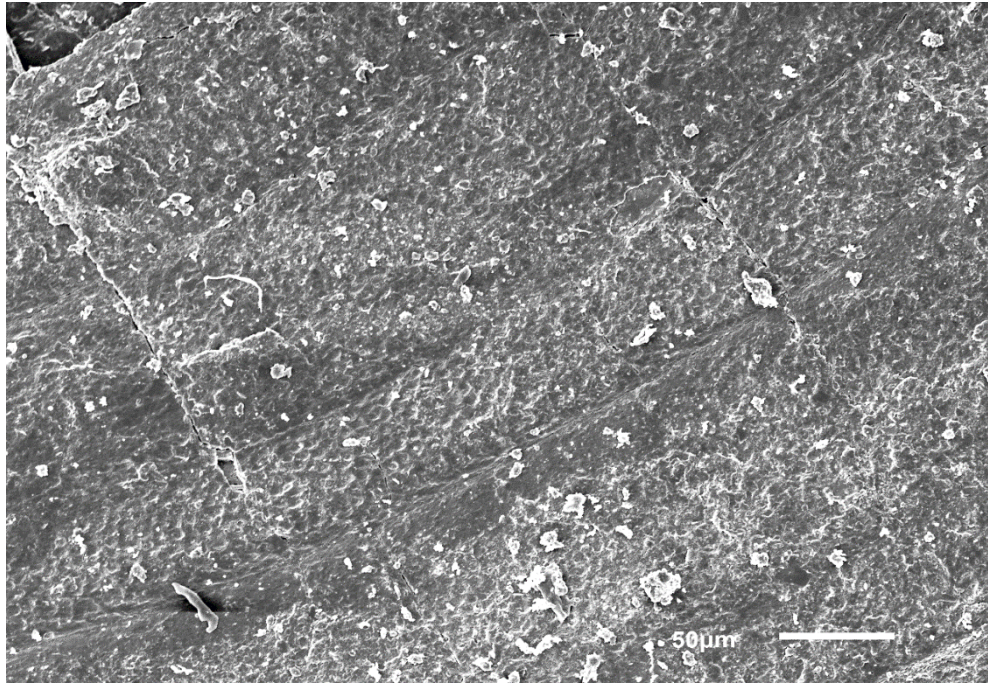
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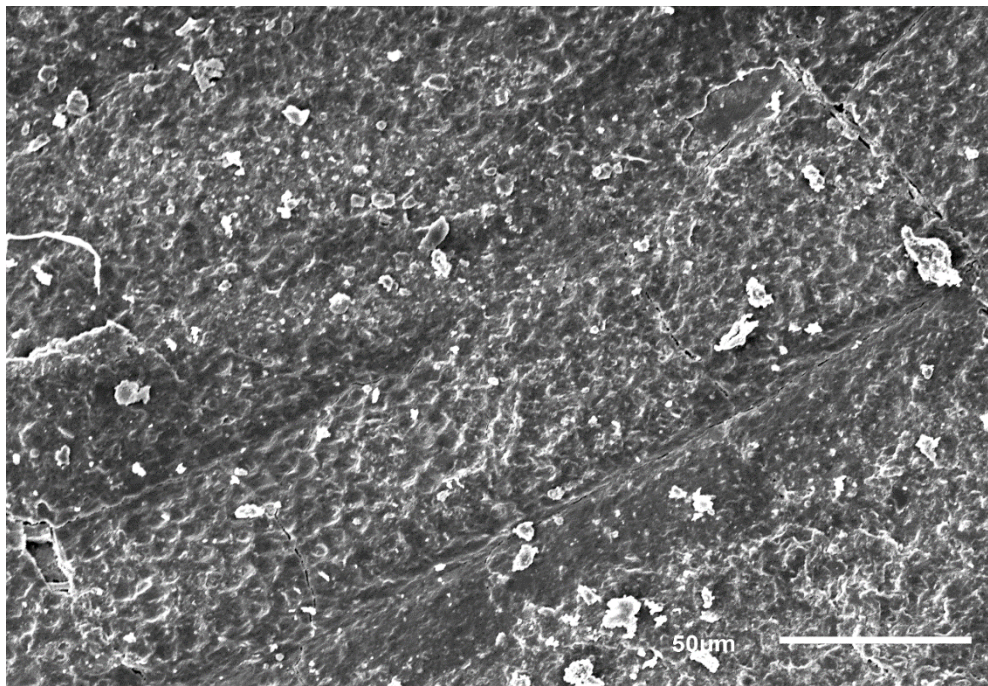
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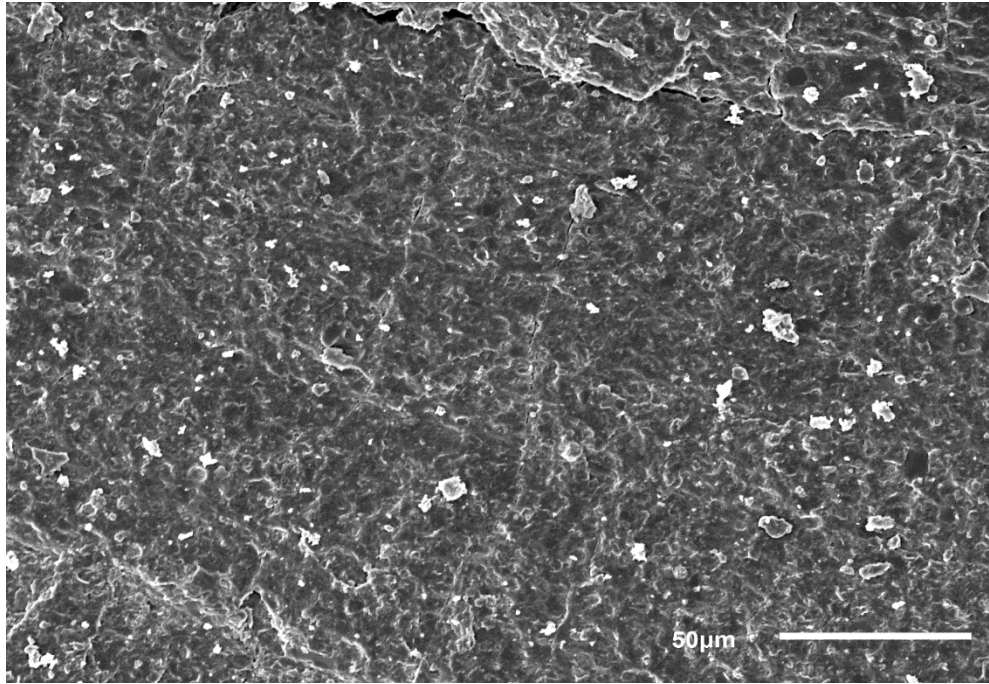
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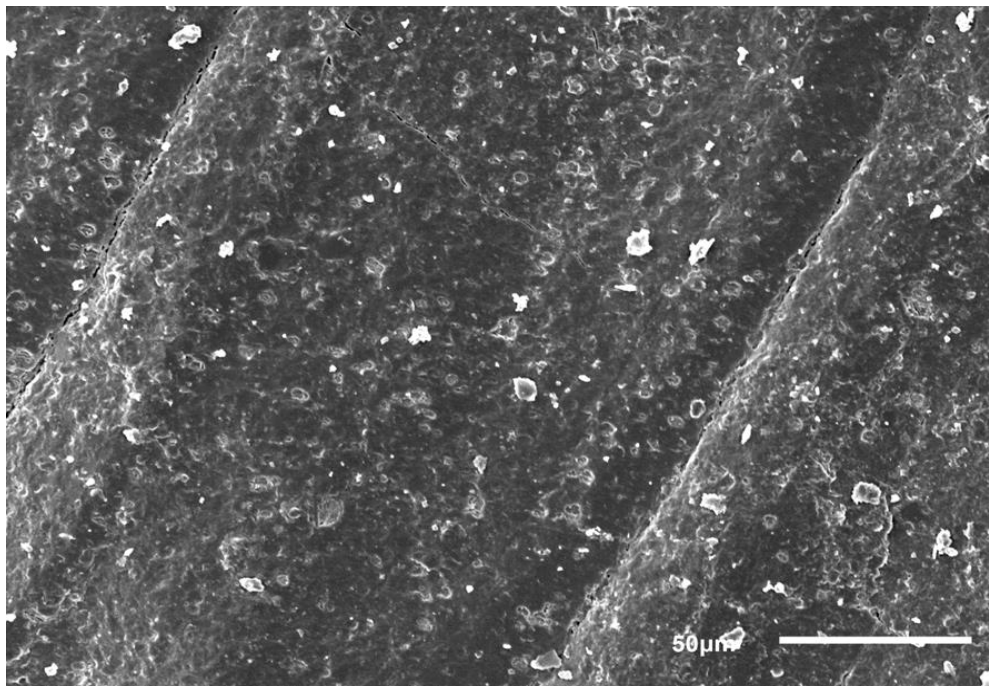
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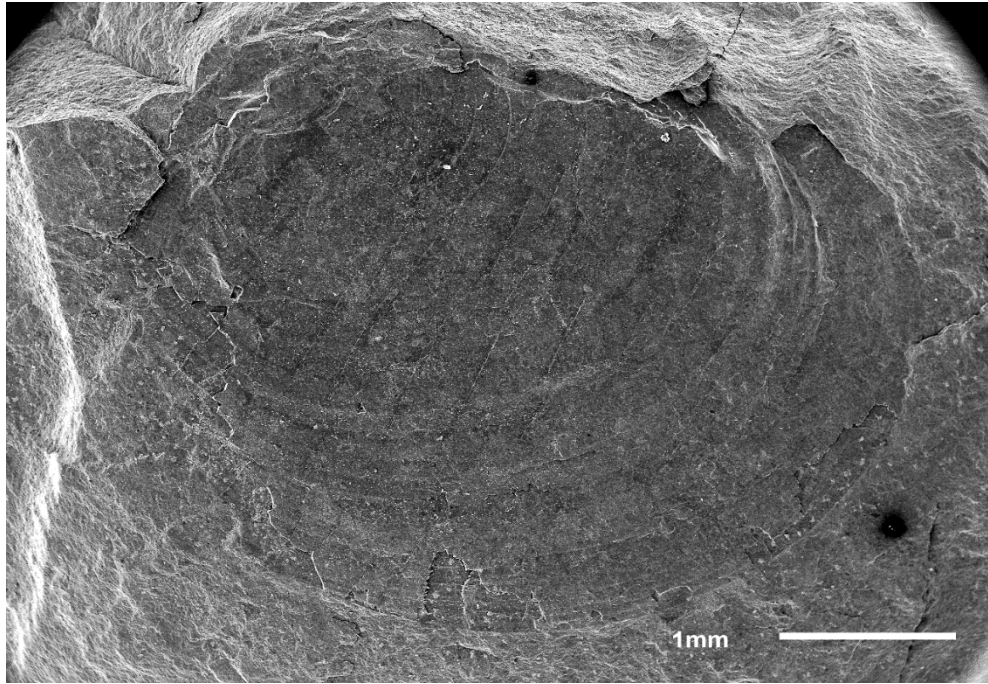
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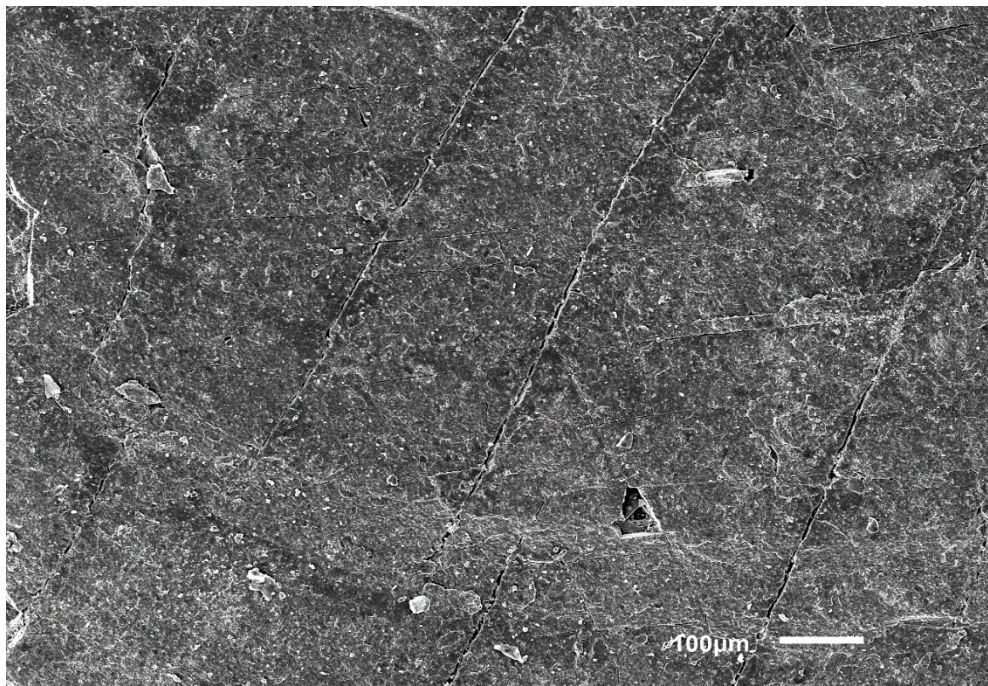
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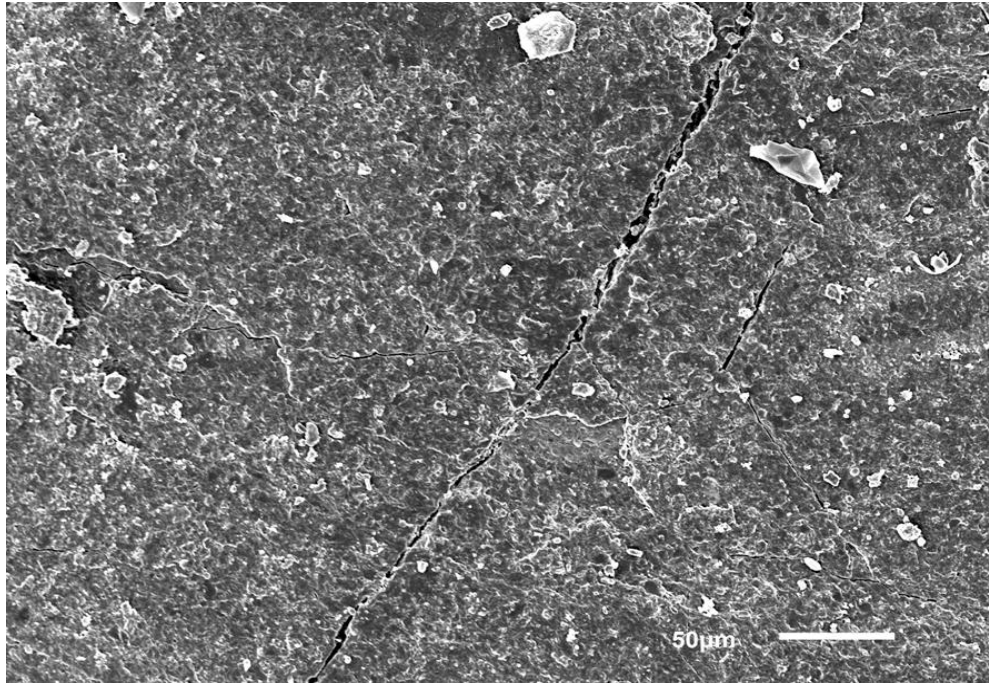
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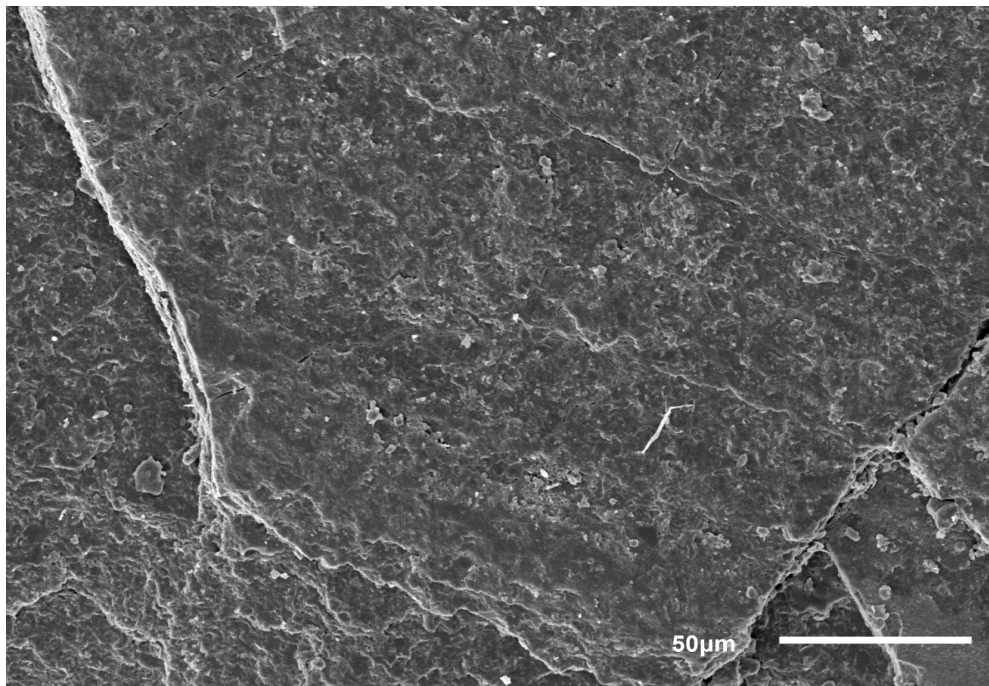
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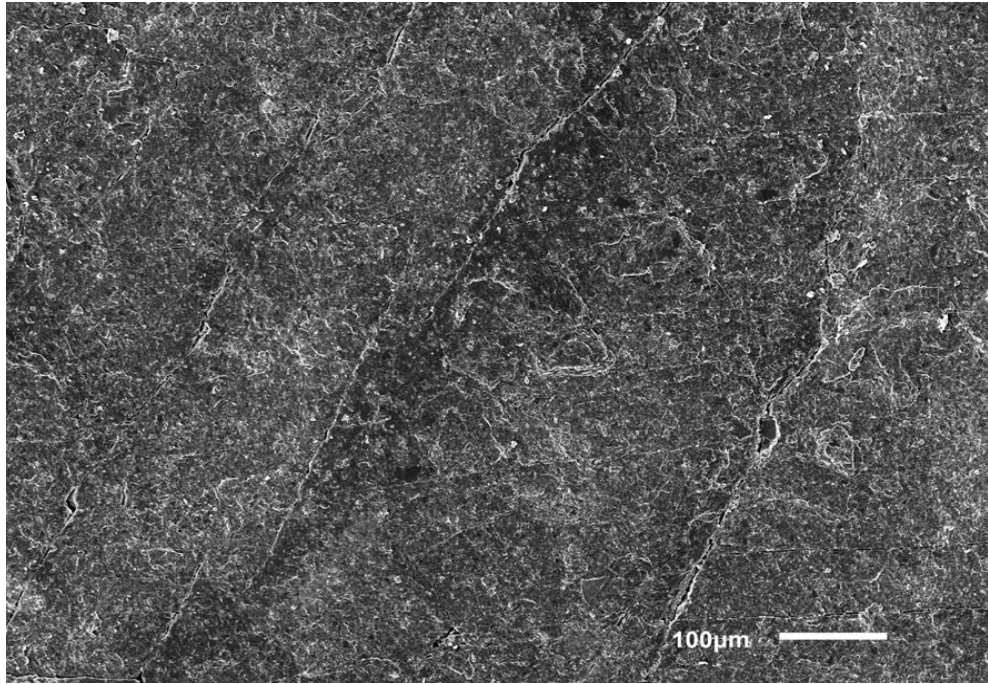
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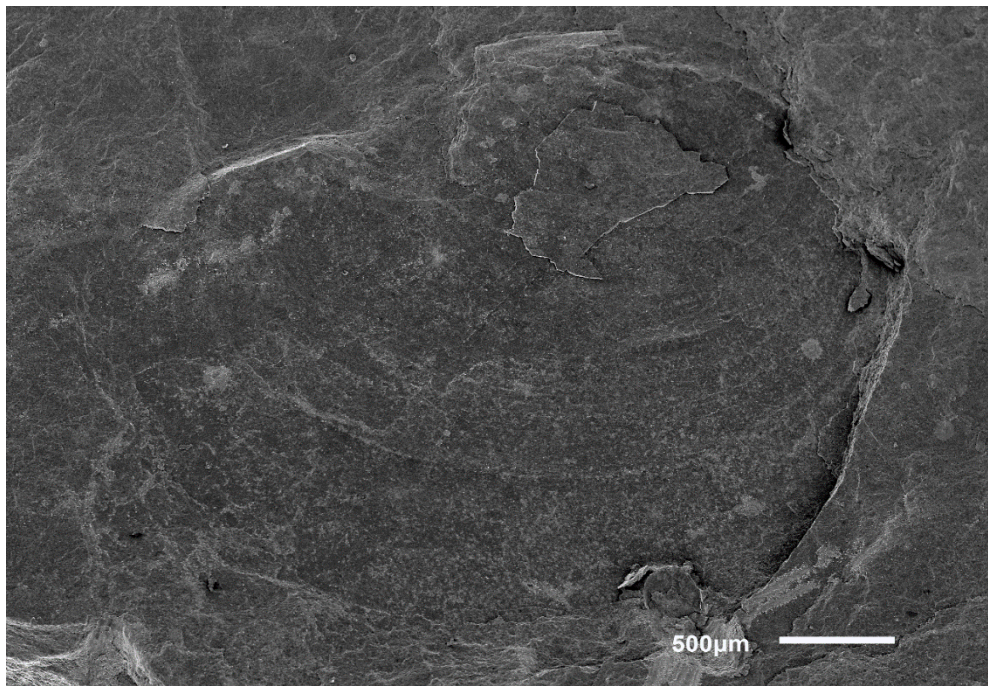
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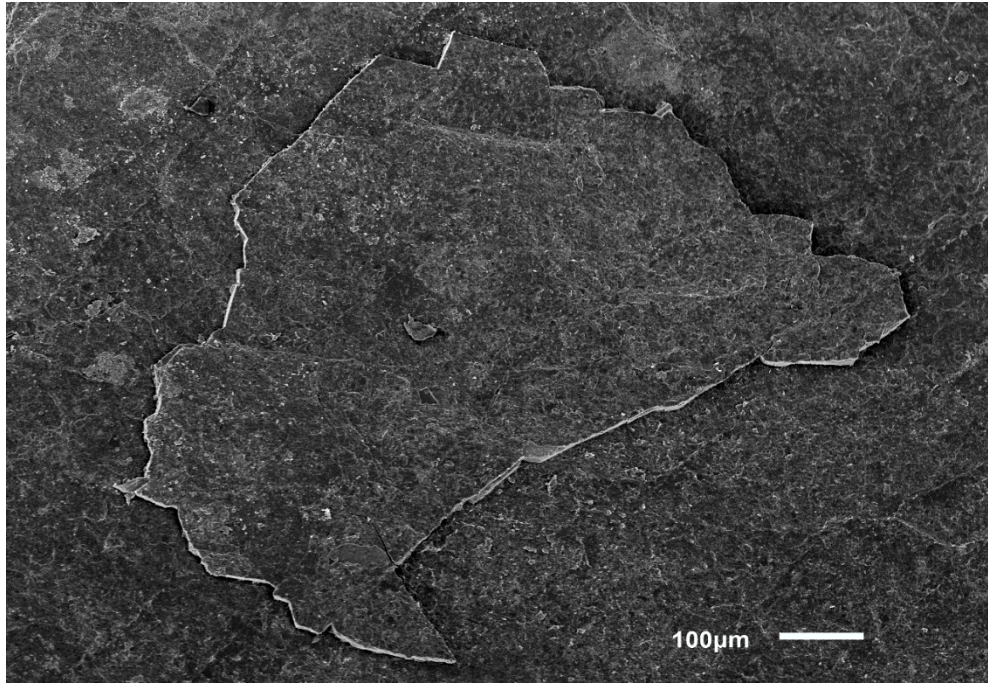
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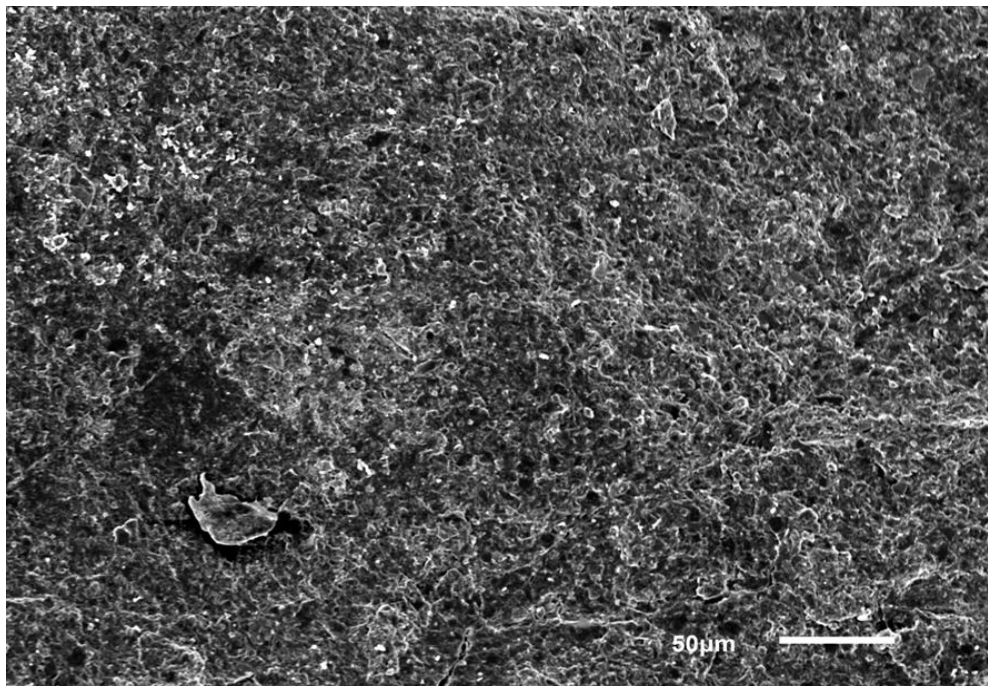
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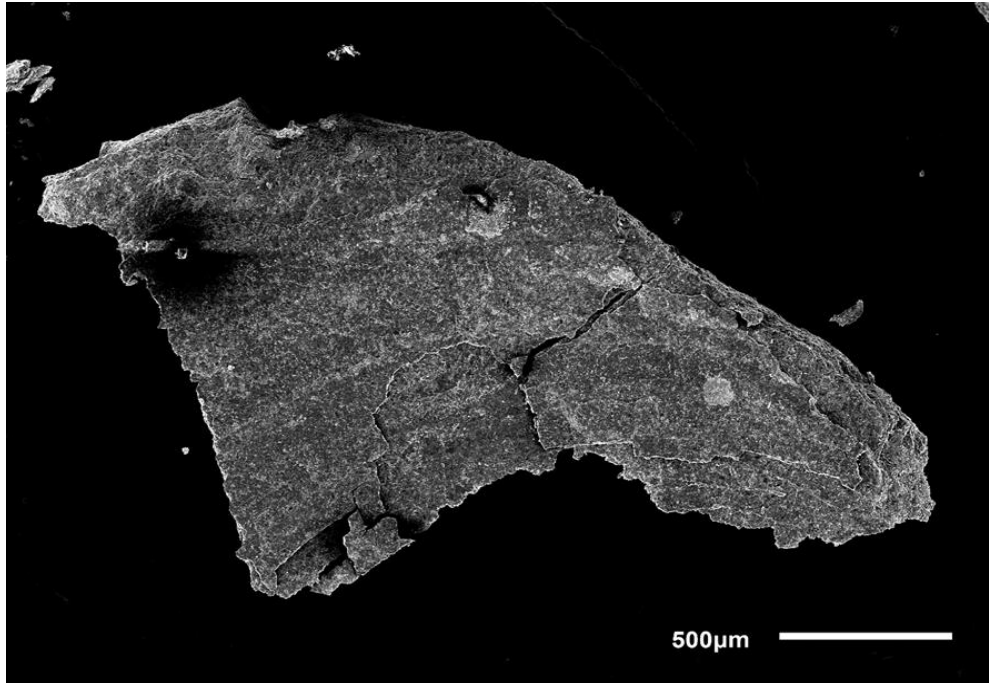
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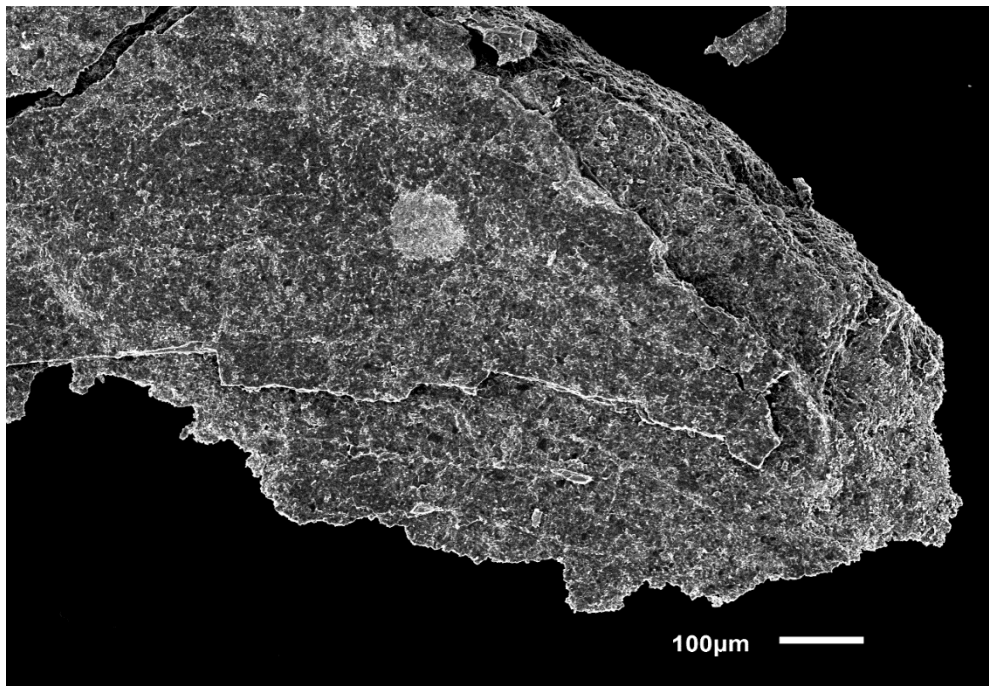
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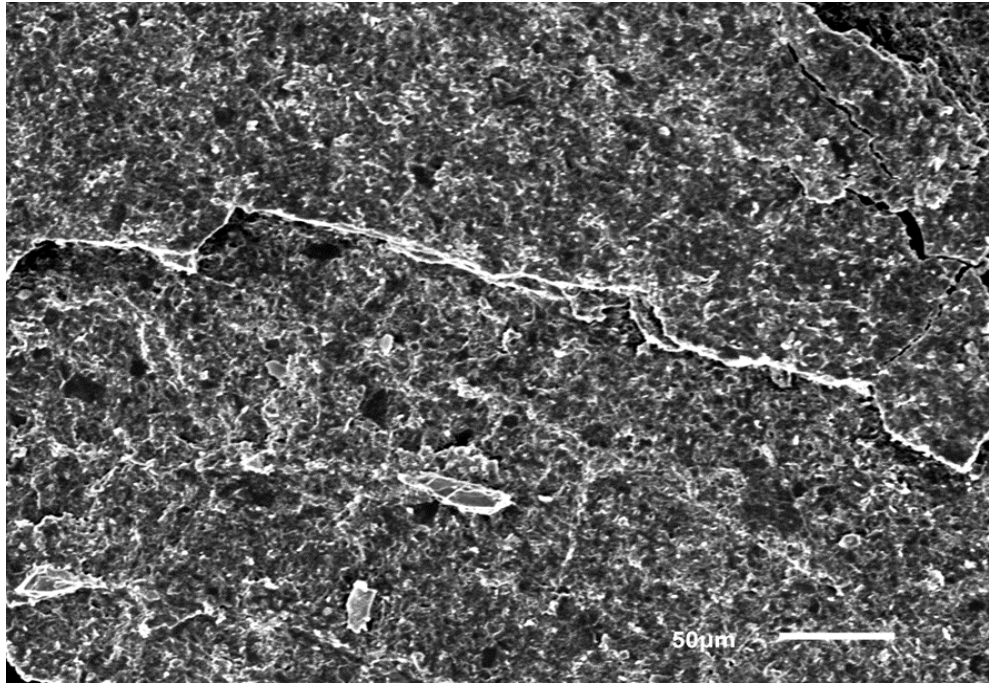
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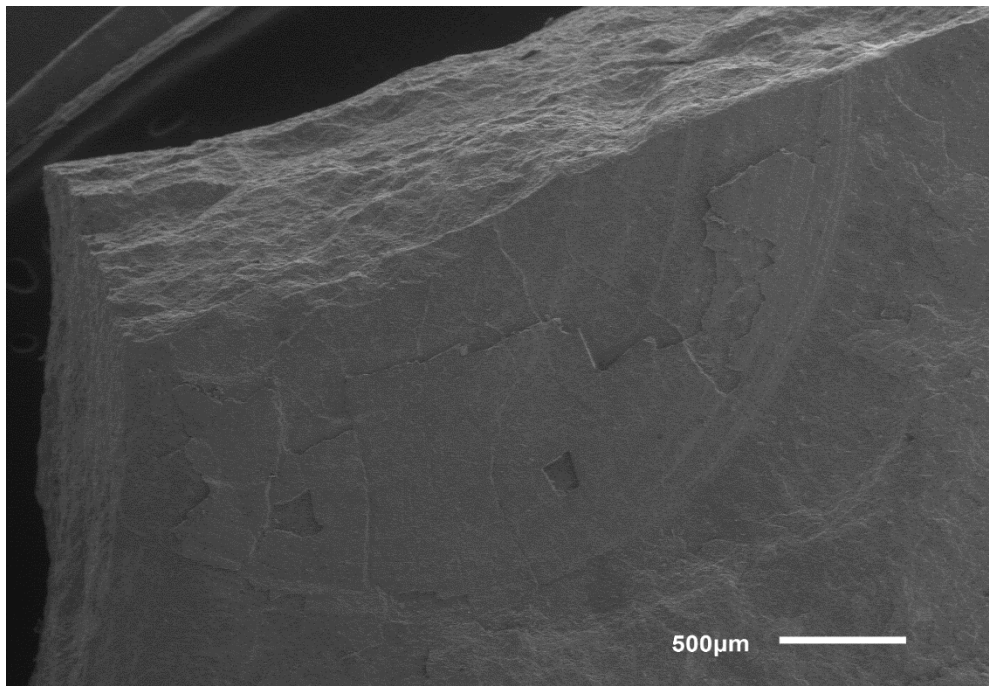
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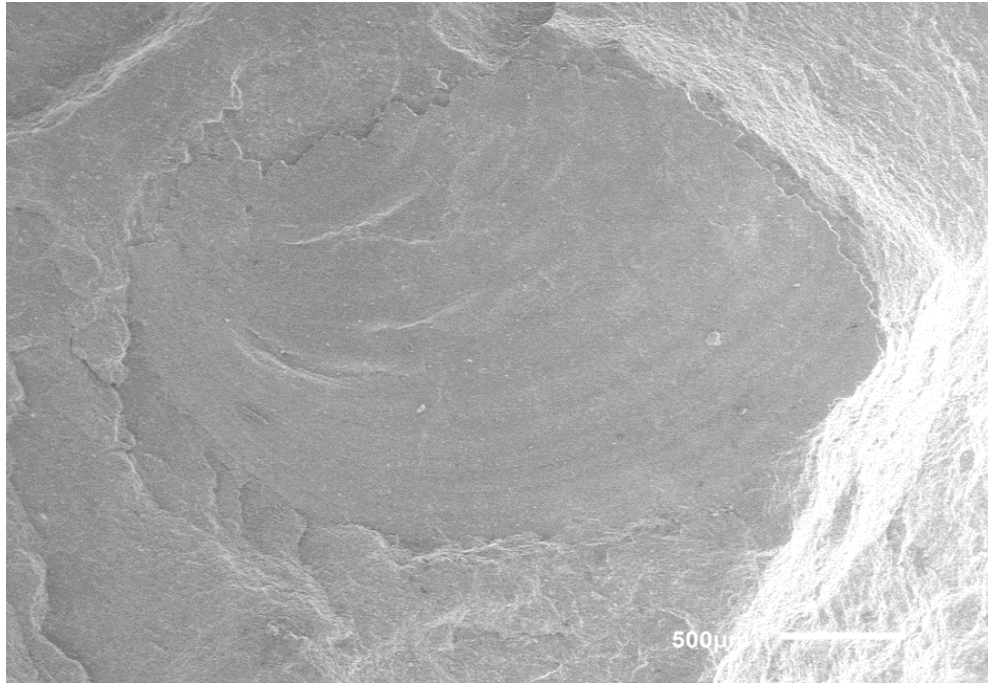
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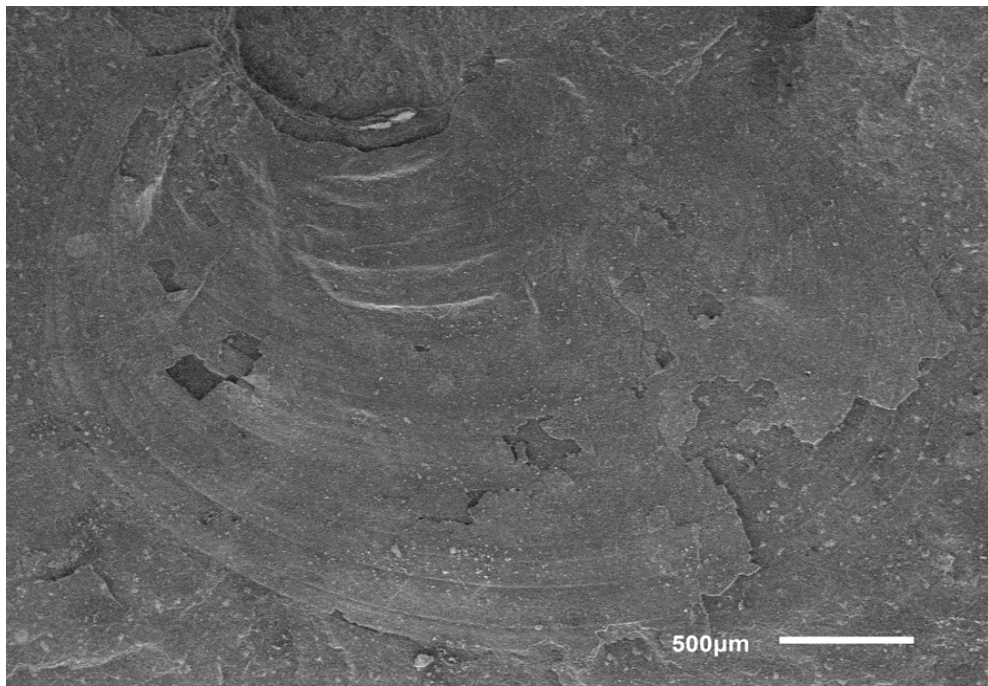
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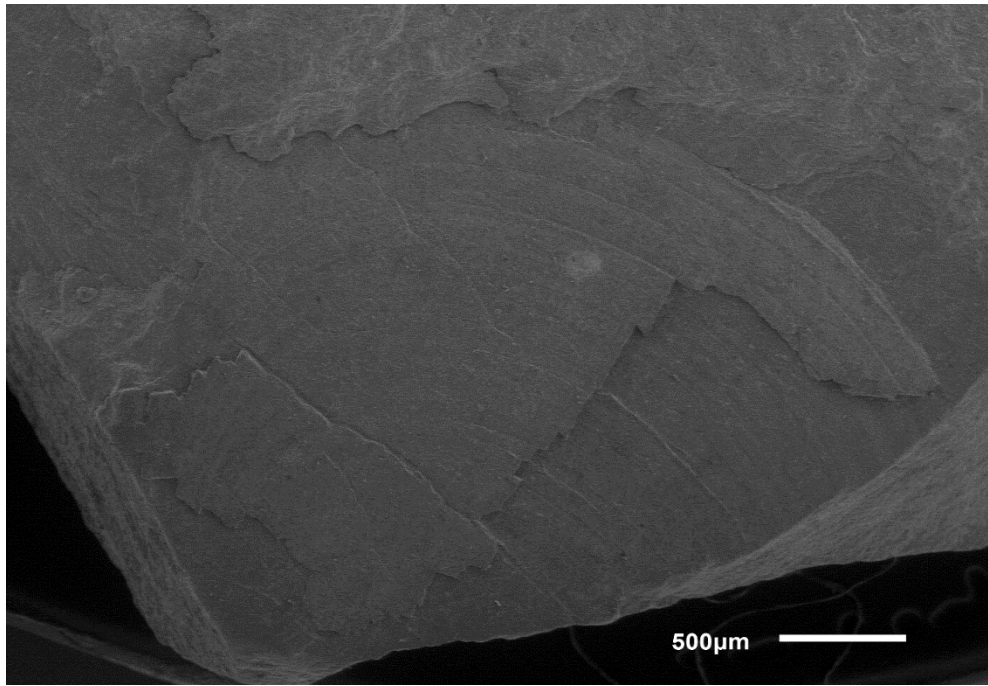
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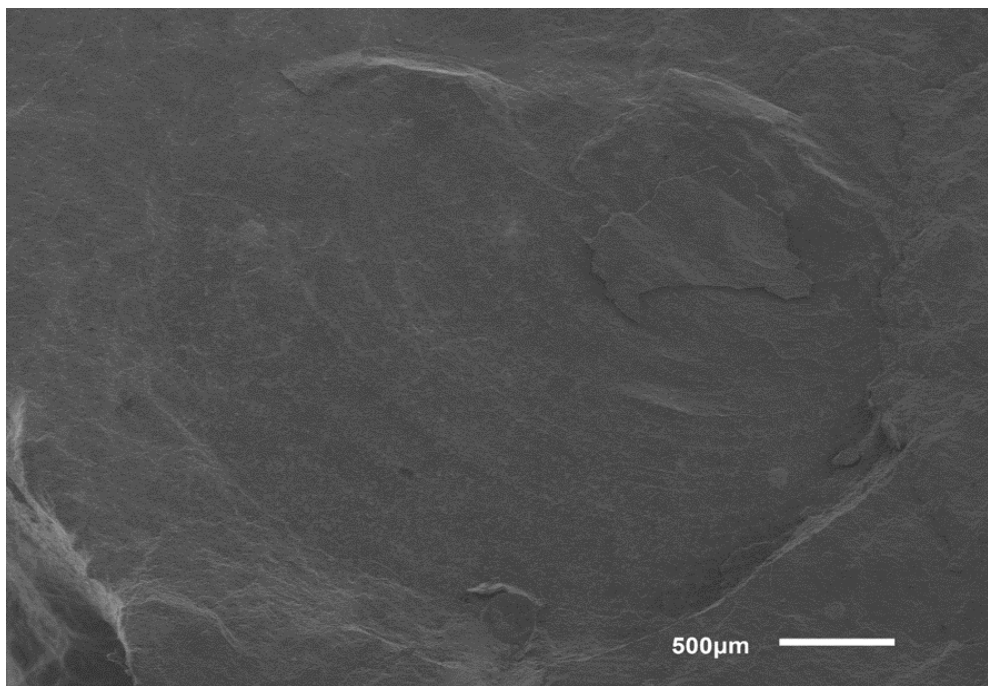
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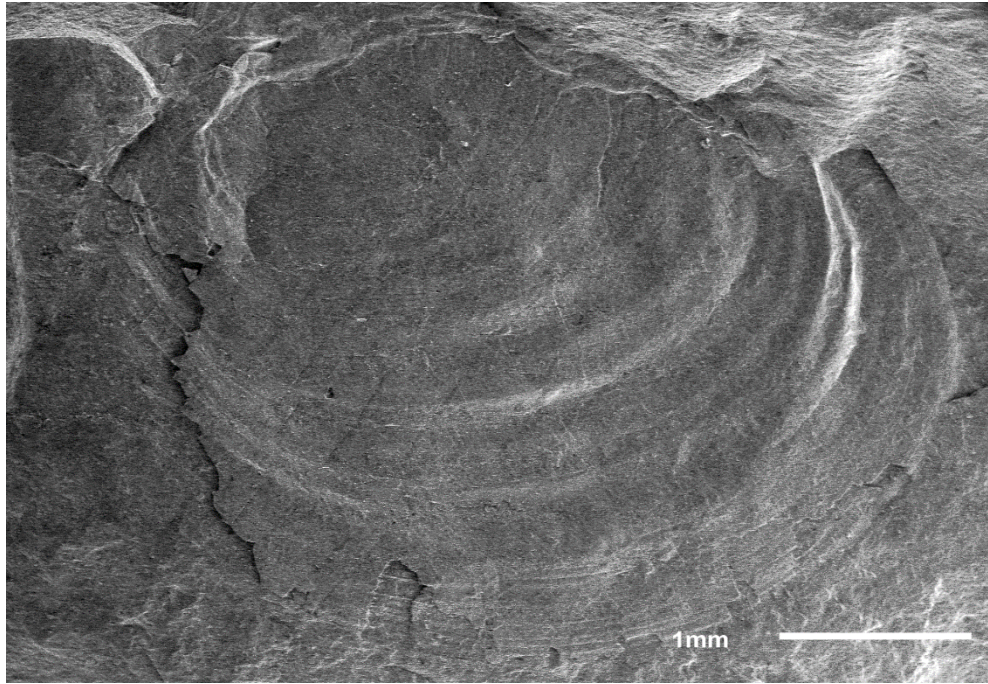
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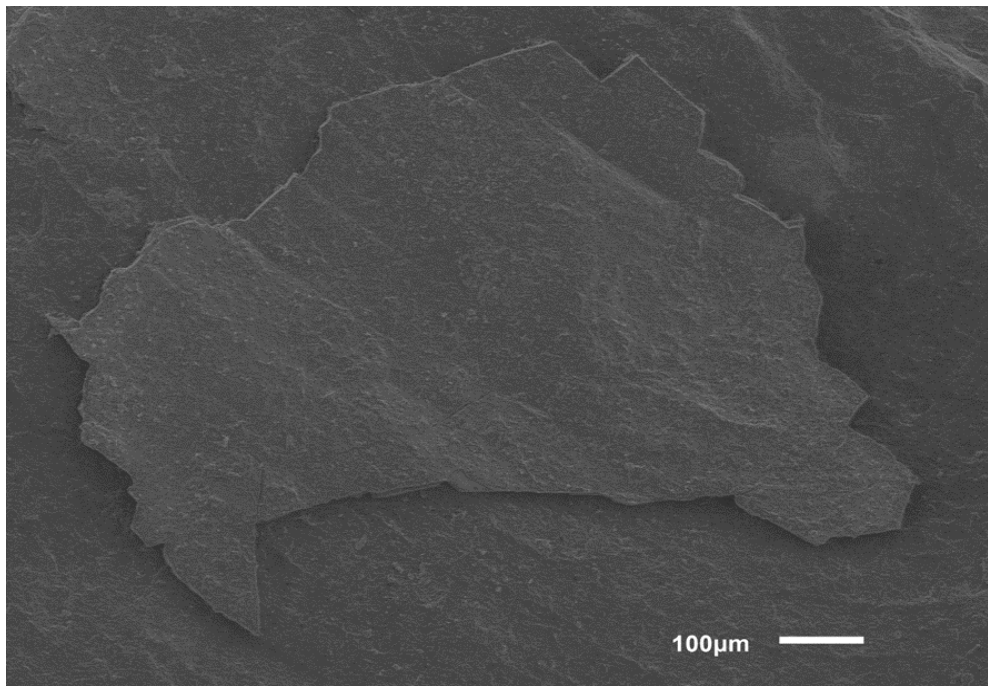
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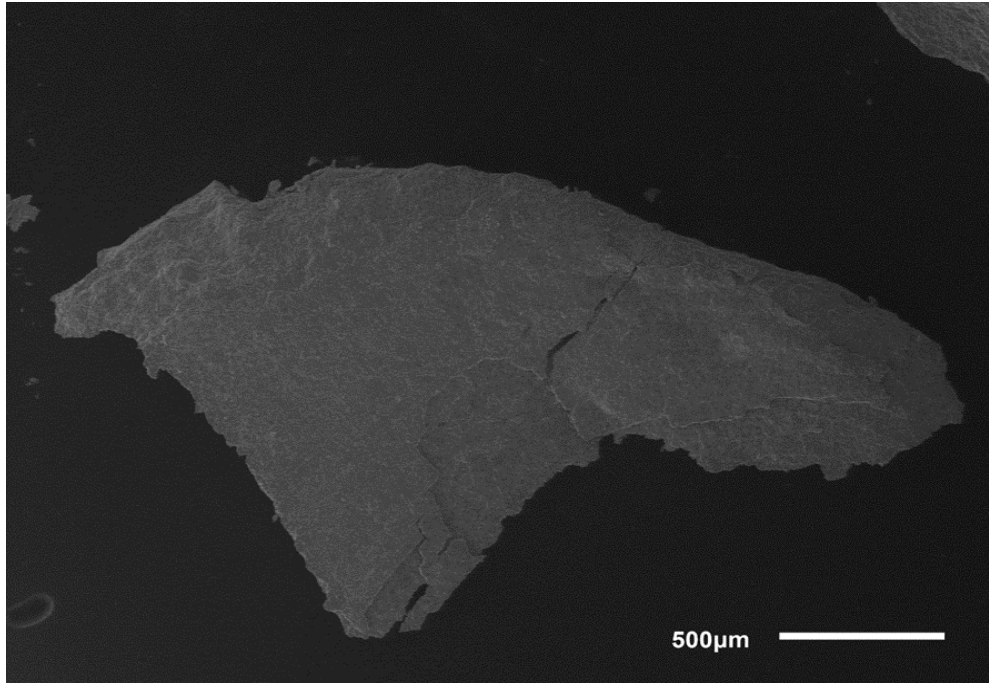
NHMW 2021/0123/0459; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0452; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0450; layer 1 (Po -50 - 0 cm)



NHMW 2021/0123/0477; layer 4 (Po 300 - 320 cm)