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Phosphatic cuticle in thylacocephalans: a taphonomic case study of *Austriocaris* (Arthropoda, Thylacocephala) from the Fossil-Lagerstätte Polzberg (Reingraben shales, Carnian, Upper Triassic, Lower Austria)

Angela FORCHIELLI[1)2)*)] & Peter PERVESLER[2)]

KEYWORDS

conservation deposit
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[1)] Freie Universität Berlin, Malteserstraße 74-100, Haus D, 12249 Berlin, Germany;
[2)] Universität Wien, Geozentrum, Althanstrasse 14, A-1090 Vienna, Austria;
[*)] Corresponding author, geoange@hotmail.it

Abstract

Thylacocephala PINNA, ARDUINI, PESARINI & TERUZZI 1982, is a recently established group of bivalved arthropods that exists since the Cambrian and is geographically widely distributed. This group was extensively studied with respect to its taxonomy, morphology and ecology, but the taphonomic pathways involved in their preservation have not received the same attention. In this study, the cuticle of the thylacocephalan *Austriocaris* GLAESSNER, 1931 from Polzberg (Upper Triassic, Lower Austria) is analyzed and compared with material from the Cambrian (Stage 3 and 4) and with other members of the Thylacocephala.

The apatitic layer of the carapace of this bivalved arthropod is compact and no evidence of original ultrastructures has been found at this stage of research, but its carapace contains organic matter (probably in the form of kerogen, due to the presence of C, S and N in the semi-qualitative energy dispersive X-ray analyses). *Austriocaris* had a primary phosphatic cuticle, which is shared by all the members of this group. The taphonomical processes that occurred at the Polzberg Fossil-Lagerstätte are most likely more complicated than hitherto expected, and probably influenced by a taxonomic factor.

Die jüngst etablierte doppelklappige Arthropodengruppe Thylacocephala PINNA, ARDUINI, PESARINI & TERUZZI 1982 ist seit dem Kambrium weit verbreitet. Morphologie, Taxonomie und Ökologie dieser Tiere wurden eingehend erforscht, die Modellierung taphonomischer Prozesse jedoch nicht in gleicher Weise behandelt. In der vorliegenden Studie wird die Kutikula des Thylacocephalen *Austriocaris* (Glaessner, 1931) der Lokalität Polzberg (Obertrias, Niederösterreich) analysiert und mit kambrischem (Stufe 3 und 4) Material und anderen Vertretern der Thylacocephalen verglichen.

Die Apatit-Schicht des Carapax dieser zweiklappigen Arthropoden ist kompakt und bislang gab es keine Beweise für ursprüngliche Ultra-Strukturen. Ein erster Hinweis auf organische Substanz (möglicherweise in Form von Kerogen, aufgrund des Vorhandenseins von C, S und N in der semi-qualitativen energiedispersiven Röntgen-Analyse) ist in der Schale gefunden worden. *Austriocaris* besaß, wie auch alle anderen Vertreter dieser Gruppe, eine primär phosphatische Kutikula. Die taphonomischen Prozesse, welche an der Fossillagerstätte Polzberg auftraten, waren vermutlich komplizierter als bisher vermutet und wahrscheinlich auch durch einen taxonomischen Faktor beeinflusst.

1. Introduction

The preservation of highly volatile tissues and soft parts is rare in the Earth history, but provides a huge amount of important information. Seilacher (1970, 1990) called such deposits where soft-bodied fossils occur Konservat-Lagerstätten. The present study deals with the preservation of the cuticle in Thylacocephala PINNA, ARDUINI, PESARINI & TERUZZI 1982, using material from the conservation deposit Polzberg in the Reingraben shales, comparing it with literature data of other thylacocephalans preserved in different Lagerstätten and with bradoriids, Cambrian bivalved arthropods that also had a primary phosphatic cuticle.

The Reingraben shales are distributed in the Reifling basin between Polzberg and Großreifling, Austria. Most of the known occurrences contain remains of fossil fishes (Trauth, 1948; Mostler and Scheuring, 1974; Griffith, 1977). The sediment consists of millimeter laminated, dark grey, brownish weathered, slightly bituminous marls, with clearly visible bright/dark stratification without any bioturbation (Krystyn, 1991).

Although the Late Triassic Polzberg Fossil-Lagerstätte in Lower Austria (Fig. 1) and its fauna were locally studied and published already in the 19th century (e.g. Stur, 1886; Teller, 1891), it remained poorly known. Few studies were focused on the taphonomic pathways of its fauna over the past decades. In 1885 and 1909, two fossil mines were driven into the basal part of the Reingraben shales. The yield of the mines (Glaessner, 1931) – approximately 100 fish remains, several arthropods and hundreds of white, chalky ammonites (*Austrotrachyceras* sp.) – is stored in the collections of the Museum of Natural History and the Geological Survey of Austria, both in Vienna. To date, there are only few papers (Doguzhaeva et al., 2006; 2007 a, b) dealing with the preservational pathways of the Polzberg cephalopods.

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Fossil plants from the stratigraphically younger Lunz Fossil-Lagerstätte are usually preserved as compressions, often with optimally preserved cuticles (e.g. Pott et al., 2010). The geological setting of the Lunz Fossil-Lagerstätte was extensively studied, and all the authors agree with a multifacies environment. The Lunz strata comprise all three major facies: marine, brackish and freshwater (Yen, 1965). The sandstones exposed at Lunz are interpreted as deposits of a subaquatic delta that changed slowly to swampy coal-building environments, probably with an occasional brackish influence (Meller et al., 2011 and references therein). A similar hypothesis is also supported by Kustatscher et al. (2011): "Lunz am See comprises alluvial- fluviatile/ limnic- brackish facies".

On the contrary, the olderr Reingraben shales, with a predominantly nektonic fauna, are interpreted as deposits of a deeper marine environment (Hornung and Brandner, 2005; Hornung et al., 2007). Often there is an overlap and a mixture of information between Lunz and Polzberg Lagerstätten in the collections and older scientific works, where the fauna of the Polzberg Lagerstätte is referred to the Lunz Lagerstätte; but there is not any connection between the two Lagerstätten: age, environment and also taphonomic pathways are completely different.

2. Material and methods

The Triassic material investigated in the present study was collected over the last century from the Reingraben shales at Polzberg and is deposited in the collections of the Museum of Natural History Vienna (NHMW) and the Geological Survey of Austria (GBA) Vienna. The original material of *Austriocaris* described by Glaessner (1931) is stored in the NHM Vienna (holotype) and the GBA Vienna (paratypes). The stratigraphic terminology used herein is according to Piller et al. (2004).

The Cambrian material of the present study belongs to the Chengjiang and Guanshan Fauna (Cambrian, Stage 3 and 4) and was collected in 2008 and 2009 in the Burgess Shale-type Lagerstätten of Yunnan Province (South China).

Energy-dispersive X-ray (EDX) analyses of the Polzberg material were conducted at the Department of Lithospheric Research of the University of Vienna using an APOLLO XV Sili-

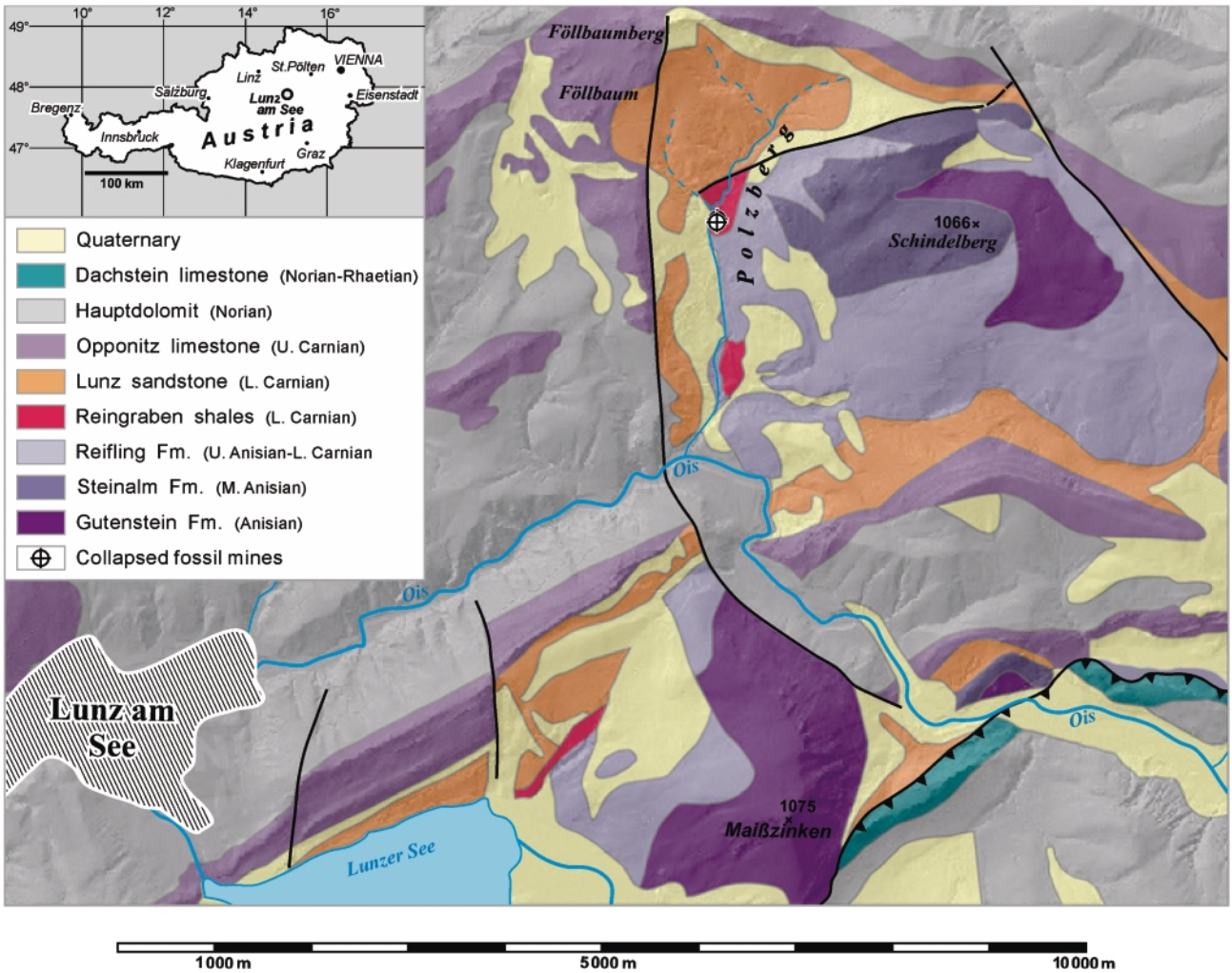

Figure 1: Regional geology of the Lunz area; distribution of the Lunz sandstone and Reingraben shales with position of the collapsed fossil mines mentioned in Glaessner (1931). Map prepared after the geological map "Geologische Karte der Republik Österreich"der GBA 1:50.000 Sheet Ybbsitz 71 (GBA, Wien, 1988) and Sheet Mariazell 72 (GBA, Wien, 1997), and the laser scan data of the Land Niederösterreich, BEV (Bundesamt für Eich- und Vermessungswesen).

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con Drift Detector coupled to a low vacuum scanning electron microscope (SEM) FEI INSPECT S50; uncoated and unpolished fossils were analyzed using 15kV voltages. Elemental mapping and EDX analyses of sample NHMW 2012/ 0228/

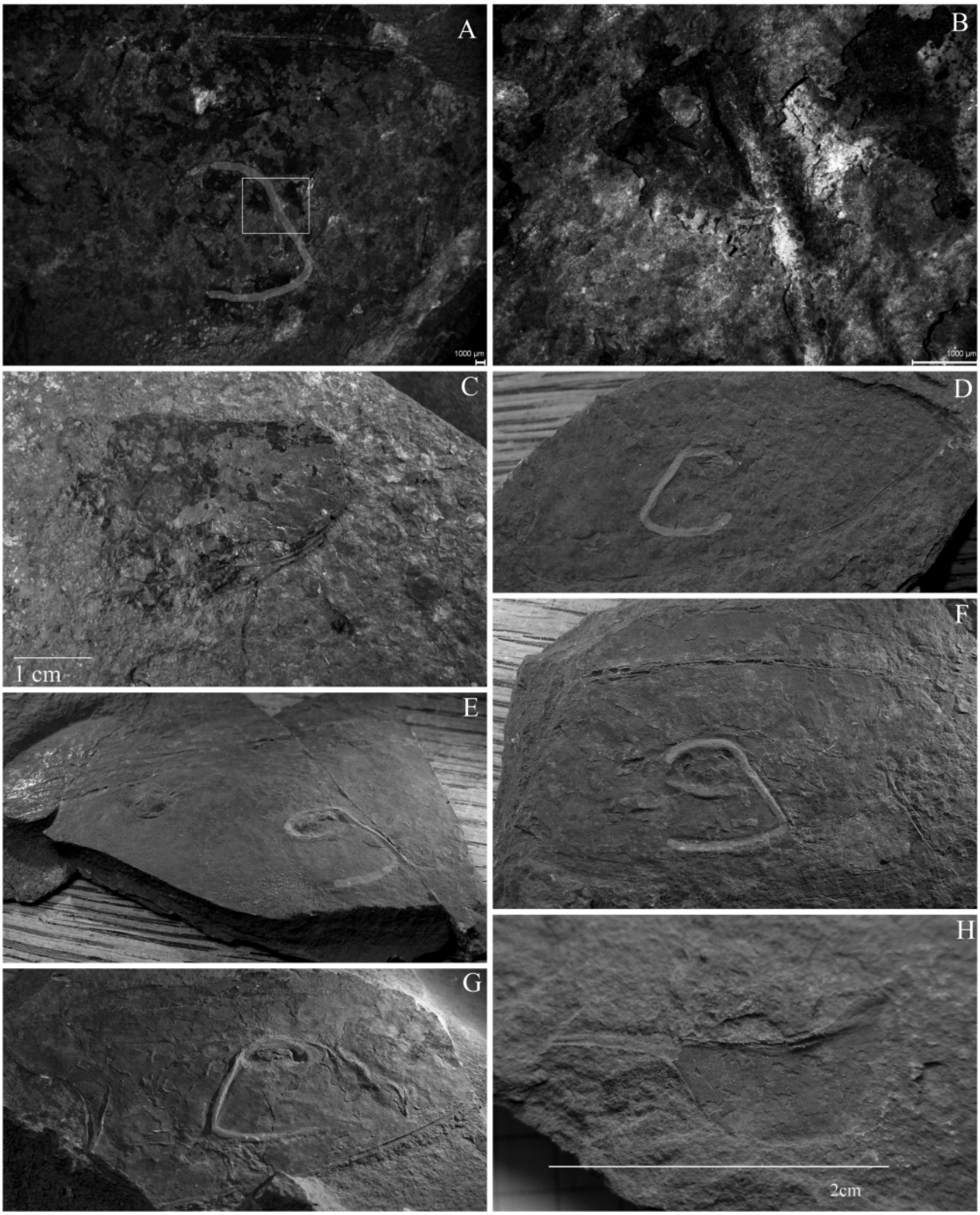

Figure 2: Morphological characteristics of *Austriocaris* Glaessner, 1931. A- The > structure (over drawings in semi-transparent color in the figure) in specimen NHMW 2012/ 0228/ 0007. B- Close up of figure A, the 3D structure is well visible. C- NHMW 2012/ 0228/ 0006 preserved with the two valves compressed, but slightly out of the alignment. D, E, F, G- the > structure (over drawings in semi-transparent color in the figure) in several specimens repository number NHMW 2012/ 228/ 0003; NHMW 2012/ 0228/ 0005; NHMW 2012/ 0228/ 0001 and NHMW 2012/ 0228/0004 respectively. H- The pointed rostrum in specimen NHMW 2012/ 0228/ 0009, total length of the specimens is 2 cm.

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0008 and Cambrian material were performed using an Inca analyzer X-max 50 mm², with Moxtex polycarbonate window (Oxford Instruments), coupled to an environmental SEM (ZEISS-SUPRA 40VP); the unpolished and uncoated sample was analyzed using 15 kV voltages.

Light microscopy (of sample NHMW 2012/ 0228/ 0007) was carried out using a digital DHS MicroCam 3.3 (3.3 Mega Pixel) attached to a LEICA MZ75 stereomicroscope.

A thin section of matrix layers was analyzed with a Cameca SX 100 Microprobe to discern the nature of the clay minerals. A section of the thin section (29.050 x 750 µm) was line scanned (20 kV, 80ms, 50 lines 1740 pts per line) with a wavelength dispersive spectrometer (WDS) detector for iron (Fe), magnesium (Mg), sulfur (S) and phosphorus (P) and with an energy dispersive spectrometer (EDS) detector for aluminum (Al), silicon (Si), potassium (K), calcium (Ca) and titanium (Ti).

3. Morphology and taphonomy of *Austriocaris*

The fossils of Austriocaris are oriented parallel or subparallel to the bedding planes of the shale; the carapace material is dark (black or dark brown). The fossils are flattened (in some cases apparently with the two valves closed, see Fig. 2 C and F), although some structures, such as the putative muscle imprints (Fig. 2 A-G) of the original descriptions made by Glaessner (1931), are preserved in 3D (Fig. 2 A, B, D and G).

A singular morphological characteristic was noticed in one specimen (NHMW 2012/ 0228/ 0009), which is similar but more prominent compared with the original description of *Austriocaris* GLAESSNER, 1931. This character is shared by other thylacocephalans: *Kilianicaris* Van Straelen, 1923 with a large rounded rostrum and *Pseuderichthus cretaceus* DAMES, 1886 with an elongate and pointed rostrum. This structure is very similar to the end of the posterior and anterior carapace of the Cambrian bivalved arthropod *Isoxys* WALCOTT, 1890, as already suggested by Glaessner (1931) himself (Fig. 2H): "The species which I will describe here are so similar to the older forms that their occurrence would not appear conspicuous in a Paleozoic fauna. Only the carapace is preserved. It consists of two connected shells fixed along a straight line. The shell is thin, soft and pliable. The two valves close in a small gap, a proximal spindle-shaped short curved rostrum. The rear end of the carapace was extracted (like *Isoxys*, Archaeostraken and other) into a strong center peak. The carapace is deeply cut on both sides of the tip, suggesting the presence of a well-developed abdomen. The surface of the shell shows a median keel and two approximately parallel lateral keels. The edge is (similar to the higher malacostracan) surrounded by a bead and a furrow. Behind the center of the shell there is a > shaped furrow, which appears at the inside as a bulge. The opening of the angle is directed forward. Eye spots and any other sculptures occurring in Archaeostraca are lacking. Nothing of the abdomen, the telson and furca is visible. As the rock is appropriate to preserve very thin shells, one must assume that the abdominal segments had no solid shell".

Austriocaris has at least 8 radially arranged gills; the most posterior gill lies almost horizontally over a battery of 9 to 10 posterior limb protopods that occupy the postero-ventral sector of the carapace and that lie just inside its margin (Rolfe, 1985).

4. Phylogenetic position of *Austriocaris* and the Thylacocephala

Among the arthropod genera represented in the Polzberg Fauna, we focus on *Austriocaris* because of unpublished material deposited at the Natural History Museum Vienna. Since the description of the genus by Glaessner (1931), *Austriocaris*

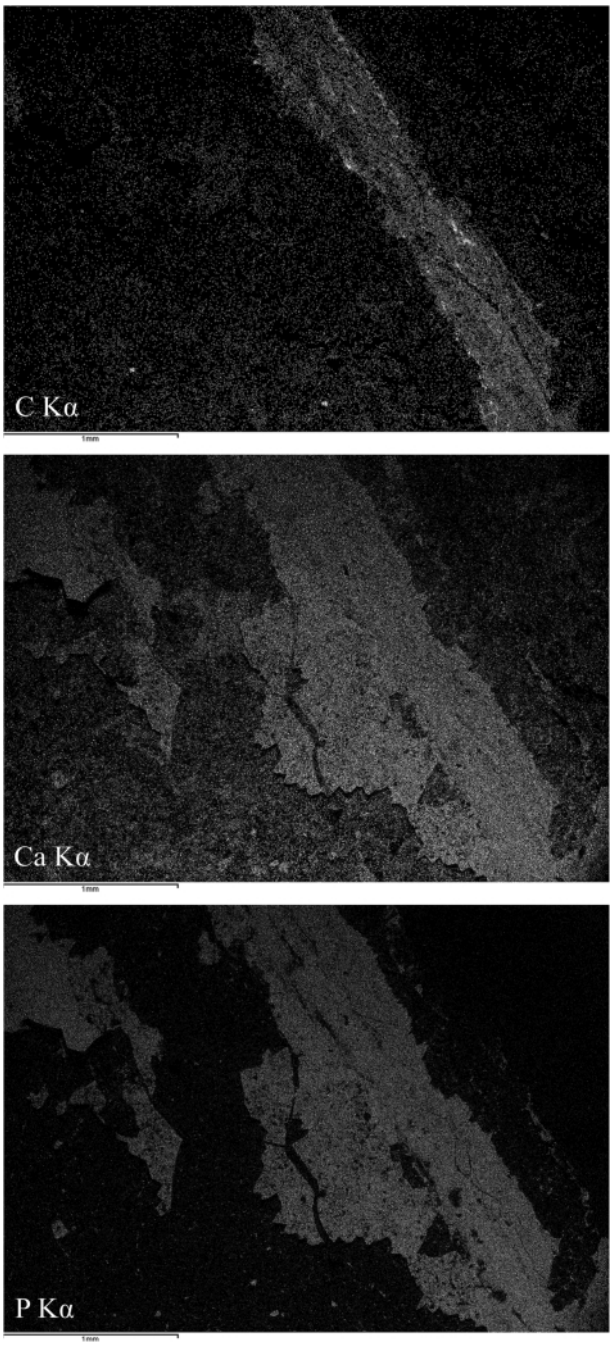

Figure 3: Elemental mapping analyses of specimen NHMW 2012/ 0228/ 0008.

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has not been taphonomically further analyzed. The phylogenetic position of *Austriocaris* was debated in the early 1980s by three different working groups (using material from northern Italy, Pinna et al., 1982; from the French Fossil-Lagerstätte La Voulte-sur-Rhône, Secrétan, 1983 and Australian material, Briggs and Rolfe, 1983), and phylogenetic work continued by Schram (1990), and Schram et al. (1999). Its origin was analyzed by Vannier et al. (2006). According to these latest papers, *Austriocaris* belongs to the Thylacocephala.

The Thylacocephala are arthropods, but the affinity of this group with the crustaceans is still an open issue. They are described as arthropods with a bivalved carapace up to 200 mm long (Rolfe, 1992), but also as an unusual group of extinct fossils, possibly related to the crustaceans, characterized by a bivalved carapace covering the head, trunk, and abdominal limb region, with large raptorial appendages situated anteriorly (Lange et al., 2001). The taxonomic history of the group is complex (see overview in Schram et al., 1999) and two orders are currently recognized (Schram, 1990): Conchyliocariida SECRÉTAN, 1983 (to which *Austriocaris* belongs, Sepkoski, 2002 via paleobiology database) and Concavicarida BRIGGS & ROLFE, 1983 (Stigall and Hendricks, 2007). Thylacocephala range from the Early Cambrian of China (*Zhenghecaris*, VANNIER, CHEN, HUANG, CHARBONNIER & WANG, 2006) to the middle Triassic of China (*Yangzicaris* SHEN, 1983), Late Triassic of Austria (*Austriocaris* GLAESSNER, 1931), the Jurassic of France and Germany (*Paraostenia* SECRÉTAN, 1983, Dollocaris VAN STRAELEN, 1923, *Kilianicaris* VAN STRAELEN, 1923, *Clausocaris* POLZ, 1989) and Italy (*Ostenocaris*, ARDUINI, PINNA AND TERUZZI, 1984) up to the Cretaceous of Lebanon (*Pseuderichthus* DAMES, 1886; *Protozoea* DAMES, 1886 and *Thylacocephalus* LANGE, HOF, SCHRAM, AND STEEMAN, 2001).

The thylacocephalan key diagnostic characters are the presence of a bivalved carapace enclosing the entire body, a large anterior optic notch (spherical or drop-shaped, possibly stalked), large raptorial limbs, gills in the anterior trunk region and a series of posterior trunk segments bearing limbs (Schram et al., 1999).

5. Results

The carapaces of all samples of the Polzberg material analyzed in this study show a compact layer, which is not preserved continuously in the whole carapace. Element mappings performed on a portion of one of the carapace show that it is composed mainly of phosphorus, calcium and carbon (Fig. 3). Energy dispersive X-ray analyses performed in several areas document the presence (with maximum peaks in percentage of the total weight) of carbon (67.8), phosphorus (20.3), calcium (34.1), fluorine (6.3), nitrogen (4.5) and in some spots also sulphur (4.0), in the carapace of *Austriocaris*, (Fig. 4 A and B). The analyses effectuated on the matrix show two slight differences in the percentage of Si and Ca in the composition (Fig. 4 C and D), but generally the matrix contains the following elements (average made of several measurements) in percentage of the total weight: carbon (27.5%), silicon (26.2% but with a maximum of 40%), potassium (1-2.6%) calcium (21%), aluminum (9%), iron (3.4%), sulfur (2-3%) and

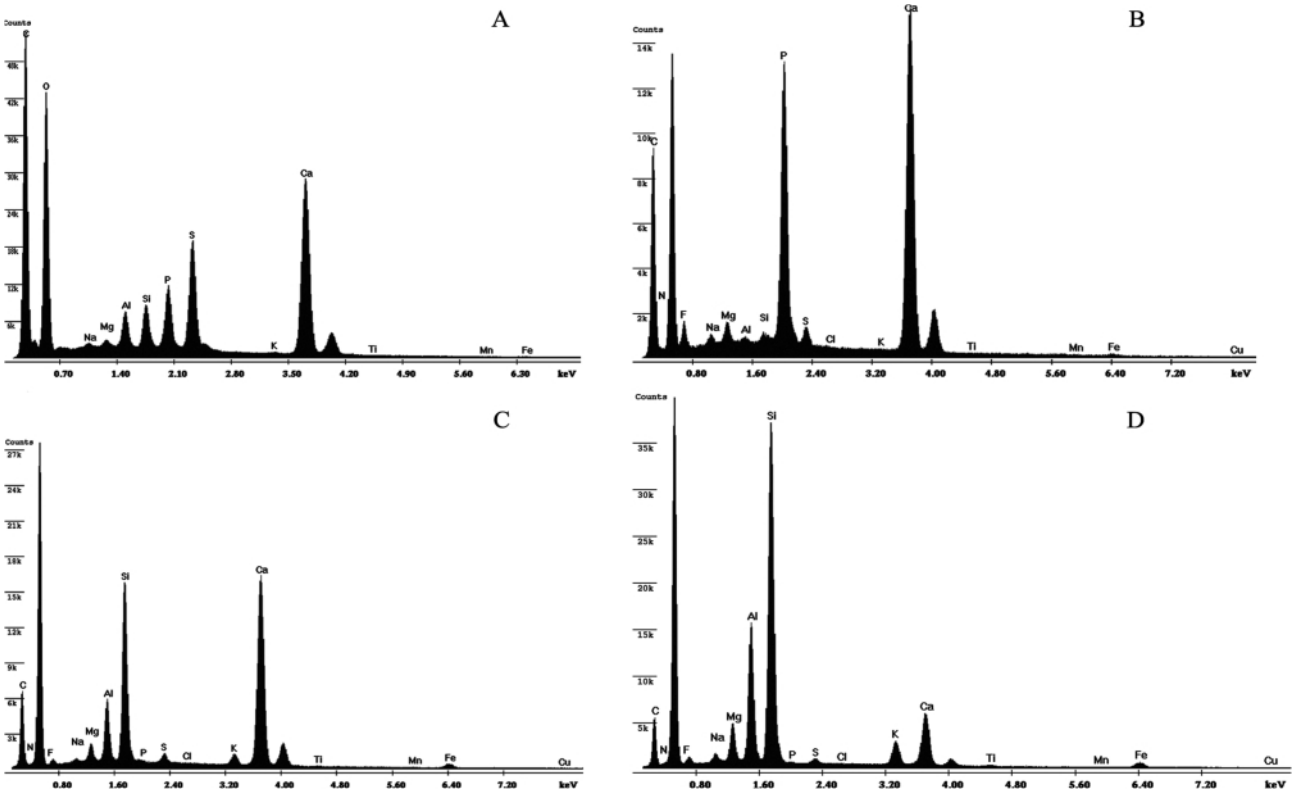

Figure 4: EDX analyses of specimen NHMW 2012/ 0228/ 0002. A, B- analyses performed inside the carapace; C, D- analyses performed on the matrix.

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magnesium (3.2%).

Mass accumulations of the bivalve *Halobia* BRONN, 1830 have been found in several layers of the strata, often preserved in butterfly positions (Fig. 5). A very similar situation is present in the Callovian La Voulte Lagerstätte, in this case the bivalve is *Bositra buchi* (ROEMER, 1836) (see introduction in Charbonnier et al., 2007 and also pictures in Charbonnier, 2009 and Fischer, 2003). The shells of *Halobia* are mostly white, similar to the abundant ammonite shells, with very rare exceptions showing a dark color similar to the carapace of *Austriocaris*.

The thin section shows an extremely finely laminated matrix, with a large quantity of shells. Two alternating beds are observed (Fig. 6): a darker, finer grained bed and another paler, laminated bed, similar to the first but coarser, with a higher portion of silt. There is a difference in the clay mineral amount of this couplet of layers. The darker layers show an enrichment of clay mineral elements (Al, Si, K), whilst the paler layers contain more calcium as along with clay minerals. Small pyrite crystals and framboids are distributed in both layers (Fig. 6).

The Cambrian material analyzed belongs to the bradoriids, one of the rare arthropod groups supposed to have a phosphatic cuticle. Bradoriids are very common small bivalved arthropods (e.g. 81.1% of the relative species abundances in the Chengjiang Fauna, Zhao et al., 2009) in the Early Cambrian of Yunnan Province. Elemental mappings performed on several specimens of *Kunmingella douvillei* MANSUY, 1912 from the Chengjiang and Guanshan faunas show the presence of calcium and phosphorus in the form of a thick and homogeneous layer (Fig. 7). Neither phosphorus nor calcium were detected in the surrounding matrix (Fig. 7). The analyzed bradoriids co-occur together with linguliform brachiopods with preserved primary organo-phosphatic shells (Forchielli et al., in press), priapulids, also with primary organo-phosphatic plates preserved (Forchielli et al., 2010). Other metazoan groups such as sponges (Forchielli et al., 2012), trilobites and other bivalved arthropods are also present in the assemblage but lack any phosphatization (primary or secondary). The material analyzed embraces a wide range of alteration/ weathering stages, from unaltered/ unweathered to completely altered/ weathered. The unweathered material analyzed shows no pyrite inside the shell of these earliest Cambrian bivalved arthropods; the taphonomical pathway that involves early diagenetic pyrite replacement, later pseudomorphed by iron minerals, proposed for this group in the Chengjiang Lagerstätte by e.g. Gabbott et al. (2004) and more recently by Hou et al. (2010) can therefore not be validated here.

6. Discussion

6.1 Phosphatic cuticle in arthropods

A recent study demonstrates that the oldest arthropod cuticles that retain traces of their major original components, chitin and protein, are not approximately 25 myrs old, as previously assumed (Briggs, 2003), but 417 myrs old (Cody et al., 2011). Organic tissues such as cuticles may occur within the fossil

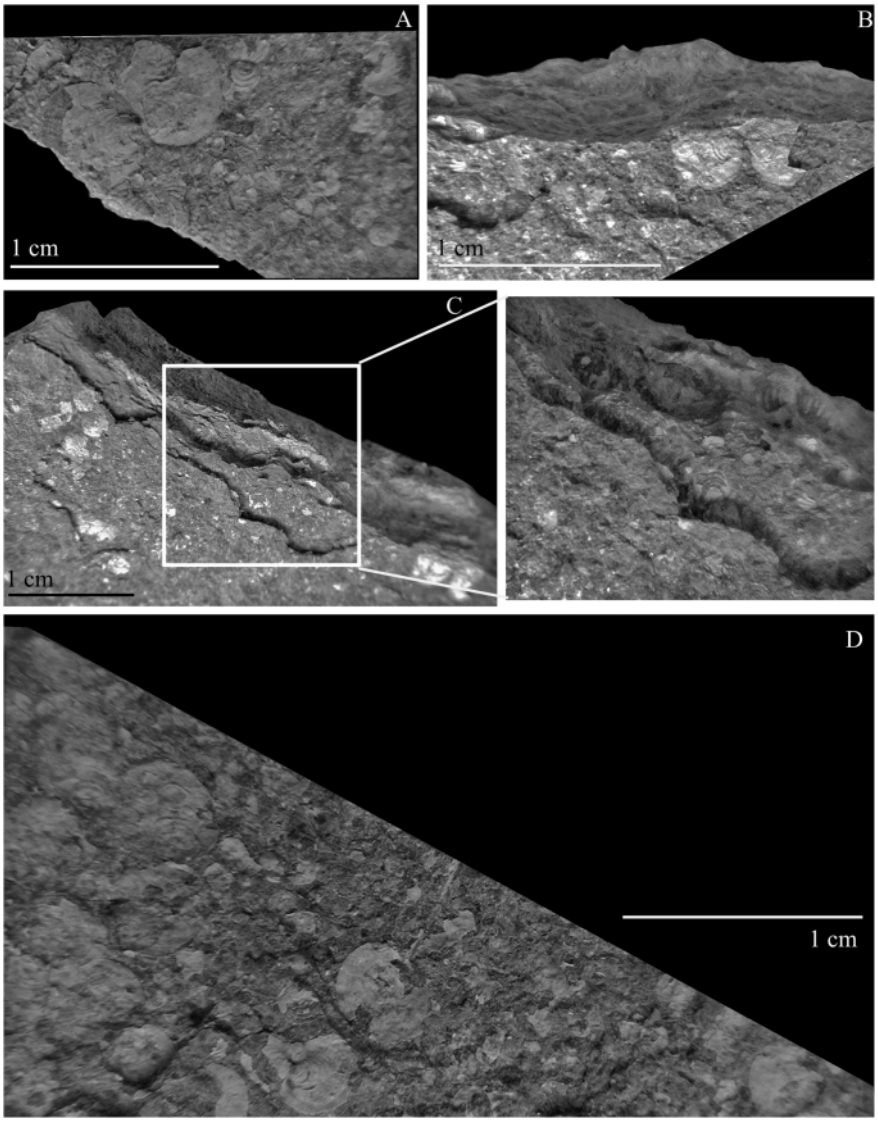

Figure 5: Mass accumulation layers of the bivalve Halobia BRONN, 1830 often preserved in butterfly position. A, D- Several exemplars of *Halobia* preserved in butterfly position. B, C- Mass accumulation layers of *Halobia*, several layers are visible. In C the close up of the white frame is on the right part of the figure.

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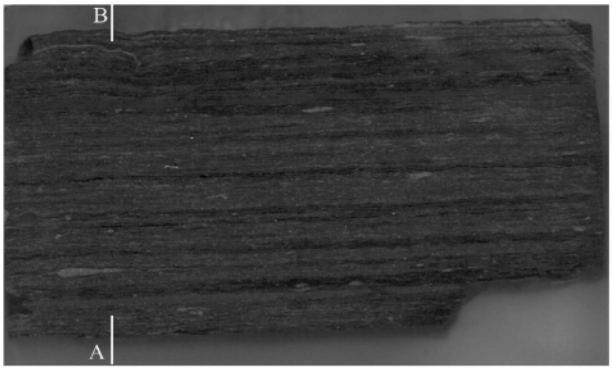
record as organic remains, only if transformed during diagenesis from their original composition to geopolymers with a significant aliphatic component (Gupta, 2011). Arthropods are the most important group that use chitin as a structural biopolymer (Baas et al., 1995 and references therein). Biosynthesis of chitin utilizes carbon, nitrogen, and oxygen atoms with dietary and environmental isotopic signals and embeds them into a large organic macromolecule where isotopic exchange of carbon, nitrogen and oxygen is negligible or impossible as long as amino sugar remains are chemically preserved. Preservation of the original chemistry of the arthropod cuticles is favoured by their thickness and degree of sclerotization, and the presence of biominerals. The exoskeleton of modern arthropods varies in chemical composition among different taxa (Lin et al., 2011). Chitin fibres in crustacean carapaces are associated with carbonate that diffuses and precipitates after the fibrous components have been excreted and stabilized.

Primary phosphatized cuticles are rare among arthropods. Examples are bradoriids and phosphatocopines; the first group was, and is, an issue of debate concerning the primary or secondary nature of its cuticle (see, e.g., Lin et al., 2011). Our analyses on *Kunmingella* HUO, 1965 from the Chengjiang Fauna demonstrate that the phosphorus in the cuticle is primary. Lin et al. (2011) reported that *Phytophilaspis* IVANTSOV, 1999, an enigmatic arthropod from the Sinsk Lagerstätte (Siberia), also had a phosphatic cuticle, together with the trilobite *Ellipsocephalus* ZENKER, 1833 and the aglaspidids, suggesting that a phosphatic exoskeleton evolved more than once among major Cambrian arthropod groups.

6.2. Preservation and lifestyle of Thylacocephala

Biases also operate at the Konservat-Lagerstätten level (Briggs, 2003), as peaks in the occurrence of Konservat-Lagerstätten through geological time tend to correspond to the prevalence of particular environments (Allison, 1988) or are the result of particular events in the history of life (Briggs, 2001). Deltas are a particularly important site for exceptional preservation in the Carboniferous, due to the prevalence of broad coastal plain environments (Allison and Briggs, 1991). An example of this exceptional preservation in a Carboniferous lacustrine delta environment is represented by the Syncarid crustaceans from the Montceau-les-Mines Lagerstätte (Perrier et al., 2006). A comparable example occurs in the Triassic, where it is represented by the laminated silts of the Grès à Voltzia Formation in north-eastern France (Briggs and Gall, 1990). The taphonomic window represented by these early Mesozoic deltaic environments is often induced by microbial mats, and reflects the prevailing environmental conditions. A broad coastal delta plain provided a setting in which restricted water bodies such as interdistributary bays and lagoons could form (Allison and Briggs, 1991). Salinity was variable (due to mixing of normal marine and fresh water) in a tidally influenced estuarine-deltaic environment and may have been instrumental in inhibiting decay. Deltaic Konservat-Lagerstätten form a faunal (but plants may also benefit of these conditions, see e.g. Charbonnier et al., 2008) continuum, together with excep-



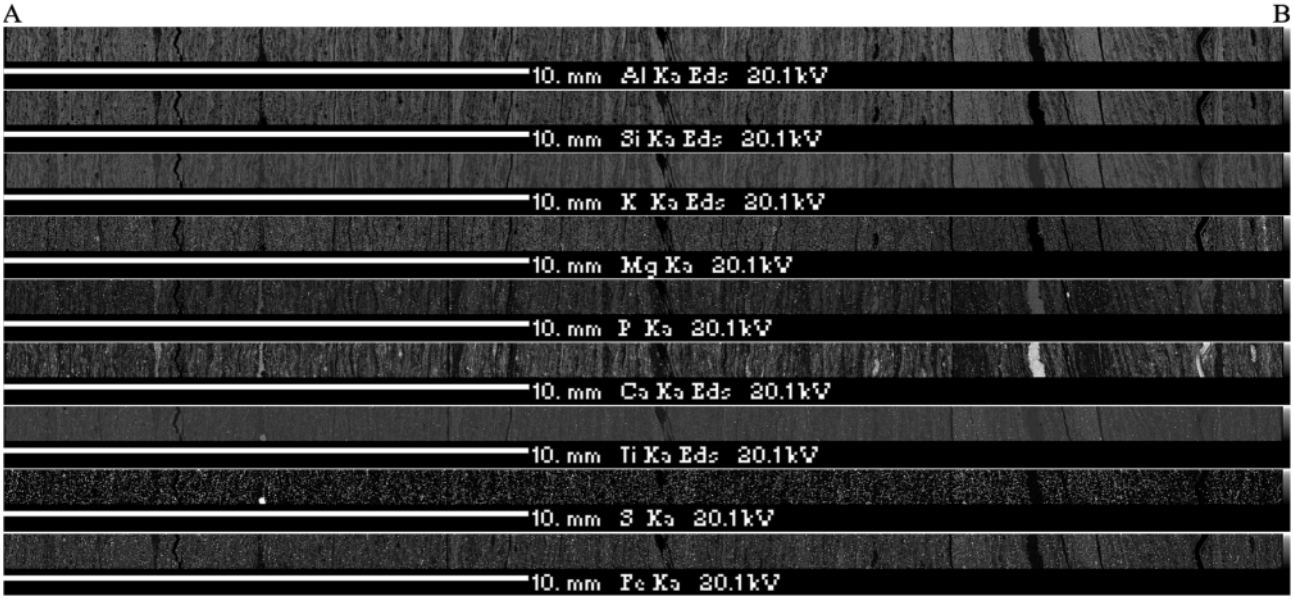


Figure 6: Microbeam analyses: the thin section measures 4.5 cm in length and is 2.5 cm high. The A-B transect represents the scan line, the results of which are reported in the lower part, element by element.

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tionally preserved biota in other contemporaneous environments, which can be traced from the Early Carboniferous to the Triassic (Allison and Briggs, 1991 and references therein).

Phosphatization of soft tissues and skeletal remains has varied through the Phanerozoic with peaks in the Cambrian to Early Ordovician, and from the Cretaceous through to the Eocene. Phosphatization favors the preservation of recalcitrant tissues that are resistant to decay and those that are already enriched with phosphate (Dornbos, 2011). Non-specific phosphatization of tissues considered to have low potential for phosphatization, such as plant and non-phosphatic cuticles, and large-sized organisms is rare but possible, also outside the marine setting (e.g. Arena, 2008).

Today, several fossils are assigned to the Thylacocephala, in several Lagerstätten and fossil sites from the Cambrian to the Cretaceous in different geographic areas. The Jurassic soft-bodied biota from La Voultesur-Rhône (France) (Charbonnier et al., 2010) has yielded a number of remarkable Thylacocephala, besides a variety of other fossils. Quantitative analyses, performed by Charbonnier et al. (2010), of 388 arthropods preserved in nodules reveal that Thylacocephala are dominant (33%) in this Lagerstätte with solenocerid shrimps (22%), coleiid crustaceans (15%) and penaeid shrimps (10%) making up the most of the assemblage. The Thylacocephala are preserved with soft parts (e.g. muscles, gut) replicated in apatite and coated by pyrite. Many of the fossils of this Fossil-Lagerstätte are fully three-dimensionally preserved in calcite or siderite concretions; those in the sediment are normally partially flat-tened. The preservation style is distinctive and characterized by the replacement of soft tissues by a number of different minerals controlled by subtle variations in the chemistry of the organisms (Wilby, 1993; Wilby et al., 1996).

Pinna (1985) reported 398 thylacocephalans in the Jurassic Osteno (Italy) fossiliferous association, collected between 1964 and 1979, which represent the 28.9% of the fauna in terms of number of individual specimens. The fossiliferous rocks of Osteno consist of microcrystalline calcite with granules of pyrite and have originally siliceous material (like sponges and radiolarians) now totally or partially replaced by calcite. The specimens of this Lagerstätte are exceptionally well preserved. In many of them, Pinna (1985) reports that besides the chitinous carapace, the compound eyes (that he erroneously interpreted as the cephalic sac), the three pairs of cephalic appendages, the segmented thorax with short thoracopods and the recessed abdomen have also been preserved. In some specimens the branchiae, the muscles and the stomach with its gastric contents are preserved, too (Pinna, 1985). The organisms preserved in the Osteno deposits are almost exclusively non-calcareous organisms, such as crustaceans (Garassino, 1996), polychaetes (Pinna and Teruzzi, 1982), fishes (Duffin, 1998) and plants (Pinna, 1985). In this Fossil-Lagerstätte the animals are replicated by amorphous calcium phosphate, whereas the land plants underwent carbonization (Pinna, 1985).

Data about the preservational pathways of some concavicarids from the Late Devonian of Australia (Briggs and Rolfe, 1983) show that in this locality, Thylacocephala are preserved in apatite and form the nucleus of the concretions found in this outcrop (Allison and Briggs, 1991). Phyllocarid crustaceans from the same outcrop show a cuticle composition dominated by calcite with variable amounts of diagenetic apatite (Briggs et al., 2011), whilst soft tissue preservation in fishes shows apatite composition with some calcite (Briggs et al., 2011 and references therein).

These few, but spectacular, described examples of conservation in Lagerstätten indicate that the preservation of Thylacocephala (Table 1) is in each case very similar, implying a taxonomic factor involved in their preservation. In some cases the phosphatic cuticle of this group could have acted as a phosphatization source even if the milieu was not phosphorous rich.

Literature data show that the majority of the members (and putative ones: *Isoxys*, *Tuzoia* WALCOTT, 1912) of the Thylacocephala, which have been found with preserved soft parts (e.g. Hu, 2005; Vannier et al., 2006 and references therein; Charbonnier et al. 2010) possess a great raptorial appendage (not well suitable for a benthic life style) and large eyes, ma-

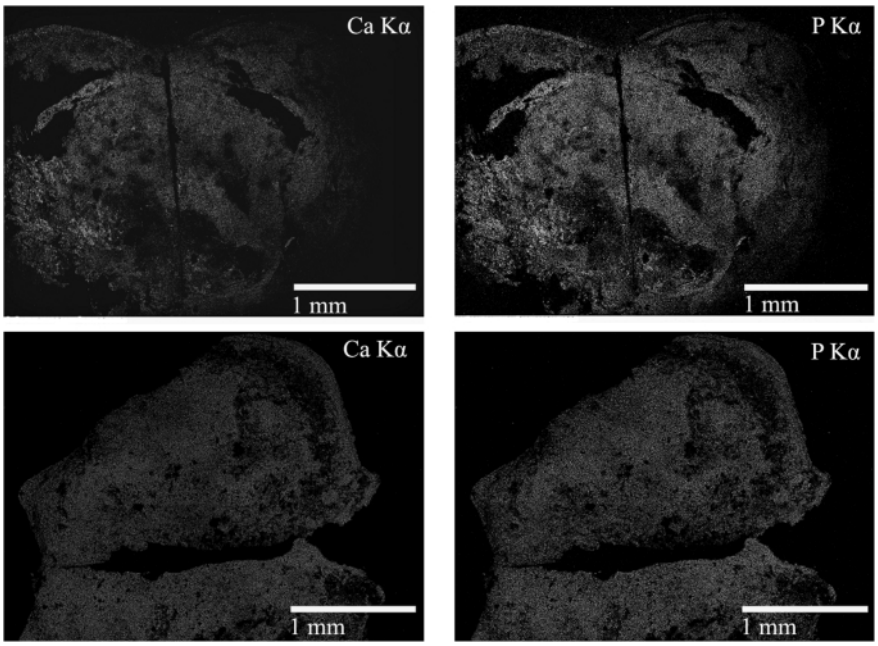

Figure 7: Elemental mapping of the carapace (preserved in butterfly position) of two Cambrian bradoriids from the Chengjiang (upper specimen, AF Lao2009) and Guanshan (lower specimen, AF Shit up 0911) faunas from Yunnan province (South China). Both specimens are housed at the FU Berlin, Institute of Geosciences collection.

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TABLE 1: Overview of all the Thylacocephala and their preservation pathways. Modified after Vannier et al. (2006).

Genera	Age	Occurrence	Preservation	References
Ainiktozoon Scourfield, 1937	Early Silurian	Scotland	Phosphatization	Scourfield 1937; Van der Brugghen et al. 1997
Ankitokazocaris Arduini, 1990	Early Triassic	Italy	no data	Arduini 1990
Atropicaris Arduini and Brasca, 1984	Late Triassic	Italy	no data	Arduini and Brasca 1984; Arduini 1988
Austriocaris Glaessner, 1931	Late Triassic	Austria	Apatite + C (this paper)	Glaessner 1931; Rolfe 1969, 1985; this paper
Clausocaris Polz, 1989	Late Jurassic (Tithonian) / Middle Jurassic (Callovian)/Late Triassic (Norian)	Germany / France/ Italy	organic matter since it reacts to UV light /phosphatization covered by pyrite/ no data	Polz 1989,1990, 1992, 1993 Arduini 1992
Concavicaris Rolfe, 1961	Devonian (Eifelian)–Carboniferous (mid–Pennsylvanian)	France, Czech Rep., Australia, USA	no data/Mold	Chlupáč 1963; Briggs & Rolfe 1983; Schram 1990; Stigall & Hendricks 2007
Convexicaris Schram, 1990	Carboniferous (mid–Pennsylvanian)	USA	no data	Schram 1990
Coreocaris Kobayashi, 1937	Early Permian	South Korea	no data	Kobayashi 1937
Dollocaris Van Straelen, 1923	Middle Jurassic (Callovian) /Late Jurassic	France /Germany	phosphatization covered by pyrite	Secrétan 1983, 1985; Secrétan and Riou 1983; Fröhlich et al. 1992; Polz, 2001
Harrycaris Briggs and Rolfe, 1983	Late Devonian (Frasnian)	W. Australia	phosphatization	Briggs and Rolfe 1983
Kilianicaris Van Straelen, 1923	Middle Jurassic (Callovian)	France	phosphatization covered by pyrite	Van Straelen 1923
Mayrocaris Polz, 1994	Late Jurassic (Tithonian)	Germany	no data (but probably like *Clausocaris* from Germany)	Arduini 1990; Polz 1994
Microcaris Pinna, 1974	Late Triassic	Italy	no data	Pinna 1974; Dalla Vecchia, 1992
Ostenocaris Arduini, Pinna, and Teruzzi, 1984	Early Jurassic (Sinemurian)	Italy	phosphatization	Pinna 1974; Arduini et al. 1980, 1984; Alessandrello et al. 1991
Paraostenia Secrétan, 1985	Middle Jurassic (Callovian)	France	phosphatization covered by pyrite	Fröhlich et al. 1992
Proboscicaris Rolfe, 1962	Middle Cambrian	Bohemia/ British Columbia / USA	no data/no data/internal mold and carbonaceous rest	Chlupáč and Kordule, 2002; Rolfe, 1962; Robinson & Richards, 1981
Protozoea Dames, 1886	Late Cretaceous (Santonian)	Lebanon	phosphatized muscle	Schram et al. 1999;
Pseuderichthus Dames, 1886	Late Cretaceous (Santonian)/ Jurassic	Lebanon - Germany	phosphatized muscle	Schram et al. 1999
Thylacocephalus Lange, Hof, Schram, and Steeman, 2001	Late Cretaceous (Santonian)	Lebanon	patch of phosphatized soft tissue	Lange et al. 2001
Rugocaris Tintori, Bigi, Crugnola, and Danini, 1986	Early Jurassic (Pliensbachian)	Italy	no data	Tintori et al. 1986
Yangzicaris Shen, 1983	Middle Triassic	China	no data	Shen 1983
Unnamed form (in Mikulic et al. 1985)	Silurian (Llandovery)	USA	Fluorapatite	Mikulic et al. 1985
Unnamed form -putative- (in Page et al., 2010)	Late Ordovician (Katian)	UK	authigenic phyllosilicate	Page et al., 2010
Zhenghecaris	Early Cambrian	China	no data	Vannier et al., 2006

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king it likely that the Thylacocephala were swimming predators, despite the Thylacocephala have been previously interpreted by Pinna (1985) as benthonic necrophagous organisms based on *Ostenocaris*, lacking developed sense organs, without eyes, and having a cephalon modified into a large cephalic sac that acted as an attachment device on soft marine bottoms . This interpretation was wrong: the cephalic sac correspond in fact to the compound eyes. In a recent paper Paterson et al. (2011) affirm that the compound eyes of some Jurassic thylacocephalans were even bigger than those of the Cambrian top predator *Anomalocaris* WHITEAVES 1892. Shen (1983) described *Yangzicaris* from the Anisian Stage (Middle Triassic) of China as being very similar to Austriocaris and interpreted it as adaptable to the brackish environment. He thus suggested a palaeoenvironment of *Yangzicaris* close to the sea shore. *Dollocaris* was defined by Secrétan (1985) as a predator lurking at the sea bottom or semi-burrowed in the sediment. Rolfe (1985) and later Charbonnier (2009) proposed *Paraostenia* as a mesopelagic predator, and compared it to the hyperid amphipods. Polz (1992) made a reconstruction of the mode of life of several Thylacocephala: *Paraostenia*, *Ostenocaris*, *Dollocaris* (based on previously published papers) and *Clausocaris*. He proposed a mixture of active and passive locomotion for *Clausocaris*, and suggested that the Thylacocephala developed several modes of life, as the classes existed from the Cambrian (e.g. *Proboscicaris* ROLFE 1962, *Isoxys*, *Tuzoia*) for a period of more than 400 million years, and spread over the oceans with a plausible range of morphological adaptations.

Linking *Isoxys* and *Tuzoia* to the Thylacocephala, as Polz (1992) had already done, Vannier et al. (2006) propose an Early Cambrian origin of the Thylacocephala. The carapace of *Isoxys* was compared with the Thylacocephala by Rolfe (1985) as well as Arduini and Pinna (1989), and the similarities between *Austriocaris* and *Isoxys* were already noticed by Glaessner (1931). Soft parts recorded for *Isoxys* comprise of raptorial appendages, prominent eyes (Hu, 2005; Garciá-Bellido et al., 2009a), large and robust antennulae composed of about seven articles armed with spines and inner lamella (Stein et al., 2010), 13 trunk appendages with an uniform biramous design, exopod fringed with marginal setae, a tube-like gut with probable digestive glands (Garciá-Bellido et al., 2009b) and 17 imbricated gill lamellae along the posterior margin (Fu et al., 2011). Even if the observation of two pairs of antennae in a thylacocephalan seems to support the opinion that thylacocephalans may be related to crustaceans (Lange et al., 2001) not all the scientists agree with this interpretation. However, the fossil record includes other taxa that are equipped with two pairs of antennae without being crown-group crustaceans; for instance, Phosphatocopida MÜLLER 1964 with two pairs of antennae as well as a mandibular-like development of the third pair of cephalic appendages (Lange et al., 2001 and references therein). These so-called crustaceomorphs do not fall within the clade of the crown-group crustaceans, but they nevertheless resolve immediately basal to this crown-group in cladistic analyses (Lange et al., 2001 and references therein).

Concerning carapace architecture and eyes, *Tuzoia* resembles *Isoxys* and *Zhenghecaris*, both from the Early Cambrian of China (Vannier et al., 2006; 2007). The latter was already placed into the Thylacocephala group by Vannier et al. (2006). *Tuzoia* has a domelike carapace, not strongly mineralized with a reticulated pattern (similar to those of other bivalved arthropod from the Burgess Shale, such as *Perspicaris recondita* BRIGGS, 1977; *Proboscicaris* and *Isoxys* from the Chengjiang Biota) and spiny marginal and lateral processes (Vannier et al., 2007). Recovered soft parts account for a pair of simple segmented antennae, stalked compound eyes, and some evidence of internal structure, probably related to the digestive system (Vannier et al., 2007).

All of the features described –light carapace (probably chitinophosphatic, based on analyses and literature data), stalked/prominent eyes, raptorial appendages and the stomach content of *Ostenocaris*: fish remains, arm hooks of cephalopods, and parts of arthropods, (Pinna, 1985)– are consistent with a free swimming predatory lifestyle of the Thylacocephala, *Isoxys* and *Tuzoia*.

6.3. Taphonomic pathways of the Polzberg Fossil-Lagerstätte

The presence of soft part preservation in arthropods, cephalopods and fishes from the Polzberg Fossil-Lagerstätte characterizes it as a conservation deposit. Conservation deposits range from those in which the soft parts have decayed but complete articulated skeletons are preserved, to those in which soft parts are also preserved (Allison and Briggs, 1991). On the contrary, the nearby Lunz Fossil-Lagerstätte was defined by Meller et al. (2011) as a Konzentrat- Lagerstätte; the replacement of plant soft tissue by minerals is more common than in animals, as the cell membranes of animals are more prone to decay than plant cell walls (Briggs, 2003).

Data from previous studies show that in this Fossil-Lagerstätte, fossil plants are usually preserved as compressions,often with optimally preserved cuticles (Pott et al., 2010); insects are also preserved as compressions. As suggested by Meller at al. (2011), the fossilization potential of insects and leaves is to some extent comparable, and parallels in chemistry as well as in the ultrastructure of their respective durable organic matter are also recognizable. Preservation of organic carbon can be supported by transformation of ist delicate framework to substances able to survive time and burial. However, the most important factor in the long-term preservation of the chemistry of both plant and animal cuticles (arthropod cuticles, for example, consist of chitin fibres in a protein matrix, Schaefer et al., 1987) is diagenetic alteration into longchain hydrocarbons of an aliphatic composition (aliphatic polymers are characteristically highly insoluble and immobile, Briggs, 1999) similar to some kerogens (Briggs, 1999; Stankiewicz et al., 2000). This transformation (or “in situ” polymerization, *sensu* Gupta et al., 2006) to a more stable composition takes place over time

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without requiring especially high temperatures and pressures (although elevated temperature and pressure accelerate the process, Briggs et al., 2000) and accounts for most of the fossil record of terrestrial and marine arthropods that lacked a biomineralized exoskeleton (Gupta et al., 2006).

With regard to preservation in the Polzberg Fossil-Lagerstätte, the other analyzed group (cephalopods: Doguzhaeva et al., 2006, 2007 a, b) shows no presence of phosphorus. The black sheets, the material on their inner surface, the ink and the arm hooks consist of carbon, occasionally with minor amounts of sulfur. The shell is composed of calcium carbonate. The carbon composition and granular ultrastructure of arm hooks, ink, and soft tissue remains indicate that the non-mineralized structures are pseudomorphosed by carbon (carbonization), possibly due to C-accumulating bacteria (Doguzhaeva et al., 2007b). The surrounding sediment was not supplying enough phosphorous to allow more extensive soft-part phosphatization, since the mantle and the putative ink sac of the cephalopods are preserved as carbon replacement. This indicates that preservation of soft tissue at this site was not controlled by a phosphorus rich medium (in a P-rich milieu many soft tissues in cephalopods are normally replicated in apatite; see, e.g., Doguzhaeva et al., 2007a). In order for apatite to precipitate, the phosphorous concentration has to be sufficiently high to inhibit the precipitation of calcite or aragonite. The shells of these cephalopods are made of extremely pure calcium carbonate, most probably in the form of aragonite, and with the original ultrastructure still preserved (Doguzhaeva et al., 2007a). These authors also suggest that the lack of significant amounts of iron and calcium indicates that neither pyrite nor calcite is of importance as a preservational element in this substance. Iron presence is not significant (absent or with maximum of 1.32%) inside the carapace of *Austriocaris* and reaches 3.4% in the matrix. This carapace shows an apatitic layer and the detected organic remains in the carapace are composed of carbon, nitrogen and sometimes sulfur, point to kerogen. The presence of the phosphorus only inside the shell of this bivalved arthropod, together with the fact that apatite is absent from the surrounding matrix and was not detected in the cephalopods (Doguzhaeva et al., 2007a, b), strongly suggests that *Austriocaris* had a primary phosphatized cuticle. Lack of trace elements in the shells of cephalopods analyzed by Doguzhaeva et al., (2007a) indicates that the specimens have undergone virtually no replacement during fossilization. It is likely that most of the phosphorus of the actual diagenetic layer in *Austriocaris* was derived from decaying tissues of the carcasses and the carapaces of the *Austriocaris* themselves. In laboratory experiments (e.g. Briggs & Kear, 1993) only crustaceans yielded phosphatized soft tissue in the absence of a significant external source of phosphorus. This arthropod therefore had a primary organo-phosphatic carapace, as suggested also by the high level of organic matter in its cuticle.

Polzberg is missing in the most important papers and books on Fossil-Lagerstätten and exceptional preservation (e.g. Allison and Briggs, 1991; Pinna and Meischner, 2000; Selden and Nudds, 2012). As stated by Doguzhaeva et al. (2007a) with regard to cephalopods, carbon replacement of non-biomineralized structures is the preservation pathway at the locality of Polzberg, Austria. This hypothesis is confirmed by our data, with the abundant presence of organic remains detected in the carapace of the bivalved arthropod Austriocaris. The local phosphatization of its carapace, together with primary bio-aragonite preserved in the cephalopods, and the calcitic shell of the bivalve *Halobia* suggest that the preservation model is more complicated than so far assumed, and was probably influenced by a taxonomic factor. Furthermore, the presence of accumulation strata of juvenile specimens of the bivalve *Halobia*, often found in butterfly positions, and the fine horizontal lamination suggest deposition in a low energy setting, or at least indicate a lack of bottom currents. *Halobia* can also be used as an indicator of occasionally low oxygen environments according to Hopkin and McRoberts (2005) and McRoberts (2001). The same situation was proposed for *Bositra buchi* by Oschmann (1994a, b) and Röhl et al. (2001). Anoxia does not inhibit decay, but it may increase the possibility of soft part preservation.

Preliminary data from new outcrops in the Polzberg area show a fauna with a nektonic prevalence: fishes and cephalopods dominate the extremely well preserved soft bodied fauna. The organic material in the sediment, the presence of pyrite crystals (Fig. 6), the absence of sessile organisms and the lack of bioturbation suggest dysoxic to anoxic bottom conditions of the Reingraben Shales.

7. Conclusions

The Upper Triassic Fossil-Lagerstätte Polzberg in the Reingraben Shales can be classified as a conservation deposit. Analyses performed on several specimens of Austriocaris show an organo-phosphatic shell with a compact apatitic layer, and suggest that the taphonomic pathways of this Fossil-Lagerstätte are more complicated than hitherto expected: if phosphatization took place during fossil diagenesis, this process of phosphatization was selective. The co-occurrence of cephalopods with the putative ink sac preserved as carbonaceous compression and the shell as aragonite suggests that the carcass of *Austriocaris* itself was the source of the phosphorus and that this bivalved arthropod had a primary phosphatic cuticle. Data from previous publications together with the presented analyses suggest similar preservational pathways of the Thylacocephala in different fossil Konservat-Lagerstätten ranging from the Devonian to the Cretaceous and with different settings, supporting a primary phosphatic cuticle for this bivalved arthropod.

Although primary phosphatized cuticles are rare among arthropods, analyses based on Thylacocephala, bradoriids, and literature data about phosphatocopines, trilobites and aglaspidids suggest that a phosphatic cuticle may have evolved several times among different arthropod groups.

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Angela FORCHIELLI[1)2)*)] & Peter PERVESLER[2)]

[1)] Freie Universität Berlin, Malteserstraße 74-100, Haus D, 12249 Berlin, Germany;

[2)] Universität Wien, Geozentrum, Althanstrasse 14, A-1090 Vienna, Austria;

[*)] Corresponding author, geoange@hotmail.it

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