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Palaeobiological significance of damaged and fragmented thylacocephalan carapaces from the Upper Devonian of Poland

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ABSTRACT

This paper investigates thylacocephalan (?Crustacea) carapaces from the lower Famennian of the Holy Cross Mountains, Poland in order to check whether predation-related activities has influenced the mode of carapace preservation. Analysis of 225 specimens reveals that 71% of carapaces consist of complete/nearly complete specimens, and those that are incomplete have experienced purely taphonomic processes. The remaining 29% of specimens, are damaged and fragmented carapaces, the preservation patterns of which point to biological modifications due to predation. These damaged carapaces range from those that have some portions missing, to those totally fragmented into small pieces scattered on bedding planes. The damaged specimens lacking some portions of the carapace are similar to those described previously from the Frasnian of Australia, where they are interpreted to evidence fish predation. The loosely scattered cuticle fragments are very similar to those reported from the Pennsylvanian of the USA that are interpreted as shark regurgitates. We interpret the damaged and fragmented thylacocephalans from Poland as evidence for fish predation, consistent with previous evidence from fragmented cuticle preserved within coprolites. However, as the majority of cuticle fragments occurring within coprolites in previous studies are difficult to distinguish, the simple calculation of predation intensity is much lower (13%) to that obtained in the present study (29%). Thus, analysis of thylacocephalan carapace preservation conducted here, may serve as a calibrating tool for the assessment of a general predation intensity in a given palaeoenvironment based solely on coprolite data.

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1. Introduction

The Class Thylacocephala [Pinna et al., 1982](#) belong to a group of rather enigmatic marine arthropods which are currently grouped with crustaceans ([Lange et al., 2001](#); [Haug et al., 2014](#)). Thylacocephalans are known from the Silurian to the Upper Cretaceous ([Schram et al., 1999](#); [Schram, 2014](#); [Haug et al., 2014](#)), but some Lower Cambrian forms classified to thylacocephalans also occur ([Vannier et al., 2006](#)). Their geographic distribution is wide, and thylacocephalans are documented from all continents except Antarctica and South America ([Hegna et al., 2014](#)). The most characteristic features of thylacocephalans are a bivalved carapace enclosing almost the entire body; large, compound eyes present in many species; three pairs of long, subchalcate raptorial appendages on the anterior part of the body; and a series of small, paddle-like limbs in the posterior part ([Rolfe, 1985, 1992](#); [Briggs and Rolfe, 1983](#); [Vannier et al., 2006](#); [Charbonnier et al., 2010](#); [Schram, 2014](#)).

The mode of life of thylacocephalans was a subject of a debate (see e.g., [Rolfe, 1985](#)), but currently it is accepted that at least some species were pelagic predators, as evidenced from their large, spiny raptorial appendages and cuticular pores which might have played a role as bioluminescent photophores (e.g., [Secrétan, 1985](#); [Rolfe, 1985](#); [Vannier et al., 2006](#); [Charbonnier et al., 2010](#)). The occurrence of some species in deep-water facies, as evidenced from lithology and faunal association (e.g., [Charbonnier et al., 2010](#); [Zatoń et al., 2014](#)), attests to a pelagic life-style. Even the stomach contents, including fish remains or coleoid hooks, found in Lower Jurassic *Ostenocaris* ([Pinna et al., 1985](#)) may indicate that thylacocephalans were active nektonic predators; however, their scavenging mode of life is enigmatic and lacks evidence for or against.

Thylacocephalans were also predated upon by various organisms. [Pinna et al. \(1985\)](#) found fragmented thylacocephalan cuticle in the stomach contents of other thylacocephalans, and [Williams \(1990\)](#) found a complete carapace within the body cavity of a cladosealachian shark from the Famennian of Ohio. Late Devonian thylacocephalan remains were also detected in numerous gastric residues from the Gogo Formation of Australia by [Briggs and Rolfe \(1983\)](#), and recently fragmented cuticle of *Concavicaris* were found within some coprolites from the lower Famennian of Poland by

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Zatoń and Rakociński (2014). Apart of these, other evidence for predation on thylacocephalans in the fossil record consists of damaged and fragmented carapaces from the upper Frasnian of Australia (Briggs and Rolfe, 1983) and upper Carboniferous of Indiana, USA (Zangerl and Richardson, 1963). The data on the predation-related fragmentation patterns of thylacocephalan carapaces presented by Briggs and Rolfe (1983) is the only known such study conducted to date.

We focus on thylacocephalans from the lower Famennian of the Holy Cross Mountains, Poland. Having a sufficiently large sample, we analyze their state of preservation in order to check whether any mode of their preservation could be attributed to predation activity, and if so, how frequently they suffered predation and what animal was responsible for their death.

2. Material and methods

2.1. Material provenance

Thylacocephalan specimens were collected from the lower Famennian portion of the Upper Devonian section at Kowala quarry in the Holy Cross Mountains, central Poland (Fig. 1). Kowala quarry is confined to the Gałęzice-Bolechowice Syncline in the southwestern part of the southern Kielce Region. In palaeogeographical terms, the area is situated in the Chęciny-Zbrza Basin

(cf. Szulczewski, 1971; Racki et al., 2002). The fossils were mainly collected from the trench located in the north-central part of the Kowala quarry (N 50°47'43.476", E 20°33'53.568"), but some specimens were also collected from coeval deposits exposed in the western quarry wall (for details see Zatoń and Rakociński, 2014). The deposits consist of alternating thin-bedded, laminated, dark, carbonaceous shales or marls and thin-bedded, grey, micritic limestones, which stratigraphically cover the *Palmatolepis crepida* standard conodont Zone and the Pw (*Puteoscortum williereae*) acritarch Zone, which correlates with the uppermost *Palmatolepis triangularis* and *P. crepida* conodont zones (Filipiak, 2009). The thickness of the fossil-bearing deposits spans some 21 m of the lower Famennian interval, being confined within the H-4 unit of Racki and Szulczewski (1996). The majority of specimens are preserved in dark shales and marls, but some may be found in the intercalating micritic limestones (Zatoń et al., 2014).

2.2. Methods

In total, 294 specimens were collected. Where possible, the parts and counterparts of thylacocephalans were gathered. All fossil remains (whole and fragmented) were collected in order to avoid bias towards better preserved specimens. After first inspection, 69 specimens were discarded as their true preservation is unclear due to incompleteness of the rock slabs, and the

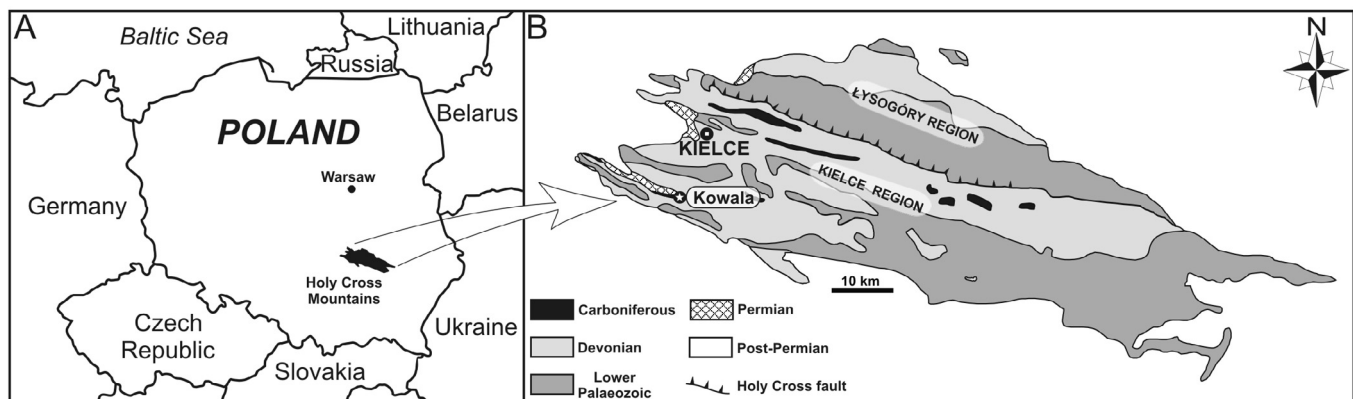


Fig. 1. Locality and geological background of the Kowala Quarry. (A) Locality of the Holy Cross Mountains in Poland. (B) Geological sketch-map of the Holy Cross Mountains with the Kowala quarry indicated. Adapted from Zatoń and Rakociński (2014) and based on Marynowski et al. (2000).

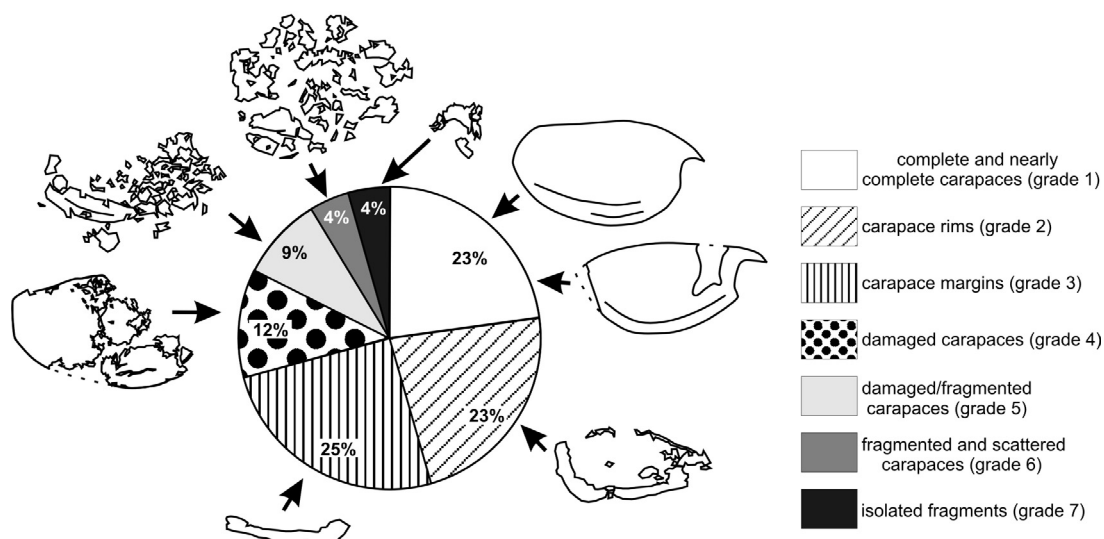


Fig. 2. Graphical presentation of a range of thylacocephalans' state of preservation along with percentage contribution of the each type (grade).

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