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Patterns of cornulitid encrustation on the Late Devonian brachiopod shells from Russia

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ABSTRACT

Upper Devonian brachiopods from the Central Devonian Field, Russia have been investigated with respect to encrustation patterns of cornulitids. These Palaeozoic encrusters were very characteristic component of shelly substrates during the Devonian and may serve as valuable objects for palaeoecological studies, especially those concerning the encrusters-host relationships. On the basis of rich material, it has been shown that cornulitid abundance significantly increased in the lower Famennian. Their disparity also increased from one morphotype (robust) present in the upper Frasnian to two distinct morphotypes (robust and slender, presumably representing two different species) in the lower Famennian. The analysis of the spatial occurrence of cornulitids on two dominant lower Famennian brachiopod species (*Cyrtospirifer zadonicus* and *Ripidiorhynchus huotinus*) showed, that these encrusters preferred the marginal parts of the shells. This, together with a dominant directional growth of cornulitids toward the commissure, indicates that cornulitids benefited from food brought by feeding currents produced by the brachiopod's lophophore. The unequivocal evidence for *syn vivo* association of the cornulitids and their brachiopod hosts is the presence of distinct shell malformations caused by cornulitid growth affecting the host's shell-secreting epithelium, preserved on some lower Famennian specimens. Interestingly, these malformations were caused by a slender cornulitid morphotype only. Thus, it is evident that during food gathering from the inhalant currents, this cornulitid species exerted a distinct, negative effect on the brachiopod – a deviation of its shell growth. In this case, we may consider this particular cornulitid species as ectoparasite rather than commensal with respect to its host.

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1. Introduction

Cornulitids are exclusively Palaeozoic tubicolous fossils. They first appeared in the Middle Ordovician and ranged up to the Upper Carboniferous (Zhan and Vinn, 2007; Vinn, 2010). Characterized by small, calcitic conical shells, cornulitids have been placed in the family Cornulitidae by Fisher (1962), although their exact zoological affinity is still uncertain. Formerly, cornulitids have been affiliated with such taxa as annelids, cnidarians, molluscs or bryozoans (see Vinn and Mutvei, 2005; Zhan and Vinn, 2007 for review). With respect to morphology and microstructural details, cornulitids are similar to other enigmatic fossils – tentaculitids (see Vinn and Mutvei, 2009). Despite different lifestyles (substrate-cemented in cornulitids and free-living in tentaculitids), it has been proposed that some tentaculitids could have derived from cornulitids (Dzik, 1991). Currently, cornulitids are hypothesized to

represent the phoronid-related or even calcified phoronid lophophorates (Vinn and Mutvei, 2009; Taylor et al., 2010). Whether they were more or less phylogenetically linked with phoronids is unresolved; however, the lophophorate nature of cornulitids is better supported by the finds of the cornulitid-like fossils from the Cambrian with lophophore-like structures preserved (Yang et al., 2013).

Cornulitid tubeworms are well-known as encrusters of any hard substrates and are especially common as inhabitants of various fossil invertebrate skeletons as either epibionts (e.g., Richards, 1974; Morris and Felton, 1993) or endobionts (Vinn and Wilson, 2010; Vinn, 2016). Cornulitids have been recognized as especially common encrusters of brachiopod shells (e.g., Richards, 1974; Bordeaux and Brett, 1990; Zhan and Vinn, 2007) with whom they could have had either symbiotic (e.g. Brezinski, 1984; Zhan and Vinn, 2007) or parasitic (Richards, 1974; Kesling et al., 1980) relationship. Thus, characterized by cemented, calcitic tubes and directional growth, cornulitids are useful fossils in palaeobiological studies, especially those concerning the host-epibiont relationships.

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In the present paper we analyze the Upper Devonian brachiopod shells with respect to the occurrence of cornulitid encrusters. The main aims of the present study are: 1) to investigate the morphological diversity and abundance of cornulitids encrusting brachiopod shells, 2) documentation of the patterns of encrustation of cornulitids on the brachiopod shells in order to find any preferences with respect to the host, and 3) to find out whether the investigated cornulitid-brachiopod host associations were characterized by a symbiotic or parasitic relationship.

2. Material and methods

2.1. Material provenance

The cornulitids under study have been found encrusting brachiopod shells and isolated valves collected in two localities, Khlevnoe and Kamenka, situated north to the Voronezh city along the Don River bank in southern part of the Central Devonian Field, Russia (Fig. 1). The material was collected during the joined Polish-Russian field trip in 2012.

In Khlevnoe, the shallow marine upper Frasnian carbonate deposits in the form of limestones, marly limestones, marls and subordinate clays occur (e.g., Sokiran, 2002; Filipiak and Zbukova, 2006). These deposits represent the regional Evlanovo Horizon which corresponds to the Upper *rhenana* standard conodont Zone (see Sokiran, 2002) and the *Aurora speciosa* (AS) miospore Subzone of the *Cristatisporites deliquescens*–*Verrucosiporites evlanensis* (DE) miospore Zone (Filipiak and Zbukova, 2006). The deposits of the Evlanovo Horizon at Khlevnoe attains 9 m (Filipiak and Zbukova, 2006) and are rich in various fossils, such as brachiopods, gastropods, tabulate and rugose corals, as well as various encrusting taxa. The encrusted brachiopod fauna is dominated by spiriferids (*Cyrtospirifer*, *Theodossia*), atrypids (*Variatrypa*) and productids (*Donalosisa*) (Sokiran, 2002; Zatoń and Krawczyński, 2011; Zatoń et al., 2017).

In the Kamenka locality, the material come from the so-called upper quarry where the lower Famennian deposits represented by various limestones and clays with abundant brachiopods, bivalves,

gastropods, crinoids and various encrusting taxa occur. Here, the encrusted brachiopods are mostly represented by rhynchonellids (*Ripidiorhynchus huotinus* [= *Orophomesorhynchus huotinus* according to Sartenaer, 2001]) and spiriferids (*Cyrtospirifer zadonicus*) (Sokiran, 2002; Zatoń and Krawczyński, 2011; Zatoń et al., 2017). The deposits attain 14 m in thickness and mainly represent the regional Zadonsk Horizon, which correspond to the *crepida* standard conodont Zone (see Sokiran, 2002) and the *Convolutispora zadonica* (Za) miospore Subzone of the *Cyrtospora cristifera*–*Diaphanospora zadonica* (CZ) miospore Zone (Filipiak and Zbukova, 2006). The deposits of the Zadonsk Horizon are here capped by 2 m thick dolomitic limestone representing the Elets Horizon, corresponding to the *rhomboidea* conodont Zone (Sokiran, 2002).

2.2. Methods

The encrusted brachiopod material consists of both complete shells and isolated valves (pedicle and brachial). Sometimes the shell may be complete but only one valve is visible while the second one is embedded in indurated sediment, which was difficult to be removed without damaging its outermost shell layer with encrusters. Thus, we treated a particular valve, even in the complete shells, as a single specimen (substrate, see Zatoń et al., 2017). This approach enlarges the sample size for our analysis and has no negative impact on the results concerning the spatial distribution and orientation of particular cornulitids on a given valve.

The material used for the present study include 504 valves from the upper Frasnian and 586 valves from the lower Famennian. The all brachiopod specimens were carefully observed under the binocular microscope in order to search for cornulitid encrusters, and such data as cornulitid number (abundance), diversity and their preferences with respect to the brachiopod host were noted. For cornulitid abundance and diversity, all the brachiopod species encountered have been inspected. However, in order to check the colonization preference with respect to the brachiopod host, only numerically the most abundant encrusted brachiopods were chosen. These include the lower Famennian *Cyrtospirifer zadonicus*

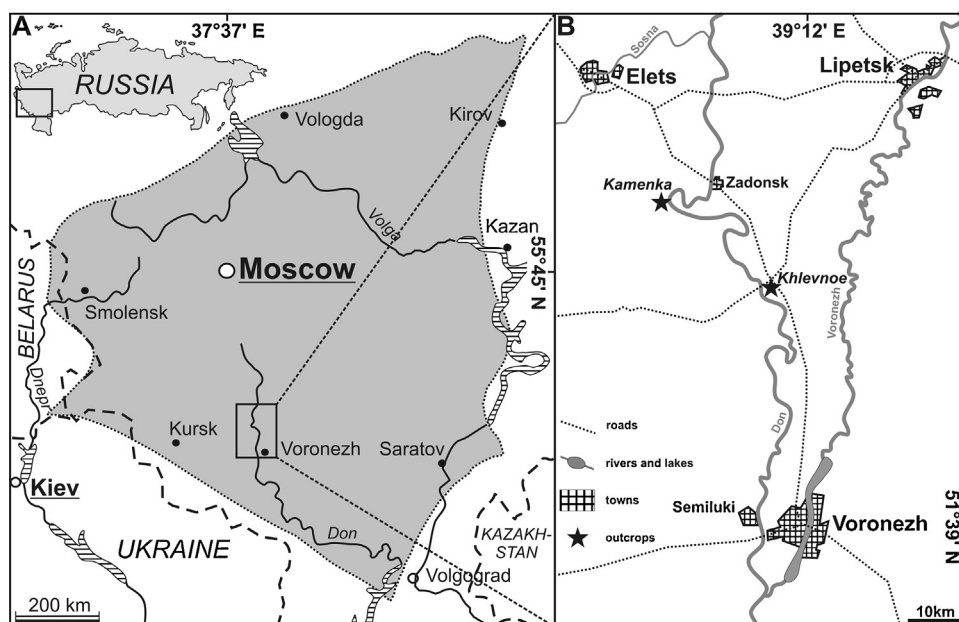


Fig. 1. A. Geological sketch-map of the Central Devonian Field (shaded area) in Russia with the investigated area indicated. B. Locations of the investigated sites at Khlevnoe and Kamenka (adopted from Zatoń et al., 2017, as modified after Sokiran, 2002, and Zatoń and Krawczyński, 2011).

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