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The youngest record of "Housean pits" in Late Devonian ammonoids

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An unusual occurrence of parasitic "Housean pits" in an internal mould of an ammonoid referred to as *Felisporadoceras* cf. *subvaricatum* (Sobolew, 1914) from the middle Famennian of Poland is described here. Until now, the youngest goniatites showing pitting on the internal moulds were known from the Middle Devonian (early Givetian). This material probably constitutes the youngest record of this phenomenon in goniatites.

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INTRODUCTION

Over five decades ago, House (1960) noted for the first time Devonian ammonoids (from the Early and Middle Devonian: Emsian–Givetian of England, Algeria and Germany) with more or less regularly distributed pits in the internal moulds. Similar pits were later described in detail by Chlupáč and Turek (1983) from almost the same stratigraphic levels in Bohemia, and by De Baets *et al.* (2011) from Morocco, Algeria and Germany. They were also mentioned and/or illustrated by Davis and Mapes (1999), Belka *et al*. (1999), Klug (2002), as well as Korn and Klug (2002) from Early and Middle Devonian goniatites. Similar structures are also known in Silurian nautiloids (see e.g., Manda and Turek, 2009; Turek and Manda, 2010). Additionally, Keupp (1986) described pits in the internal moulds of Early Jurassic ammonoids. These pits resemble (in shape and size) individual larger pits in some Devonian ammonoids (type 4 *sensu* De Baets *et al*., 2011); however, the pits in Jurassic specimens are not paired (see Keupp, 1986, figs. 1–2). Hengsbach (1996) named all these structures "*forma concreta*". Davis and Mapes (1999) named all pits in the internal moulds of Devonian ammonoids as "Housean pits", in honour of Michael R. House who first documented this phenomenon (see also Becker and Kirchgasser, 2007; De Baets *et al*., 2011).

Recently, De Baets *et al*. (2011) published a detailed study of this kind of shell malformation from Early and Middle Devonian ammonoids. Based on shape, size and arrangement of the pits, five types of the "Housean pits" can be differentiated accordingly (for detail see De Baets *et al*., 2011). Remarkably, they provide evidence for the parasitic origin of these structures (see De Baets *et al*., 2011). In addition, because of the lack of knowledge of "Housean pits" from younger strata, they concluded that the parasites probably became either extinct or stopped causing the formation of the "Housean pits" after the Middle Devonian. However, the present discovery of "Housean pits" in the middle Famennian *Felisporadoceras* from Poland is evidence that the fossil record of this phenomenon continues at least into the middle Famennian.

GEOLOGICAL SETTING

The specimen described here come from the well-known Kowala section of the Holy Cross Mountains, Poland (Fig. 1A). One specimen was found in 2010 by L. Marynowski in dark grey marly shales (in rubble), directly near the northern quarry wall, where a middle Famennian rhythmic succession of limestones and marly shales with pyritized fauna (Fig. 1B; KPG horizon *sensu* Marynowski *et al*., 2007) belonging to the unit J (*sensu* Berkowski, 2002) is exposed. The stratigraphic setting of this unit has been determined using ammonoids (Rakociński, 2006) and includes two zones, *Pernoceras dorsatum* and *Pseudoclymenia pseudogoniatites*, which corre-

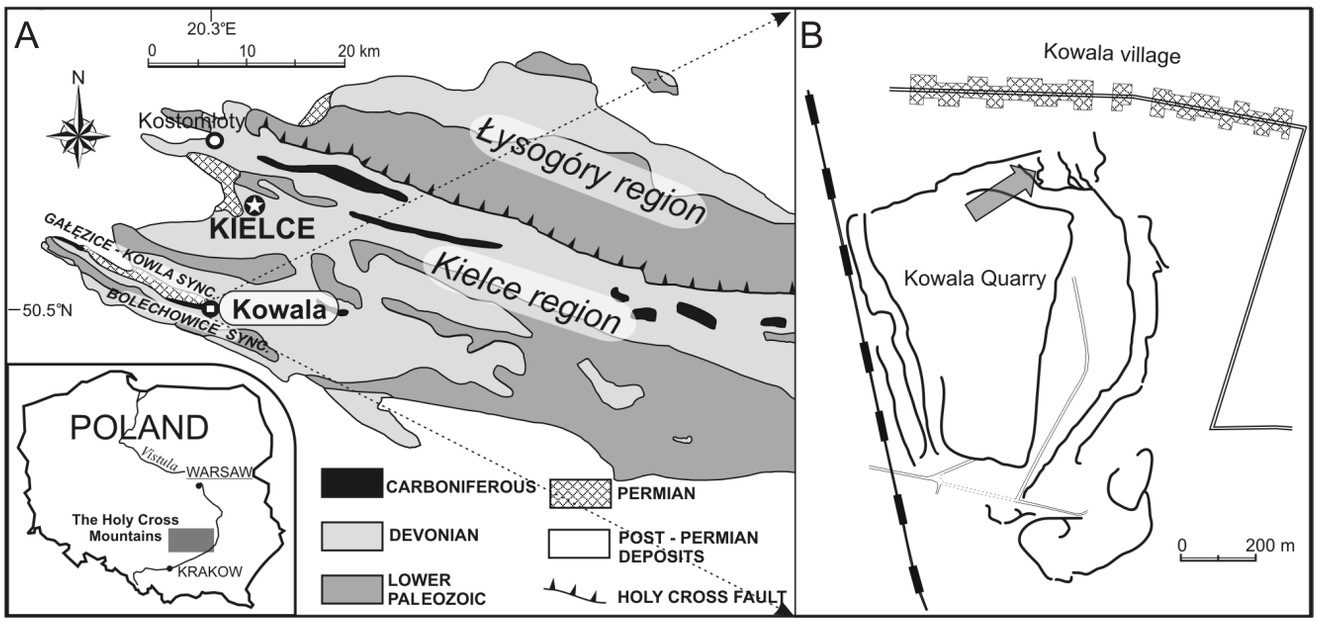

Fig. 1A – simplified geological map of the western and central part of the Holy Cross Mountains showing the location of the Kowala Quarry; B – schematic map of the Kowala Quarry (Marynowski *et al.*, 2007); the arrow indicates the position of the KPG – goniatite level where *Felisporadoceras* with "Housean pits" was discovered

spond to the latest *marginifera* conodont zone (see also Marynowski *et al*., 2007, fig. 3). For more detailed information concerning the geology and sedimentology of this part of the succession at Kowala Quarry see, e.g., Racki and Szulczewski (1996), Berkowski (2002) and Marynowski *et al*. (2007).

DESCRIPTION OF THE NEW SPECIMEN WITH "HOUSEAN PITS"

The goniatite is small (17 mm in diameter) and preserves much of the body chamber and the phragmocone. The specimen was identified as *Felisporadoceras* cf. *subvaricatum* (Sobolew, 1914) and is preserved as pyritized internal mould. It is partly overgrown by a second generation of pyrite (Fig. 2B; *cf*. Brett and Baird, 1986, fig. 9D).

The pits are subcircular, shallow and small (diameter *ca*. 0.5 mm – both in spiral and radial diameter; *cf*. De Baets *et al*., 2011; Fig. 1), and they are chaotically arranged. These certainly represent "Housean pits" of type 2 or a transitional form between type 1 and type 2 *sensu* De Baets *et al*. (2011). The pits of type 1 are larger than in type 2; they are lengthened in spiral direction and are thus more or less oval. The pits of type 2 are relatively small and numerous; they are chaotically arranged or in more or less radial rows. In this transitional form, the pits have an intermediate size (for details see De Baets *et al*., 2011). The pits in *Felisporadoceras* occur mainly on the ventral side of the phragmocone (Fig. 2B, C) and only a few are visible on the flank of the body chamber (Fig. 2A). In this specimen there is no pattern or regular arrangement of the pits.

DISCUSSION

Although pits on the internal moulds of Devonian ammonoids have been known for several decades, their origin has been intensively disputed since than. The "Housean pits" correspond to a marked local thickening of the inner shell wall. House (1960) tentatively suggested that these pits represent the moulds of pearls that must have formed *syn vivo* on the inner wall of the body chamber. Despite the fact that he lacked evidence, House (1960) explained that these pits probably represent traces of enclosed parasites or foreign particles that entered the space between the mantle and the shell, causing an irritation and formation of a pearl-like structure (for more details see De Baets *et al*., 2011). Davis and Mapes (1999) proposed a parasitic origin of these structures, but the firm evidence is still lacking in their consideration. Keupp (1986) also suggested that these structures might have been caused by parasites. Recently, De Baets *et al*. (2011) published a comprehensive study of this type of shell malformation in Early and Middle Devonian ammonoids. Based on new material from Morocco, they provided substantial support for the parasite hypothesis. De Baets *et al*. (2011) reported a unique finding of tiny tubes, which are located inside the ammonoid shell wall and were overgrown by the innermost layer of cephalopod shell, thus forming pearls.

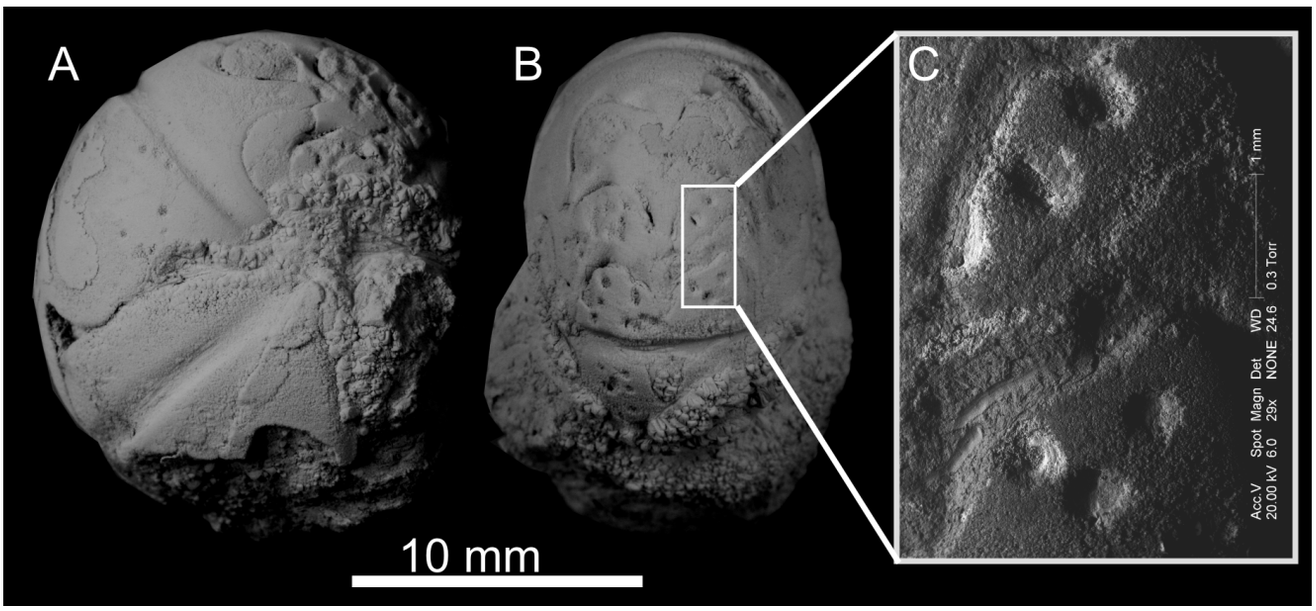

Fig. 2. "Housean pits" on *Felisporadoceras* cf. *subvaricatum* (Sobolew, 1914) GIUS4-3541-KW-21HP from the middle Famennian, Kowala Quarry

A – rare pits on the lateral side of the body chamber; **B** – ventral view of a specimen showing dense pits on internal mould of the phragmocone; **C** – detailed view of part B; GIUS – Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland.

These details of the ammonoid pearls were visible in longitudinal sections of some *Sellanarcestes* shells. De Baets *et al*. (2011) suggested that digenetic trematodes might have been responsible for the formation of the tubes and the pearls surrounding them, based on the similarity between Devonian ammonoid pearls and pearls occurring in Recent bivalves. In their opinion, the parasites responsible for the pit formation either became extinct or stopped causing this after the Middle Devonian (see De Baets *et al*., 2011). By contrast, the present discovery of "Housean pits" in the middle Famennian *Felisporadoceras* from the Holy Cross Mountains proves that this phenomenon occurred much longer, at least until the middle Famennian.

In modern environments, trematodes often utilize molluscs as intermediate hosts (Littlewood and Donovan, 2003; Littlewood, 2006; De Baets *et al*., 2011; Huntley and Scarponi, 2012) and cause the formation of pearls (e.g., Conway Morris, 1981; Cremonte and Ituarte, 2003), while vertebrates (e.g., fish, bird or mammal) are often the terminal hosts (e.g., Huntley and Scarponi, 2012). A parasitic origin for the "Housean pits" of the Kowala specimen is here tentatively proposed and supported by the occurrence of parasitic traces in juvenile and small-sized acanthodian and placoderm fishes from the Late Devonian of Latvia (Upeniece, 2001, 2011; Littlewood and Donovan, 2003), as well as in sarcopterygians and placoderms from the Late Devonian of Latvia and Russia (Lukševics *et al.,* 2009), which were potentially the final hosts to the (?) trematodes.

Remarkably, *Felisporadoceras* belongs to the Tornoceratacеae, which derives from the Anarcestaceae. Most other occurrences of "Housean pits" were documented from the Anarcestaceae, which fits well together when considering the parasite-ammonoid co-evolution suggested by De Baets *et al*. (2011). It appears like the parasites that infested the earlier ammonoids cleaved to one large group of ammonoids, also in the Late Devonian. It appears like the parasites that infested the earlier ammonoids cleaved to one large group of ammonoids, also in the Late Devonian (Klug, pers. comm.).

CONCLUSIONS

The hypothesis that ammonoids were intermediate hosts to parasites (perhaps trematodes) until the Late Devonian (perhaps with fish as terminal hosts) can be supported by the occurrence of "Housean pits" in the internal mould of ammonoids from Poland. However, further research on Late Devonian cephalopods is still needed to better understand the ammonoid-parasite co-evolution, and their conjectural demise, possibly during the end-Devonian Hangenberg biotic crisis.

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