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Discussion

Drill holes in tests of the echinoid *Echinocyamus linearis* from the *Heterostegina* Sands (middle Miocene, Poland) record the predation of cassid gastropods. There is no evidence that some of the drill holes are the result of eulimid parasitism, as has been suggested in critical comments. Also, contrary to the critical suggestions, not all drill holes can be classified within the ichnospecies *Oichnus simplex*. Although the drill holes differ distinctly in outline morphology, they were probably produced by only one cassid species, *Semicassis miolaevigata*.

Introduction

Drill holes observed on tests of the clypeasteroid echinoid *Echinocyamus linearis* from the middle Miocene Korytnica Basin documented in the paper of Ceranka and Złotnik (2003) were originally interpreted as the record of predation of cassid gastropods. However, a cassid origin for the drill holes was partially questioned by Donovan and Pickerill (2004). The same authors also critically commented the nomenclature used by Ceranka and Złotnik (2003). In the light of recent knowledge of palaeobiology and ichnology of the drill holes, we find the argumentation of Donovan and Pickerill (2004) to be unconvincing.

The origin of drill holes

Predatory cassids and parasitic eulimids are two gastropod groups that can drill in echinoid tests. The drill holes made by these drillers are often undistinguishable. Fortunately, beside the drill holes, eulimids can also leave attachment scars on the tests of their hosts. Apart from that, the drill holes made by eulimids are sometimes healed by the echinoids. In case of cassid-echinoid interactions, such phenomena have not been observed (see Kowalewski and Nebelsick 2003 and literature cited there). Both attachment scars and healed drill holes can be therefore considered as diagnostic for eulimid drillers.

As previously reported, neither attachment scars nor healed drill holes have been found in the material. Because of this, we excluded eulimids as potential borers. Consequently all the drill holes observed on tests of *E. linearis* were attributed to cassids (Ceranka and Złotnik 2003). Contrary to our original diagnosis, Donovan and Pickerill (2004) suggest, however, that some of the analysed drill holes could be the result of eulimid parasitism. They argue that eulimids leave attachment scars only occasion-

ally and, because of this, their diagnostic value is low. The rarity of attachment scars postulated by Donovan and Pickerill is a major point of their argument and they support it by the authority of Kowalewski and Nebelsick (2003).

Laboratory observations of recent eulimids parasitizing on echinoids indicate, however, that attachment scars are produced frequently by eulimids. Lützen and Nielsen (1975) show that *Echineulima mittrei* and *Echineulima eburnea* leave very deep attachment scars in the tests of their hosts and this is typical for these eulimid species. Warén and Crossland (1991) reported that all drill holes produced by another eulimid species, *Hypermastus obliquistomus* were surrounded by attachment scars. Attachment scars were also observed when echinoids were infested by three other eulimids, *Hypermastus orstomi*, *Hypermastus mareticola*, and *Clypeastericola* sp. (Warén et al. 1991). Thus, attachment scars appear to be typical for eulimids.

Also the conclusions of Kowalewski and Nebelsick (2003), when carefully studied, seem to constitute rather poor support for Donovan and Pickerill's argumentation. Indeed, as it was cited by the latter authors, Kowalewski and Nebelsick (2003) wrote that they "cannot provide reliable diagnostic guidelines for differentiating unambiguosly drill holes made by eulimids from those made by cassids". However, despite this, they finally concluded that the presence of attachment scars could be used as an "indirect" criterion for identifying eulimid drill holes. Moreover, they do not suggest that attachment scars are produced by eulimids extremely rarely. All in all, the conclusions of Kowalewski and Nebelsick (2003) seem to be generally less radical than those presented by Donovan and Pickerill (2004).

In such circumstances the lack of attachment scars in our large collection of *Echinocyamus* from the Korytnica Basin (over 7200 complete tests bearing more that 300 borings) becomes a very strong argument against the eulimid origin of the drill holes.

The lack of healed drill holes (not commented broadly by Donovan and Pickerill) may also indicate that eulimids should be excluded as potential borers. Preliminary observations of Warén et al. (1994) showed that two out of twenty five holes produced by *Hypermastus mareticola* were repaired by the hosts. These results suggest that test reparation by infested echinoids does not occur only accidentally. If the echinoids from the Korytnica Basin would have been indeed infested by eulimids, at least some healed drill holes should be observed in the material.

The distribution of body fossils within the investigated deposits also suggests that the drill holes were produced by cassids rather than by cassids and eulimids. As we reported previously, almost all drilled tests (277 out of 278) were collected from the Heterostegina Sands, characterised by the lack of any fossil eulimids, whereas cassid remains have been found there (Gutowski 1984; Ceranka and Złotnik 2003). Thus, the eulimid origin of some of the drill holes proposed by Donovan and Pickerill is unparsimonious. In the subsequent part of their discussion, Donovan and Pickerill suggest that eulimids may have occured in the palaeobiocoenosis but they have not been preserved due to their small size. Indeed, large and thick-shelled cassids are undoubtly characterised by a higher fossilization potential than the small and thin-shelled eulimids. In addition the fossil record of the Heterostegina Sands is strongly biased, as all the aragonitic remains, including gastropod shells, are preserved there only as internal moulds (Gutowski 1984; Ceranka and Złotnik 2003). However, beside the cassids (and many other large gastropods) also some smaller snails, such as nassarids, have been reported from the discussed deposits (see Gutowski 1984). The preservation potential of nassarids and eulimids most probably does not differ dramatically. Although the eulimid shells are usually slightly thinner and more elongate that those typical of nassarids, the size of the shells of these two groups is comparable. Taphonomic loss as an explanation for the absence of eulimids in the Heterostegina Sands proposed by Donovan and Pickerill is therefore not obvious.

Disproportion between the size of the drill holes and the size of fossil cassids was the last controversial issue. The drill holes are reletively small (0.04-1.80 mm in diameter, with a mean of 0.26 mm) when compared to the size of cassids remains (shell height ca. 3-6 cm) (Ceranka and Złotnik 2003; see also Złotnik and Ceranka 2005, this volume). Laboratory observations of Recent cassids clearly show that such large cassids as those recognised from the Heterostegina Sands should produce larger drill holes. Donovan and Pickerill state, therefore, that the cassid origin of small drill holes is not supported enough by the occurrence of appropriate body fossils (remains of small cassids). This is, however, incorrect argumentation because the large cassids at the earliest stage of development were obviously smaller. Consequently, at that stage of development they had to drill smaller drill holes. The occurence of large cassids may therefore be a strong argument on cassid origin of small drill holes.

Ichnology

The analysed drill holes were illustrated and described in detail in our paper but their ichnotaxonomic position has not been considered. It was critically commented on by Donovan and Pickerill, who stated that the bioerosional structures should be obviously classified to the appropriate ichnotaxa according to the rules of ichnological nomenclature. However, there are at least three important reasons that incline us to avoid ichnotaxonomic names: (1) The drill holes were probably produced by only one cassid species, *Semicassis miolaevigata* (Złotnik and Ceranka 2005, this

volume). We believe that there is no need to introduce ichnotaxonomic names when the borer is identified at a specific level. (2) Diversified morphology of the cassid drill holes does not correspond to the taxonomic diversity of the cassid borers. The results of laboratory observations of Hughes and Hughes (1971) show that even one cassid species preying on a single species of echinoid prey can produce many morphotypes of drill holes. The discussed drill holes also significantly vary in outline morphology (see Ceranka and Złotnik 2003: fig. 1; Złotnik and Ceranka 2005: fig 4). Because of this, they can not be simply classified to ichnospecies Oichnus simplex, as it has been proposed by Donovan and Pickerill. In fact, some of the drill holes are so irregular in outline that they cannot be attributed even to the ichnogenus Oichnus. Labelling the drill holes that were produced by one cassid species with different ichnogeneric names is unacceptable to us. (3) The palaebiological and palaeocological aspects of drilling predation were the main subjects of our considerations (Ceranka and Złotnik 2003). Ichnotaxonomic names would not provide any important information either to drill hole palaeobiology nor to palaeoecological interpretations presented in the discussed paper.

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