Traces of cassid snails predation upon the echinoids from the Middle Miocene of Poland

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Drill holes on tests of *Echinocyamus linearis* from the Middle Miocene Korytnica Basin represent the first well documented fossil record of cassid predation from Poland. These traces complement the ecological information on the size and structure of cassid populations recorded by body fossils. The high number of drill holes recognised from the *Heterostegina* Sands, the uppermost part of the Korytnica depositional sequence, indicates the occurrence of a large cassid population during the late stage of development of the Korytnica Basin. The small size of most of the drill holes indicates that juvenile gastropods of the family Cassidae, which are not preserved in the fossil record of the investigated area, were also present in the cassid populations.

Key words: Cassidae, echinoids, drill holes, predation, population structure, taphonomy, Middle Miocene, Poland.

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Introduction

Recent representatives of the family Cassidae are predatory gastropods that drill in tests of echinoids to consume their internal soft tissues (Hughes and Hughes 1971, 1981; Kowalewski and Nebelsick 2003). Drill holes in fossil echinoids attributed to cassids have been recorded from the Cretaceous and Tertiary. The oldest, Cretaceous drill holes were reported only from the Coniacian (Smith 1984) and Santonian (Rose and Cross 1993). However, beginning with the Late Eocene, the record of drilling predation upon echinoids continues without any major stratigraphic gaps (for review see Nebelsick and Kowalewski 1999 and literature cited therein). In contrast to the fairly good stratigraphic record of these drill holes, their geographic distribution, especially during the Palaeogene and Neogene epochs, is restricted to areas where most of the investigations of this phenomenon have been conducted, namely Australia (McNamara 1994), New Zealand (Beu et al. 1972) and Northern America (Gibson and Watson 1989). In particular, very little is known about the distribution of the drill holes in Neogene deposits of Europe. A short note on the occurrence of some gastropod drillings in tests of Miocene echinoids collected from certain undetermined localities from Malta and Poland appeared in the synthetic paper of Kowalewski and Nebelsick (2003). These drill holes neither have been illustrated nor described in detail making it impossible to determine whether they record predatory or parasitic interactions.

Drilled tests of the clypeasteroid *Echinocyamus linearis* Capeder, 1906 described in the present paper, form the first well documented fossil record of gastropod predation upon echinoids recognised from Poland. They may also represent the first well documented record of the gastropod-echinoid predatory interactions from the Parathetys. Material for this study comes from the Korytnica Clays and from the overlying *Heterostegina* Sands, deposited within the Korytnica Basin during the Middle Miocene transgression of the Parathetys sea on the southern slopes of the Holy Cross Mountains (see Radwański 1969; Bałuk and Radwański 1977).

The specimens are housed at the Faculty of Geology, Warsaw University, Poland (abbreviated MWG or BkK).

Drill hole morphology and identification of borer

The analysed drill holes are usually cylindrical in shape and their axis is perpendicular to the test surface. The outline of most of the traces is circular and smooth (see Fig. 1A, C). Some irregular holes also occur, but are less abundant (52 out of 316). The shapes of the latter traces appear to be strongly related to the morphology of the echinoid test because their outlines are often defined by outlines of ambulacral pores and/or by plates margins (see Fig. 1B, D, E). All drillings are complete and unrepaired. Most of them (246 out of 277) are single. The diameter of the drill holes ranges from 0.06 to 1.8 mm with a mean of 0.28 mm.

Many lines of evidence point to the cassid origin for these drill holes. First, single, perpendicular, circular to subcircular, lacking attachments scars and complete penetrations are typical for drillings produced by predators (see Carriker and Yochelson 1968; Carriker 1981; Kitchell et al. 1981; Rohr 1991; Kowalewski and Flessa 1994) and cassids are the

Table 1. Fossil cassids and traces of their predatory activity (drill holes) recognised from the investigated material. $FQD = \frac{DT}{NT} \times 100\%$. The number following the sign "±" is a confidence interval computed from the following formula (Łomnicki 1995): $p \mp 1.96\sqrt{\frac{p(1-p)}{n}}$, where p denotes the proportion of one kind of fossil (such as drilled tests) observed in the collection of n specimens.

Deposit		Korytnica Clays	*Heterostegina* Sands
portion of the investigated deposit (PD)		1500 kg	200 kg
cassid remains		3 incomplete shells of *S. miolaevigata*	–
drill holes on tests of *E. linearis*	total number of tests (NT)	12	7290
	total number of drilled tests (DT)	1	277
	number of single-drilled tests (SD)	1	246
	number of drill holes (ND)	1	316
	drilling frequency (FQD)	too few specimens for reliable estimation	3.8 ± 0.2%

only well documented drilling predators on Recent echinoids. Second, the presence of cassid shells (or their internal moulds) in the associated sediments (see Tables 1, 2 and Fig. 2) indicates that cassids and echinoids co-occurred within the benthic communities of the Korytnica Basin during the Middle Miocene. Third, the drill hole size and morphology correspond closely to drill holes made by Recent cassids (see Hughes and Hughes 1971, 1981; Nebelsick and Kowalewski 1999).

Other than Cassidae, the only well-documented present-day gastropods that drill echinoids are the parasitic eulimids. However, it is highly unlikely that the analysed damages are of eulimid origin, because no healed drill holes or attachment scars (typical of some of the eulimid-echinoid interactions—see Warén and Crossland 1991; Warén et al. 1994) have been found in the material. Moreover, almost all (277 out of 278) drilled echinoid tests were collected from the *Heterostegina* Sands, a deposit characterised by the lack of any fossil eulimids. The frequency of multiple drill holes recognised here (11%) is also lower than those typical of Recent eulimids (ca. 20%, see Warén et al. 1994).

Echinoids are also known to be bored by cirripedes, annelid worms, or clionid sponges (Gibson and Watson 1989; Rose and Cross 1993; Cross and Rose 1994), however, characteristic drill holes made by these sedentary organisms have not been recognised in the tests of *E. linearis*.

Palaeoecological and taphonomic implications

Frequency of cassid shells *versus* frequency of drill holes and size of cassid populations.—Cassid shells (or their internal moulds) and drill holes in echinoids attributed to them represent two sources of data establishing the presence of Cassidae in the benthic communities of the Korytnica Basin. However, the ecological information provided by body fossils is quite different from that found in the trace fossils, and the complementary use of both data is necessary to provide a fuller picture of the palaeoecology of Korytnica. For example, the numerical distribution of these two kinds of fossils in the clays differs significantly from that in the overlying sands. Also, the size of cassid population from the *Heterostegina* Sands recorded by body fossils seems to differ significantly from that recorded by drill holes.

Drilled echinoids and cassids are both relatively rare in the clays. Only three fragments of *S. miolevigata* shells and one drilled test of *E. linearis* were recovered from the material collected in this study (see Table 1). However, almost 180 specimens of very well preserved cassid shells (mostly of *S. miolevigata*) reported from the clays by previous authors, clearly indicate the occurrence of at least one large cassid population within the basin during the sedimentation of clays (see Table 2).

In comparison to the clays, the number of cassids described hitherto from the overlying sands is extremely low. Only one specimen of *S. miolevigata* was found there by Andrzej Radwański (personal communication 2002) and no more than 5–7 specimens identifiable to generic level were described from the sands by Gutowski (1984) (Jacek Gutowski personal communication 2002). No cassids have been found in the material investigated during this study (see Tables 1 and 2).

The very low number of cassid remains from the sands, corresponds well to the generally low abundance of gastropods in these deposits (Bałuk and Radwański 1977; Gutowski 1984). This situation is opposite to that for the clays, where gastropods are numerically dominant (Bałuk and Radwański 1977; Hoffman 1977; Kowalewski 1990).

The low number of cassids from the sands is likely a result of taphonomic bias caused by shell dissolution. This interpretation is strongly supported by the results of Gutowski

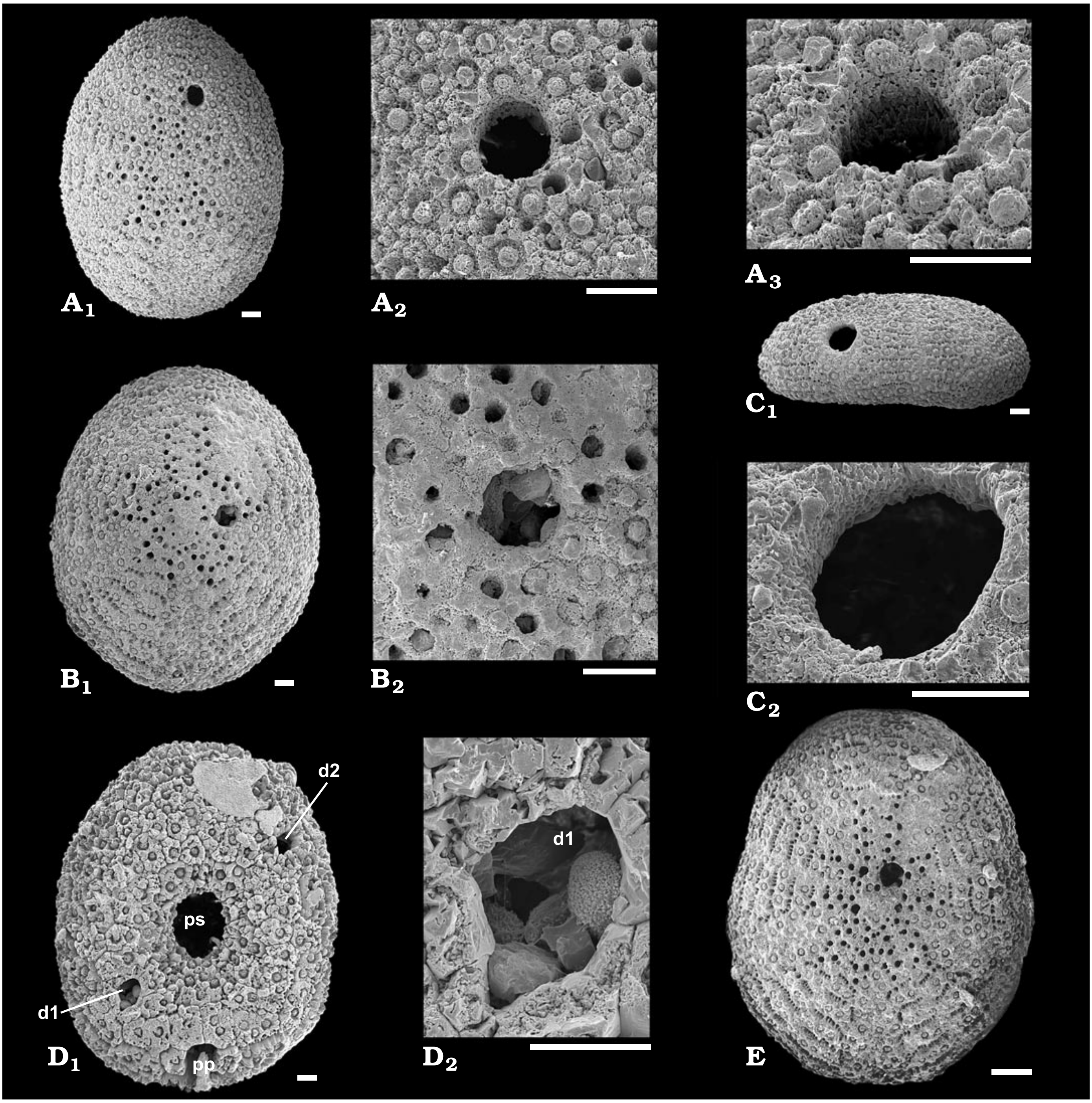

Fig. 1. Drilled tests of *Echinocyamus linearis* Capeder, 1906 from the Korytnica Basin. **A$_1$**. Single, cylindrical drill hole on aboral side of MWG/ZI/32/005, *Heterostegina* Sands. **A$_2$**, **A$_3$**. Close-ups of the drill hole in different views. **B$_1$**. Single irregular drill hole on aboral side of MWG/ZI/32/006 test, *Heterostegina* Sands and its close-up (**B$_2$**). **C$_1$**. Single, circular drill hole on aboral side of MWG/ZI/32/007, *Heterostegina* Sands and its close-up (**C$_2$**). **D$_1$**. Double, irregular drill holes on oral side of MWG/ZI/32/008, *Heterostegina* Sands; d1, d2, drill holes; ps, peristom; pp, periproct. **D$_2$**. Close-up of the drill hole d1. **E**. Single, irregular drill hole on aboral side of MWG/ZI/32/009, Korytnica Clays. Scale bars 200 μm.

(1984), who recognised that (1) all the organisms possessing primarily aragonitic shells preserved within the discussed deposits are represented only as casts or internal moulds and (2) calcitic remains are much more abundant there than all the other kinds of fossils.

In contrast to body fossils, traces of predation attributed here to Cassidae are common within the sands with more than 270 drilled specimens of *E. linearis* found (see Table 1). They are in fact the only record of the occurrence of a large cassid population within the benthic community of the Korytnica Basin during its late stage of development, when the *Heterostegina* Sands were deposited.

Table 2. Cassids recognised hitherto from the Korytnica Basin. Based on Pusch (1837), Friedberg (1912), Kowalewski (1930), Bałuk and Radwański (1977), Gutowski (1984), Bałuk (1977), Jacek Gutowski (personal communication 2002), Andrzej Radwański (personal communication 2002) and the present study.

Cassid species	Number of specimens	
	Korytnica Clays	*Heterostegina* Sands
Semicassis miolaevigata Sacco, 1890	ca. 150 shells	1 internal mould
Cypraecassis cypraeiformis (Borson, 1820)	10 shells	–
Cassidaria cingulifera Hoernes and Auinger, 1884	ca. 15 shells	–
Cassis sp.	–	not more than 5–7 internal moulds
total	ca. 175 shells	not more than 6–8 internal moulds

Height of cassid shells *versus* diameter of drill holes and structure of cassid populations.—All cassid shells collected from the Korytnica Clays are relatively large. The height of unbroken specimens ranges from 25 to 67 mm (see Bałuk 1995). The largest shell, reconstructed from fragmented remains of *S. miolaevigata* was most probably up to 85 mm in height (Bałuk and Radwański 1977). Remains of the few Cassidae from the overlying sands are also characterised by relatively large dimensions. The internal mould of the illustrated specimen of *S. miolevigata* (Fig. 2E) is 38 mm high and this is a typical value for the Cassidae from the sands (Jacek Gutowski personal communication 2002).

In contrast to the body fossils, drill holes attributed to the Cassidae are very small. 99% of the drill holes (312 out of 316 borings) recognised from the *Heterostegina* Sands are below 1.0 mm in diameter, with an average size of only 0.28 mm. The only drill hole recognised from the underlying clays is also very small, as its diameter is below 0.3 mm.

Although cassids usually produce small drill holes relative to their size (Hughes and Hughes 1971), laboratory studies on Recent Cassidae clearly show that fully grown individuals such as those recognised from the Korytnica Basin usually drill holes, which are over 2 mm in diameter (see Hughes and Hughes 1981). The discordance between the size of the drill holes, and the height of the cassid shells in the Korytnica Basin indicates that most of the investigated drill holes were produced by juvenile forms, which have not been preserved.

The lack of small fossil cassids in the sands can be easily explained as being a result of taphonomic bias since the preservation state of all gastropod fossils recognised within the discussed deposit (internal moulds or casts) does not favour the fossilisation of juvenile forms. However, the absence of juvenile shells in the clays is more difficult to explain because many smaller and thinner-shelled gastropods and bivalves have been preserved there. Moreover, the glossy surface of most of the mollusc fossils, and the preserved colour patterns on some gastropod and barnacle shells (Bałuk and Radwański 1977), indicate unusually favourable fossilisation conditions in the Korytnica Clays. On the other hand, the lack of larval gastropod shells within the clays is in contrast to their occurrence in many other fossil clayey deposits (see Kaim 2001 for example), suggesting that some as yet indeterminate factors (compaction?, dissolution?) caused the disappearance of these particularly fragile (or poorly calcified ?) remains from the fossil record of Korytnica.

Whatever the reason, for the absence of juvenile cassids in both the clays and the sands, the small drill holes recognised here on tests of *E. linearis* indicate that such small forms were in fact present in the live populations. This shows the importance of using trace fossils for reconstructing ecological information on population structure.

Occurrence of large cassid shells and the absence of large drill holes on the co-occurring *E. linearis* suggest that adult cassids most probably preyed upon other (larger) kind of prey. Among twenty echinoid species described hitherto from the Korytnica Basin (see Mączyńska 1977, 1987), representatives of the genera *Centrostephanus*, *Cidaris* and *Schizaster* seem to be large enough to be the potential source of food for adult cassids. Unfortunately, these echinoids are

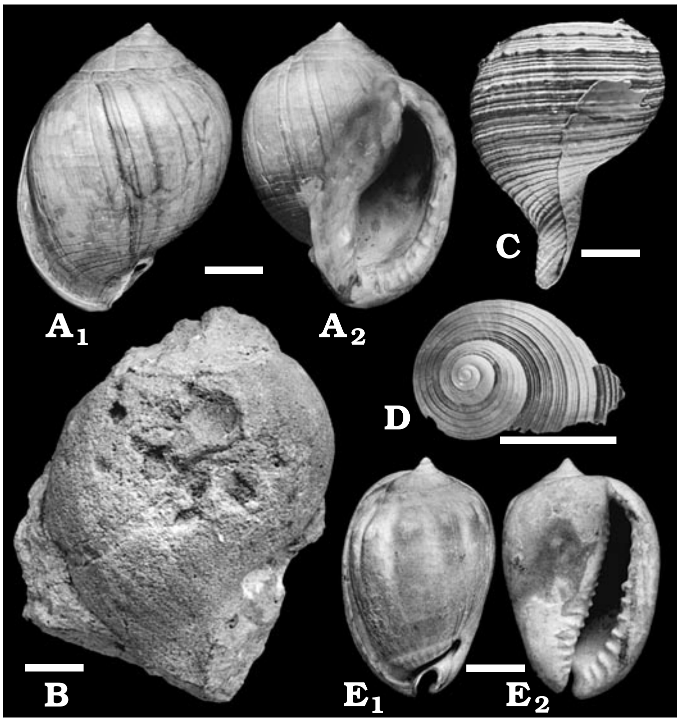

Fig. 2. Cassids from the Korytnica Basin. **A**, **B**. *Semicassis miolaevigata* Sacco, 1890. **A**. Shell MWG/ZI/32/002 in abapertural (A_1) and apertural (A_2) views, Korytnica Clays. **B**. Internal mould MWG/ZI/32/003, *Heterostegina* Sands. **C**, **D**. *Cassidaria cingulifera* Hoernes and Auinger, 1884. **C**. Incomplete shell BkK-G476 in latero-apertural view, Korytnica Clays. **D**. Incomplete shell BkK-G475 in apical view, Korytnica Clays. **E**. *Cypraecassis cypraeiformis* (Borson, 1820), shell MWG/ZI/32/001 in abapertural (E_1) and apertural (E_2) views, Korytnica Clays. Scale bars 1 cm. Photographs A, B, E taken by B. Malinowska, C, D taken by B. Drozd. Specimens BkK-G475-476 were previously illustrated by Bałuk (1995).

very rare, and when found their tests are usually largely disarticulated and show no traces of cassid predation. However, laboratory studies of Hughes and Hughes (1971) indicate that some cassid predation on echinoids occurs without drilling and has no chance of being preserved in the fossil record. In fact, the drilling behaviour is not obligatory for even a single cassid species (Hughes and Hughes 1971).

Drilling predation frequency.—The drill hole frequency for *Echinocyamus linearis* from the *Heterostegina* Sands is less than 4% (277 out of 7290 specimens are drilled). This is a very low value when compared to the drilling predation frequency recognised by Nebelsick and Kowalewski (1999) for recent species of *Echinocyamus* from the Red Sea (60–80%). However, it does fall within the generally broad range of drilling-predation intensities reported for fossil and recent echinoids, which is from ca. 2–3% to over 60% (see Kowalewski and Nebelsick 2003).

Due to the very low number of echinoid specimens in the underlying clays, the drilling frequency in the clays can only serve as a rough approximation (only eight echinoid tests were found there and only one of them was drilled—see Table 1) and comparisons between drilling intensities in the clays and sands would not be informative.

Geographical distribution of borers.—Representatives of the Cassidae found at the Korytnica Basin are characterised by a relatively wide geographic distribution within the Neogene (mostly Miocene) deposits of Europe.

S. miolaevigata was described from the Miocene of Austria (Hörnes 1856), Croatia (Eremija 1971), Hungary (Csepreghy-Meznerics 1956, 1969; Strausz 1966), Bulgaria (Kojumdgieva 1960) and France (Cossmann and Peyrot 1924). *C. cypraeiformis* was recognised within the Miocene deposits of Austria (Hörnes 1856; Hoernes and Auinger 1884), Hungary (Csepreghy-Meznerics 1956; Strausz 1966) Croatia (Eremija 1959) and France (Cossmann and Peyrot 1924). *C. cingulifera* is known from the Miocene of Austria (Hoernes and Auinger 1884), Bulgaria (Kojumdgieva 1960) and Hungary (Csepreghy-Meznerics 1954).

The distribution pattern of these cassids suggests that traces of their predation will likely be found soon in many other localities of the European Neogene, especially the Miocene deposits of Central Parathetys, where the discussed species appear most commonly (Miocene of Austria, Bulgaria, and Hungary).

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