

Patterns of drilling predation of cassid gastropods preying on echinoids from the middle Miocene of Poland

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Test-drilling predation by cassid gastropods on minute clypeasteroid echinoids has been studied in the fossil assemblage of the *Heterostegina* Sands (middle Miocene, Holy Cross Mountains, Poland). The analysed prey, collected from two sublithofacies of the *Heterostegina* Sands (coarse-grained *Heterostegina* Sands and fine-grained *Heterostegina* Sands), represent three species of *Echinocyamus* (*E. linearis*, *E. pusillus* and *E. pseudopusillus*). The drill holes were produced presumably by one cassid species, *Semicassis miolaevigata*. The investigation showed that drilling predation intensities varied among the prey species. Within both fine- and coarse-grained sands, *E. linearis* was drilled more frequently than *E. pusillus*. An intermediate value of drilling predation was recognised for *E. pseudopusillus*. The intensities of drilling predation recognised for some of the prey species (*E. pusillus*) varied also between (but never within) the sublithofacies. Drilling predation was both size- and site-selective. Larger individuals of *E. linearis* and *E. pusillus* were attacked more frequently and the aboral side of the test of all *Echinocyamus* species was drilled preferentially. An extremely high concentration of drill holes was observed in the apical disc and petals. Results obtained for the most abundant prey (*E. linearis*) indicate that the predatory behaviour of large cassids was somewhat different from those typical of small cassids. Large cassids drilled and consumed their prey almost always individually, whereas small cassids sometimes preyed upon the urchins in a group. Large cassids displayed also a higher site-selectivity. They more frequently drilled in the petals and apical disc. The patterns of drilling predation were most likely controlled by the potential energetic value of prey (measured by the internal volume/test thickness ratio), prey and predator mobility, prey mode of life, thickness and porosity of the prey's tests, as well as by the proportions between the size of the prey and size of the predator. The results suggest that the mode of life of the prey and its test structure can influence the drill hole morphology.

Key words: Cassidae, echinoids, drill holes, drilling predation, predatory behaviour, middle Miocene, Poland.

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Introduction

Recent representatives of the family Cassidae are predatory gastropods that can 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 reported from the Upper Cretaceous (Rose and Cross 1993) and the Tertiary (Beu et al. 1972; Gibson and Watson 1989; McNamara 1994; Ceranka and Złotnik 2003; Kowalewski and Nebelsick 2003).

This paper deals with the patterns of drilling predation displayed by cassids preying on three echinoid species, *Echinocyamus linearis* Capeder, 1906, *Echinocyamus pusillus* (Müller, 1776) and *Echinocyamus pseudopusillus* Cotteau, 1895, from the middle Miocene *Heterostegina* Sands (Holy Cross Mountains, central Poland). The morphology of the drill holes, drilling intensity, size- and site-selectivity and the relation of the predatory behaviour to the size of the predator, are analysed in detail. The results have been interpreted with the use of laboratory observations of Recent cassids preying on echinoids (Hughes and Hughes 1971, 1981) and the theoretical model of predator-prey interactions proposed by Kitchell et al. (1981).

The drilling activity of the Cassidae from the *Heterostegina* Sands was first recognised and described in our previous paper (Ceranka and Złotnik 2003); however, the topics of this study have not been discussed there. Many results presented here differ distinctly from those described by Nebelsick and Kowalewski (1999), who studied the drilling behaviour of cassids preying on Recent representative of *Echinocyamus*. These differences seem to be even more important in view of the fact that the dataset presented by the latter authors remained, until now, the only comprehensive case study of cassid–*Echinocyamus* interactions. Some of the predator-prey interactions examined in this study (e.g., relation of the predator size to the site of the attack) have not been explored previously for either Recent or fossil cassids.

Materials and methods

The material for this study comes from the *Heterostegina* Sands, deposited within the Korytnica Basin, a terminal part of a shallow bay which developed during the middle Mio-

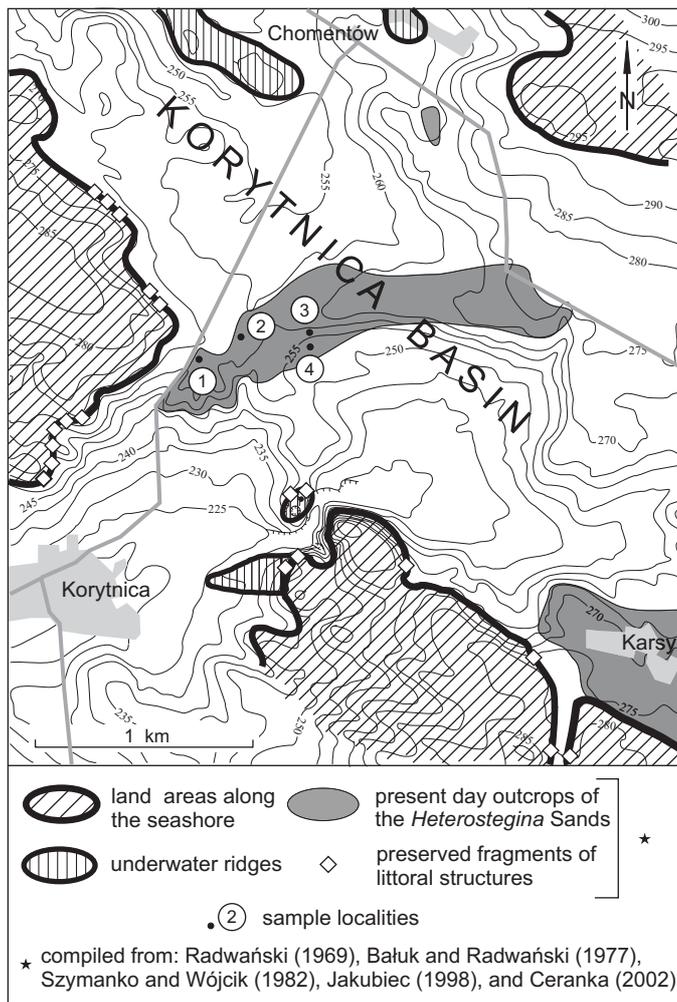


Fig. 1. Palaeoenvironmental sketch of the Korytnica Basin with sample localities (adapted from Złotnik 2003).

cene transgression of the Parathety Sea on the southern slopes of the Holy Cross Mountains, central Poland (see Radwański 1969; Bałuk and Radwański 1977; Gutowski 1984). Fossils were collected from four bulk-sediment samples, ~20 kg each (Fig. 1).

The grain-size analysis of sediment sample, made it possible to distinguish two sublithofacies within the investigated deposits. They are referred to here as “coarse-grained” and “fine-grained” sands. Each of the sublithofacies is represented by two samples (Fig. 2).

Complete echinoid tests belonging to three clypeasteroid species, *Echinocyamus linearis*, *Echinocyamus pusillus* and *Echinocyamus pseudopusillus* were obtained for the analysis. Out of 7923 tests collected, 353 were drilled (Table 1). The length of both the drilled and undrilled tests were measured under a binocular microscope with a precision of 0.05 mm. The maximum diameter (maximum length) of the drill holes was measured with the precision of 0.025 mm. When the analysed drill hole was composed of two evidently different parts, a circular one preserved only partially and a sec-

ond, irregular in outline, the maximum diameter of the circular part of the hole was measured (or estimated) only. The rejection of the irregular parts of the complex holes from the morphometric analysis is justified by the results of laboratory observations of Hughes and Hughes (1971) as well as by some observations on drill hole morphology and taphonomy presented in this paper (see next paragraph). These clearly show that the irregular parts of such complex drill holes are either of taphonomic origin or, if they were produced by the predator, they were made without drilling and are situated outside the drilling area.

The diameter of a cassid hole made in an echinoid test directly corresponds to the size of the predator (Hughes and Hughes 1981). Drill holes exceeding 0.4 mm (termed here as large drill holes) will be considered here as recording large cassids, whereas those smaller than 0.4 mm (small drill holes)—as recording small cassids. The terms large and small cassids were also used in our previous paper (Ceranka and Złotnik 2003); however, they have been defined differently there.

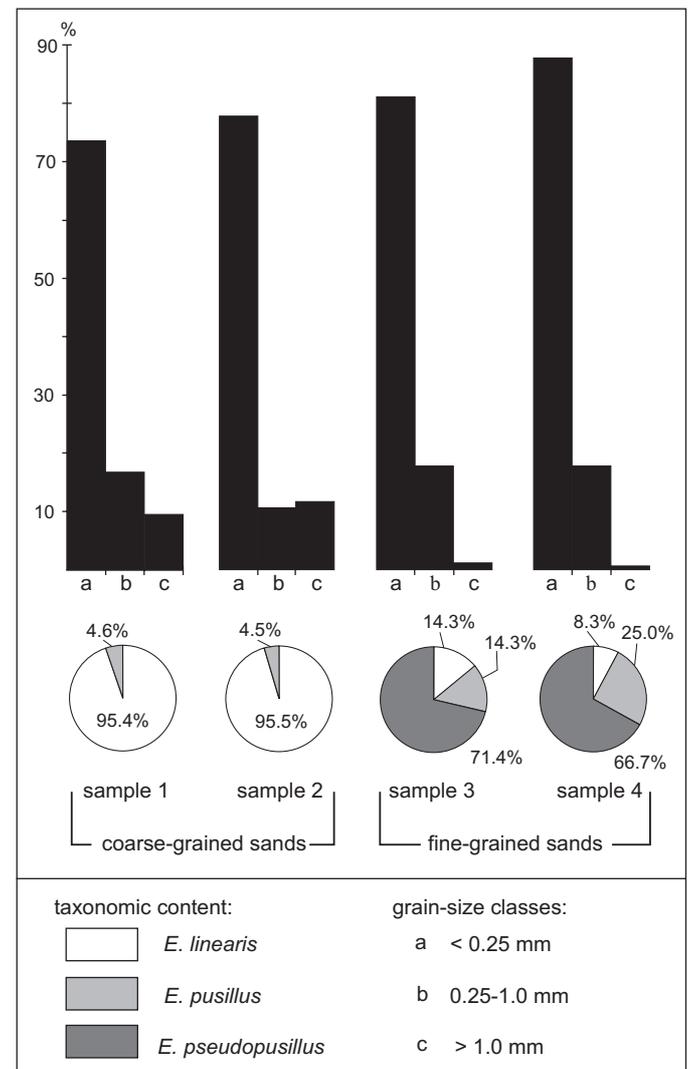


Fig. 2. Relative abundances of *Echinocyamus* species in particular samples compared to the results of grain-size analysis of the samples.

Table 1. Basic numerical and morphometric data on drilled and undrilled tests of *Echinocyamus* species and drill holes. Confidence intervals calculated from the formula $\bar{x} \pm 1.96 \frac{\delta}{\sqrt{n}}$, where \bar{x} denotes mean value, δ standart deviation, and n number of specimens (Łomnicki 1995).

variable	prey species	<i>E. linearis</i>			<i>E. pusillus</i>			<i>E. pseudopusillus</i>			Total		
	facies	coarse-grained sands	fine-grained sands	total	coarse-grained sands	fine-grained sands	total	coarse-grained sands	fine-grained sands	total	coarse-grained sands	fine-grained sands	total
Number of echinoid tests													
total		7290	34	7324	350	52	402	-	197	197	7640	283	7923
with no drill holes		7012	33	7045	320	38	358	-	167	167	7332	238	7570
with drill holes		278	1	279	30	14	44	-	30	30	308	45	353
with single drill holes		247	1	248	27	13	40	-	21	21	274	35	309
with multiple drill holes		31	-	31	3	1	4	-	9	9	34	10	44
with two drill holes		26	-	26	3	1	4	-	9	9	29	10	39
with three drill holes		3	-	3	-	-	-	-	-	-	3	-	3
with four drill holes		2	-	2	-	-	-	-	-	-	2	-	2
Test length (mm)													
range													
minimum		1.35	1.50	1.35	1.35	1.60	1.35	-	1.45	1.45	1.35	1.45	1.35
maximum		4.40	3.50	4.40	6.00	4.10	6.00	-	4.30	4.30	6.00	4.30	6.00
mean		2.40	2.42	2.40	2.70	2.68	2.70	-	2.59	2.59	2.42	2.59	2.42
95% confidence interval around mean value													
lower limit		2.39	2.23	2.39	2.65	2.53	2.54	-	2.52	2.52	2.41	2.53	2.41
upper limit		2.41	3.32	2.41	2.75	3.18	3.17	-	2.66	2.66	2.43	2.65	2.43
Number of drill holes													
total		316	1	317	33	15	48	-	39	39	349	55	404
small drill holes		262	1	263	27	13	40	-	36	36	286	50	336
large drill holes		54	-	54	6	2	8	-	3	3	60	5	65
single drill holes		247	1	248	27	13	40	-	21	21	274	35	309
multiple drill holes		69	-	69	6	2	8	-	18	18	75	20	95
small single drill holes		194	1	195	21	11	32	-	18	18	215	30	245
large single drill holes		53	-	53	6	2	8	-	3	3	59	5	64
small multiple drill holes		68	-	68	6	2	8	-	18	18	74	20	94
large multiple drill holes		1	-	1	-	-	-	-	-	-	1	0	1
Drill hole diameter (mm)													
range													
minimum		0.06	0.20	0.06	0.06	0.06	0.06	-	0.04	0.04	0.06	0.04	0.04
maximum		1.80	0.20	1.80	0.86	0.48	0.86	-	0.90	0.90	1.80	0.90	1.80
mean		0.28	-	0.28	0.24	0.24	0.24	-	0.18	0.18	0.27	0.20	0.26
95% confidence intervals around mean value													
lower limit		0.26	-	0.26	0.19	0.18	0.20	-	0.12	0.12	0.25	0.15	0.24
upper limit		0.28	-	0.28	0.29	0.30	0.28	-	0.14	0.14	0.29	0.25	0.28

Site-selective drilling has been assessed as follows: first, the relative frequency of the drill holes was calculated separately for the ambulacra, interambulacra, apical disc and many other natural sectors of the echinoid test. The relative area of each sector (proportion of the area of a given sector to the area of the entire echinoid test) was also estimated with the use of virtual, three-dimensional models of echinoid tests. Next, the theoretical frequencies of drill holes expected in the case of random (non-site-selective) drilling were determined for each sector. We simply assumed that with random drilling the number of drill holes found in a sector should be proportional to the area of that sector. Finally, the drill hole frequencies expected in the case of random drilling were compared with the relative frequencies of drill holes calcu-

lated directly from the dataset. When the differences were statistically significant, the positioning of drill holes was considered as site-selective. An analogous procedure was also applied separately to the aboral and oral side of test, however, only in such cases when the number of drill holes observed on tests of a given species of prey was large enough for reliable estimations (Fig. 3, Table 2). Due to similar reasons, the distributions of large and small drill holes were examined separately only for the most abundant prey.

The estimation of prey value to the predator (ratio of the energetic value of the prey's soft tissues consumed by the predator to the energy required for search, recognition and handling of prey – the benefit/cost ratio) is an important part of predator-prey interactions analysis (see Kitchell et al.

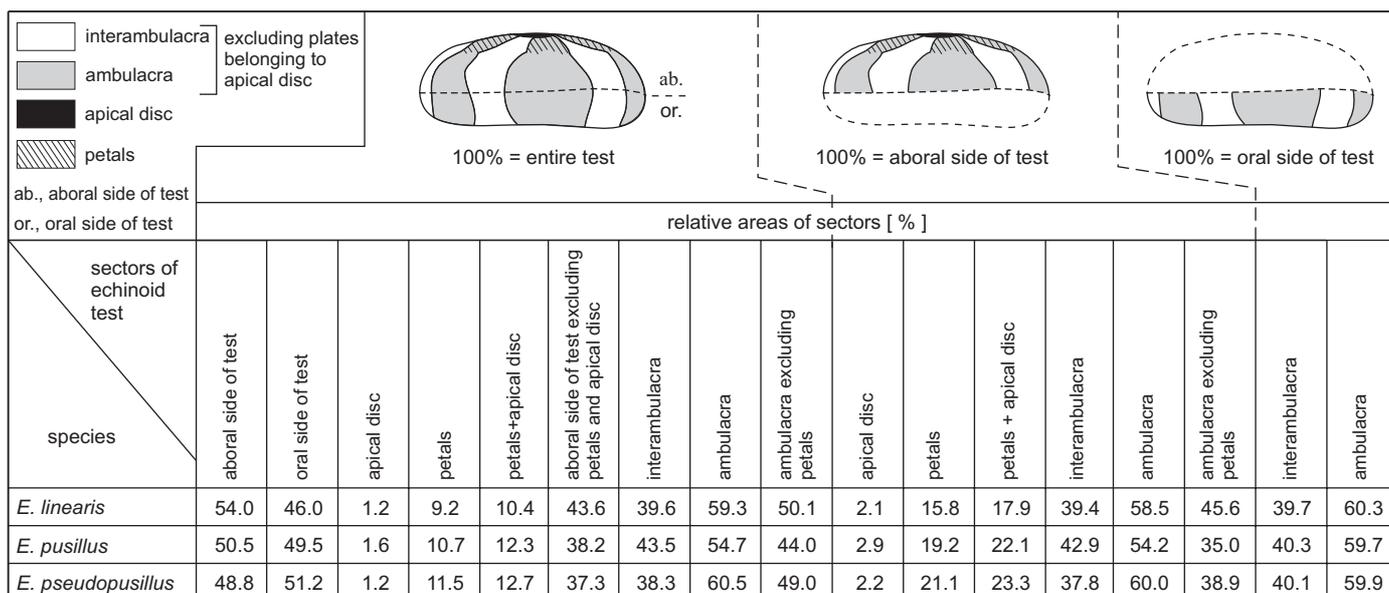


Fig. 3. Analysed sectors of *Echinocyamus* tests and their relative areas.

Table 2. Formulas used for calculations of the relative frequencies of drill holes in particular sectors of *Echinocyamus* tests.

1	$(\text{number of drill holes on aboral side of test} / \text{number of drill holes on entire test}) \times 100\%$
2	$(\text{number of drill holes on oral side of test} / \text{number of drill holes on entire test}) \times 100\%$
3	$(\text{number of drill holes on apical disc} / \text{number of drill holes on entire test}) \times 100\%$
4	$(\text{number of drill holes on petals} / \text{number of drill holes on entire test}) \times 100\%$
5	$(\text{summarised number of drill holes on petals and apical disc} / \text{number of drill holes on entire test}) \times 100\%$
6	$(\text{number of drill holes on aboral side of test excluding petals and apical disc} / \text{number of drill holes on entire test}) \times 100\%$
7	$(\text{number of drill holes on interambulacra} / \text{number of drill holes on entire test}) \times 100\%$
8	$(\text{number of drill holes on ambulacra} / \text{number of drill holes on entire test}) \times 100\%$
9	$(\text{number of drill holes on ambulacra excluding petals} / \text{number of drill holes on entire test}) \times 100\%$
10	$(\text{number of drill holes on apical disc} / \text{number of drill holes on aboral side of test}) \times 100\%$
11	$(\text{number of drill holes on petals} / \text{number of drill holes on aboral side of test}) \times 100\%$
12	$(\text{summarised number of drill holes on petals and apical disc} / \text{number of drill holes on aboral side of test}) \times 100\%$
13	$(\text{number of drill holes on aboral parts of interambulacra} / \text{number of drill holes on aboral side of test}) \times 100\%$
14	$(\text{number of drill holes on aboral parts of ambulacra} / \text{number of drill holes on aboral side of test}) \times 100\%$
15	$(\text{number of drill holes on aboral parts of ambulacra excluding petals} / \text{number of drill holes on aboral side of test}) \times 100\%$
16	$(\text{number of drill holes on oral parts of interambulacra} / \text{number of drill holes on aboral side of test}) \times 100\%$
17	$(\text{number of drill holes on oral parts of ambulacra} / \text{number of drill holes on aboral side of test}) \times 100\%$

1981; Kitchell 1986; Leighton 2002). Particularly, the value of a given prey with respect to the values of other prey should be known. The ratio of the internal volume of the shell to the shell thickness is usually considered as a good measure of prey value to the shell-drilling predator (Kitchell et al. 1981; Kitchell 1986; Kelley 1988, 1989; Anderson et al. 1991; Dietl and Alexander 2000; Dietl 2000, 2003; but see also Leighton 2002). The formula, introduced primarily by Kitchell et al. (1981) (and until now tested exclusively on mollusc prey—see references above), can be applied when the drilling time is proportional to the shell thickness and all the

soft tissues are consumed by the predator. Additionally, the drilling time/capturing time ratio is desirable.

Although the relationship between drilling time and thickness of echinoid test has not been studied for Recent cassids, some elements of cassid drilling techniques described by Hughes and Hughes (1981) (cutting of test and its dissolution—see below) indicate that the drilling time should indeed increase when the echinoid test becomes thicker. Hughes and Hughes (1971) showed also that cassids usually consume almost all soft tissues of the attacked echinoid and abandon their prey rarely, mainly due to unfavourable

changes of abiotic environmental conditions (see Hughes and Hughes 1981). Kitchell's formula seems therefore to be very useful in the analysis of cassid–echinoid interactions. Unfortunately, the relatively short drilling time recognised for Recent cassids is comparable to the time of prey capture (Hughes and Hughes 1981) and, because of this, the values of echinoid preys to the cassid predators calculated from the discussed formula should be treated only as rough approximations (see Kitchell et al. 1981).

Due to technical difficulties (small size of specimens and complex internal shape of the echinoid tests) we have estimated the values of the analysed preys from a slightly modified version of Kitchell's formula. Namely, we have replaced the internal volume of the echinoid test by the internal volume of a virtual cuboid defined by internal length, width and height of the test. The values calculated thereby are undoubtedly overestimated, however, the proposed modification seems to be a reasonable proxy useful for comparative analyses, as all the analysed preys are similar in shape. That is, the energetic value of prey should be comparable among specimens, both within and across species.

The predator-prey interactions recorded by drill holes have been analysed separately for each prey species. Representatives of the same species collected from two different sublithofacies were also examined separately. The analysis of drilling predation patterns focused mostly on *E. linearis* and *E. pusillus* from the coarse-grained sands and *E. pseudopusillus* from the fine-grained sands. *E. linearis* and *E. pusillus* from the fine-grained sands were usually excluded from the investigations because the number of their tests was, in most cases, too low for reliable estimations (Table 1). The relation between the size of the predator and the site of attack was analysed exclusively for the most abundant prey species, *E. linearis* from the coarse-grained sands.

Institutional abbreviations.—The studied specimens are housed in the Faculty of Geology, Warsaw University, Poland (abbreviated MWG).

The origin of drill holes

The origin of drill holes observed in tests of *E. linearis* from the *Heterostegina* Sands was discussed in detail in our previous paper (see Ceranka and Złotnik 2003 and references cited therein). The results presented there can be briefly summarised as follows: (1) The penetrations observed in tests of *E. linearis* are typical for drillings produced by predators (Carriker and Yochelson 1968; Carriker 1981; Kitchell et al. 1981; Rohr 1991; Kowalewski and Flessa 1994) and cassids are the only well-documented drilling predators on Recent echinoids. (2) 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). (3) The presence of fossil cassids in the *Heterostegina* Sands indicates that cassids and echinoids co-occurred within the

benthic communities of the Korytnica Basin. (4) Apart from Cassidae, the only well-documented present-day gastropods that drill echinoids are parasitic eulimids. However, eulimids have not been reported from the *Heterostegina* Sands and no healed drill holes or attachment scars typical of some of the eulimid–echinoid interactions (Lützen and Nielsen 1975; Warén and Crossland 1991; Warén et al. 1994) have been found in the studied material.

Because the material collected for this study also comes from the *Heterostegina* Sands and the morphology of the studied drill holes (including drill holes observed in *E. pusillus* and *E. pseudopusillus*) does not differ significantly from those attributed to Cassidae previously (Ceranka and Złotnik 2003), all the analysed drill holes are considered here to be of cassid origin.

The results of previous studies (Gutowski 1984; Ceranka and Złotnik 2003) suggest that the drill holes were produced by one cassid species, *Semicassis miolaevigata* Sacco, 1890. The internal mould of *S. miolaevigata* figured in Ceranka and Złotnik (2003: fig. 2B) is the only illustrated specimen of the Cassidae from the *Heterostegina* Sands. Other specimens, determined previously by Gutowski (1984) at the generic level, most probably also belong to *S. miolaevigata* (Wacław Bałuk, personal communication 2003).

The cassid origin of the drill holes proposed in our previous paper (Ceranka and Złotnik 2003) was partially questioned by Donovan and Pickerill (2004). Somewhat contrary to our original diagnosis they had suggested that some of the drill holes could have been produced by eulimids. A reply to Donovan and Pickerill's critical comments with detailed argumentation against the eulimid origin of the drill holes has been presented recently by Złotnik and Ceranka (2005).

Size, morphology and structure of the prey's test

The analysed prey species are represented by small specimens (test length = 1.4–6.0 mm). *E. linearis* is slightly smaller (mean test length = 2.4 mm) than *E. pusillus* and *E. pseudopusillus* (mean test length 2.6 and 2.7 mm respectively) and the difference is statistically significant (Table 1). In all species studied, the uppermost part of the aboral side of the test is almost completely dominated by an apical disc and a large petalodium (see Fig. 4O and schemes of echinoid tests on Fig 3). Both the peristome and periproct are located on the oral side of the tests (Fig. 4D).

All *Echinocyamus* species are characterised by the occurrence of internal supports (Durham 1966). These structures make the echinoid test more resistant to mechanical destruction. The strength of the echinoid test also obviously increases when the test becomes thicker. Both the test thickness and size of internal supports usually vary among the analysed prey. *E. linearis* is characterised by relatively thick test and well developed internal supports. The thickness of *E.*

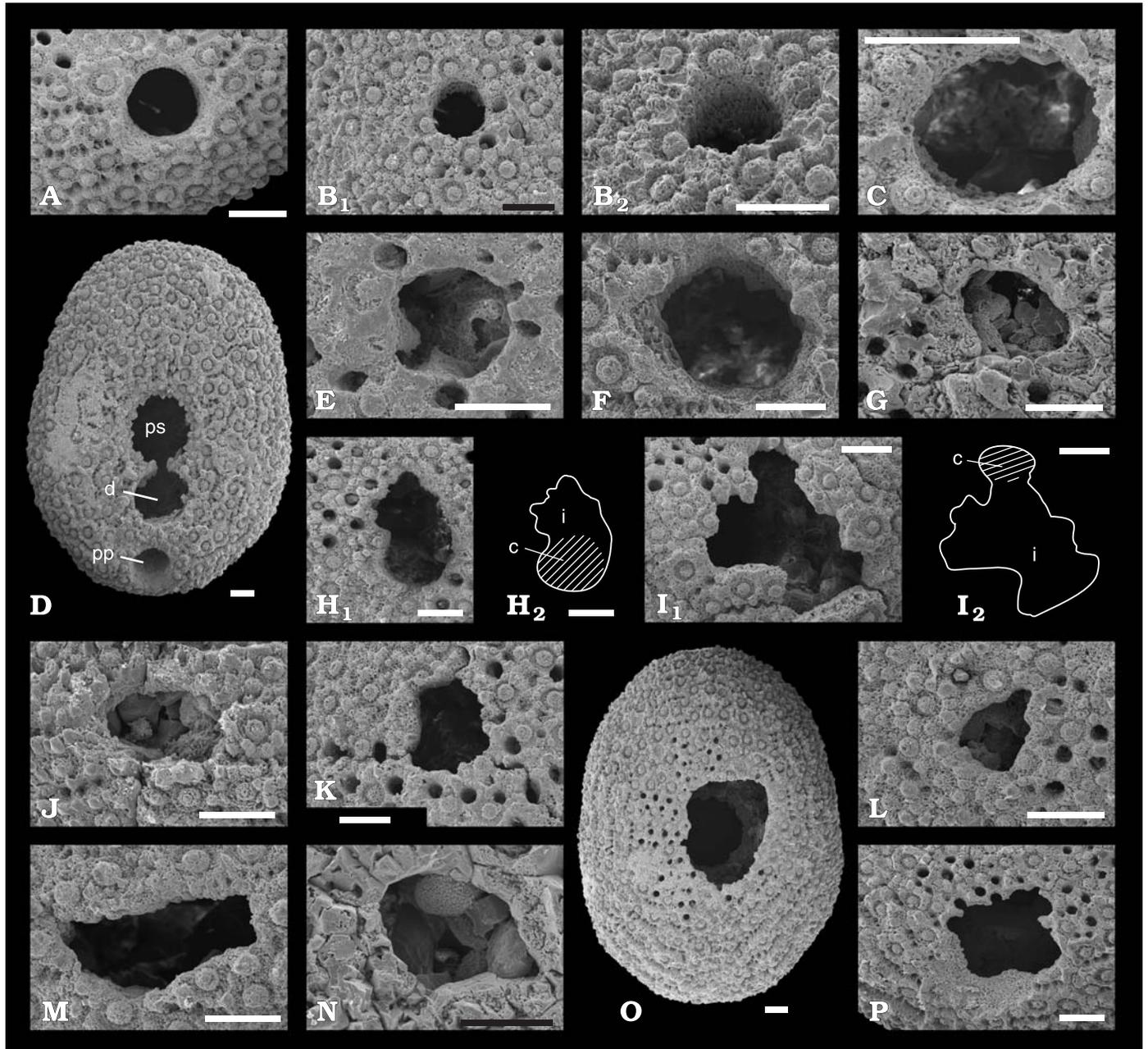


Fig. 4. Morphotypes of drill holes observed on tests of *Echinocyamus linearis*. **A–F**. Circular drill holes. **A**. Circular drill hole on MWG/ZI/022. **B**. Circular drill hole on MWG/ZI/005 in view perpendicular to the test surface (**B₁**) and its close up in slightly oblique view (**B₂**). Note that the walls of the drill hole are perpendicular to the test surface. **C**. Circular (subcircular) drill hole on MWG/ZI/023. **D**. Circular drill hole on oral side of MWG/ZI/024; d, drill hole; ps, peristome; pp, periproct. **E**. Circular (subcircular) drill hole on MWG/ZI/025. **F**. Circular (subcircular) drill hole on MWG/ZI/026. **G**. Drill hole transitional in outline circular (subcircular)/irregular on MWG/ZI/027. **H, I**. Complex drill holes on MWG/ZI/028 (**H₁**) and MWG/ZI/29 (**I₁**) with explanatory drawings (**H₂** and **I₂**); c, circular part of drill hole; i, irregular part of drill hole. **J–P**. Irregular drill holes. **J**. Irregular drill hole on MWG/ZI/030. **K**. Irregular drill hole on MWG/ZI/031. Note three radial crevices running from the drill hole margin. **L**. Irregular drill hole on MWG/ZI/032. Drill hole outline slightly modified due to the occurrence of ambulacral pore. **M**. Irregular drill hole? on MWG/ZI/033. The upper part of drill hole appears to be partially defined by series of ambulacral pores. **N**. Irregular drill hole on MWG/ZI/008. Drill hole margin apparently defined by the plate margins. **O**. Large irregular drill hole on aboral side of MWG/ZI/034. **P**. Irregular drill hole on MWG/ZI/035. Drill hole outline strongly modified due to the occurrence of ambulacral pores. All specimens collected from coarse-grained *Heterostegina* Sands. Scale bars 0.2 mm.

pusillus tests do not differ significantly from the thickness of *E. linearis*, but internal supports of *E. pusillus* are usually more delicate. *E. pseudopusillus* is characterised by the occurrence of rudimentary internal supports and its tests are distinctly thinner than tests of the other echinoids studied

(Figs. 5 and 6A). A rough comparison of the prey's test structure suggests that the most delicate test of *E. pseudopusillus* should be relatively vulnerable to mechanical destruction. Consequently, the robust test of *E. linearis* should be relatively strong. The preservation state of the collected speci-

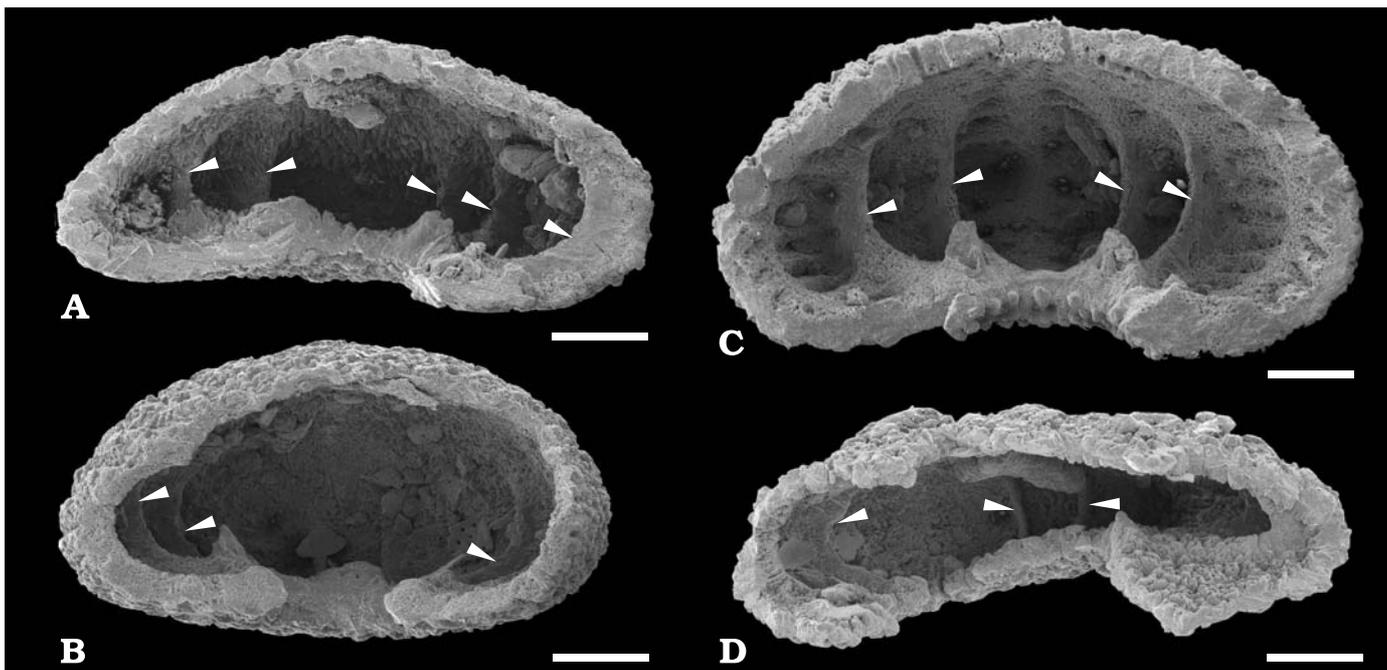


Fig. 5. Cross-sections of *Echinocyamus* tests. **A, B.** *Echinocyamus pusillus*, MWG/ZI/018 (**A**), MWG/ZI/019 (**B**). **C.** *Echinocyamus linearis*, MWG/ZI/020. **D.** *Echinocyamus pseudopusillus*, MWG/ZI/021; internal supports indicated by white arrows. Scale bars 0.5 mm.

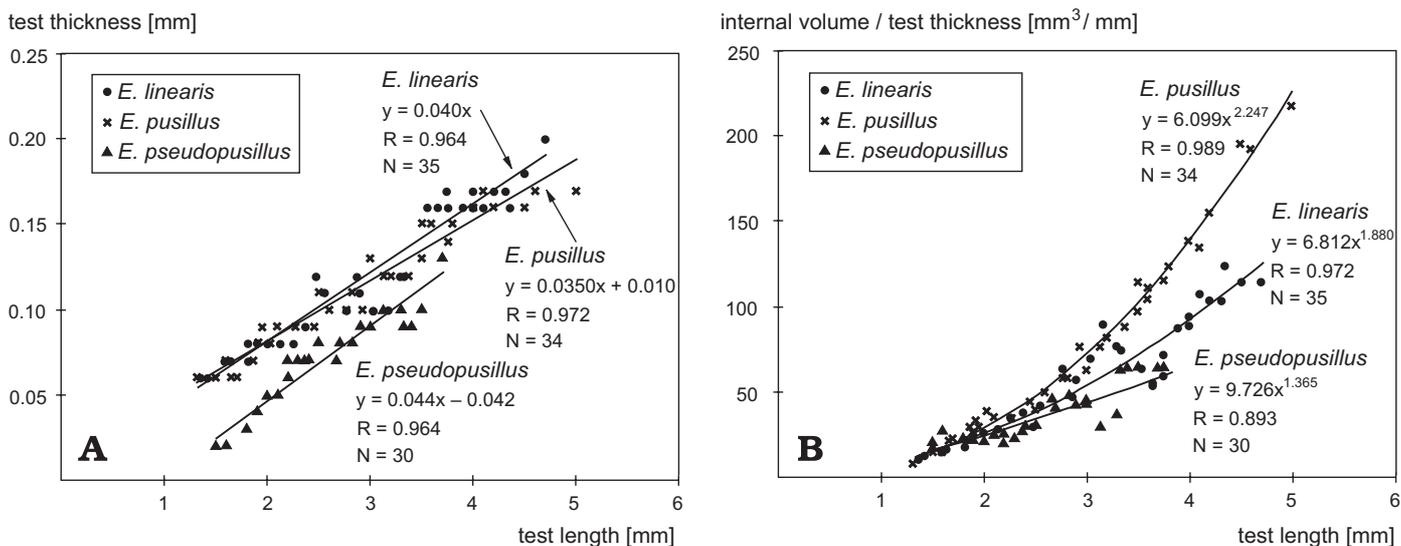


Fig. 6. Relationships between test thickness and test length (**A**) and benefit-cost curves (**B**) of *Echinocyamus* species from the *Heterostegina* Sands; N, number of specimens; R, Pearson's correlation coefficient. Test thickness measured at the upper part of interambulacra situated between petals.

mens perfectly confirms these conclusions. The frequencies of broken tests observed in the material were ca. 1%, 15%, and 30% for *E. linearis*, *E. pusillus*, and *E. pseudopusillus* respectively. It should be also mentioned that the few specimens evidently damaged (flattened) by compaction belong exclusively to *E. pusillus* or *E. pseudopusillus*. Our observations of the broken specimens showed that the aboral side of the test of *Echinocyamus* is slightly thinner. Particularly, the petalodium seems to be the thinnest of all parts of the tests. In contrast, the apical disc seems to be relatively thick.

The size and distribution of tubercles on the test surface do not vary among the prey species. This means that the spines of the studied representatives of *Echinocyamus* (not found in the material) were similar in size and their distribution on the test was almost identical for all the analysed prey. Spines of Recent *Echinocyamus* are, however, short and blunt and they are not an effective defence against cassid predation. In fact, all *Echinocyamus* species are devoid of any antipredatory defences and, because of this, they are easily accessible food source for predators (see

Mc Namara 1990 for detailed review of the defensive strategies in echinoids).

Mode of life and habitat of prey

E. pusillus from the *Heterostegina* Sands most probably lived on the bottom surface, as Recent representatives of this species are epibenthic browsers (Telford et al. 1983). The epifaunal mode of life postulated here for *E. pusillus* from the Korytnica Basin is also supported by morphological data. Detailed studies of Ceranka (2002) showed that the areols of the discussed species are almost symmetrical, and this is a feature typical of Recent epifaunal clypeasteroids.

The morphology of test of other prey indicates that they lived within the sediment. The areols at both the oral and aboral side of tests of *E. linearis* and *E. pseudopusillus* are posteriorly enlarged (Ceranka 2002), which is a feature characteristic of Recent infaunal clypeasteroids (Smith 1984). The extremely high antero-posterior asymmetry of the areols recognised for *E. linearis* (see Ceranka 2002) indicates that this species could have been a very efficient burrower (compare Smith 1984).

The relative frequencies of two echinoid species, *E. linearis* and *E. pseudopusillus* vary significantly between the two facies. Detailed numerical data show that the habitats of these two prey barely overlap (Fig. 2). *E. pseudopusillus* lived exclusively within fine-grained sands, whereas *E. linearis* mostly inhabited coarse-grained sands and rarely appeared in the fine-grained facies (Fig. 2). The distribution pattern recognised here suggests that *E. linearis* inhabited a somewhat higher-energy environment in comparison to *E. pseudopusillus*. The relative abundance of the third species, *E. pusillus*, does not vary distinctly between the facies (Fig. 2). It indicates that this species inhabited the bottom surface irrespective of sediment nature and could live both in higher- and lower-energy environments.

Morphology and size of drill holes

The drill holes are relatively small. The maximum drill hole diameter ranges from 0.04 mm to 1.8 mm, with a mean of 0.26 mm (Table 1). The size frequency distributions of drill holes recognised for all prey species are highly right-skewed and generally unimodal, with small drill holes (below 0.4 mm in diameter) dominating (Fig. 7).

The analysed drill holes are ca. three times smaller than those recognised by Nebelsick and Kowalewski (1999) for a Recent representative of *Echinocyamus* (*E. crispus*) from the Red Sea. This fact indicates that drill holes documented in this study were probably produced by smaller cassids, since the diameter of a cassid drill hole correlates positively with the size of the predator (Hughes and Hughes 1981).

The drill holes vary substantially in outline morphology. The observed differences allow us to distinguish three morphological types of the drill holes: circular, irregular and complex. The circular drill holes are characterised by a very regular circular or subcircular outline (Fig. 4A–F). The irregular drill holes are usually polygonal in outline, with the perimeter often defined by plate margins and/or by series of ambulacral pores arranged in regular rows (Fig. 4G, J–P). The complex drill holes consist of two conjoined outlines, where one is circular but preserved only partially, and the other is irregular (Fig. 4H, I). The outline of many drill holes is additionally modified due to the presence of many natural holes (peristome, periproct, unipores, ambulacral pores) penetrating the test (Fig. 4D, L, P). The walls of all the drill holes are perpendicular to the test surface (Fig. 4B). The distribution of the particular types of the drill holes varies distinctly among the prey species. The circular drill holes predominate in tests of *E. linearis*. The irregular holes occur most frequently in tests of *E. pusillus* and *E. pseudopusillus* (Fig. 8).

Drilling techniques of Recent cassids described in detail by Hughes and Hughes (1981) seem to explain well the morpho-

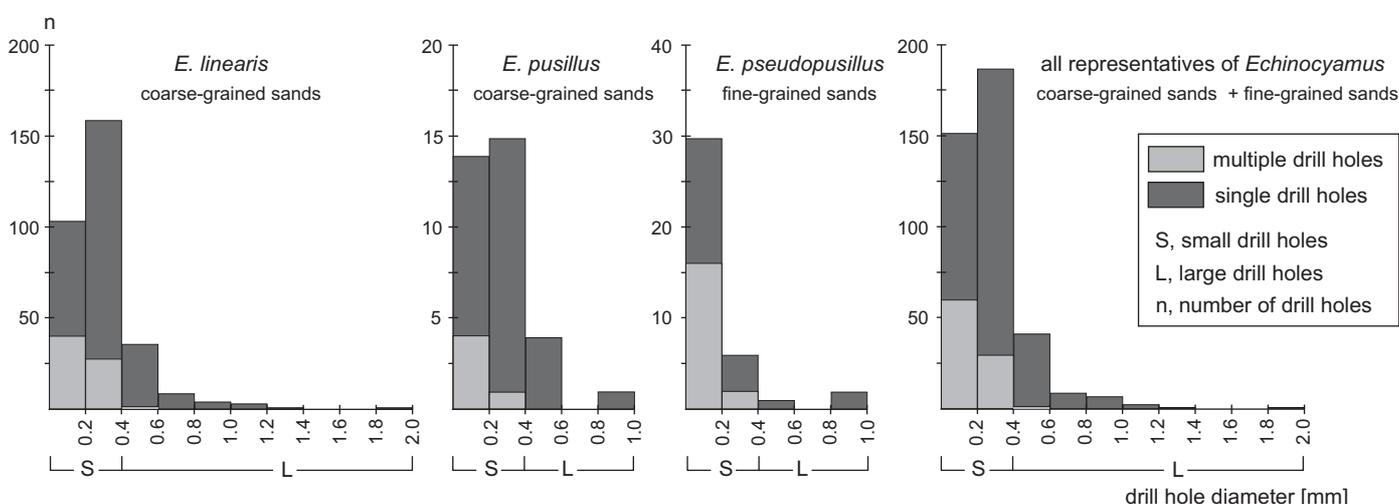
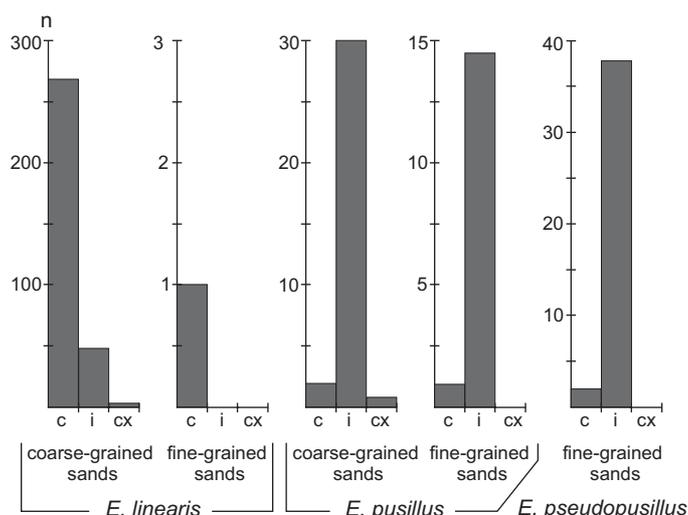


Fig. 7. Size-frequency distributions of drill holes observed on tests of *Echinocyamus* species.



drill holes: c, circular; i, irregular; cx, complex; n, number of drill holes

Fig. 8. Numerical distribution of the particular morphotypes of drill holes within the studied *Echinocyanus* species.

logical diversity of the drill holes observed in the studied material. As described by these authors, the extant cassids cut a circular groove in the test with the mechanical use of radula aided by acid digestion. The disc of test cut out thereby is then pushed inwards or is displaced by the test. Thus, a circular, cylindrical perforation with straight walls is formed. Due to the secretion of acid after penetration, the plates of the test become loosened and the test is easily crushed. Because of this, some delicate tests collapse under the predator during feeding. The latter observation suggests that the irregular drill holes (also produced by Recent cassids—see Hughes and Hughes 1971) are formed by the dissolution and crushing of the margins of the perforation during consumption of the prey. One cannot exclude, however, the possibility that cassids sometimes remove the disc and adjacent parts of the test simultaneously, creating an irregular perforation before feeding. In turn, the origin of complex drill holes seems to be evident. They are produced when the margins of circular perforations are damaged only partially by the predator.

The morphology of the drill hole primarily formed by the activity of predator is sometimes modified later by postmortem dissolution, transportation or other taphonomic processes (see de Cauwer 1985; Roy et al. 1994; Nebelsick and Kowalewski 1999). Because some of the studied echinoid tests are evidently flattened by compaction, we suspect that compaction influenced also the morphology of some of the analysed drill holes. A drill hole presented in Fig. 4K seems to have been affected by the initial stages of taphonomic alternation. The next, imaginary step of destruction of the illustrated drill hole seems to be easily predictable, as three radial crevices perpendicular to the drill hole margin clearly define the area of the test that is vulnerable to possible collapse. The proportion between the length of the crevices and the drill hole diameter suggests that in this particular case the poten-

tial hole produced by compaction would be three to four times larger than the primary drill hole produced by the predator. This example of possible taphonomic alternation suggests that some of the analysed irregular drill holes could be significantly enlarged by compaction. We suspect that the irregular parts of some complex drill holes could be also enlarged (or even could be produced) in a similar manner. The number of drill holes modified by compaction cannot, however, be estimated because it is impossible to distinguish an irregular or complex drill hole produced directly by the predator from those produced (or altered) by taphonomic processes.

The distribution of the particular types of drill holes among the prey species indicates that the mode of life of the prey and the structure of the prey's test strongly influenced the morphology of drill holes. Circular drill holes predominate in the robust tests of infaunal prey (*E. linearis*). When the prey is epifaunal (*E. pusillus*) or its tests are delicate (*E. pseudopusillus*), most of the observed drill holes are irregular in outline. The distribution pattern seems to be clear, as the thin-walled tests of *E. pseudopusillus*, which are devoid of strong internal supports, could be easily crushed by the predator during drilling or feeding. The margins of drill holes produced in the delicate tests of *E. pseudopusillus* could also be easily damaged by compaction. The reverse argumentation applies to *E. linearis*. Its robust tests are relatively resistant to mechanical destruction and, because of this, the number of irregular drill holes recognised for this species is relatively low. The resistance of *E. pusillus* tests is intermediate between the resistance of *E. pseudopusillus* and of *E. linearis*. Surprisingly, the relative frequency of irregular drill holes observed in test of *E. pusillus* is very high and does not differ significantly from those recognised for *E. pseudopusillus* (Fig. 8; $p > 0.5$, chi-squared goodness-of-fit test). This phenomenon can be explained by the epifaunal mode of life of *E. pusillus*, as empty tests of this species abandoned by the predator after feeding and lying at the bottom surface, could be damaged by epibenthic organisms or abiotic factors. The last explanation seems to be even more probable, considering that the *Heterostegina* Sands were, in general, deposited in high-energy environment (Gutowski 1984).

Drilling predation intensities

The frequency of drilled tests varies notably both among the prey species and across the facies (Fig. 9B; Table 3). Within a given environment, the drilling predation rates recognised for particular prey do not seem to change in any substantial matter (Fig. 9A; Table 3). The only possible exceptions (variations in drilling predation intensities recognised for *E. pusillus* and *E. linearis* within the fine-grained sands) are most probably statistical artifacts caused by the small size of samples (Fig. 9A; Table 3).

Both within the fine- and coarse-grained sands, *E. pusillus* was drilled more frequently than *E. linearis*. The third

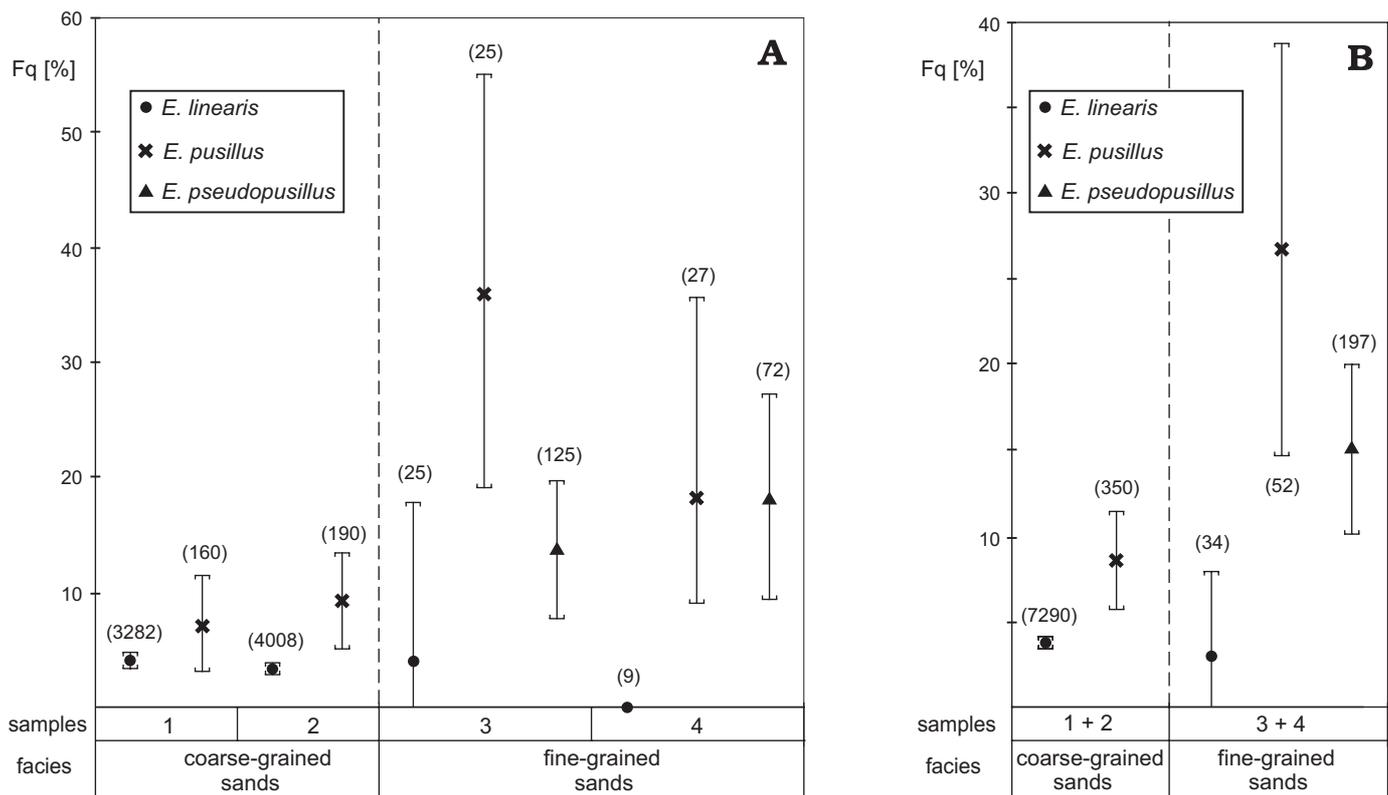


Fig. 9. Intensities of drilling predation observed within particular samples (A) and facies (B). Confidence intervals for large samples (30 specimens or more) computed from the formula $p \pm 1.96 \sqrt{\frac{p(1-p)}{n}}$, where p denotes the proportion of one kind of fossil observed in the collection of n specimens (Łomnicki 1995). Confidence intervals for small samples (less than 30 specimens) derived from Weber (1964: Table 8a).

prey, *E. pseudopusillus* is known only from the fine-grained sands and within this sublithofacies the drilling predation intensity recognised for this species seems to be intermediate (Fig. 9B; Table 3).

Kitchell's et al. (1981) model of predator-prey interactions assumes that prey characterised by higher energetic values for predators, if available, should be drilled more frequently. The relatively high predation rates consistency for *E. pusillus* are concordant with the predictions of the model, as the energetic value of this species (measured by internal volume/test thickness ratio) was indeed the highest (Fig. 6B). The intermediate value of the drilling predation rate recognised for *E. pseudopusillus*, however, contradicts the predictions of the model because the value of this prey species was evidently the lowest (Fig. 6B). This means that the interspecific variation in drilling predation intensities can be explained by Kitchell's et al. (1981) model only partially and another explanation needs to be considered.

The results of Hughes and Hughes (1981) shows that cassids prey on both infaunal and epifaunal echinoids and detect their prey by olfaction. Metabolites produced by an echinoid should diffuse within the water environment faster when they are excreted by an animal not within the sediment, but directly to the water mass, above the bottom surface. The relatively high predation rates recognised for *E. pusillus* may

therefore reflect the possibility that this epifaunal species could have been easier to detect by the predator than echinoids which lived within the sediment (*E. linearis* and *E. pseudopusillus*). This is with agreement of Hughes and Hughes (1981), who stated that time optimisation rather than energy optimisation strategy is used by extant cassids.

The interspecific variation in the drilling predation rates recognised among the infaunal prey may also be a result of their different mobility. Most likely, *E. linearis*, which was a very efficient burrower (see previous paragraphs for more details), moved much faster than *E. pseudopusillus*, thus avoiding attack more frequently. It is noteworthy that echinoids usually move faster than cassids and often escape if alarmed before they are covered by the predator (see Hughes and Hughes 1981).

Within the coarse-grained sands the proportions of drilled test of *E. linearis* and *E. pusillus*, when estimated exclusively for tests bearing large drill holes, are almost identical to those calculated for each species for tests with small drill holes (Fig. 10A), and the two ratios indistinguishable from one another statistically ($p > 0.99$, Fisher's exact test). This may indicate that the diet of small cassids does not differ significantly from the diet of large cassids.

A reliable comparison of the drilling predation intensities across the sublithofacies was possible exclusively for *E.*

Table 3. Results of Student's t-test for differences in the drilling predation intensities between: samples, sublithofacies and prey species; ns, non significant differences ($p > 0.05$).

drilling intensities	modulus of t-value	significance
between samples		
coarse-grained <i>Heterostegina</i> Sands		
<i>E. linearis</i>	1.199	ns
<i>E. pusillus</i>	0.657	ns
fine-grained <i>Heterostegina</i> Sands		
<i>E. linearis</i>	0.609	ns
<i>E. pusillus</i>	1.420	ns
<i>E. pseudopusillus</i>	0.838	ns
between sublithofacies		
<i>E. linearis</i>	0.265	ns
<i>E. pusillus</i>	3.955	$p < 0.001$
between species		
coarse grained <i>Heterostegina</i> Sands		
<i>E. linearis</i> – <i>E. pusillus</i>	4.421	$p < 0.001$
fine-grained <i>Heterostegina</i> Sands		
<i>E. linearis</i> – <i>E. pusillus</i>	2.865	$p < 0.01$
<i>E. linearis</i> – <i>E. pseudopusillus</i>	1.941	$p < 0.05$
<i>E. pusillus</i> – <i>E. pseudopusillus</i>	1.967	$p < 0.05$

pusillus because only this species occurs frequently in both coarse- and fine-grained sands. The analysis showed that *E. pusillus* from fine-grained sands was attacked more frequently (Fig. 9B; Table 3). The higher predation rate recognised for *E. pusillus* from the fine-grained facies may simply suggest that the proportion between the number of cassids and the number of echinoids could be higher in that community which inhabited a lower energy environment. Unfortunately, this preliminary hypothesis cannot be easily tested by the examination of the body fossils. This is because the preservation state of cassids (internal moulds) differs distinctly from the preservation state of echinoids (original tests) and there is no doubt that the ratios of cassids to echinoids as recorded by body fossils are strongly biased (Ceranka and Złotnik 2003; see also Gutowski 1984).

The intensities of drilling predation by cassid gastropods on *Echinocyamus* can be potentially overestimated due to test destruction by other durophagous (test-crushing) preda-

tors (Kowalewski and Nebelsick 2003). Both crushed tests and the remains of crabs (the most common group of test-crushing predators—see Kowalewski and Nebelsick 2003) have been found in the material. The intensity of crushing predation is, however, difficult to evaluate since the tests crushed by predators are usually indistinguishable from those destroyed by abiotic factors. Fortunately, the upper limit of the crushing predation rate can be easily estimated, as its value is obviously never higher than the total frequency of the crushed tests observed in the material.

The analysis shows that *E. linearis* was attacked by test-crushing predators very rarely, as no more than 1% of its tests are destroyed. This means that the intensities of drilling predation recognised for this species have not been biased in any substantial matter. The highest frequencies of crushed tests recognised for *E. pusillus* (ca. 15%) and *E. pseudopusillus* (ca. 30%) may imply that drilling predation intensities recognised for these species may be slightly overestimated (by ca. 1–2% for *E. pusillus* and ca. 5–6% for *E. pseudopusillus*). However, it should be emphasised again that the frequencies of the crushed tests determine only the highest potential rates of crushing predation, whereas the real intensities were probably lower. We believe, therefore, that drilling predation rates recognised for *E. pusillus* and *E. pseudopusillus* also have also not been notably biased. Finally, it is also highly unlikely that the higher intensity of drilling predation recognised for *E. pusillus* from the fine-grained sand was caused by higher intensity of crushing predation within this facies. This is because the frequencies of crushed tests of *E. pusillus* within the coarse- and fine-grained sands were almost identical (ca. 15% for each facies).

Values of the drilling predation intensities recognised here for three *Echinocyamus* species (4–35%) are much lower than the drilling predation frequencies observed in the Recent populations of *Echinocyamus* from the Red Sea (70–90%) (Nebelsick and Kowalewski 1999). The observed difference may confirm the increase of intensity of drilling predation/parasitism on echinoids recognised by Kowalewski and Nebelsick (2003: fig. 6) in a large time interval. However, many other explanations are also possible. It cannot be excluded that drilling predation intensities recognised here for the Miocene representatives of *Echinocyamus* from the Korytnica Basin differ from those reported by Nebelsick and Kowalewski (1999) for Recent *Echinocyamus* from the Red Sea because: (1) the studied prey differ in size and (2) belong to different species, (3) they were attacked by different species of cassid borers as well as (4) lived in different environments and (5) belonged to different ecosystems (compare Nebelsick and Kowalewski 1999).

Size selectivity

Size-selective drilling has been recognised in two analysed prey, *E. linearis* and *E. pusillus* from the coarse-grained sands. The investigation showed that the larger tests of both

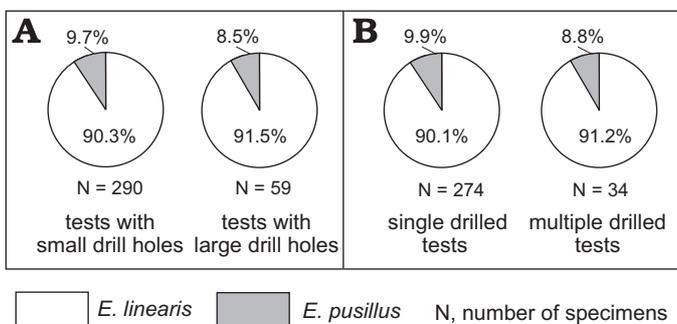


Fig. 10. Relative abundances of drilled tests of *E. linearis* and drilled tests of *E. pusillus* bearing small and large drill holes (A) and relative abundances of single and multiple drilled tests of the same species (B). All specimens collected from the coarse-grained *Heterostegina* Sands.

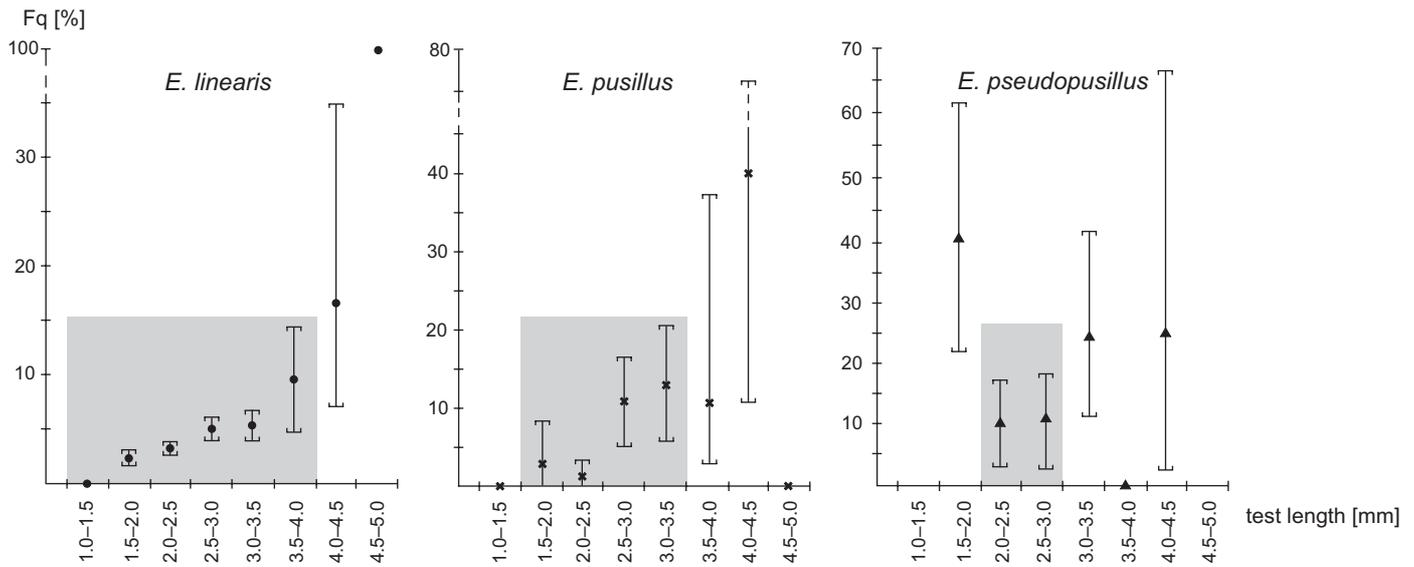


Fig. 11. Drilling predation intensities recognised for the particular size classes of preys; Fq, relative frequency of drill holes; grey areas indicate size classes represented by 30 or more specimens. *E. linearis* and *E. pusillus* collected from the coarse-grained *Heterostegina* Sands, and *E. pseudopusillus* from the fine-grained *Heterostegina* Sands. Confidence intervals computed from the formulas presented in captions to Fig. 9.

species were generally drilled more frequently. Particularly, specimens exceeding 2.5 mm in length were drilled more frequently than the smaller ones. The size selectivity is even more distinct when the size classes of prey represented by less than 30 specimens are rejected from the analysis (Fig. 11). Size-selective drilling displayed by cassids preying on *E. linearis* and *E. pusillus* can be explained perfectly by Kitchell's et al. (1981) model, as the energetic value of the echinoid prey increases when the echinoid test becomes larger (Fig. 6B). The relationship between the size of prey and intensity of drilling predation was also studied for *E. pseudopusillus* from the fine-grained sands. The investigation showed only that specimens from 2.0 to 3.0 mm in length were drilled less frequently than the smaller ones; however, the overall pattern of the size-selectivity for cassids preying on *E. pseudopusillus* cannot be evaluated reliably. This is because most of size classes of prey were represented by less than 30 specimens, resulting in very wide confidence intervals (Fig. 11).

The results presented here differ distinctly from the results of Nebelsick and Kowalewski (1999), who studied cassid-*Echinocyamus* interactions in Recent environments. Their investigations clearly showed that cassid drilling predation on Recent *Echinocyamus* is not size-selective.

The weak ($r = 0.29$), but statistically significant ($p < 0.001$) positive correlation between the drill hole diameter and the length of the prey test recognised for *E. linearis* may imply that larger cassids preferentially preyed on larger echinoids (Fig. 12). Such preference agrees with the expectations of Kitchell's et al. (1981) model since larger prey, if accessible to the predator, should be drilled preferentially. However, the observed correlation may also be the result of specific drilling techniques applied by cassids: the larger the predator and the smaller the

prey are, the higher the chance for the destruction of prey test during drilling or feeding. The drilling predation of large cassids upon small echinoids would be, therefore, underestimated in the fossil record. The difference between the mobility of the prey and the mobility of the predator can also be partially responsible for the observed correlation. This is because larger prey attacked by smaller predators should have a higher survival chance. This means that the larger echinoids could have been attacked successfully mostly by larger predators.

A slightly higher, but still weak correlation ($r = 0.36$, $p < 0.0001$) between the size of the predator and the size of prey was recognised by Nebelsick and Kowalewski (1999) for Recent *Echinocyamus* drilled by cassids.

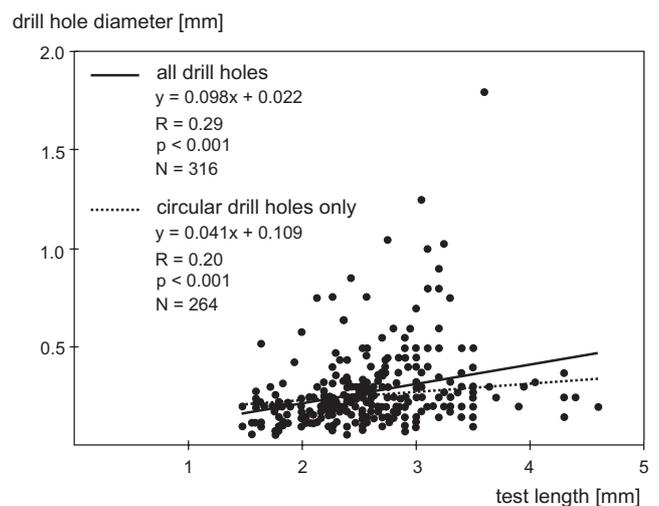


Fig. 12. Relationship between the size of drilled *Echinocyamus linearis* and the size (maximum diameter) of the drill holes; N, number of specimens; R, Pearson's correlation coefficient; p, probability of significance of R. All specimens collected from coarse-grained *Heterostegina* Sands.

Intraspecific site-selectivity

The drill holes observed on tests of *E. linearis* were not positioned randomly. The investigation shows that the aboral side of tests of this species was drilled preferentially. The preference displayed by cassids was evident, as 85% of the drill holes were situated on the aboral side of test (only 52% were expected there in the case of random drilling). Detailed numerical data shows that the dorsal preference displayed by cassids was mainly a result of a great concentration of drill holes on the petals and apical disc. The frequencies of drill holes observed in each of the mentioned sectors were ca. 4–7 times higher than the theoretical frequencies of drill holes expected for these sectors in the case of random drilling. In fact, more than 50% of all drill holes found in tests of *E. linearis* are situated on the petals or apical disc. The remaining part of the aboral side of test (aboral side excluding petals and apical disc) was not drilled preferentially, as the drilling predation frequency recognised for this sector was somewhat lower than expected in the case of random drilling. The oral side of the *E. linearis* test was evidently avoided by the predator. The drilling predation frequencies recognised for this sector were ca. four times lower than expected in case of random drilling (Fig. 13A, Table 4).

The distribution of drill holes on the ambulacra and interambulacra was the subject of a separate study. The analysis showed that the relative frequencies of drill holes on the interambulacra of *E. linearis* were lower than expected. The ambulacra of this species seem to be drilled preferentially. However, when the petals were rejected from the analysis, the relative frequency of drill holes on the ambulacra was distinctly lower than expected (Fig. 13A, Table 4). This means that preferential drilling recognised here for the ambulacra is only a result of the enormous concentration of drill holes on the petals. We suggest, therefore, that there was no significant correlation between the positioning of drill holes and the presence of ambulacra and interambulacra. The random distribution of the drill holes on the oral side of the test, where the morphology and structure of both the ambulacra and interambulacra is relatively homogenous confirms well this suggestion (Fig. 13A, Table 4).

The similar (but statistically less significant) pattern of site selectivity was recognised for two other analysed prey, *E. pusillus* from the coarse-grained sands and *E. pseudopusillus* from the fine-grained sands (Fig. 13B, C, Table 5).

The dorsal (aboral) preference displayed by cassids from the Korytnica Basin and recognised also for Recent cassids preying on *Echinocyamus* (Nebelsick and Kowalewski 1999)

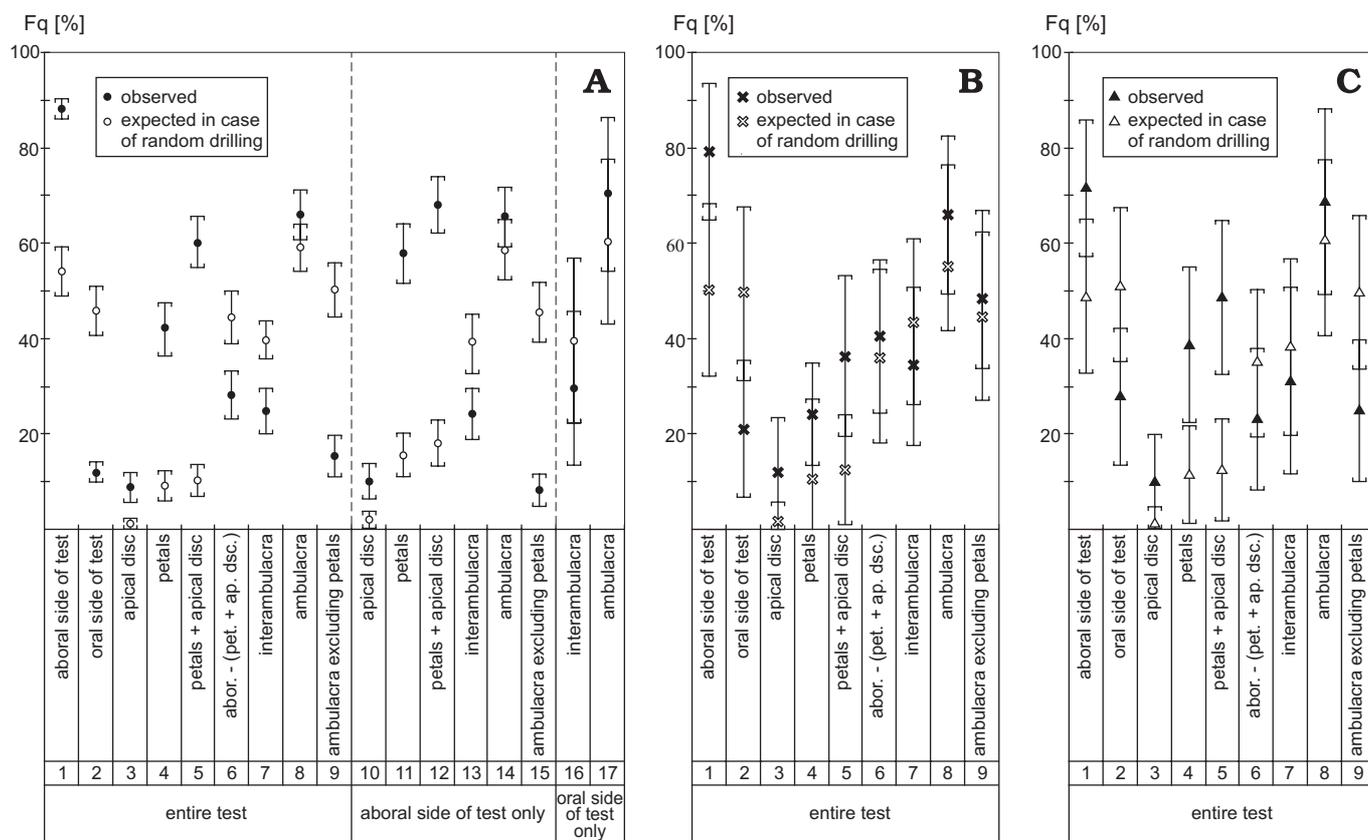


Fig. 13. Distribution of drill holes within the particular sectors of the tests of *Echinocyamus linearis* (A), *Echinocyamus pusillus* (B), and *Echinocyamus pseudopusillus* (C); Fq, relative frequency of drill holes. *E. linearis* and *E. pusillus* collected from the coarse-grained *Heterostegina* Sands, and *E. pseudopusillus* from the fine-grained *Heterostegina* Sands. Fq for particular sectors computed from the formulas presented in Table 2, the numbers of formulas in Table 2 correspond to the numbers attributed here to the particular sectors. Confidence intervals computed from the formulas presented in captions to Fig. 9; abor. - (pet. + ap. disc.), aboral side of test excluding petals and apical disc.

Table 4. Results of Student's t-test for drill hole-site selectivity on tests of *E. linearis* from the coarse-grained *Heterostegina* Sands. Positive values of t indicate preferential drilling, negative values of t indicate avoiding of a sector by driller; ns, non significant difference ($p > 0.05$) between the observed number of drill holes in a given sector and the number of drill holes expected in this sector in case of random drilling; abor. - (pet. + ap. dsc.), aboral side of test excluding petals and apical disc.

investigated part of test sector	small drill holes		large drill holes		all drill holes	
	t	significance	t	significance	t	significance
entire test						
aboral side of test	8.289	$p < 0.001$	4.805	$p < 0.001$	9.516	$p < 0.001$
oral side of test	- 8.289	$p < 0.001$	- 4.805	$p < 0.001$	- 9.516	$p < 0.001$
apical disc	2.666	$p < 0.01$	3.752	$p < 0.001$	4.404	$p < 0.001$
petals	8.678	$p < 0.001$	6.324	$p < 0.001$	9.536	$p < 0.001$
petals + apical disc	9.406	$p < 0.001$	8.744	$p < 0.001$	11.120	$p < 0.001$
abor. - (pet. + ap. dsc.)	- 0.996	ns	- 5.487	$p < 0.001$	- 1.687	ns ($0.05 < p < 0.1$)
interambulacra	- 3.623	$p < 0.001$	- 4.529	$p < 0.001$	- 5.025	$p < 0.001$
ambulacra	2.524	$p < 0.02$	1.205	ns	2.795	$p < 0.01$
ambulacra excluding petals	- 5.313	$p < 0.001$	- 5.717	$p < 0.001$	- 5.734	$p < 0.001$
aboral side of test only						
apical disc	2.170	$p < 0.05$	3.608	$p < 0.05$	3.917	$p < 0.001$
petals	7.512	$p < 0.001$	5.771	$p < 0.001$	8.164	$p < 0.001$
petals + apical disc	8.196	$p < 0.001$	8.428	$p < 0.001$	9.778	$p < 0.001$
interambulacra	- 3.397	$p < 0.001$	- 4.995	$p < 0.001$	- 4.992	$p < 0.001$
ambulacra	2.400	$p < 0.02$	1.493	ns	2.808	$p < 0.01$
ambulacra excluding petals	- 5.669	$p < 0.001$	- 5.176	$p < 0.001$	- 5.928	$p < 0.001$
oral side of test only						
interambulacra	- 1.159	ns	0.662	ns	- 0.903	ns
ambulacra	1.159	ns	- 0.662	ns	0.903	ns

Table 5. Results of Student's t-test for drill hole-site selectivity on tests of *E. pusillus* from the coarse-grained *Heterostegina* Sands and *E. pseudopusillus* from the fine-grained *Heterostegina* Sands. Positive values of t indicate preferential drilling, negative values of t indicate avoiding of a sector by driller; ns, non significant difference ($p > 0.05$) between the observed number of drill holes in a given sector and the number of drill holes expected in this sector in case of random drilling; abor. - (pet. + ap. dsc.), aboral side of test excluding petals and apical disc.

sector	<i>E. pusillus</i>		<i>E. pseudopusillus</i>	
	t	significance	t	significance
aboral side of test	2.359	$p < 0.02$	2.082	$p < 0.05$
oral side of test	- 2.359	$p < 0.02$	- 2.082	$p < 0.05$
apical disc	1.709	ns, $0.05 < p < 0.1$	1.700	ns, $0.05 < p < 0.1$
petals	1.460	ns	2.746	$p < 0.01$
petals + apical disc	2.264	$p < 0.05$	3.435	$p < 0.01$
abor. - (pet. + ap. dsc.)	0.351	ns	- 1.357	ns
interambulacra	- 1.122	ns	- 0.938	ns
ambulacra	0.223	ns	0.093	ns
ambulacra excl. petals	- 0.885	ns	- 2.382	$p < 0.02$

Table 6. Results of Student's t-test for differences in the distribution of small and large drill holes on tests of *E. linearis* from the coarse grained *Heterostegina* Sands. Positive values of t indicate higher frequencies of large drill holes; ns, non significant differences ($p > 0.05$); abor. - (pet. + ap. dsc.), aboral side of test excluding petals and apical disc.

investigated part of test sector	t	significance
entire test		
aboral side of test	1.544	ns
oral side of test	- 1.544	ns
apical disc	4.846	$p < 0.001$
petals	3.507	$p < 0.001$
petals + apical disc	6.295	$p < 0.001$
abor. - (pet. + ap. dsc.)	- 5.612	$p < 0.001$
interambulacra	- 3.455	$p < 0.001$
ambulacra	0.076	ns
ambulacra excluding petals	- 4.069	$p < 0.001$
aboral side of test only		
apical disc	4.579	$p < 0.001$
petals	3.087	$p < 0.001$
petals + apical disc	6.048	$p < 0.001$
interambulacra	- 3.959	$p < 0.001$
ambulacra	0.457	ns
ambulacra excluding petals	- 3.191	$p < 0.01$
oral side of test only		
interambulacra	1.460	ns
ambulacra	- 1.460	ns

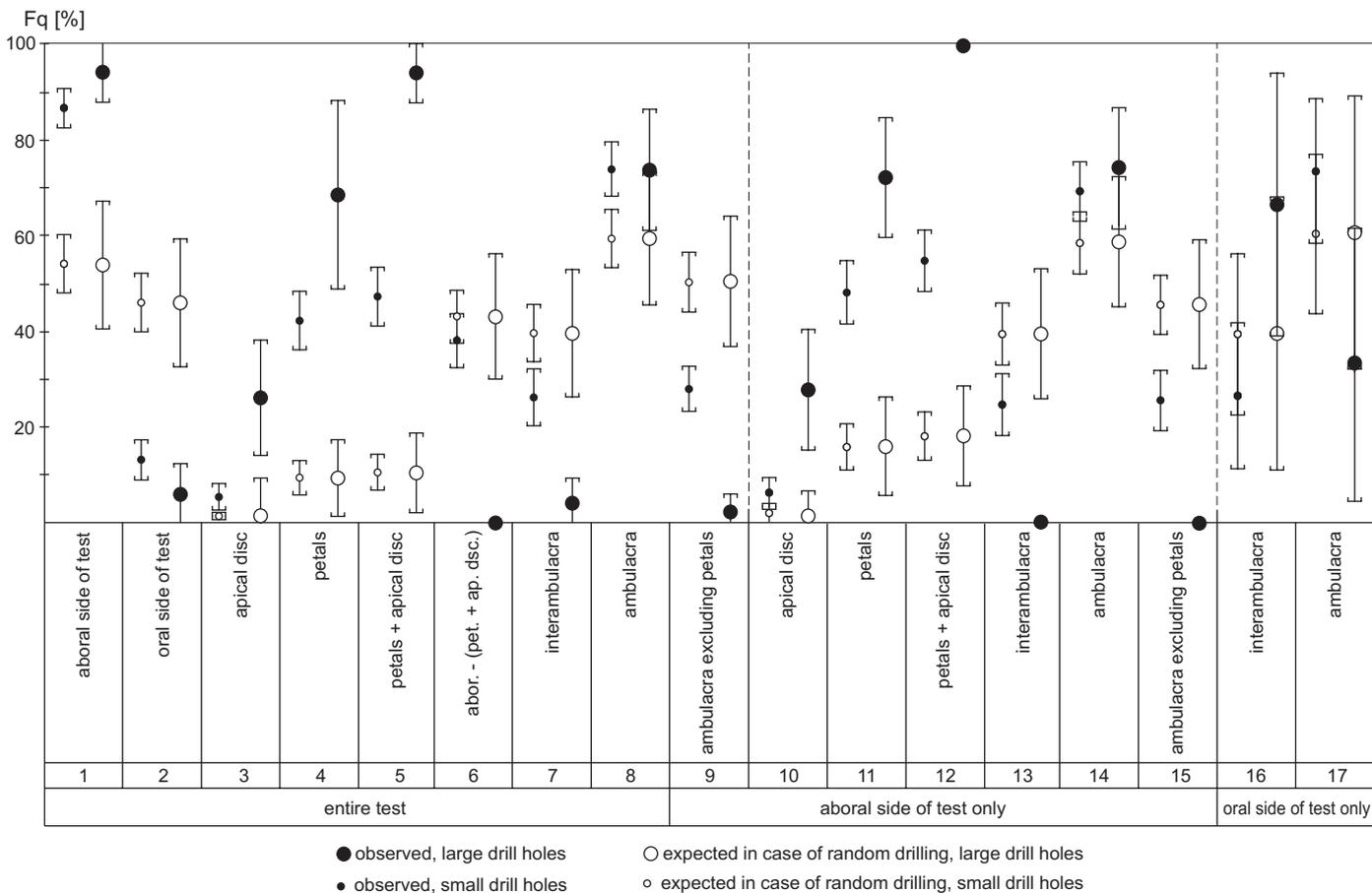


Fig. 14. Distribution of small and large drill holes within particular sectors of tests of *Echinocyamus linearis*; Fq, relative frequency of the drill holes; abor. - (pet. + ap. dsc.), aboral side of test excluding petals and apical disc. Fq for particular sectors computed from the formulas presented in Table 2, the numbers of formulas in Table 2 correspond to the numbers attributed here to the particular sectors. Confidence intervals computed from the formulas presented in captions to Fig. 9.

could have been caused by many different factors. Nebelsick and Kowalewski (1999) suggested that cassids prefer the aboral side of the echinoid test because the gonads and other nutritious organs are situated there. Gibson and Watson (1989) assumed that the aboral side of the test is the surface that would have been first encountered by a gastropod as it either attacked an echinoid on the sediment surface or burrowed into the sediment in search of its prey. Laboratory observations of Hughes and Hughes (1981) are consistent with this assumption. We suggest that the discussed preference may also be partially forced by specific methods of capturing and handling of prey applied by cassids. Hughes and Hughes (1981) showed that, before they start drilling, cassids usually mount up on the urchin and cover its aboral surface. This means that the aboral surface is the part of echinoid test that lies directly under the predator. Notably, a gastropod that covers the aboral side of an echinoid and drills this side of an urchin can intrude almost the entire proboscis into its prey. In contrast, a predator which occupies the aboral side of the echinoid test, but drills its oral surface, can use only part of its proboscis in order to penetrate the prey (Hughes and Hughes 1981: fig. 5C). In the latter case some parts of the soft tissues most probably can not

be consumed without changing the position of the gastropod on the test surface.

The pattern of site selectivity displayed by cassids is also concordant with the predictions of Kitchell's et al. (1981) model because such preferential drilling as that described above increases the net energy gain for the predator. This is because the aboral side of the *Echinocyamus* test is generally thinner, and the thinner the test, the shorter the drilling time.

The occurrence of many large ambulacral pores in petals and the occurrence of gonopores in the apical disc may explain well the relatively high frequency of drill holes observed in these sectors. Gibson and Watson (1989) suggested that these regions of the aboral side of the echinoid test which are characterised by the occurrence of numerous pores should be especially attractive for predators because the soft parts of echinoids are exposed very well there. Although the argumentation of Gibson and Watson (1989) certainly is viable, one cannot exclude the possibility that the very high frequency of drill holes observed in the apical sectors of the echinoid test is forced simply by the specific methods of attack, capture and handling of prey applied by cassids (ex-

tending the proboscis toward the top of an urchin and mounting upon the urchin—see Hughes and Hughes 1981).

The relatively high number of drill holes observed on the petals agrees with the predictions of Kitchell et al. (1981) because most probably this highly porous and relatively thin part of echinoid could be drilled through faster than other parts of the echinoid test. However, the relatively high abundance of drill holes observed on the apical disc can not be explained by Kitchell's et al. (1981) model because this part of the *Echinocyamus* test is relatively thick.

A reliable comparison of the distribution of small vs. large drill holes was possible exclusively for the most abundant prey species, *E. linearis* from the coarse-grained sands. The analysis showed that the distribution of both types of drill holes on the test surface was very similar. The relative frequencies of both large and small drill holes were higher than expected on the petals, apical disc and generally on the dorsal side of test. The distribution of large and small drill holes on both the ambulacra and interambulacra was also comparable (Fig. 14; Table 6). These concordant patterns suggest that site-selectivity displayed by large cassids was very similar to that displayed by small cassids.

Although both large and small cassids drilled the same sectors of echinoid test preferentially, the relative frequencies of drill holes produced by these two-size classes of drillers were usually different for particular sectors. Detailed numerical data showed that the concentration of large drill holes on petals and apical disc (25.9%, petals; 68.5%, apical disc; 94.4%, petals and apical disc) was significantly higher than the concentration of small drill holes in the mentioned sectors (5.3%, petals; 42.2%, apical disc; 53.1%, petals and apical disc) (Fig. 14; Table 6). This means that large cassids displayed a significantly higher site-selectivity.

Multiple drill holes

Twelve per cent (44 out of 353) of drilled echinoid tests bear two, three or sometimes four drill holes (Table 1 and Fig. 15A–G). Drill holes situated on a single test usually differ in size and the distances between them are relatively long (Fig. 15A, C, D, G). This suggests that multiple perforations were produced by several cassid predators which attacked different parts of a single urchin. This is consistent with laboratory observations of Recent cassids (Hughes and Hughes 1971), which showed that a single echinoid prey is sometimes attacked simultaneously by more than one predator.

Although the acts of simultaneous predation of several cassid individuals upon a single echinoid prey explain well the origin of most of the multiple drill holes, a double drilled specimen of *E. linearis* illustrated on Fig. 15F suggests that multiple drillings can be also produced by cassids in a somewhat different manner. The figured drill holes lie very close to one another and it seems improbable that they were produced by two cassid individuals which simultaneously preyed upon an urchin. We believe that these particular holes

record two successive rather than two simultaneous acts of drilling predation. Because the discussed drill holes differ in size, they were most probably produced by two different predators. The first predator drilled through the test, but was forced to abandon its prey. The second predator bored its drill hole just beside the previous perforation and consumed the rest of the soft tissues.

The ratios of multiple drilled tests relative to the number of tests with single perforations calculated for *E. linearis* and *E. pusillus* from the coarse-grained sands are almost identical (Fig. 10B) and the two ratios indistinguishable statistically from one another ($p > 0.99$, Fisher's exact test). This may indicate that the prey species preferences displayed by cassids did not change when they attacked in a group. Unfortunately, due to the low number of specimens no reliable comparisons were possible for the representatives of *Echinocyamus* from the fine-grained sands.

Almost 30% (94 out of 336) of the small drill holes are multiple. The large drill holes are, however, almost always single. In fact only one large drill hole was found among multiply drilled *Echinocyamus* tests. This means that only 1.5% (1 out of 64) of all large drill holes are multiple (Fig. 7 and Table 1). The results presented here indicate that the predatory behaviour of small cassids was somewhat different from that displayed by large cassids. The small cassids sometimes preyed upon urchins in a group whereas large cassids almost always drilled and consumed their prey individually. We suggest that the observed change of predatory behaviour could have been forced directly by the ontogenetic increase of the size of the predator. This is because the larger predator, the larger area of an echinoid test covered by predator during drilling and feeding and consequently the smaller the remaining part of test which can be attacked by other potential drillers. The proposed explanation for the extremely low number of multiple large drill holes is confirmed by laboratory observations of Hughes and Hughes (1981) as they show that relatively large cassids preying on distinctly smaller echinoids cover the entire aboral side of their tests. Noteworthy, for each of the prey species, the mean length of multiple drilled tests does not differ significantly from the mean length of a test with a single perforation. Also the length ranges of multiply and single drilled tests strongly overlap (Fig 16). This lack of any detectable correlation between the size of the prey the frequency of multiple drilling suggest that group attacks were not forced by the larger size of the prey.

Possible taphonomic biases

Drilling predation makes the prey skeleton more prone to mechanical destruction and dissolution (Roy et al. 1994 and results of this study below, but see also Zushin and Stanton 2001). This can generate serious taphonomic biases because the intensity of drilling predation may be underestimated due to preferential destruction of the drilled skeletons. Specifically, the relative frequency of multiple drilled skeletons

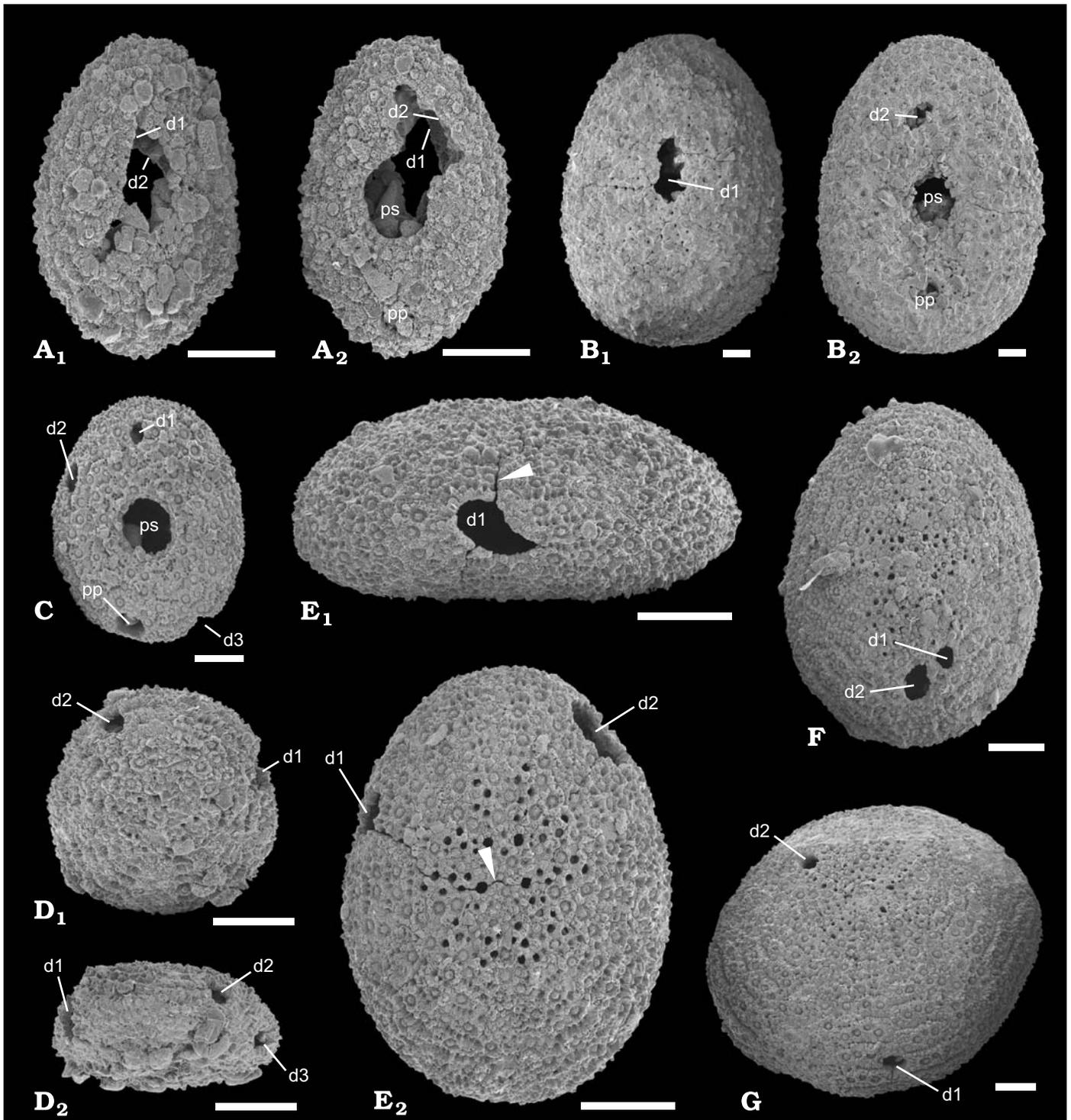


Fig. 15. Tests of representatives of *Echinocyamus* bearing multiple drill holes. **A.** *Echinocyamus pseudopusillus*. Double drilled MWG/ZI/036 in aboral (A₁) and oral (A₂) views. **B.** *Echinocyamus pusillus*. Double drilled MWG/ZI/037 in aboral (B₁) and oral (B₂) views. **C–G.** *Echinocyamus linearis*. **C.** MWG/ZI/038 bearing three drill holes in oral view. **D.** Juvenile specimen (MWG/ZI/039) bearing three drill holes in aboral (D₁) and slightly (D₂) oblique views. **E.** Double drilled MWG/ZI/040 in lateral (E₁) and aboral (E₂) views. Note the crevice connecting the drill holes (white arrow) and its oral prolongation (see E₁). **F.** Double drilled MWG/ZI/041 in aboral view. Note extremely short distance between the drill holes. **G.** Double drilled MWG/ZI/042 in oblique view; ps, peristome; pp, periproct; d1, d2, d3, drill holes. *E. linearis* and *E. pusillus* collected from the coarse-grained *Heterostegina* Sands, and *E. pseudopusillus* from the fine-grained *Heterostegina* Sands. Scale bars 0.5 mm.

may be underestimated as they are presumably characterised by an even higher vulnerability to mechanical destruction.

For similar reasons the frequently drilled species may be underestimated relative to other species in a given fossil assem-

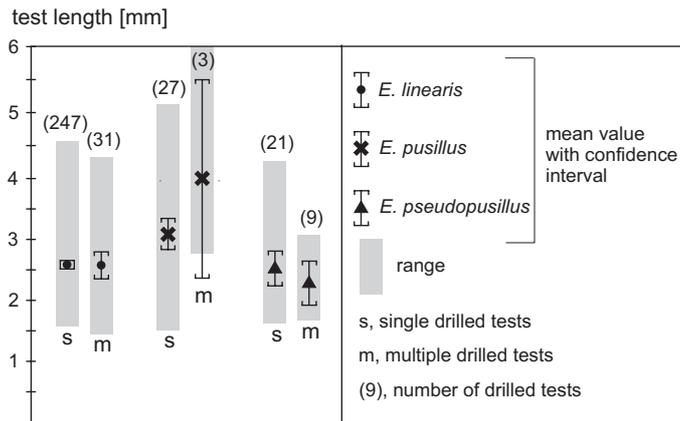


Fig. 16. Mean values and ranges of tests lengths of single and multiple drilled tests for the particular *Echinocyamus* species. *E. linearis* and *E. pusillus* collected from the coarse-grained *Heterostegina* Sands, *E. pseudopusillus*, from the fine-grained *Heterostegina* Sands. Formula used for confidence intervals estimations, see captions to Table 1.

blage (cf. Nebelsick and Kowalewski 1999). On the other hand, some perforations may be produced directly by taphonomic processes. In such cases the number of drilled skeletons may be overestimated because the holes of taphonomic origin are sometimes undistinguishable from drill holes produced by predators. The positive correlation between the drill hole size and the size of drilled prey can also be generated by taphonomic alternation. This is because the larger the drill hole and the smaller the prey, the higher the chance for destruction of the prey's shell (cf. Nebelsick and Kowalewski 1999). Finally, as discussed previously, taphonomic processes can influence the drill holes size and morphology.

The analysed record of drilling predation can potentially be affected by all the biases mentioned. The double drilled test of *E. linearis* collected from the coarse-grained sands, presented in Fig. 15E, was evidently weakened by the drilling activity of cassids. The illustrated specimen represents, in fact, the initial stage of mechanical destruction of the test. The relatively high number of irregular drill holes recognised for *E. pusillus* and *E. pseudopusillus* indicates that some abiotic factors could also influence the drill morphology (see Fig. 8 and the text on the morphology of drill holes above). This means that some of the studied tests and some of the drill holes had undergone postmortem alternation. The preservation state of the analysed fossils suggests, however, that this alternation was relatively weak. Among the collected tests, unbroken specimens predominate significantly (ca. 97% of tests are complete; $p < 0.001$, chi-square goodness-of-fit test) and only three tests evidently flattened by compaction were observed in the material. All details of the test morphology are usually perfectly preserved and no evidence for abrasion or postmortem dissolution of tests has been found. Indeed, representatives of *Echinocyamus* from the *Heterostegina* Sands constitute one of the best preserved echinoid faunas known from the Miocene deposits of the world (Ceranka 2002). We believe therefore that the studied record of drilling predation has not been biased

in any substantial matter and it reflects well the true interactions between the cassids and echinoids.

The lack of any serious taphonomic biases postulated here seems to be even more probable, as most conclusions have been derived from the analysis of tests of *E. linearis*, characterised by a relatively high resistance to mechanical destruction.

Summary and conclusions

Test-drilling predation by cassid gastropods on minute clypeasteroid echinoids has been studied in the fossil assemblage of the *Heterostegina* Sands (middle Miocene, Holy Cross Mountains, Poland). The analysed prey, collected from two sublithofacies of the *Heterostegina* Sands (coarse- and fine-grained sands), represent three species of *Echinocyamus*, *E. linearis*, *E. pusillus*, and *E. pseudopusillus*. The drill holes were presumably produced by one cassid species, *Semicassis miolaevigata*.

The investigation showed that drilling predation intensities varied both among the prey species and across the lithofacies. Within both fine- and coarse-grained sands, *E. linearis* was drilled more frequently than *E. pusillus*. An intermediate value of drilling predation was recognised for *E. pseudopusillus*. Echinoids from the fine-grained sands appeared to be drilled more frequently. Within particular sublithofacies, the drilling predation intensities calculated for each of the analysed prey do not change in any substantial matter.

Drilling predation was both size- and site-selective. The larger individuals of *E. linearis* and *E. pusillus* were attacked more frequently and the aboral side of test of all *Echinocyamus* species was drilled preferentially. Particularly, the extremely high number of drill holes was situated in the upper part of the echinoid test (petals and apical disc).

The predatory behaviour displayed by small cassids was somewhat different from those typical of large cassids. Large cassids drilled and consumed their prey almost always individually, whereas small cassids sometimes preyed upon the urchins in a group. Large cassids displayed also a higher site-selectivity. They more frequently drilled the petals and apical disc. The positive correlation between the drill holes size and the size of the prey recognised here for *E. linearis* may also indicate that larger cassids preyed more frequently on larger echinoids. Despite all the mentioned differences, the general pattern of drilling predation displayed by the small and large cassids was, however, fairly similar, both in term of stereotypy and diet.

The interactions between the cassids and echinoids recorded by analysed drill holes were controlled by many different factors. Among them the potential energetic value of prey (measured by internal volume/test thickness ratio), prey and predator mobility, mode of life of prey, thickness and porosity of the prey test and the ratio of prey size to the predator size appear to be the most important controlling processes. The general strategy applied by cassids preying on echinoids, if exist-

ing, remains, however, unrecognised. Some of the results suggest that cassids preferred prey characterised by a higher energetic value. The others indicate that the discussed predators were rather time-optimising than energy-optimising drillers.

The distribution pattern of particular morphotypes of drill holes among the prey species suggests that the mode of life of prey and its test structure could have influenced the drill hole morphology. Circular drill holes predominated in the robust test of infaunal *E. linearis*. When the prey was epifaunal (*E. pusillus*) or its tests were delicate (*E. pseudo-pusillus*), the observed drill holes were usually irregular in outline. The presented data indicate that the shape of a cassid drill hole cannot be used in order to identify a potential borer.

The patterns of drilling predation recognised here for cassids preying on echinoids are in many cases very similar to the patterns displayed by muricid and/or naticid drillers, two well-known groups of gastropod predators that prey on molluscs. Both muricid and naticid drillers select their prey species (see Taylor 1970; Taylor et al. 1980, 1983; Harper and Morton 1997 for muricid data and Taylor 1970; Hoffman et al. 1974; Taylor et al. 1980, 1983; Kitchell et al. 1981; Hoffman and Martinell 1984; Kelley 1988; Kohn and Arua 1999 for naticid data). Also both groups of borers non-randomly locate their drill holes on mollusc shells (see Harper and Morton 1997 for muricid data and Ansell 1960; Berg and Nishenko 1975; Negus 1975; Kelley 1988; Anderson 1992; Dietl and Alexander 1995, 1997 for naticid data). The increase of site selectivity during ontogeny has been reported for naticids (Złotnik 2001). The diameter of naticid drill holes also correlates positively with the size of the prey (Ansell 1960; Kitchell 1986; Kelley 1988; Kowalewski 1990; Anderson et al. 1991). Finally, multiple drill holes are produced by both muricid (Harper and Morton 1997) and naticid (Hoffman et al. 1974; Kitchell et al. 1986) drillers. In this case, however, it should be emphasised that muricid and naticid multiple drill holes are interpreted differently. In fact, only muricid multiple drill holes are comparable to those typically produced by cassids because only muricids can prey upon a single prey in a group (Harper and Morton 1997).

The similarities between the patterns of drilling predation displayed by cassids and those displayed by gastropods that drill in shells of mollusc prey are fairly intriguing since the cassid drilling techniques differ distinctly from those displayed by naticid or muricid drillers (compare Hughes and Hughes 1971; 1981 with Carriker 1981). Also, the structure of the echinoid test is not comparable with the structure of a bivalve or gastropod shell. Similar patterns of drilling predation recognised for major groups of gastropod borers may imply that the interactions between the shell-drilling gastropod predators and their preys are controlled strongly by general factors such as size and mobility of prey, size and mobility of predator or thickness of prey's shell. However, it should be emphasised that cassid-echinoid interactions are insufficiently known to postulate any far-reaching conclusions. The presented concept should therefore be treated only as a preliminary hypothesis, which needs to be confirmed by future studies.

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