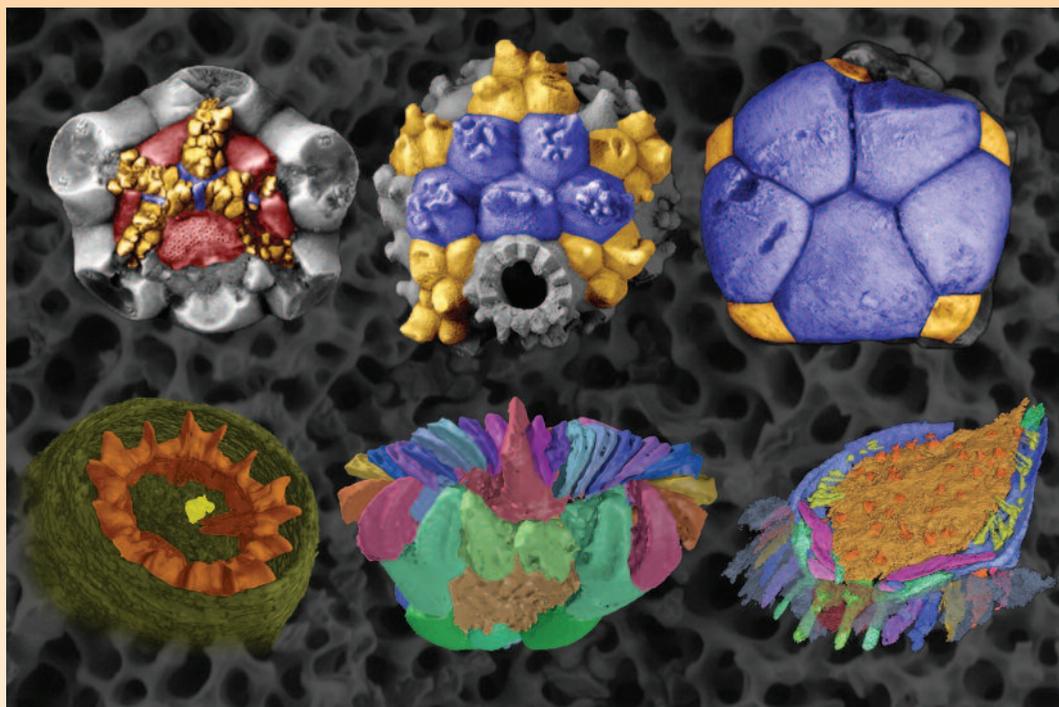


PROGRESS IN ECHINODERM PALAEOBIOLOGY



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SNEAKY SNAILS: HOW DRILLHOLES CAN AFFECT PALEONTOLOGICAL ANALYSES OF THE MINUTE CLYPEASTEROID ECHINOID *ECHINOCYAMUS*?

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INTRODUCTION

Drilling in marine invertebrate shells is a common feeding strategy for a variety of predatory and parasitic gastropods. Naticids, muricids, capulids, nudibranchs, eulimids as well as the group of tonnaceans including cassids, cymatiids, tonnids, and some pulmonats are known drilling predators in marine environments (Bromley, 1981; Carriker, 1981; Kelley, 1988; Hoffmeister *et al.*, 2004). Most of these drilling gastropods predate on a restricted variety of prey. Naticids, muricids and capulids, cymatiids and some pulmonats drill in other mollusks or barnacles (Carriker and Yochelson, 1968; Bromley, 1981; Palmer, 1982; Kelley, 2001; Kelley and Hansen, 2006). Nudibranchs are known to drill in calcareous polychaete tubes (Young, 1969), while cassids and eulimids drill in echinoids (Hughes and Hughes, 1971, 1981; Warén and Crossland, 1991; Warén *et al.*, 1994). Drilling in shells leave predatory drillholes (Fig. 1A), which can be attributed to a specific predator due to characteristic morphological features. Drilling frequencies and the drillhole size can give detailed insights into fossil predator-prey interactions. Cassid gastropods are known predators of echinoids producing characteristic drillhole morphologies (Fig. 1B) and sizes (Hughes and Hughes, 1971, 1981). There has, however, been little study on the effects of taphonomic bias with respect to drillhole morphologies and preservation (Nebelsick and Kowalewski, 1999; Ceranka and Złotnik, 2003; Grun *et al.*, 2014).

This analysis includes numerous Recent and fossil tests of the clypeasteroid echinoid *Echinocyamus pusillus* from Recent nearshore environments around Giglio Island (Mediterranean Sea) and fossil specimens from Astrup and Doberg (northern Germany): with trace fossils (*Oichnus*) interpreted as drillholes. Tests were analyzed for: (1) drilling rates, (2) drillhole size, (3) size selectivity, (4) site selectivity, (5) drillhole morphology, (6) drilling based test-destructions, and (7) taphonomic alterations.

STUDIED FAUNA

The genus *Echinocyamus*, a minute clypeasteroid echinoid, is used for analysis since it is easy to collect, abundant in a various habitats and occurs in Recent as well as in the Cenozoic fossil record. The behavior, morphology and predator-prey interactions of this genus has been described by several authors (Mortensen, 1927, 1948; Nichols, 1959; Ghiold, 1982; Telford *et al.*, 1983; Nebelsick and Kowalewski, 1999; Kowalewski and Nebelsick, 2003; Ziegler *et al.*, 2008; Grun *et al.*, 2014). *Echinocyamus* shows a wide distribution occurring in shallow waters down to 1250 m depth, burrowing in the sediment. The flattened calcareous test is oval to sub-elliptical in outline, up to 15 mm in length and

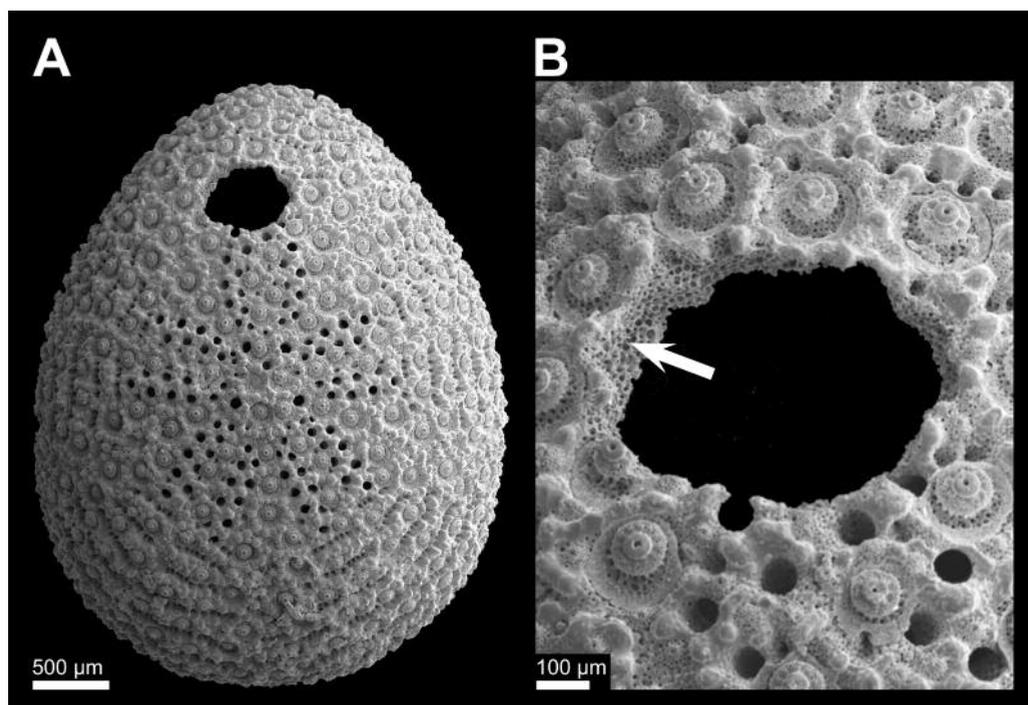


Figure 1. Photomicrographs of a Recent *Echinocyamus pusillus* test from nearshore environments around Giglio Island (Italy, Mediterranean Sea). (A) The elliptical test shows a drillhole in the anterior part. (B) In the detailed view the presence of microstructures (tubercles, knobs and pores in a ragged drillhole outline. The arrow indicates the concave cross-section of the drillhole.

entirely covered by minute spines. The aboral test side contains the apical disc and the petals; the oral test side is characterized by the slightly depressed peristome and periproct. The skeleton also features an internal support system which connects the oral and aboral sides of the test which leads to a high preservation potential.

TAPHONOMY

Despite its high preservation potential, specimens of *Echinocyamus* are subjected to taphonomic effects which can dramatically bias Recent and fossil samples, depending on the environment in which the individuals occur. High energy environments with low sedimentation rates are more likely to result in test destruction than low energy environments associated with high sedimentation rates. Additionally, drillholes can be potentially affect the stability of the echinoid tests, especially when large drillholes occur in small individuals leading to a size bias of preserved specimens.

MORPHOLOGY, FREQUENCIES AND TAPHONOMIC BIAS

Analyses of drilling frequencies show similar rates with 15 % for Recent samples around Giglio Island and for Oligocene samples from northern Germany. These drilling rates are in contrast to those found by Nebelsick and Kowalewski (1999) with a drilling frequency of up to 70 % for environments in the Red Sea. Analyzed tests show predominantly single drillholes. Predators do not seem to actively choose prey items by test size since correlations between tests length and drillhole length are absent or low. The distribution pattern of drillholes shows a high selectivity of the predator for the aboral side of the test, especially for the petal area which contains the respiratory

tube feet. Predators do not prefer the anterior or posterior parts of the echinoids test as both show similar drilling frequencies. Drillhole morphology (Fig. 1B) is highly affected by the microstructure of the skeleton; the drillhole outline is irregular if drilled within pore rich areas or is smoother if the cassid drill into areas without pores. Drillholes are concave shaped in the cross-section which is due to stereom differentiation of the echinoid test plates (Figure 1B, arrow).

The lack of very small individuals with large drillholes may be indicative for a biased size distribution of Recent drilled tests due to handling effects of the predator. The test size distribution of drilled and undrilled tests suggests that drilled test do not seem to be subjected to preferential test destruction than non-drilled test. Further predation and drillhole based biases are discussed.

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