

# Signs of predation in the Middle Jurassic of south-central Poland: evidence from echinoderm taphonomy

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Distinct faunal aggregates are described from the Middle Jurassic (uppermost Bajocian/lowermost Bathonian and Middle Bathonian) clay deposits of Częstochowa area, south-central Poland. These aggregates are composed of molluscs (scaphopods, gastropods, bivalves, ammonites and belemnites), articulate brachiopods and echinoderms (asteroids, crinoids and echinoids). A large percentage of the fossils, especially bivalves, are fragmented, but some fossils are complete. Although most of the fossils are crushed and fragmented, they are still identifiable to at least the genus level. Thorough statistical analysis of taphonomic features indicates that the preservation of asteroid marginal plates is distinct from the ossicles derived from the host clays. The high frequency of bite marks and the good state of preservation suggest that the accumulations are the products of predation activities and most probably are the effect of regurgitation. Taking into account the rich and diverse fauna, the predator was a bottom-feeding generalist. Possible predators include palaeospinacid sharks, a tooth of which was collected from the same bedding surface, but not associated with regurgitated remains. Although the bite marks on the asteroid ossicles point to sharks as potential producers of regurgitates, other vertebrates, like durophagous pycnodontiform fish, cannot be excluded. □ *Jurassic, Poland, predation, regurgitates, starfish, taphonomy, vertebrates.*

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Digestive residues are of great palaeobiological importance, especially for study of the feeding preferences of marine vertebrates, predator-prey relationship and evolution of food web structure (Pollard 1990; Sato & Tanabe 1998; Neumann 2000; Chin 2002; Northwood 2005; Vannier & Chen 2005). This is particularly interesting for the time of the Mesozoic Marine Revolution (e.g. Vermeij 1977; Kelley & Hansen 2001; Walker & Brett 2002; Harper 2006), when both the predation (durophagous predators) and the frequency of predation-resistant morphologies (armoured preys) increased significantly (Kelley & Hansen 2001; but see also Oji *et al.* 2003). Compared to coprolites, where digestive processes destroy the majority of swallowed elements, regurgitates contain better-preserved and recognizable food remains; skeletal elements especially are less affected by the digestive processes. When preserved as fossils, regurgitates, contrary to coprolites, are generally lacking a phosphatic matrix (Pollard 1990). This is due to a short residence time of food particles in the digestive tract, and regurgitates are therefore better suited for retrieving ecological information. By sampling some otherwise rare taxa or preserving fragile skeletons, regurgitates can also further our understanding of

fossil biodiversity. In practice, fossil regurgitates are preserved as aggregates of skeletal elements without much distinctive features, and the problem of how to formally identify them in sedimentary rocks remains. Aggregates of faunal remains can be derived from various sedimentary or biotic processes including hydrodynamic or taphonomic sorting, wash-over of fine sediments, original patchy distribution of communities, regurgitates or coprolites of predators/scavengers. Only a fine taphonomic analysis of the bioclasts should help identify the possible causes for given fossil aggregates and recognition of regurgitates.

Middle Jurassic (Upper Bajocian through Bathonian) clays from the Polish Jura are known for their well-preserved micro- and macrofauna including gastropods (Kaim 2004), brachiopods (Wiśniewska-Żelichowska 1978), ammonites (Majewski 1997; Matyja & Wierzbowski 2000; Zatoń & Marynowski 2004, 2006; Kopik 2006), belemnites and diverse echinoderm ossicles (Gedl *et al.* 2003). Fossils of the clays are usually scattered throughout the sedimentary rocks or enclosed in carbonate concretions, commonly preserving original aragonitic shell material. In some locations, aggregates of densely packed fossil remains occur. The fossil aggregates are best observed on the

weathered surfaces of the clay-pits, usually on the floors of particular exploitation levels. All invertebrate fossil groups known from the surrounding sedimentary rocks are identifiable from jumbled remains, with echinoderms, bivalves and/or brachiopods dominating. Skeletal elements of organisms with multi-element skeletons such as echinoderms are always found dissociated. For comparison, accumulations of skeletal elements rich in dissociated echinoderm ossicles, renowned as 'echinoderm lenses' are common in Cretaceous deposits, and have usually been interpreted as regurgitates (e.g. Wright & Wright 1940; Breton 1992; Villier 1995). The densely packed fossil aggregates from the Middle Jurassic of Poland may be an equivalent.

Compared to other common fossil groups, echinoderm skeletal elements well record a high variety of taphonomic processes (Améziac-Cominardi & Roux 1987; Meyer *et al.* 1989; Donovan 1991; Llewellyn & Messing 1993; Baumiller *et al.* 1995; Nebelsick 1999a, b). Comparative and quantitative approaches of echinoderm preservation allow precise assessments of ecological and taphonomic processes (Brett & Baird 1986; Meyer *et al.* 1989; Nebelsick 1999b; Gahn & Baumiller 2004).

Dead starfish individuals are disarticulated into a jumble of plates during a timespan ranging from hours, in the case of ingestion by predators, to a few weeks in examples of natural decay of organic tissues (Blake 1967; Breton 1992). Biting of sharp teeth causes deep notches and scars on ossicle surfaces, which are recognizable on fossil ossicles (Neumann 2000). Note that the occurrence of bite marks does not prove that a predator killed the individuals. Extant forms commonly bear non-lethal bite marks (Mah 2005) on the marginal plates and bite marks could also be due to scavengers. Disarticulated, isolated plates become hard elements at the surface of the sediment. They can undergo mechanical abrasion and chemical corrosion, which should smooth the ornament and the edges of the plates. Various encrusting organisms can settle on disarticulated ossicles and Breton (1992) described various traces produced by bioeroding organisms. In life, the skeleton of a starfish is made up of a dense reticulate network of high magnesian calcite fibres, the stereom. During early diagenesis, the stereom is modified into low magnesian calcite, new calcite precipitates synaxially and the skeletal plates gain the characteristics of single calcite crystals. Fractures occurring before and after diagenesis can be clearly distinguished. The former are irregular to conchoidal, whereas the latter occur through calcite cleavage.

The plates from the marginal frame are large and robust skeletal elements in most starfishes. Marginal

plates have a good preservation potential and most aspects of their taphonomic and diagenetic history can be described from their surface aspect.

The present paper describes and compares the taphonomic features of starfish ossicles (marginal plates) collected from the aggregates and clays of the Mid-Jurassic of the Polish Jura. Statistical comparison of preservation states of ossicles found in aggregates and in a reference sample of the surrounding sedimentary rocks should help in recognizing the remains of predation activities from other types of accumulations.

## Geological setting and palaeogeography

In the Middle Jurassic, the Polish Basin was the easternmost part of the Mid-European Epicontinental Basin (Dadlez 1989). It was bordered to the north by the Fennoscandian Shield, to the east by the Belarussian High and Ukrainian Shield, and to the southwest by the Bohemian Massif (Fig. 1A). The Fennoscandian Shield and Bohemian Massif are considered to be the main sources of clastic deposits that infilled the basin (Dadlez 1997). To the south, the Polish Basin was not clearly separated from the northwest margin of Tethys. The epicontinental Polish Basin was connected with Tethys at least during transgressive pulses (Dayczak-Calikowska *et al.* 1997), but the geographical connections to Poland are still unclear. According to Dayczak-Calikowska & Moryc (1988), the Moravian Gate on the west was closed at least until the late Bathonian transgression, and the connection with Tethys was possible through the East Carpathian Gate via Mid-Polish Trough in the southeast. Świdrowska (1994) suggested that at least the Aalenian transgression entered from the west, through the Germanic Basin.

The Middle Jurassic deposits are best exposed in the monoclinical structure referred to as the Polish Jura Chain, which extends from a southeast to northwest direction in south and central Poland (Fig. 1B). The Upper Bajocian and Bathonian deposit exposed in this area consists of a monotonous sequence of black and dark-grey clays, intercalated with more or less continuous levels of carbonate concretions or massive siderites, forming the ore-bearing Częstochowa Clay Formation (e.g. Kopik 1998; Matyja & Wierzbowski 2000). The sediments originated in epicratonic basin.

All fossil material discussed in this paper originate from two working brick-pits named 'Sowa' and 'Gnaszyn', located at Kawodrza Górna and Gnaszyn Dolny, respectively, approximately 10 km southwest of Częstochowa (Fig. 1C). Taking into account the North-West European ammonite zonation, the clays exposed in the 'Sowa' brick-pit represent the

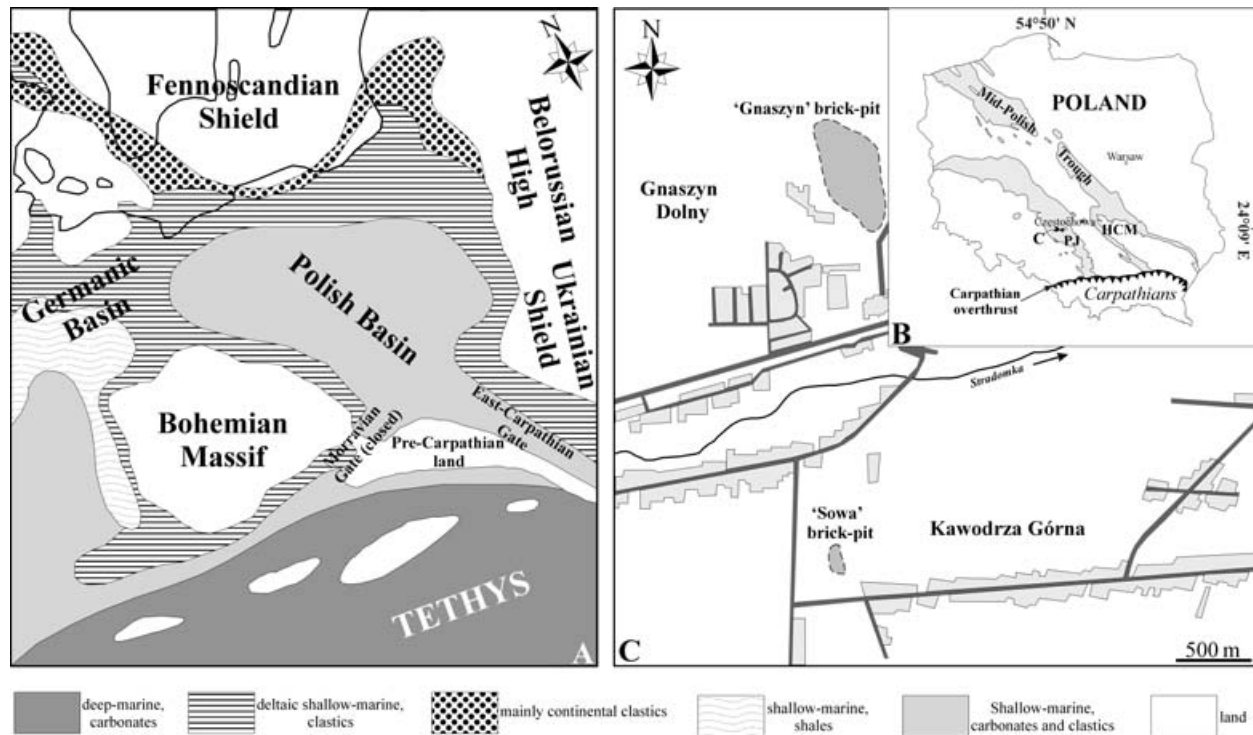


Fig. 1. □A. Palaeogeographic map showing the location of the Polish Basin during the Bajocian–Bathonian times (after Ziegler 1990; modified). □B. The map of Poland with Jurassic sedimentary rocks in grey. PJ – Polish Jura Chain, HCM – Holy Cross Mountains; black square indicates the study area. □C. Location of the ‘Sowa’ and ‘Gnaszyn’ brick-pits in the study area.

uppermost Bajocian and lowermost Bathonian, dated as the Bomfordi Subzone of Parkinsoni Zone and Convergens Subzone of Zigzag Zone, respectively (Matyja & Wierzbowski 2000; Zatoń & Marynowski 2004, 2006). In the ‘Gnaszyn’ brick-pit, the sedimentary rocks are Middle Bathonian (Subcontractus and Morrisi Chrones) and late Bathonian (Hodsoni Chron = Bremeri and early Retrocostatum Chron in Submediterranean zonation) (Majewski 1997; Zatoń *et al.* 2006; Matyja & Wierzbowski 2006).

## Material and methods

### Collection and treatment of samples

In total, nine samples (fossil aggregates) were collected from the weathered bedding-planes of the investigated exposures: two samples from the uppermost Bajocian/lowermost Bathonian interval at the ‘Sowa’ brick-pit, and seven samples from the Middle Bathonian (Morrisi Zone) at the ‘Gnaszyn’ brick-pit. Additionally, one sample (Gnaszyn-HS) was derived from the host clays of the ‘Gnaszyn’ brick-pit for comparative analysis. Some samples were photographed in the field (Fig. 2) and all were examined macroscopically. After initial examination, the samples were disinte-

grated in hot water and sieved through meshes of 0.315 mm diameter. The obtained material was then dried and examined using a binocular microscope. Among starfish ossicles, only the marginal plates were sorted. Fossil remains were determined to genus and species level if possible. The material is housed at the Department of Ecosystem Stratigraphy, Faculty of Earth Sciences in Sosnowiec, Poland under catalogue acronyms GIUS 8-3433-1 to GIUS 8-3433-8, except for asteroid ossicles that are deposited at Centre de Sédimentologie-Paléontologie, Université de Provence, Marseille (numbers VIL 001 to VIL 009).

### Analyzing taphonomic processes from starfish ossicles

Ossicles preserved in fossil regurgitates should have experienced a taphonomic history distinct from that of the surrounding sedimentary rocks, because of the ingestion and preservation in patches. Taphonomic and diagenetic alterations of ossicles were explored using a scanning electron microscope (SEM, see Fig. 3). The taphonomy of the sampled aggregates was characterized semiquantitatively, which allows statistical comparisons of samples (e.g. Meyer *et al.* 1989; Llewellyn & Messing 1993; Nebelsick 1999a; Gahn & Baumiller 2004). Six taphonomic variables

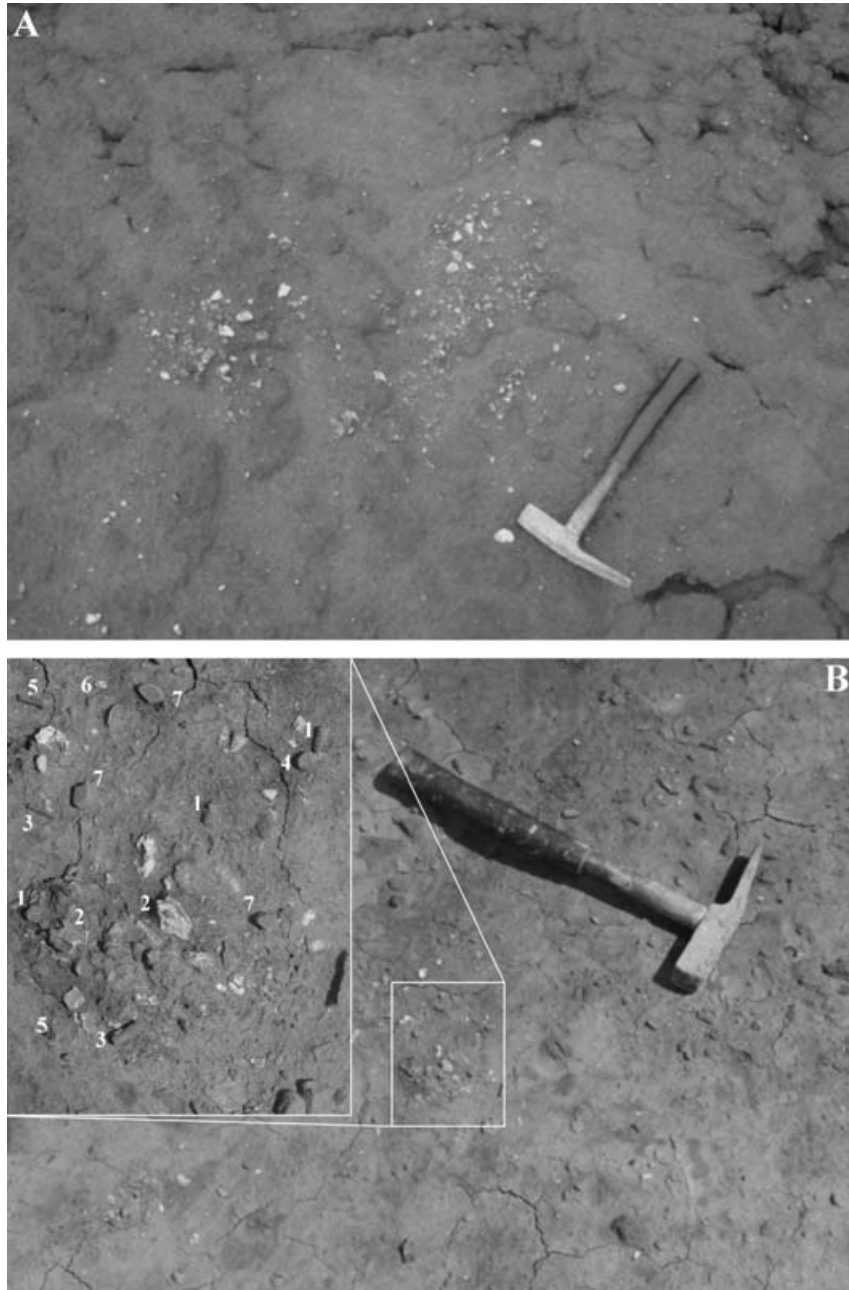


Fig. 2. □A. Scattered uppermost Bajocian/lowermost Bathonian regurgitates at 'Sowa' brick-pit. The components of the aggregate at the right could have undergone some dispersion due to the post-excavation exposure on the bedding plane, as well. □B. Clumped Middle Bathonian regurgitated remains at 'Gnaszyn' brick-pit; 1 – gastropods, 2 – trioniid bivalves, 3 – belemnites, 4 – rhynchonellid brachiopod, 5 – echinoid spines, 6 – echinoid coronal plate, 7 – asteroid plates. The hammer is 30 cm long.

were described for each of the marginal plates from observation under a binocular microscope:

- 1 The overall quality of preservation was coded from 0 in the case of ossicles with the whole surface altered to 3 in the case of a perfectly preserved plate.
- 2 The bite marks were counted from 0 to 2, and ossicles with three or more bite marks are coded equally as 3.
- 3 The intensity of bioerosion was coded between 0 for ossicles without any traces and 3 for highly decayed plates.
- 4 The encrusting organisms were counted in the same manner as bite marks.
- 5 The alteration, whether mechanical or chemical, was coded between 0 for plates with ornament perfectly preserved and 3 for completely smoothed

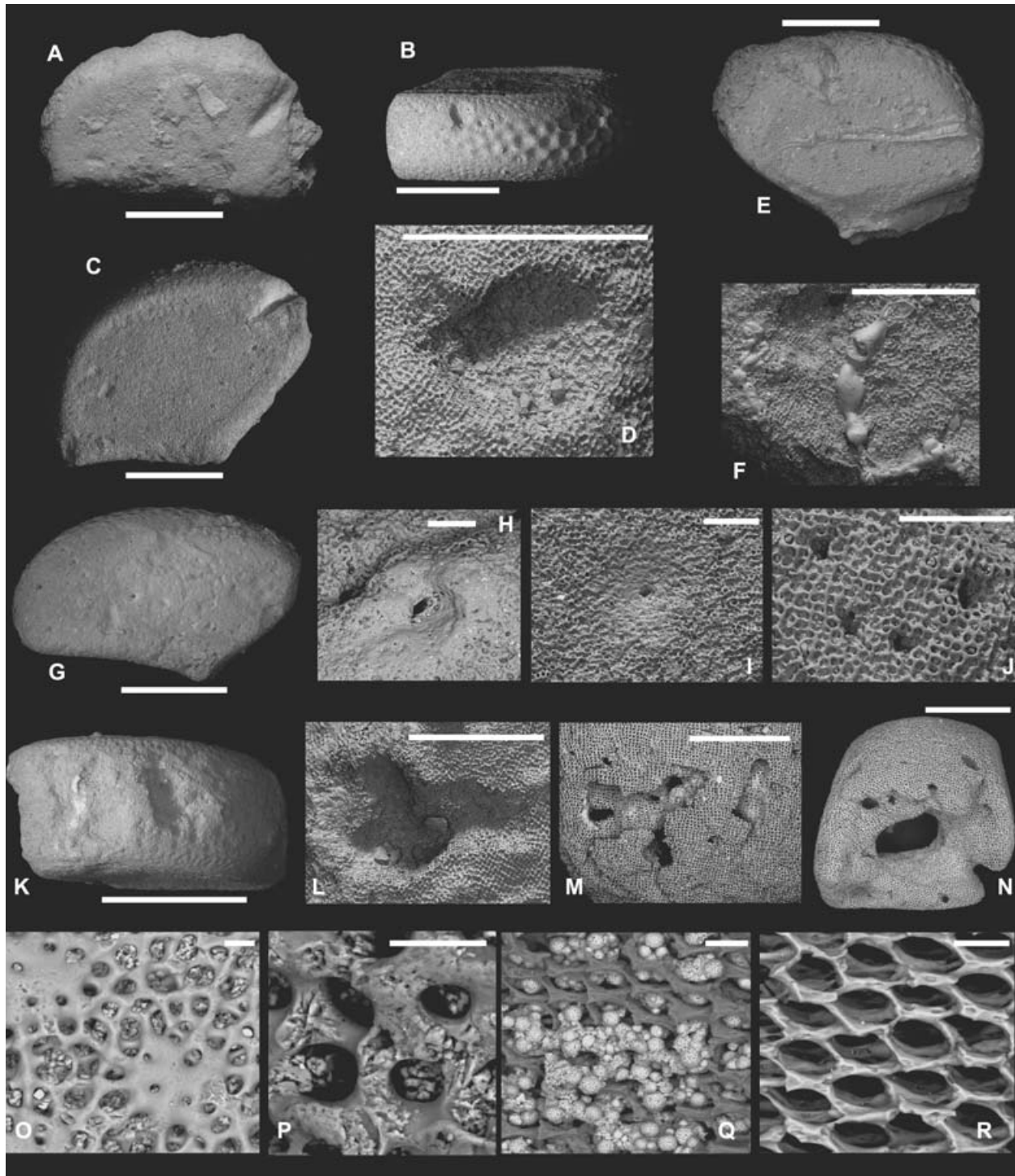


Fig. 3. Taphonomic features observed on marginal plates of astropectinid starfish. □A–D. Bite marks. A. Inferomarginal plate. B. Superomarginal plate. C. Superomarginal plate. D. Detail of the marks. □E, F. Encrusting organisms. E. Tube of a serpulid worm on the lateral side of a superomarginal plate. F. Encrusting foraminifer of the genus *Bullopora*. □G–J. Bioerosion traces: tiny borings. G. Superomarginal plate of astropectinid species with several tiny pits. H. Detail of pits flush with the skeletal surface. I. and J. Two sunken tiny pits and associated with an abrasion and modification of the stereom structure. □K–N. Bioerosion traces: large corrosion structures due to sponges. K. External surface of an inferomarginal plate with ornament altered by large size bioerosion traces. L. Detail of an irregular depression at the plate surface. M. Detail of a surface, showing the irregular aspect of the corrosion and the galleries connecting the pits. N. Marginal plate partially destroyed by intense bioerosion. □O–R. Microstructure preservation. O. Well-preserved structure of the stereom of an ornamented external surface. P. Stereom structure modified by calcite overgrowth synaxially to the skeleton fibers. Q. Framboid pyrite in the skeletal network. R. Dissolution of the stereom structure on an ossicle surface. Scale-bars: A–C, E, G, K 2 mm; D, F, L–N: 500  $\mu\text{m}$ ; H–J 100  $\mu\text{m}$ ; O–R 20  $\mu\text{m}$ .

Table 1. List of taxa occurring in the investigated accumulations.

Taxa	Samples							
	Sowa 1	Sowa 2	Gnaszyn 1 and 1'	Gnaszyn 2	Gnaszyn 3	Gnaszyn 4	Gnaszyn 5	Gnaszyn 6
<b>Gastropoda</b>								
<i>Cryptaulax</i> sp.		•	•		•	•	•	•
<i>Spinigera</i> sp.					•		•	
<i>Turcica</i> sp.		•				•	•	
<i>Calliotropis</i> sp.					•			
Calliotropidae indet.				•				•
<b>Scaphopoda</b>								
<i>Dentalium</i> sp.			•		•	•	•	•
<b>Bivalvia</b>								
<i>Corbula</i> sp.		•	•		•	•		
<i>Liostraea</i> sp.	•	•		•		•	•	•
' <i>Trigonia</i> ' sp.	•	•	•	•	•	•	•	•
<i>Myophorella</i> sp.		•						
<i>Gervillia</i> sp.		•						
<i>Pholadomya</i> sp.		•						
<i>Isognomon</i> sp.						•		
<i>Pleuromya</i> sp.		•	•		•			•
<i>Astarte</i> sp.			•	•		•		
Pectinidae indet.		•	•	•	•	•	•	•
<b>Belemnoida</b>								
Belemnitidae indet.				•	•	•	•	•
<b>Ammonoidea</b>								
<i>Morrsiceras</i>			•		•			
Tulitidae indet.					•			
Perisphinctidae indet.						•	•	•
<b>Brachiopoda</b>								
<i>Cardinirhynchia</i> sp.	•	•		•		•	•	•
<i>Capillirhynchia</i> sp.				•	•			
<i>Formosarhynchia</i> sp.	•							
Terebratulida indet.		•		•	•	•		•
<b>Crinoidea</b>								
<i>Balanocrinus</i> sp.		•		•	•	•	•	•
<i>Balanocrinus</i> cf. <i>subteres</i>					•			
<i>Chariocrinus</i> sp.	•					•	•	•
<i>Chariochnus</i> cf. <i>andreae</i>		•		•	•	•		
<i>Chariocrinus andreae</i>						•	•	
Isocrinida indet.					•	•	•	•
Millericrinida indet.						•		•
Comatulida indet.						•		
<b>Echinoidea</b>								
Echinoid plates/spines		•	•	•	•	•	•	•
<b>Asteroidea</b>								
Astropectinid and goniasterid remains	•	•	•	•	•	•	•	
<b>Vertebrata</b>								
Bone remains (fish?)					•			
Shark tooth	•							

outer surface (note that it remains difficult to distinguish the respective effects of mechanical or chemical alterations, without thorough observation using an electronic microscope).

- 6 The fractures were counted and their occurrences before or after diagenetic changes determined.

We calculated for all variables and all samples the mean value and a standard error, which gives the degree of variability. Searching for features specific of aggregates, we tested for differences between the accumulations (with  $n > 5$ ) and the reference sample (taken from the surrounding clays of the Gnaszyn brick-pit) using non-parametric Mann–Whitney tests.

## Results

### *Composition of the assemblages*

The fossil aggregates are densely packed within a clay matrix. They are semi-discrete or dispersed, but still spatially definable, round to elliptical aggregates ranging from 60 to 200 mm, or slightly more, in diameter. All the fossil aggregates contain abundant and diverse fossils. The fossil diversity from each fossil aggregate sample is listed in Table 1. The macro-invertebrate fauna consists of epifaunal to infaunal organisms. All large shells, such as trigoniid bivalves,

Table 2. Preservation and taphonomic characteristics of the starfish ossicles collected from the accumulations and the host clay. Each sample is described by the number of ossicles (*n*), the mean values (Mean) and standard errors (SE) for the six variables. Too few starfish ossicles were collected in the samples Gnaszyn 3, 4 and 6; statistics are not relevant, but the mean values are given for information.

	<i>n</i>	Preservation		Bite marks		Bioerosion		Encrusting		Fractures		Abrasion	
		Mean	SE	Mean	SE	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Gnaszyn-HS*	32	1.344	0.166	0	0	1.062	0.168	0.188	0.095	0.219	0.074	1.531	0.168
Gnaszyn 1	33	2.212	0.143	1.03	0.22	0.303	0.092	0.424	0.151	0.515	0.116	0.394	0.106
Gnaszyn 5	31	1.516	0.179	0.71	0.168	1.258	0.146	0.677	0.224	0.387	0.11	0.935	0.122
Gnaszyn 2	11	1.636	0.338	0.273	0.195	1	0.302	0.818	0.464	0.636	0.244	0.636	0.203
Gnaszyn 1'	9	1.778	0.278	0.556	0.242	0.889	0.2	0.778	0.547	0.444	0.176	0.778	0.278
Gnaszyn 3	3	1.333	0.882	0	0	1.333	0.882	1.667	0.333	0.333	0.333	1.333	0.882
Gnaszyn 4	3	1	0.577	0.333	0.333	2	0.577	5.333	1.453	0.333	0.333	2	0
Gnaszyn 6	2	1	0	1	1	2	0	0	0	0.5	0.5	1	0
Sowa 1	110	1.782	0.087	0.109	0.042	1.282	0.087	0.173	0.05	0.164	0.04	0.845	0.079
Sowa 2	15	1.933	0.267	0.933	0.3	0.8	0.175	0.733	0.206	0.067	0.067	1	0.218

\*Shaded line highlights results for the reference sample taken from the clay surrounding accumulations.

oysters, some rhynchonellid and terebratulid brachiopods, and ammonites, are fragmented. Smaller fossils are usually preserved whole, but some, especially complete brachiopods, are flattened due to post-depositional compaction. The echinoderms are preserved as isolated ossicles (asteroids, echinoids), or more or less articulated elements (columnals and pluricolumnals of crinoids). Belemnite rostra, together with asteroid and echinoid ossicles, possess distinct etched surfaces. Some of the fossils are encrusted by foraminifers, serpulids and/or oysters. On many asteroid marginal ossicles, bite marks are observed (Fig. 3A–D). Only two samples, from 'Sowa' and 'Gnaszyn' brick-pits, contain a shark tooth and a small bone fragment, respectively. In addition, small wood fragments are also present.

### Taphonomic features on starfish ossicles

*Alteration of ossicle structure.* – On average, the fine skeletal structures of the collected ossicles show a good state of preservation. The original stereom mesh is generally preserved. In the most well-preserved specimens, the stereom looks similar to that of living echinoderms, although filled by clays (Fig. 3O). Calcite overgrowths are rare and of very limited extent to the surface of the skeletal ossicles (Fig. 3P). Small pyrite crystals occur in some ossicles, where they grow within the cavities of the stereom mesh (Fig. 3Q). Micro-corrosion, as described by Améziane-Cominardi & Roux (1987) on extant material, is not recognized. The most common alterations of the microstructure are dissolution, wear or breakage of the stereom associated to alteration of the ossicle surface (Fig. 3R).

*Encrusting organisms.* – About 25% of the collected ossicles are encrusted by at least one recognizable

organism. The foraminifer *Bullopora* sp. is the most commonly encountered form (Fig. 3F), representing more than 70% of cases, but serpulids are also frequent (Fig. 3E). Only two juvenile oysters have been identified. The encrusters can be attached to any part of the ossicles, either the external face or the articulation faces (Fig. 3E), which demonstrates that encrusting organisms settled on isolated ossicles lying on the sediment surface, and after the complete breaking and decay of the starfish body. The frequency and the number of encrusting organisms are highly variable among samples, and between ossicles within a sample (Table 2).

*Bite marks.* – Specific scratches, scores and pits imprinted in stereom are interpreted as bite marks of different angles and strength on the ossicle (Fig. 3A–D). Scratches are understood here as shallow, but clean, cuts in the stereom of the ossicle surface. Scores are more conspicuous cuts, approximately of 0.5 to 1.0 mm wide and up to 3.0 mm long (Fig. 3A, C). They have distinctive, flattened oblique sides, forming a straight angular groove. Pits were produced as the imprint of a blunt point perpendicular to the surface of the ossicle. The outline of the holes is elliptical, generally with an angular bottom (Fig. 3B, D). They are never very deep (about 0.1–0.3 mm) and measure 0.5 to 1.0 mm in maximum dimension. All bite marks are suggestive of a unique type of predator or scavenger with blunt pointed teeth, with a width of about 1 mm at their tip. In fossil accumulations, a mean of 24% of marginal plates bear bite marks (Table 2). In most plates they occur on the outer face or on the external part of the lateral faces. In some cases, biting seems to be the cause of plate fractures. We were unable to recognize regenerated stereom as illustrated by Neumann (2000), which suggests that bites were all lethal or produced after death.

Table 3. Correlation among the variables estimated by *P*-value of Spearman rank correlation test. Lower-left and the upper-right parts of the table consider the samples from the 'Gnaszyn' and 'Sowa' brick-pits respectively. Significant values are in bold.

	Preservation	Bioerosion	Abrasion	Encrusting	Bite marks	Fractures
Preservation	–	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.27	0.47	<b>0.01</b>
Bioerosion	<b>&lt;0.001</b>	–	<b>&lt;0.001</b>	0.33	0.61	0.14
Abrasion	<b>&lt;0.001</b>	<b>0.01</b>	–	0.97	<b>0.02</b>	0.96
Encrusting	0.49	0.86	0.19	–	0.38	0.98
Bite marks	0.81	0.87	0.84	0.17	–	<b>0.08</b>
Fractures	<b>0.01</b>	0.16	0.71	0.31	0.39	–

*Bioerosion traces.* – The traces of corrosion due to encrusting or foraging organisms are very similar to those mentioned by Villier *et al.* (2004) on material from the Lower Jurassic clays of western France. Two thirds of the ossicles show obvious traces of bioerosion which is the major cause for ossicle alteration (Table 2). Two types of traces are easily distinguished; tiny pits and large irregular depressions.

Tiny pits occur in one third of marginal plates. Any face of an ossicle may be pitted by tiny holes (diameter 20 to 50  $\mu\text{m}$ ), digging relatively deep (Fig. 3G–J). At the margins of the openings, the stereom mesh does not look broken, but rather etched. In most cases, the tiny holes are placed in a rounded depression where the stereom is more or less altered (Fig. 3H, I). Various types of infaunal borers are able to produce such holes in carbonate skeletons, including fungi, sipunculans, phoronidians, polychaetes worms and acrothoracican cirripeds (de Saint-Seine 1955; Hutchings 1986; Breton 1992). It is unclear, however, which of these organisms may have lived in boreholes in echinoderm ossicles.

Large, irregular depressions are very common, occurring in 46% of the marginal plates. They are large structures, generally 0.1 to 0.5 mm in length, and can cover most parts of ossicles (Fig. 3K–N). Both the outline and the bottom of the depression are smooth and irregular. The largest pits are prolonged laterally by galleries (Fig. 3M, N). In cases of intense bioerosion, the decay extends deep into the ossicle and can form a wide cavity, which weakens the ossicle structure (Fig. 3N). Thus, intensely corroded plates are commonly found fragmented. There is no evidence of fracture of the stereom in such traces, and the encrusting organism probably induced the corrosion through chemical processes. Similar corruptions of ossicles are common in the Cretaceous and Breton (1992) suggested that encrusting sponges might be responsible.

#### *Compared taphonomy of the sampled levels*

The analysis of correlation between the variables shows that the mean preservation of ossicles is directly

related to the intensity of bioerosion and alteration by etching and mechanical abrasion (Table 3). During maceration on the sediment surface, ossicles are subjected to post-mortem etching, mechanical erosion and bioerosion that modify the aspects of the skeletal structure. Correlations of the variables suggest that preservation is related to the residence time of ossicles in the superficial layers of the sediment. The mean preservation is highly variable between samples but the lowest value is recorded for the reference sample, collected from the host clays (Table 2). The potentially better preservation in aggregates is related to a significantly lower degree of alteration of the ossicle surface.

Bite marks are common features in all aggregates with a frequency ranging from 10% of ossicles bitten up to a mean of one bite mark per ossicle. No evidence of bite mark was recognized in the ossicles collected in the reference sample.

The frequency of encrusted organisms varies independently of the other variables analyzed. Their occurrence is likely related to the time the ossicles stayed exposed at the surface of the sediment. The two lowest values are for the reference sample and 'Sowa' 1. In the other aggregates, frequency of encrusted organisms is extremely variable from one ossicle to another (Table 2).

Two variables constantly distinguish the preservation of ossicles from aggregates and from the sediment: bite marks and alteration (Table 4). Preservation in aggregates is also characterized by high standard errors (except for surface alteration). However, the sample of 'Sowa' 1 makes an exception to the rule. Despite a good preservation state due to a reduced level of surface alteration, all characteristics of 'Sowa' 1 do not differ significantly from that of the surrounding sedimentary rocks. In contrast to the other accumulation from the same level, 'Sowa' 1 does not show a high frequency of bite marks. The sample 'Sowa' 1 also differs by its low taxonomic diversity (Table 1), composed mainly of rhynchonellid brachiopods and starfish with a few bivalve fragments and crinoid ossicles.



Table 4. Statistical comparison of the accumulations and the reference sample from the surrounding sediment based on non-parametric Mann–Whitney tests.

	Sowa 1			Sowa 2								
	<i>U</i>	<i>P</i>	Sign.	<i>U</i>	<i>p</i>	Sign.	<i>U</i>	<i>p</i>	Sign.	<i>U</i>	<i>p</i>	Sign.
Preservation	-2.288	0.022	*	-1.947	0.515	NS						
Bioerosion	-1.239	0.215	NS	-0.757	0.449	NS						
Abrasion	-3.611	<0.001	**	-1.879	0.06	*						
Encrusting	-0.083	0.934	NS	-3.15	0.002	**						
Bite marks	-1.564	0.118	NS	-4.128	<0.001	**						
Fractures	-0.932	0.351	NS	-1.279	0.2	NS						

	Gnaszyn 1			Gnaszyn 1'			Gnaszyn 2			Gnaszyn 5		
	<i>U</i>	<i>P</i>	Sign.	<i>U</i>	<i>p</i>	Sign.	<i>U</i>	<i>p</i>	Sign.	<i>U</i>	<i>p</i>	Sign.
Preservation	-3.524	0.004	**	-1.213	0.225	NS	-0.114	0.416	NS	-0.776	0.438	NS
Bioerosion	-3.618	<0.001	**	-0.304	0.761	NS	-0.22	0.826	NS	-1.045	0.296	NS
Abrasion	-4.735	<0.001	**	-2.04	0.041	*	-2.69	0.007	**	-2.625	0.009	**
Encrusting	-1.43	0.152	NS	-1.443	0.149	NS	-1.765	0.078	*	-2.309	0.021	*
Bite marks	-4.273	<0.001	**	-3.917	<0.001	**	-2.441	0.015	*	-4.241	0.002	**
Fractures	-1.91	0.056	*	-1.333	0.182	NS	-1.724	0.085	*	-1.041	0.298	NS

*U*, test value; *p*, probability associated to the test significance; Sign., level of significance; NS, non-significant, \*significant; \*\*highly significant.

## Discussion

The taphonomic analysis demonstrates that the preservation of ossicles from the aggregates found in the Middle Jurassic of Poland derives from processes different from those occurring in the surrounding clays. Among the various causes for shell accumulation, those involving low sedimentation rate, hydrodynamic sorting and reworking of the sediment are unlikely because of the reduced mechanical abrasion of ossicles in aggregates, except for the sample 'Sowa' 1. Local aggregation of brachiopod shells may reflect the initial structure of benthic communities at 'Sowa'. In soft-bottom environments, brachiopods live frequently aggregated into patches where they are attached one to each other. Transported by currents, skeletal elements can accumulate mechanically within a brachiopod clump. This latter hypothesis is compatible with the composition and the preservation of the sample 'Sowa' 1.

The high frequency of bite marks strongly supports the intervention of a predator or scavenger for all other aggregates. The constantly flattened rounded shape of the aggregates dismisses the hypothesis of accumulation in burrows or shelters. Most taphonomic features fit the hypotheses of faeces or regurgitates. Skeletal elements preserved in fossil faeces or regurgitates experienced a taphonomic history distinct from that of the surrounding sedimentary rocks, because of the ingestion and preservation in patches. Faeces or regurgitates lying at the sediment surface are indeed cohesive, specific microenvironments, potentially favorable to preservation. Skeletal remains in

contact with the sediment may never be exposed to borer and encrusting organisms, while ossicles in contact with the sea water have a preservation potential similar to that of the surrounding mud. This explains why preservation is so variable between starfish ossicles of a single aggregate. In case of a long residence time before burial, most ossicles from aggregates would develop to a state of preservation similar to that of isolated ossicles lying on the sea bottom. Thus, the differences of preservation between accumulations can be explained by different exposure times and conditions before burial. Ossicles from the aggregates suffered very limited surface alteration (both mechanical and chemical), which is more attested for regurgitates than faeces. For comparison, similar preservation conditions were described in the so-called 'echinoderm lenses' of the Late Cretaceous that are interpreted as predator regurgitates. On the one hand, Breton (1992) showed that 'echinoderm lenses' have ossicles better preserved on average than isolated ossicles collected from the sediment. On the other hand, bite marks are particularly frequent in some, but not all, 'echinoderm lenses' (Neumann 2000).

The sampled regurgitates all have similar faunal content. Some of the fossils, even tiny echinoderm ossicles, were encrusted with serpulids, foraminifers or oysters. This attests that the remains were exposed for a variable period of time on the seafloor, after they were regurgitated. Some of the fossils could have been introduced or exported by currents or biotic activity at the sediment surface, but the dispersion must have been limited, because all remains are rather close to each other, forming well-defined clumps. The

presence of many different faunal groups in regurgitates, the majority of which are benthic, attests that a predator was rather a bottom-feeding generalist, having a low degree of specialization (Hattin 1996; Neumann 2000). However, the composition of prey distinguished the Middle Jurassic regurgitates from the Cretaceous 'echinoderm lenses' that were probably produced by selective echinoderm predators. Similar aggregates, in shape and fragmentation pattern, were presented by Grawe-Baumeister *et al.* (2000, pl. 1; Fig. 1) from the Kimmeridgian Lithographic Limestones. They were interpreted as regurgitated by durophagous fish *Gyrodus*.

The presence of semi-infaunal scaphopods, infaunal bivalves or even wood fragments indicates that the predator used to swallow large portions of bottom sediment together with the main food particles. Durophagous vertebrates, such as extant rays, feed on similar fauna often regurgitating stomach contents (Hattin 1996), and teleosts, like Sparidae, are also known to regurgitate (G. Cuny, personal communication, 2004). Apart from clearly benthic species, there are also juvenile ammonites and belemnite rostra within the aggregates. While belemnite rostra are fragmented, the small ammonite shells are often complete. Sato & Tanabe (1998), describing the stomach contents of a Cretaceous plesiosaur, noticed the complete absence of ammonite shells, while the aptychi were preserved. They concluded that small ammonites might have been swallowed whole and then their shells were affected by stomach acid. Here, the preserved ammonite shells additionally point to short residence time of swallowed fauna in the digestive tract of a predator and the regurgitated nature of these aggregates.

The predator that produced the regurgitate aggregates is impossible to identify without a clear association of the fossil regurgitates with the fossil remains of the predator preserved in the same bedding plane. An excellent example was presented by Sato & Tanabe (1998). These authors found the stomach content within the skeleton of a Cretaceous plesiosaur, giving the first direct evidence of its diet. An Early Jurassic ichthyosaur was described by Pollard (1968) with its gastric content, consisting of belemnite hooks, still preserved within the skeleton. The Jurassic hybodont shark *Hybodus* has also been found with gastric residues consisting of numerous belemnite rostra preserved between its pectoral fins, also giving information on its feeding habits (see Pollard 1990). Many skeletons belonging to theropod dinosaurs also contain the bony remains of their prey (Farlow & Holtz 2002). Buffetaut *et al.* (2004), for example, reported an evidence of spinosaurid dinosaur preying on the pterosaur. Dalsatt *et al.* (2006) reported the

presence of fish remains in the early Cretaceous bird *Confuciusornis* in its alimentary system.

However, most coprolites or regurgitates are found unassociated with their producers' skeletons. Additional diagenesis, especially of coprolites, hinders assignment to specific producers (Pollard 1990; Chin 2002). Thus, we can only suspect a potential predator. Hattin (1996) assigned Cretaceous regurgitates to *Ptychodus*, which was the only durophagous fish among the Cretaceous vertebrates of the Kansas area. Sometimes, teeth can co-occur with regurgitates, allowing the possibility that they belong to the producer of such remains. Neumann (2000) gave a similar interpretation for durophagous shark teeth *Heterodontus* co-occurring with regurgitates.

Some provisional conclusions can be drawn although the vertebrate assemblages from the study area are currently under research (A. Kaim, personal communication, 2004). In one sample from the 'Sowa' brick-pit (sample 'Sowa' 1), a shark anterior tooth has been found. It was tentatively assigned to the orthacodontid neoselachian *Sphenodus* (Fig. 4). The tooth was probably accumulated by current in the brachiopod clumps, like the echinoderm ossicles. Moreover, the tearing dentition of *Sphenodus longidens* or the clutching dentition of *Sphenodus macer* is indicative of a diet consisting mainly of soft-bodied preys, which is incompatible with the diversity of organisms found in the aggregates (Böttcher & Duffin 2000; G. Cuny, personal communication, 2004). Thus, it is hardly possible that the tooth belonged to the aggregate's producer.

Another complete tooth, assigned to palaeospinacid neoselachian *Synechodus* (Fig. 4), was found in the same clay-pit and the same bedding surface, but not associated with regurgitates. Palaeospinacids were rather small (< 1 m in length) benthopelagic sharks (Kriwet 2003a) inhabiting mostly offshore, shelf regions (Kriwet 2003b; Underwood & Ward 2004). *Synechodus* is regarded as a weak swimmer, with a strongly heterodont dentition suggesting a varied diet of both soft-bodied and shelled organisms (Underwood *et al.* 1999; Underwood 2002). However, the anterior and anterolateral teeth of *Synechodus* are hardly compatible with a full hard-shelled diet. This shark could be rather an ambush predator (Underwood 2002) and therefore, the fauna occurring in the fossil aggregates would not be the usual diet of *Synechodus* (G. Cuny, personal communication, 2004). The bite marks on the asteroid marginal ossicles seem to be made by a single type of predator, probably a shark. *Synechodus* could be a potential producer, even if its tooth was not associated with regurgitated remains. Other durophagous sharks or pycnodontiform fishes, although not recognized yet, may be responsible of

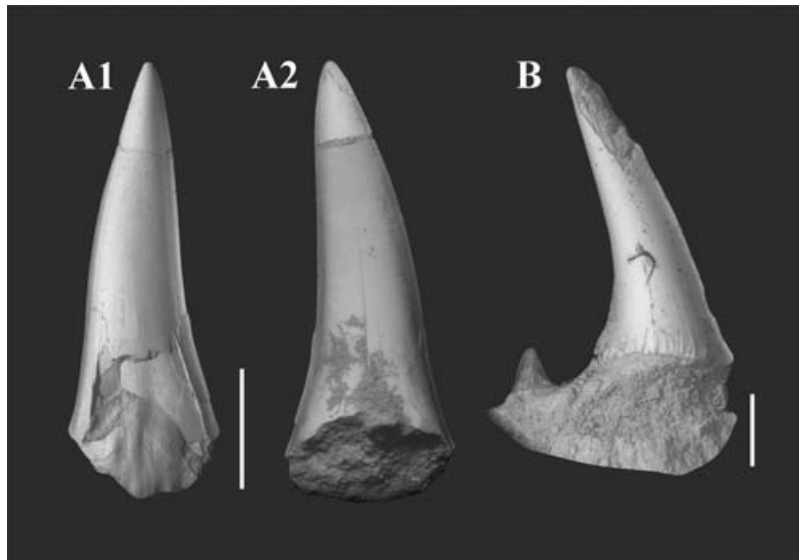


Fig. 4. □A. *Sphenodus* sp. found in one sample from 'Sowa' brick-pit (sample 'Sowa' 1) in labial (A1) and lingual view (A2), specimen deposited at the Faculty of Earth Sciences, Department of Ecosystem Stratigraphy at Sosnowiec, under the collection number GIUS 8-2512. □B. *Synechodus* sp. (lingual view) found loose in the sediment at 'Sowa' brick-pit, close to accumulations. Scale bars 1 mm.

the aggregates' formation as well (e.g. Poyato-Ariza & Wenz 2002).

The regurgitated remains under discussion provide additional important information. As mentioned above, after regurgitation, the remains could be easily dispersed by currents and/or scavengers and thus may have introduced significant bias to the fossil record. Mobile predators, like sharks, feeding in various parts of the basin, can regurgitate undigested remains in different places on the basin floor. Therefore, sampling such clay deposits without caution may significantly bias our palaeoecological data. In order to obtain the unbiased palaeoecological results, we should avoid sampling the sediments where such faunal aggregates are clearly visible. On the other hand, however, such regurgitates offer a valuable insight into the faunal diversity of the epicontinental basin on a wider scale, which can be reduced due to limited number of exposures representing the same time interval.

## Conclusions

The faunal aggregates from the Middle Jurassic clays of the Polish Jura most probably represent regurgitates, as evidenced from the taphonomy of the fossil remains and especially the asteroid ossicles. They provide an example of marine vertebrate diet and indirect evidence of predator-prey interactions in the fossil record. The presence of diverse benthic and nectobenthic fauna points to a bottom-feeding generalist. The state of preservation of the regurgi-

tated invertebrate fauna indicates that they were either fragmented or swallowed whole by predators. Although the potential predators are unknown, benthic-pelagic sharks may be suspected. Among the teeth found in the 'Sowa' brick-pit, some could belong to palaeospinacid neoselachians. However, other predators, like durophagous pycnodontiform fishes may have been responsible, as well.

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