DUROPHAGOUS PREDATION ON MIDDLE JURASSIC MOLLUSCS, AS EVIDENCED FROM SHELL FRAGMENTATION

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Abstract: Durophagous (shell-crushing) predation is known from the beginning of the Phanerozoic, but it has been suggested that modern intensity was not reached until the Late Cretaceous and Early Cenozoic, when specialized marine durophagous taxa increased in diversity. In this paper, evidence of durophagous predation on Middle Jurassic communities of molluscan prey is presented on the basis of distinct accumulations of fossil remains in the Polish Jura (south-central Poland) that contain characteristic, angular shell fragments with sharp, non-abraded margins. The diverse fossil content of the accumulations studied, consisting of either benthic or nektic/nekto-benthic taxa, indicates that the potential predatory taxon was an opportunistic generalist, most probably fish. On the basis of taphonomic observations, the faunal accumulations are interpreted to represent regurgitated remains (pellets). The common occurrence of such accumulations in the Middle Jurassic clays of the Polish Jura indicates that durophagous predation has been intense since the mid-Mesozoic, at least locally.

Key words: Predation, durophagy, shell fragmentation, Jurassic, Mesozoic Marine Revolution.

ALTHOUGH durophagous (shell-crushing) predation is known from the Early Cambrian, a marked increase in diversity of marine families of specialized shell-crushing predators occurred during Late Cretaceous and Early Cenozoic times (e.g. Vermeij 1977, 1987, 2002; Bambach 2002; Walker and Brett 2002; Oji *et al.* 2003; Harper 2006). Many of the taxa concerned were present by the beginning of the Mesozoic (Walker and Brett 2002; Harper 2006), but the fossil record of durophagous predation during Triassic and Jurassic times is sparse (Harper 2006).

Fragmented shell material caused by the shell-crushing predation is a highly significant component of shelly assemblages from a number of modern environmental settings (Cadée 1994; Cate and Evans 1994). Despite this, uncertainty exists as to whether the shell-fragmentation was caused by durophagy or physical factors (e.g. water agitation or compaction). Although previous studies have aimed to differentiate between fragments resulting from predatation and those caused by physical processes (e.g. Cadée 1994), Oji *et al.* (2003) showed experimentally a marked difference between shell breakage owing to transport and that produced by shell-crushing predators. They found that transported shells were only infrequently broken and possessed abraded margins. In contrast, angular shell fragments with sharp margins, found in numerous Cenozoic shell beds in Japan, were attributed to durophagous predators. Their research also showed that such angular shell fragments substantially increased during the Early Cenozoic, coinciding with the radiation of durophagous teleost fishes and decapod crustaceans.

Little is, however, known about the activities of possible durophages in the Jurassic. Here we present the evidence of shell-crushing predation in the Upper Bajocian–Middle Bathonian (Middle Jurassic) fossil accumulations in the Polish Jura.

GEOLOGICAL SETTING

Upper Bajocian–Bathonian (Middle Jurassic) sediments of the Polish Jura (Text-fig. 1) consist of dark grey marine clays that were deposited in an epicontinental sea. The clays, referred to as the ore-bearing Częstochowa Clay Formation, form a monotonous sequence intercalated with numerous horizons of carbonate concretions and massive siderite beds. They crop out in several active clay pits in both southern and northern parts of the Polish Jura and range in age from latest Bajocian to Late Bathonian (Majewski 1997, 2000; Kopik 1998; Matyja and Wierzbowski 2000, 2006; Zatoń and Marynowski 2004, 2006). They are very rich in fossils, which occur in both the clays and the carbonate concretions. In the clays they are usually scattered, but in some places they form distinct, subcircular to oval accumulations, best exposed

upon dry bedding planes. These are the main subject of the present paper. The accumulations studied come from active clay pits in the region of Gnaszyn and Kawodrza, near Częstochowa (south-central Poland; Text-fig. 1), where uppermost Bajocian (Parkinsoni Zone, Bomfordi Subzone)–Lower Bathonian (Zigzag Zone, Convergens to Macrescens zones: 'Sowa'/'Gliński' clay-pits) and Middle/ Upper Bathonian (Subcontractus to Retrocostatum zones: 'Gnaszyn' clay-pit) unconsolidated, dark grey clays are well exposed (Matyja and Wierzbowski 2000, 2006; Zatoń and Marynowski 2004, 2006; Zatoń et al. 2006).

MATERIAL AND METHODS

Eleven samples were collected in April 2006 for taphonomic analysis: six from the uppermost Bajocian/lowermost Bathonian transitional deposits, one from the lowermost Bathonian (Convergens Subzone, 'Sowa'/ 'Gliński' clay-pits), and four from the Middle Bathonian (Morrisi Zone, 'Gnaszyn' clay-pit).

The accumulations were photographed in the field and their general characteristics (e.g. shape, size) were noted. The portion of the bedding planes with the accumulations were then carefully transported from the field to the laboratory, where they were closely examined. The main aim of this procedure was to find out whether the shell fragments occur throughout the each sample, and to examine their features (e.g. angularity, sharpness of the margins, size range). This assured us that shell fragmentation is primary and could not be produced artificially by the later washing procedure. The samples were then carefully washed from the clay sediment and the whole residue was inspected under a binocular microscope. The following taphonomic features were noted: presence or absence of abrasion, dissolution, bioerosion and epibiontic cover. Because the fauna occurring in the accumulations also consists of multi-element skeletons (echinoderms) and the samples were different sizes (volumes), the frequency of fossils in each sample is relative and was estimated visually as single (1–5 elements), common (6–30) and abundant (more than 30 elements of a given group per sample).

In order to show the size distribution of the shell fragments in a particular sample, all bivalve shell fragments (being the most numerous) were measured by dry sieving using a series of sieves with mesh sizes ranging from 1.25 to 20 mm. All fragments from a particular mesh range (20–10, 10–5, 5–3.15, 3.15–2.5, 2.5–1.25 mm) were then counted and the results plotted. Univariate analysis, as standard deviation and coefficient of variation (CV), were
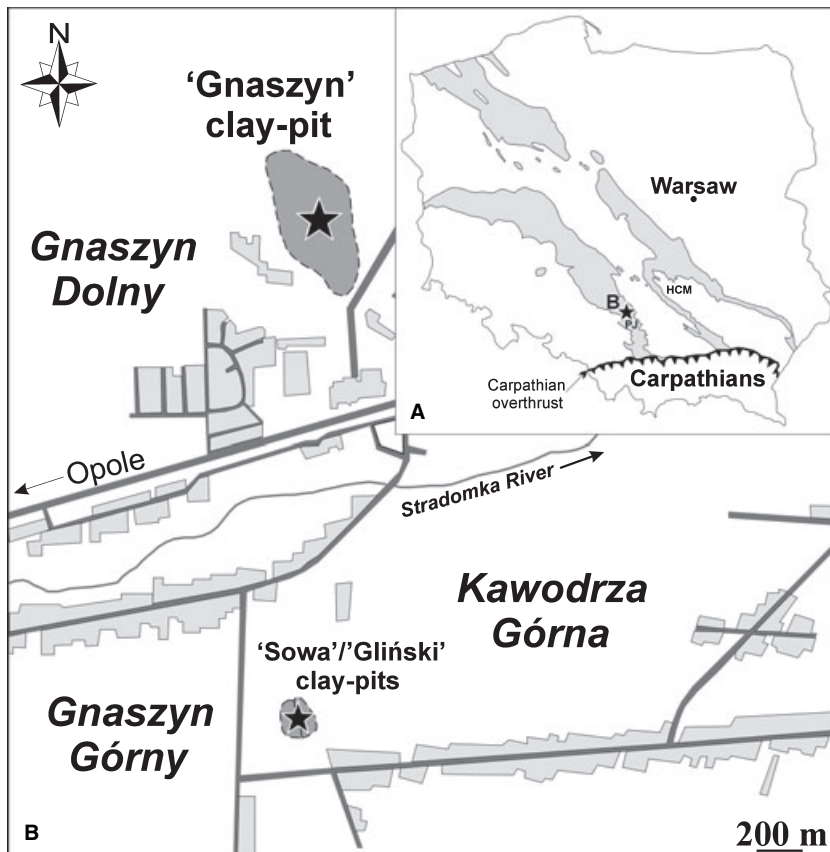
TEXT-FIG. 1. A, map of Poland with Jurassic deposits (shaded) and investigated area indicated (asterisk, B); PJ, Polish Jura; HCM, Holy Cross Mountains. B, enlargement of the investigated Gnaszyn/Kawodrza area near Częstochowa, with the sampled clay-pits indicated (asterisks) (modified after Zatoń et al. 2006).

used. The usefulness of the CV results from the comparison of normalized values in different samples.

The general taxonomic composition and relative frequency of fossil occurrences in each sample are given in Table 1. All of the material is housed at the Faculty of Earth Sciences, University of Silesia, Sosnowiec, under catalogue numbers GIUS 8-3435–3445.

RESULTS

On the bedding planes, the accumulations are more or less oval to subcircular in shape, from *c.* 56 up to 167 mm in diameter. They can occur as single or several accumulations on one plane, but distinctly separated from each other. The fossils in the accumulations are mixed and packed in their centres but may be more or less dispersed at their margins (Text-fig. 2A–D). In the field, some of the accumulations still retained their three-dimensional state, without any scattering of the bioclasts at their margins (Text-fig. 2D).

As is seen in Table 1, each sample comprises several taxonomic groups, but in quite different proportions. Most common are echinoderm ossicles and fragmented shells, mainly of bivalves. However, some almost complete valves and shells of small individuals also occur (see below). Small gastropods dominated by Trochidae (*Calliotropis*, *Turcica*) and Cerithiidae (*Cryptaulax*) also occur as near-complete specimens, although they all lack their apertures and some lack the apical part of the shell. Single specimens may also occur only as fragments of whorls. Many have a sideritic coating, and single specimens are partly pyritized (sample S4). Fragmented bivalve shells, mostly belonging to thick-shelled Trigoniidae (*Trigonia*, *Myophoria*), are most numerous in uppermost Bajocian/Lower Bathonian samples, but in the Middle Bathonian assemblages they still exceed in number the fragments belonging to other bivalve groups (Table 1). The rest of bivalves, which may also occur as fragments, are oysters (Gryphaeidae). Belemnites occur only as fragmented rostra. In all of the samples, shell fragments have angular, sharp edges (Text-fig. 2E). Cardiids, corbulids and nuculids represent small or juvenile specimens, and very often occur as complete single valves or shells. As for the gastropods, in places the surfaces of bivalves are coated with siderite.

The fragments vary in size, but the frequency of particular sizes differed between the samples (Text-fig. 3). The CV values calculated for particular samples show that although the shell fragments in them vary it is possible to distinguish two groups of samples in which the variation is similar. The first comprises samples S6, S2, Gn2, S4, Gl1, S1, for which the CV ranges from 79.9 to 69.5 per cent. The second consists of samples Gn3, Gn1, S3, S5 and Gn4, for which the CV is lower, ranging from 65.4 to 52.0 per cent. Taking into account the total amount of bioclasts from a particular fraction from all the samples, it is evident, that the 5–3.15-mm fraction predominates. CV values of particular fractions in all samples, however, clearly indicate that the 20–10 and 10–5-mm fractions are the most variable (Table 2).

Some of the asteroid ossicles possess distinct bite marks (Text-fig. 4); the external surfaces of many fossils, on the other hand, show signs of dissolution and bioerosion, and are encrusted by epibionts. These also occur, however, on the isolated ossicles of echinoderms, including articular facets of crinoids, and the inner surfaces of shell fragments (encrusted mainly by foraminifers).
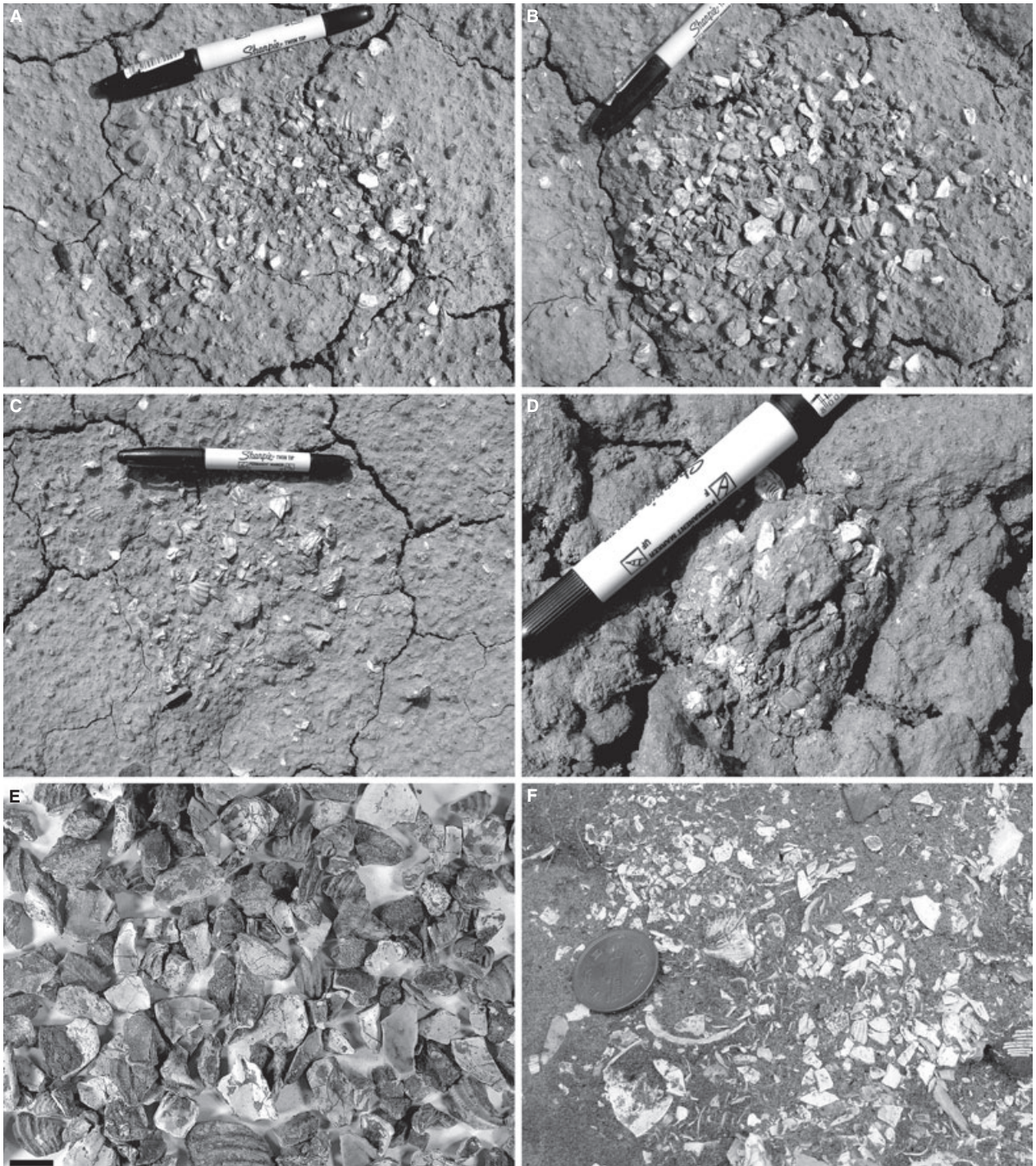
DISCUSSION

All of the features noted above, i.e. the randomness of the shell-fragment sizes, their angular and sharp margins with no traces of abrasion, and the association of different groups of organisms, the majority of which are benthic, suggest that they were produced by shell-crushing (durophagous) opportunistic generalists, most probably fishes. Stomatopods and brachyuran crabs must be excluded because, although well differentiated in the Jurassic, they did not evolve shell-breaking limbs until the Paleocene and Eocene (Vermeij 1987). Overall, the shell fragments resemble those retrieved from the digestive tracts of the durophagous fish *Pogonias* by Cate and Evans (1994), and those described from Palaeogene–Neogene strata in Japan (Oji *et al.* 2003) (Text-fig. 2F). Cate and Evans (1994) also recorded whole gastropods, even with soft parts still preserved, and complete valves of bivalves. Taking into account the gastropod investigations, the Upper Bajocian/Lower Bathonian sediments under discussion were deposited in a much shallower (photic zone) environment than those of mid Bathonian age, which represent deeper (outer shelf) biotopes (Dr A. Kaim, pers. comm. 2004). Thus, the prey remains studied represent two different bathymetric settings.

The role of physical factors must be excluded, because none of the shell fragments, in particular their margins, is abraded. The presence of fossils of varying size, ranging from tiny echinoderm ossicles through to larger shell fragments, in each accumulation also means that transport leading to sorting of the bioclasts was not involved. Moreover, the accumulations are still well-packed in their centres. Dispersion at their margins, however, could have been caused by gentle water movement or later activities of scavengers retrieving any remaining digestible organic matter. The patterns of occurrence of the accumulations and their diverse faunal content may suggest that they represent regurgitated pellets and/or defecated remains (coprolites) (see Hattin 1996; Neumann 2000), expelled as an ingestible part of food consumed by a predator. The regurgitation of

TABLE 1. Diversity of fossils in the samples investigated, and their relative frequency: +, single; ++, common; +++, abundant. The frequency of occurrence of a particular fossil group in a given sample is expressed relative to that sample. S1–S6, uppermost Bajocian/lowermost Bathonian samples; Gl1, Lower Bathonian sample; Gn1–Gn4, Middle Bathonian samples.

| Samples (catalogue number) Taxa	S1 (Gius 8-3435)	S2 (Gius 8-3436)	S3 (Gius 8-3437)	S4 (Gius 8-3438)	S5 (Gius 8-3439)	S6 (Gius 8-3440)	Gl1 (Gius 8-3441)	Gn1 (Gius 8-3442)	Gn2 (Gius 8-3443)	Gn3 (Gius 8-3444)	Gn4 (Gius 8-3445)
Gastropods	+	+	+	+	+			++	++	+	+
Trochidae	+	+	+	+	+			++	++	+	
Cerithiidae	+	+	+		+					+	+
Pseudozygopleuridae			+								
Aporrhaidae			+								
Mathildidae	+										
'Pleurotomariidae'	+							+	+		
Indet. fragments								+	+		
Scaphopods		++	+	+	+	+		+			+
Bivalves	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	++
Trigoniidae	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	++
Cardiidae	+										
Corbulidae		+	+	+	+			+	+		+
Arcidae			+	+					+		
Nuculidae	+	+	+		+		+	+			
Pectiniidae	+			+	+			+			
Gryphaeidae	+	+	+		+	+	+		+		
Plicatulidae		+						+			
Indet. fragments				+		+				+	
Belemnites (*Belemnopsis* and/or *Hibolites*)	+	+		+	+	++	+	+	+	+	+
Ammonites (Perisphinctidae indet.)						+	+	++	++	+	+
Rhynchonellid brachiopods	+	+	+++	+	+	+++		+		+	
Terebratulid brachiopods	+		+	+	+		+	+	+		
Bryozoans (Cyclostomata)		+	+					+			
Crinoids (Isocrinidae)	++	+++	+++	+++	++	+++	+++	+++	++	+	+
Regular echinoids	+	+		+	+	+	++	++	+	+	+
Asteroids (Astropectinidae/ Goniasteridae)	+	+	+	+	+	+	+	++	+	+	+
Ophiuroids	+	+				+			+	+	
Wood remains	+	+						+			

TEXT-FIG. 2. *In situ* accumulations of fossil remains from A–C, the uppermost Bajocian/lowermost Bathonian, and D, Middle Bathonian ore-bearing Częstochowa Clay Formation of the Polish Jura; marker as a scale bar 14 cm long. E, separated shell fragments from the Lower Bathonian sample; note that the fragments possess distinct angularity and sharp-edged margins. F, shell fragments from the Upper Pliocene Dainichi Formation, Kakegawa Group, central Japan, shown for comparison (photograph courtesy of Tatsuo Oji, University of Tokyo).

food remains is known in such durophagous generalists as extant rays, sharks (Hattin 1996) and many groups of teleost fishes. Extant fishes of Sciaenidae, Labridae or flounders, on the other hand, do break shells and then pass the fragmented shell material through their digestive tracts (see Zuschin *et al.* 2003), which ends up in faeces.

TABLE 2. Absolute number of the shell fragments from a particular mesh-size range in the samples analysed. SD, standard deviation; CV, coefficient of variation.

| Fraction	S1	S2	S3	S4	S5	S6	Gl1	Gn1	Gn2	Gn3	Gn4	Total	Mean	SD	CV
20–10 mm	0	3	0	0	4	2	29	2	0	0	0	40	3.6	8.1	223.8%
10–5 mm	114	190	21	26	52	52	356	45	12	10	16	894	81.3	101.0	124.3%
5–3.15 mm	216	278	16	76	95	38	300	131	82	34	21	1287	117.0	97.9	83.6%
3.15–2.5 mm	106	100	12	37	78	19	79	85	98	22	21	657	59.7	35.6	59.6%
2.5–1.25 mm	69	52	8	26	108	7	112	136	130	28	23	699	63.5	47.4	74.7%
Total	505	623	57	165	337	118	876	399	322	94	81				
Mean	101	124.6	11.4	33	67.4	23.6	175.2	79.8	64.4	18.8	16.2				
SD	70.2	98.5	7.1	24.7	36.8	18.9	128.8	51.1	50.3	12.3	8.4				
CV	69.5%	79.0%	62.7%	74.9%	54.6%	79.9%	73.5%	64.1%	78.1%	65.4%	52.0%				
Accumulation size	135 mm	167 mm	56 mm	84 mm	140 mm	76 mm	155 mm	148 mm	125 mm	77 mm	72 mm				
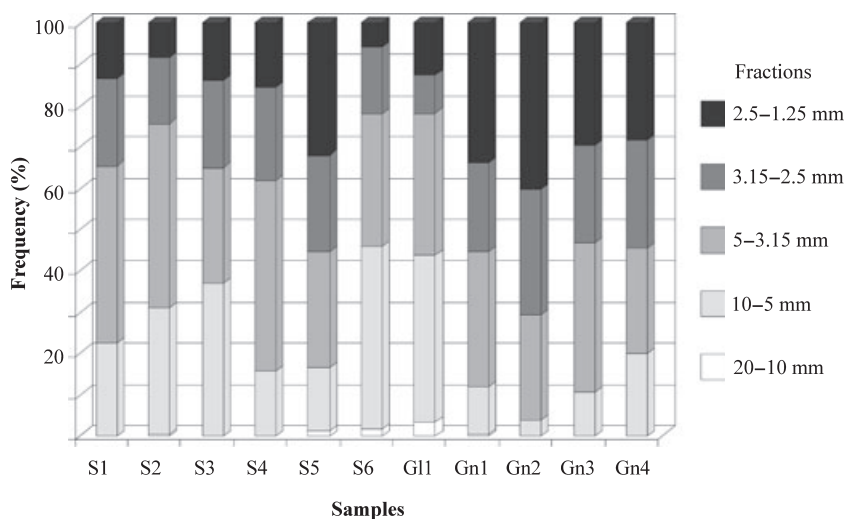
TEXT-FIG. 3. Size-frequency distribution of the shell fragments in the samples analysed.

However, carnivorous vertebrate coprolites and regurgitates differ in their composition. The former are composed of calcium phosphate (see Pollard 1990; Chin 2002; Northwood 2005), and the swallowed particles are more affected by digestive processes than regurgitates and, therefore, less recognizable as fossils (see Chin 2002). Regurgitated remains will have spent only a short time in the digestive tract. Coprolites are also frequently replaced by siderite, limonite or silica during diagenesis (see Pollard 1990), which certainly strengthens them, allowing preservation of their original form. They may retain features such as spiral folding or vascular markings, which reflect the morphology of the intestine of a predator (Pollard 1990).

The aggregations investigated did not undergo any post-burial transformation into calcite or siderite, mineral phases that are very common in the Middle Jurassic sediments under discussion, to form concretions of different shapes and sizes. Instead, the bioclasts are packed together on the bedding planes. The fragments also clearly point to

a regurgitate rather than a faecal origin. The bivalve remains and belemnite rostra bear clear signs of dissolution, most probably digestive fluids, and the fossils are still easily recognizable. The presence of ammonite shell fragments in the accumulations may additionally support a regurgitation origin. It has been documented (Sato and Tanabe 1998) that ammonites swallowed by a plesiosaur lost their shells owing to their complete dissolution in its stomach. The calcitic aptychi (ammonite jaws), on the other hand, were still preserved. In the Middle Bathonian samples, many thin, aragonitic ammonite shell fragments are preserved, still showing multicoloured iridescence of the shell nacre. Thus, they must have been in the digestive tract of a predator for a very short time to avoid complete dissolution.

Extant birds (eiders and shelducks) also produce faeces consisting of numerous angular shell fragments with sharp margins (Cadée 1994) that are quite similar to those investigated here (except for their small size). However,
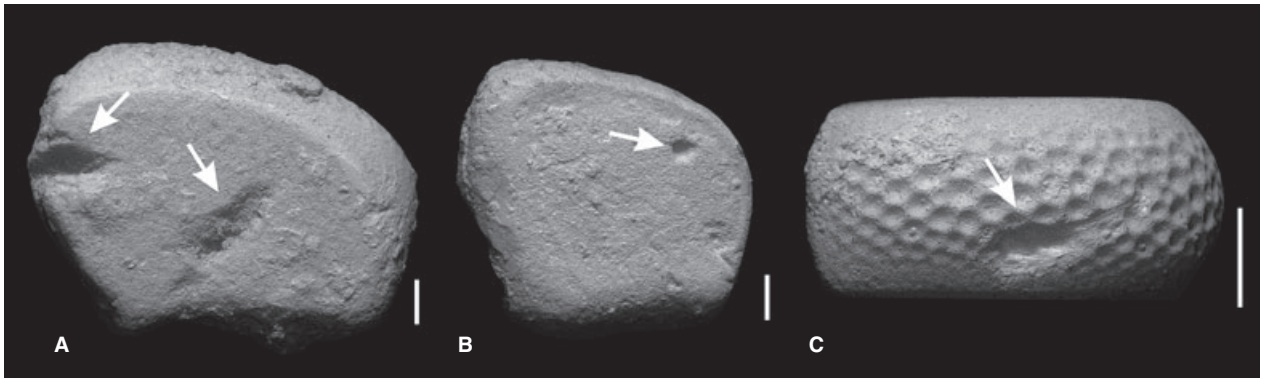
TEXT-FIG. 4. A–C, bite-marks (arrows) on isolated marginal plates of asteroids from accumulations in the uppermost Bajocian/lowermost Bathonian transition at the 'Sowa'/'Gliński' clay pits (Kawodrza Górna). Scale bars represent 1 mm.

birds did not evolve until later so comparison of their faeces with material produced by Middle Jurassic fishes is inappropriate.

Although the fish fauna of the Middle Jurassic clays of the Polish Jura have not been described so far, some selachian and teleostean teeth have been recorded by one of us (MZ). Thus, the possibility that the accumulations under discussion could have been produced by such predators cannot be dismissed. Reptile remains are currently unknown from the sediments.

Taking into account the relative frequency of faunal remains in the samples investigated, it may be assumed that, apart of echinoderms, the most preferred prey was trignoiid bivalves. The other bivalve groups do not appear to have been included in the predator's usual diet. The tiny gastropods and brachiopods recorded must have been swallowed incidentally because in the majority of cases they are preserved as nearly complete shells or valves. The small number of the largest shell fragments (20–10-mm fraction) may not necessarily attest to generally small predators; rather, it may simply indicate that some of the bivalve prey (especially thick-shelled trigoniids) was less crushed by the predator's jaws.

The lack of apertures in the small gastropods, however, could have been an effect of post-regurgitation scavenging upon the individuals that still possessed soft parts or of later predation if the gastropods were still alive. Thus, some time-averaging of the faunal remains after they were expelled must have occurred, as also evidenced by the presence of epibionts on, and signs of bioerosion of, numerous bioclasts. Post-regurgitation fouling of bioclasts by various encrusters (mainly serpulids, cyclostomatous bryozoans and foraminifers) is apparent from the general lack of broken epibionts on the fragmented shells. Moreover, their presence on isolated ossicles of echinoderms and the inner surfaces of shell fragments clearly indicate that the remains were encrusted after they were expelled by the predator. Although the distinct bite marks pre-served on some of the asteroid (Astropectiniidae and Goniasteridae) ossicles (Text-fig. 4) may represent post-regurgitation activity of scavengers, they could also have been produced prior to death (Zaton *et al.* 2007). In the latter case, apart from the crushed shells, they may, in addition, provide evidence of durophagous activity during the formation of the accumulations under discussion.

The role of compaction, which may produce similar shell fragments, has been suggested (see Vermeij 2002), but may be excluded here. It was observed in the field that thick-shelled trigoniid bivalves usually occur as single valves, isolated from each other. Although they may indeed be broken owing to compaction, the resulting fragments are still close together. Such a fragmentation pattern as a result of compaction has been reported by Zuschin *et al.* (2003), and is in marked contrast to the fragmented shell accumulations, all of which are amalgamated and derived from different individuals.

CONCLUSIONS

The shell fragments described possess distinct taphonomic features (angular fragments with sharp, not abraded, margins) and, combined with their sedimentological context, suggest biomechanical production. As indigestible remains, they may have been regurgitated by predators to form characteristic fossil aggregations. In the Middle Jurassic sediments investigated, they occur on almost all exploitation levels that are weathered enough for the accumulations to be clearly visible. Thus, it seems that such remnants of durophagous predation are rather common in the area investigated. If the increase in abundance of angular shell fragments from the early Palaeogene onward is real, as suggested by Oji *et al.* (2003), who supported their observations with data showing an increase in shell-crushing organisms, intense durophagous predation was established much earlier, at least locally. Our evidence in

support of this conclusion may of course be partly a result of favourable taphonomic conditions that prevailed locally in the clays we have examined, but it may also imply that shell-crushing activities were common in the mid Mesozoic times, during so called Mesozoic Marine Revolution.

REFERENCES

BAMBACH, R. K. 2002. Supporting predators: changes in the global ecosystem inferred from changes in predator diversity. 319–352. *In* KOWALEWSKI, M. and KELLEY, P. H. (eds). *The fossil record of predation*. The Paleontological Society, Papers, **8**, 398 pp.

CADÉE, G. C. 1994. Eider, Shelduck, and other predators, the main producers of shell fragmentation in the Wadden Sea: palaeoecological implications. *Palaeontology*, **37**, 181–202.

CATE, A. S. and EVANS, I. 1994. Taphonomic significance of the biomechanical fragmentation of live molluscan shell material by a bottom-feeding fish (*Pogonias cromis*) in Texas coastal bays. *Palaios*, **9**, 254–274.

CHIN, K. 2002. Analyses of coprolites produced by carnivorous vertebrates. 43–49. *In* KOWALEWSKI, M. and KELLEY, P. H. (eds). *The fossil record of predation*. The Paleontological Society, Papers, **8**, 398 pp.

HARPER, E. 2006. Dissecting post-Palaeozoic arms races. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 322–343.

HATTIN, D. E. 1996. Fossilized regurgitate from Smoky Hill Member of Niobrara Chalk (Upper Cretaceous) of Kansas, USA. *Cretaceous Research*, **17**, 443–450.

KOPIK, J. 1998. Lower to Middle Jurassic of the north-eastern margin of the Upper Silesian Coal Basin. *Prace Państwowego Instytutu Geologicznego*, **378**, 67–130 [In Polish, English summary].

MAJEWSKI, W. 1997. Ammonites from the ore-bearing clays of the environs of Częstochowa. Unpublished MSc thesis, University of Warsaw, 99 pp. [In Polish].

—— 2000. Middle Jurassic concretions from Częstochowa (Poland) as indicators of sedimentation rates. *Acta Geologica Polonica*, **50**, 431–439.

MATYJA, B. A. and WIERZBOWSKI, A. 2000. Ammonites and stratigraphy of the uppermost Bajocian and Lower Bathonian between Częstochowa and Wieluń, central Poland. *Acta Geologica Polonica*, **50**, 191–209.

—— 2006. Field Trip B1 – Biostratigraphical framework from Bajocian to Oxfordian. 149–155. *In* WIERZBOWSKI, A., AUBRECHT, R., GOLONKA, J., GUTOWSKI, J., KROBICKI, M., MATYJA, B. A., PIEŃKOWSKI, G. and UCHMAN, A. (eds). *Jurassic of Poland and adjacent Slovakian Carpathians. Field trip guidebook*. 7th International Congress on the Jurassic System, 6–18 September 2006, Kraków, Poland, 235 pp.

NEUMANN, C. 2000. Evidence of predation on Cretaceous sea stars from north-west Germany. *Lethaia*, **33**, 65–70.

NORTHWOOD, C. 2005. Early Triassic coprolites from Australia and their palaeobiological significance. *Palaeontology*, **48**, 49–68.

OJI, T., OGAYA, C. and SATO, T. 2003. Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology*, **29**, 520–526.

POLLARD, J. E. 1990. Evidence for diet. 362–367. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology: a synthesis*. Blackwell Publishing, Oxford, 583 pp.

SATO, T. and TANABE, K. 1998. Cretaceous plesiosaurs ate ammonites. *Nature*, **394**, 629–630.

WALKER, S. E. and BRETT, C. E. 2002. Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? 119–193. *In* KOWALEWSKI, M. and KELLEY, P. H. (eds). *The fossil record of predation*. The Paleontological Society, Papers, **8**, 398 pp.

VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.

—— 1987. *Evolution and escalation. An ecological history of life*. Princeton University Press, Princeton, NJ, xv + 527 pp.

—— 2002. Evolution in the consumer age: predators and the history of life. 375–393. *In* KOWALEWSKI, M. and KELLEY, P. H. (eds). *The fossil record of predation*. The Paleontological Society, Papers, **8**, 398 pp.

ZATOŃ, M. and MARYNOWSKI, L. 2004. Konzentrat-Lagerstatte – type carbonate concretions from the uppermost Bajocian (Middle Jurassic) of the Częstochowa area, south-central Poland. *Geological Quarterly*, **48**, 339–350.

—— —— 2006. Ammonite fauna from uppermost Bajocian (Middle Jurassic) calcitic concretions from the Polish Jura – biogeographical and taphonomical implications. *Geobios*, **39**, 426–442.

—— BARBACKA, M., MARYNOWSKI, L. and KRZYS-TANEK, J. 2006. *Sagenopteris* (Caytoniales) with its possible preserved biomarkers from the Bathonian of the Polish Jura, south-central Poland. *Neues Jahrbuch für Geologie und Paläontologie, Monatschefte*, **7**, 385–402.

—— VILLIER, L. and SALAMON, M. A. 2007. Signs of predation in the Middle Jurassic of south-central Poland: evidence from echinoderm taphonomy. *Lethaia*, **40**, 139–151.

ZUSCHIN, M., STACHOWITSCH, M. and STANTON, R. J. Jr 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews*, **63**, 33–82.