SHARK PREDATION OF DINANTIAN BRACHIOPODS FROM THE DERBYSHIRE DOME

by

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Summary

Gigantoproductid brachiopods collected from the Eyam Limestones Formation (late Brigantian) of the Derbyshire Dome occasionally display shell malformation. Some of these malformations originated by repair of damage which was inflicted during the life of the gigantoproductid. This damage is thought to have been caused during an unsuccessful predatory attack. The predators were most likely to have been bottom-feeding sharks whose remains have been found in association with the damaged shells.

Introduction

The fossils studied were collected from bioclastic limestones which crop out around Monyash in the central part of the Derbyshire Dome (Fig. 1). The damaged brachiopod shells and associated shark fossils were found at two localities: Once a Week Quarry (SK 15756805) and Upper Bricks Quarry (SK 149687), Fig. 1. A list of the brachiopod and shark fauna is given in the appendix.

These bioclastic limestones form a distinctive facies consisting mainly of crinoidal grainstone and packstone which occurs at the top of the Eyam Limestones in the Monyash area. This facies has been referred to previously as the "flat-reef" facies of the Eyam Limestones by Stevenson & Gaunt (1971) and Aitkenhead *et al.* (1985). These limestones commonly display cross-bedding of different sizes which indicates the former presence of bedforms ranging from ripples, which had wavelengths of a few centimetres, to sand-waves and mega-ripples which had wavelengths of over 25 m. These limestones were deposited in part of a bioclastic sand-body which formed in association with the western margin of the Derbyshire carbonate platform (Gutteridge 1983). A shark fauna described by Ford (1964) from near Wirksworth was collected from limestones which are the same stratigraphic age and were deposited in a similar environmental setting to those described here.

The preservation of the gigantoproductids ranges from disarticulated, fragmented and abraded shells in well-sorted limestones, to whole, unabraded valves in poorly-sorted limestones. The fauna described here was collected from the poorly-sorted limestones. In addition to the gigantoproductids, the poorly-sorted limestones contain articulated crinoid stems and *in situ* coral colonies within a matrix of ripple-laminated sand—to gravel-sized bioclastic sediment. These poorly-sorted limestones pass laterally into the cross-bedded well-sorted limestones suggesting that the poorly-sorted limestones accumulated in the troughs of larger bedforms. The gigantoproductids are interpreted to have lived on the rippled bioclastic sand and gravel substrate in the troughs of mega-ripples. The gigantoproductids probably maintained their positions on the shifting sand substrate by their bulk and hydrodynamic shape (cf. Ferguson 1978).

Shell types affected and the nature of the damage

A list of the brachiopod and shark fauna collected from Once a Week Quarry and Upper Bricks Quarry is given in the appendix to this paper. Shell damage has only been observed on the pedicle valves of finely-ribbed gigantoproductids, whereas other productaceans and spiriferaceans show no evidence of shell damage.

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Three types of shell-damage have been recognised:

1. The shell is fractured in an interlocking pattern rather like a jig-saw. The fractures cut across the ribbing. Examples of this type of damage are shown by Plate 1a and b.
2. The ribs are deflected about a point indentation in the shell. The indentation does not penetrate the shell. Parallel growth of the ribs is resumed either immediately (e.g. Plate 1c) or following a short linear scar parallel to the ribs (e.g. Plate 1b).
3. The ribs are deflected about a point indentation which occurs at the origin of a persistent groove parallel to the ribs. This groove is often present throughout the subsequent growth of the shell (e.g. Plate 1d).

Damage of types 2 and 3 is found only on the lateral areas of the pedicle valves not more than several centimetres from the umbo (measured along the ribs) which suggests that attacks may have been limited to small shells.

There is no evidence of subsequent shell growth following the type 1 damage. This damage, therefore, either caused the death of the gigantoproductid or occurred after its death. Since the shell fragments have remained in place after fracturing, this type of damage did not occur at the sediment surface because the shell fragments would have been dispersed by reworking. Type 1 shell damage was probably caused after death by compaction of the gigantoproductid valve during shallow burial.

Shell damage, types 2 and 3, have both been repaired by subsequent shell growth, these types of damage were, therefore, inflicted during growth of the gigantoproductid and were non-fatal. The important difference between types 2 and 3 damage is in the mode of repair and subsequent growth of the shell. In the case of type 2 damage, normal growth was resumed, whereas in the case of type 3 damage, the gigantoproductid suffered a permanent malformation.

Rudwick (1970) showed that growth and shell secretion by the mantle takes place at the posterior margin in modern brachiopods. If the mantle is damaged this will presumably result in a disruption of its shell-secreting capability. Severe damage to the mantle may permanently impair the normal secretion of shell material. The difference between type 2 and type 3 shell damage is interpreted as one of degree. In the case of type 2 damage, the mantle eventually recovered, whereas type 3 damage resulted in the permanent impairment of the ability of the mantle to secrete shell material.

Cause of the shell damage

In addition to reworking and compactive fracturing after death, shell damage may occur in the following ways:

(*a*) *Growth Interference*

Malformation of the hard parts of sedentary organisms may be produced if the organism grows against an obstruction. Such an obstruction may be an inanimate object or other sedentary organisms growing in close proximity to the organism. The likelihood of growth interference is lessened if the organism has a degree of mobility. Ferguson (1978) suggested that gigantoproductids rested on the sediment surface and position was maintained by their bulk and hydrodynamic shape. He also showed experimentally that gigantoproductids were able to rotate in response to changing current direction. These gigantoproductids are found in association with rippled bioclastic sand in the troughs of large-scale bedforms. They are inferred to have lived on a shifting bioclastic sand substrate in a manner similar to that proposed by Ferguson (1978). The gigantoproductids were probably mobile and unlikely to develop growth malformation by jamming against other shells.

(*b*) *Damage by epifauna*

Brunton (1966) described shell damage to Dinantian brachiopods caused by colonisation of the shell surface by sponges and bryozoans. He inferred that the sponges colonised the living brachiopods whereas colonisation by bryozoans took place on disarticulated shells after death.

Sponges produce small borings, pits or holes up to 1.5 mm in diameter which are often aligned along ribs. Colonisation by bryozoans produces a ramifying network of tubes up to 0.1 mm in diameter. These networks commonly radiate from several points on the shell which presumably represent the initial sites of colonisation.

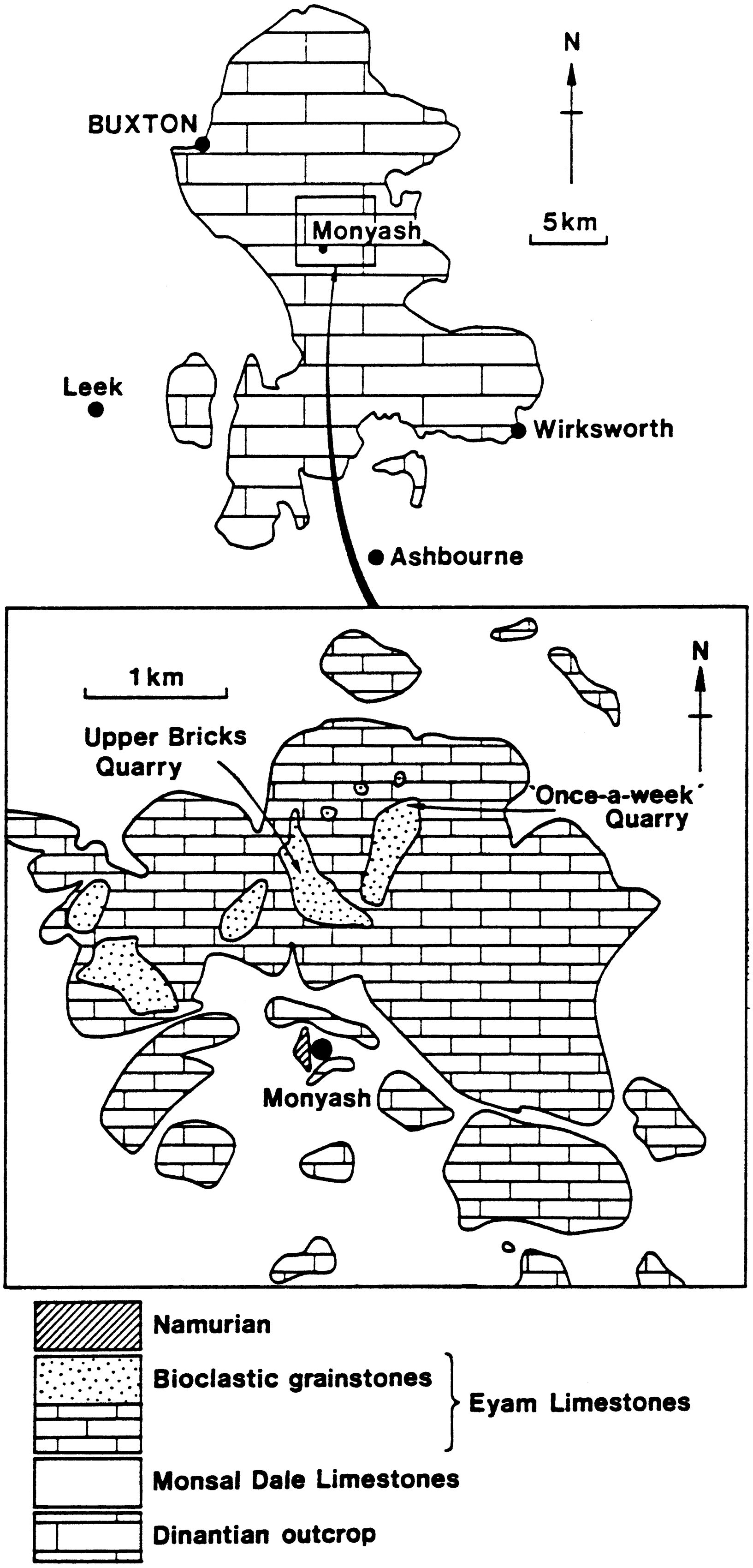

Fig. 1. Location map showing sample sites and outcrop of bioclastic sand bodies within the Eyam Limestones Formation around Monyash, Derbyshire.

The damage described here differs morphologically from that inflicted by sponges and bryozoans. Additionally, the damage caused by bryozoans was probably inflicted after death of the brachiopod, whereas types 2 and 3 damage were caused whilst the gigantoproductids were alive.

(*c*) *Predation*

Brunton (1966), Carter (1968) and Mundy (1982) list the following organisms which, at various geological times are thought to have preyed on brachiopods and bivalves:

Birds
Marine mammals
Arthropods (Crabs and Lobsters)
Gastropods
Asteroids (Starfish)
Cephalopods
Fish

Birds, marine mammals, crabs and lobsters did not evolve until the Mesozoic and therefore cannot have preyed upon the gigantoproductids described here.

Gastropod predation on bivalves and brachiopods produces circular holes several millimetres in diameter which often have bevelled edges (Brunton 1966, Carter 1968). These differ from the shell damage described here which is a localised crushing or breakage of the shell rather than a neatly-bored hole. The lack of gastropod remains in the associated sediments also make it unlikely that gastropods caused the observed shell damage.

Recent asteroids are known to prey on bivalves by opening the valves by force (Carter 1968) and it is likely that they preyed on bivalves and brachiopods in a similar way in the past. Alexander (1981) suggested that asteroid predation inflicts only minor damage such as flaking or chipping where the shell was gripped by a foot. This damage is unlikely to be recognised in the geological record as it would be indistinguishable from, or obliterated by, the results of abrasion during sedimentary reworking.

Predation by cephalopods (e.g. goniatites) has been proposed by Mundy (1982) to account for damaged brachiopod shells found in Dinantian carbonate mud mounds. He suggested that the goniatites preyed on the brachiopods by nicking at the posterior and lateral margins of the shell with their mandibles. This type of damage is similar to the types 2 and 3 damage described here, however, cephalopod remains have not been found in these sediments.

Predatory attacks by fish have also been invoked to account for various types of damage to brachiopod shells. The type of damage described is often inflicted at a point and matches the morphology of teeth found in association with damaged shells (e.g. Alexander 1981). Brunton (1966) and Mundy (1982) described and figured conjugate damage inflicted by jawed predators inferred by them to be fish. Additional evidence of fish predation cited by Bishop (1975) and Alexander (1981) is the presence of shell remains in gastric residues and coprolites.

Fish remains are present in association with the damaged gigantoproductids. Examples include cf. *Petalorhynchus* (Plate 1e), *Orodus* sp. (Plate 1f) and cf. *Petalodus* (Plate 1g). A more complete faunal list is given in the appendix.

The shell-malformations present in these gigantoproductids were initiated at a point and could have been inflicted by petalodontid teeth. Gigantoproductid valves only display damage at single points and, owing to disarticulation, there is no indication of conjugate damage. Thus, it is not possible to infer the configuration of teeth in the predators' jaws. In the fauna listed below, the main brachiopodophages were probably *Cladodus*, the petalodonts and the chimaeroids, as the other sharks had teeth which were too small to crush the shells (David Ward personal communication 1988).

Of the suspected predators discussed, only fish remains have been found in association with the damaged shells. Since these belong to sharks which are likely to have been predators or scavengers it is logical to ascribe the shell damage to them.

Adaptations of brachiopods against predation

Mundy (1982) showed that smooth shells show more evidence of attempted predation than more strongly ornamented shells. Alexander (1981) also suggested that increased plication of brachiopods through the Mississippian may have been an adaptation against increasing shark predation. In this study the finely-ribbed gigantoproductid shells show evidence of predation whereas the coarsely-ribbed shells of the *Spirifer bisulcatus* group do not. This may reflect selective predation such as that described from recent brachiopod faunas by Rudwick (1970 p. 161). Alternatively, the biconvex shape of the spiriferaceam shell was stronger than the concavo-convex shape of the gigantoproductids and so more resistant to predatory attack. The lack of evidence of attempted predation on the spriferaceans may equally imply that their shells were readily crushed, leaving no evidence of predation.

Conclusions

Three types of damage to Dinantian gigantoproductid brachiopods has been recognised:

1. Unrepaired interlocking fractures which were caused after death of the brachiopod by compaction of the sediment.

2. Indentation or crushing at a point which was completely repaired. This damage may not have permanently affected the ability of the mantle to secrete shell material.

3. A linear groove originating at a point which formed a permanent feature of the gigantoproductid during subsequent growth. This damage may have pemanently affected the ability of the mantle to secrete normal shell material.

The second and third types of damage were probably inflicted by a predator during an unsuccessful predatory attack. The damage differs from that inflicted by gastropods and asteroids and is unlikely to have been caused by cephalopods because their remains have not been found in association with the damaged shells.

The damage is thought to have been caused by fish predators, probably *Cladodus*, petalodont and chimaeroid sharks because the teeth of these fish match the shell damage and occur in association with the gigantoproductids.

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Appendix

Faunal list of brachiopod and shark specimens collected from Once a Week Quarry and Upper Bricks Quarry.

Brachiopoda

Antiquatonia hindi (Muir-Wood)
A.insculpta (Muir-Wood)
A.sp.
Avonia sp.
Dictyoclostus sp.
dictyoclostid
echinoconchid
Eomarginifera cf. *lobatus laqueatus* (Muir-Wood)
Gigantoproductus cf. *crassiventer* (Prentice)
G. cf. *moderatus* (Schvetsov)
G.sp. (Prentice)
gigantoproductid
Latiproducutus latissimus s.l. (J. Sowerby)
Productus cf. *muricatus* (Phillips)
Schizophoria sp.
Semiplanus sp.
Spirifer bisulcatus group (J. Sowerby)
cf. *Striatifera*

Pisces

Euselachian

Anachronistes fordi (Duffin & Ward)

Hybodont

Lissodus sp.

Petalodonts

Petalodus acuminatus (Agassiz)
Petalodus spp.
Petalorhynchus psitticanus (M'Coy)
Ctenoptychius lobatus (Etheridge)

Orodonts

Orodus sp.

Cladodonts

Cladodus miribilis (Agassiz)
Cladodus spp.

Cenocanthids

Diplodus sp.
Oracanthus sp.

Uncertain affinity

Harpagondens ferrox (Turner)

Chimaeroids

Deltodus spp.

Plate 1 (facing page)

Plate 1. Damaged gigantoproductid brachiopods and fish remains collected from Once a Week Quarry (SK 15756805).

(*a*) Pedicle valve of a *Gigantoproductus* sp. showing an interlocking fracture pattern (Type 1 damage) which cuts across the ribbing and was probably caused by compaction of the surrounding sediment. (x1.25). No. SF104, Department of Geology, University of Manchester Collection.

(*b*) Pedicle valve of a gigantoproductid showing a compactive fracture (Type 1 damage), (f) and a predation scar (p) around which the ribs are deflected and normal growth is resumed after a short scar (Type 2 damage). (x2.5). No. SF108, Department of Geology, University of Manchester Collection.

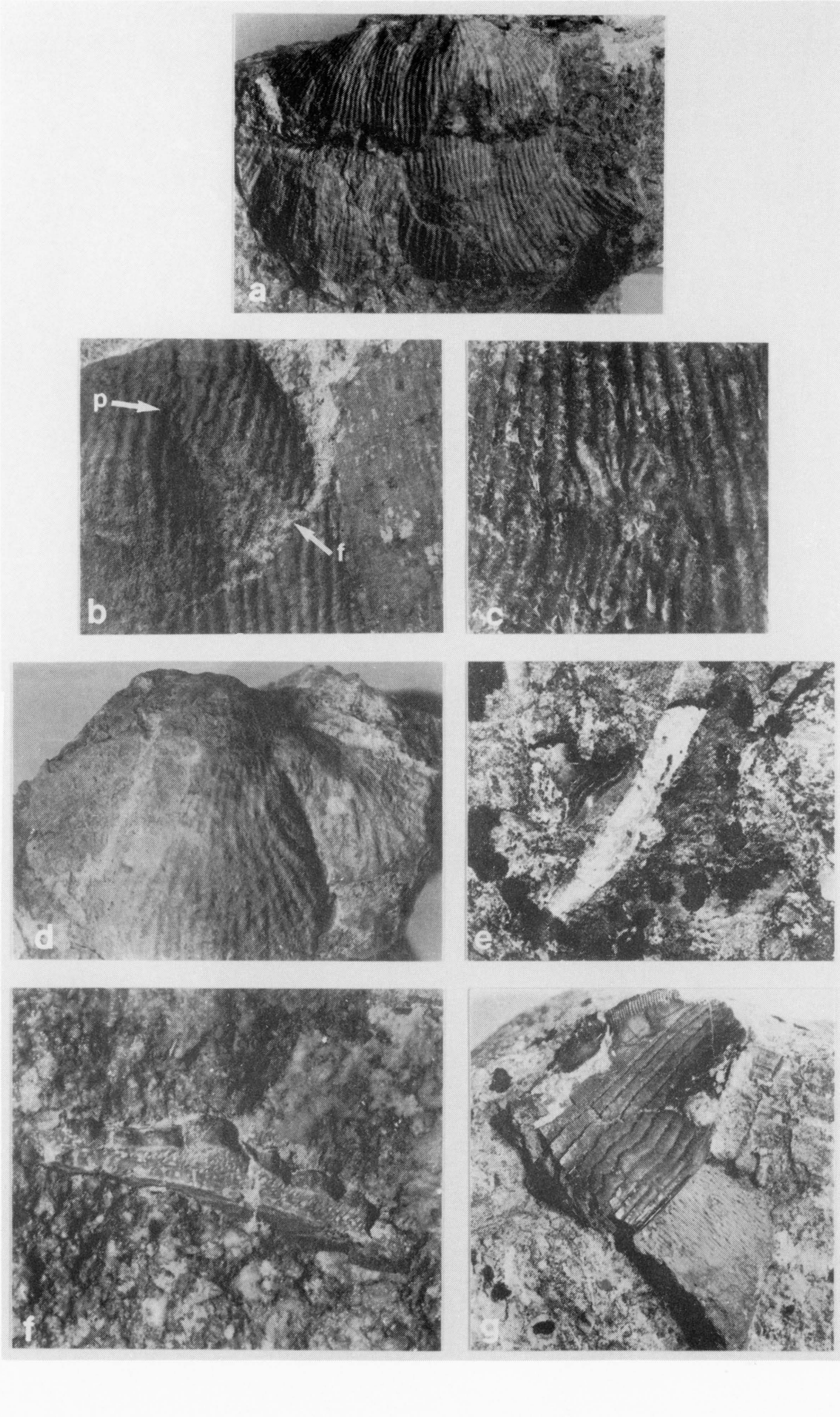
(*c*) Left lateral area of the pedicle valve of a *Gigantoproductus* sp showing deflection of ribs about a point indentation with subsequent resumption of normal growth (Type 2 damage). This damage was probably inflicted by a petalodontid tooth. (x3.5). No. SF106, Department of Geology, University of Manchester Collection.

(*d*) A groove originating from a point on the pedicle valve of a gigantoproductid. This is an example of type 3 damage which persists throughout the subsequent growth of the brachiopod. This damage was probably inflicted during an unsuccessful predatory attack. (x2). NO. SF107, Department of Geology, University of Manchester Collection.

(*e*) cf. *Petalorhynchus* (x3).

(*f*) cf. *Orodus* (x1.25).

(*g*) cf. *Petalodus* (x2.25).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