ON ELASMOBRANCH DERMAL DENTICLES FROM THE RHAETIC BONE BED AT BARNSTONE, NOTTINGHAMSHIRE

by

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Summary

Elasmobranch dermal denticles from Rhaetic bone beds are described including a new minute form. Their affinities with the family Dalatidae, various hybodont genera and the family Squalorajidae are discussed.

Introduction

Dermal denticles are small tooth-like structures which protrude from the skin of sharks giving it a roughness which has caused it to be known as shagreen. In text-fig.1, fig.2, the typical parts of a denticle are illustrated, following the terms used by Applegate (1967).

The majority of the denticles forming the subject of this paper were collected from the Barnstone Railway Cutting, approximately 850 metres east of Barnstone, Nottinghamshire, (SK 739358). Here a section exposing the Rhaetic Bone Bed was excavated by Members of the East Midland Geological Society, (Sykes, Cargill and Fryer, 1970).

The Barnstone denticles, along with others found in Rhaetic bone bed exposures of additional localities including Aust, Axminster, Gainsborough, Lavernock and Penarth, fall into three groups, two of which (A and B) are common, and one (C) is rare. Each group has its exclusively distinguishing characteristic features. Denticles of one of the common groups (A) are much smaller than the other two and are considered, on the comparison with the upper teeth and general Dalatiid characteristics, to have affinities with the fish species *Dalatias barnstonensis* Sykes (1971). The common group, (B), of large dermal denticles can be referred, (by comparison with established hybodont denticles) to genera of hybodonts. The third group (C), which are large in size, conical in shape but quite rare in occurrence, are considered to be dermal denticles of Chimaeroid fish.

Samples of bone bed weighing 183 grams from both Gainsborough and Barnstone yielded the following count of *D. barnstonensis* teeth and dermal denticles. The Gainsborough Bone Bed, because of its pyritic matrix, did not yield as many specimens as did the more friable Barnstone Bone Bed.

Table 1 - Specimens of teeth and denticles from Rhaetic Bone Bed

	D. Barnstonensis Teeth		Dermal denticles		
	Upper Jaw	Lower Jaw	Minute [A]	Hybodont [B]	Rare [C]
Gainsborough	1	3	55	10	1
Barnstone	3	3	278	22	0

Mercian Geologist, Vol.5, No.1.
1974. pp.49-64, 3 text-figs. Plate 3.

TABLE 2 SHOWING THE COMBINATIONS OF FEATURES IN 80 WHOLE RHAETIAN DERMAL DENTICLES

		Crowns	Pointed	Medium Broad	Broad	Triple Keeled	Bifurcate Keels	Extra Keels	Upper View Quadrate	U.V.Quad & Pointed Rear	U.V.Rounded	U.Surface Flattened	U.S. Part Smooth	U. Surface Smooth	Lateral Points	*Pedicels*	Broad	Medium	Slender	Sub-Square	Laterally Compressed	Transversely Comp.	Short	Medium	Long	*Basal Plates*	Sub-Square	Laterally Compressed	Med. Trans. Compressed	Transversely Comp.
			12	54	14	5	65	10	42	19	11	10	15	9	13		19	50	11	35	4	41	33	45	2		30	4	34	12
Crowns		80																												
Pointed	12		12	0	0	5	7	0	0	4	0	0	0	0	4		2	10	0	11	1	0	5	7	0		12	0	0	0
Medium Broad	54		0	54	0	0	44	10	39	15	0	7	15	8	5		17	32	5	22	3	29	23	29	2		16	4	28	6
Broad	14		0	0	14	0	14	0	3	0	11	3	0	1	4		0	8	6	2	0	12	5	9	0		2	0	6	6
Triple Keeled	5		5	0	0	5	0	0	1	1	0	0	0	0	2		1	4	0	5	0	0	5	0	0		5	0	0	0
Bifurcate Keels	65		7	44	14	0	65	0	33	16	11	10	8	8	11		15	40	10	26	4	35	23	40	2		24	4	28	9
Extra Keels	10		0	10	0	0	0	10	0	0	0	3	7	1	2		3	6	1	4	0	6	5	5	0		1	0	6	3
Upper View Quadrate	42		0	39	3	1	33	0	42	0	0	8	12	6	1		12	28	2	19	2	21	18	23	1		15	2	21	4
U.V. Quad & Pointed Rear	19		4	15	0	1	16	0	0	19	0	1	3	1	3		5	11	3	7	2	10	8	10	1		6	2	9	2
U.V. Rounded	11		0	0	11	0	11	0	0	0	11	0	0	1	4		2	3	6	1	0	10	3	8	0		1	0	4	6
U. Surface Flattened	10		0	7	3	0	10	3	8	1	0	10	3	4	0		4	5	1	6	1	0	4	6	0		6	0	2	2
U.S. Part Smooth	15		0	15	0	0	8	7	12	3	0	3	15	0	1		6	7	2	7	1	5	7	8	0		6	2	7	0
U. Surface Smooth	9		0	8	1	0	8	1	6	1	1	4	0	9	0		5	2	2	6	1	2	4	5	0		3	2	2	2
Lateral Points	13		4	5	4	2	11	2	1	3	4	0	1	0	13		2	7	4	2	1	8	10	1	2		3	1	6	3
Pedicels																80														
Broad	19		2	17	0	1	15	3	12	5	2	4	6	5	2		19	0	0	12	1	6	12	7	0		10	0	8	1
Medium	50		10	32	8	4	40	6	28	11	3	5	7	2	7		0	50	0	20	3	27	20	30	0		19	3	19	9
Slender	11		0	5	6	0	10	1	2	3	6	1	2	2	4		0	0	11	3	0	8	1	8	2		1	1	7	2
Sub-Square	35		11	22	2	5	26	4	19	7	1	6	7	6	2		12	20	3	35	0	0	14	21	0		29	0	5	1
Laterally Compressed	4		1	3	0	0	4	0	2	2	0	1	1	1	1		1	3	0	0	4	0	1	3	0		0	4	0	0
Transversely Comp.	41		0	29	12	0	35	6	21	10	10	0	5	2	8		6	27	8	0	0	1	18	21	2		1	0	29	11
Short	33		5	23	5	5	23	5	18	8	3	4	7	4	10		12	20	1	14	1	18	33	0	0		11	3	16	3
Medium	45		7	29	9	0	40	5	23	10	8	6	8	5	1		7	30	8	21	3	21	0	45	0		19	1	17	8
Long	2		0	2	0	0	2	0	1	1	0	0	0	0	2		0	0	2	0	0	2	0	0	2		0	0	1	1
Basal Plates																										80				
Sub-Square	30		12	16	2	5	24	1	15	6	1	6	6	3	3		10	19	1	29	0	1	11	19	0		30	0	0	0
Laterally Compressed	4		0	4	0	0	4	0	2	2	0	0	2	2	1		0	3	1	0	4	0	3	1	0		0	4	0	0
Med. Trans. Compressed	34		0	28	6	0	28	6	21	9	4	2	7	2	6		8	19	7	5	0	29	16	17	1		0	0	34	0
Transversely Comp.	12		0	6	6	0	9	3	4	2	6	2	0	2	3		1	9	2	1	0	11	3	8	1		0	0	0	12

EXPLANATION OF TABLE 2

Individual characteristics of the CROWNS, PEDICELS and BASAL PLATES are listed under those headings on the left.

In each case, the figure in the first column on the left shows how many of the eighty denticles have that particular characteristic.

Subsequent figures along the row enumerate the quantities of other characteristics (listed above) held by denticles of that particular group.

EXAMPLE: Under the heading CROWNS on row No.7 is listed the characteristic of 'quadrate upper view'; the first column of figures shows, that, out of the eighty, there are 42 denticles with this feature.

By consulting the figures along the row, under the characteristics listed above, it is possible to note that out of the 42 denticles with a quadrate upper view, 12 of them have crowns with the upper surface partly smooth, only 2 of them have slender pedicels, 21 of them have a basal plate which is average or medium transversely compressed, and so on.

Dalatiid Dermal Denticles (Group A)

The minute denticles are quite common in the finer residues from Barnstone. Many of them are broken, especially the large and more fragile ones, but a large number are preserved whole. In order to obtain an estimate of the relative amounts of the various types of these denticles, a further total extraction of 280 specimens was taken from an unspecified amount of bone bed, including complete and broken examples. The denticles display a great diversity in the combinations of their minor features. To assess this diversity, the chief morphological features of each part of the denticles were listed (Table 2) and eighty of the complete specimens were closely examined, their characteristic features being plotted in Table 2.

From an inspection of the whole of the denticles it was possible to note the major commonly occurring groupings of characteristics and to define distinct types. The denticles fall broadly into three chief groups (Nos. 1, 2 and 3) and two minor groups (Nos. 4 and 5). Groups 1, 2 and 3 have variations on the common type which are either extreme forms or intermediate between the groups. Table No. 2 generally confirms the broad outlines of these groupings but it also shows the complexity of individual specimen types.

The three samples of minute, group A, denticles were divided in the following manner:

Table 3 - Minute Denticles (Group A)

Type Nos.	1	1a	1b	2	2a	2b	3	3a	3b	4	5	total
Locality												
G	1	0	0	32	0	5	10	1	2	4	0	55
B.1.	15	15	1	131	4	15	66	13	8	8	2	278
B.2.	10	18	3	133	4	6	69	114	4	10	9	280

Key to Table 3:-

G = Gainsborough (Wollaton Museum, Nottingham, Chamberlain Collection)

B.1. = Barnstone 183 grams (278 denticles grouped under No. Zr9681, Institute of Geological Sciences, London. (I.G.S).

B.2. = Barnstone second sample (denticles 1-80, Zr9682 and 200 denticles, Zr9683, I.G.S.).

The following is a general summary of the characteristics of the various types of minute denticle (Group A):-

Type No.1, pl. 3, figs. 1-2; text-fig.1, fig.1; text-fig.2, fig.8.

Basal Plates are expanded and mostly sub-square.

Pedicels are upright and of medium width.

Crowns are pointed and inclined posteriorly at an angle of approximately 45°.

Keels extend from the basal plate to the crown tip, approximately half of the denticles having bifurcate keels, apparently a random feature.

EXPLANATION OF TEXT-FIGURE 1

Rhaetian Denticles illustrating the
Relationships of the Types

Fig. 1 Type No. 1 Zr9684, upper view (.6mm × .4 mm), anterior view (.5 mm × .4 mm), lateral view (.5 mm × .5 mm).

Fig. 2 Lateral view showing denticle features, Zr9685, (.4mm × .5mm).

Fig. 3 Illustration of Basal Plate shapes (Table 2), a, laterally compressed, Zr9686, (.4mm × .3mm). b, Sub-square, Zr9687, (.3mm × .3mm). c, medium transversely compressed, Zr9688, (.4mm × .25mm). d, transversely compressed, Zr9689, (.5mm × .2 mm).

Fig. 4 Type No. 1a Zr9690, upper view (.5mm × .4 mm), anterior view (.5mm × .4mm), lateral view (.5mm × .5 mm).

Fig. 5 Type No. 2b Zr9691, upper view (.4mm × .4mm), anterior view (.4mm × .4mm), lateral view (.4mm × .4mm).

Fig. 6 Type No. 1b Zr9692, upper view (.4mm × .2 mm), anterior view (.6mm × .2 mm), lateral view (.6mm × .3mm).

Fig. 7 Type No. 2 Zr9693, upper view (.3mm × .5mm), anterior view (.4mm × .5mm), lateral view (.4mm × .6mm).

Fig. 8 Type No. 3b Zr9694, upper view (.6mm × .7 mm), anterior view (.9mm × .7 mm), lateral view (.9mm × .7 mm).

Fig. 9 Type No. 2a Zr9695, upper view (.3mm × .4mm), anterior view (.4 × .4), lateral view (.4mm × .4mm).

Fig. 10 Type No. 3a Zr9696, upper view (.4mm × .5mm), anterior view (.5mm × .5mm), lateral view (.5mm × .5mm).

Fig. 11 Type No. 5 Zr9697, upper view (.4mm × .2 mm), anterior view (.7 mm × .2 mm), lateral view (.7 mm × .5mm).

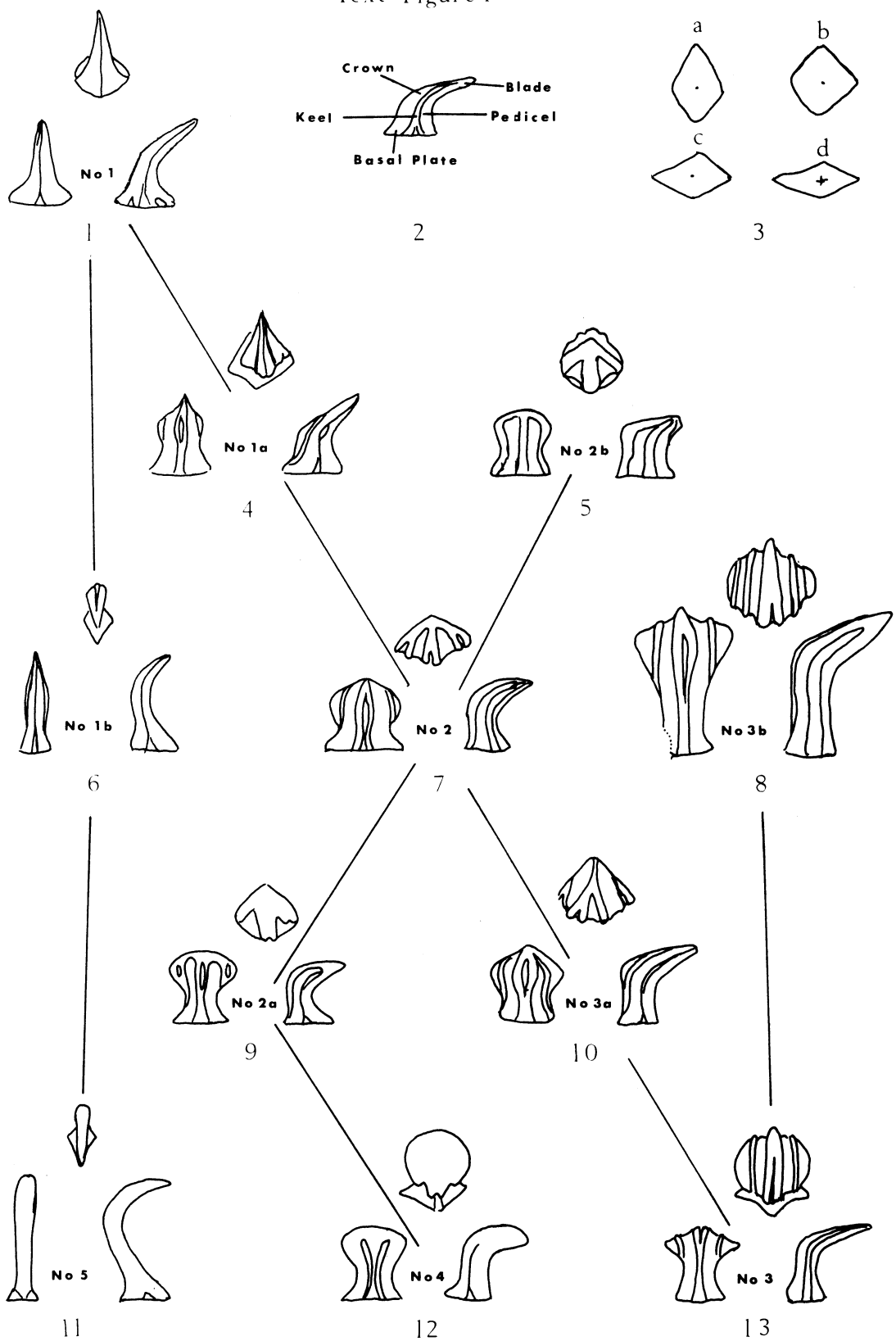
Fig. 12 Type No. 4 Zr9698, upper view (.5mm × .4mm), anterior view (.5mm × .4mm), lateral view (.5mm × .5mm).

Fig. 13 Type No. 3 Zr9699, upper view (.5mm × .5mm), anterior view (.5mm × .5mm), lateral view (.5mm × .5mm).

All denticles are drawn to the same scale and the quoted measurements are of heights and widths respectively in each figure. In each case the upper figure is an upper view, the one on the left an anterior view and the one on the right a lateral view.

Specimens are deposited in the Institute of Geological Sciences, London and numbered Zr9684 to Zr9699.

Text-Figure 1



Type No. 1a, pl. 3, fig. 3; text-fig. 1, fig. 4

The crown is wider especially near the base, some having lateral points. These denticles are transitional to type no. 2.

Type No. 1b, text-fig. 1, fig. 6

The pedicels and crowns are more rounded in section and on some, the pedicels are inclined anteriorly, resembling type no. 5 though keeled; the crowns are rather inflated.

Type No. 2, pl. 3, figs. 4-5; text-fig. 1, figs. 2 & 7; text-fig. 2, figs. 5-6.

Basal Plates are generally less expanded than in type no. 1; about 25% are subsquare and most of the rest transversely compressed.

Pedicels are upright, tending to be short and broad with many being rather transversely compressed.

Crowns are inclined posteriorly at a low angle from the horizontal and they all have a short blade and a quadrate upper view. Many have the whole or part of the upper surface smooth and without keels.

Specimens of no. 2 type are the commonest and have the most varied forms.

Type No. 2a, text-fig. 1, fig. 9

The basal plate is rather smaller; the pedicel narrower and the crown develops a rounded posterior edge. The lateral keels are faint or missing and the hollow between the keels deepened. Denticles of type 2a are transitional to those of type no. 4.

Type No. 2b, text-fig. 1, fig. 5

Specimens allocated to this sub-division are an extreme form almost without blade extension of the crown. The upper surface is almost horizontal and often smooth. Some are very broad with extra keels and some have short keels on the posterior face.

Type No. 3, pl. 3, figs. 7-8; text-fig. 1, fig. 13; text-fig. 2, figs. 15-16.

Basal Plates are usually widespread laterally and transversely compressed.

Pedicels are generally of medium width or narrow.

Crowns are all broad, nearly all of them having bifurcate keels; most of the lateral ones ending as separate points near the tip.

Denticles of no. 3 type are mostly transversely compressed in all their features.

Type No. 3a, text-fig. 1, fig. 10

Basal plate and pedicel are transversely compressed. The crown is less rounded in upper view and narrower. Lateral keels may or may not reach the tip of the crown. Type 3a denticles are intermediate in morphology between types no. 2 and no. 3.

Type No. 3b, text-fig. 1, fig. 8

Specimens of this type are larger than the rest. They have narrow, transversely compressed basal plates; elongate, narrow pedicels and broad, high-angled crowns. The keels are strong, ending in distinct points.

Type No. 4, pl. 3, fig. 6; text-fig. 1, fig. 12; text-fig. 2, fig. 7

The basal plates are transversely compressed and the pedicel is so narrow that most of the crowns are detached. The horizontally inclined crown has a smooth, convex upper surface with a rounded posterior edge. Most denticles of this type have two deep grooves which extend from the basal plate to part of the upper surface of the crown.

Type No. 5, pl. 3, fig. 9; text-fig. 1, fig. 11

Specimens of type no. 5 have a quadrate basal plate that narrows to a smooth needle-like hook which is circular in section. This hook inclines anteriorly from the basal plate and then curves sharply posteriorly to a pointed tip. Denticles of this group may be clasper hooks such as occur on the claspers of the male sharks.

Discussion on the affinity of Group A denticles

Size and distribution of Minute Denticles

The minute denticles from Barnstone range in size from a height of approximately 0.3 mm and a length of 0.2 mm to a height of 0.9 mm and a length of 0.7 mm. The majority of the denticles are approximately 0.5 mm high and 0.5 mm long.

If these denticles belong to *D. barnstonensis* the teeth of the same species should occur with the same strata. This has proved to be so at nine localities and though specimens are sometimes rare, all bone beds examined have yielded specimens of the teeth and denticles. (Sykes, 1974).

Dermal Denticles of the Order Squalea

In the Order Squalea, to which the Family Dalatiidae belongs, there is a variation in dermal denticles between plate-like and spiny types. White (1957, p. 59) considers that there was possibly a development from one type to the other, with the plate-like type being the more primitive. Characteristics of the minute Rhaetian denticles are to be found in many of the denticles of modern squalid sharks. Many like *Isistius braziliensis* are minute and have a quadrated basal plate. Some have triple keels, *Somniosus microcephalus* (text-fig. 2, figs. 9-10) having both single and bifurcate keels. *Squalus acanthus* (text-fig. 2, figs. 11-12), *Centroscymnus coelolepis* and others have distinct quadrate pedicels and blade-like, transversely compressed crowns, whilst those of *Etmopterus hillanus* are quadrate with an expanded base and a curved, pointed crown (all figures in Bigelow and Schroeder, 1948).

Most of the species in the Order Squalea have varying forms of denticles on different parts of their body.

Dermal Denticles of the recent species, *Dalatias licha*

Specimens of *Dalatias licha* in the British Museum (Nat. Hist.) show that over the body as a whole the denticles have an expanded quadrate base which narrows to a low, broad pedicel. The crowns have a quadrate upper view with slightly concave sides; they are inclined posteriorly at an angle of about 45°. On the dorsal surface of the fish the crowns are wider and more rounded. The denticles have three keels which are bifurcate on the broader denticles (text-fig. 2, figs. 1-2). Under the snout the denticles are strongly transversely compressed. Their basal plates are expanded and they have upright pedicels with crowns inclined posteriorly almost at right angles having a rather rounded upper view. There are rather faint single and bifurcate keels which on some denticles do not extend across the smooth upper surface of the crown (text-fig. 2, fig. 3). On the denticles towards the tail of the fish, the crowns narrow and become pointed. The expanded quadrate base narrows to a short upright pedicel, the crowns

EXPLANATION OF TEXT-FIGURE 2

Fig. 1 *Dalatias licha* (Bonaterre) 1788, outline of median section of body denticle (after Daniels, 1934, p. 32).

Fig. 2 *Dalatias licha*, upper view of body denticle (after Bigelow and Schroeder, 1948, p. 502) (.8 mm × 9 mm).

Fig. 3 *Dalatias licha*, upper view of denticle from the ventral surface of the snout (after Bigelow and Schroeder, 1948, p. 502) (0.9 mm × 0.9 mm).

Fig. 4 *Dalatias licha*, lateral view of tail denticle, Zr9700, (0.8 mm × 1.0 mm).

Fig. 5 Rhaetian denticle, type No. 2, lateral view, Zr9701, (0.4 mm × 0.4 mm).

Fig. 6 Same specimen as figure No. 5, upper view (0.3 mm × 0.4 mm).

Fig. 7 Rhaetian denticle, type No. 4, upper view, Zr9702 (.4 mm × .4 mm).

Fig. 8 Rhaetian denticle, type No. 1, lateral view, Zr9703 (0.5 mm × 0.4 mm).

Fig. 9 *Somniosus microcephalus* (Block & Schneider, 1801), lateral view (after Bigelow & Schroeder, 1948, p. 517) (.9 mm × 1.1).

Fig. 10 *Somniosus microcephalus*, upper view (after Bigelow & Schroeder, 1948, p. 517) (1.2 mm × 1.1 mm).

Fig. 11 *Squalus acanthus* Linnaeus, 1758, upper view (after White 1937, pl. 4) (app. .8 mm × .6 mm).

Fig. 12 *Squalus acanthus* posterior view (after White, 1937, pl. 4) (app. .6 mm × .6 mm).

Fig. 13 *Dalatias barnstonensis* Sykes, 1970, upper tooth, lateral view (after Sykes, 1970, pl. 21) (3.2 mm × 1.0 mm).

Fig. 14 *Dalatias licha*, upper tooth, lateral view (after Casier, 1961, p. 20) (6.0 mm × 1.3 mm).

Fig. 15 Rhaetian denticle, type No. 3, upper view, Zr9704 (0.3 mm × 0.4 mm).

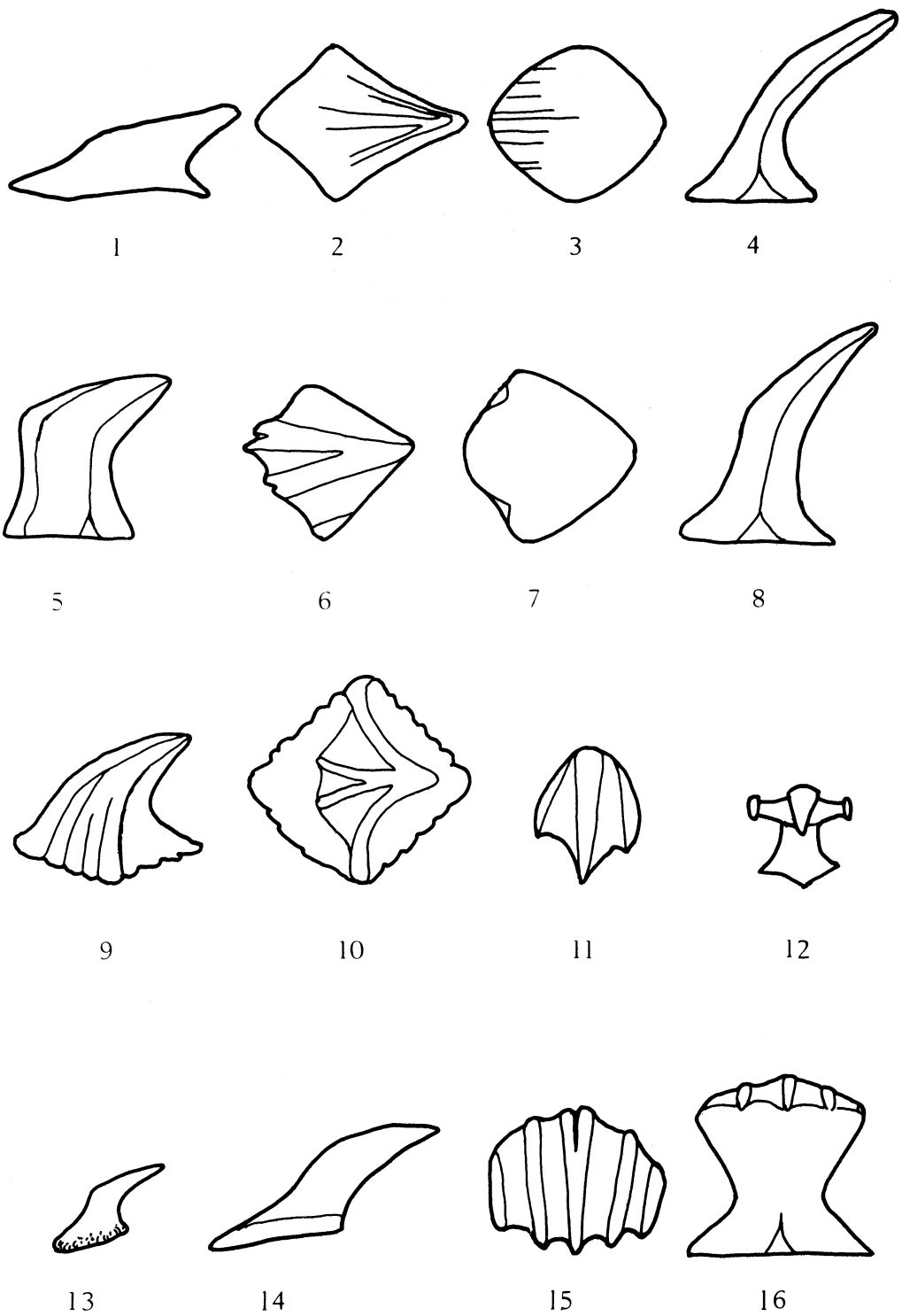
Fig. 16 Same specimen as figure No. 15, posterior view (0.4 mm × 0.4 mm).

The teeth (figs. 13 & 14) are drawn to the same scale; figures 1, 2, 3, 9, 10, 11 & 12 are all to a scale four times the size of the teeth; figures 4, 5, 7, 8, 15 & 16 are all to a scale ten times the size of the teeth.

The quoted measurements are of the height and width respectively in each figure.

Specimens numbered Zr9700 to Zr9704 are deposited in the Institute of Geological Sciences, London.

Text Figure 2



inclined posteriorly at approximately 45° (text-fig. 2, fig.4). The fins have much smaller denticles with narrower pedicels and pointed crowns.

Comparison between the Group A Denticles and those of *Dalatias licha*

The Rhaetian minute denticles (Group A) and those of the recent species *D. licha* have several features in common. Both forms of denticles are small, ranging in width from about one-fifth to one-eighth of the width of the respective teeth. They both have a flat based, quadrate, expanded basal plate, though the expansion is greater in *D. licha* along with a tendency for the basal plate to have more acute corners.

The pedicels of both types are quadrate though in *D. licha* they are shorter and less upright.

The crowns of the majority of denticles of both Group A and *D. licha* have a quadrate upper view varying in breadth and posterior elongation from denticle to denticle. They are both ornamented with keels which generally extend from the basal plate to the tip of the crown. On the Rhaetian denticles the keels are mostly bifurcate with some having extra keels. This feature of bifurcate keels is also present in some of the *D. licha* denticles.

The minute pointed denticles of *D. licha* and the pointed Rhaetian denticles show the greatest similarity between the two forms (text-fig. 2, figs. 4, 8).

Relationship of Teeth and Denticles

Shark teeth and denticles are closely related. The denticles have the same internal structure as the teeth and could be regarded as specialised dermal denticles (Applegate, 1967, p. 45).

The species *D. barnstonensis* was largely based on a comparison of Rhaetian teeth with those of *D. licha*. The similarities between the tail and fin denticles and the upper teeth of *D. licha* (text-fig. 2, figs. 4 and 14) suggest a similar compatibility between the denticles and teeth of *D. barnstonensis* Apart from the differences of ornamentation and in the nature of the roots and basal plates, such a resemblance is found between the upper teeth of *D. barnstonensis* and the pointed Rhaetian denticles (text-fig. 2, figs. 8 and 13). If the Rhaetian denticles are from *D. barnstonensis* the differences in the teeth of the two species may well be reflected by differences in their respective denticles. The upper teeth of *D. barnstonensis* differ from those of *D. licha* in being slightly angled at the base of the crown; this feature is present in most of the no. 1 type Rhaetian denticles and not in those of *D. licha*. Another feature is the development of side points on some of the type no. 1 Rhaetian denticles comparing with the lateral points on the upper teeth of *D. barnstonensis* and in contrast to the absence of side points in *D. licha*. The lower teeth of *D. barnstonensis* have more strongly developed serrations which may be reflected in the stronger ornamentation of the Rhaetian denticles as a whole.

Position of Denticles

It has been pointed out (White, 1937, p. 61) that the denticles of sharks are flatter and less strongly keeled in the least exposed parts of the body and they are typical on the flanks and dorsal surface. If this is the case with the Rhaetian denticles it is possible that those of types no. 2 and 2b, with a smooth and flattened upper surface, came from the belly of the fish whilst those modified type no. 4 are from under the snout (text-fig. 2, figs. 3 and 7). Those with a partly smooth upper surface being intermediate to type no. 2 found on the flanks and then a continuing modification to the most armoured type no. 3 on the dorsal surface.

Possibility of association with Hybodont Sharks

With such an abundance of the type A denticles and a predominance of hybodont teeth in the bone bed, it is open to consideration that the type A denticles and hybodont teeth must go

together. A conclusion upon statistical evidence alone would ignore all the comparative morphological evidence that link type A denticles with *D. barnstonensis* teeth. Amongst the minute denticles the nearest approach to a hybodont denticle is in the small number of specimens allocated to the type no.2b which are, however, a minor variation. Possible explanations why the teeth should be rare and the denticles common are that originally there were many more denticles than teeth on each fish and their minute size may have helped them to move more easily with the current after deposition thus avoiding abrasion. The teeth have a spongy interior which makes them more fragile than the more solid denticles. It is therefore considered that the type A denticles show closer affinity to Dalatiids than to Hybodonts.

Hybodont Denticles (Group B)

The hybodont genera *Hybodus* and *Acrodus* are closely related (Day, 1864) and dermal denticles from Liassic species of hybodonts such as *Acrodus nobilis*, *Acrodus anningae* and *Hybodus becherei* are very similar. Many of them consist of a round, well-defined basal plate with a domed crown bearing longitudinal ridges (text-fig.3, fig.1). Others have a number of narrow crowns spread laterally on a basal plate (Woodward, 1889, pl.8, figs. 2-5).

Denticles of the Triassic species *Lissodus africanus* (Brown) are also described (Brough, 1935, p.40) as being shaped like a pointed dome with a ridged surface. Stensiö (1921, pl.1 fig.14) figures a domed type of dermal denticle (text-fig.3, fig.2) which he considers to be a hybodont though found in isolation detached from the fish. He also figures (1921, p.25, fig.9) poorly preserved denticles of a Triassic species *Acrodus oppenheimeri* Stensiö, the denticles of which are laterally extended (text-fig.3, figs. 3-4).

In the Rhaetic bone bed at Barnstone, prior to the finding of the dalatiid, *D. barnstonensis* the Elasmobranch species, as recognised from teeth and jaw fragments, all belonged to the hybodont genera *Hybodus*, *Acrodus* and *Polyacrodus*.

The commoner (Group B) of the two groups of large denticles found at Barnstone can be related to each other by transitional types and are associated with hybodont sharks (Sykes et al 1970, p.254, pl.17, figs. 1-5, text-fig.5, figs. 8-9). The denticles of group B range in size from 1.0 to 1.5 mm in height and 1.0 to 3.0 mm in length.

The simplest of these Rhaetian hybodont type denticles have a single, fluted, stud-like crown on a spreading, subcircular base which has a concave undersurface (text-fig.3, figs.5-6). Some of the denticles have two to six crowns on a similar base, a number having the rear crowns inclined rearwards. There are denticles which are extended laterally and have narrower, rearward inclined crowns. These are transitional to the commonest type which consist of a number of striated, closely packed crowns on a base which is considerably extended laterally. The crowns are narrow and all are curved rearwards. The pedicel on this latter type is merely a narrowing above the base which is similar to that figured by Stensiö (text-fig.3, figs. 3 and 7).

Hybodont dermal denticles are generally not very well known but there is sufficient evidence to link these Rhaetian denticles with hybodont species.

Chimaeriforme Dermal Denticles (Group C)

Rare specimens of the Holocephalon *Squaloraja* have been found in the Rhaetic rocks of Beer Crowcombe (More, 1861) and thought to have been found in the bone bed at Redland, Bristol (Short, 1904). This genus belongs to the family Squalorajidae in the Order Chimaeriformes. The dermal denticles of the primitive Chimaeriformes are based on cone-like structures (Patterson, 1965) and in addition, some denticles have well developed or divided crowns. The basal plates are large and expanded, usually striated or fluted with a concave undersurface.

EXPLANATION OF TEXT-FIGURE 3

Figures 1 to 8 hybodont dermal denticles.

Fig. 1 *Hybodus delabechei*, lateral view of head denticle (after Woodward, 1889, p. 260, pl. 8, fig. 3) (3.7 mm × 3.3 mm).

Fig. 2 Hybodont denticle, general view (after Stensiö, 1921, pl. 1, fig. 14).

Fig. 3 *Acrodus oppenheimeri* Stensiö, 1921, lateral view (after Stensiö, 1921, p. 25, fig. 9) (.8 mm × .9 mm).

Fig. 4 *Acrodus oppenheimeri*, anterior view (after Stensiö, 1921, p. 25, fig. 9) (.8 mm × 1.0 mm).

Fig. 5 Rhaetian hybodont denticle, lateral view, Zr9705 (1.1 mm × 2.0 mm).

Fig. 6 Same specimen as figure No. 5, upper view (1.7 mm × 2.0 mm).

Fig. 7 Rhaetian hybodont denticle, lateral view, Zr9706 (.9 mm × 1.4 mm).

Fig. 8 Same specimen as figure No. 7, anterior view (1.3 mm × 1.4 mm).

Fig. 9 *Menaspis armata* Ewald, lateral view of enlarged median denticle (after Patterson, 1965, p. 170, fig. 36) (5 mm × 3 mm), size of average body denticle is app. 2 mm × 1 mm).

Fig. 10 *Menaspis armata*, lateral view of enlarged median denticle (after Patterson, 1965, p. 124, fig. 12) (3 mm × 2.6 mm).

Fig. 11 *Squaloraja polyspondyla* Agassiz, upper view of dorsal denticle (after Patterson, 1965, p. 124, fig. 12) (4.0 mm × 1.5 mm).

Fig. 12 *Squaloraja polyspondyla*, upper view of dorsal denticle (Patterson, 1965, p. 124, fig. 12) (2.5 mm × 2.1 mm).

Fig. 13 Rhaetian denticle, Barnstone, lateral view, Zr9707, (3.0 mm × 2.2 mm).

Fig. 14 Rhaetian denticle, Barnstone, upper view (after Sykes, et al, 1970, pl. 17, fig. 6) (2.4 mm × 2.2 mm).

Fig. 15 Rhaetian denticle, Barnstone, lateral view, Zr9708 (2.2 mm × 1.6 mm).

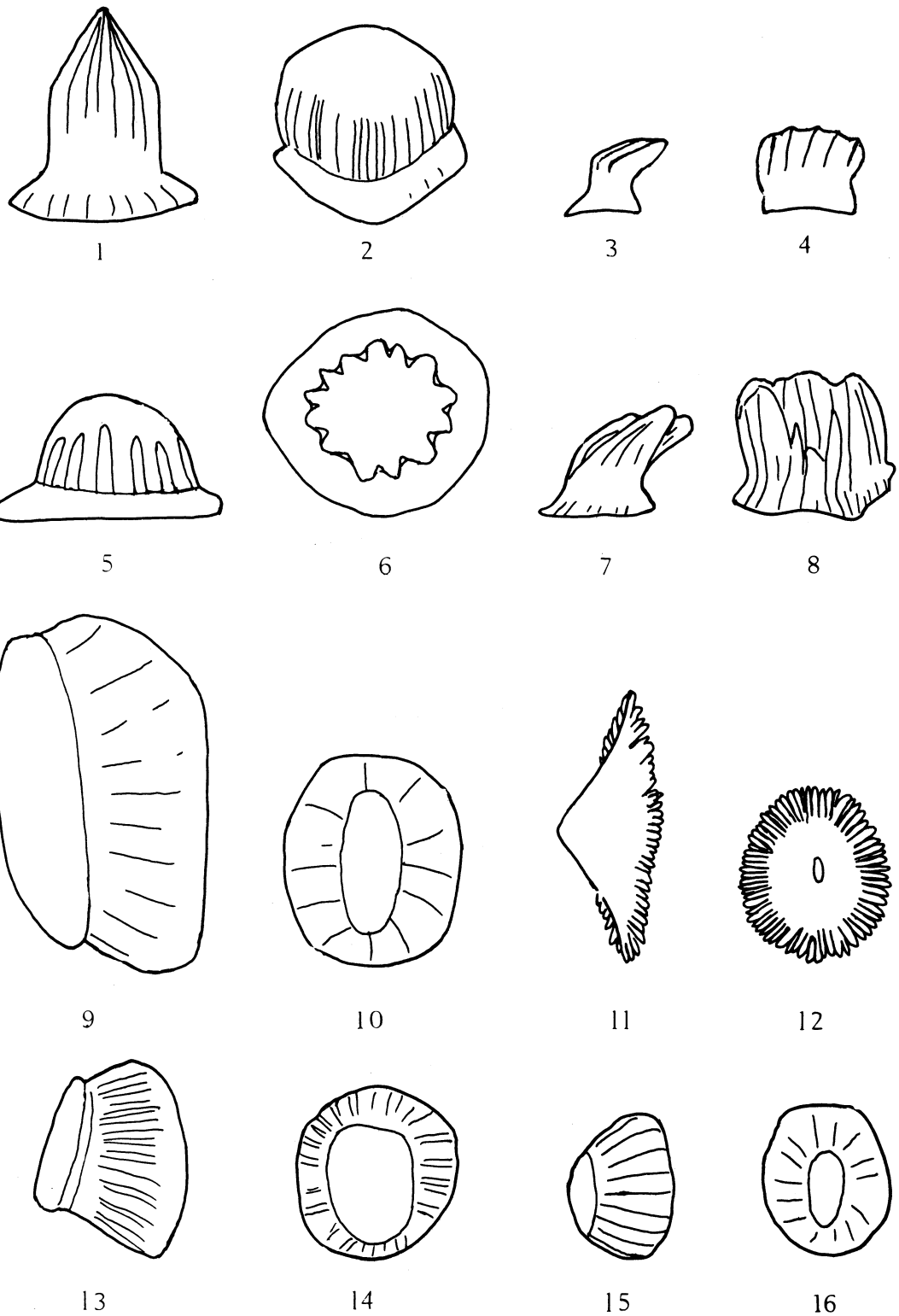
Fig. 16 Same specimen as figure No. 15, upper view (2.2 mm × 1.9 mm).

Figures 1 & 2 are drawn to the same scale; figures 3 to 8 are all drawn to a scale twice the size of figures 1 & 2; figures 9 to 16 are all drawn to a scale of 17 to 14 times the size of figures 1 & 2.

The quoted figures are of the height and width respectively in each figure.

Specimens numbered Zr9705 to Zr9708 are deposited in the institute of Geological Sciences.

Text-Figure 3



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The rare type of Rhaetian denticles vary in size from 1.2 to 2.2mm high and 2.0 to 3.0mm long. They consist of a simple rounded, conical structure with a smooth, depressed crown which varies in size between denticles (Sykes et al., 1970, p. 255, pl.17, fig. 6, text-fig. 5, fig.10). The basal plate is large and radially grooved with a slightly concave undersurface. They compare closely (text-fig. 3, figs. 9-10, 13-14) with the denticles of the Chimaeriformes *Menaspis armarta* Ewald (Patterson, 1965, p.170) and generally (text-fig. 3, figs. 11, 12, 15 and 16) with the denticles of *Squaloraja polyspondyla* Agassiz (Patterson, 1965, p. 124).

There is, therefore, good comparative evidence that the group C denticles belong to the rare Rhaetian genus *Squaloraja*.

Conclusions

The dermal denticles of the Rhaetic bone bed samples can be classified into three distinct groupings, the denticles of one group being smaller than those of the other two. One of the larger, group B, denticles, which are common, are associated with hybodont sharks. The other larger, group C, denticles are quite rare and have affinities with a rare Rhaetian Holocephalon. The third, common and minute, group A denticles, show affinities with the species *D. barnstonensis*.

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EXPLANATION OF PLATE 3

Fig. 1 Dermal denticle type No. 1, lateral view ×100, No. Zr9709.

Fig. 2 Dermal denticle type No. 1, upper anterior view, ×50, No. Zr9710.

Fig. 3 Dermal denticle type No. 1a, anterior view, ×85, No. Zr9711.

Fig. 4 Dermal denticle type No. 2, upper view, with extra median keel, ×130, No. Zr9712.

Fig. 5 Same specimen as Fig. 4, general anterior view, ×130.

Fig. 6 Dermal denticle type No. 4, upper anterior view ×90, No. Zr9713.

Fig. 7 Dermal denticle type No. 3, upper view, ×120, No. Zr9714.

Fig. 8 Dermal denticle type No. 3, general anterior view, ×85, No. Zr9715.

Fig. 9 Dermal denticle type No. 5, lateral view, ×80, No. Zr.9716.

All specimens in the Institute of Geological Sciences, London, Nos. Zr9709, ZR9716.

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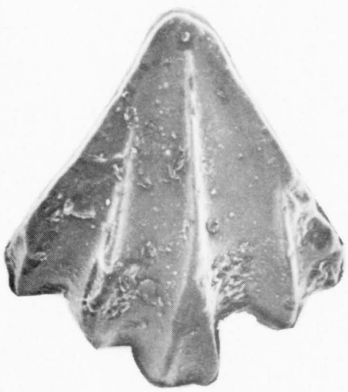

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Rhaetian Elasmobranch dermal denticles