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SELACHIAN FAUNAS FROM THE EARLIEST CRETACEOUS  
PURBECK GROUP OF DORSET, SOUTHERN ENGLAND

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ABSTRACT. Abundant selachian remains have been recovered from a number of horizons through the Purbeck Group at Durlston Bay, Lulworth Cove and Stair Hole in southern England. The remains, primarily teeth, but additionally fin spines and dermal denticles, belong to selachians from two major groups, the Hybodontoida and the Rhinobatoidei. The assemblage of hybodont sharks is quite diverse, comprising six species from the four genera '*Hybodus*', *Egertonodus*, *Polyacrodus* and *Lonchidion*. The rhinobatoid rays include two species, one belonging to the genus *Belemnobatis* and another, larger, indeterminate ray. Within the Purbeck fauna, two species are new: *Lonchidion inflexum* sp. nov. and *Belemnobatis variabilis* sp. nov. Within the entirely non-marine succession of the Purbeck Group, the beds containing ray teeth also contain molluscs indicative of more saline intervals. In all of the sampled beds, the hybodont faunas recovered were relatively homogenous.

THE Purbeck Group of southern England consists of a carbonate-dominated succession of lagoonal sediments of Tithonian (Jurassic) to Valanginian (Cretaceous) age. The Lulworth Formation, which comprises the lower part of the succession, consists of micritic limestones and marls with subsidiary molluscan and

ostracod bioclastic limestones, shales and evaporites. It is probable that sedimentation was dominantly within restricted settings, with evidence for rapid fluctuations in palaeosalinity. This is overlain by the Durlston Formation, in which rapidly alternating bioclastic limestones and shales dominate. Diverse molluscan and ostracod faunas suggest that environments with palaeosalinities from freshwater to almost fully marine were present, although there is no evidence for open marine conditions at any time. For more information of probable palaeoenvironments, see elsewhere within this volume.

## MATERIAL AND METHODS

Selachian material was principally obtained by acid dissolving of limestones from a number of horizons within the Purbeck Group of Dorset (Text-fig. 1). Samples were collected from 16 horizons throughout the uppermost Lulworth Formation and the Durlston Formation at Durlston Bay (Text-fig. 2), Lulworth Cove and Stair Hole (Text-fig. 3), with samples collected from all of the named lithostratigraphic units throughout this interval. Samples were principally collected from bioclastic horizons in which vertebrate material was seen in the field, although selachian material was also obtained from limestones of similar lithologies that appeared barren of vertebrate remains when collected. These varied in size from 1 kg to 25 kg, with a total of almost 100 kg being processed. Limestones were dissolved in buffered 15-20 per cent acetic acid, with insoluble material being removed regularly. This was washed and picked for vertebrate material in fractions down to 355  $\mu\text{m}$ .

Selachian remains frequently proved to be very abundant, with some samples yielding several tens of recognizable teeth and denticles per kg. A number of larger hybodont teeth and fin spines were also collected by surface picking in the field.

Many of the samples containing selachian material also produced abundant examples of other vertebrate remains. Fragmentary fossils of actinopterygian fish are common. These are relatively diverse in some samples, but are invariably dominated by teeth and scales of semionotiformes and small teeth possibly assignable to amiiformes. Fragmentary reptile remains are common in some samples, with many fragments being recognizable as chelonian. Small crocodylian remains are locally abundant, with teeth probably assignable to *Theriosuchus* being especially common. Other vertebrate material was rare, but a sample from a bone-rich lens at the base of bed DB223 (of Clements 1992) at Durlston Bay yielded three lissamphibian jaw fragments, two partial theropod teeth and a mammal tooth.

The style and quality of preservation of selachian teeth is relatively consistent throughout the samples. Teeth generally show low to moderate abrasion (stages 0 to 2 of Fiorillo (1988) and Cook (1995)). The degree of abrasion is often highly variable within an individual sample, and there is no strong relationship between degree of abrasion and lithology. It is therefore likely that many of the studied samples contain a mixture of autochthonous and parautochthonous elements. The bulk of hybodont teeth lack a root, probably due to taphonomic loss of the porous root, although, where it is present, it is generally well preserved.

Bioerosion of teeth is sporadically present. This is especially frequent on the roots of batoid teeth, which invariably have hyphate borings of *Mycelites*, which can be recognised as having completely destroyed the root in some cases. These borings are strongly substrate specific (Underwood *et al.* 1999b). They are rare on hybodont teeth and of variable frequency on actinopterygian remains.

The taxonomy and the descriptive tooth terminology is based on Cappetta (1987). All photographed specimens were coated with gold and photographed using a SEM. Illustrated specimens are deposited in The Natural History Museum, London and prefixed P denoting Pisces.

## SYSTEMATIC PALAEOLOGY

Superfamily HYBODONTOIDEA Zangerl, 1981

Family HYBODONTIDAE Owen, 1846

Genus EGERTONODUS Maisey, 1987

*Type species.* *Hybodus basanus* Egerton, 1845, from the Aptian or Barremian, Lower Cretaceous of the Isle of Wight, southern England.

*Remarks.* The separation of the genus *Egertonodus* from *Hybodus* by Maisey (1987) was based primarily on cranial anatomy and scale morphology. The teeth have a morphology very similar to that of *Hybodus reticulatus*, the type species of

*Hybodus*, and consequently, isolated teeth of other nominal *Hybodus* species cannot readily be assigned to *Egertonodus*. We therefore consider that *Egertonodus* should be regarded as a monotypic genus until cranial material of other nominal *Hybodus* species is studied.

*Egertonodus basanus* (Egerton, 1845)

Plate 1, figures 2-3, 5-6

\*.1845 *Hybodus basanus* Egerton, p. 197, pl. 4.

.1916 *Hybodus basanus* Egerton; Woodward, p. 5, pl. 1, figs 1-3; pl. 2, fig. 1.

v.1966 *Hybodus basanus* Egerton; Patterson, p. 288, text-figs 1-3.

v.1983 *Hybodus basanus* Egerton; Maisey, p. 1, figs 2-10, 12-18, 21-25.

1987 *Egertonodus basanus* (Egerton); Maisey, p. 27.

.1990 *Egertonodus basanus* (Egerton); Batchelor and Ward, p. 184, pl. 1, fig. 1.

1993 *Egertonodus basanus* (Egerton); Duffin and Sigogneau-Russell, p. 182, text-fig. 5.

*Material*. Two complete tooth-crowns and several hundred incomplete teeth.

*Description*. Teeth of this species have a high and slender cusp, and generally two pairs of lateral cusplets. The proximal pair reaches almost half the height of the cusp and the distal pair is lower. The cusp is lingually inclined and, on most teeth, the apex bends back labially, giving the cusp a slight sigmoidal curvature in lateral

view. All cusps are rounded in cross section. In anterior teeth, the cusp is straight and the cusplets are bent towards it. In lateral teeth, both the cusp and the cusplets are inclined posteriorly. All cusps on lateral teeth tend to be lower. Ornamentation consists of fine vertical folds. These are straight and bifurcate only rarely towards the base of the crown. They are present on all cusps, and are more pronounced on the labial side, where they reach half the height of the cusp. Above, the cusp is smooth, other than a cutting edge, which is continuous across all cusps. The teeth are up to 10 mm wide and 6 mm high. Only partial roots are preserved on a few specimens. They display a typically hybodont root structure with large foramina, especially on the basal part of the root, and smaller foramina close to the crown-root junction.

*Remarks.* The dentition and the heterodonty pattern of this species is well known from several more or less complete skulls housed in The Natural History Museum, London. Maisey (1983) suggested that '*Hybodus*' *ensis* Woodward, 1916 and *Polyacrodus parvidens* (Woodward, 1916), two tooth-based species also found in the Purbeck and Wealden of southern England, would be junior synonyms of *E. basanus*. One of us (JR) has studied the material of *E. basanus* in The Natural History Museum and come to the conclusion that there is no evidence to support this statement. Several characters separate the three species (see below). There are also localities where teeth of *E. basanus* are found in large numbers that lack teeth of '*H.*' *ensis*-type.

*Type species.* *Hybodus reticulatus* Agassiz, 1837, from the Sinemurian, Lower Jurassic of Lyme Regis, southern England.

*Remarks.* Teeth of the type species, *H. reticulatus*, have a high and slender cusp with a circular cross-section, a morphology quite different from that of some other nominal *Hybodus* species. It is therefore considered that *Hybodus* is best regarded as a form genus (see also Rees 1998), which may be polyphyletic, until the problems of hybodont taxonomy are resolved by future work.

*'Hybodus' ensis* Woodward, 1916

Text-figures 4-5

\*p.1916 *Hybodus ensis* Woodward, p. 11, pl. 2, figs 2-7 *non* pl. 3, figs 1-3.

v.1966 *Hybodus ensis* Woodward; Patterson, p. 292, text-figs 4-5.

*Material.* Nineteen isolated cusps and one almost complete crown.

*Description.* The main cusp is high, broad and labio-lingually compressed, particularly in larger teeth. Only one pair of small cusplets, well separated from the cusp, appear to be present. These are also compressed and have a triangular outline. The surface of the crown is almost smooth with weak vertical folds present mainly on the basal parts of the crown. The cutting edges are prominent



and are irregularly, weakly, serrated on large teeth. The labial face is almost flat while the lingual side is convex. There is a moderate degree of heterodonty, some teeth have a very broad and flattened cusp while the cusp in other teeth of the same size is more slender and narrow. The most complete tooth is 14 mm wide and 8 mm high, but larger isolated cusps were recorded.

*Remarks.* Serrations of the cutting edges are rare in hybodont sharks and was previously limited to *Priohybodus arambourgi* d'Erasmus, 1960, from the Upper Jurassic and Lower Cretaceous of northern Africa (Cappetta 1987) and *Thaiodus rucha*e Cappetta, Buffetaut and Suteethorn, 1990, from the Lower Cretaceous of Thailand. Teeth of *P. arambourgi* are symmetrical and have a broad and flattened outline. The root is not as porous as in most hybodonts and there is only a single row of larger foramina on the lower part of the root. The teeth of *T. rucha*e are very low and lack a well developed cusp. They are extremely expanded mesio-distally. Neither of these species are particularly closely related to '*H.*' *ensis* or to each other. Therefore, it is likely that serrations have arisen several times within the Hybodontoida, as they have within the Neoselachii (Cappetta 1987).

The type of heterodonty in '*H.*' *ensis* cannot be determined at this stage, but it may well be dignathic, a rare type within hybodonts, although it was previously noted by Patterson (1966) in the dentition of *Polyacrodus brevicostatus* (Patterson, 1966).

Woodward (1916) illustrated three isolated dorsal fin spines and assigned them to '*H. 'ensis*'. As fin spines are taxonomically indeterminable at the moment, there is no reason to consider the teeth and spines to be conspecific.

Family POLYACRODONTIDAE Glikman, 1964

*Remarks.* This family is partly being revised by the authors and the results will be published elsewhere. Our conclusions are that *Lonchidion*, a genus considered to be a junior synonym of *Lissodus* by Duffin (1985), in fact is valid as originally described by Estes (1964). This is based on morphological differences of the teeth, *Lissodus s.s.* have a tooth morphology characterized by a heavy crown with a prominent labial protuberance, giving the teeth a triangular outline in occlusal view. The root is smaller than the crown and the crown-root junction is very incised. Teeth of *Lonchidion* are gracile, and narrow in occlusal view. The labial protuberance is much more narrow than in *Lissodus s.s.* and it often forms a separate cusplet. The root is generally larger than the crown.

Genus LONCHIDION Estes, 1964

*Lonchidion inflexum* sp. nov.

Plate 2, figures 1-3, 6-8, 13-15

*Derivation of name.* From the latin *inflexus* meaning bent, referring to the angled crowns of the teeth.

*Holotype.* P. 65437, an anterolateral tooth-crown from Bed DB239 at Durlston Bay.

*Paratypes.* P. 65438, an anterior tooth-crown from Bed DB181 at Durlston Bay and P. 65439, a lateral tooth-crown from Bed DB239 at Durlston Bay.

*Material.* Several complete and frequent broken crowns, although no complete teeth.

*Diagnosis.* Small species of *Lonchidion* with an angled crown when viewed occlusally, the distal parts of the crown being inclined lingually. Distal tips of the crown are bent labially. The labial protuberance is very rounded. The crown-root junction is slightly incised.

*Description.* The teeth are low and the main cusp is only weakly developed, except on extreme anterior teeth where it forms a low cone. There are usually two pairs of very poorly developed lateral cusplets. When viewed occlusally, teeth are seen to have a sharply angled curvature, giving a rather 'V-shaped' profile. This curvature is centred around the main cusp, with angles of down to 87° being present in anterior teeth. The degree of inclination is somewhat variable, being highest in

anterior teeth. On most teeth, the most distal tips of the crown are curved labially, giving these teeth a 'zig-zag shape' in occlusal view. A moderately developed, rounded labial protuberance is present on the main cusp. There is also a small lingual protuberance on some teeth. The degree of ornamentation is variable, consisting of fine to moderate, non-bifurcating folds, usually present to some degree on both lingual and labial faces. Where folds are present, they are never strong but sometimes quite dense and appear to be more developed on lateral teeth. The crown shoulder is quite well developed in most teeth. The maximum width of the teeth is slightly over two mm. The root morphology is unknown.

*Remarks.* The strongly angled crown of the teeth separates this species from all other *Lonchidion* species except *L. noncostatus* (Duffin and Thies, 1997) from the Kimmeridgian of northwest Germany. However, *L. noncostatus* may be separated by the presence of a more pronounced occlusal crest and stronger cusplets. In addition, the teeth of *L. noncostatus* are not as strongly angled as teeth of *L. inflexum* and lack the labially bent distal tips of the crown.

*Lonchidion crenulatum* (Patterson, 1966)

Plate 2, figures 4-5, 9-12

v.1966 *Lonchidion breve crenulatum* Patterson, p. 316, text-figs 17-18.

pv.1966 *Lonchidion heterodon* Patterson, p. 326, text-fig. 25C *non* text-fig. 25A-B, D.

\*.1985 *Lissodus crenulatus* (Patterson); Duffin, p. 110, text-figs 4, pl. 1, fig. 2.

*Material.* Several teeth, a few of them complete with roots.

*Description.* The teeth are very gracile with a clearly marked, but low, central cusp. There are three pairs of minute lateral cusplets, although these may be very poorly developed and appear more like rather irregular serrations. The labial protuberance is weak. Ornamentation is limited to weak vertical folds descending from each of the cusp and cusplets, reaching as far as the crown shoulder. The crown shoulder is only slightly developed on the labial side of the crown. The crown is thinner than the root both labially and lingually. The root is typical for *Lonchidion*, with large foramina on the lower parts of the root and a few, irregularly placed, small circular foramina close to the crown-root junction. The teeth are up to two mm in width.

*Remarks.* This species was originally described as a subspecies of *Lonchidion breve* by Patterson (1966) but was considered a separate species by Duffin (1985) when he recognized *Lissodus crenulatus* as a formal species. We agree that *L. crenulatum* is a valid species but believe that it should remain in the genus *Lonchidion*. Another species from the Purbeck of Dorset, *L. heterodon* Patterson, 1966 was based on an assemblage of *L. crenulatum* and *Polyacrodus rugianus* (Ansorge, 1990), with the holotype being the only remaining figured *L. heterodon* specimen. The species is probably assignable to the genus *Polyacrodus*.

Genus POLYACRODUS Jaekel, 1889

*Polyacrodus parvidens* (Woodward, 1916)

Plate 1, figures 1, 4, 8-9

\*.1916 *Hybodus parvidens* Woodward, p. 12, pl. 2, figs 8-14.

v.1966 *Hybodus parvidens* Woodward; Patterson, p. 296, text-figs. 6-9.

1982 *Hybodus parvidens* Woodward; Estes and Sanchíz, p. 22, fig. 1A-B.

1987 *Polyacrodus parvidens* (Woodward); Cappetta, p. 37.

p.1990 *Lissodus rugianus* Ansoerge, p. 136, figs. 10-11 *non* figs. 4-9, 12-15

1993 *Polyacrodus parvidens* (Woodward); Hervat and Hervat, P. 43-48, figs. 1-8.

*Material.* Two complete and hundreds of incomplete teeth.

*Description.* Teeth of this species have a high and slender cusp and are equipped with two to three pairs of lateral cusplets. The cusp is ornamented with a longitudinal keel on the labial side, forming a small, but sharp-edged, protuberance. Vertical folds are present over much of the crown, reaching the apex of all cusps. They are coarse, but not particularly dense, and often bifurcating. These folds tend to be finer on the lingual face. The cutting edges are moderately developed, and are continuous across the crown. There is a moderate degree of heterodonty present, with lower lateral teeth being posteriorly inclined. The root morphology is characterized by a porous structure with large irregular foramina on the lower part

of the root and smaller circular foramina close to the crown-root junction. The root is strongly inclined lingually and has a flat basal face.

*Remarks.* The high cusp of *P. parvidens* makes the teeth rather like teeth of *Hybodus reticulatus*, the type species of *Hybodus*, although the keel on the cusp shows that they belong to another genus. Lateral teeth of *P. parvidens* are lower than equivalent teeth of *Hybodus s. s.*, demonstrating a greater degree of heterodonty. Even though the teeth of *P. parvidens* are quite different from those of *P. polycyphus*, the type species of *Polyacrodus*, we agree with Cappetta (1987) in including *P. parvidens* in *Polyacrodus*, awaiting a revision of the genus.

*Polyacrodus rugianus* (Ansorge, 1990)

Plate 1, figures 7, 10-12

pv.1966 *Lonchidion heterodon* Patterson, p. 326, text-fig. 25B *non* text-fig. 25A, C-D.

p\*.1990 *Lissodus rugianus* Ansorge, p. 136, figs 4-9, 14-15 *non* figs 10-11.

*Material.* A few complete and several incomplete teeth.

*Description.* This species have relatively low-crowned teeth that are expanded mesio-distally. The cusp is moderately low and there are two to three pairs of low lateral cusplets. In lateral teeth, the cusp and cusplets are very low. The proximal

pair of cusplets are situated far from the cusp. The teeth are ornamented with a few, coarse folds, descending from the tips of the cusp and the cusplets. On the cusp, there is a moderate labial protuberance. The occlusal crest is fairly strong. The foramina in the root are situated rather irregularly and there is no clear delimitation between small and larger foramina. The root is quite high and concave on the labial side. The lingual rootface is flat. In width, the teeth measure up to 2.5 mm.

*Remarks.* The overall tooth morphology of this species, with clearly demarcated cusp and cusplets, in combination with a weak labial protuberance and coarse folds makes *P. rugianus* assignable to *Polyacrodus s. l.* The teeth figured by Ansorge (1990) cannot all be included in *P. rugianus*, figures 10-11 are teeth of *P. parvidens* and the placoid scales (figs 12-13) cannot be assigned to any species with certainty.

Another small-toothed hybodont, *Polyacrodus heterodon* (Patterson, 1966), has previously been recorded in the Purbeck of Dorset. No specimens of this species were encountered during this study and therefore it is only known from the holotype.

Order RAJIFORMES Berg, 1940

Suborder RHINOBATOIDEI Fowler, 1941

Incertae familiae



*Remarks.* The two genera *Spathobatis* Thiollière, 1854, and *Belemnobatis* Thiollière, 1854, are well known from complete skeletons from the Upper Jurassic (Cappetta 1987). These were excluded from the rhinobatidoid clade by Brito and Séret (1996) but no new family was created. We agree, however, with Cavin *et al.* (1995) in their view that *Belemnobatis* and *Spathobatis* are undoubtedly members of the suborder Rhinobatoidei but we believe that they may be members of a separate family, distinguished by the shape of the hypobranchials (Brito and Séret 1996) and the presence of two short dorsal fin spines.

A third batoid genus, *Asterodermus*, is also recorded from the Upper Jurassic. The type species, *A. platypterus* Agassiz, 1843, is based on an incomplete skeleton with no preserved head or dentition. The distinctive placoid scales were considered diagnostic of *Asterodermus* by Thies (1995), who assigned isolated scales from the Kimmeridgian of northern Germany to *Asterodermus*, despite them being associated with teeth assigned to *Spathobatis*. In the Purbeck material described herein, there are also numerous scales of the *Asterodermus* type. It is therefore probable that this type of scales were present on both *Spathobatis* and *Belemnobatis*, with *Asterodermus* probably being synonymous with one of these genera. To avoid parataxonomy, only partial fish with the dentition preserved ought to be used taxonomically. We suggest that *Asterodermus* is considered a *nomen dubium* until diagnostic skeletal characters are described.

Isolated teeth of *Spathobatis* and *Belemnobatis* can, according to Cavin *et al.* (1995), be separated by a number of characters. The distinction is not clear,

however, since many teeth in the Purbeck collection display characters typical of both genera. Generally, teeth of *Spathobatis* have a higher crown with a demarcated cusp, while teeth of *Belemnobatis* are lower and transversely expanded (Cappetta 1987). The lingual uvula is wide in *Spathobatis* and more narrow in *Belemnobatis* (Cavin *et al.* 1995).

Genus BELEMNOBATHIS Thiollière, 1854

*Belemnobatis variabilis* sp. nov.

Plate 3, figures 1-11; Plate 4, figures 1-4

*Derivation of name.* Refers to the wide range of variation within the dentition of this species.

*Holotype.* P. 65442, an anterior (male?) tooth from Bed DB181 at Durlston Bay.

*Paratypes.* P. 65443, a lateral female tooth, P. 65444, a lateral male tooth and P. 65445, a symphyseal? tooth, all from Bed DB181 at Durlston Bay.

*Material.* More than 500 teeth, most of them complete.

*Diagnosis.* A highly heterodont species of *Belemnobatis* where the variations occur in both absence or presence of a well developed central cusp, strength of the

transverse crest and size of the labial protuberance. The median lingual uvula is well developed and rounded. The labial projection is not very large but the labial protuberance may be strong. On the labial rim of the teeth, there is a small number of weak folds. The basal foramen of the root is wide and the root lobes widely separated.

*Description.* This species is characterized by a strong heterodonty, probably of both monognathic and gynandric type. As in many extant batoids, it is assumed that teeth with a more pointed cusp are from males (e.g. Herman *et al.* 1997). The anterior teeth are strongly convex on the lingual side and the crown projects labially over the root. Male anterior teeth have a high and pointed cusp while anterior teeth of females are lower. Lateral teeth are more mesiodistally expanded, with a cusp either lacking (in females) or very poorly developed (in males). Female teeth are more labially expanded than male teeth. The transverse crest is well developed, being straight in lateral teeth and forming a sinus in anterior teeth. The median lingual uvula is straight and quite narrow in female teeth, while in male teeth, it is generally slightly wider. Juvenile teeth have a more narrow, tapering uvula and symphyseals? (extreme anteriors) have a wider uvula, occasionally slightly crenulated close to the lower rim. Marginal lingual uvulas are very poorly developed. On the labial side, the protuberance is quite strong, and on most teeth flanked by small irregular folds on the rim of the crown. The crown-root junction is incised on anterior teeth while lateral teeth have a root that is smaller than the crown. The root is quite low and projected lingually. Below the median lingual

uvula, there is a notch in the root. Two foramina are placed near the crown on each side of the median lingual uvula. In basal view, the root is divided in two lobes by a wide nutritive groove. No specimens were recorded in which the root lobes had fused to form a secondary hemiaulacorhize condition, as in many extant (e.g. Herman *et al.* 1997) and Mesozoic (CJU, pers. obs.) batoids. The teeth range in size from 0.5 to 1.2 mm.

*Remarks.* There are several species of *Belemnobatis* known from the Upper Jurassic and Lower Cretaceous (Cavin *et al.* 1995). The presence of folds on the labial rim of the crown separates teeth of *B. variabilis* from teeth of the following species: *B. sismondae* Thiollière, 1854 from the Kimmeridgian of northern France; *B. weneri* (Thies, 1983) from the Callovian of southern England; *B. moorbergensis* (Thies, 1983) from the Toarcian-Aalenian of northern Germany; and an undescribed species from the Bathonian of southern England (see Young 1982). Teeth of *B. morinicus* (Sauvage, 1873) from the Tithonian of northern France are less transversely expanded and with a less irregular labial rim of the crown than teeth of *B. variabilis*. *B. morinicus* also appears to be less heterodont than *B. variabilis*. ‘*Rhinobatos*’ *picteti* Cappetta, 1975, from the Aptian of southern France have a general tooth morphology very close to that of *B. sismondae*, the type species of *Belemnobatis*, and is here considered a species of this genus. Teeth of *B. picteti* have a more pronounced labial projection of the crown and a less pronounced labial protuberance compared to teeth of *B. variabilis*. *B. picteti* is also less heterodont and the teeth have a tapering lingual

uvula (present only in juvenile teeth of *B. variabilis*) and a smaller basal foramen than teeth of *B. variabilis*. High degrees of monognathic heterodonty are also seen in *Spathobatis rugosus* Underwood, Mitchell and Veltkamp, 1999a and in a *Spathobatis* from the Kimmeridgian of southern England (CJU, pers. obs.)

Rhinobatoidei indet.

Plate 4, figures 5-12

*Material.* Ten teeth, most of them complete.

*Description.* The teeth are massive with a low crown. The transverse crest is almost absent. There is a heavy, strongly convex lingual uvula, tapering in some teeth. The labial protuberance is strong and overhangs the root in all teeth, dipping down slightly. The variation is not striking but some teeth have a flat occlusal surface and a trace of a transverse crest (males?) while other teeth are more rounded (females?). The root is low and characterized by a wide median groove on the basal face. On the lingual face of the root, there are two large foramina placed on the sides of the lingual uvula. The width of the teeth varies from 1.1 to 1.7 mm

*Remarks.* The teeth described herein represent a species that is closely related to '*Rhinobatos*' *halteri* Biddle and Landemaine, 1988, from the Barremian to Albian of France (Biddle and Landemaine 1988; Biddle 1993) and Spain (Kriwet 1999). Our material and '*R.*' *halteri* may represent a new genus. The teeth are clearly different

from teeth of most *Rhinobatos* in lacking marginal lingual uvulas. They have a morphology that is more like that of the extant *Trygonorrhina*, although the teeth are lower and lack crenulations on the base of the crown.

#### OTHER SELACHIAN REMAINS

Although teeth are the most readily identified selachian remains within the Purbeck Group, other remains are also present in the form of denticles and dorsal and cephalic spines.

Dermal denticles are abundant and were recorded in almost all the samples studied. The most abundant of these are non-growing hybodontid scales (of Reif 1978). These are generically indeterminate, since the form of hybodontid scales varies greatly according to their position on the shark. Placoid scales were recorded from samples containing batoid teeth. These are of a morphology referred to *Asterodermus* by Thies (1995), but the majority can here be assigned to *Belemnobatis* by association with the teeth.

Fin spines are the largest and most conspicuous selachian elements recorded from the Purbeck Group. All fin spines so far recorded can be assigned to hybodonts. It is probable that fin spines of *Belemnobatis* are also present. That none have been recognised is probably due to their small size and the lack of restudy of older collections. Hybodont fin spines have been referred to a number of species within the genera *Asteracanthus* and *Hybodus* (Woodward 1919). The following species from the Purbeck Group must be considered *nomina dubia* as

they are based on isolated spines only; *Hybodus strictus* Agassiz, 1837, *Asteracanthus verrucosus* Egerton, 1854, and *A. semiverrucosus* Egerton, 1854. The referral of spines ornamented with granulae to *Asteracanthus* cannot be justified, as none of the characteristic and conspicuous teeth of this genus have been recorded in the Purbeck Group. The assignment of fin spines and teeth to the same species (e.g. Woodward 1919; Patterson 1966) is unjustified unless demonstrably associated teeth and post-cranial remains are found. At present, therefore, hybodont fin spines should be regarded as taxonomically indeterminate.

A small number of incomplete cephalic spines was also recorded, but as the case with fin spines, they are not taxonomically distinctive.

## PALAEOECOLOGY

In all the material sampled for selachians, the composition of the hybodont assemblage is relatively uniform. This also seems to be true of the associated actinopterygian faunas. The occurrence of rhinobatoid rays with this hybodont and actinopterygian fauna represents a far more localised association, apparently only present within the Corbula Beds, a unit known to have had a greater degree of marine influence.

Hybodonts are well known to have been common and diverse within non-marine environments during the Mesozoic (e.g. Patterson 1966; Duffin and Thies 1997). It is evident, however, from the uniformity of the hybodont assemblage that hybodont faunas were not particularly salinity controlled.

Although there are a number of taxa of extant non-marine batoids, Mesozoic ray remains are usually associated with a diverse neoselachian fauna in sediments deposited within fully marine environments. Despite this, the association of hybodonts and batoids in the near or complete absence of other neoselachian sharks is known from the Jurassic of Germany (Duffin and Thies 1997) and the Cretaceous of Brazil (e.g. Martill 1993) and Texas (Thurmond 1971). It is therefore probable that some taxa of rays (initially rhinobatoids and later dasyatids and sclerorhynchoids) were able to tolerate lower salinities than other neoselachians through much of the Jurassic and Cretaceous.

The feeding preferences of hybodont sharks are poorly known, with direct evidence (such as preserved gut contents) being unknown within non-marine taxa. Evidence of diet must therefore be deduced from the functional morphology of the dentitions. It is probable that species with a high and slender cusp producing a tearing-type dentition (of Cappetta 1987), such as *E. basanus*, and *P. parvidens*, preyed largely on small bony fishes. The broad, flattened cusp of '*H. ensis*' may have produced more of a cutting dentition, especially since some teeth were equipped with serrated cutting edges. This, in association with the relatively large size of the teeth, may indicate a diet of larger animals, possibly including small reptiles. The low-crowned teeth of *Lonchidion* spp. and *P. rugianus* appear to have a morphology suitable for clutching small prey items. The overall arrangement of these teeth, however, probably produced a dentition where several teeth in each file were used to form a crushing dentition. This may be similar to the situation present within many extant orectolobid sharks (such as within the Hemiscylliidae)



and some dasyatid rays (such as within the Gymnuridae). It is likely that these sharks were generalists, feeding on shelly molluscs, crustaceans and some small fish. The teeth of the rhinobatoid rays are highly indicative of a crushing-type dentition (of Cappetta 1987), specialised for feeding on shelled invertebrates.

## PALAEOBIOGEOGRAPHY

Hybodont faunas from the British Purbeck are very similar to those from the overlying Wealden succession, despite the differences in stratigraphic level and the change from carbonate to clastic-dominated facies. The two large species in the Purbeck, *E. basanus* and '*H.*' *ensis* are also present in the Wealden, whilst the Wealden *P. brevicostatus* is absent within the Purbeck.

*E. basanus* is a widespread element in Early Cretaceous lagoonal and fluvial sediments outside Britain, being known from Morocco (Duffin and Sigogneau-Russell 1993) and Sweden (JR, pers. obs.). Fragmentary teeth probably referable to *E. basanus* are also found in Germany (Ansorge 1990) and Spain (Soler-Gijón and Poyato-Ariza 1995). '*H.*' *ensis*, in contrast, is unknown outside southern England. Like *E. basanus*, *P. parvidens* is known from sites across Europe in Germany (recorded by Ansorge 1990 as *Lissodus rugianus*), France (Hervat and Hervat 1993) and Sweden (JR, pers. obs.). Teeth of very similar morphology to *P. parvidens* are also present in the Aptian and Albian of Texas (Thurmond 1971; Welton and Farish 1993).

Smaller hybodonts tend to be more restricted in both their stratigraphical and geographical distribution, with most species being known from a single stratigraphical level and geographical area, with few species being common to the Purbeck and Wealden groups. However, the presence of *P. rugianus* at several other sites across northern Europe, such as northern Germany (Ansorge 1990) and southern Sweden (JR, pers. obs.) indicates that this is partly due to lack of study.

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### EXPLANATION OF PLATE 1

Figs 1, 4, 8-9. *Polyacrodus parvidens* (Woodward, 1916). 1, 4, P.65434; Bed DB239, juvenile tooth: 1, labial, and 4, lingual views; x 45. 8-9, P. 65433; Bed DB181, lateral tooth: 8, labial, and 9, lingual views; x 24.

Figs 2-3, 5-6. *Egertonodus basanus* (Egerton, 1845). 2-3, P. 65431; Bed DB239, antero-lateral tooth: 2, lingual, and 3, labial views; x 8. 5-6. P. 65432; Bed DB239, anterior tooth: 5, lingual, and 6, labial views; x 8.

Figs 7, 10-12. *Polyacrodus rugianus* (Ansorge, 1990). 7, 10, P. 65435; Bed DB189, lateral tooth: 7, labial, and 10, lingual views; x 35. 11-12, P. 65436; Bed DB239, anterior tooth: 11, labial, and 12, lingual views; x 27.

All specimens from the Durlston Formation, Durlston Bay, Dorset.

### EXPLANATION OF PLATE 2

Figs 1-3, 6-8, 13-15. *Lonchidion inflexum* sp. nov. 1-3, P. 65437; Bed DB239; holotype; anterolateral tooth-crown: 1, labial, 2, occlusal, and 3, lingual views. 6-8, P. 65438; Bed DB181; paratype; anterior tooth-crown: 6, lingual, 7, occlusal, and 8, labial views. 13-15, P. 65439; Bed DB239; paratype; lateral tooth-crown: 13, labial, 14, lingual and, 15, occlusal views. All specimens from the Durlston Formation, Durlston Bay, Dorset. All x 45.

Figs 4-5, 9-12. *Lonchidion crenulatum* (Patterson, 1966). 4-5, 9, P. 65440; Sampled No 1, Durlston Formation, Lulworth Cove, Dorset; lateral tooth: 4, lingual, 5, labial and, 6, occlusal views. 10-12, P. 65441; Bed DB239, Durlston Formation, Durlston Bay, Dorset; anterior tooth-crown: 10, labial, 11, occlusal and, 12, lingual views. All x 45.

#### EXPLANATION OF PLATE 3

Figs 1-11. *Belemnobatis variabilis* sp. nov. 1-3, 11, P. 65443; paratype; lateral female tooth: 1, occlusal, 2, lateral, 3, labial and 11, basal views. 4-6, 10. P. 65442; holotype; anterior (male?) tooth: 4, lateral, 5, occlusal, 6, labial and 10, basal views. 7-9, P. 65445; paratype; symphyseal? tooth: 7, occlusal, 8, lateral and, 9, labial views. All specimens from Bed DB181, Durlston Formation, Durlston Bay, Dorset; x 60.

#### EXPLANATION OF PLATE 4

Figs 1-4. *Belemnobatis variabilis* sp. nov. 1-2, P. 65444; paratype; lateral male tooth: 1, labial and, 2, occlusal views. 3-4, P. 65446; juvenile female tooth: 3, occlusal and, 4, labial views; x 60.

Figs 5-12. Rhinobatoidei indet. 5-8, P. 65447; male? tooth: 5, basal, 6, lateral, 7, labial and, 8, occlusal views. 9-12, P. 65448; female? tooth: 9, lateral, 10, basal, 11, occlusal and, 12, labial views; x 50.

All specimens from Bed DB181, Durlston Formation, Durlston Bay, Dorset.

TEXT-FIG 1. Locality map showing Durlston Bay, Lulworth Cove and Stair Hole. Striped areas indicate the distribution of the Purbeck Group.

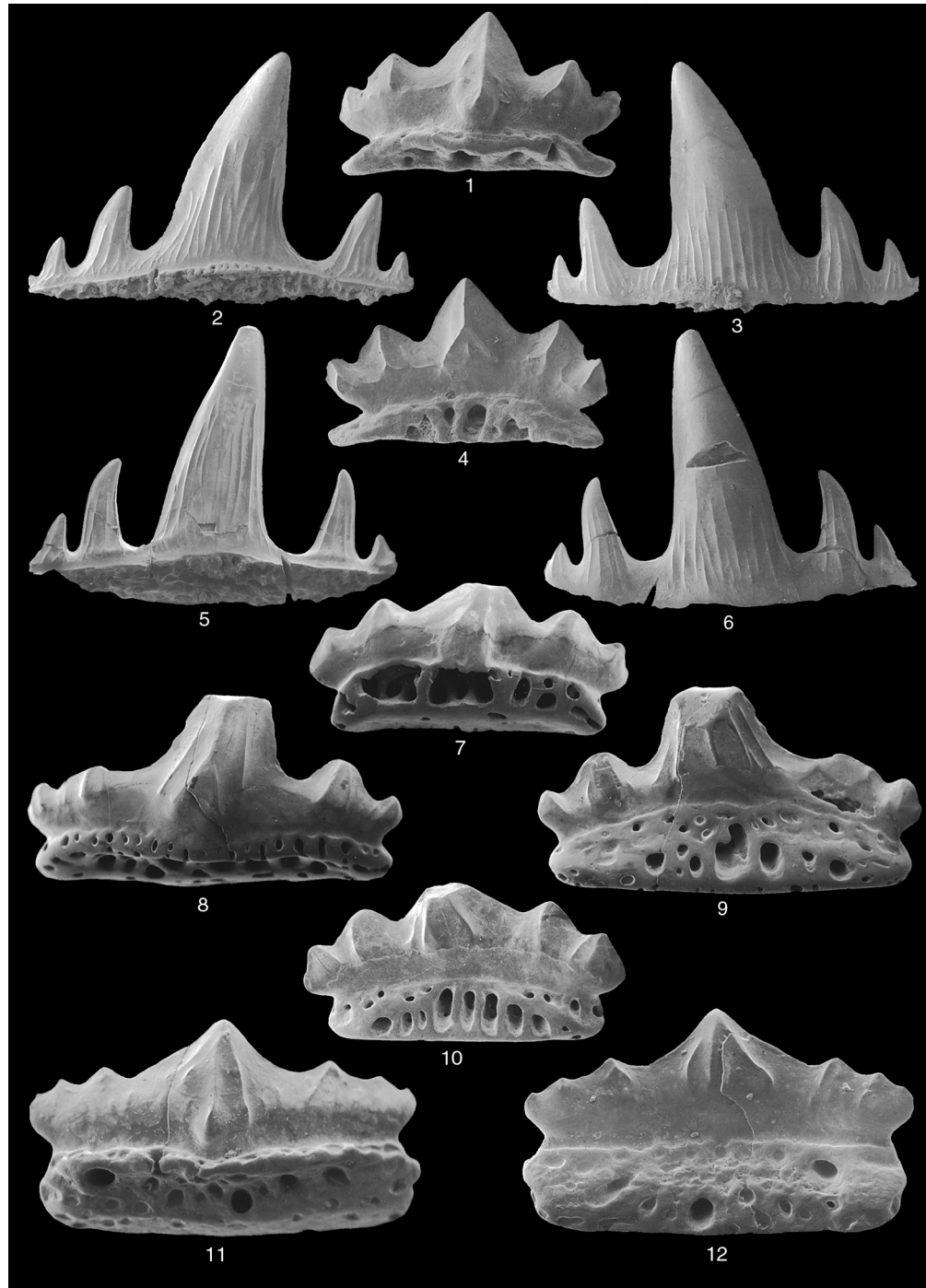
TEXT-FIG 2. Distribution of vertebrate remains in the Purbeck succession at Durlston Bay. The log is based on Clements (1992). Abbreviations: B.S.L., Broken Shell Limestone; Fw., Freshwater.

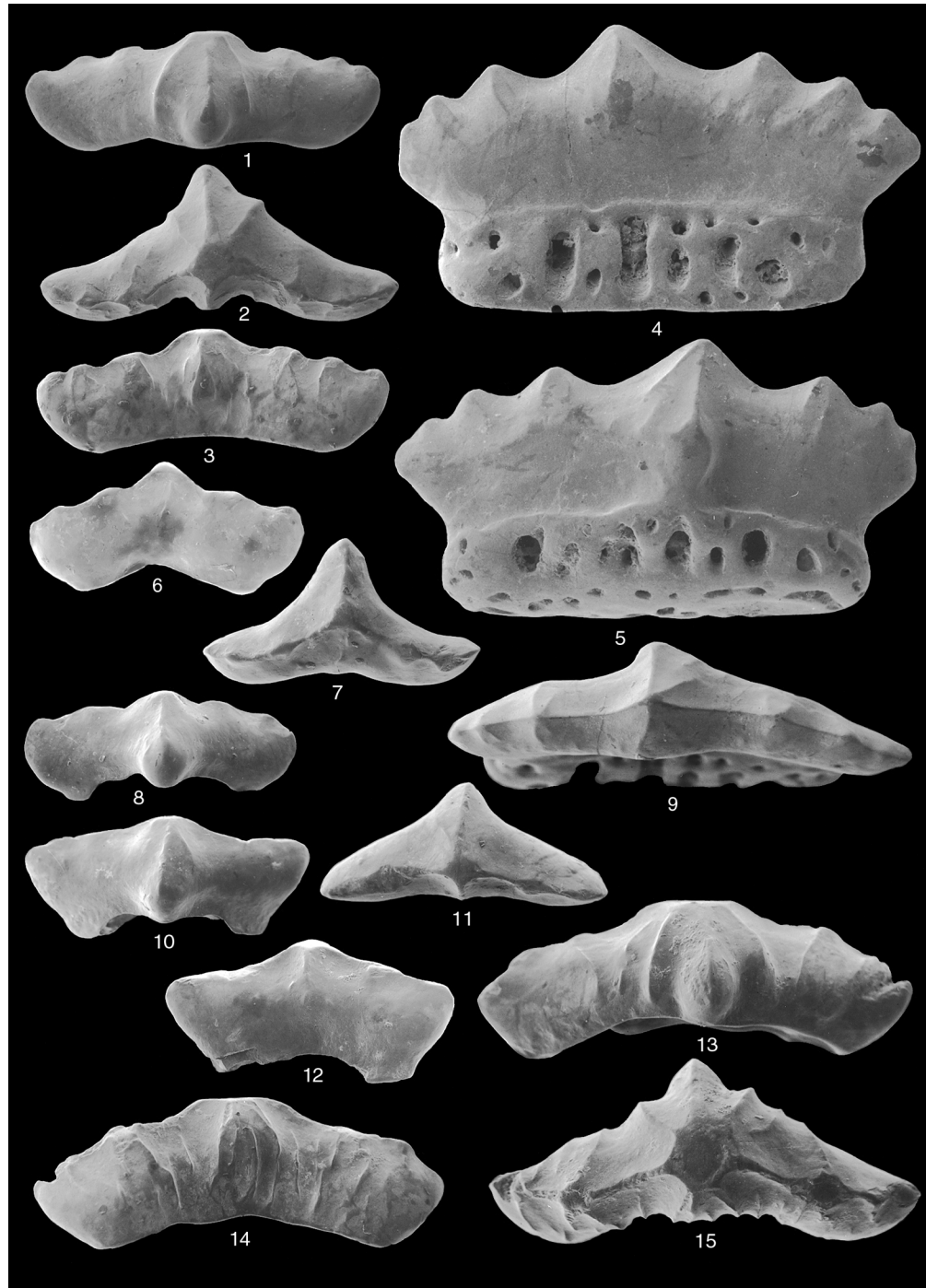
TEXT-FIG 3. Distribution of vertebrate remains in the Purbeck of Lulworth Cove and Stair Hole. The logs were measured by CJU in January 1999. Correlation is based on lithological and faunal characteristics. This differs from the correlation of Westhead and Mather (1996). Abbreviations: C.B., Cinder Bed; Fw., Freshwater; Lst., Limestone.

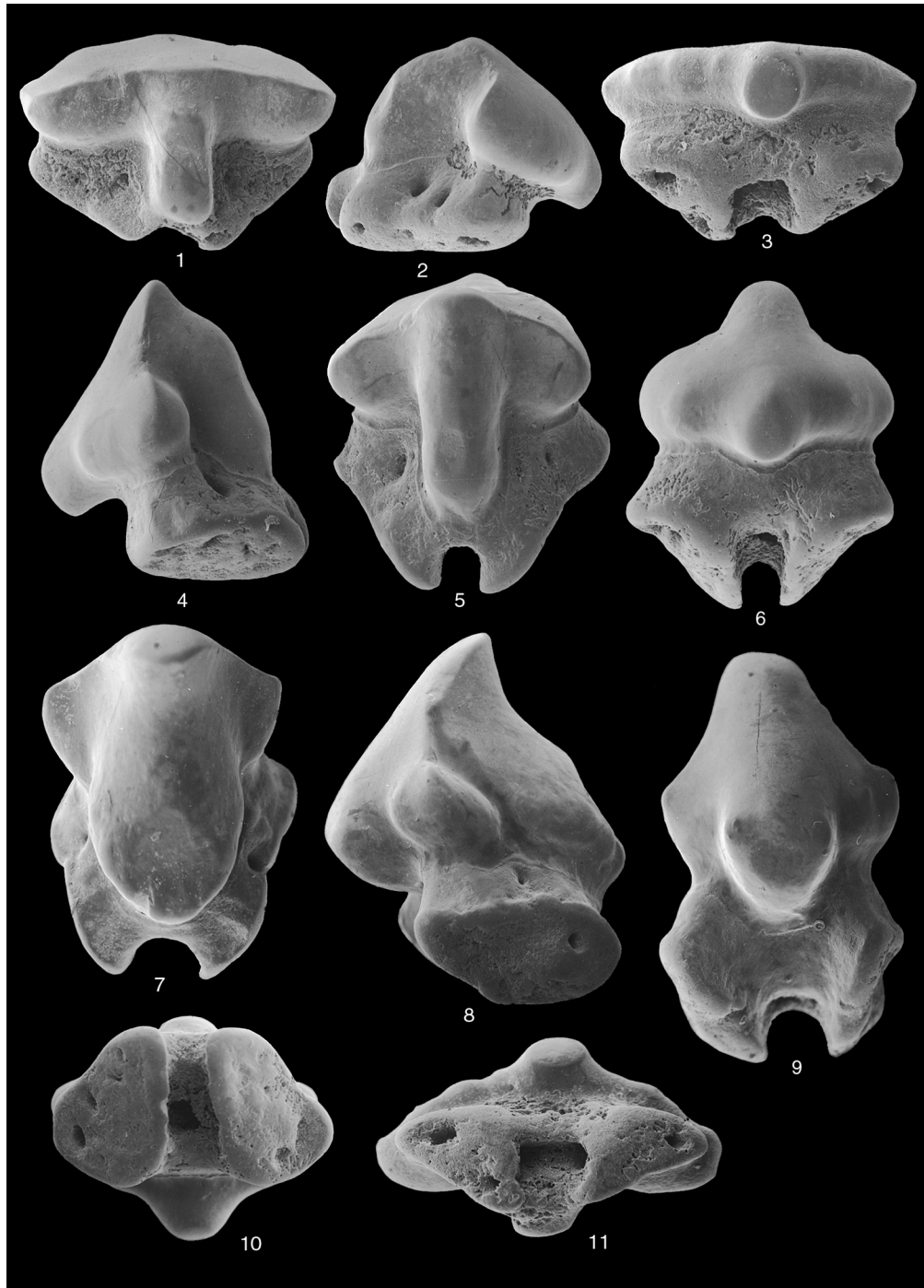
TEXT-FIG 4. Drawings of teeth of '*Hybodus*' *ensis* (Woodward, 1916). A, D, P. 65428; Bed DB189, Durlston Formation, Durlston Bay, Dorset; incomplete tooth-

crown: A, lingual and, B, labial views. B-C, P. 65429; Bed DB223, Durlston Formation, Durlston Bay, Dorset; incomplete tooth-crown: B, lingual and, C, labial views. E-F, P. 65430; surface collected from somewhere within the top 5 m of the Purbeck Group at Stair Hole; incomplete tooth-crown: E, lingual and F, labial views. All x 6.

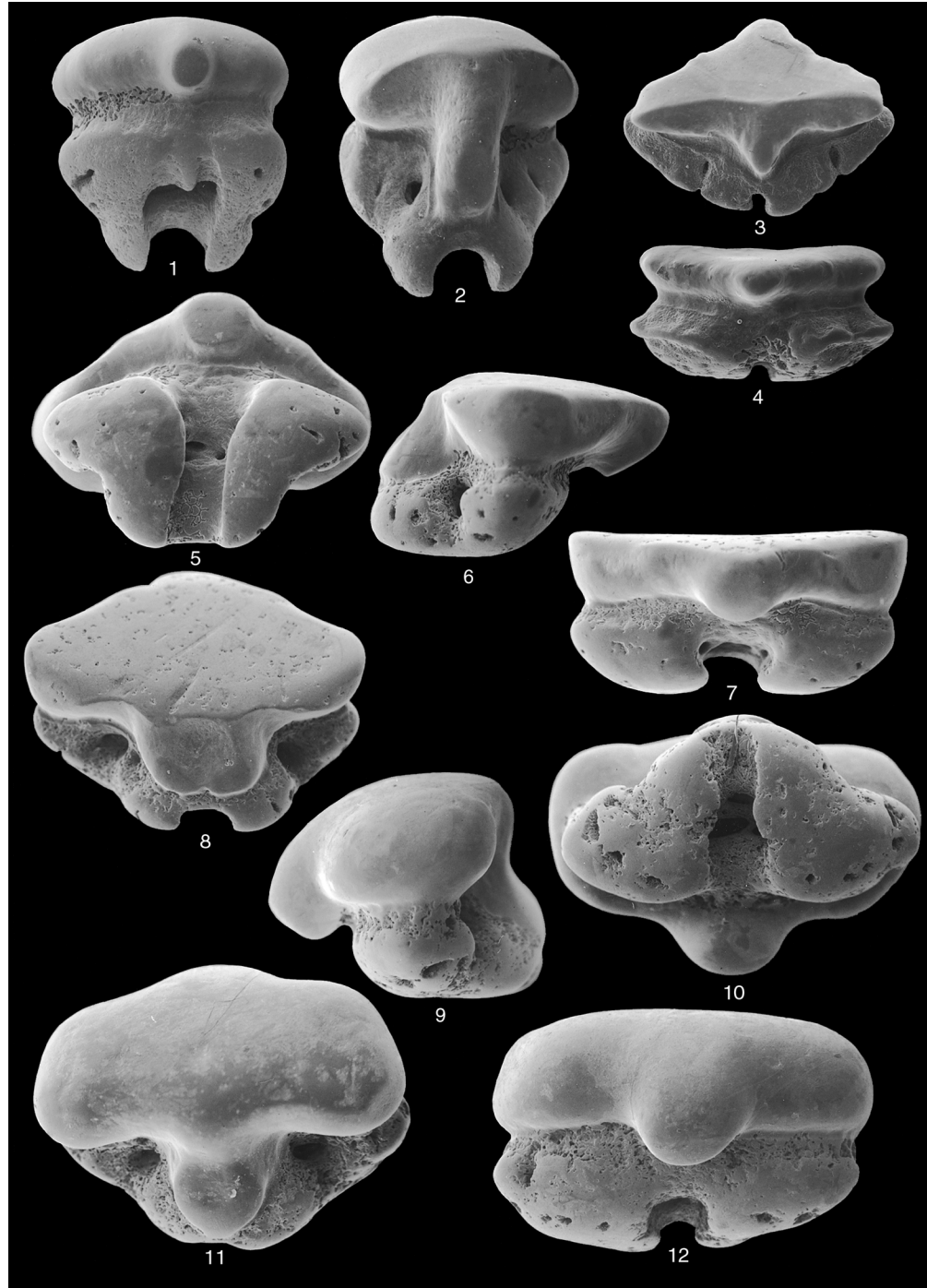
TEXT-FIG 5. Variations in the serrations of the cutting edges in '*Hybodus*' *ensis* (Woodward, 1916). A-C, P. 65430; surface collected from somewhere within the top 5 m of the Purbeck Group at Stair Hole; incomplete tooth-crown: A, C, details of the midpart of the cusp, x 14, B, detail of the area where the cusp meets the toothbase, x 35.

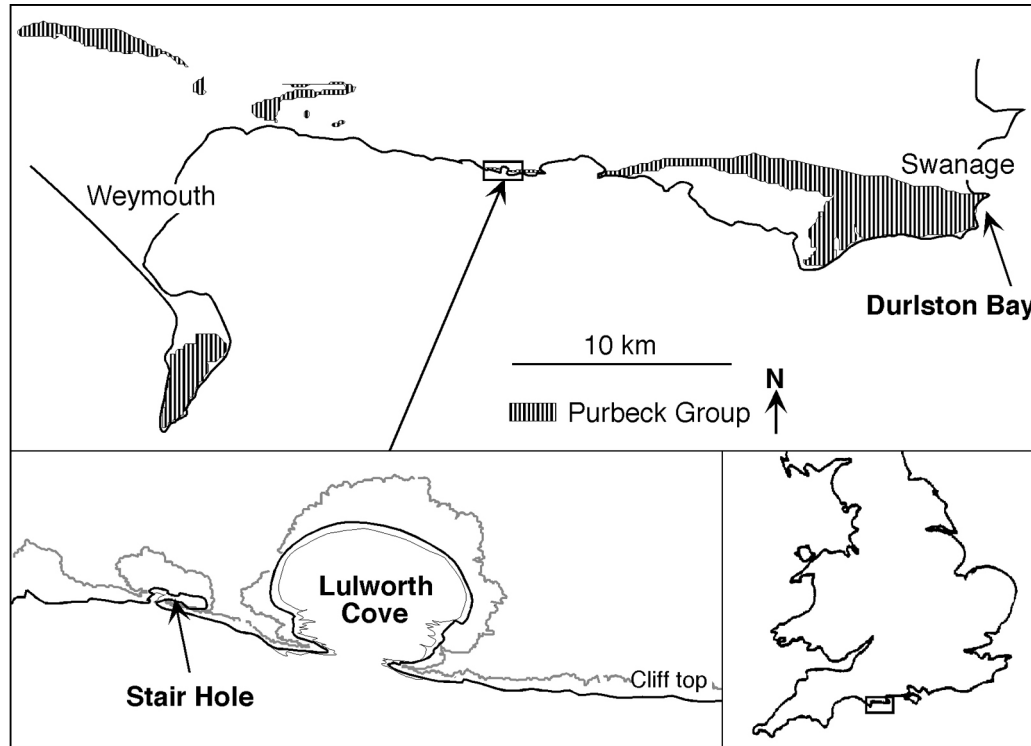


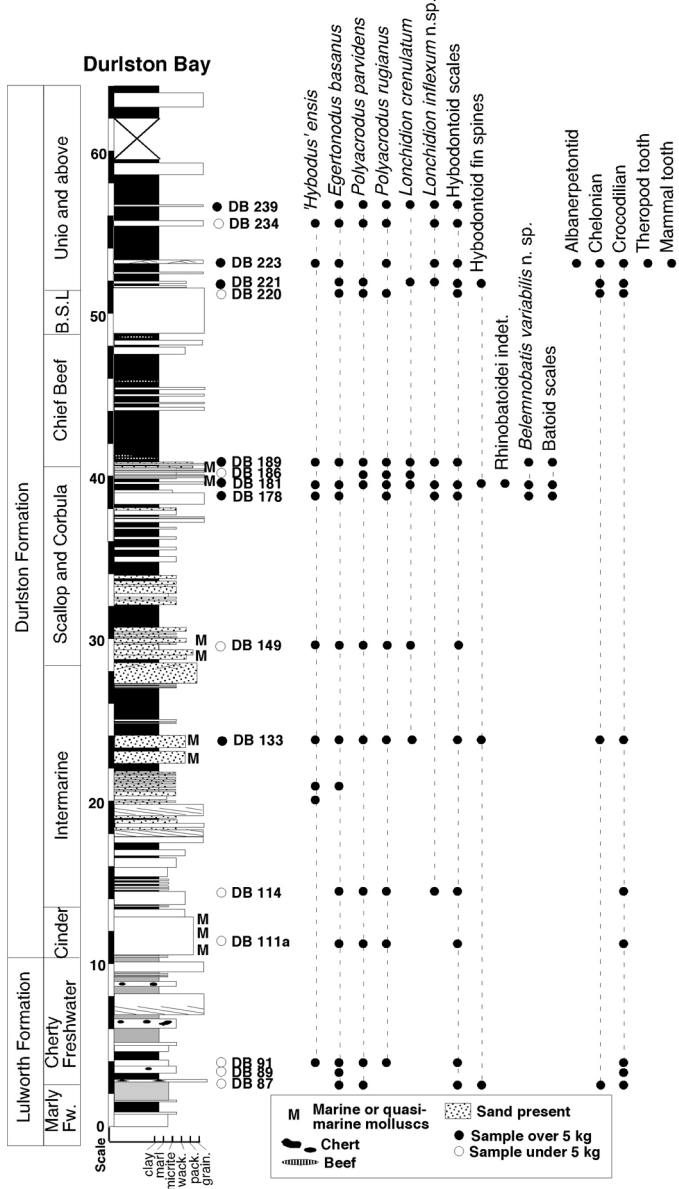




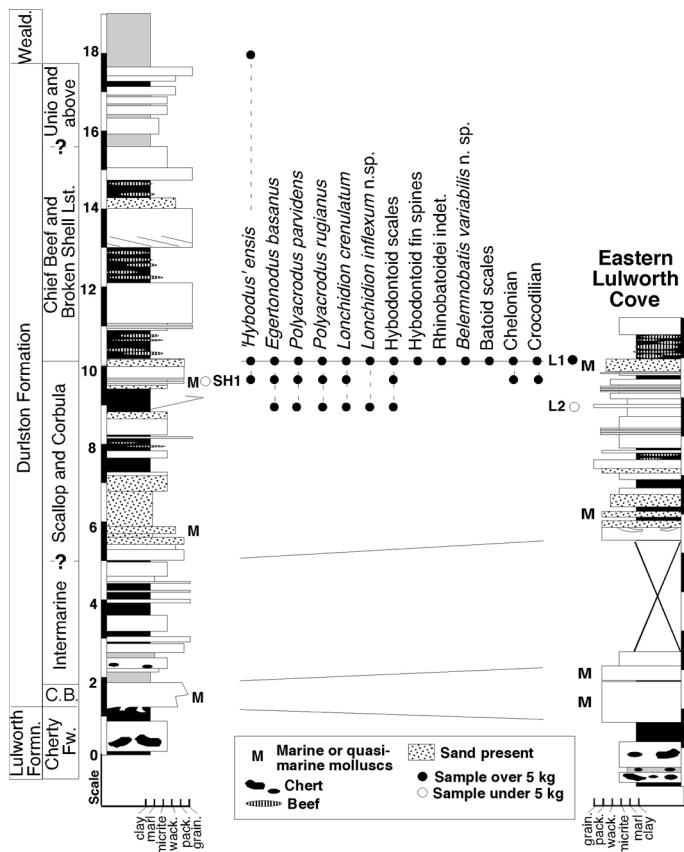


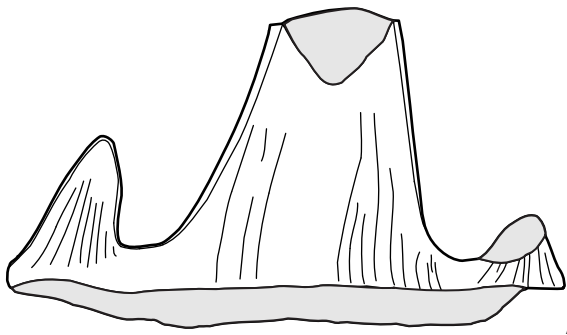




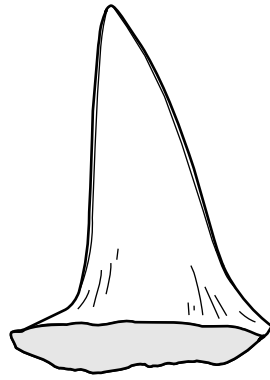


### Central Stair Hole

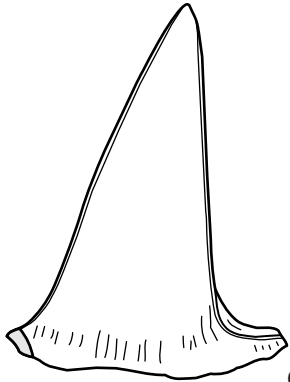




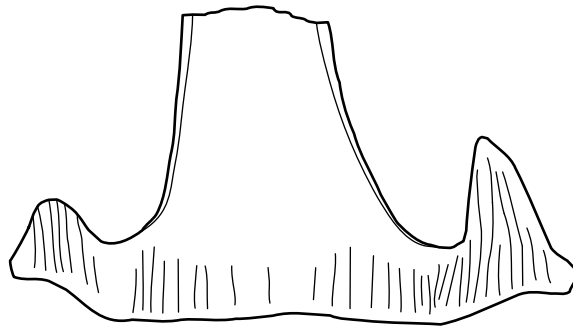
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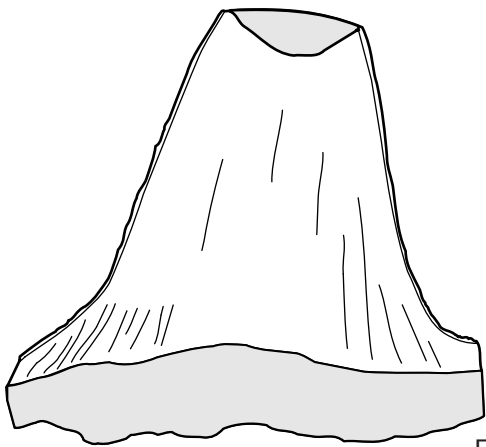
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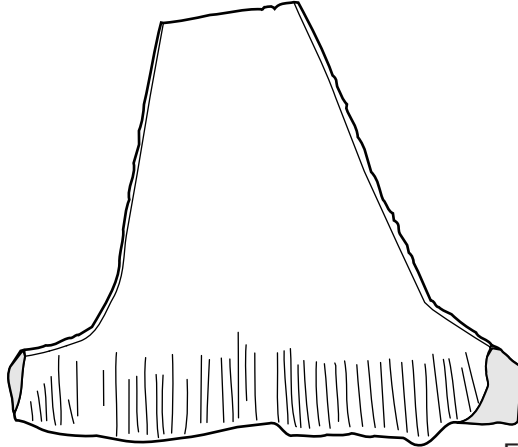
C



D



E



F

