# BONE-BEDS: A REVIEW OF THEIR CLASSIFICATION, OCCURRENCE, GENESIS, DIAGENESIS, GEOCHEMISTRY, PALAEOECOLOGY, WEATHERING, AND MICROBIOTAS

by

David D. J. Antia

## Summary

The term *bone-bed* is redefined to include only deposits containing more than 18% phosphatic material. Such deposits are divided into three major groups (a) Lithobonebeds, (b) Biobonebeds, and (c) Pelbonebeds, on the composition of their phosphatic clasts.

The concept of bone-bed prefossilisation is critically examined and some bone-beds previously considered to be prefossilised deposits, for example the West German Muschelkalk Grenzbonebed, deemed to be primary bone-bed deposits.

A review of bone-beds from Europe and America, of Silurian to Modern age forms the main section of this paper and includes models for their formation. Vertebrate mortality and decomposition and subsequent weathering and diagenesis are all considered.

New data regarding the environments, geochemistry, sedimentology and palaeontology of the British Ludlow-Downton, German Beyrichiankalk (Upper Downton), Irish Carboniferous (Tournasian), German Triassic (Muschelkalk, Lettenkeuper), British Rhaetic, Miocene/Pleistocene, and Holocene bone-beds is included.

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## 1 - Introduction

Since 1236 bone-beds of all ages (Ordovician - Recent) have been described from rocks of many countries, but there is no single account of them. Furthermore there is no single definition of bone-beds used by all authors and no attempt has been made to compare and contrast these accumulations of bone, teeth, scales and other remains of fish, reptiles and vertebrates. This article begins with a definition of phosphorites - a group of deposits, which include bone-beds, and indicates a scheme for the classification of phosphorites and bone-beds.

The accumulation and subsequent history of modern vertebrate deposits is then outlined and followed by a review of some Silurian to Pliocene bone-beds. A comparison is made between the recent and fossil bone-beds and conclusions are drawn regarding the palaeoecology, syndepositional weathering and microbiotas of the fossil layers.

## 2 - Previous use of the term bone-bed

Invariably rocks termed bone-beds contain "abundant" fish scales, teeth, bones, coprolites, phosphatic concretions and nodules, phosphatic moulds and casts of shells, and phosphatic invertebrate exo-, or endo-, skeletons. Some of these deposits can contain conodonts, crustacea, calcareous shells, pebbles, quartz, heavy minerals, feldspar, clays, glauconite and calcite. Locally within a bone-bed any one clast type may dominate (See Reif, 1969; 1971).

The term bone-bed was originally applied to a recent marine deposit rich in vertebrate remains (Lyell 1834) and later to the English Rhaetic bone-bed which was described as "being composed of fragments of teeth and bones in an extraordinary manner" (Roberts, 1839, p.20). Later, Murchison (1852) termed the earlier described (Murchison, 1837, 1839) Ludlow Fish Bed, the Ludlow Bone-Bed. Page (1859, p.93) cited both the Ludlow and Rhaetic Bone-Beds as examples of bone-beds, defined as "A term applied to several thin strata or layers containing innumerable fragments of fossil bones, scales, teeth coprolites and other organic debris". This definition has been accepted by Howell (1957, p.35), while Challinor (1967,p.29) considers a bone-bed to be "a bed of rock composed of fossil bones, teeth etc., of vertebrates" (also Murawski, 1972). More recently (Reif, 1976) defined bone-beds as "sediments which are enriched in highly fractured and abraded vertebrate bones. Very often the bone fraction is well-sorted with grain sizes of fine to coarse gravel. Bone-beds appear abruptly in sections which are otherwise poor in vertebrate remains; as a rule they have high lateral persistence (up to 50,000 km$^2$) and a thickness of several mm up to 20 cm; often they form series of 2 to 20 layers within one section".

None of these definitions of the term bone-bed are satisfactory as they do not define precisely what a bone-bed is, i.e. how much vertebrate material is required to call a deposit a bone-bed. The current definitions have been even further confused by the interchangeable useage of the terms bone-bed and fish-bed which are regarded as synonymous by Howell (1957, p.109).

In this study it is proposed that the term bone-bed should not be applied to zones or layers of bone-bed material but only to a single layer of vertebrate rich sediment. A group of bone-beds should be called bone-bed facies (e.g. Allen, 1974a, p.126, Facies A).

Some authors (e.g. Reif, 1976) believe that a bone-bed should be traceable over a wide area (up to 50,000 km$^2$). However, some named bone-beds only occur with certainty in their type sections, e.g. the Temeside Bone-Bed and the Downton Bone-Bed of the Welsh Borders (Elles & Slater, 1906). It is therefore suggested that the term 'bone-bed' be applicable to deposits found either in only one locality or proved to occur over a wide area.

The term bone-bed should have no genetic connotations since different bone-beds were formed under different conditions (see Section 6) and there is general disagreement as to how some bone-beds formed.

Recent studies of four well established bone-beds -the Ludlow Bone-Bed, the British Rhaetic (Sykes, 1977) and West German Rhaetic Bone-Beds, (Reif, 1969) and that of the West German Muschelkalk (Reif, 1969) have shown (Table 1) that all these deposits contain at least 4.7% phosphatic material. This suggests that a lower limit of 4.5% phosphatic material can be used in the redefinition of the term bone-bed.

Table 1. Quartz and phosphate compositions of Bone-Beds (values gives as weight percents).

| Bone-Bed | Quartz | Phosphate | Source |
|---|---|---|---|
| Ludlow Bone-Bed | 0.001 - 71 | 5 - 85 | Antia (Unpub.) |
| Muschelkalk Grenzbonebed | 11.5 - 69 | 18 - 40 | Reif, 1969 |
| British Rhaetic | 13.5 - 48.7 | 4.74 - 33.7 | Sykes, 1977 |
| German Rhaetic | 18.9 - 55 | 6 - 35 | Reif, 1969 |

With this percentage of phosphate, bone-beds fall within the general definition of phosphorites containing apatite as a dominant constituent (Cressman & Swanson, 1964, p.307) i.e. $P_2O_4 = 2 - 24^{+}\%$ (Swanson, 1973, p.786). Common usage of the term phosphorite includes vertebrate rich deposits, phosphatic shell and phosphatic nodular or peletal deposits, though a survey of the literature indicates a trend to restrict phosphorite to the latter type of deposit, except for the purpose of commercial exploitation. Since all three kinds of deposits merge into each other this study will define the parameters of the phosphatic deposits outlined.

## 2.1 Phosphatic deposits

Definition - "A phosphatic deposit is a rock or sediment containing more than 4.5% by weight of apatite". These deposits may be broadly classified with respect to apatite abundance on a three point graph (text-fig. 1a), and further subdivided on the basis of their dominant phosphatic clast (text-fig. 1b):

1. Phosphatic concretions, nodules, pellets and coprolites - Phosphorites
2. Phosphatic invertebrate shells - Phosphatic shell beds
3. Vertebrate bones, teeth and scales - Vertebrate beds

### 2.1.1. Phosphorites

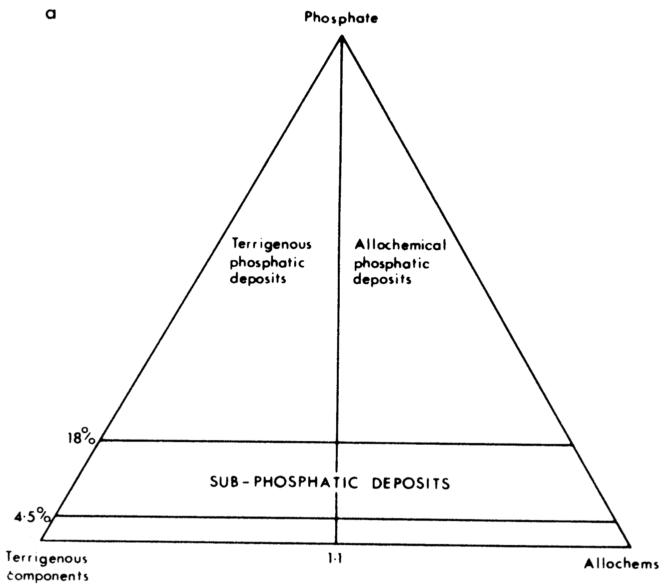
Definition - "A phosphorite is a phosphatic deposit in which the phosphatic component contains less than 30% vertebrate material; and a ratio of phosphatic pebble to phosphatic invertebrate shell, greater than 1:1 i.e. $1{:}1 \rightarrow \infty{:}1$".

Classification - Such deposits may be subdivided on the basis of their invertebrate and vertebrate compositions (text-fig. 1b), and/or, on their pebble components. Phosphorite deposits containing less than 19.5% $P_2O_5$ are commonly termed sub-phosphorites (Swanson, 1970).

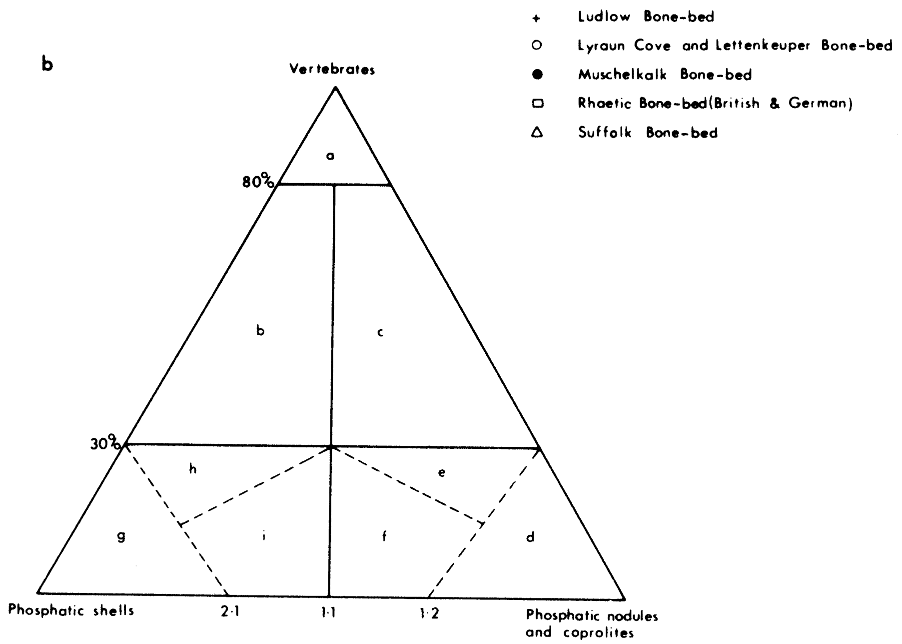
Example - The phosphorites of the Permian Phosphoria Formation of the central U.S.A. (Sheldon, 1963; Cressman & Swanson, 1964).

Note: These deposits include those made entirely of faecal pellets, e.g. guano.

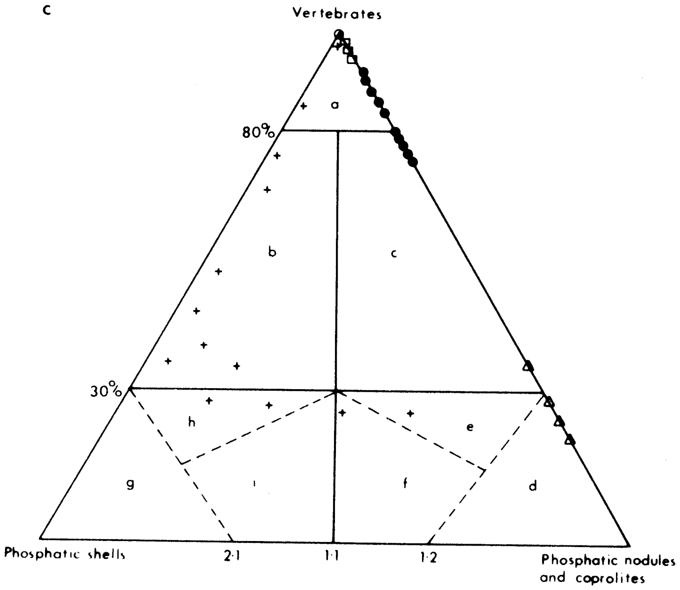
a



b



c



Text-fig.1a - Component graph for the recognition of phosphatic deposits.

Text-fig.1b - Classification of phosphatic debris deposits

a = Lithobonebeds
b = Phosphatic shell bone-bed (Biobonebed)
c = Phosphatic nodule bone-bed (Pelbonebed)
d = Phosphorite
e = Vertebrate rich phosphorite
f = Phosphatic shell rich phosphorite
g = Phosphatic shell bed
h = Vertebrate rich phosphatic shell bed
i = Phosphatic nodule enriched phosphatic shell bed

Text-fig.1c - Classification of bone-beds
Key to bone-bed classifications (a - i) given in 1b.

### 2.1.2. Phosphatic shell beds

Definition - "A phosphatic shell bed contains less than 30% vertebrate material and a ratio of phosphatic shells to phosphatic pebbles of greater than 1:1 i.e. 1:1 → ∞:1." Such deposits can be subdivided on the basis of their phosphatic components (text-fig. 1b).

Examples - Layers F69 and F68 of the (Permian) Franson Tongue of the Park City Formation (Central, U.S.A.) and the basal *Orbiculoidea* layer of the Mede Park Member of the Phosphoria Formation (Permian - Central U.S.A.). (McKelvey *et al.*, 1959; Branson, 1916; Yochelson, 1968).

### 2.1.3. Vertebrate Beds

Definition - "A vertebrate bed is a phosphatic deposit in which the phosphatic component contains ≥ 30% vertebrate debris".

Classification - Vertebrate Beds can be divided into two types of deposits, those made of whole articulated vertebrates, and, deposits made of disarticulated vertebrate remains. It is suggested that the former deposits be named after their dominant constituent member, i.e. Fish beds refer to rocks made up of whole articulated fishes. (pl. 14, fig. a). The term bone-bed should be applied only to the latter kind of deposit, thus a bone-bed may be defined as a single layer or lens of a vertebrate rich deposit (containing ≥ 4.5% phosphatic material of which ≥ 30% is fragmented and/or disarticulated vertebrate material).

### 2.2. Bone-bed classification

Two attempts to classify bone-beds have been made. The first (Reif, 1969; 1971) divided Triassic bone-beds into deposits which had been diagenetically altered (prefossilised) prior to accumulation in the bone-bed and deposits in which the vertebrate fragments had not been diagenetically altered prior to accumulation and concentration in the bone-bed. These two groups were each subdivided on the basis of their matrix into calcareous, marly, sandy-clayey and sandy bone-beds.

The second attempt (Sykes 1977) to classify bone-beds, this time of Rhaetian age, discussed the possibility of dividing them into primary and secondary deposits but came to the conclusion that all bone-beds showed some secondary characteristics. The four groups of Sykes' classification are:

1. Part primary bone-beds - recognised by the random orientation of the fossils, lack of bedding, lack of abrasion of fossils.
2. Secondary bone-beds - recognised by well developed bedded layers, wear on the clasts and aligned fossils.
3. Scatter bone-beds - recognised as mudstones containing evenly distributed, disseminated vertebrate material, but variable in geographical extent.
4. Trace bone-beds - recognised as thin, often single layers, of grains and patches of vertebrate material.

Both classifications are primarily genetic with superimposed secondary sedimentological criteria. That of Reif is inadequate, mainly because it does not consider the variability or density of phosphatic debris in a bone-bed. Sykes' classification fails because in a low energy environment with minimal current activity a secondary deposit would contain those characters attributed to a primary deposit. Conversely, in a high energy environment secondary characteristics can be superimposed upon a mainly primary deposit.

In this article a classificatory scheme is outlined which acknowledges that the vertebrate component of a bone-bed is variable as are the proportions of allochems, matrix and clasts.

An initial classification (text-fig. 1b) can be based on the bone-beds phosphatic component, dividing them into three groups: (a) Lithobonebeds, (b) Biobonebeds, (c) Pelbonebeds. Those bone-beds containing between 4.5 and 18% apatite should be described as Sub-lithobonebeds, Sub-biobonebeds and Sub-pelbonebeds.

Table 2. General bone-bed terminology.

| BONE - BED | | | |
|---|---|---|---|
| Mud supported sediment | | Grain supported sediment | |
| Less than 10 grains | More than 10 grains | | |
| Floatstone | Wackestone | Grainstone | Terminology |
| Lyraun Cove Bone-Bed | Muschelkalk Grenzbonebed | Ludlow Bone-Bed | Examples |

Bone-beds can be further subdivided on the basis of matrix and clast to produce a descriptive terminology (Table 2) and may be secondarily subdivided into:

1. Carbonate bone-beds
   (a) Micritic bone-beds are those containing a matrix which contains more than 50% lime mud.
   (b) Sparitic bone-beds are those containing more than 50% calcite (or dolomite) spar cement in the matrix.
2. Non-Carbonate bone-beds
   (a) Clayey bone-beds are those in which clay forms a dominant component of the matrix.
   (b) Carbonaceous bone-beds are those in which carbon is a dominant constituent in a clay matrix i.e.>10% volatiles.
   (c) Limonitic (or haematitic) bone-beds are those in which limonite (or haematite) is the dominant cement.

Many bone-beds contain pebbles, quartz sand, glauconite, pyrite, calcareous shells, trace fossils, sedimentary structures, heavy minerals, etc. These features should be included in an individual bone-beds description.

Examples of the different types of bone-beds are given in text-fig. 1c.

## 3 - Prefossilisation

Some authors (e.g. Reif, 1971; 1974; 1976; Duffin & Gazdzicki, 1977) have suggested that many bone-beds are prefossilised deposits. The concept of prefossilisation suggests that the vertebrate material under consideration has been buried after death of the animal and diagenetically altered (phosphatised) at a low Eh and normal to alkali pH's in the sediment prior to its exhumation and concentration into a bone-bed (Reif, 1971; 1976).

Reif (1969, p. 71; 1971, p.390) suggested four ways by which prefossilised vertebrate material may be recognised.

1. Fracture patterns of bone fragments
   (a) Recent bones show a predominantly fibrous breakage surfaces.
   (b) Sub-fossilised bones never have fibrous breakage surfaces and are easily worn down during sedimentation.
   (c) Fossil bones when broken have smooth breakage surfaces.

On the basis of these observations Reif (1971) suggested that the presence of smooth breakage surfaces and rounding on the bone fragments in a bone-bed indicates that they have been reworked from an earlier sediment, after they had been fossilised, before being concentrated to form a bone-bed.

2. Size distribution of quartz and vertebrate material.

Secondly, Reif (1971) suggested that while recent bone debris is less dense than quartz, fossil bone is as dense or even denser than quartz (Table 3). Therefore, if quartz and bone fragments are found together and the maximum values of their size distributions lie at the same point, then it follows that their densities must have been approximately the same during the formation of the deposit and the bone material must be prefossilised.

3. The third criterion for prefossilisation is the presence of high polish on the grains surface.

4. The phosphatisation of bone reduces its inherent elasticity and suggested that fossil bones are less likely to be well rounded.

Table 3. Quartz, Apatite, Bone, Fossil Bone and Collophane densities.
(After Dana, 1858: Rogers, 1922; 1924; Deer *et al.*, 1962)

| Quartz | Recent Bone | Fossil Bone | Collophane | Apatite |
|---|---|---|---|---|
| 2.5 - 2.8 | 1.9 - 2.0 | 2.6 - 2.94 | 2.6 - 2.92 | 3.1 - 3.35 |

These criteria are all very subjective and provide no real test of whether or not a fossil vertebrate fragment has been prefossilised or not, because:

1. Observed smooth fracture patterns may be a result of processing fossilised material, and since studies on fracture patterns have not been done on scales or teeth (the dominant components of many bone-beds) the value of fracture pattern studies must still be in doubt. Similarly, Schafer (1972) has noted that unaltered fish scales in recent sediments are often worn or rounded.

2. Application of the equivalence principal suggests that clasts of similar densities will have similar size distributions. However, Reif's application of the theory forgets (a) that many bone-bed sediments contain no quartz grains (even locally in the Muschelkalk Grenzbonebed, his type example of a prefossilised bone-bed), (b) vertebrate material (unaltered) present in many modern sediments possess the same size modal peaks as quartz grains in the same sediment (Schafer, 1972). This observation may result because clay infilling pores in the vertebrate material may help to increase its density, or because of the differing aerodynamic properties of rounded quartz grains and vertebrate fragments, or because of diagensis (see Section 8).

3. Grain polish is by itself a dubious criterion, since many marine carbonate grains show a high polish, due to either abrasive high energy current activity or to diagenetic mineral coatings on the exterior of the grain (Farrow, pers. com. 1978). Broken surfaces of polished *Acrodus lateralis*, a shark's tooth from the Muschelkalk Grenzbonebed, *Thelodus parvidens*, a fish scale from the Ludlow Bone-Bed, and whale bones from the Suffolk Bone-Bed, are characteristically dull; thus suggesting that the polish is an exterior property of the vertebrate material and may result from abrasive or diagenetic processes.

4. The elasticity of vertebrate material is thought to decrease with increasing prefossilisation. Yet supposedly prefossilised (Reif, 1969; 1971; 1974; 1976; pers. com. 1976; 1977) specimens of *Acrodus lateralis* from the Muschelkalk Grenzbonebed occur in a variety of abrasive states ranging from well rounded worn spheres to angular broken fragments to whole teeth. This surely suggests that the inherent elasticity (i.e. ability to round with wear) of the grains has not been markedly affected by prefossilisation.

Reif (1971) regards the vertebrate material from both the Muschelkalk Grenzbonebed and the Rhaetic Bone-Bed to be made of francolite (a fluoro-carbonate-apatite). Modern bones and teeth are made of a microcrystalline arrangement of hydroxy-apatite in collagen (Glimcher and Krane, 1968). Thus alteration of the bones and teeth has presumably occurred such that:

$$\underset{\text{hydroxy-apatite}}{Ca_5(PO_4)_3OH} + \text{collagen} \rightarrow \underset{\text{francolite}}{(Ca_3F)_2(P,C)_6(O,OH\ F)_{24}(Ca,C)_4} .$$

This reaction doubtless reflects the combined effects of initial and subsequent diagenesis on the vertebrate remains, if they have been prefossilised.

Reif (1976; pers. com. 1976; 1977) also regards the Upper Silurian Ludlow Bone-Bed as a prefossilised deposit. If this is so, then a geochemical proof may be forthcoming. The thelodont fish species (*Thelodus parvidens*), which dominates the vertebrate faunas of the Ludlow Bone-Bed and the sediments immediately above and below the bone-bed, occurs in two geochemical states.

1. In the bone-bed the thelodonts tend to be made of a fluorapatite and have a polished orange-yellowy appearance (Table 4, col.6).
2. In the sediments below the bone-bed the thelodonts tend to be made of a carbonate apatite and have a white chalky appearance (Table 4, col.4).

Though both geochemical thelodont forms occur in sediments representing aerobic conditions, Burnett (1977) has shown that aerobic sediment surfaces are found above anoxic microenvironments a few centimeters below the sediment/water interface. The thelodont scales present in low densities in the sediments below the bone-bed were possibly excavated by currents after they had been altered to a carbonate apatite in a subsurface anoxic environment prior to concentration in a bone-bed (cf. Antia & Whitaker, 1978). The alteration to fluorapatite would therefore be a result of diagenesis after bone-bed deposition.

If this prefossilisation model is correct then there could be a difference in the abrasive appearance of the scales occurring in the two sediment types, and the geochemical composition of the phosphatic clasts in the bone-bed ought not to be related to the matrix of the bone-beds.

1. Abrasive features

   The thelodont scales from the two sediment types though differing in chemical composition show no difference in abrasive features. In both instances the scales vary from unworn forms to partly worn forms to very well worn and rounded forms. Many of the more rounded scales are bored. These observations suggest that scales deposited in both environments were abraded on the sediment surface.

Table 4. Dry X-ray powder diffraction (X.R.D.) analysis results for
(1) Carbonate apatite (after Smith *et al.*, 1974)
(2) A phosphatic pebble from the Ludlow Bone-Bed
(3) '*Serpulites*' *longissimus*, *Orbiculoidea rugata*, *Lingula* sp.
(4) Thelodont fish (*Thelodus parvidens*).
Both (3) and (4) represent samples collected from the Upper Whitcliffe sediments of Aston Munslow (Salop).
(5) Fluorapatite (after Smith *et al.*, 1974)
(6) *Thelodus parvidens*
(7) '*Serpulites*' *longissimus*, *Orbiculoidea rugata* and *Lingula* sp.
Both (6) and (7) were obtained from the Ludlow Bone-Bed at Aston Munslow.

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|
| 2.78 | 2.78 | 2.79 | 2.79 | 2.80 | 2.79 | 2.80 |
| 2.68 | 2.68 | 2.69 | 2.69 | 2.70 | 2.70 | 2.70 |
| 3.46 | - | 3.43 | 3.46 | 2.77 | 2.78 | 2.76 |
| 2.23 | 2.23 | 2.24 | 2.25 | 3.44 | 3.44 | 3.43 |
| 1.93 | 1.92 | 1.93 | 1.93 | 2.62 | 2.62 | 2.61 |
| 1.84 | 1.83 | 1.83 | 1.83 | 1.84 | 1.83 | 1.85 |
| 3.04 | 3.03 | 3.05 | 3.04 | 1.94 | 1.92 | 1.93 |
| 2.62 | 2.61 | 2.62 | 2.62 | - | - | - |

Table 5. The chemical composition of the clasts of the phosphatic components in the Ludlow Bone-Bed (Upper Silurian).
F = fluorapatite; C = carbonate apatite;
(F) = some fluorapatite present.
Localities are located on text-fig.4, p.114.

| Locality | Phosphatic component | | Sediment | | |
|---|---|---|---|---|---|
| | Thelodont | Invertebrate | Lime-stone | Mud-silt | Sand |
| Usk | C | C | - | - | + |
| Longhope | F | C | - | + | - |
| Priors Frome | F | C | - | + | - |
| Rushall | C | C | - | - | + |
| Kington | F | F | + | - | - |
| Downton | F | F | + | - | - |
| Deepwood | F | C | - | + | - |
| Ashely Moor | F | F | + | - | - |
| Ludford | F | F | + | - | - |
| Siefton | F | - | - | + | - |
| Corfton | F | F | + | - | - |
| Aston Munslow | F | F | + | - | - |
| Shipton | F | C(F) | - | + | - |
| Brockton | F | C | - | + | - |
| Netherton | F | C | - | + | - |
| Lye | C | C | - | - | + |

2. Relationship of phosphatic clast to matrix.

In the bone-bed three types of phosphatic clasts occur, carbonate apatite pebbles (Table 4, col. 2), thelodonts and other fish remains, and phosphatic invertebrate remains (pl. 14, figs. b,c) of *'Serpulites' longissimus*, *Orbiculoidea rugata*, and *Lingula* sp. Below the bone-bed the latter two remains tend to be made of a carbonate apatite (Table 4, col. 3 and 4) while in the bone-bed they occur in both a carbonate apatite (Table 5) and a fluorapatite state (Table 4, col. 6 and 7; Table 5).

Examination of the chemical composition of the two main clast types (Table 5) suggest that the clast composition is related to the nature of the matrix of the bone-bed such that:

(a) Calcareous bone-beds only have fluorapatite (phosphatic) biological clasts.

(b) Muddy and silty bone-beds have fluorapatite fish remains and carbonate apatite phosphatic shell debris.

(c) Porous poorly cemented quartz sand bone-beds contain only carbonate apatite phosphatic clasts.

This apparent relationship between chemical composition and matrix type suggests that the chemical composition of the vertebrate and invertebrate remains may be a result of post depositional diagensis, and could indicate that the scales were not prefossilised prior to inclusion in the bone-bed.

This conclusion is borne out by the presence of borings on the fish scales and not on the invertebrate fragments in the bone-beds, where both have the same chemical composition. Since the borings are specific to the thelodonts, it must be assumed there were nutritional or chemical differences between the two clast types. If this assumption is correct then it is likely that the scales were unaltered when bored, i.e. were composed of a hydroxy apatite + collagen with an enamel-like coating on their crown (Beevers & McIntyre, 1946) or carbonate apatite + collagen (Osmond & Swain, 1959). Study of boring density and distribution on the scales suggests that the crown has fewer borings than the cusp of the thelodont denticles, thus adding support to this hypothesis. The vertebrate clasts in other bone-beds show no such relationship between clast composition and sediment (Table 6).

Table 6. Geochemical composition of bone-beds

| Bone-Bed | Chemistry | | Sediment | | |
|---|---|---|---|---|---|
| | fluorapatite | francolite | black clay | carbonate | sand |
| Lyraun Cove | + | - | + | - | - |
| Rhaetic (British) | - | + | + | - | - |
| Rhaetic (German) | - | + | - | - | + |
| Muschelkalk | - | + | + | + | + |
| Lettenkeuper | - | + | + | - | - |
| Suffolk | + | + | - | - | + |

These observations suggest that the chemical composition of the phosphatic clasts in prefossilised bone-beds are not markedly affected by diagenesis in the sediment of the bone-beds, while in primary bone-beds (i.e. bone-beds which are not produced by the reworking of older sediment) there may be a marked relationship between clast composition and sediment type.

Since marine prefossilised bone-beds exist and are actively being formed, (i.e. bone-beds containing diagenetically altered vertebrate material) see Reid (1890), Baturin (1970) Frey *et al.* (1975), the chemical processes which could lead to the prefossilisation of vertebrate material will be considered here.

1. The environments of prefossilisation, - 3.1
2. Conditions favourable to prefossilisation, - 3.2
3. A geochemical model for prefossilisation, - 3.3

Reif (1976) and Baturin (1970) have noted that prefossilisation involves the phosphatisation of bones (considered to be made of a hydroxy apatite (Glimcher & Krane, 1968 ) and teeth (considered to be made of either a carbonate apatite (Osmond & Swain, 1959) or a hydroxy apatite (Beevers & McIntyre, 1946)). This phosphatisation involves the replacement of collagen and existing apatites with fluorapatites thus increasing their densities without altering their internal structures (Paine 1937). Since they are replacing an amorphous structure, their densities will remain the same as that for collophane (Rogers, 1917; 1922; 1924) - see Table, 3, p. 99. Collophane is a term applied to any amorphous apatite (Deer *et al.*, 1962).

## 3.1 The environments of prefossilisation

Vertebrate remains are unlikely to be phosphatised by direct, ocean water - vertebrate reactions (Burnett, 1974), but could be altered by pore waters in a sediment. To date, only two regions of active phosphatisation are known, the Peru-Chilean shelf and the South West African Shelf seas. In both regions phosphatisation occurs within anoxic alkali sediment pore waters (Baturin, 1970; 1971; Burnett, 1977).

Actively forming phosphatised vertebrate concentrations may result from the erosion by marine and estuarine currents of older sediments (Miocene - Pleistocene) (e.g. the vertebrate concentrates of Georgia (U.S.A.) estuaries (Frey *et al.* 1975) and the Florida shelf (Burnett & Gomberg, 1977)), or recent ( ≥ 30,000 years) phosphatic shelf sediments (Baturin, 1969; 1970).

These limited studies have suggested that vertebrate phosphatisation may occur in the anoxic alkali pore waters of some sediments.

## 3.2 Conditions favourable to prefossilisation

There are four major characteristics of natural aqueous solutions which favour the prefossilisation of vertebrate remains in the pore waters of sediments.

1. High dissolved inorganic phosphate content.
2. High Ca/Mg ratio.
3. High pH.
4. Suitable nucleation sites.

Phosphates may be supplied to anoxic pore waters in sediments from the reduction of hydrous ferric oxides which bind phosphate to their surfaces under oxidising conditions (Stumm & Leckie, 1970) and the decomposition of phosphorous containing organic matter. The contribution from the decaying organic matter is the more significant (Burnett, 1974). If large quantities of vertebrate material are to be prefossilised by the pore waters of organic rich sediments, then the $PO_4^{3-}$ content of the interstitial fluids must be continually replenished, while the material is being prefossilised.

The precipitation of apatite is inhibited by $Mg^{2+}$ ions (Bachra *et al.*, 1965; Martens & Harriss, 1970). However, diagenetic reactions in anoxic pore waters can raise the Ca/Mg ratio to beyond that of the Ca/Mg threshold value (Broecker, 1974; Burnett, 1974) to allow apatite to precipitate. Many reactions in anoxic pore waters would have this effect, for example the replacement of $Fe^{3+}$ by $Mg^{2+}$ in clays (Drever, 1971).

For prefossilisation to occur a high pH is required (Krumbein & Garrels, 1952; Goldberg & Parker, 1960; Robertson, 1966; Pytkowicz & Kester, 1967), because at low pH's apatite is 'soluble'. Experiments have shown (Berner, 1969) that the decomposition of fish and molluscan organic matter is accompanied by a rise in pH, which results from the formation of $NH_4^+$ and other nitrogenous bases, and from the breakdown of proteins and other biochemical compounds, pH is also affected by other variables such as the release of $CO_2$ into the pore waters during the oxidation of organic materials.

However, an increase in pH favours $CaCO_3$ precipitation (Gulbrandsen, 1969) and as dissolved carbonate species in sea water are several orders of magnitude higher than the phosphate species, a coprecipitation of apatite and calcite would result in the apatite being completely overwhelmed by calcium carbonate. Therefore if apatite is to be precipitated with minimal calcite, the dissolved $PO_4^{3-}$ content of the pore waters would have to be raised to the point where $Ca^{2+}$ concentrations in the pore waters are controlled by apatite rather than carbonate equilibria.

Discussions on the availability of suitable sites for apatite growth suggest that calcite forms the best surface for apatite nucleation (Stumm & Morgan, 1970) as epitaxial overgrowths and catalyses the precipitation of apatite around specific nuclei (Stumm & Leckie, 1970). When calcite is absent from the sediment, siliceous skeletal debris, brachiopod shells, fish bones and scales, apatite and feldspar crystals appear to be favoured sites for authogenic apatite growth (Deer *et al.*, 1962; Stumm & Leckie, 1970; Burnett, 1977). Clasts already enriched in apatite are preferentially chosen for authogenic apatite growth and replacement (i.e. prefossilisation). (Konta, 1959).

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See Appendix - 2, p.168, for additional note.

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## 3.3. A geochemical model for bone-bed prefossilisation

The following is a general geochemical model which may represent the most likely combination of events which could result in the phosphatisation of vertebrate (and invertebrate) material by pore water solutions in sediment, prior to the newly phosphatised materials reworking and inclusion into a 'prefossilised' bone-bed deposit. Since both vertebrate, invertebrate and coprolitic material can be prefossilised (Reif, 1969; 1971· 1976; Duffin & Gazdzicki, 1977), the model will consider apatite precipitation.

During periods of increased sea water temperature inorganic apatite precipitation may take place within the anoxic pore waters of sediment (Burnett, 1974; 1977). Within about 15 cm of the sediment/water interface, the $PO_4^{3-}$ ion concentrations present in these anoxic pore waters can increase to about 1000 x those of the surrounding aerobic surface waters before precipitating around a suitable nucleation site. (Brooks *et al.*, 1968; D'Anglejan, 1968; Bray *et al.*, 1975; Sholkovitz, 1973.) Phosphatisation replaces the original nucleation site preserving its internal structure and including fluorine within its crystal lattices. (Paine, 1937; Kortnig, 1968; Reif, 1969; Antia & Whitaker, 1978.)

Apatite precipitation is initiated when the pore waters are supersaturated with respect to $PO_4^{3-}$ and undersaturated with respect to oxygen. Sustained periods of apatite precipitation require a constant supply of organic phosphorous to the pore waters, so consequently such a region must have a high biological productivity to provide a large input of organic phosphorous into the sediment. Inhibitory $Mg^{2+}$ ions would be removed by diagenetic reactions (Bachra *et al.*, 1965; Martens & Harriss, 1970) involving both the solid and fluid phases of the sediment.

General types of reactions likely to occur in the pore waters within the sediment during early diagenesis are summarised below:

1. $SO_4^{2-}$ + 'organic matter' $\rightarrow H_2S + HCO_3^- + HOP_4^{2-} + NH_4^+ + CH_4$
   The probable C:N:P: ratio based on that for modern plankton (Richards, 1965) is 106:16:1, and
2. $2Fe^{3+}$clay $+ 3Mg^{2+} + 4S \rightleftharpoons 3Mg^{2+}$clay $+ 2FeS_2$ (pyrite), and/or
3. $2CaCO_3$ M $+ Mg^{2+} \rightleftharpoons CaMg(CO_3)_2 + Ca^{2+}$, and/or
4. $Al_2Si_2O_5(OH)_4 + 5Mg^{2+} + 10HCO_3 + H_4SiO_4 \rightleftharpoons Mg_5Al_2Si_3O_{10}(OH)_8 + 10CO_2 + 3H_2O$, and
5. $5Ca^{2+} + 3HPO_4^{2-} + F^- \rightleftharpoons Ca_5(PO_4)_3F + 3H^+$ .

The resultant authogenic prefossilised particles may be concentrated into vertebrate rich deposits by changes in sea level dynamics (Baturin, 1971). Since during periods of regression the fine grained fraction of the sediment will be eroded away to concentrate the prefossilised material, initially into a coarse grained sediment and ultimately into a bone-bed. In this sort of situation electrical neutrality in the pore waters is probably maintained by counterbalancing the changes in $Ca^{2+}$ and $Mg^{2+}$ concentration, $NH_4^+$ production, and the change in $SO_4^{2-}$ content with a coincident rise in $HCO_3^-$ (Sayles, *et al.*, 1974). i.e.

$$\Delta Ca^{2+} + \Delta Mg^{2+} + NH_4^+ - \Delta SO_4^{2-} = \Delta HCO_3^-$$

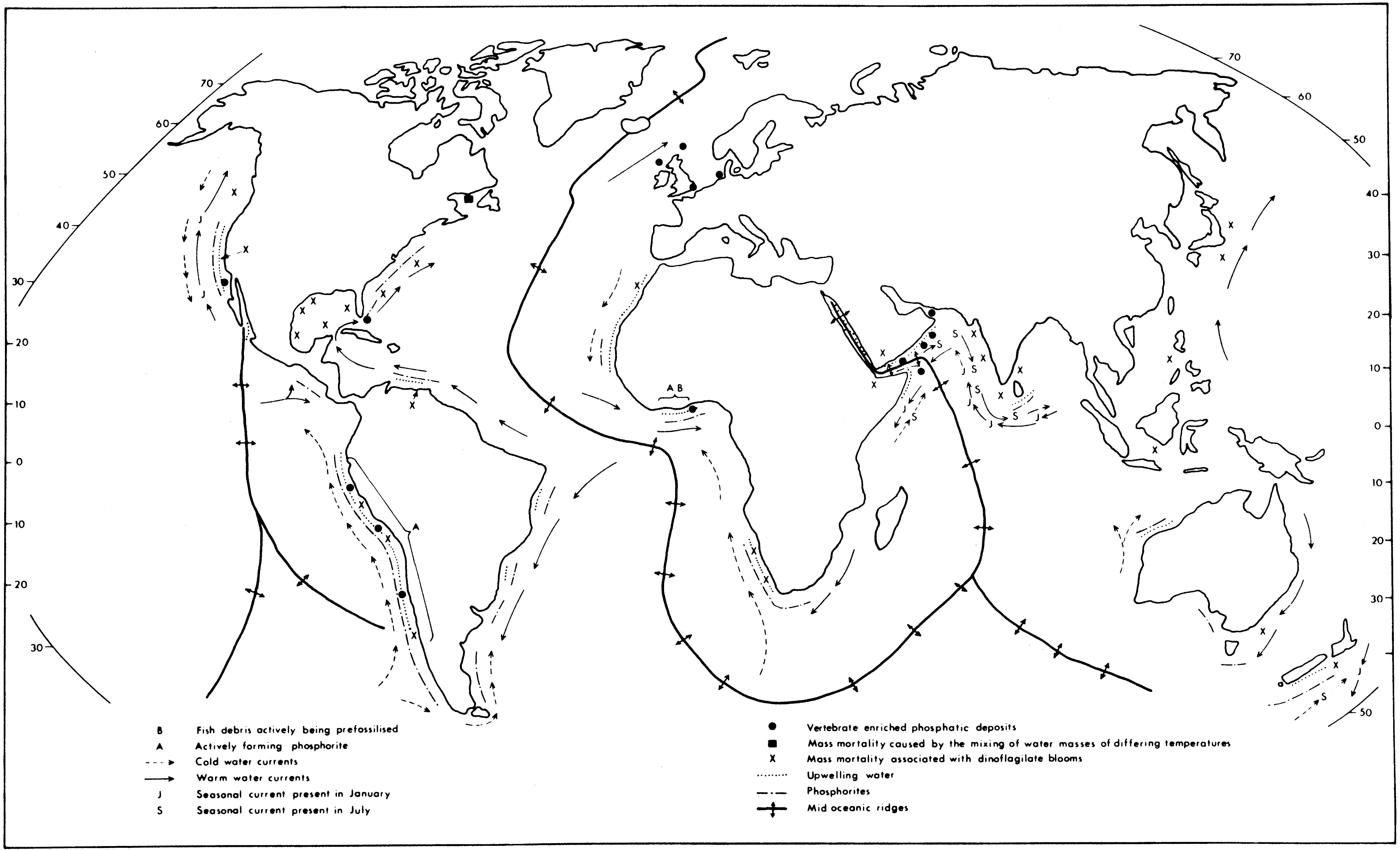
## 4 - On the occurrence and genesis of vertebrate rich deposits

Studied deposits rich in disarticulated vertebrate remains on the modern sea shelf commonly occur in association with coprolites, phosphatic nodules and phosphatic brachiopod shells. They almost all occur in areas of increased nutrient content of the water, and are commonly associated with regions of upwelling waters (McKelvey, 1967; also text-fig. 2). However, only two regions of vertebrate accumulation are regions of active sea bed phosphatisation today. These are off the Peru-Chile coast (Veeh *et al.*, 1973; Burnett, *et al.*, 1973; Burnett 1974: 1977; Manheim *et al.*, 1975; Burnett & Veeh, 1977) and the South West African coast (Baturin, 1969; Baturin *et al.*, 1972; Veeh *et al.*, 1974). Other phosphatic deposits found on the surface of the sea-floor (e.g. California coast, Florida coast, New Zealand Coast, South African coast, and Tasmanian coast) have been shown (Kolodny & Kaplan, 1970; Burnett & Gomberg, 1977 to be of Upper Pleistocene age.

In addition to the above phosphatic deposits unconfirmed reports exist of vertebrate sands off the U.K. notably near Rockall and Shetland. These deposits were noted by Lyell (1868: p.576, vol. 2; 3rd ed. 1834, vol. 3) as "A bed of fish bones (off Rockall).... extending for 2 miles along the bottom of the sea in 10 - 90 fathoms of water, at the eastern extremity .... of Rockall bank fish bones were met with .... Analogous formations are in progress in the submarine tracts extending from the Shetland Isles to the North of Ireland". At "(Lat.61° 51' Long. 6°30') Fish bones occur in extraordinary profusion .... this 'bone bed' .... is 3½ miles in length and 45 fathoms under water". More recent work by Dr. J.B. Wilson (pers. comm. 1977) has revealed very high concentrations of fish otoliths in the Rockall region.

### 4.1 Recent examples

Sediments on the S.W. African shelf and Peru - Chile shelves (text-fig. 2) consist of black muds formed at depths between 150 and 50 m. The surface waters of these regions are very rich in diatom phytoplankton, and are biologically very productive, because upwelling coastal waters bring up nutrient salts (Bakun 1978; Savidge & Foster 1978). The upwelling waters result in a massive phytoplankton production on the shelf, and consequently a large biogenic input into the underlying sediment (50 - 150 m depth). The low $O_2$ content of these waters allows much of the biogenic material to be input into the sediment (Baturin, 1971). This sediment becomes enriched (Baturin, 1969; 1971) in organic carbon (5-20%) and phosphorous (0.1 - 1%). In the sediments the P:C ratio varies from 1:25 to 1:60, whereas living diatoms have a ratio of 1:25 (Lisitsyn, 1969).



Text-fig.2. Map showing the distribution of oceanic currents, areas of mass mortality, regions of upwelling and vertebrate accumulation at the present time. Compiled after David (1944; 1947); Brongersama-Sanders (1956); McKelvey (1967) and the Times Atlas of the World (1974).

Both areas have alkaline reducing pore waters (Table 7) enriched in phosphorous, in which the phosphorous content of the pore waters increases with depth below the sediment/ water interface (Burnett, 1977).

Table 7. Composition of pore waters in regions of phosphatisation on shelf seas

| Locality | Eh | pH | Source |
|---|---|---|---|
| California | -200mv | 7.2 - 7.8 | D'Anglejan, 1967 |
| West Africa | -300mv | 7.2 - 8.0 | Baturin, 1969; 1971 |
| Peru/Chile | - | 6 - 7 | Burnett, 1974; 1971 |

On both the Chilean and African shelves phosphorous oversaturation of the interstitial waters leads to its precipitation in separate microzones within the sediment (i.e., where the microenvironment is most alkaline) (Baturin, 1969; 1971; Burnett, 1974; 1977). In the Peruvian shelf this microzone is situated at 15 cm below the sediment/water interface (Burnett, 1977). This precipitation induces a decrease of phosphorous concentration in the pore waters of far below 0.1 $mg.l^{-1}$ and its redistribution in the sediments results in either the formation (Baturin, 1969; 1970; 1971) of scattered soft nodules consisting of an impure gel-like calcium phosphate (5 - 10 $P_2O_5$) or nucleation around and/or replacement of biogenic tissue, e.g. bones, scales, teeth, shells, etc. (Konta, 1956; D'Anglejan, 1967; Baturin, 1970; 1971; Burnett, 1977).

The process surrounding the phosphatic replacement of biogenic material is poorly understood, but may relate to the much better known sequences of phosphatisation of the gel-like phosphatic nodules in the sediment, many of which contain 'densely packed' fish debris (Baturin, 1971).

Further diagenetic processes result in the lithification of the nodules, depletion in $SiO_2$, $Al_2O_3$, Fe, $H_2O$ and C as shown in Table 8 and enrichment in $P_2O_5$, CaO, $CO_2$ and F; there is also an increase in trace elements such as uranium, gold, and vanadium (Yasgrev, 1971; Burnett, 1974). The end product of these changes is very similar to those resulting in the formation of the phosphatic nodules in the Muschelkalk Grenzbonebed (Table 8).

Table 8. The composition of stages in the phosphatisation of mud to produce a phosphatic nodule (after Baturin, 1969; 1971). Note the similarity of the composition of the hard nodule to that of a phosphatic nodule (?coprolite) from the Muschelkalk Grenzbonebed (Reif 1971).

| Stage | $P_2O_5$ | CaO | $CO_2$ | F | $SiO_2$ | $Al_2O_3$ | $Fe_2O_3$ | MgO | Organic C |
|---|---|---|---|---|---|---|---|---|---|
| 1. Diatomaceous mud | 0.62 | 3.0 | 2.43 | Tr. | 50 | - | 1.0 | - | 5.35 |
| 2. Phosphatised D. mud | 5.10 | 6.9 | 1.17 | 0.3 | 49.18 | 2.0 | 1.24 | 2.5 | 3.4 |
| 3. Soft nodules | 23.85 | 35.9 | 5.30 | 2.45 | 14.80 | 0.45 | 0.80 | 1.7 | 1.8 |
| 4. Friable nodules | 27.70 | 42.27 | 5.34 | 2.70 | 4.87 | 0.38 | 1.00 | 1.3 | 1.0 |
| 5. Hard nodules | 32.74 | 46.42 | 6.33 | 3.02 | 0.15 | 0.04 | 0.20 | 1.7 | 0.9 |
| 6. Nodule Muschelkalk Grenzbonebed | 31.50 | 50.1 | 4.81 | - | 0.42 | - | 1.44 | 0.5 | - |

Chemical analyses of bone and fossil bone show that during diagensis vertebrate fragments become enriched in $P_2O_5$, CaO, $CO_2$ and F (Rogers, 1924; Baturin, 1970; Reif, 1971) and the trace elements gold, titanium, vanadium and uranium (Yasgrev & Nikitin, 1970; Yasgrev, 1971). The net similarity in the enrichment of phosphatic nodules and bone noted here suggests that similar chemical reactions take place concurrently during diagensis in the two types of material (Baturin, 1970).

These recent deposits contain about 7% phosphate material (Baturin, 1971), reworking of these deposits caused by changes in sea level dynamics could produce remanee ('prefossilised') deposits containing more than 20% phosphatic material, such as those on the Peru - Chile shelves (Burnett, 1974).

Many actively forming vertebrate and phosphate rich deposits are formed by the reworking of older sediments. Such deposits can be concentrated on either an aerobic (Burnett Gomberg, 1977) or anaerobic benthos (Frey *et al.*, 1975). Examples of the former include the Florida phosphorites, produced by the active erosion of Pliocene limestones, and those of California which may still be actively forming, but are most likely derived from slightly earlier sediments. On the Trinidad shelf these deposits are found strewn over the surface of a hard ground (Kolewijn, 1958). Another example of the latter kind of deposit are the vertebrate assemblages of the Georgia Estuaries (Western U.S.A.) produced by the active erosion of vertebrate rich Miocene and Pleistocene beds.

Vertebrate accumulations of diagenetically unaltered fish material have been recorded in the Arabian Sea, Red Sea and Persian Gulf (Stubbings, 1939), (text-fig. 2), and off the Californian coast (David, 1944; 1947). Fish bones have been recorded from the Black Sea (Andrussow, 1893; Murray, 1900; Archangnelski, 1927), and in association with coprolites near the mouth of the River Congo. High densities of the boney plates of teliost fish have been recorded (Schafer, 1966; 1972) on the swash marks on the intertidal mudflats of the Island of Mellum (West Germany). Here the fish debris has the same modal size distributions as the associated shell debris. These sediments contain up to 250 vertebra to a $m^2$ area of sediment. On the West German East Frisian Islands and the Island of Sylt (text-fig. 2) large fish fragments are found (Schafer, 1972) associated with coarse shell debris. On the mudflats, beaches which are exposed to a powerful swash contain vertebrate fragments which are markedly size sorted (Schafer, 1972). Similarly intertidal mudflat deposits situated on the Elbe & Wesser River mouths are enriched in worn and polished boney sturgeon plates. An extensive review of the occurrence of articulated fish on the benthos is given by Brongersama-Sanders (1949; 1957).

### 4.2. Models for the formation of marine bone-beds

Over the years a number of ideas relating to the formation of deposits of vertebrate remains have been found. These theories can be divided into two major groups.

1. Primary deposits - produced by the primary concentration of disarticulated vertebrate material.
2. Secondary deposits - produced by reworking and concentration from older sediments.

#### 4.2.1. Primary deposits

Two major groups of theories regarding the genesis of primary deposits exist. The first considers the deposit to have formed over a long period of time as a condensation deposit. The second considers the vertebrate material to have been deposited, disarticulated and concentrated shortly after a catastrophe to produce a bone-bed resulting from an initial mass mortality deposit.

### 4.2.1.1 Condensation deposits

These are deposits formed over a long period of time by the withholding of sediment from an area, or when fish were the dominant faunas of the seas (Orton, 1878; p.628). The concentration of the deposits could also be the result of the reworking of excrementations matter representing the hard indigestable parts of fishes, which have served as food for larger kinds. Thus the fragmentary and worn appearance of the vertebrate debris could be attributable to the crushing maceration and partial digestion which they have suffered. Such deposits may form in a nook or bay where large and small fish congregate (Newbery, 1889; p.30). Fourthly, acidic anoxic bottom conditions could dissolve calcareous invertebrate material, leaving a deposit rich in phosphatic animal tissue.

### 4.2.1.2 Mass mortality deposits

These deposits are formed over short periods of time by the mass mortality of vertebrate organisms and may result from:

1. An Act of God

   The best documented example of this kind of mass mortality is given in the Old Testament of the Bible (Exodus, ch. 6: v. 17-21). "... I am the Lord: behold ... the water that is in the Nile ... shall be turned to blood and the fish in the Nile shall die ... All the water that was in the Nile turned to blood and the fish in the Nile died". (R.S.V. Trans. 1973).

2. Cold waves

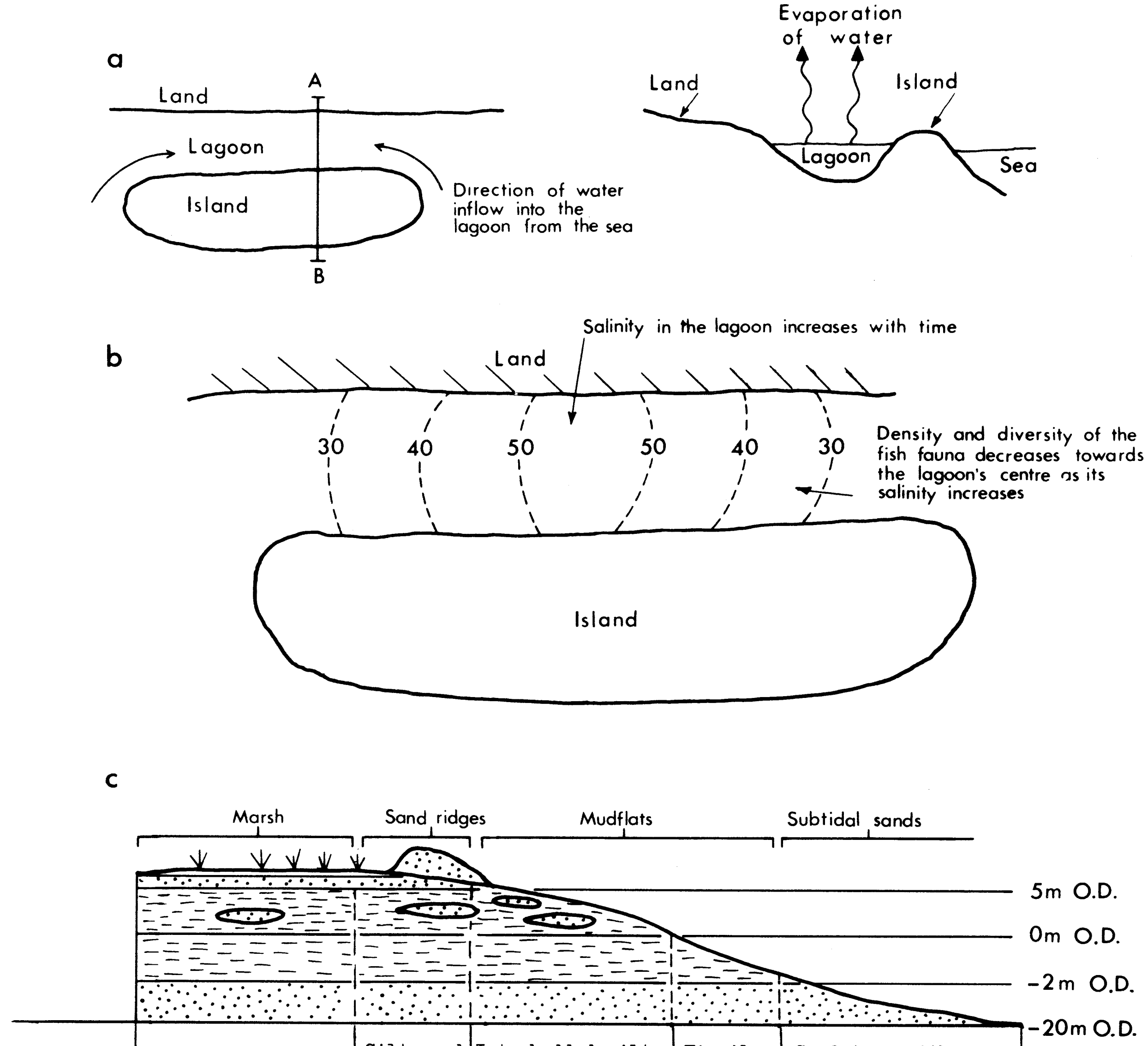
   In shallow waters, hard cold, sudden temperature drops can cause mass mortalities among fishes (Storey & Gudger, 1936; Gunter 1945, 1947). Such mass mortalities have been documented along the U.S. Gulf coast. Here a cold spell kills fishes every few years. Similar effects have been recorded (Storey, 1937; Gunter, 1947) along the west Florida coast and the Texas coast. These cold waves are less severe on the invertebrates, though they too are killed in the colder water (Gunter, 1941; Davis, 1963). The fish killed either sink to the bottom or are swept ashore (Gunter, 1947). In the Gulf Coast these deposits tend to be cyclic occurring every 6 - 14 years. The vertebrate fauna takes some three years to recover from one of these freezes (Gunter, 1945).

3. Oversalinity

   The salinities of restricted bays and coastal lagoons along the Texas coast increases drastically during dry years causing mass mortalities among fish (Gunter, 1947). These lagoons may cover some 1,400 km$^2$ and are separated from the sea by an island (text-fig. 3). In normal years the salinity of the lagoons gradually increases till the lagoon is barren of fish. Periodic hurricanes bring in a new influx of lower salinity salt water (normal marine) and allow the barren lagoon to be colonised by a new abundant fish fauna (Hildebrand, 1969).

4. Warm waves

   Some regions contain an abundant fish fauna living in a nutrient rich cold current of water near the cold currents junction with a warm current. Changes in the relative position of this junction can cause mass mortalities within the fish fauna. Examples of this kind of mass mortality have been recorded (Murphy, 1926; Mears, 1943) along the Peruvian coast, at the junction of the southward warm equatorial current and the cold northward coastal current (text-fig.2).



| | | | | | |
|---|---|---|---|---|---|
| Sediment | Mudstone | Silts and sandstone | Interbedded silts muds and sands | Fissile shales | Sandstone with phosphatic nodules |
| Structure | Dessication structures and calcareous nodules | | Symmetric ripples = 10 - 15 cm | | |
| Biogenic Structures | Rootlets | | | | Bioturbation |
| Fossils | Plants | | Rare brachiopods | Brachio-pods and crinoids | Brachiopods, fish plates, crinoids, bone fragments |

Text-fig. 3. A Gulf Coast lagoon (a) showing water flow direction;
(b) the resulting salinity concentration contours; note that salinity increases as a result of an osmotic process;
(c) distribution of environments through the Catsgill cylothem.

5. Plankton blooms

   Plankton blooms of dinoflagelates which produce toxic wastes may result in mass mortalities of fish, sometimes killing in excess of a milliard fish. These planktons often colour the sea water to give the so called red water effect. (Brongersama - Sanders, 1949; 1956).

6. Storms - water mass effect

   Mortality may be caused by the mixing of adjacent 'hot' and 'cold' water masses during storms to produce layers of fish many decimetres thick on the substrate over a wide area (Verril, 1882; Huntsman, 1917; Neville, 1967).

7. Storms - stranding effect

   During storms the vast shoals of fish which congregate in coastal tidal waters near the Elbe and Weser Estuaries are often injured by being thrown on to stones and sandbars or are stranded, others are cut off in narrow creeks and thrown on to the tidal flats. (Mohr, 1952)

8. Breakdown of the food chain

   Mass mortalities may result from a breakdown in the food chain due to nutrient shortages, etc. (Heldt *et. al.*, 1947).

9. Earthquakes

   Earthquakes may severely disorientate life in coastal waters causing some species to commit mass suicide (Forbes, 1858) or die (Brongersama - Sanders, 1956).

10. Vulcanicity

    Volcanic eruptions can cause mass mortalities in the sea, either by killing off the plankton (Jenkins, 1970) or by killing the fish (Brongersama - Sanders, 1956).

11. Geochemical changes in environment

    Changes in the geochemical nature of the environment are known to produce mass mortalities of fish (Brongersama - Sanders, 1956) e.g. decrease in the oxygen content of the water; increase in the amount of cyanide in the water, etc.

### 4.2.2. Secondary deposits

Before a vertebrate deposit can be termed a bone-bed its constituent vertebrates have to be disarticulated and swept around by currents, etc. The term 'Secondary Deposit' is used here to refer to a primary vertebrate deposit which has been buried, diagenetically altered, excavated, fragmented and then further concentrated to form a bone-bed.

Since secondary bone-beds are formed by the reworking of older vertebrate deposits, by tidal, oceanic or fluvial currents, little ecological information can be derived from these deposits in intertidal, fluvial or marine environments.

## 5 - The decomposition of marine vertebrates

(after Schafer, 1972)

Three major groups of vertebrates are represented in bone-beds throughout time; they are fish (Ordovician - Recent), reptiles (Triassic - Cretaceous) and mammals (Jurassic - Recent). The dominant components are fish with lesser proportions of reptiles and/or mammals (mainly mantae and ceteans). In order to more fully comprehend the formation of a primary bone-bed deposit it is necessary to have some understanding of the history of the vertebrates in the interval between their death and accumulation in a vertebrate sand or bone-bed, i.e. their decomposition.

Unfortunately little is known about the geological aspects of vertebrate decomposition. Virtually nothing is known about the decomposition of marine reptiles or mammals though their processes of decomposition may be similar.

1. Decomposition of whales - physical and mechanical effects:
   - (a) Death of the whale
   - (b) Animal sinks to sea-floor
   - (c) Floated off the sea-floor (not necessarily to the surface) by decomposition gases
   - (d) Carcass may drift for weeks
   - (e) Skin ruptures and the now loosely held skeletal parts fall to the ground from the floating carcass and may be spread over a very wide area
   - (f) If the whale dies in a restricted or partly enclosed basin less than 400 x 600 km in size, then it generally reaches a beach before it disintegrates. In this instance constant battering onto the shore and refloating aids the break up of the animal.

2. Decomposition of fishes - physical and mechanical effects:
   - (a) Death of fish
   - (b) Animal sinks to the sea-floor with its back directed downwards
   - (c) Within 12 hours of death decomposition gases accumulate in the abdomen
   - (d) 3-4 days after death the decomposition gases float the fish ventral side up off the sediment
   - (e) 4-6 days after death the skin ruptures and the carcasses sink to the bottom and disintegrate rapidly
   - (f) 15-20 days after death only the skeleton (inc. scales) is left and may be broken up and rolled by currents and waves

Vertebrate remains are absent from many sediments even though the surface waters of these regions abound in fish, e.g. the west coast of Scotland. This absence may be explained if vertebrate remains provide an important food source for detritivores and scavengers, or if they are removed from the region by high current activity into deeper waters. At present no data exists to support the latter hypothesis. It is, however, known that echinoids and carniverous invertebrates are fond of fish bones and rapidly consume them (Johansen, 1929; Wasmund, 1935; p.50).

These latter observations suggest that it is unlikely that vertebrate deposits would accumulate today on an aerobic substrate with a low sedimentation rate swept by weak currents. It is more likely that they will accumulate in areas of high sedimentation rates and high energy (e.g. a tidally swept area), areas of abnormal conditions (e.g. high salinity as in a Texas type lagoon) or areas possessing an anoxic substrate (e.g. areas below the oxygen minimum depth), because they are less likely to support vertebrate bone detritivores or because they are removed into a less favourable environment, for detritivores. However, prior to the diversification and increase in abundance of echinoids in the late Triassic and Early Jurassic bone-beds were relatively common sediment types. Their gradual disappearance from aerobic environments during the Mesozoic may be linked to the rise in abundance of these efficient omniverous detritivores.

## 6 - Bone-beds through time

Bone-beds are not a phenomena restricted to Holocene sediments, they are found in a variety of environments and facies throughout geological time. The purpose of this section is to consider the environmental location of many of these bone-beds to see if any patterns of bone-bed genesis can be determined.

### 6.1 British Upper Silurian Bone-Beds

In the Palaeozoic the first bone-beds are found as thin loosely consolidated quartz rich vertebrate sands in the Ordovician (Behre and Johnson, 1933), but they do not become abundant until the Silurian. In the British Silurian the first bone-beds are recorded in the Leintwardine Beds (Middle Ludlow) as shelly layers containing phosphatic nodules (Cherns, 1977). The overlying Whitcliffe Beds (Upper Ludlow) contain a variety of bone-beds (Squirrel, 1959; Cave & White, 1971; 1978) culminating in the Ludlow Bone-Bed at the base of the overlying Downtonian Series of sediments (Upper Silurian). The Downtonian contains a large number of bone-beds, many of which are currently unrecorded in the literature.

### 6.1.1 Upper Ludlow Bone-Beds

Vertebrate deposits in the Upper Ludlow (Whitcliffe Beds) occur in two major facies (termed here Facies A and Facies B) and form discontinuous bone-beds traceable over distances of less than 1 km.

1. Facies A consists of an interbedded sequence of quartz silts, locally enriched in muscovite mica, but with few shells. Alternating silt units (5 - 10 cm thick) have flat erosive bases. The internal structure of inphase current ripple lamination or parallel lamination has been largely destroyed by bioturbation. The facies contains shell bands 1 - 15 mm thick which have an erosive lower contact and are made of commutated shell fragments. They frequently contain ostracod carapaces and occasionally a high density of fish scales associated with euhedral biotite crystals. The shell or bone-bed layers acted as an impassable substrate for burrowing organisms in the sediments overlying the deposit.

   The absence of lenticular or flaser bedding suggests that these marine sediments were not formed as subtidal tidal deposits. The sharp erosive contacts between silt layers and the high intensity of bioturbation destroying in some instances the internal lamination of the deposit suggest that sedimentation was episodic on an aerobic benthos, and that the sedimentation might be related to the effects of storm activities (Watkins & Berry, 1977) bringing in fresh sediments onto a shallow ( ≥ - 50 m O.D.) sea-floor.

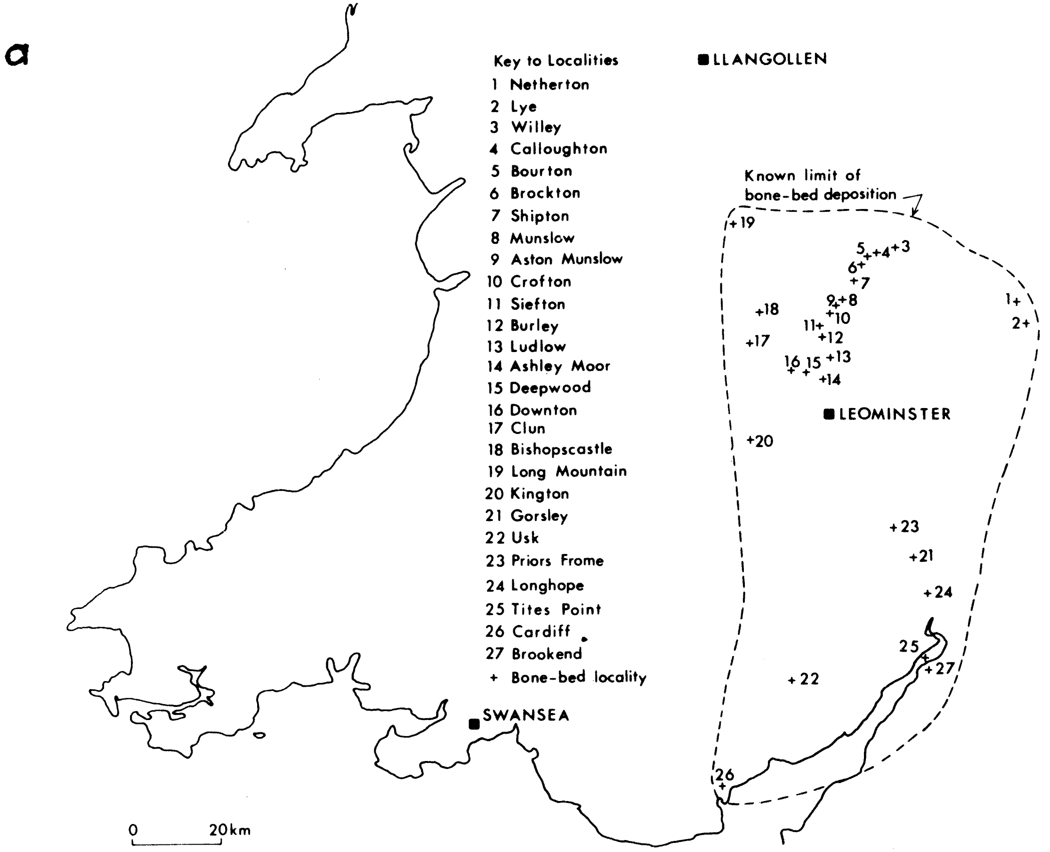
   The presence of biotite in the bone-beds may be a result of diagenetic reactions, though the sequence above and below the deposits contains no biotite. It is more likely that the biotite is derived from bentonites, which are biotite rich, and that a bentonite ashfall could have been responsible for the death of the fish in the bone-bed.

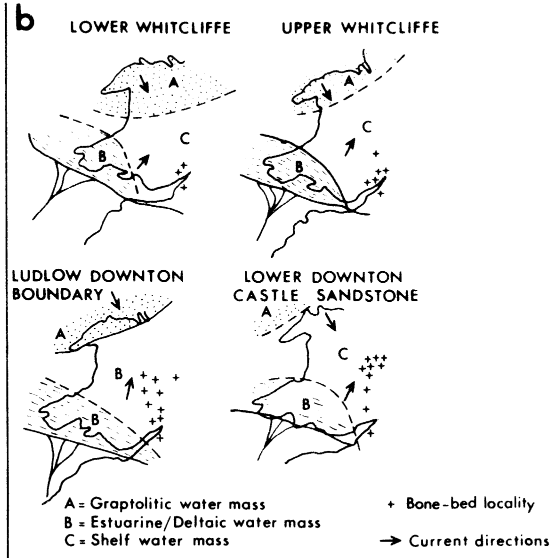
Text-fig.4a. Map of Wales and the Borderlands showing the localities containing deposits assigned to the Ludlow Bone-Bed.

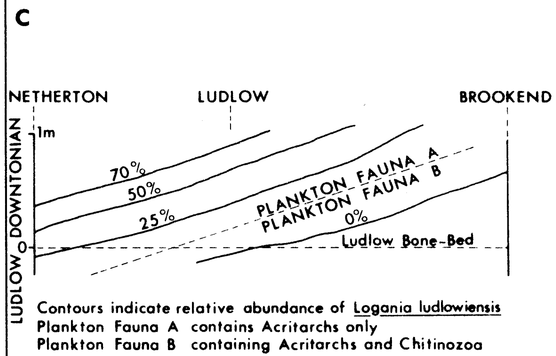
Text-fig.4b. Location of bone-beds, Plankton masses and Palaeogeography in the Upper Silurian (adapted from Watkins & Berry, 1977).

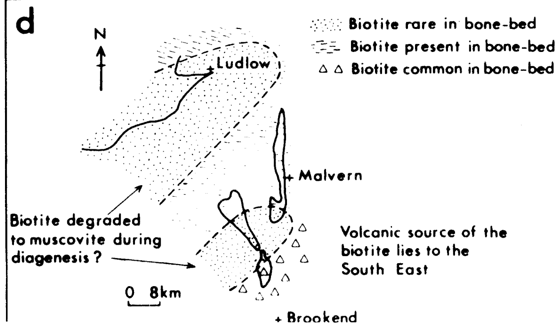
Text-fig.4c. Thelodont Species and Plankton distributions in the Upper Silurian.

Text-fig.4d. Distribution of Biotite in the Ludlow Bone-Bed (Modified after Tucker, 1960).









2. Facies B consits of an interbedded sequence of lenticular bedded silts and clayey silts. Individual units range in thickness from 0.5 to 8 cm. The clayey silts commonly contain *Chondrites*. The silts may be made of quartz (0.005 - 0.15 mm grain size), shell debris (0.2 - 3.0 mm grain size) and, rarely, fish scales (0.08 - 0.95 mm grain size). These latter deposits occasionally form thin bone-beds (1 - 6 mm thick) and may have formed in a subtidal ( -30 - 0 m O.D.) shelf region of oscillating tidal currents with an aerobic benthos.

### 6.1.2. Downtonian Bone-Beds

In the Downtonian, bone-beds are a fairly common sediment type and are present in a variety of facies, including some named bone-beds.

1. The Ludlow Bone-Bed is a stratigraphically important horizon which was once considered to mark the Silurian/Devonian boundary but now marks the basal layer of the Downton series (Upper Silurian), Holland *et at.*, (1963). The Bone-Bed has been recorded over a wide area (text-fig. 4a) and may be described as either a bone-bed facies (Allen, 1974a) containing a number of bone-beds within a short vertical sequence of strata (ca. 25 cm) or as the basal vertebrate sand layer marking the junction of the Whitcliffian and Downtonian faunas. This is the sense in which the term is used here.

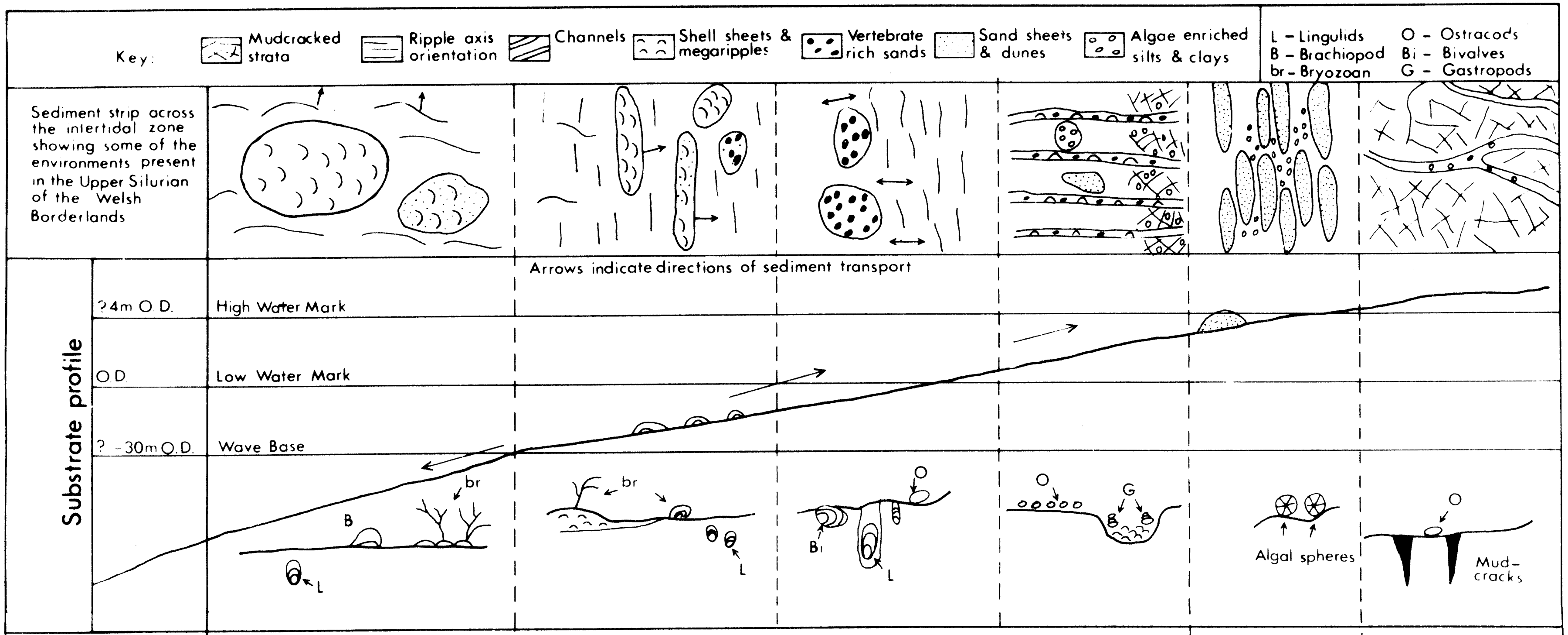
   The Bone-Bed may be described as a lenticular bedded sand (1 - 130 mm thick) composed of thelodont fish scales (0.06 - 1.2 mm grain size), phosphatic shell fragments (0.15 - 30.0 mm grain size), phosphatic nodules (0.35 - 25.3 mm grain size), and rare quartz grains (0.04 - 3.5 mm), see cover and pl. 14, figs. b,c. Thelodont scales, which may or may not be worn, form the dominant part of the bone-bed (pl.14, figs. d,e,f).

   Examination of the rare quartz grains show a variety of grain types, varying from quartz shards (pl. 14, fig. k), rounded grains showing evidence of eolean abrasion (pl. 14, fig. g), euhedral crystals (pl. 14, fig. h) some of which contain worn edges (pl. 14, fig. i) and high energy intertidal crescent shaped abrasion chips (pl. 14, fig. j).

   The features present on the quartz grains suggest that the Ludlow Bone-Bed is an intertidal deposit (cf. Krinsley & Doornkamp, 1973). This interpretation is supported by the fauna and lenticular bedded nature of the deposit, suggesting deposition in a region of tidal flow (cf. Reineck & Singh, 1975; Allen, 1974a; Antia & Whitaker, 1978).

2. Facies C - In the sediments immediately overlying the Ludlow Bone-Bed a number of other bone-beds are present. These occur in an interbedded sequence of intertidal (Allen, 1974a) lenticular and flaser bedded silts as either discontinuous rippled sand sheets ( $\leq$ 5 mm thick) forming an integral part of a lenticular bedded strata, (e.g. the Downton Bone-Bed of Elles and Slater, 1906), laminae within rippled silts, or as thin vertebrate sand sheets (0.1 cm thick). Burrows within the facies are commonly infilled with vertebrate sand. The bone-beds contain thelodont fish scales and phosphatic shell fragments.

3. Facies D - At Ludlow about 1 m above the Ludlow Bone-Bed is a mud-cracked channeled series of flaser bedded silts and clays. The channels are infilled with abundant thelodont fish scales associated with ostracod and molluscan shell debris forming bone-beds (1 - 3 cm thick) infilling runnel like channels. The sediments of this facies bear some morphological similarities to the modern mudmound facies found high in the intertidal zone (Greensmith & Tucker, 1967).



| | | | | | | |
|---|---|---|---|---|---|---|
| Environment | Muds, silts and shell sheets | Tidally influenced, shell gravels and muds | Mudcracks | Runneled muds mudcracked at top of zone | Chenier or Dune sands | Marsh sediments |
| Bone-beds | FACIES A | FACIES B | Ludlow Bone-Bed and FACIES C | FACIES D | | TEMESIDE Bone-Beds |
| Sedimentary structures | Shell sheets, silt wedges, current ripples | Shell sheets and mega-ripples Current rippled and lenticular bedded muds and silt | Lenticular bedded silts and muds | Mudcracks, runnels | Trough cross bedding | Mudcracked channels calcite glaebules |
| Biogenic structures | *Chondrites* burrows | *Chondrites* burrows | U-shaped burrows | U-shaped burrows | | |
| Ecology | **Epifauna = Lingulid brachiopods & bivalves** | Lingulid brachiopods and bivalves | Lingulid brachiopods and bivalves | | | |
| | Epifauna = **Articulate brachio-pods and ostracods** | Articulate brachiopods and ostracods | Endobyssate bivalves and ostracods | Ostracods Algae small gastropods | Algae *Pachytheca* | Ostracods |
| | Encrusting fauna = Bryozoans | Bryozoans | | | | |

Text-fig.5. The environments of Upper Silurian (Whitcliffe/Downtonian) bone-bed deposition.

4. The Temeside Bone-Bed (Elles & Slater, 1906) is a channel infill deposit which cuts into a series fine-grained red clays (grain size $\leq 0.03$ mm) which are extensively mudcracked and contain calcite glaebules, indicating that the deposit is cutting into supratidal sediments (Allen, 1974b). The bone-bed contains abundant plant fragments, fish scales and pellets, fish spines and rare angular quartz grains (pl. 14, fig. 6). Fish remains include those of thelodonts (*Thelodus parvidens, Logania ludlowiensis, T. trilobatus*), acanthodians (*Gomphoncus murchisoni, G. tennustriata*), and the cyphaspid, *Hemicyclaspis murchisoni*. The lowest Gedinnian conodont, *Ozarkodina remscheidensis*, has been recorded from a bone-bed infilling a scour hollow 60 cm below the Temeside Bone-Bed at Ludlow (GR S0522742).

### 6.1.3 The ecological significance and faunas of the bone-beds

As discussed earlier (p.100-102) the British Upper Silurian bone-beds may be primary deposits and therefore reflect the composition of the fish schools in the overlying waters (David, 1944). The deposits are located in a number of environments both subtidally and intertidally (text-fig. 5) and may represent mass mortality deposits in which the fish have been broken up after death. They do not mark stratigraphical faunal breaks, though some do represent a facies change (e.g. the Ludlow Bone-Bed). In this latter instance much of the fauna found immediately above the Bone-Bed has been recorded elsewhere from horizons below bone-bed (e.g. Hoppe, 1931; Atkins, pers. com. 1978).

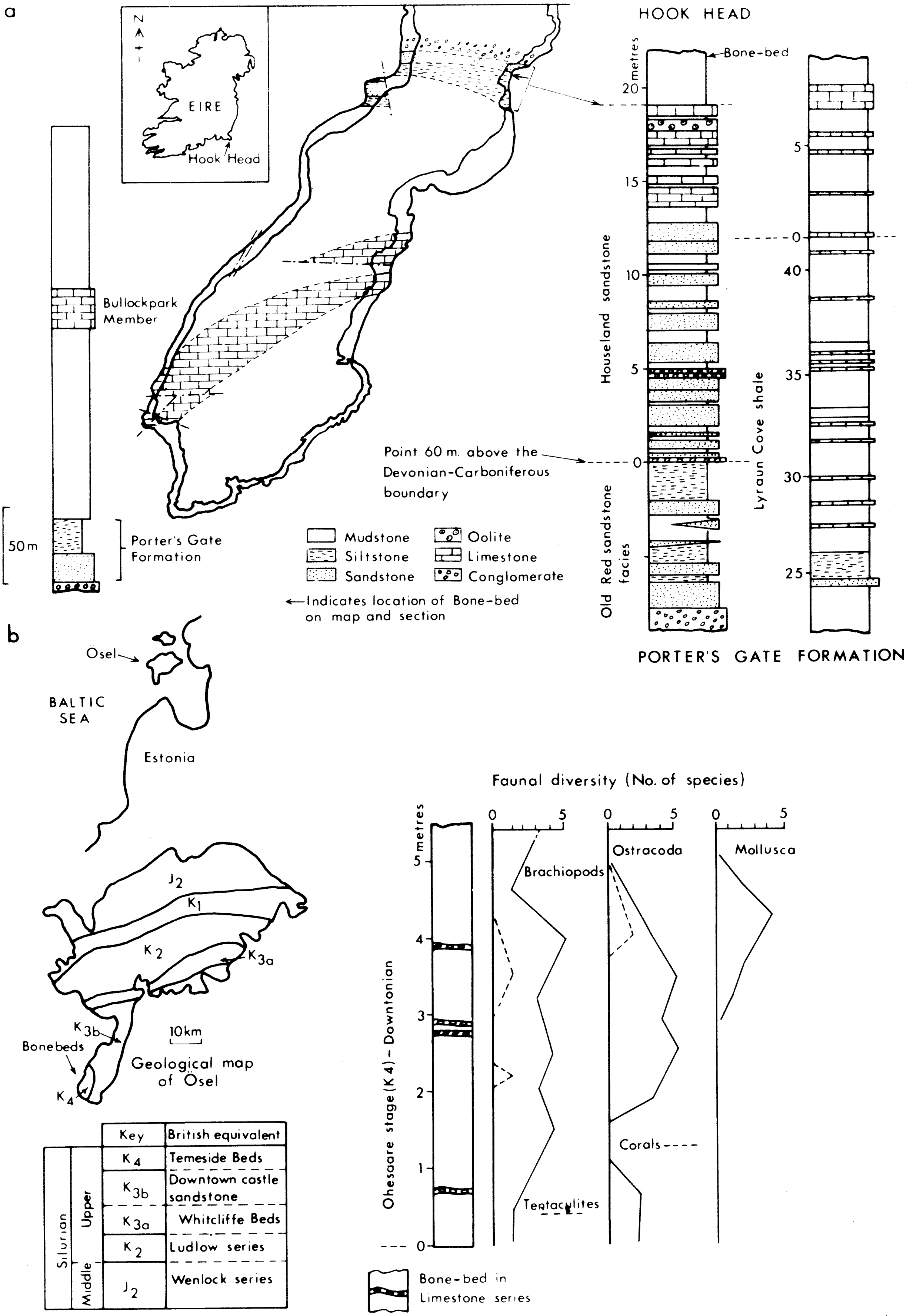
If the bone-beds do represent mass mortality deposits then they may have formed as a result of volcanic activity, since many of the deposits contain euhedral biotite (text-fig. 4d), a common constituent of local bentonites.

If this catastrophic interpretation of mortality is correct then study of the bone-beds should allow an ecological model for the Ludlow fish fauna to be considered. As many sections contain multiple bone-beds, changes in the composition of the fish faunas will be reflected in the deposits. The location of the Upper Silurian bone-beds, and plankton masses and a palaeogeography are given in text-fig. 4b. This figure illustrates the effect of the northward migrating southern estuarine/deltaic environment on the distribution of bone-beds and water masses and suggest that the schools of fish were confined to a relatively narrow northward migrating belt (100 km wide) on the shelf sea.

Examination of the faunal composition of these resulting deposits allows variations in fish school composition with distance and time to be studied. Study of the two dominant fish species present in the bone-beds (*Logania ludlowiensis* and *Thelodus parvidens* (pl. 14, figs. b, e, f) in relation to the plankton composition of the waters (data from Richardson & Lister, 1969; Swanson & Dorning, 1977; Dorning, oral com. 1977; White, oral com. 1978) allows the following observations to be made (text-fig. 4c).

1. Throughout the Upper Ludlow (Turner, 1973; pers. com. 1977) *Thelodus parvidens* forms the dominant fish remains in the sediments and bone-beds, suggesting that it was the dominant species of fish present in the overlying waters.

2. The change in relative abundance of *Logania ludlowiensis* making it the dominant species in the bone-beds is apparently related to a change in the composition of the plankton faunas (text-fig. 4c). A possible interpretation of this change could suggest that the fish schools dominated by *T. parvidens* were plankton feeders, while the schools dominated by *L. ludlowiensis* may have also utilised another food source (e.g. benthic algae). Thus increased nutritional pressure on *T. parvidens* due to a decrease in the diversity of its food supply, coinciding with a southward migration of part of the *L. ludowiensis* population (Turner, 1973) feeding on ?plankton and ?algae may have allowed it to compete successfully with *T. parvidens* for dominance in the local fish schools.



Text-fig. 6 a. Location map and section showing the position of the Lyraun Cove Bone-Bed.
b. Map of the Island of Osel (Estonia) showing the bone-bed outcrop.
Stratigraphy after Kaljo & Sarv (1966).

After the mass mortality of fish (however caused), decomposition and disaggregation, the fish scales were transported into a number of environments.

1. The environment of death

   No articulated thelodont fish have been recorded from the Whitcliffe or Downtonian sediments though some whole cyathaspid headshields were recorded above the Ludlow Bone-Bed at Tites Point (Tites Point collection I.G.S. Lond.).

   If the fish died in a littoral or sublittoral environment not influenced by strong or oscillating currents, complete fish skeletons would be expected. The *Cyathaspis* headshield noted here occurs in littoral sediments and the fish was by nature a "mudgrubber" (David, 1956) and thus more likely to be preserved in its entirety.

   Thus the fish probably died in a region affected by subtidal current and were broken up by them. The disarticulated scales were then rolled around on the sediment surface and some colonised by algae (see Section 10). The scales may then have been transported from their environment of death both seaward and landward (text-fig. 5), before being concentrated in a bone-bed.

2. The ecology of the bone-beds

   Many bone-beds contain or are associated with *in-situ* faunas. The bone-bed facies A and B contain no such faunas though the sediments above and below contain an endemic fauna of brachiopods, bivalves and bryozoans. The Ludlow Bone-Bed contains a fauna of burrowing bivalves and the bone-bed facies C and D occur is sediments containing an autochthonous necrocenosis of ostracods, bivalves and gastropods. The Temeside Bone-Bed occurs in sediments containing a carapace fauna of rare ostracods. Since only the Ludlow Bone-Bed contains evidence of an in place fauna it is probable that the vertebrate sands did not form a good ecological habitat. The ecological habitats of the bone-bed environments are illustrated in text-fig. 5.

### 6.2 The Upper Silurian Bone-Beds of Osel

Deposits termed bone-beds have been recorded (Hoppe, 1931; Gross, 1967; 1971) on the Estonian Island of Saaremaa (Osel) in the Downtonian Ohesaare (K4) Stage (text-fig. 6). The bone-beds may be described as thin layers (5 - 23 cm thick) of either crystalline limestones with fish debris (K4c) or as sandy crystalline limestones rich in fish debris (K4a). Although the dominant vertebrate remains are thelodont scales a total of 27 vertebrate species belonging to the Thelodonti, Acanthodei, Actinopterygil, Heterostraci and Arthrodira have been recorded (Mark-Kurik, 1969). The bone-beds may be correlated with those of the Temeside shales of the British Upper Silurian sequence (cf. Cocks *et al.* 1972; Turner, 1973). They occur in a sequence of thin interbedded marls, clays and limestones (Hoppe, 1931). Locally some of the limestones are bioturbated, others dominated by a shelly fauna (text-fig. 6). The faunas across the bone-beds are dominated by crinoid ossicles, ostracods and brachiopods. The presence of the brachiopods *Salopina* sp., *Protochonetes ludloviensis*, *Microsphaeridiorhynchus nucula* suggest that the bone-bed sediments were formed in a shallow marine environment (cf. Calef & Hancock (1974; on the *Salopina* community), Lawson (1975; on the *Salopina-Protochonetes* association), and Boucot (1975; on Benthic assemblage 2)) above wave base. This conclusion is supported by other general sedimentology, palaeontology and ecostratigraphy studies from Estonia at this stratigraphic level, (Gailite 1972; Kaljo & Jurgenson, 1977; Kaljo oral com. 1978).

### 6.3 Bone-beds of the Beyrichienkalk erratics

Within north German glacial drift are a large number of glacial erratics from a marine Upper Silurian formation termed the Beyrichienkalk.

A large percentage of these erratics contain vertebrate remains (Romer, 1955) which have been described by Gross (1947) and some contain bone-beds (Brotzen, 1933). Samples of a Beyrichien bone-bed were obtained by the present author from Dr. Jahnke of Göttingen University. This material obtained from Loc. 22 Heiligenhafer, Geschiebe, N. Germany (Göttingen, Geology and Palaeontology Institute locality number) may be described as a vertebrate coccinia within an ostracod limestone.

The limestone sediment in which the bone-bed occurs may be described as a sparite containing orthocones, nuculoid bivalves, small bellerophon-like gastropods, small rhynchonellid brachiopods, or thick brachiopods and ostracods. The ostracod species observed by the author include ?*Aparchites sinuatus* Hall, *Bythocypris* cf. *phillipsiana* (Jones & Hall) *Nodibeyrichia pustulosa* Hall and all occur as a carapace fauna. These ostracods suggest by comparison with those of Nova Scotia (Copeland, 1960, 1964) and those of Britain (Straw & Woodward, 1932; Shaw, 1969) that the sediments are of Upper Downtonian age.

The bone-bed itself may be described as a wackestone made of thelodont and acanthodian scales. Ostracod carapaces are common, but in most cases their interior has been replaced during diagenesis by phosphate. Similar internal phosphatic casts and moulds of small bellarophontid gastropods are common. Lingulid brachiopods (*Lingula* cf. *missindenesis* Straw) with both valves joined, are present within some small phosphatic nodules. The phosphatic elements present in the bone-bed are dominated ( $\geq$ 80%) by fish remains belonging to the genera *Gonioporus*, *Katoporus*, *Thelodus*, *Logania*, *Nosteolopis* and *Gomphonchus*. These remains are poorly abraded and are dominated by poorly weathered scales. Some of the scales contain algal solution pits of the type illustrated in pl. 18, fig. e. The grain size of the phosphatic elements of the bone-bed is in the range 0.2 - 1.2 mm.

The bone-bed is regarded (Romer, 1955; Halstead & Turner, 1973) as having formed in an estuarine or near shore marine shelf environment. This interpretation is supported by the presence of a marine invertebrate fauna belonging to the near shore benthic assemblage 2 of Boucot (1975).

### 6.4 Devonian bone-beds

Accumulations of fragmented vertebrate debris have been recorded in the Lower Devonian Catsgill Delta facies and the Middle Devonian Limestones of Ohio, U.S.A.

#### 6.4.1 The Catsgill Delta Facies

The Lower Devonian Catsgill Facies represents a deltaic sequence of interbedded sandstones and conglomerates in the north eastern states of the U.S.A. (Allen & Friend, 1969) which allowed the development of a prograding muddy marine shore line to the south of the delta (text-fig. 3, p. 99) in Pennsylvania (Walker & Harms, 1971). Similar estuary/deltaic associations with prograding muddy shore lines are found adjoining the Thames Estuary (Greensmith & Tucker, 1967; 1975; Antia, 1977), the Mississippi Delta (Gould & McFarlan, 1959) and elsewhere (Price, 1955).

These prograding muddy shore lines may form chenier plains (Price, 1955), which are swept by a mud laden subtidal traction current. The coarse debris (sand, shells, pebbles, vertebrate debris, etc.) is concentrated into lag concentrates by storms, currents and wave activity, and migrated across the intertidal zone to accumulate as ridges of sand, shell and cobble on the junction of the tidal mudflats and the supratidal marsh.

In the Catsgill Coastal Plain environment, Walker & Harms (1971) have recorded 60 transgressions and regression of this coastline. Each transgression producing a sequence of sediments representing a variety of subtidal and intertidal environments (text-fig. 3). Similar sequences have been recorded in recent post glacial coastal plain sediments (Greensmith & Tucker, 1976).

The basal unit of each of the Catsgill transgressive sequences is a subtidal siltstone bone-bed rich in quartz, brachiopod and crinoid debris, phosphatic nodules, bone fragments and fish plates. It rests on a sharp, discordant erosive surface which is commonly bioturbated.

### 6.4.2 Middle Devonian bone-beds of the Central U.S.A.

Four bone-beds have been described (Wells, 1943; 1944; 1947) from the Delaware and Upper Columbus Formations of the Middle Devonian (Late Ulsterian) limestones of central Ohio (text-fig. 7h).

The bone-beds are local concentrations or zones of pelopsammic material outcropping over a wide area, which formed in a shallow shelf sea near a land area (text-fig. 7a). The phosphatic organic constituents are generally worn scales, teeth, plates and bone fragments of agnathid, arthrodiran, ptyctodontid, scanthodian, selachian and crossopterygian fishes. Other less common constituents include conodonts, arenaceous foraminifera, ostracods, scolecodonts, sponge spicules, and lycopod spore exines. Locally crinoid ossicles, corals, bryozoans, gastropods, brachiopods, and bivalves dominate the fauna. The phosphatic component of the bone-beds is made of a carbonate apatite (Westgate & Fischer, 1933).

The individual bone-beds may be described as follows:

1. The First Ohio Bone-Bed (text-fig. 7h) consists of a thin (5 - 8 cm thick) vertebrate sand rich in angular, rounded and frosted quartz grains ( ≤0.3 mm long) and accessory chert.
2. The Second Ohio Bone-Bed (text-fig. 7h) covers an area of several hundred square kilometres (Orton, 1878) and consists of a thin (0 - 40 cm thick) vertebrate and crinoidal diastemic sand containing limestone intraclasts, chert, and angular, rounded and frosted quartz grains ( ≤ 0.8 mm).
3. The Third Ohio Bone-Bed (text-fig. 7h) forms the topmost bed of the Columbus limestone (Stauffer, 1909) and is an extensive, 0 - 32 cm thick, diastemic vertebrate sand rich in coarse crinoidal debris, containing well rounded and frosted quartz grains ( ≤ 0.5 mm). Some of the vertebrate remains have been replaced by opal. The deposit rests on an erosive surface in the Columbus Limestone which cuts through corals and brachiopod shells and marks an important faunal change (Table 9). Locally the bone-bed infills a channelled and mudcracked underlying surface (text-fig. 7b, c, d).
4. The Fourth Ohio Bone-Bed (text-fig. 7h) is a crinoidal vertebrate sand (5 - 8 cm thick) containing phosphatic nodules and rounded frosted quartz and chert grains ( ≤ 1 mm).

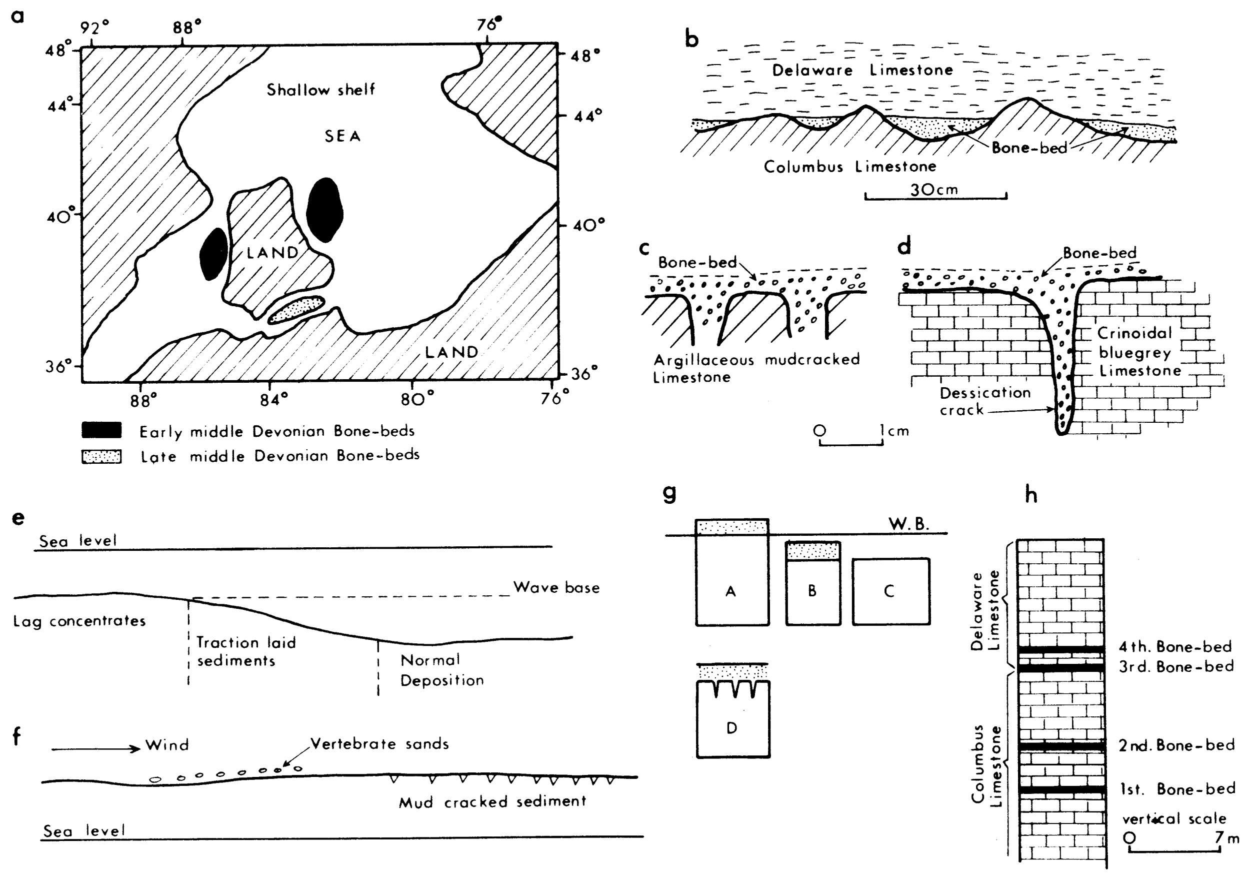
Three other bone-beds of local extent have been recorded from the Middle Devonian of Ohio, Indiana and Kentucky. The East Liberty Bone-Bed (Newberry, 1873) is a diastemic dolomitic vertebrate sand (0 - 30 cm thick) rich in pyrite, phosphatic nodules and rounded, frosted and rutilated quartz grains. Secondly, the Rocky Branch Bone-Bed (Foersets, 1906) is a calcareous vertebrate sand (5 cm thick) containing rolled frosted quartz grains and phosphatic nodules some of which are internal phosphatic moulds of gastropods, bivalves and pelmatozoans. The third one is the Kiddville Bone-Bed (Wells, 1944), a thin vertebrate sand rich is spores, inarticulate brachiopods, fragmented conodonts, phosphatic nodules, and rounded, frosted, polished and rutilated quartz grains, some of which occur as perfect euhedral overgrowths.

Table 9. Faunas across the Columbus/Delaware limestone boundary (Westgate & Fischer, 1933).

1 = *Nucleocrinus verneudi*;
2 = *Spirifer acuminatus*
3 = *S. duodenarius*;
4 = *Reticularia fimbriata*;
5 = *Leptaena rhombiodalis*;
6 = *Stropheodonta demissa*;
7 = *S. perlana*;
8 = *Rhipidomella vanuxemi*;
9 = *Delthyris consobrina*;
10 = *Martinia maia*;

C = common; P = present; R = rare

| | Species | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Delaware Limestone | - | - | - | - | P | P | P | P | C | C |
| Bone-bed | - | - | - | R | C | C | C | C | C | C |
| Top of Columbus Limestone | C | C | C | C | - | - | - | - | - | - |
| Columbus Limestone | P | P | P | P | P | P | P | P | - | - |



Text-fig.7. Middle Devonian Bone-beds

(a) Palaeogeography
(b-d) Sections through the third bone-bed
(e-g) Environments of bone-bed deposition

A = bone-beds formed as lag concentrates W.B. = Wave Base
B = bone-beds concentrated by traction currents
C = normal deposition (no bone-beds formed)
D = bone-beds formed as lag concentrates in the intertidal zone.

(h) The stratigraphic location of the bone-beds

Data for fig. obtained from Westgate & Fischer (1934), and Wells (1944).

A variety of models have been proposed to account for the origin and distribution of the Ohio Bone-Beds. The early models suggested that they formed as a condensation deposit, a mass mortality deposit or from the reworking of coprolites and they are summarised by Wells (1944).

Wells (1944) following examination of the bone-beds decided that:

1. The vertebrates were fragmented after death and transported.
2. All the bone-beds have a uniform mode or origin.
3. They are associated with diastems resulting from fluctuations with respect to wave base on the bottom of a very shallow sea.
4. In some places they represent lag concentrates, in others rapid subaqueous accumulations of coarser material transported from areas of lag concentration with a bipassing of finer particles (text-fig. 7e, 7g).

Subsequent (post 1947) detailed biostratigraphic work utilising a foraminifera zonal scheme (Conkin & Conkin, 1975) has shown that the sections described by Wells (1944) contain a total of 16 bone-beds (Conkin, 1969; Conkin *et al.*, 1972; 1973) and that the bone-beds are associated with paracontinuities. These are disconformities which exhibit a slight though clearly discernable channelling and a small but significant faunal discontinuity. Conkin & Conkin (1975) note that the rocks which overlie paracontinuities in the Delaware and Columbus Limestones often contain a basal detrital unit, such as a bone-bed.

However, since these more recent accounts of the Ohio, Devonian bone-beds supply no appreciable new sedimentological, petrographic and environmental information relating to these bone-beds, the interpretation of Wells (1944; 1947), outlined here, remains the best available account of their formation and petrology.

### 6.5. A Tournaisian (L. Carboniferous) bone-bed from Hook Head, Co. Wexford, Eire

Although the geology, palaeoenvironments and palaeontology of the Hook Head peninsula (text-fig. 6, p.118) have been extensively described (Smyth, 1930; Sleeman *et al.*, 1974; Sleeman, 1977), little is known about the nature of the phosphatic nodules and fish debris of the Lyraun Cove Member of the Tournaisian Porters Gate Formation.

The fish debris is disseminated throughout the Lyraun Cove Member but is concentrated in a thin dark grey shelly fine-grained siltstone containing about 15% shell, 25% fish debris, and 5 - 10% pyrite; termed here the Lyraun Cove Bone-Bed (text-fig. 6).

The shelly debris of the bone-bed consists of crinoid ossicles, smooth ostracods and small brachiopods (? *Spirifer tornacensis* de Kon). The fish debris comprises worn and fragmented blue grey fish scales ( ≥ 99%), rare teeth ( ≤ 1%) and conodonts (Johnston pers. com. 1978). The pyrite forms small (0.1 - 0.4 mm) nodules of framboidal pyrite or as internal moulds of ostracods and gastropods. Some fish scales have acted as a nuclei for pyrite growth in the concretions and are partially engulfed. The pyrite has a diagenetic origin. Both the fish and shell debris occur within the same size range 0.1 - 1 mm (modal range (0.3 - 0.5 mm).

The early Hook Head Tournaisian sediments represent a marine transgression and show a gradual transition from a fluviatile to a marine environment. The sediments pass up from a fining-up sequence of conglomerates, sandstones and siltstones in the Old Red Sandstone facies represented by the Old Town Bay Formation (text-fig. 6), into a series of flaserbedded sandstones containing bipolar cross stratification and trace fossils. This latter sediment type is represented by the Houseland Member of the Porters Gate Formation and is thought to have been deposited in a variety of intertidal and shallow subtidal marine environments (Sleeman *et al.*, 1974; Sleeman, 1977).

The Houseland Member is overlain by the Lyraun Cove Member, which comprises a sequence of grey sand lensed mudstones and bioturbated siltstones containing ossilation ripples (text-fig.6). Phosphatic nodules and fish remains are common throughout the sequence. The Member is considered to represent a low energy shallow marine environment rarely influenced by tidal currents and storms (Sleeman, 1977). The overlying Hookhead Formation represents a shallow water open shelf tidally influenced marine environment (Sleeman *et al.*, 1974). Thus the Lyraun Cove Bone-Bed accumulated in a low energy marine environment. This environmental interpretation is not supported by the well sorted and fragmented nature of the beds clasts, but these may have been swept into the environment as a well sorted lag concentrate.

The presence of pyrite and phosphate nodules in the Member suggest that sediment pore waters were both sulphurous and anoxic (Eh -200 to -300; pH 6 - 7; Berner, 1970; Baturin, 1971), when the nodules formed, and may suggest that the Lyraun Cove Bone-Bed is a transported deposit of shell and fish debris, possibly transported during a storm, from a tidally influenced environment to this environment presenting ?foetid bottom conditions.

### 6.6. The German Middle/Upper Triassic Bone-Beds

Bone-beds have been recorded (Wagner, 1913; Aust, 1969; Reif, 1969; 1971; 1974; 1976; Bachmann & Gwinner, 1971; Gwinner & Hinkelbein, 1976, etc.) from the Upper Muschelkalk (mo3) and Lower Lettenkeuper (kul) of south west Germany, within a standard stratigraphic profile across the Muschelkalk/Keuper boundary which may be presented as follows, from base to top (after Reif, 1974):

1. Obere Terebratelbank (mo3) - A blue grey limestone (40 - 50 cm thick) containing convolute bedding, stylolites, and rare bone-beds.

2. Frankische Grenzschichten (mo3) - A blue grey glauconitic shelly limestone locally interbedded with ostracod rich clays (the *Bairdia* Ton) and occasional conglomeratic layers (0 - 100 cm thick).

3. The Grenzbonebed (mo3) - Rippled bone-bed (4 - 20 cm thick) rich in fish debris and coprolites, often with a rich trace fossil fauna on its upper surface.

4. The Untervitriolschiefer (kul) - Grey laminated clays 40 - 80 cm thick) occasionally rippled locally containing layers rich in ostracod debris.

5. Wagner's Plattenhorizon (kul) - A grey siltstone rich in bone debris (8 - 15 cm thick) locally flaser bedded.

6. The Oberevitriolschiefer (kul) - Grey laminated clays (40 - 60 cm thick) occasionally rippled, locally flaser bedded towards the upper part of the unit.

7. The Blaubank (kul) - A blue grey limestone (20 - 40 cm thick) with local patches of diagenetically dissolved calcite or gypsum crystals (Porenkalk (Reif, 1974) and shell debris. Bone-beds are commonly developed at the units base. Stylolites are common.

8. The Dolomitsche Mergelschiefer (kul) - A sequence of alternating blue grey dolomitic limestones, silts, clays and grits with occasional layers of fish and coprolite debris (60 - 100 cm thick).

9. The Untere Dolomite (kul) - Blue grey dolomite locally rippled, with some sandy layers (40 - 80 cm thick).

10. The Estherien-Schichten (kul) - Black shales with interbedded cross-bedded sandstones rich in plant debris (2 - 10 m thick).

11. The Upper Lettenkeuper (kul) - Black shales with interbedded dolomites, bone-beds and algal stromatolites (5 - 15 m thick).

The most important of the bone-beds is the Grenzbonebed which forms the uppermost layer of the Frankische Grenzschichten. Within the Frankische Grenschichten are a number of thin (1 - 3 cm thick) discontinuous bone-beds traceable only a few metres, but owing to their relative position in the quarry faces, usually 30 - 70 m above the ground, they have proved difficult to study in depth. However, like the Grenzbonebed they may represent "condensation" or omission deposits (Reif, 1971) and may provide evidence of a slow down in the deposition rate of the Muschelkalk Limestone towards its top.

The thick bone-bed forming the top of the Muschelkalk Limestone (the Grenzbonebed) marks both a facies and a faunal change (Table 10) and may represent a change in the axis of the Muschelkalk Basin (Reif pers. com. 1977).

### 6.6.1. The Grenzbonebed

The Grenzbonebed (pl.15, fig.h) has been extensively described by Reif (1969; 1971; 1974; 1976) and Aust (1969). It is a thin deposit (0.5 - 30 cm thick) of rippled or parallel laminated carbonate clay or sand enriched in vertebrate debris and phosphatic nodules, including coprolites. The ripples tend to be symmetric low wavelength (7 - 15 cm) subtidal current ripples.

Within the bone-bed four facies are present - conglomeratic, sandy, clayey, and carbonate; their general distribution pattern is indicated in text-fig. 8, and their description follows:

1. The conglomeratic facies

   A deposit 5 - 20 cm thick composed of platy subrounded to angular pebbles (0.5 - 20 cm across), sometimes imbricated, in a vertebrate rich matrix. The pebbles are comprised of micrite, shelly bioclastic micrite and reworked vertebrate rich micrite, and are often bored.

2. The sandy facies

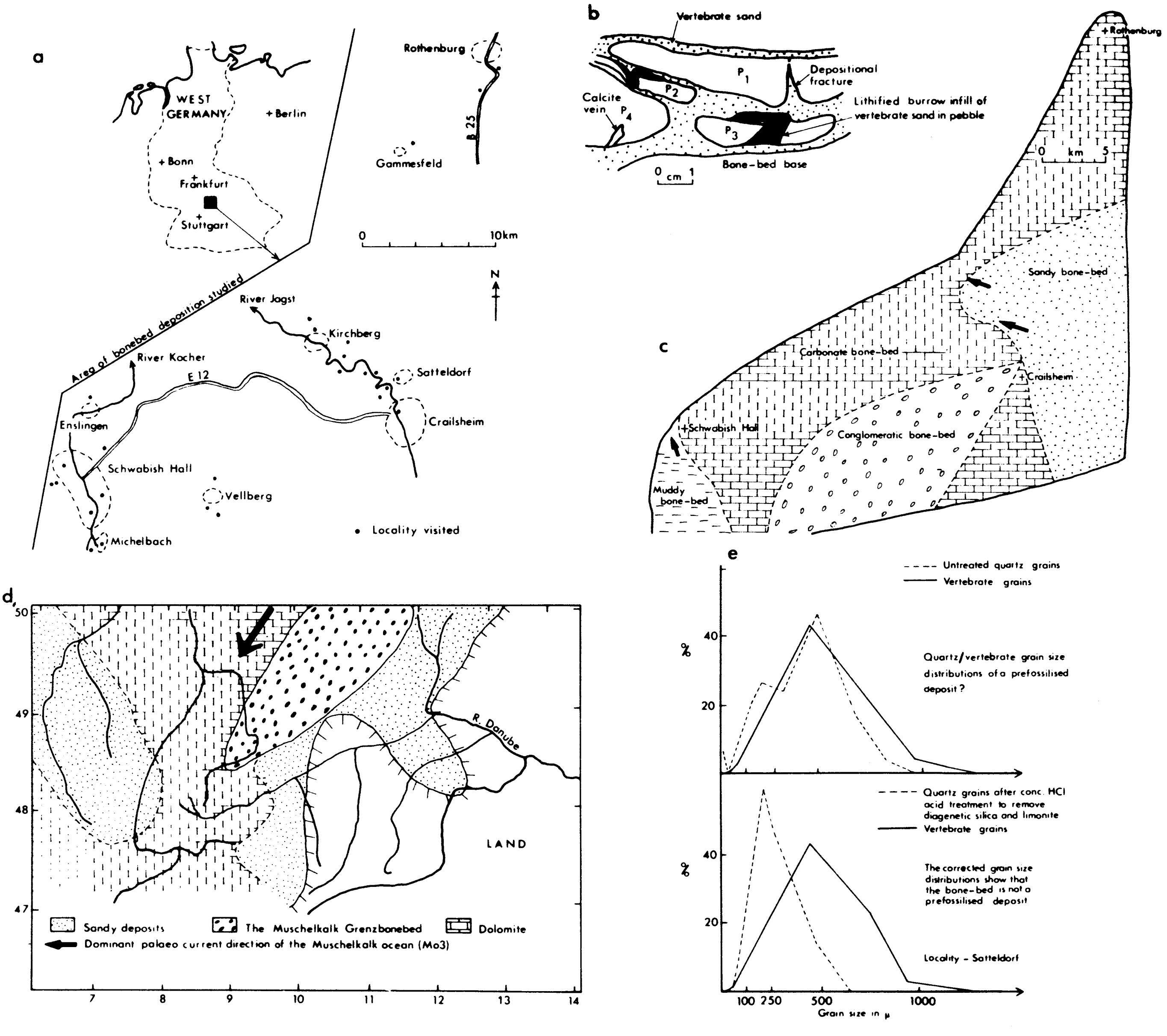
   A quartz sand deposit enriched in vertebrate remains. Both the quartz and vertebrate clasts may occur as well rounded high spherocity grains. The quartz grains are often coated by limonite (pl.15, fig.g) and by diagenetic silica (pl.15, figs. d,e).

3. The clay facies

   Thin deposits (less than 8 cm thick) of grey clay enriched in fish scales, normally parallel laminated, though ripple laminated clays have been recorded within the facies.

4. The carbonate facies

   Poorly bedded micrite deposits rich in vertebrate debris. S.E.M. studies of the sediments of this facies show that locally the vertebrate clasts may be rounded (pl.15, figs. j,l) though many of the clasts are angular (pl.15, figs. c,f) or unabraded (pl.15, figs. g,h). Many of the clast surfaces are chipped and uneven as a result of abrasive processes (pl.15, fig.i). The matrix of the limestone is rich in both calcite (pl.15, fig.c) and dolomite crystals (pl.15, fig.b) and rare clays. Some of the vertebrate clasts in the bone-bed are bored (pl.15, fig.k), possessing a boring diameter between 0.004 and 0.010, mm. Their general morphology is very different to the algal dissolution pits recorded on vertebrate clasts in the Ludlow Bone-Bed by Antia & Whitaker (1978) (pl.18, fig.c; pl.19, figs. d,e). They may, however, represent algal borings similar to those described by Bathurst (1975).



Text-fig.8. a Location map of sections through the Muschelkalk Grenzbonebed examined.
b Tracing of pl. 14, fig. n, explaining the features present.
c Facies distributions in the Muschelkalk Grenzbonebed.
d Palaeogeography of the Muschelkalk Grenzbonebed.
e Grain size distributions in the Muschelkalk Grenzbonebed.

Table 10. Ranked faunal distributions across the Muschelkalk/Keuper boundary (Mo3/Ku1) in South West Germany based on unpublished researches of the author. The individual stratigraphic units (1 - 11) are described in the text.

| Species | Stratigraphic Unit | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Brachiopoda | | | | | | | | | | | |
| *Coenothyris vulgaris* (Sch.) | 1 | 1 | 1 | - | - | - | - | - | - | - | - |
| *Lingula tenuissima* Bronn | - | - | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 |
| Gastropoda | | | | | | | | | | | |
| *Loxonema obsoletum* Zieten | - | 8 | - | - | - | - | - | - | - | - | - |
| *Omphaloptycha pyramidata* (Ko.) | - | 9 | - | - | - | - | - | - | - | - | - |
| Cephalopoda | | | | | | | | | | | |
| *Ceratites semipartitus* Mont. | 5 | 12 | - | - | - | - | - | - | - | - | - |
| Bivalia | | | | | | | | | | | |
| *Anoplophora lettica* Quen. | - | - | - | - | 2 | - | 2 | - | - | - | 2 |
| *A. brevis* Schaur | - | - | - | - | - | - | 4 | 2 | 1 | - | - |
| *Enantiostreon difforme* (Sch.) | 3 | 3 | 4 | - | - | - | - | - | - | - | - |
| *Gervilleia costata* Sch. | - | 4 | - | - | - | - | - | - | - | - | - |
| *Hoernesia socialis* Sch. | 2 | 2 | 3 | - | - | - | - | - | - | - | - |
| *Myophoria intermedia* Schaur | 4 | 10 | - | - | - | - | - | - | - | - | - |
| *M. goldfussi* Alb. | - | - | - | 3 | 3 | 2 | 3 | 3 | 3 | - | 4 |
| *Mytilus eduliformis* Sch. | - | 5 | - | - | - | - | - | - | - | - | - |
| *Pecten discites* Sch. | - | 7 | - | - | - | - | - | - | - | - | - |
| Echinodermata | | | | | | | | | | | |
| *Encrinus liliiformis* Sch. | 6 | 11 | - | - | - | - | - | - | - | - | - |
| Estherids | | | | | | | | | | | |
| *Isuara minuata* Goldf. | - | 5 | - | 2 | - | - | - | - | - | 1 | 1 |

Table 11. A component analysis of the Muschelkalk Grenzbonebed

| Vertebrate Component | Locality | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Pointed teeth | 3.4 | 2.6 | 34.5 | 3.1 | 1.4 | 6.5 | 3.0 | 4.1 | - | 1.4 |
| Concavo-convex teeth | - | - | 4.2 | 1.0 | - | 0.3 | - | - | - | - |
| Flat teeth | 64.0 | 53.2 | 38.8 | 60.3 | 29.2 | 58.6 | 57.5 | 34.2 | 65.2 | 71.6 |
| Fish scales | 12.8 | 37.7 | 22.4 | 16.4 | 59.7 | 24.6 | 36.4 | 37.0 | 13.4 | 16.4 |
| Phosphatic nodules | 18.6 | 6.5 | - | 9.1 | 8.3 | 9.8 | 3.0 | 24.7 | 21.4 | 10.4 |
| Fish spines | 1.2 | - | - | - | - | - | - | - | - | - |
| Vertebra | - | - | - | - | 1.4 | - | - | - | - | - |

Key to localities:

Locality 1 - Rothenburg ob der Tauber. 1:50,000 Map No. L6726. GR 867699.
2 - Gammesfeld. Map No. L6726. GR 803674.
3 - Satteldorf. 1:35,000 Map of Kirchberg. Reference 10° 2.6' 49° 10.9'
4 - Burlesmagen. Map as for 3. Reference 10° 1.9' 49° 10.9'.
5 - Hornberg. Map as for 3. Reference 9° 59.5' 49° 13.4'.
6 - Eselsteige. Map as for 3. Reference 10° 0.8' 49° 9.8'.
7 - Schwabish Hall. 1:50,000 Map L6924. GR 524415.
8 - Klinenacker. Map No. L6924. GR 524415.
9 - Hessental. Map No. L6924. GR 555407.
10 - Enslingen. Map No. L6924. GR 549478.

The relative abundances of the major groupings of vertebrate remains may alter over a short area, and locally one fraction may dominate the fauna (Table 11).

### 6.6.2. The time period represented by the Grenzbonebed

Study of the conglomeratic fractions of the bone-bed suggest that it represents a long depositional period. Since some of the lithified limestone pebbles (derived as intraclasts from the Muschelkalk Limestone Grenzbonebed junction) contain a lithfied burrow infill of bone-bed which predates the formation of the pebbles (pl.14, fig.n; text-fig.8). Thus indicating the following processes may have occurred:

1. Semilithification of the limestone.
2. Burrowing into the semilithified sediment.
3. Burying of the burrows with a vertebrate sand.
4. Lithification of the limestone and burrow infills with a calcite clay cement.
5. Scouring and fragmentation of the substrate.
6. Transport of these fragments and inclusion in a vertebrate sand.
7. Burial and lithification of the fragments in the vertebrate sand.

The time period involved for this lithification of the limestone sediment may be a few hundred or thousand years (Bathurst, 1975).

The absence of burrows in the bone-bed suggests that the sediment was too unstable to accommodate an ichnofauna or that the substrate was too foetid/nutrient poor to support an ichnofauna or that the bone-bed was buried very soon after its deposition. The presence of trace fossils on the upper surface of the bone-bed suggests that the last interpretation may be correct.

The phosphatic elements of the bone-bed have been derived from limnofluviatile, terrestial and marine environments (Reif, 1971). They may occur as perfectly preserved vertebrate teeth, bones, etc., or as well rounded high spherocity highly abraded fragments (pl.15, fig. i). This suggests that some of the vertebrate remains have been transported over a large area and that the bone-bed is a multicomponent deposit.

These observations suggest that the bone-bed represents a period of sediment omission, during which the substrate was gradually becoming lithified, and was swept and temporarily buried by actively moving vertebrate sands.

### 6.6.3. The source of the phosphatic debris in the Grenzbonebed

Reif (1969; 1971) considers much of the vertebrate material in the Grenzbonebed to be prefossilised and suggests that it has been derived from eroded sediments and concentrated on a lithified substrate as a lag deposit. However, much of the fauna in the Grenzbonebed is not present in the underlying sediments (Schmidt, 1928) and represents faunas from a variety of environments (terrestial, limnofluvial and marine). The vertebrate remains are commonly worn and abraded with grain size distributions which differ from that of the associated quartz grains (text-fig. 8). Quartz grains are rare or absent in some of the deposits, suggesting perhaps that the bone-bed is not a prefossilised deposit.

It is therefore suggested that the bone-bed formed as a lag concentrate of vertebrate material, derived from a variety of habitats, elongated in the direction of the dominant palaeocurrents (text-fig. 8) on the surface of a lithified or semilithified carbonate mud.

### 6.6.4. The Lettenkeuper bone-beds

Within the Lettenkeuper (Upper Triassic) of West Germany (Crailsheim - Rothenburg, text-fig. 8) a number of bone-beds have been recorded (Reif, 1969; 1974) within the Keuper regression sequence. These will be considered from the base (1.) of the sequence as follows:

1. Vitriolschiefer Bone-Beds

   The Vitriolschiefer is a dark clay rich in vertebrate material. In its middle section it contains a deposit ( ≤ 15 cm thick) termed the Plattenhorizon, which contains 3 - 5 thin bone-beds varying in thickness from 0.1 to 1 cm. The Plattenhorizon is a rippled clayey silt layer resting with an erosive base on the underlying shales. The bone-beds contain little pyrite or glauconite (Reif, 1969) and are frequently associated with lingulid and bivalve shells and shell fragments. They contain a rich fauna of perfect and worn fish fragments with some rolled phosphatic nodules (?coprolites). Vertebrate fragments are in the size range 0.2 to 44 mm.

2. Blaubank Bone-Beds

   Within the Blaubank thin bone-beds ( ≤ 1 cm thick) are present (rarely more than one bone-bed at a given section). Their matrix varies from that of a shelly dolomite to a dolomite sand and contains fragments of vertebrate material (varying from perfect to trite fragments and specimens), 0.1 to 40 mm in length.

3. Dolomitischen Mergelschiefern

   Bone-beds are rare within the Dolomitischen Mergelschiefern. They occur as thin layers ( ≤ 4 mm thick) of largely unworn vertebrate fragments (bones, teeth and scales), 0.5 - 6 cm long, in a sandy matrix.

4. Unteren Dolomiten

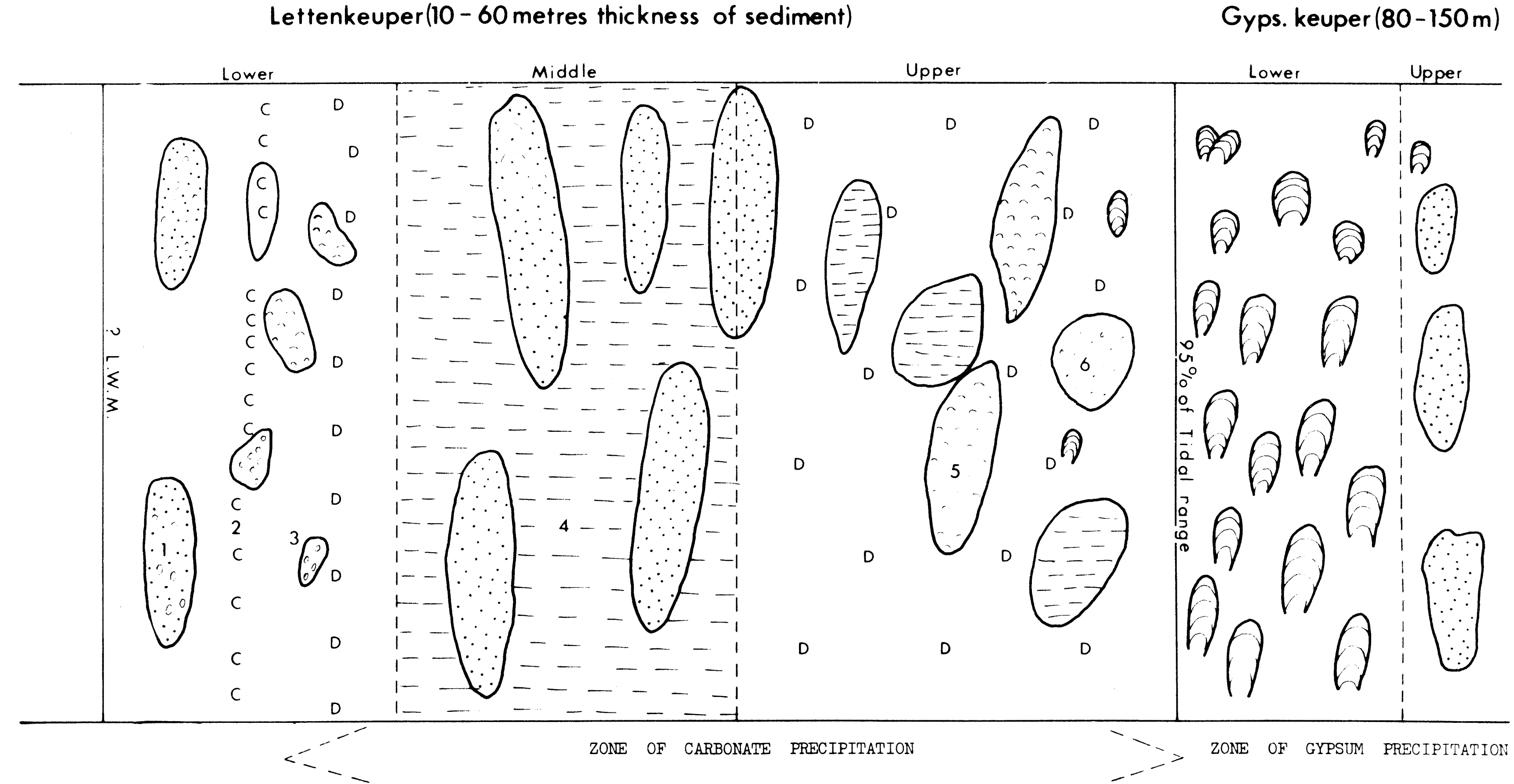
   Bone-beds are very rare in the Unteren Dolomiten but when present consist of a rippled vertebrate quartz sand ( ≤ 1 cm thick) with a dolomitic matrix. The vertebrate fragments are in the size range 0.4 to 8 mm and are poorly abraded, consisting largely of teeth and scales.

5. The Estherien-Schichten

   Within the Estherien-Schichten bone-beds are very rare, though occasionally thin vertebrate lags are found underlying the sandstone layers. These lags consist of coprolites, unworn vertebra, teeth and scales, in the size range 0.6 to 38 mm and are rarely more than one layer thick (1 - 40 mm thick).

6. The Upper Lettenkeuper

   At Michelbach (text-fig. 8) a vertebrate rich carbonaceous black clay (30 cm thick, containing 29% vertebrate remains) occurs in a sequence associated with some gypsiferous and dolomitic algal stromatolites, dolomites and thin shell layers. The horizon is rich in broken fish scales (*Gyrolepis quenstedti* Dames), 0.4 to 3 mm across, and sharks jaw bones (pl.16, fig.g) of *Acrodus lateralis* Ag.



| | | | | |
|---|---|---|---|---|
| Structure | Parallel Ripple Lamination + Lenticular Bedded Horizons | Trough Cross Bedding and Parallel Lamination | Rare Algal Stromatolites, Parallel & Rippled Lamination | Algal Stromatolites |
| Environment | Foetid Mudflats with vertebrate sand sheets and rare shell sheets | Foetid Mudflats containing Migrating Perched Sand Bodies and shell sheets (?high intertidal) | High Mudflat zone with shell sheets, dolomitic muds and foetid black muds (?supratidal) | Supratidal |

Text-fig. 9. An environmental model for bone-beds in the Lettenkeuper. C = Carbonate precipitation. D = Dolomite precipitation.
1 = Vitriolschiefer Bone-beds, 2 = Blaubank, 3 = Dolomitischen Mergelschiefern and Unteren Dolomiten,
4 = Estherien - Schichten, 5 = Shell sheets in the Upper Lettenkeuper, 6 = Muddy Bone-beds in the Upper Lettenkeuper e.g. Michelbach Bone-Bed.

### 6.6.5. Environmental model for the Lettenkeuper bone-beds

Examination of the lower part of the Upper Triassic sequence of West Germany (i.e. the Lettenkeuper) shows a regression sequence passing up from the black shales of the Vitriolschiefer into a dolomitic sequence (The Blaubank to Unteren Dolomiten), containing primary carbonate or gypsum crystals (Reif, 1974). The overlying black shales contain thin shell and sand layers and trough cross-bedded sand wedges (1 - 2 m thick), rich in plant fragments (The Estherien-Schichten). These black shales and sandstones are overlain by a sequence of dolomitic marls containing rare stromatolites, black shales and shell beds, the Upper Lettenkeuper. In turn these sediments are overlain by a thick sequence of gypsiferous algal stromatolites in red and green clays, the GipsKeuper. The Lettenkeuper is interpreted as a regression sub-to supratidal sequence in text-fig. 9, deposited in a region of low terregenous sediment input.

Examination of the shell deposits in the Lettenkeuper show them to represent either a liptocenosis or taphocenosis occurring as shell sheets (0.2 - 5 cm thick). The invertebrate composition of these shell sheets and the Lettenkeuper sediments is outlined in Table 10, p.126 Examination of the shell orientations show that 80 - 100% of the shells are orientated concave down. The size distributions of the shells show that shell deposits low in the intertidal zone (e.g. in the Vitriolschiefer) are markedly transported (cf. Antia & Wood, 1977; Alexandrowicz, 1978) while those in the Upper Lettenkeuper are not; thus suggesting that the amount of shell transport decreases up the intertidal zone! Examination of the bone-beds also shows a similar pattern with the percentage of unworn vertebrate remains increasing up the intertidal zone.

### 6.7. Rhaetic bone-beds

Rhaetic bone-bed deposits have been recorded in Germany, Switzerland, France, Luxemberg, Britain and Poland (Duffin & Gazdzicki, 1977). In West Germany a bone-bed marks the Rhaetic/ Liassic boundary whilst in Britain bone-beds are found in the lower parts of the Rhaetic. Bone-beds from these two countries are perhaps the best known of the Rhaetic bone-beds and were formed on the margin of the Rhaetic sea (text-fig. 10a).

### 6.7.1. West German Rhaetic Bone-bed

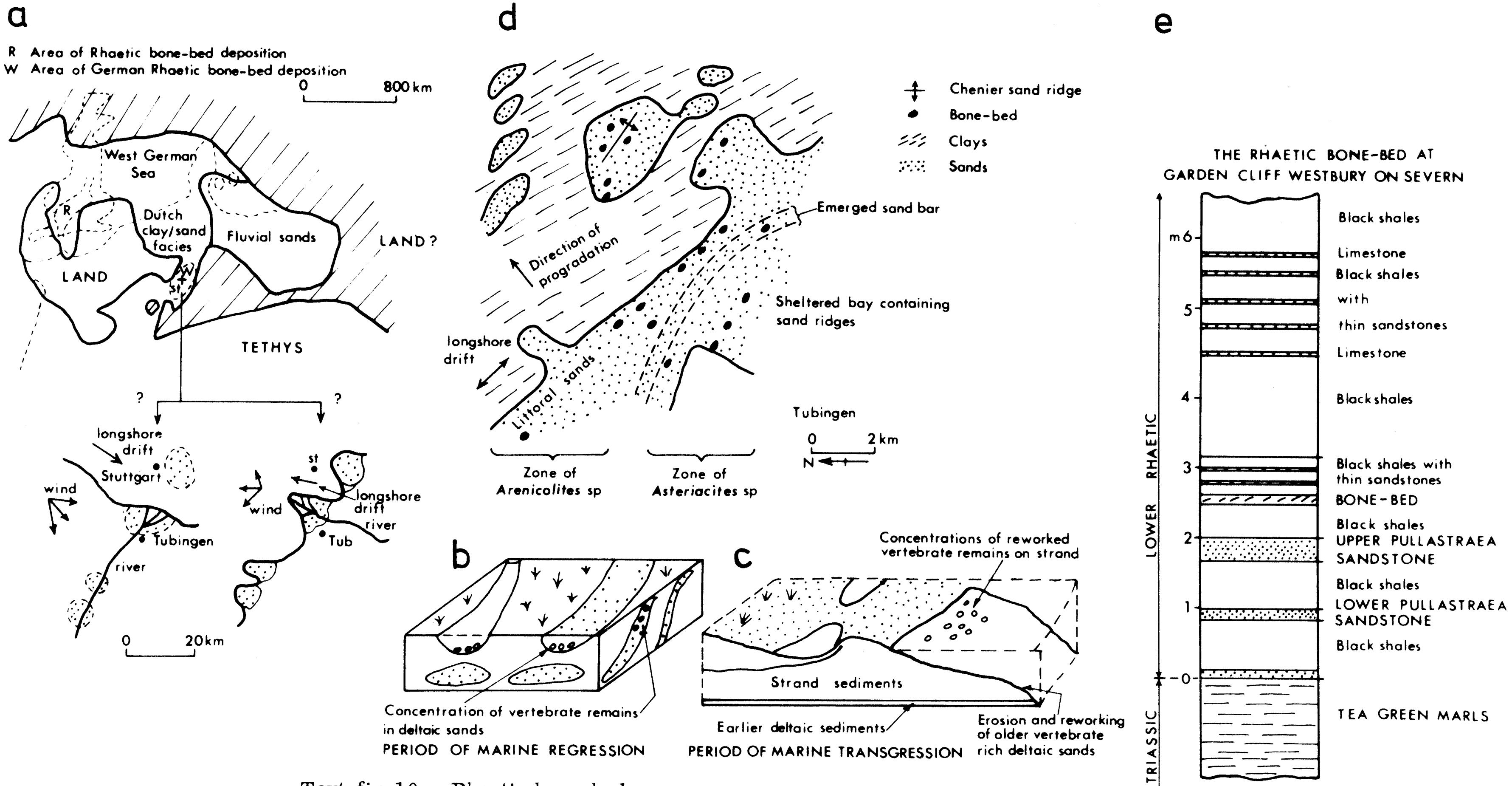
In West Germany the bone-bed (text-fig. 10a) has been extensively described both from a palaeontological (Endlich, 1870; Schmidt, 1928; Huene, 1933; Reif, 1977) and sedimentological (Aepler, 1974) stance. Vertebrate fragments are found in association with a molluscan fauna of *Rhaetavicula contorta* (Geyer & Gwinner, 1968; Aepler, 1974).

The vertebrate remains commonly have a size range 0.125 - 0.25 mm, though fragments in excess of 2 cm in length are known and include worn and unworn remains of the sharks *Hybodus* and *Acrodus*, the dipnoid fish *Ceratodus*, the ganoid fish *Saurichthys* and the reptiles *Triglyphus* and *Microlestes*. (Schmidt, 1928; Geyer & Gwinner, 1968).

During his study of the sedimentology of Rhaetic bone-beds Aepler (1974) observed three different environmental settings for bone-bed deposition, viz:

1. Lagoonal placer deposits,
2. In deltaic deposits during periods of regression,
3. In intertidal chenier plain type sediments deposited during periods of transgression,

and suggested the following model to account for the deposition of the German bone-beds. Aepler (1974) envisaged an initial deltaic model (text-fig. 10b) of sediment deposition in which primary vertebrate deposits were included in lagoonal sediments deposited in small lagoons between channels in a prograding Rhaetic delta during period of stable or falling sea level. Channel switching caused by transported sediment choking the river channels may have preceded the reworking of vertebrate remains in the lagoonal sediments causing them to be redeposited within a sequence of deltaic sands (text-fig. 10b). Subsequent rises in sea level led to a marine transgression. The net outcome of this transgression was a reworking of vertebrate



Text-fig.10. Rhaetic bone-beds.

a = Palaeogeography of the Rhaetic oceans.
b = Regression Delta bone-beds.
c = Transgression Delta bone-beds.
d = Facies distributions in the German Rhaetic intertidal zone.
e = Section through the British Rhaetic Bone-bed.

material in the deltaic sands (text-fig. 10c) and its migration and concentration on a chenier-like coastal plain (text-fig. 10d), containing chenier sand dunes up to 1 m high and 2 to 8 km long. The vertebrate concentrates occur in the sandy facies of the coastal plain and form both uni- and bi-modal deposits with a mean size skewness distribution indicative of a littoral beach or dune sand environment. Two trace fossil faunas have been recorded which appear to be depth stratified (text-fig. 10d). The fauna occurring in the higher part of the intertidal zone is of *Arenicolites*, a U-shaped burrow resembling those produced by *Corophium* in the model intertidal zone. Like *Corophium* its modern ?equivalent, *Arenicolites* occurs on small muddy banks within the zone some 5 - 20 cm high. The lower part of the Rhaetic intertidal or high subtidal zone contains *Asteriacites* (ophorioid nesting traces).

### 6.7.2. British Rhaetic Bone-Beds

British Rhaetic bone-beds have been recorded in Somerset, Gwent, Glamorganshire, Dorset, Leicestershire, Nottinghamshire, Yorkshire and Northern Ireland (Sykes, 1977; Arkell, 1933). In Scotland vertebrate remains do occur (Tyrrell, 1928), but not in sufficient quantities to constitute a bone-bed. The Rhaetic bone-beds have been the subject of many reviews (e.g. Wickes, 1904; Sykes, 1977; Hamilton, 1977) and are most abundant in the Lower Rhaetic. (Sully and Westbury Beds - Table 12).

Table 12. The divisions of the British Upper Triassic.
(after Kent 1968, Taylor 1968)

| | Ostracod Zone | Lithological Unit | Thickness |
|---|---|---|---|
| Upper Rhaetic | *Hungarella moorei* | Watchet Beds | 0 - 2.3 m |
| | | Langport Beds | 0 - 8 m |
| | | Cotham Beds | 0 - 8 m |
| Lower Rhaetic | *H. bristolensis* | Westbury Beds | 0.3 - 15 m |
| | *H. martini* | | |
| | *Rhombocythere penarthensis* | Sully Beds | 0 - 4.2 m |
| 'Keuper' | - - - - - - - - - | Tea Green Marls | 3 - 30 m |
| | | Red marls(undiff) | 10 - 170 m |

They are contained within a sequence of interbedded black shales, sandstones and limestones (text-fig. 10e). Much of the vertebrate fauna present in the bone-beds and associated strata has been illustrated by Schmidt (1928) and Duffin (1978).

Many theories have been proposed to account for the origin of these bone-beds ranging from a sudden massacre of vertebrates, to a temporary abundance of vertebrate life, to a condensation deposit. Likewise many different environmental models for the Lower Rhaetic have been proposed. These range from deposition in an anoxic subtidal environment (Kendall & Wroot, 1924) through to deposition on an intertidal mudflat (Short, 1904; McKerrow, 1978). The Keuper - Rhaetic - Liassic sediments of Britain are commonly considered to represent a marine transgression, which started in the ?late Keuper (Arkell, 1933).

Prior to this marine transgression, central and southern Britain formed a very extensive sabkha environment (Nickless *et al.*, 1976; Jeans, 1978) which deposited the Keuper Marls and resulted in the formation of evaporite deposits. This period of stable water level and sabkha formation was succeeded by a gradual relative increase in sea level, which led to a marine transgression over the sabka plain from south to north, such that an ostracod zone of the standard Rhaetian sequence is missing from the Nottinghamshire Rhaetic rocks (Anderson, 1964). The absence of this zone does not imply a faunal break at the junction of the Tea Green Marls and the Rhaetic, but rather a later arrival of the transgressive marine sediments in this area.

Commonly the 'start' of the marine transgression is marked by a 2 - 3 cm thick layer of vertebrate rich marl (Richardson, 1911), which is succeeded by 3 - 4 m of unfossiliferous marlstones and may have been deposited in a supratidal environment. The succeeding sediment is a bone-bed containing pebbles of the underlying marl and remains of the fish *Hybodus*, *Acrodus*, *Gyrolepsis* and *Ledidotus* and the mollusc *Rhaetavicula contorta*, and may represent a transported deposit formed low in the intertidal zone. The overlying sediments consist initially of interbedded sandstones and shales containing shell beds of *R. contorta* and *Pleurophorous* in association with ?darwinulid ostracods (Richardson, 1911; Anderson, 1964) which may represent an oligohaline to mesohaline intertidal environment (Morkhoven, 1963). The sands and shales are succeeded by black shales containing interbedded, lenticular bedded and flaser bedded shelly limestones, bioturbated sandstones and bone-beds, including *the* Rhaetic Bone-Bed.

Faunal diversity increases up the sediment sequence, and the fauna includes a number of mesohaline to fully marine ostracods (Anderson, 1964; Morkhoven, 1963), numerous trace fossils (pl.16, fig.c; pl.19, fig.h), the coral *Heterastraea* (Richardson, 1905), the molluscs *Protocardia rhaetica*, *R. contorta*, *Chlamys valoniensis*, *Cardium cloacinum*, and the starfish *Ophiolepis damesii* (Harrison, 1876). In Arran the ?Westbury Beds contain the estherid *Isuara minuata* (Newton, 1901). This latter species occurs, in association with plant debris in the Bristol district (Sollas, 1901) and, in great abundance in the Cotham Beds (Arkell, 1933), which are considered to represent an intertidal deposit (Mckerrow, 1978).

The bone-beds vary in thickness from 0.1 to 15 cm, are locally flaser bedded and consist of dark muddy quartz sands locally enriched in vertebrate fragments (pl.16, figs. f,g,h), coprolites (containing shell gragments, crustacean and vertebrate remains, and quartz grains), and phosphatic nodules.

The vertebrate remains vary from perfect to highly abraded teeth, scales and bones belonging to reptiles, elasmobranch, ganoid and dipnoid fish. The reptile remains present include vertebra of the archosaurian *Rysosteus*, and teeth and bones referable to *Ichthyosaurus* and *Plesiosaurus* (cf. Arkell, 1933; Duffin, 1978). The fish remains include the teeth and fin spines of the hybodont sharks *Hybodus*, *Acrodus* and *Nemacanthus*; the earliest euselachian sharks *Pseudodalatias barnstonensis* (Sykes), (Sykes, 1971, 1974; Reif, 1978); the ganoid fish (primitive boney fish) *Bigeria* and *Gyrolepis* and dental plates of the dipnoid lungfish *Ceratodus*.

It has been suggested (Wickes, 1908; Kendall & Wroot, 1924; Neville, 1967) that the rounded vein quartz pebbles present in the bone-beds could be stomach stones (gastroliths) which were swallowed by marine reptiles to aid digestion (Wieland, 1907).

Many hypotheses have been advanced to account for the bone-beds. These include (1) mass mortality due to the effects of increased salinity as the 'marine' animals entered the hypersaline Keuper lakes (Jukes-Browne, 1892), (2) formation as a storm deposit (Short, 1904; Neville, 1967), (3) concentration due to a reduced rate of sediment deposition (Richardson, 1901; Kendall & Wroot, 1924; Arkell, 1933), (4) concentration due to wave action (Donovan, 1955; Hamilton, 1977), (5) lag concentration resulting from the reworking of vertebrate poor sediments (Duffin & Gazdzicki, 1977) and (6) a mass mortality caused by reduced salinity resulting from an influx of fresh water (Kent, 1968).

The bone-beds are often local in extent (Arkell, 1933) and are highly variable in composition, for example, Short (1904) notes that at Redland (ST 585753) *Acrodus minimus* is the dominant vertebrate, while at Chipping Sodbury and Penarth (ST 186697) *Saurichthys* and *Sphaerodus minimus* are the dominant forms respectively. This variability coupled with the knowledge that in 1867 a violent storm in the Bay of Fundy drove fish into shallow water and onto the shore, so that fish were piled to a depth in excess of 30 cm on the coast, led Short (1904, p.182) and later Neville (1967) to suggest that bone-beds result from storm deposition in shallow coastal waters. The presence of numerous local islands in the Rhaetic sea (Richardson, 1901; Arkell, 1933) some of whose coastlines are closely associated with bone-bed localities (Richardson, 1901; Sykes, 1977) gives credence to this model. The presence in the bone-beds of mudballs (Short, 1904) and bone-bed material infilling sun cracks (Woodward, 1888) appears to confirm a coastal or mudflat depositional site for some of the bone-beds, (Greensmith & Tucker, 1973).

Hamilton (1977) came to the conclusion that the bone-beds are formed as strand line deposits, which have been winnowed and abraded by wave action and shore line currents, and that some of the vertebrate material may have been derived through a reworking of the Keuper sediments. However, it is possible that some of the bone-beds represent subtidal deposits (Duffin, pers. com. 1978).

If Kents (1968) environmental model for the Westbury Beds is accepted here, then the Westbury Beds represented a broad shallow estuarine environment containing small islands, and considerable local variation in temperature, salinity and oxygenation, in which circulation was impeded by widespread growth of aquatic weed. Such an environment is inherently unstable. Fluctuations in any of the physical or chemical variables in the environment (e.g. oxygenation, temperature, salinity, etc) caused by any number of external or internal processes (e.g. a storm, a plankton bloom, etc) could have resulted in a fish mortality and ultimately concentration of the fish remains into a vertebrate sand (bone-bed) of local extent in both subtidal and intertidal environments (Wells, 1944).

### 6.8. Middle Jurassic bone-beds on the Scottish Island of Eigg (text-fig. 11)

The presence of a bone-bed on the Island of Eigg in the Middle Jurassic *Mytilus* shales of the Great Estuarine Series was first noted by Miller (1858; p. 75 & 219). Later work by Barrow & Tait (in Harker, 1908), Hudson (1962; 1963a, b; 1964; 1966) and Hudson & Harris (in press) has described their faunas and established the bone-beds stratigraphical position.

Hudson (1966) records 3 vertebrate rich (bone-bed) horizons (labelled 1 - 3) which he considers to have been deposited in a coastal lagoon.

#### Bone-bed 1 (Hugh Millers Reptile Bed)

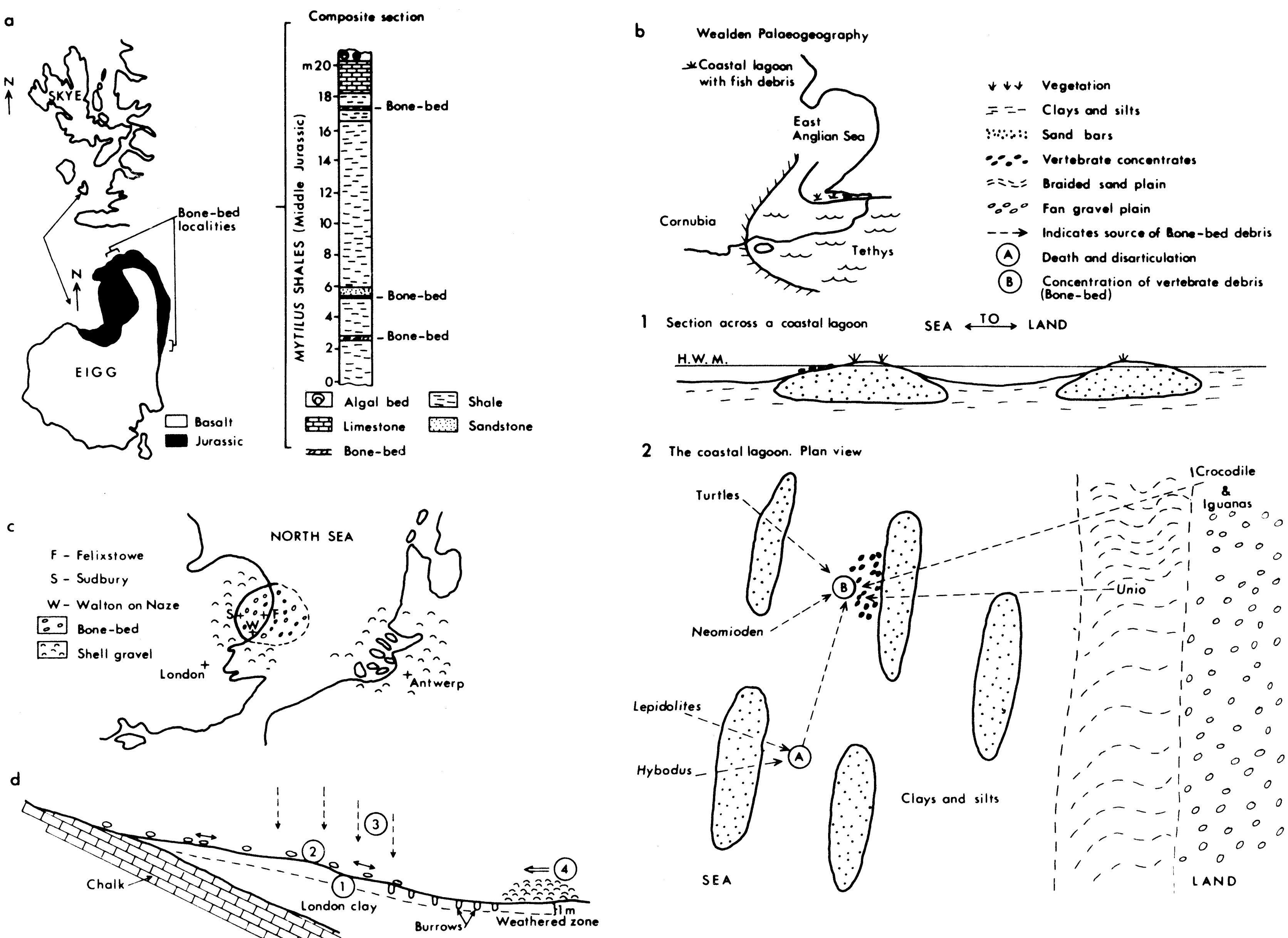
A vertebrate rich dark grey shelly limestone, 15 cm thick, extending for at least 3 km laterally. The vertebrate component is black in colour (?fluorapatite or ?francolite) comprising phosphatic fish teeth, scales and fin spines, and reptilean bones. The dominant fish include the sharks *Hybodus*, *Acrodus* and the holostean *Lepidotus*. The reptile remains include disarticulated specimens of plesiosaurs, turtles, tortoises, crocodiles and pterodactyls. The bones and fish remains are fragmented (Hudson, 1966; p. 276). Secondary pyrite is common throughout the deposit and has replaced some of the shells (e.g. ostracods). The invertebrate shell component of the bone-beds contains abundant small gastropods (*Globularia hebridica*, *Cylindrobullina inermis* and *Tornus praecursor*) and bivalves (*Unio andersoni* and *Mytilus strathairdensis*). Hudson (1963a, b) regards the gastropods as euryhaline species; *Mytilus strathairdensis* is considered (Hudson, 1963a, b) to have lived in brackish marine water (salinity between 16.5 and 9 pp. thousand) and *Unio andersoni* is considered (Hudson, 1963a, b; Tan & Hudson, 1974) to have lived in freshwater (salinity 0.5 - 3 pp. thousand). If this conclusion is correct then postmortum intermixing of brackish and freshwater species must have taken place during the processes forming the bone-bed.

#### Bone-bed 2 (The Complex Bed)

The lowest parts of the Complex Bed (text-fig. 11) consist of well rounded quartz grains associated with abundant rounded partly pyritised fragments of fish phosphate associated with *Mytilus strathairdensis* and may have been deposited in brackish marine waters (Hudson, 1966).

#### Bone-bed 3 (The Fish Bed)

A *Mytilus* shell limestone (5 cm thick), containing abundant black phosphatic fish debris (about 10% by volume). This debris consists of fish otoliths and the teeth, spines and scales of the sharks *Hybodus* and *Acrodus*. Most of the sharks teeth are worn and the abundance of *Mytilus* may suggest that the bone-bed was formed subtidaly in brackish marine conditions.



Text-fig.11. For explanation see facing page 137.

## 6.9. The Wealden Bone-beds (Cretaceous)

Within the Wealden Beds of Britain a number of bone-bed horizons have been recorded (Allen, 1949; 1975). These bone-beds may be described as buff sands, poorly sorted, containing commutated scales, teeth and bones (1 - 45 mm in length) of *Lepidotus* and *Hybodus*; the bones and teeth of reptiles (crocodiles, turtles and iguanas) and teeth of small mammals. They are associated with detritial quartz, glauconite, the casts/moulds of the molluscs *Viviparus*, *Neomiodon* and *Unio*; and abundant ostracod carapaces of *Theriosyrioecum fittoni* (Mantell) (Allen, 1949; 1975; Anderson, 1964).

Originally these deposits were considered to be the product of floods shifting over a subareal deltaic plain, containing scattered evershifting lagoons (Kirkaldy, 1939) and were regarded as freshwater - brackish water estuarine deposits by Allen (1949). However, analysis of the clasts show that the deposits contain multienvironmental components:

1. *Hybodus* is generally considered to be a marine shark (Duffin, pers. com. 1977).
2. *Lepidotus* is found in sediments containing freshwater and marine shells (Allen *et al.*, 1973) and may be a euryhaline form.
3. The reptiles noted could all be found in a littoral or deltaic environment, and the mammals noted were presumably terrestrial.
4. The glauconite is considered to be a derived component from eroded Jurassic strata. The individual glauconite grains represent abraded foraminiferal moulds (Allen *et al.*, 1964).
5. The molluscs noted belong to the following salinity environments:
   (1) *Unio* - fresh water environments (Hudson, pers. com. 1975)
   (2) *Viviparus* - fresh brackish water environments (Allen & Keith, 1964)
   (3) *Neomioden* - marine water environments (Allen *et al.*, 1973)
6. *Theriosynoecum* is a fresh - brackish water ostracod genus (Morkhoven, 1963).

The bone-beds occur as sand lenticles or scour/channel fill deposits on sands in a cyclothemic type sequence:

1. Clay rich in rootlets
2. Bone-beds
3. Cross-bedded sands
4. Ostracod rich dark shales, at base.

This cyclothemic pattern was initially described in terms of an estuarine/deltaic environment (Allen, 1949; 1954), but fits equally well the coastal lagoonal model recently proposed for the Wealden (Allen 1975), text-fig. 11. Using this model the sources of the bone-bed components can be identified and suggest that postmortum faunal mixing due to current and/or wave activity occurred in the Wealden lagoons.

The initial cause of death of the fishes is indeterminable at present though in modern coastal lagoons episodic mass mortalities of fish take place for a variety of reasons every 6 - 14 years (Gunther, 1947).

Elsewhere in the Wealden and on the Isle of Wight, thin layers (0.5 - 3 mm) of fish debris (vertebrae, bones, and scales) are associated with a rich ostracod fauna (observed in conjunction with B.A. Wood).

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Text-fig.11. a. The Geology of the Island of Eigg (After Hudson, 1966). b. An environmental model of bone-bed deposition in the Wealden Beds (Modified after Allen, 1975). c. Location map of the Suffolk Bone-Bed. d. Depositional model for the Suffolk Bone-Bed. 1 = The Miocene/Pliocene North Sea sea-floor of London Clay was weathered and eroded by the sea, excavating phosphatic nodules and vertebrate remainé within the deposit. 2 = These were then rolled around on the sea-floor to form a remains deposit of both worn and unworn derived fossils. 3 = Contributions to the content of the bone-bed were made from the overlying waters. 4 = The bone-bed was then buried by migrating shell sheets composed of commutated shell fragments.

### 6.10. The Suffolk Bone-Bed (Lower Pleistocene)

The Suffolk Bone-Bed occurs at the base of the British (East Anglian) Pleistocene Crag deposits (Chatwin, 1937) and may have been the first British deposit in which vertebrate remains were noted (Ralphe, circa. 1236). The bone-bed was mined for phosphate in the nineteenth century, yielding 3,000 to 12,000 tons annually (Reid, 1890). It may be described as a thin (15 to 30 cm thick) coarse-grained quartz sand (grain size 1.5 to 3 mm), containing well rounded sandstone pebbles (Miocene age; 5 - 26 cm in diameter), flint pebbles, bored phosphatised pebbles of London Clay, phosphatised arthropods (e.g. crabs), black phosphatised sharks teeth, rolled bone fragments, fish dental plates, mineralised and porous bone fragments. Most of the phosphatic pebbles are in the size range 1 to 23 cm. A variety of the phosphatic clasts are illustrated in pl.16, figs. h-p.

Examination of the Suffolk Bone-Bed in the Sudbury district, Walton-on-the-Naze and at Felixstowe (text-fig. 11) allow the following generalisation to be made:

1. The bone-bed rests on an uneven erosional surface which cuts across the London Clay, Reading and Thanet Beds, and the Chalk. This erosional surface on the London Clay undulates and contains small shallow scour channels (up to 1 m in width). The surface is underlain by a 1 m thick weathered zone, and is extensively bored (densities varying between 30 and 300 borings per square metre have been observed at Walton-on-the-Naze). The overlying one-bed consists of a coarse quartz sand with some commutated shell debris, infilling the borings and forming a nodule rich vertebrate sand. The phosphatic clasts are well sorted and tend to be concentrated in hollows on the London Clay surface such that one hollow may contain an abundance of cetean fragments and another phosphatic nodules.

2. The phosphatic clasts in the bone-bed are mainly phosphatised nodules of London Clay, 2 - 12 cm long, usually rounded and bored; cetean bones, 1 - 26 cm long, often mineralised and bored; ear and rib bones are almost always mineralised broken rounded and polished; vertebrae were only recorded as unmineralised light porous bone; sharks teeth, 0.5 - 15 cm long, usually black in colour, varying in preservation from perfect to worn and broken teeth, the first parts to be removed by abrasion being the roots; fish remains (0.5 - 4 cm long) as chiefly worn and rounded dental plates; mammal remains (0.5 - 17 cm long) as worn and rounded teeth and bones; and phosphatised arthropods (replaced crabs, etc).

3. The shell gravels overlying the bone-bed commonly contain articulated, slightly gaping, derived valves of *Glycimeris glycimeris* (pl.18, figs.i-j). The size distributions of these valves suggest that they may represent an indigenous fauna in the shell gravels (Appendix - 1, p.167) which was buried alive during the last major reworking of the shell gravel by currents, etc. (cf. Thomas, 1975). If *G. glycimeris* hasn't changed its life habits since the Pliocene then it is probable that the bone-beds were buried by actively moving, aerobic current swept subtidal shell deposits formed in a shallow shelf sea, between -15 and -75 m O.D. cf. Tebble (1966); Thomas (1975).

4. The bone-bed is overlain by the Pliocene Coralline Crag in the Aldebury/ Orford district (Boswell, 1928) and the Pleistocene Red Crag at Walton-on-the-Naze and elsewhere (Reid, 1890; Harmer, 1900; Boswell, 1928; 1929). Thus suggesting that the top of the bone-bed is diachronous.

### 6.10.1. Depositional model for the Suffolk Bone-Bed (text-fig. 11c, p.136)

The Bone-bed contains a variety of phosphatic clasts derived from a variety of sources. Some of the material has been derived from the London Clay (e.g. the phosphatic nodules, phosphatised arthropods, some sharks teeth and bone), while the remainder has been derived either from now eroded Miocene/Pliocene deposits or has been concentrated in the bone-bed from a contemperaneous fauna. An interpretation of the bone-beds depositional history may be presented as follows:

1. The Miocene/Pliocene sea floor had a base of London Clay which was weathered to a depth of 1 m below the sediment water interface. This clay deposit was extensively attacked by biogenic activity and scouring currents, to produce an extensively scoured and bored surface to the sea floor. Phosphatic clasts derived from the London Clay were concentrated into a well sorted lag deposit on the surface of this sea floor (text-fig. 11). Many of the clasts show signs of marked abrasion. The phosphatic nodules show evidence of 'Pholad' borings (pl.16, fig.k) and along with the cetean rib bones small ( ≤ 1 cm) circular depressions (pl.16, fig.i) which may represent barnacle or limpet 'borings'. Thus the bone-bed contained a rich indigenous fauna, only known from its trace fossils, which colonised a variety of hardground substrates represented by the London Clay, the phosphatic nodules and the vertebrate fragments.

2. Contributions of cetean bones, sharks teeth, phosphatic nodules and fish remains were made to the accumulating bone-bed from the surrounding waters abd the eroded sediments above the London Clay (text-fig.11).

3. This bone-bed or vertebrate sand was eventually buried by migrating shell sheets (text-fig. 11).

Throughout the Red Crag vertebrate remains (rolled sharks teeth, rolled bone and fish dental plates) can be found usually as well rounded black sand grains (1 - 4 mm) and more rarely as readily identifyable remains. Occasionally thin (1 - 2 cm thick) bone-beds are present and contain about 20% quartz sand, 50 - 60% shell, and 20 - 30% vertebrate remains. At Brightwell (GR TM251431, near Ipswich) the bone-bed's vertebrate component is in the size range 0.3 - 4.0 cm and consists of 60% rolled and worn black bone fragments, 30% rolled and worn blue grey and black sharks teeth and 10% rolled and worn fish dental plates. These bone-beds represent lag concentrations on shell gravel surfaces and contain both indigenous and London Clay derived vertebrate remains.

### 6.11. The Rockall Bone-Bed (Recent)

The continental slope sediments around Rockall contain a historically important bone-bed (Lyell, 1834, vol. 3). However, it still remains unsampled in modern times.

Recently, June/July 1978, Dr. G.E. Farrow and colleagues have sampled the continental slope sediments around Rockall. Although they did not record Lyell's bone-bed, they did record a very high concentration (? < 5%) of fish otoliths in the sediment (Farrow, oral com., 1978; Pye, oral com., 1978).

Samples of the sediment and otoliths given to the author for examination, by Dr. Farrow, from 57° 9.2'N 14° 57.6' sampled at a depth of 387 m may be described as follows:

1. The sediment is a carbonate sand (mean grain size 300 ), rich in foraminifera which dominate the sediment (≃ 65%) and occur as whole shells and fragments. Bivalve shell fragments are common (≃ 10%). Lithic fragments, quartz grains and sponge spicules are present (≃ 25%) and the former vary from elongate subangular large (1 mm long) grains to compact high sphero-city well rounded grains (300 $\mu$ long). The remainder of the sediment is made of a mixture of otoliths, shells and small pebbles.

2. Large shells and shell fragments are present ( ≥ 1 cm). The bivalve shell material recorded mainly belonged to the bivalve genus *Artica*. All the bivalve shells were disarticulated (about half were fragmented) and on all specimens the external ornament was starting to flake off. Most of the remaining shell debris belonged to calcareous tube worms. Some of these fragments were colonised by fenestrate bryozoans. Many of the shell fragments contain ?fungal and ?algal micro-borings.

3. Within the sediment are a number of pebbles. These fall into two groups - lithic rock fragments (5 - 20 mm in length) and lithified rounded carbonate pebbles (2 - 6 cm) with the same composition as the surrounding sediment (i.e. that of a foraminiferal quartz sand).

   The lithic rock fragments are sometimes colonised by calcareous tube worms, while the more friable carbonate pebbles may be extensively bored. Boring diameters vary from ≤1 to 5 mm.

4. The fish otoliths present in the sample examined vary in colour from a dull pink to white to cream to cream-grey. They vary in length from 6 mm to 14 mm with a mean length of 9.1 mm. 30% of the otoliths are chipped. They show no evidence of abrasive rounding, though some chip marks are present. The weathering features of the otoliths may be described as follows: (A detailed account of clast weathering in bone-beds is given in section 7)

Five stages of weathering were observed on the otoliths and these stages can be related to those recorded by Behrensmeyer (1978) and summarised in section 7. The proportions of otoliths in each weathering stage, at a number of points in the Rockall Trough, sampled by Dr G.E. Farrow and co-workers, are given in Table 13.

The weathering stages observed form a continuum ranging from unweathered to highly weathered, implying that material is being continually added to the deposit at a very slow rate and that individual otoliths may have lain on the sediment surface for more than 15 years and possibly for several hundred.

Table 13. Weathering stages present on Otoliths from the seabed near Rockall. Key to the weathering stages is given in Table 14, p.142.

| Locality | Depth | Sample Size | Weathering Stage 0 | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|---|---|
| 57° 9.2'N 14° 57.6'W | 387 m | 21 | 0 | 31 | 69 | 0 | 0 | 0 |
| 57° 36.9'N 14° 0.2'W | 175 m | 1 | 100 | 0 | 0 | 0 | 0 | 0 |
| 57° 28.0'N 13° 07.2'W | 270 m | 11 | 9 | 18 | 54 | 18 | 0 | 0 |
| 57° 3.3'N 15° 0.5'W | 250 m | 21 | 9 | 19 | 62 | 5 | 5 | 0 |
| 57° 34.9'N 14° 30.8'W | 220 m | 40 | 13 | 23 | 50 | 10 | 5 | 0 |
| 57° 37.7'N 13° 37.3'W | 180 m | 28 | 18 | 21 | 36 | 14 | 11 | 0 |
| 57° 19.5'N 14° 51.6'W | 260 m | 11 | 18 | 27 | 27 | 27 | 0 | 0 |

The unweathered otoliths range from unbored to highly bored material, containing gastropod radula marks which often expose a very complex network of fungal borings present just below the otolith's surface (pl.17, fig.6). Some of these otoliths show a mosaic pattern of cracks under the light microscope (weathering stage 1). Most of these cracks are not visible under the Scanning Electron Microscope. However, some of them appear to form the initial sites of concentric outer layer peeling (pl.17, fig.a, weathering stage 2). This peeling becomes very marked on some of the more weathered otoliths (pl.17, figs. d, e) and eventually patchyly exposes the inner structure of the otolith (pl.17, fig.c, weathering stage 3). Continued weathering further degenerates the otoliths exposing just the internal structure and often forming deep cracks (weathering stage 4).

Thus it could be inferred from the data presented here that the Rockall Bone-Bed described by Lyell (1834) may present a similar set of weathering, abrasion and microbiotal features and represent a condensation deposit.

### 6.12. Bone-bed genesis - a conclusion

Bone-beds have been recorded in a variety of subtidal and intertidal environments and tend to form as lag concentrates. They may result from the reworking of older, vertebrate poor, sediments to produce a secondary bone-bed or form from a primary concentration of drifting vertebrate material on the seafloor. However, examination of the bone-beds through time suggests that no single model of bone-bed genesis will suffice and that for most of the deposits insufficient data exists for a valid environmental model of bone-bed genesis to be made.

## 7 - Bone weathering

Vertebrate remains, including bones, decompose on and in the sediment. This decomposition, which forms a normal part of nutrient recycling within the oceans, also determines whether or not a bone will survive to become fossilised. The fossilisation of bone is therefore dependant on the intensity and rate of the various destructive processes and the chance for permanent burial prior to total destruction. In this context the term bone embraces teeth and scales.

At the present time little is known about how these processes affect bones or how they may consequently bias the vertebrate fossil record in bone-beds. As a result most authors (e.g. Wells, 1944; Reif, 1969, 1971, 1976; Aepler, 1974; Allen, 1974a; Sykes, 1977; Antia & Whitaker, 1978) have ignored suggestions (e.g. Behrensmeyer, 1978) that some grain size biasing in vertebrate assemblages could be due to weathering. Instead they regard wave and current activity as the primary cause of grain size biasing in bone-beds.

Following recent advancements in the study of the bone weathering, Behrensmeyer (1978, p.151) has outlined a time related six stage scale of bone weathering, and the features characterising each weathering stage are listed in Table 14, p. 142. The establishment of a time related scale of bone weathering has important implications for future bone-bed research because it enables:

1. an estimate of the time interval between the death of the fish and the permanent burial of the bone-bed to be made;
2. it enables the amount of grain size biasing in a bone-bed caused by weathering to be assessed;
3. it may help to determine whether or not a given bone-bed developed as a 'direct' result of a mass mortality.

For the purposes of this study a preliminary examination of bone-bed weathering has been made by the author, to assess the practical value of weathering as a tool for the interpretation of bone-beds.

Table 14. Weathering stages observable in a variety of bone-beds.
Weathering stages 0 - 5 are explained as follows (after Behrensmeyer, 1978):

| | |
|---|---|
| 0 | Vertebrate material shows no sign of cracking or flaking due to weathering. |
| 1 | Cracks parallel to the fibre structure appear. In some bones a mosaic cracking of surfaces may develop. |
| 2 | Outermost thin concentric layers of cyamine show flaking, usually with cracks in the initial stages. |
| 3 | The internal fibrous structure starts to appear patchily over the 'bone' surface. |
| 4 | The fibrous structure of the 'bone' is clearly visible. Weathering has penetrated the inner cavities, cracks are open and have splintered or rounded edges. |
| 5 | Vertebrate material falls apart, in situ, is fragile, and easily broken by moving. |

| | | Weathering Stages | | | | | |
|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4 | 5 |
| 1. | Upper Whitcliffe Bone-Beds (Ludlow Series, Upper Silurian, U.K.) | | | | | | |
| | *Thelodus* spp. (scales) | + | + | - | - | - | - |
| | *Logania* sp. (scales) | + | + | - | - | - | - |
| | ?*Gomphonchus* sp. (spine fragments) | - | + | + | - | - | - |
| 2. | Ludlow Bone-Bed (Downton Series, Upper Silurian, U.K.) | | | | | | |
| | *Thelodus* spp. | + | + | + | - | - | - |
| | *Logania* spp. | + | + | - | - | - | - |
| | ?*Gomphonchus* sp. (fragments) | - | + | + | + | - | - |
| | *Gomphonchus* sp. (scales) | + | + | - | - | - | - |
| | *Gomphonchus* sp. (fin spine) | - | - | + | + | + | - |
| | *Nosteolopis* sp. (scale) | + | + | - | - | - | - |
| | *Cythaspis* sp. (headshield) | - | - | - | + | + | + |
| 3. | Lower Downton Castle Sandstone Bone-Beds (Downton Series, Upper Silurian, U.K.) | | | | | | |
| | *Thelodus* spp. (scales) | + | + | + | - | - | - |
| | *Logania* sp. (scales) | + | + | - | - | - | - |
| | *Gomphonchus* sp. (fragments) | - | + | + | + | - | - |
| | *Gomphonchus* sp. (fin spine) | - | - | + | + | + | - |
| | *Sclerodus* sp. (headshield) | - | - | - | - | + | + |
| | *Cythaspis* sp. (headshield) | - | - | - | + | + | + |
| | *Climatius* sp. (fin spine) | - | - | + | + | + | - |
| 4. | Temeside Bone-Bed (Downton Series, Upper Silurian, U.K.) | | | | | | |
| | *Thelodus* sp. (scales) | - | - | + | + | - | - |
| | *Logania* sp. (scales) | - | + | + | - | - | - |
| | *Climatius* sp. (fin spine) | - | - | - | + | + | + |
| | *Gomphonchus* sp. (fin spine) | - | - | - | + | + | - |
| | *Gomphonchus* sp. (fragments) | - | - | - | + | + | - |
| | *Cythaspis* sp. (fragments) | - | - | - | + | + | - |
| 5. | Muschelkalk Grenzbonebed (Middle Triassic, West Germany) | | | | | | |
| | *Acrodus* spp. (teeth) | - | + | + | - | - | - |
| | *Hybodus* sp. (teeth) | - | + | + | - | - | - |
| | *Gyrolepis* sp. (scales) | - | - | + | + | - | - |
| | *Colobodus* sp. (scales) | - | + | + | + | - | - |
| | *Saurichthys* sp. (teeth) | - | + | + | - | - | - |
| | Reptilian bones | - | - | - | + | + | - |
| | *Acrodus* sp. (fin spine) | - | - | + | + | - | - |
| 6. | Lettenkeuper Bone-Beds (Upper Triassic, West Germany) | | | | | | |
| | *Acrodus* spp. (teeth) | - | + | + | - | - | - |
| | *Acrodus* sp. (jaw bone) | - | - | - | + | + | - |
| | *Gyrolepis* sp. (scales) | - | - | + | + | - | - |
| | Reptilian bones | - | - | - | + | + | - |
| 7. | Rhaetic bone-beds (British and West German) | | | | | | |
| | *Acrodus* sp. (teeth) | - | + | + | + | - | - |
| | *Hybodus* sp. (teeth) | - | + | + | - | - | - |
| | *Rysosteus* (fin spines) | - | - | + | + | - | - |
| | Reptilian bones | - | - | + | + | + | - |
| 8. | Suffolk Bone-Bed (Miocene/Pliocene, U.K.) | | | | | | |
| | Sharks teeth var. | - | + | + | + | - | - |
| | Cetean bones | - | - | - | + | + | - |
| 9. | Crag bone-beds (Lower Pleistocene, U.K.) | | | | | | |
| | Sharks teeth var. | - | + | + | + | - | - |
| | Fish dental plates var. | - | + | + | - | - | - |
| | Cetean bones | - | - | - | + | + | - |

## 7.1. Weathering versus abrasion

Bone weathering produces a distinctive set of external features which can be grouped in a number of stages (Table 14). These stages differ from those produced by abrasion in the following respects:

abrasion can produce small chip marks on the grain surface (pl.14, fig.i; 16, fig.f), and/or, remove large chunks off the ends of bone surface (pl.14, fig.o; 16, fig.g), and/or, round individual grain surfaces (pl.15, fig.l; 16, fig.d).

Weathering features are always superimposed on the grain, thus a highly rounded and abraded bone fragment need only show (pl.15, fig. j) features associated with weathering stage 1 (cracks parallel to the fibre structure), while a less abraded scale (pl.14, fig.o) can show features associated with weathering stage 2 (outermost thin layers of cyamine start to peel off). Similar weathering stage 2 features are also present on highly abraded bone fragments (pl.16, fig.d). Weathering can also aid abrasive processes. Another example, (pl.16, fig.b) illustrates a tooth which, having reached weathering stage 1, split along a crack parallel to its fibre structure during an abrasion phase in its depositional history. Thus weathering and abrasion both produce distinctive features which may be superimposed on each other.

## 7.2. Assessing differential weathering

Differing bone types can weather at slightly different rates (Behrensmeyer, 1978, p.153). Similarly differential weathering can occur on a single bone. In the latter case the bones are usually more weathered on the lower than the upper surfaces (Behrensmeyer, 1978, p.154). As a result of the weathering process, vertebrate material could be preferentially destroyed and removed from the deposit it was accumulating in, by weathering, thus biasing the grain size distributions of the deposit. Individual grains could be partially destroyed after accumulation in the bone-bed, before the bone-beds burial, thereby altering the grain size distribution of the deposit. In the Suffolk Bone-Bed sharks teeth, which have had their pulp destroyed by weathering, are present (pl.16, fig.j).

If different types of vertebrate material weather at different rates, an examination of bone-bed cumulates should support this hypothesis. Nine bone-beds were examined with this point in mind and the weathering stages of the various vertebrate components are noted in Table 14.

The results show that in each bone-bed teeth and scales are comparatively unweathered, while fin spines, headshields and endoskeletal bones were markedly weathered. Thus suggesting that either the scales and teeth were more recent additions to the vertebrate faunas or that different vertebrate material weathered at different rates. Since it is unreasonable to suggest that the scales and teeth are more recent additions to the faunas (Reif, 1969; 1971), it is probable that the different types of vertebrate material weathered at different rates. The cyamine outer coatings of the teeth and scales may have helped to shield them from rapid weathering and disintegration, while the less well protected and more fibrous fin spines and bones may have weathered more rapidly.

In all the bone-beds examined (Table 14) it was the least weathered fraction which dominated the fauna. However, since this fraction (usually teeth and scales) represents the smallest grain size elements of the fauna, it may result from a mixture of both current activity, concentrating the finer particles into a unimodal assemblage, and weathering removing some of the less resistant (and sometimes larger) clasts.

The data presented here (Table 14) seems to support Behrensmeyer's (1978) hypothesis that bone weathering can result in or could casue grain size biases in vertebrate assemblages. The palaeoecological implications of such an observation are that prior to compositional reconstructions of marine vertebrate faunas from a fossil assemblage, the extent of faunal depletion due to weathering has to be assessed. Further, a unimodal vertebrate condensation deposit forming in a region of slack current activity could owe its unimodality to weathering rather than sedimentological processes. Thirdly, in some marine vertebrate deposits (e.g. the Ludlow Bone-Bed, the Muschelkalk Grenzbonebed and the Rhaetic Bone-Bed) algal and fungal borings are commonest on the least weathered components of the deposit (Antia & Whitaker, 1978; Duffin, pers. com., 1978) perhaps indicating a substrate preference for poorly weathered material which is likely to be on the sea bed for a long period of time.

### 7.3. Weathering rates

A scale (Table 14) of bone weathering rates has been outlined by Behrensmeyer (1978, p.157). However, in the previous section it was noted that different bone types weather at different rates. Thus for Behrensmeyer's (1978) scale of weathering rates to have any palaeoecological or sedimentological significance a scheme of correction factors has to be developed. To obtain a correction factor value it was assumed that fin spines and bone weather at the same rate in the sea, as those in terrestrial lake bed and soil environments (Table 15).

The dominant weathering peak of these bones was then tabulated against the dominant weathering peak of the teeth and scales (Table 15). From this tabulated data the possible residence time on the sediment surface represented by each weathering stage present on the teeth and scales was determined (Table 15). This theoretical relationship between weathering stage and time may bear little similarity to the real time intervals represented by the weathering scales, but can be used to indicate a relative time sequence of events in the fossil record.

### 7.4. On the significance of weathering stages and rates

An analysis of the relative abundances of each of the various weathering stages on fish scales in a number of bone-beds should give an estimate of the minimum residence time of the scales on the substrate surface. This would then help to determine if the bone-beds formed as the result of a single mortality, a number of mortalities, a condensed sequence, or from the reworking of vertebrate poor sediments.

In each bone-bed listed in Table 16, 150 - 400 thelodont scales were examined for weathering features using a scanning electron microscope and the results recorded in Table 14. The scales were extracted using 30% acetic acid solution from their matrix, then washed in 30% hydrogen peroxide solution. In a test sample taken from the Ludlow Bone-Bed at Ludlow it was shown (Table 16) that there is no significant differences in the weathering features observed on the acid treated scales and on untreated scales present in the sediment.

Most of the results listed in Table 16 show a low incidence of weathering stage 1. The relatively high abundance of weathering stage 0 (up to 94%) may suggest that most of the scales had a low residence time on the substrate ( ≤ 6 years) but the presence of weathered scales in low abundances in stage 1 and 2 suggests that some scales may have been drifting on the substrate surface for more than 6 years.

The presence of abundance peaks in weathering stage 0 and 2 (e.g. Rushall) suggests two major 'short' periods of scale addition to the substrate separated by at least 6 years and may be longer than 15 years (i.e. not a steady inflow of vertebrate material). If the scale assemblages do result from mass mortalities, than 6 - 15 years may indicate the minimum time interval between any two mass mortalities (cf. 7 years recorded between recurring recent mass mortalities by Gunter, 1947).

In almost all the intertidal and shelf bone-beds (i.e. those of the Whitcliffe Beds, Ludlow Bone-Bed, Downton Castle Sandstone) the least weathered scales dominate the faunas, suggesting a fairly rapid ( ≤ 6 years) burial. However, it is interesting to note (Table 16) that the scales in higher intertidal sediments (Ludlow, Downton Castle Sandstone, Bone-beds 11 and 12) are dominated by weathering stage 2, indicating a longer preburial residence period on the substrate. A similar situation is observable in the supratidal bone-beds of the Temeside Beds (Table 16).

### 7.5. Bone weathering - conclusions

Since work on bone weathering and its application is in its infancy, readers are advised to regard the ideas and statements in this section as hypotheses which need testing through additional research on recent and fossil bones. However, the points which should be emphasised are that bone weathering can reveal information regarding the differential weathering and destruction of clasts, and important data concerning the relative residence times of the vertebrate material on the substrate and the genesis of the deposit.

Table 15. Weathering stages related to the number of years since the death of the animal
Column 1 and 2 based on Behrensmeyer (1978)

| Possible range in years since death of the fin spines and bones | Weathering stage present on the fin spines & bones | Weathering stage present on scales and teeth corresponding to equivalent stage on fin spines, etc. | Weathering stage present on scales and teeth | Possible range in years since death of the teeth and scales |
|---|---|---|---|---|
| 0 - 1 | 0 | 0 | 0 | 0 - 6 |
| 0 - 3 | 1 | 0 | 1 | 4 - 15$^+$ |
| 2 - 6 | 2 | 0/1 | 2 | 6$^+$ - 15$^+$ |
| 4 - 15$^+$ | 3 | 0/1/2/3 | 3 | 6$^+$ - 15$^+$ |
| 6 - 15$^+$ | 4 | 1/2/3 | 4 | |
| 6 - 15$^+$ | 5 | 1/2/3 | 5 | |

Table 16. Percentages of Thelodont scales in each weathering stage.

| | | | Weathering Stage (%) | | | | Locality |
|---|---|---|---|---|---|---|---|
| | | | 0 | 1 | 2 | 3 | |
| Ludlow Bone-Bed (L.B.B.) | | | 85 | 10 | 5 | - | Ludlow |
| | | | 87 | 9 | 4 | - | Ludlow (untreated) |
| | | | 64 | 26 | 10 | - | Aston Munslow |
| | | | 62 | 24 | 14 | - | Shipton |
| | | | 73 | 16 | 11 | - | Brockton |
| | | | 82 | 11 | 7 | - | Corfton |
| | | | 69 | 6 | 25 | - | Corfton Lane |
| | | | 92 | 4 | 4 | - | Deepwood |
| | | | 94 | 4 | 2 | - | Ashley Moor |
| | | | 44 | 7 | 49 | - | Rushall |
| | | | 78 | 10 | 12 | - | Longhope |
| | | | 62 | 6 | 32 | - | Priors Frome |
| | | | 86 | 8 | 6 | - | Lye |
| | | | 19 | 6 | 75 | - | Usk |
| | | | 89 | 8 | 3 | - | Downton |
| Downton Castle Sandstone | | | | | | | |
| Bone-Bed | 1. | 1 cm above L.B.B. | 58 | 6 | 36 | - | Ludlow |
| | 2. | 3.3 cm " " | 76 | 3 | 21 | - | Ludlow |
| | 3. | 4.9 cm " " | 85 | 1 | 14 | - | Ludlow |
| | 4. | 7.1 cm " " | 81 | 4 | 15 | - | Ludlow |
| | 5. | 8.9 cm " " | 80 | 2 | 18 | - | Ludlow |
| | 6. | 9.1 cm " " | 87 | 5 | 8 | - | Ludlow |
| | 7. | 9.7 cm " " | 92 | 4 | 4 | - | Ludlow |
| | 8. | 10.1 cm " " | 93 | 6 | 1 | - | Ludlow |
| | 9. | 24.2 cm " " | 86 | 5 | 9 | - | Ludlow |
| | 10. | 53.7 cm " " | 84 | 4 | 12 | - | Ludlow |
| | 11. | 110.2 cm " " | 24 | 5 | 71 | - | Ludlow |
| | 12. | 124.9 cm " " | 30 | 4 | 65 | 1 | Ludlow |
| Bone-bed | 1. | 1.2 cm " " | 84 | 6 | 10 | - | Aston Munslow |
| | 2. | 3.6 cm " " | 82 | 9 | 9 | - | Aston Munslow |
| | 3. | 5.9 cm " " | 86 | 7 | 7 | - | Aston Munslow |
| Temeside Shales | (1) | 60 cm below T.B.B. | 3 | 4 | 86 | 7 | Ludlow |
| | (2) | Temeside Bone-Bed (T.B.B.) | - | 5 | 93 | 2 | Ludlow |
| | (3) | 25-60 cm above T.B.B. | 4 | 4 | 82 | 10 | Ludlow |
| Upper Whitcliffe Beds (Upper Ludlow) | | | | | | | |
| | | | 79 | 11 | 10 | - | Longhope |
| | | | 96 | 1 | 3 | - | Ludlow |
| | | | 38 | 18 | 46 | - | Aston Munslow |

## 8 – Diagenesis of bone-beds

In the analysis of bone-bed sediments it is important to consider the diagenesis of the sediment, since many grains change shape, size and composition during diagenesis.

### 8.1. Diagenetic clasts

Biogenic clay or mud pellets produced by the ingestion and excretion of mud by organisms may be transported as detritial particles (Pryor, 1975) and included in bone-bed sediments. These pellets are commonly altered either at the sediment water interface to glauconite (Wilson & Pittman, 1977) or in the sediment pore waters to collophane (Burnett, 1977; Weaver & Beck, 1977). The pellets are ovoid in outline and may contain an internal structure of concentric rings. They have a low grain and bulk density and will be coarser-grained than the associated quartz, fish debris and rock fragments in the sediment. Examples of deposits containing the two types of pellets are a glauconitic bone-bed at the top of the Downton Castle Sandstone in the Brookend bore hole (Cave & White, 1978), and some phosphatic pebble horizons in bone-beds in the Lower Downton Castle Sandstone. In the latter instance the phosphate, collophane, has replaced (Antia & Whitaker, 1978) the authigenic clay structure of the pellet (pl.18, fig.a). Two stages, at least, of diagenesis of the pellet are indicated, by the formation of a honeycomb clay structure in the pellet (before inclusion in the bone-bed?) and by replacement of the honeycomb structure by phosphate (carbonate apatite), possibly after inclusion in the bone-bed.

These diagenetic phosphatic pellets can be distinguished from small phosphorite nodules by an S.E.M. examination of their internal structure. Since phosphorite nodules are formed of a crystalline sheet arrangement of apatite (Baturin & Dubinchuk, 1974), they can be distinguished from coprolites on their gross morphology and internal structure.

Pyrite framboids (pl.18, fig.b) and nodules present in the Ludlow, Lyraun Cove and Rhaetic Bone-Beds are also of an authigenic nature since the nodules are unstable outside an anoxic sulphorous environment (Berner, 1970). Studies on the formation of such clasts suggest that they form in anoxic sulphurous pore waters during early sediment diagenesis at two or more centimetres depth below the sediment water interface and sometimes take years to grow (Berner, 1970; Elverhi, 1977).

Bone-bed residues occasionally contain equidimensional grains (up to 3 mm long) formed of fibrous layers of clays (pl.18, fig.g) approx. 8 - 40 $\mu$ in length. These grains formed as authigenic clay linings or infillings of pores in the sediment (Wilson & Pittman, 1977).

### 8.2. Diagenetic grain coatings

Grains within a stabilised bone-bed sediment (e.g. the Ludlow Bone-Bed) may become coated with layers of authigenic clays or cryptocrystalline silica (Antia & Whitaker, 1978). The clay coatings, which may assume a crystalline, platy or honeycomb structure (pl.18, figs. c,d,e) are absent from grain contacts and coat all grains regardless of composition (Hayes, 1970). In later diagenesis idiomorphic quartz overgrowths may attach to the quartz nuclei (pl.18, fig.h) and cover the clay coatings prior to carbonate sedimentation (pl.18, fig.l).

### 8.3. Diagenetic alteration of grain shape and texture

Diagenetic reactions can alter a quartz grain's shape and texture by either clay or silica plastering (Antia & Whitaker, 1978) such that grain surfaces become smooth or secondarily complex. Silica plastering is a form of grain growth in which the grain is coated by a thin sheet-like layer of silica. Silica plastering on a grain's surface (pl.15, figs. d,e; 18, fig.h) can alter its net shape. Examples of bone-beds containing diagenetically enlarged quartz grains are the Rhaetic and Muschelkalk Bone-Beds (text-fig. 8; pl.15, figs. d,e; 18, fig.f).

Thus examination of the diagenetic history of a bone-bed can explain the presence of glauconitic, phosphatic, pyrite and clay clasts and give an indication of the depositional geochemical environments of the pore waters. Study of the effect of diagenesis on individual grains can aid studies on the genesis of bone-beds (Antia & Whitaker, 1977; 1978) and markedly affect skewness kurtosis and modal values of grain size distributions (Wilson & Pittman, 1977; also text-fig. 8e). Failure to consider the diagenetic history of the sediment can lead to unnecessary complex and erroneous environmental models for bone-bed genesis.

## 9 - The ecological importance of primary bone-beds

Bone-beds comprised largely of fish debris and formed by the disarticulation and concentration of fish remains which died in a catastrophic event are considered here to represent primary deposits. Such mortalities may occur in a given area at rates varying between $1 \times 10^4$ to $1.4 \times 10^4$ per million years (Gunter, 1947) and each catastrophe may kill more than a milliard ($10^9$) fish (Brongersama-Sanders, 1956). In all instances these massive fish deaths, however caused, will 'accurately' reflect the composition of the fish schools in mortalities reaching the benthos (David, 1944) and this composition is reflected in the disarticulated scale faunas resulting from a mortality (David, 1944).

At the present time individual schools of fish vary in size from $0.5 \times 10^1$ to $5 \times 10^9$ individuals; occupy regions varying in length from $0.1 \times 10^1$ to $1 \times 10^6$ m, and occur in densities ranging from 0.1 to 30 individuals per $m^3$. Individual schools may be monospecific or polyspecific, though schools of many species tend to have an unstable composition and readily disband into monospecific groups (Truskanov & Shcherbino, 1963; Radakov, 1973).

Hence a study of bone-bed distribution and composition in an area containing many bone-beds could yield information regarding the composition of schools over an area and the variation of school composition with time.

Similarly, examination of scale lengths and growth lines can give useful full information regarding the natality, mortality and survivorship of a species, in addition to information regarding the effect of predation on the species (Antia & Wood, 1977). Study of these changes can yield information regarding increased or decreased predator pressure on a species, over a period of time. For example, Nikolskii (1969, p. 192) has shown that as the predation rates on a fish species increase, the mean scale size of the fish species decrease.

## 10 - The microbiotas of bone-beds

All sand grains form potential microbial environments and may support a rich biota of bacteria, algae, diatoms, hydroids, fungi, ciliates and other organisms. Of these forms only diatoms and calcareous algae contain preservable skeletons (pl.19, fig.a). Endolithic algae leave recognisable traces in the form of dissolution pits (pl.19, figs.b, e) and borings (pl.19, figs. f-h). Most other forms (e.g. fungi and bacteria) are only likely to be preserved if they are replaced during very early sediment diagenesis by silica or apatite (Antia & Whitaker, 1978).

Two important forms present in modern microbiotas, the diatoms and calcareous algae, are considered to have appeared in the middle to late Mesozoic and are therefore unlikely to be represented in early Mesozoic or Palaeozoic microbiotas.

At the present time different grain types will contain differing microbiotas and ecological successions (Sieburth, 1975). Commonly the biotas are patchily distributed over a grain's surface (Meadows & Anderson, 1966; 1968). Thus:-

1. a piece of wood will show an algal, bacterial, hydroid succession
2. a plastic bottle will show a diatom, bacterial, hydroid succession
3. an oolith will show an algae, bacteria, fungi succession (Bathurst, 1975)
4. carbonate grains from a high energy environment show an algal, diatom, bacteria, succession
5. quartz grains show a diatom, algae, bacteria, ciliate succession. If the grain is from a low energy environment it may be completely covered by its biota. If it is from a high energy environment then the biota is confined to hollows on the grain's surface. If it is from a very high energy environment then only bacteria are present on the grain's surface.

6. vertebrate grains will show a rod-shaped bacteria, algae succession. Both forms use the grain as a source of nutrition (Sieburth, 1975).

In most of these microbiotas the primary colonists produce a nutrient fish film on the surface of the grains which can support bacteria on an originally non-nutrient surface.

In the fossil record, evidence from borings has established the presence of a microbiota on many carbonate grains (Bathurst, 1975) and filaments (?fungal) have been recorded on quartz grains in association with bored vertebrate grains in the British Silurian (Antia & Whitaker, 1978).

An S.E.M. examination of vertebrate quartz and shell grains from the subtidal and intertidal environments represented by the West German Muschelkalk Grenzbonebed (pp.124-128) and the British Upper Silurian Bone-beds (pp.115-119) allowed the following observations and conclusions to be made about the patterns of microbial succession.

### 10.1. Muschelkalk Grenzbonebed (subtidal deposit formed below wave base)

No evidence of a microbial fauna was noted on the scales or quartz grains (7 specimens examined). However, endolithic algal borings were recorded on the surface of one tooth (pl. 15, fig.k). Possible algal borings have also been recorded in teeth (Duffin, 1977; pers.com.) and shell fragments (pl.19, figs.f-h) from the Rhaetic Bone-Bed. (Bone-bed 15 Blue Anchor Bay - Richardson, 1911).

### 10.2. Upper Silurian bone-beds

Two types of Upper Silurian bone-beds occur, subtidal and intertidal, both contain different non-vertebrate clast types and thus a potentially different microbial fauna.

1. Subtidal bone-beds formed above wave base consist of thin shell/vertebrate debris sheets containing a fine grained (5 - 50$\mu$) quartz sand component and a diagenetic carbonate matrix. Study of 1000 - 2000 shell fragments from such deposits revealed 3 fragments all of *Lingula* sp. which had been bored by ?endolithic algae. Examination of the Thelodont scales showed that 10 - 15% of them contained algal dissolution pits and of these about 20% contained endolithic algal borings. This suggests that algae formed the dominant "preservable" elements of the fauna of the microbiota.

2. In the low intertidal zone (e.g. the Ludlow Bone-Bed) both the vertebrate and quartz grains contain evidence of microbial colonisation (Antia & Whitaker, 1977; 1978). The quartz grains may contain silicified ?fungal filaments (pl.18, fig.k) with a distinctive branching pattern. Small silica granules patchily distributed on the surfaces of some of the quartz grains could be interpreted as silicified coccoid bacteria and some of the silicifilament mats present may represent filamentous bacteria. Development of quartz overgrowths on the quartz grains (including their epibiota) is considered to have taken place within a few years of the sediments burial in the substrata, possibly within 20 cm of the sediment water interface.

   Since the filaments cover all surfaces on the grain (i.e. are not confined to cracks and hollows on the grain) it is likely that they represent a colonisation stage within the substratum, which is post sediment stabilisation, within say, 20 cm of the sediment water interface (Meadows & Anderson, 1968).

   An S.E.M. examination of 54 quartz grains revealed 48 containing fungal filaments. Of these latter grains 2 contained "coccoid bacteria" and one "filamentous bacteria". The bacterial colonies are restricted to localised areas, forming colonies of several hundred individuals.

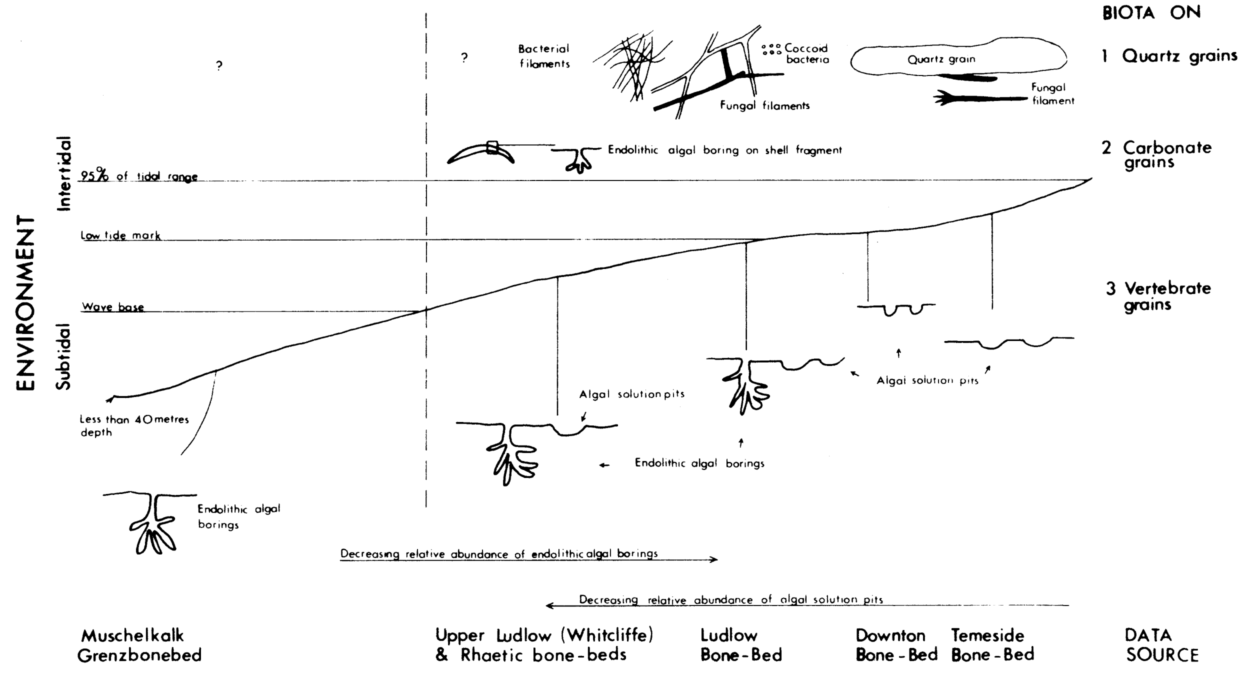
The fungal filaments are found over the entire surface of the grains and probably (in view of their widespread distribution) represent the first stages in the subsurface colonisation of these grains in an anoxic alkali environment. Later succession stages allowed colonisation by coccoid bacteria and bacterial filaments.

The invertebrate fragments show no evidence of microbes though presumably they once contained them, though the phosphatic nodules do contain phosphatised filaments of ?fungal origin (pl.19, fig.k).

The vertebrate fragments contain evidence of algae on their surfaces, both in the form of algal dissolution pits (pl.19, figs. d,e) and algal borings. These latter borings have a larger diameter and are less regularly distributed than histological pores revealed by abrasion.

5 - 40% of the thelodont scales contain algal dissolution pits (termed here Algal Form A) and of these less than 10% contain endolithic algal borings. Thus suggesting that an initial colonisation of the grains by Algal Form A was followed by a subsequent colonisation by endolithic algae, (Algal Form B).

3. Vertebrate and quartz grains from the high intertidal/supratidal zone (e.g. The Temeside Bone-Bed) were examined under the S.E.M. for a remnant microbial fauna. Of 280 thelodont scales examined only one contained evidence of a microbiota in the form of algal dissolution pits and one quartz grain contained two silicified ?fungal filaments (pl.19, figs. i-l) differing in style from those recorded in the Ludlow Bone-Bed.



Text-fig. 12. A general environmental synthesis of microbial biotas in the Lower Palaeozoic and Early Mesozoic bone-beds.

### 10.3 General microbial synthesis (text-fig.12)

In this section a new and speculative field of bone-bed analysis has been examined and the conclusions drawn regarding the distribution and diversity of (Lower Palaeozoic and early Mesozoic) microbial biotas within the subtidal and intertidal environments may be applicable to bone-beds other than those investigated. It is expected that diatoms and calcareous algae will form an important part of the microbiota of late Mesozoic and Cainozoic bone-beds and may in part replace some of the non-calcareous algal forms.

The main microbial points to arise out of this study were the comparative distribution of algal dissolution pits and algal borings on vertebrate grains. The former are located in tidally influenced environments with the latter preferring subtidal marine environments. Occasionally, early silicification on the surface of grains has preserved fungal and bacterial elements of the microbiota. Such elements appear to increase in diversity and abundance along a supra littoral to subtidal transect, though this may be a reflection of their preservation potential.

Further study of microbiotas in both recent and fossil sediments should lead to a greater understanding of the early geochemical and diagenetic conditions prevalent in the subsurface (0 - 20 cm depth) environments presented by fossil vertebrate sands (bone-beds).

Since Swinchatt (1969) has shown that sediments containing endolithic algal borings are most likely to be formed at depths of less than 40 m, and that abundant borings indicate formation at less than 18 m depth, it is unlikely that bone-beds formed in waters deeper than 40 m will contain algal borings on static grains.

## 11 — Discussion and Conclusions

This paper has sought to first produce a criterion for an improved bone-bed classification utilising both modern sedimentological terminology and the variation in the phosphatic composition of the bone-beds.

This classification, though descriptive, is important since it gives an insight into the sedimentology and diagenesis of the bone-beds. For example, the phosphatic nodules present in the bone-beds described here originate from a number of different sources:

1. Faecal droppings forming coprolites. An example of a bone-bed in which most of the phosphatic pebbles originate as faecal droppings is the U.K. Rhaetic Bone-Beds (Duffin, oral com. 1978; Mayall, oral com. 1978).

2. Phosphate nucleation and replacement of clays around suitable sites (e.g. phosphatic shells and crinoid stems). This type of nodule originated in an anoxic subsurface environment in the pore waters of a loosely consolidated sediment. Their presence may indicate that the bone-bed includes material which has been derived from the reworking of sediment containing phosphate nodules formed during early diagenesis. A good example of this type of deposit is the Ludlow Bone-Bed at Longhope (text-fig. 5). Many of these nodules contain *Trypanites* borings indicating post formational exposure.

3. Phosphate nodules are present as broken abraded internal moulds and casts of gastropods, bivalves and brachiopods. These nodules frequently contain phosphate pseudomorphing after clays (Antia & Whitaker, 1978). An example of a bone-bed containing this type of phosphatic nodule is the Ludlow Bone-Bed (Antia & Whitaker, 1978).

4. Some bone-beds (e.g. the Beyrichienkalk Bone-Beds) contain phosphate centres to the shells and carapaces of ostracods and gastropods. These nodules form during post depositional diagenesis.

5. In some bone-beds (e.g. the Upper Ludlow Bone-beds of the Brookend borehole (Cave & White 1978) bored mud pebbles are present which contain a surface rim of phosphate. This rim also lines the sides of borings into the pebbles. This phosphatisation occurred during bone-bed diagenesis. The phosphate was probably derived from partial solution of fish debris in the bone-bed.

The genetic distinction of the phosphatic nodules in bone-beds into predepositional diagenetic nodules, coprolites and postdepositional diagenetic nodules is important because it allows elimination of clasts from the original vertebrate sand cumulate. Similarly a removal of the diagenetic coatings on individual grains will enable a 'true' grain size and shape analysis of bone-beds to be made.

It is envisaged that future bone-bed sedimentological work will concentrate on scanning electron microscope analysis of abrasive features on bone-bed sediments and grain size and shape analysis.

The former analytical method has received some attention (Antia & Whitaker, 1977, 1978; Whitaker & Antia, 1978). The latter has been used by Reif (1969; 1971) to prove and dispute (Antia, this paper text-fig. 8) prefossilisation of the Muschelkalk Grenzbonebed. Weight, density, shape, rollability (a property of particles which utilises size, shape and density) and grain settling times are important properties which can influence the dynamic behaviour of sand grains during the transport and deposition of a bone-bed. Common sense dictates the belief that rounder and more spherical grains should be better transported in bottom traction (cf. MacCarthy, 1933). However, recent studies suggest that this belief may be erroneous (Winkelmolen, 1971) and that a comparative analysis of grain size and rollability could help to determine how a bone-bed formed and the source of its various components. (Passega, 1964; 1977; Winkelmolen, 1971; 1978; Veenstra and Winkelmolen, 1976).

The preliminary investigations outlined here suggest that a study on the syndepositional weathering of vertebrate clasts can reveal valuable information regarding, the relative weathering rates of different clast types, the relative residence time on the sediment surface of individual clast types and the genesis of the bone-bed.

The investigation of the distribution of bone-beds throughout the geological record suggests that bone-beds may mark major unconformities (e.g. Suffolk Bone-Bed) or para continuities (Devonian Ohio Bone-Beds). They may occur as discontinuous conformable deposits within a sediment sequence (e.g. British Upper Silurian Bone-beds). Thirdly, they commonly develop in estuarine environments and occasionally form in association with phosphorites on the continental shelf in regions of nutrient upwelling.

Although this study has reviewed the formation of some bone-bed deposits it is *not* comprehensive - other bone-beds exist but remain poorly described at the present time. Examples of these poorly described bone-beds are the Permian bone-beds of the U.S.A. (Parrish 1978), the deltaic Middle Jurassic bone-beds of Thailand (Ridd, oral com. 1978), the numerous otolith beds of the Cainozoic (Malz, 1978a, b), the Lower Devonian bone-beds of Spitzbergen (Goujet and Blieck, 1977) and those of the Lower Muschelkalk of Poland (Liszkowski, 1973).

Although bone-bed research is in its infancy, despite its early start, pre-1236, a number of conclusions regarding the findings and direction of bone-bed researches can be made:

1. Research indicates that no single mode of bone-bed formation will suffice.
2. Detailed examinations of bone weathering, bone-bed sedimentology and diagenesis can reveal important genetic and ecological information.
3. Future bone-bed research should concentrate on the sedimentology and faunas across individual bone-beds instead of treating them in isolation. In doing so they will re-appraise the various models of bone-bed genesis and the techniques for determining the genesis of individual deposits.

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## 14 - Appendix - 1 (See p.138)

A life table for some closed articulated valves of *Glycimeris glycimeris* from the Red Crag at Walton on the Naze, Essex.

Key to the columns of the Table

1 - Age interval given in number of growth rings
2 - Sample size
3 - Proportion dying in the age interval
4 - Number living at age x assuming an initial population of 10,000
5 - Number dying in interval
6 - Number of timespans lived in the interval
7 - Total number of timespans lived beyond age x
8 - Observed expectation of life at age x
9 - Proportion of survivors over the age interval

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|
| 0 | 57 | 10000 | 0.3800 | 3800 | 8100 | 16803 | 1.68 | 0.62 |
| 1 | 48 | 6200 | 0.5161 | 3200 | 4600 | 8703 | 1.40 | 0.48 |
| 2 | 22 | 3000 | 0.4889 | 1467 | 2267 | 4103 | 1.37 | 0.51 |
| 3 | 13 | 1533 | 0.5652 | 866 | 1100 | 1836 | 1.20 | 0.44 |
| 4 | 5 | 667 | 0.5000 | 333 | 501 | 736 | 1.10 | 0.50 |
| 5 | 4 | 334 | 0.8000 | 267 | 201 | 235 | 0.70 | 0.20 |
| 6 | 1 | 67 | 1.0000 | 67 | - | - | - | - |
| 7 | - | - | - | - | - | - | - | - |

David D.J. Antia
Dept. Geology
Glasgow University
Glasgow

## Appendix - 2

Since this paper went to the proof stage (Dec. 1978), a paper on the prefossilisation of fish spines has appeared (Maisey, 1978), which reveals an alternative method for the identification of prefossilised fish material, to that outlined by Reif (1969; 1971) and critically examined in Section 3, p.98, of this paper.

Maisey (1978) observed that fin spines of *Sphenacanthus* (Selachii) and *Gyracanthus* (Acanthodii) occurring in a sediment matrix of fine carbonaceous clays and micas from the Staffordshire Coal Measures (Carboniferous) commonly have the lower part of their spine lumen infilled with clays and the upper part infilled with diagenetic feldspar (albite rich plagioclase). This feldspar also infilled the pore spaces of the spine oseodentine and coated the spines exterior, but only where pieces of the spines outer wall had been broken away prior to feldspar crystallisation. The clay grains resting against the feldspar on the outer surface of the spine have not been altered and post date the feldspar crystallisation (Maisey, 1978). This latter observation led Maisey to suggest that the spines had been prefossilised prior to inclusion in the sediment, in which they were found.

However, these observations do not prove that the fin spines are prefossilised material, because both clays and feldspars are commonly produced by diagenesis within the same sediment (Waugh, 1978). Thus it could be suggested that the observations made by Maisey (1978) indicate that the precipitation of clays post-date the precipitation of feldspar within the sediment during diagenesis, after burial of the unaltered fin spine. Further indications that the fin spines were not prefossilised prior to burial in the sediment are given by the presence of diagenetic calcite, quartz, siderite and pyrite locally infilling cavities in the spines and locally replacing the apatite of the spine (Maisey, 1977; 1978). All these minerals can occur together in a sediment as products of complex diagenesis (Blanche & Whitaker, 1978).

If the fin spines observed by Maisey (1978) were fossilised prior to their inclusion in the sediment in which they were found then one of the following two observations should have been made.

1. If the vertebrate material is prefossilised then the feldspar crystallites should contain abrasion features on their external surfaces.
2. Similarly the spines could be regarded as prefossilised if it could be shown that the feldspar would not have grown in the diagenetic micro-environments presented by the sediment containing the spine through time.

Maisey (1978) observed that some of his fin spines were broken at their tips revealing the diagenetic feldspar, indicating that they may have been prefossilised, but does not say whether the breaks were of syndepositional origin or a result of laboratory processing. Similarly he does not indicate whether or not abrasion features are present on any of the feldspars on the exterior of the spines. Consequently because neither criterion outlined here were fulfilled, it remains a distinct possibility that the fin spines examined by Maisey (1978) were not prefossilised. However, the two points listed above should prove a useful test to aid determination of prefossilisation in vertebrate grains which contain diagenetic precipitates on their external surface.

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| | |
|---|---|
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## Explanation for Plate 14

(a) Oligocene fish from a lacustrine fish bed - note complete preservation of the bones and compare with the random orientation of scales in a bone-bed (pl.14, fig.d) (x 1).

(b) Bedding plane surface of the Ludlow Bone-Bed - Ludlow. Note the presence of black orientated '*Serpulites*' sp. fragments (x ½).

(c) Detail of the Ludlow Bone-Bed (x 2) showing the larger phosphatic clasts of the bone-bed. 1 = '*Serpulites*' sp. fragments; 2 = *Orbiculoidea rugata* fragment; 3 = Acanthodian fish plate (? *Gomphonchus* sp.).

(d) Detail of the Ludlow Bone-Bed showing the smaller phosphatic clasts. Note the randomly orientated *Thelodus parvidens* scales in a fine grained quartz silt matrix (x 30).

(e) A *Thelodus parvidens* Ag. scale from the Ludlow Bone-Bed (x 60).

(f) A *Logania ludlowiensis* Gross scale from the Ludlow Bone-Bed (x 60).

(g) Quartz grain from the Ludlow Bone-Bed showing a concave fracture and rounded form indicative of eolian abrasion (x 60).

(h) Diagenetic euhedral quartz overgrowth from the Ludlow Bone-Bed (x 60).

(i) Diagenetic euhedral overgrowth from the Ludlow Bone-Bed showing preburial abrasion features, e.g. rounded edges (x 50).

(j) Crescentic abrasion pit on a crystal face on an abraded quartz overgrowth from the Ludlow Bone-Bed (x 1000).

(k) Angular quartz shard (x 30) from the Ludlow Bone-Bed; derived originally from a benthonite ?(cf. Marsh, R.C., 1976, PhD. Thesis Leicester Univ.).

(l) Angular quartz grain from the Temeside Bone-Bed (x 45).

(m) *Saurichthys apicalis* Ag. from the Muschelkalk Grenzbonebed. This species forms a dominant constituent of the pointed tooth fauna of the bone-bed (x 24) - a stereopair.

(n) A polished section through the conglomeratic fraction of the Muschelkalk Grenzbonebed. Note the presence of limestone pebbles, some of which contain vertebrate sand infilled burrows (arrowed). A more detailed explanation of the section is given in the text (page 128) and in text-fig. 8.

(o) An abraded fish scale from the Muschelkalk Grenzbonebed (*Gyrolepis* sp.). Such semi-complete scales are common throughout the bone-bed (cf. pl.15, fig.h) (x 12).

# Explanation for Plate 15

(a) Detail (x 900) of the matrix of the Muschelkalk Grenzbonebed showing late diagenetic calcite crystals infilling a vug in the bone-bed's sediment.

(b) Detail (x 950) of the Muschelkalk Grenzbonebed showing the 'early' diagenetic dolomite crystals which form much of the bone-bed's sediment.

(c) Detail (x 925) of the Muschelkalk Grenzbonebed showing a fish fragment (centre), mica plates and diagenetic carbonate crystals.

(d) A quartz grain from the Muschelkalk Grenzbonebed with its diagenetic limonite coating removed. Note the semieuhedral faces of the grain indicate an earlier phase of silica precipitation during diagenesis (x 54). Arrow indicates area detailed in fig. e.

(e) Diagenetic silica plastering on the surface of quartz grain (fig. e) (x 153).

(f) Broken flat tooth of *Acrodus lateralis* Ag. in a diagenetic dolomite matriz in the Muschelkalk Grenzbonebed (x 150).

(g) Stereopair of a limonite encrusted (?originally pyrite) quartz grain from the Muschelkalk Grenzbonebed (x 45).

(h) Bedding plane surface of the Muschelkalk Grenzbonebed (x 1) showing a high density of vertebrate debris including *Gyrolepis* sp. fragments (arrowed).

(i) Detail of an abraded and solution pitted surface of an *Acrodus* tooth in the Muschelkalk Grenzbonebed (x 306).

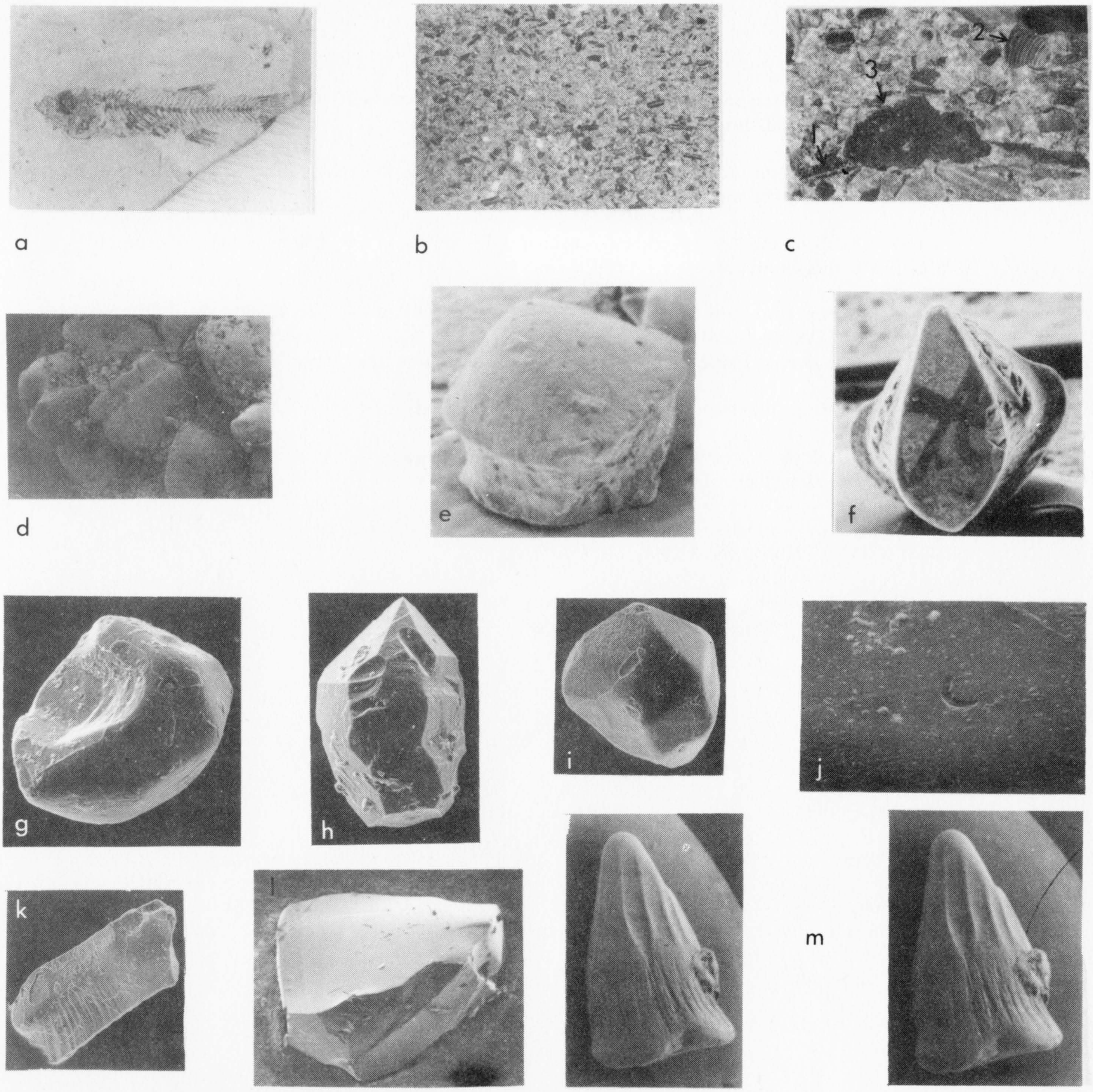
(j) Stereopair of an abrasion rounded vertebrate fragment from the Muschelkalk Grenzbonebed. Note its high sphericity. (x 60).

(k) Endolithic algal borings on a *Saurichthys* tooth from the Muschelkalk Grenzbonebed (x 920).

(l) Stereopair of an *Acrodus* tooth fragment showing a preburial break (arrowed) which has acted as a nucleous for the diagenetic growth of apatite. Rhaetic Bone-Bed. Blue Anchor locality (see Sykes, 1977, for details). (x 60).

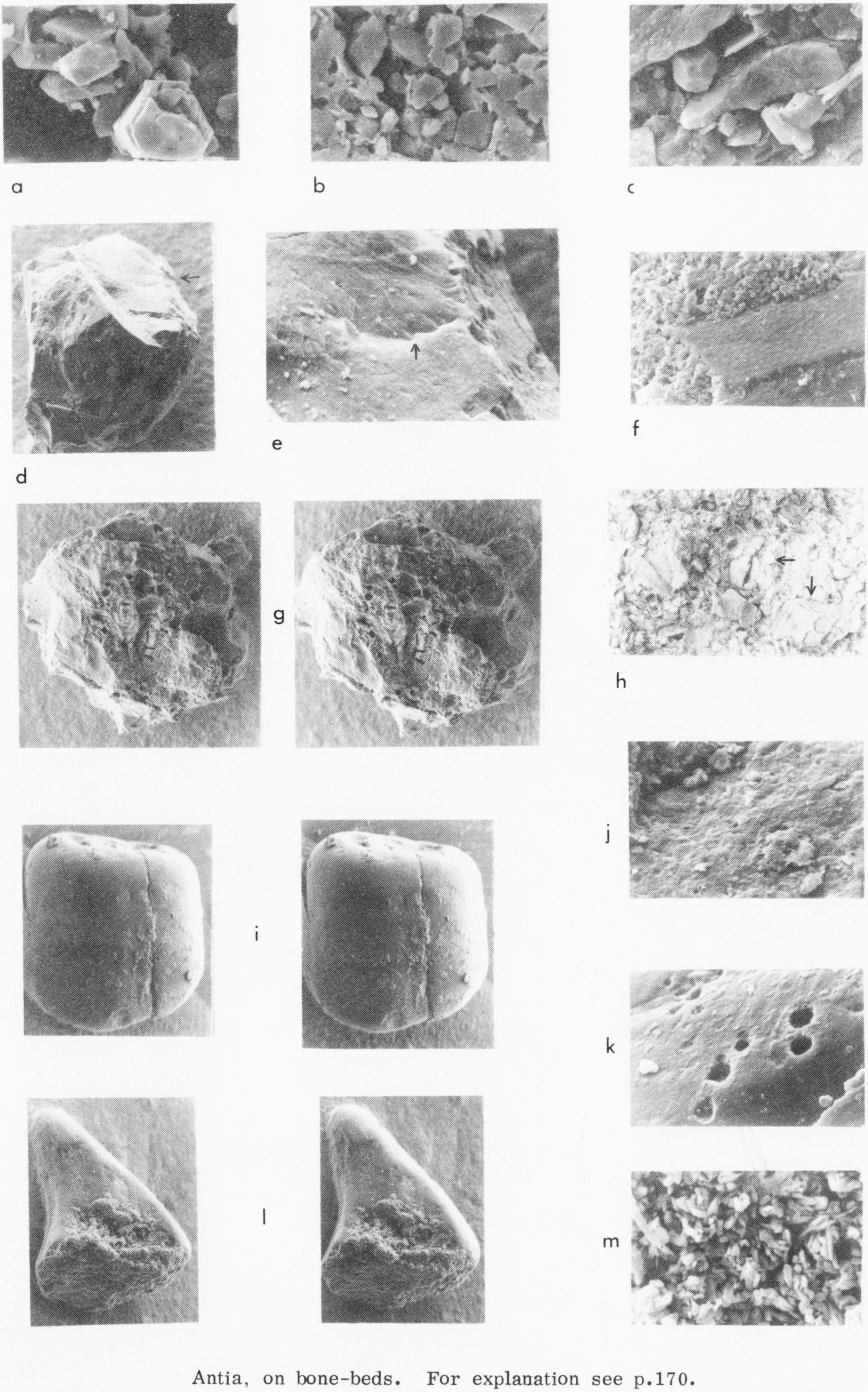
(m) Detail of the diagenetic apatite overgrowths (x 1000).

Plate 14



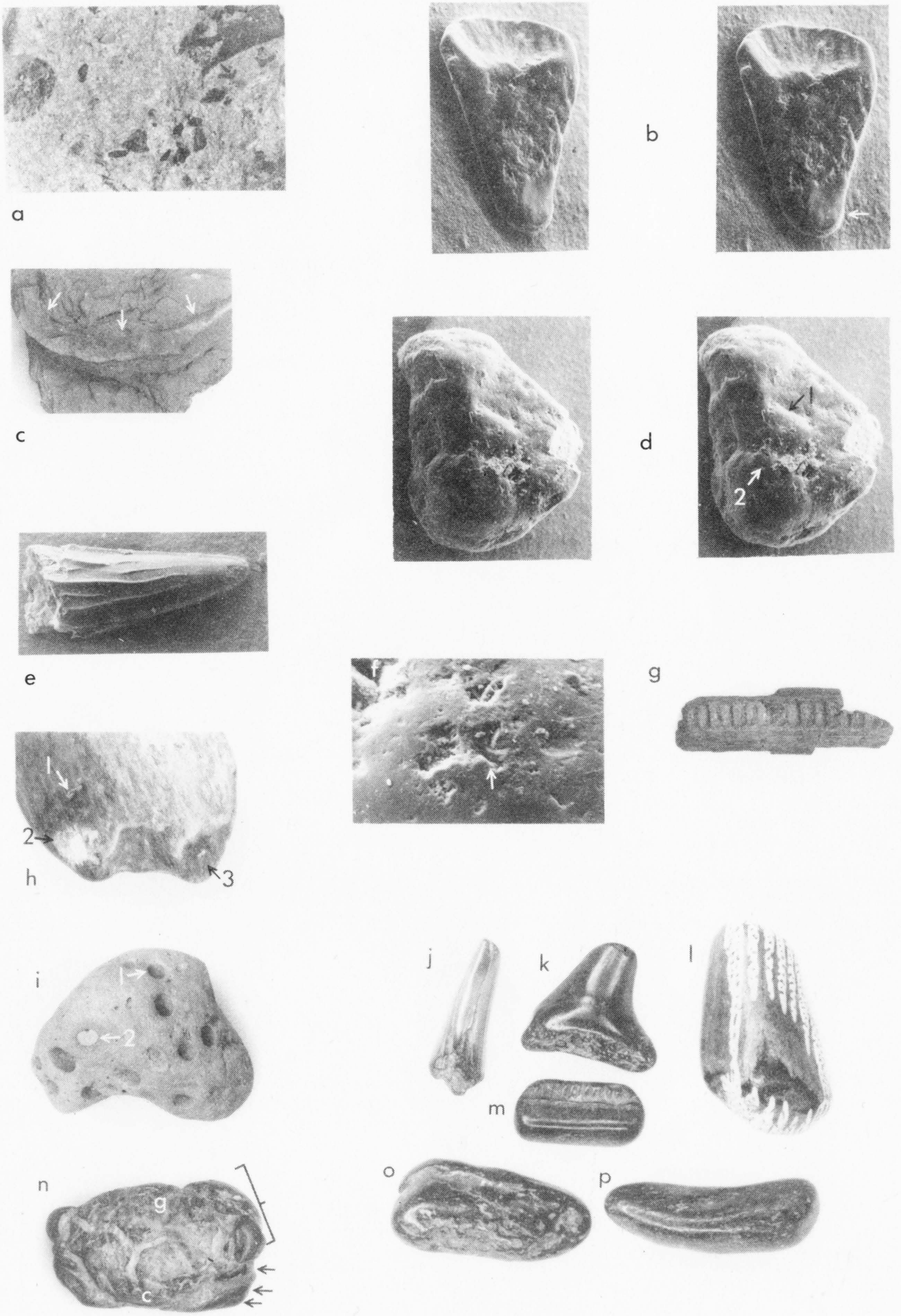
Antia, on bone-beds. For explanation see p.169.

Plate 15



Antia, on bone-beds. For explanation see p.170.

Plate 16



Antia, on bone-beds. For explanation see p.171.

## Explanation for Plate 16

(a) The Rhaetic Bone-Bed - Bedding plane surface. Westbury on Severn. (x 1).

(b) ?*Saurichthys* sp. tooth showing a syndepositional uneven fracture along its length, dividing it into two equal halves. This fracture surface has been modified during diagenesis to give in places (arrowed) a smooth fracture surface - stereopair. (x 21). Rhaetic Bone-Bed. Blue Anchor locality.

(c) A crustacean burrow from the Pullastra Sandstone underlying the Rhaetic Bone-Bed - Westbury on Severn. (x $\frac{1}{4}$).

(d) An abraded vertebrate fragment showing abrasion pits (1) and algal borings (2) from the Rhaetic Bone-Bed. Blue Anchor. - stereopair. (x 30).

(e) ?*Saurichthys* tooth from the Rhaetic Bone-Bed. Note its apparent lack of abrasive features compared to b and d and pl. 14, fig. m. These four vertebrate fragments illustrate the extreme variation in the abrasive features present in any one bone-bed. (x 28).

(f) Detail (x 225) of the abraded surface of a rounded vertebrate fragment showing abrasive chip markings (arrowed) from the Rhaetic Bone-Bed. Blue Anchor.

(g) A jawbone fragment of *Acrodus lateralis* from the Michelbach Bone-Bed, Michelbach, W. Germany. Upper Lettenkeuper. (x $\frac{1}{2}$).

(h) Mineralised (phosphate enriched) cetean bone from the Suffolk Bone-Bed ? barnacle borings (1); regions of poor mineralisation (2); and abrasion rounded fracture surfaces (3) - Walton on the Naze. (x $\frac{1}{2}$).

(i) Pebble of London Clay from the Suffolk Bone-Bed showing pholad borings (1), some of which were infilled with clay prior to their burial in the bone-bed (2). - Walton on the Naze. (x $\frac{1}{2}$).

(j) Unmineralised sharks tooth from the Suffolk Bone-Bed - Walton on the Naze. (x 2).

(k) Mineralised sharks tooth derived from the London Clay (Lower Eocene) and found in the Suffolk Bone-Bed (Pliocene/Pleistocene) - Walton on the Naze. (x 2).

(l) Mineralised abraded mammalian tooth from the Suffolk Bone-Bed. Bawdsey cliff, Felixstowe. (x 2).

(m) Mineralised fish dental plate - Suffolk Bone-Bed, Walton on the Naze. (x 2).

(n) Mineralised (phosphatised) crab derived from the London Clay and found in the Suffolk Bone-Bed, Walton on the Naze; g = gastric region; c = cardiac region; arrows indicate the walking legs; brackets indicate the claw (chela + carpus). (x $\frac{1}{2}$).

(o/p) Abraded mineralised mammalian bone fragments from a thin bone-bed in the Red Crag (Lower Pleistocene) at Brightwell, Suffolk. (x 2).

## Explanation for Plate 17

(a) Otolith - detail of surface showing ?fungal borings and the initial stages in the development of weathering stage 2 (i.e. concentric outer layer peeling). (x 450).

(b) Otolith - detail of surface showing ?fungal borings aligned parallel to the otoliths outer surface, which have been partly exposed by a gastropod boring. The ridges and grooves observable in this figure result from a scraping of the otoliths surface by a gastropod radula. This particular otolith contained no weathering features, and illustrates the high density of microbial borings present on many of the unweathered (weathering stage 0) otoliths from the Rockall Trough. (x 800).

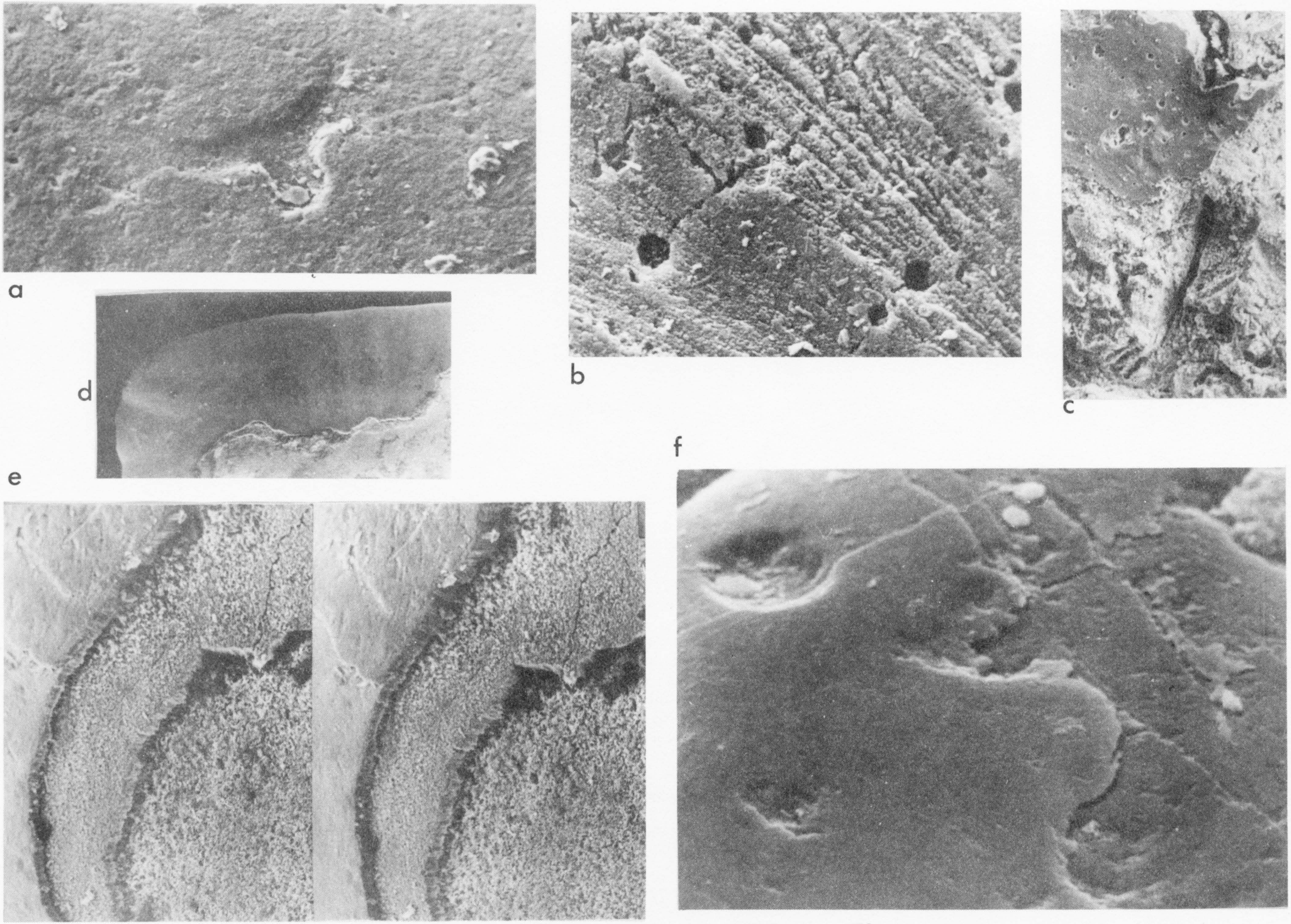
(c) Otolith - detail of the surface of a weathered otolith (weathering stage 3) showing the reminants of the resistant outer layer surrounded by the less resistant inner fiberous layer. This latter layer contains a deep crack with rounded margins, of a type which is common on the most highly weathered vertebrate remains (weathering stages 4 and 5). (x 50).

(d) Otolith - Low magnification (x 10) view of the outer surface of an otolith showing a well developed peeling of the outermost concentric layers. i.e. typical weathering stage 2 features.

(e) Stereopair showing well developed concentric layer peeling on the surface of an otolith. (x 300).

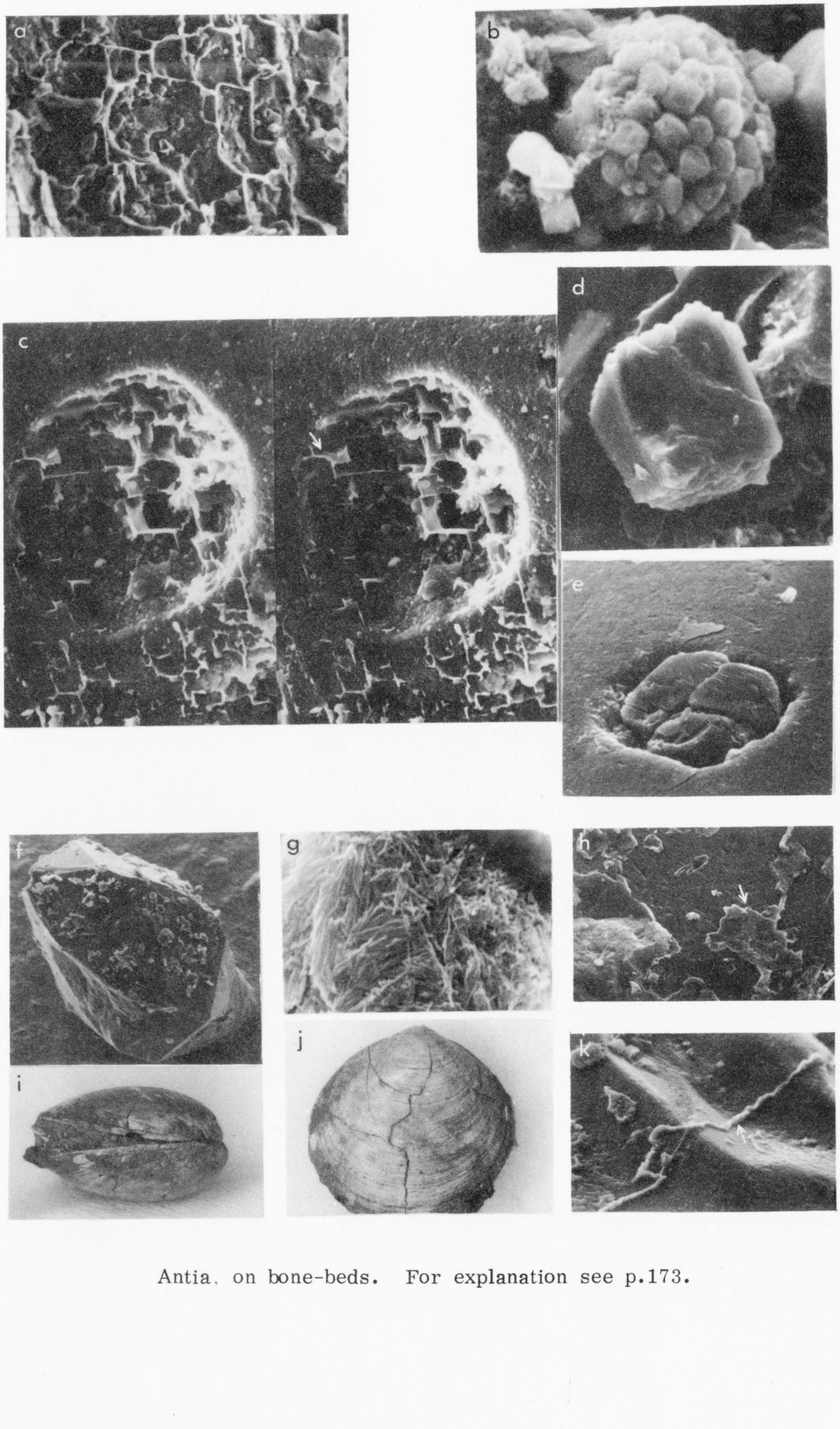
(f) The outer surface of a thelodont scale (*Thelodus parvidens*, showing algal dissolution pit (see also Section 10), concentric peeling of the outermost layers (weathering stage 2 features), abrasion chip marks, and cracks (reminant weathering stage 1 features ?) from the Ludlow Bone-Bed at Corfton (x 750).

Plate 17. Weathering and microbial features on otoliths and thelodonts.
This plate has been placed for sideways viewing.



Antia, on bone-beds. For explanation see p.172.

Plate 18



Antia, on bone-beds. For explanation see p.173.

## Explanation for Plate 18

(a) Apatite pseudomorphing after clays in a phosphatic nodule from the Ludlow Bone-Bed. (x 1000).

(b) Pyrite framboid from the Ludlow Bone-Bed (x 3000).

(c) Kaolinite infilling an algal solution pit on the surface of a thelodont scale. Note the honeycomb nature of the clay structure - stereopair. From the Ludlow Bone-Bed. (x 2500).

(d) Kaolinite crystal from the matrix of the Ludlow Bone-Bed. (x 900).

(e) Kaolinite crystals completely infilling an algal solution pit on a thelodont scales surface. (x 800).

(f) Quartz grain from the Rhaetic Bone-Bed - Blue Anchor locality. Note the euhedral diagenetic crystal faces on the grain. (x 80).

(g) A fibrous clay from a clay pebble in the Ludlow Bone-Bed. (x 2500).

(h) Silica plastering on the surface of a quartz grain in the Rhaetic Bone-Bed, Blue Anchor locality. (x 600).

(i) Articulated *Glycimeris glycimeris* shell from the Red Crag at Walton on the Naze. (x $\frac{3}{4}$).

(j) Articulated *Glycimeris glycimeris* shell. (x $\frac{3}{4}$).

(k) Silicified filament on the surface of a quartz grain in the Ludlow Bone-Bed. (x 650).

## Explanation for Plate 19

(a) Microbial flora of diatoms on a modern carbonate grain. (x 1000).

(b) Algal solution pits (x 200) on a modern carbonate grain - Sales Point, Bradwell, Essex (see Antia, 1977, for locality details).

(c) An algal bored carbonate grain from the Rhaetic Bone-Bed, Blue Anchor. (x 23).

(d) Algal solution pits on a thelodont fish scale (*Thelodus parvidens*) from the Ludlow Bone-Bed. (x 25).

(e) Detail (x 500) of the solution pits. Note their similarity to those illustrated in b.

(f) Detail (x 225) of algal borings on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor.

(g) Detail of ? fungal borings on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor. (x 450).

(h) Detail (x 263) of a large algal boring on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor.

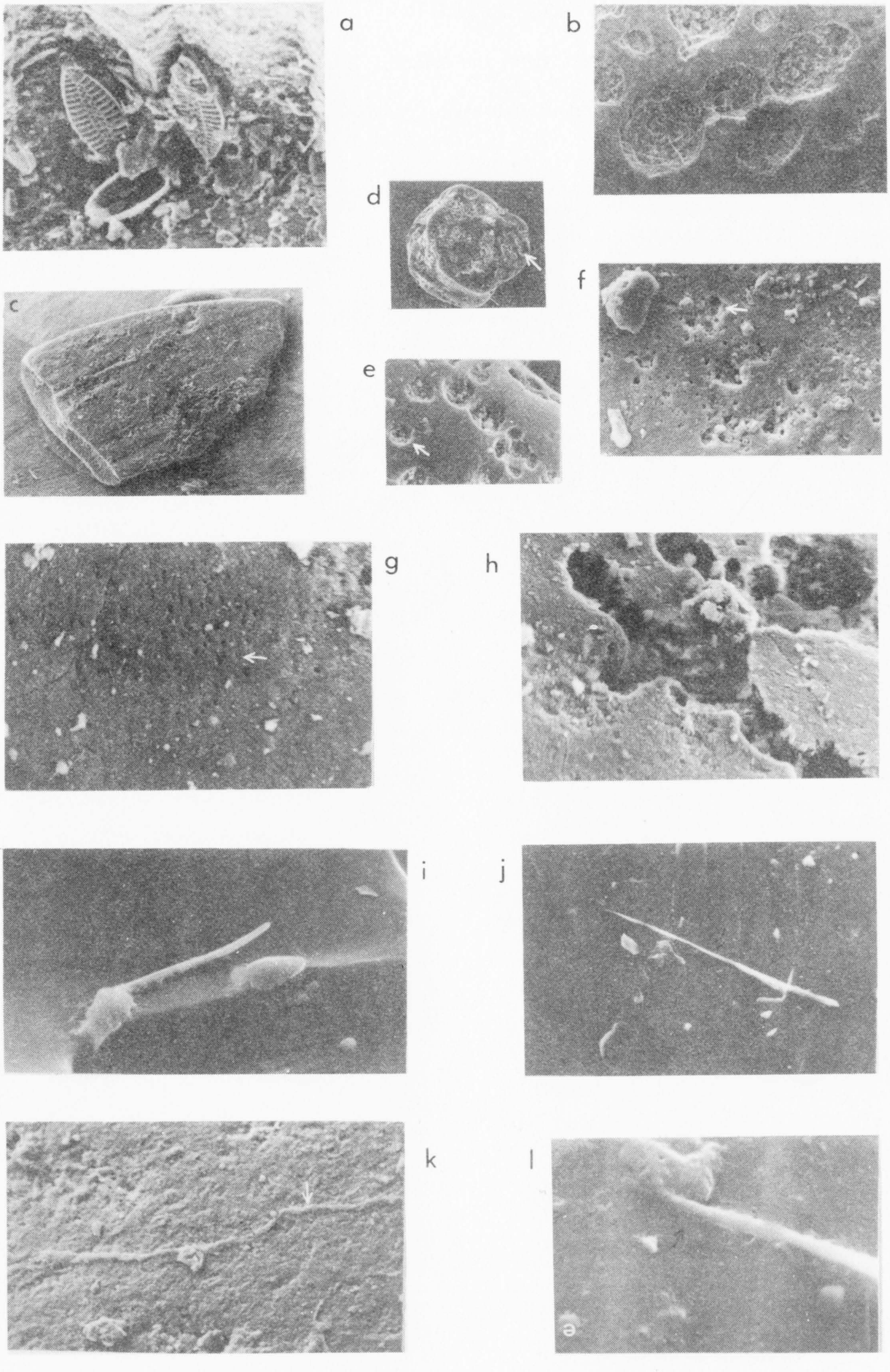
(i) Silicified fungal filament (side view) on a quartz grain from the Temeside Bone-Bed, Ludlow. (x 1000).

(j) Another silicified fungal filament (same species) on a quartz grain from the Temeside Bone-Bed, Ludlow - viewed from above. (x 250).

(k) Phosphatised fungal filament on a phosphorite nodule - Ludlow Bone-Bed, Ludlow. (x 1200).

(l) Detail of the holdfast of the silicified fungal filament illustrated in j from the Temeside Bone-Bed. (x 2500).

Plate 19



Antia, on bone-beds. For explanation see p.174.