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Late Quaternary mammal remains, spanning about 30 000 years, from excavations in Devil's Lair, Western Australia

by Jane Balme, D. Merrilees and J. K. Porter

Western Australian Museum, Francis St., Perth, W.A. 6000

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Abstract

The vertebrate component of about 100 layers in one complex of trenches excavated in 1973-76 in the sandy floor of Devil's Lair, a small cave in the extreme south west of Western Australia, has been examined. The oldest of the layers discussed dates from about 35 000 yr. B.P. and the youngest in what appears to be an uninterrupted sequence dates from about 5 000 yr. B.P. The deposit contains older layers not yet examined and one which was laid down about 300 yr B.P. after a pause in sedimentation. There are signs of ancient disturbance of the deposit by human occupants of the cave, and only stratigraphically undisturbed samples are reported.

Detailed analysis of terrestrial mammals and an indication of bats and lower vertebrates is given. Most of the mammal species were still extant in historic time, though not all in the Devil's Lair district. There is a small proportion of totally extinct species of large marsupials in the lower layers, but these are believed provisionally to be re-worked from an older deposit. Some of the extant species may have been represented in this postulated older deposit. Thus specimens of different ages are apparently asociated in the lowest layers examined. Man is believed to have been the main accumulator of bone in the upper layers, owls in the lower.

Throughout the period studied, a more varied mammal fauna persisted than is recorded in historic time. At some late Holocene period not represented in Devil's Lair, several species not known to inhabit forest disappeared from the district. This and the distribution of mammal species between 35 000 and 5 000 yr. B.P. suggest that a drier climatic regime in the Pleistocene gave way to a wetter regime in the Holocene.

Introduction

Systematic excavations in the sandy floor deposit of Devil's Lair, a small cave in the Cape Leeuwin-Cape Naturaliste region of Western Australia, were begun in 1970 under the joint direction of C. E. Dortch and D. Merrilees, of the Archaeology and Palaeontology Departments respectively of the Western Australian Museum. These excavations have yielded stone and bone artifacts, an abundance of bone, much of it highly fragmented, and sufficient charcoal to provide a series of radiocarbon dates spanning late Pleistocene and early Holocene time.

Our principal objective in this paper is to report an analysis of the bone recovered from a set of adjacent excavations in an approximately central position in the cave. These excavations were made mainly in 1974, 1975 and 1976 and have not been reported previously, but for reasons explained later we include some material recovered in 1973, part of the subject matter of the report of Baynes *et al.* (1976). These authors suggested that the bone represented remains of meals eaten in the cave by human beings who had sampled the mammal fauna of the area around the cave. Changes in the composition of this sample with time which were noted might have been due to changes in the fauna resulting from vegetational and hence presumably climatic changes in the area, or might have been due to changes in the relative proportions of forest and heath resulting from the post-glacial marine transgression, without much climatic change.

We re-examine all these suggestions in the light of our stratigraphically more finely divided sample, larger sample size, improved methods of quantifying our results, and longer time span, the last allowing us to take into account the possible effects of the pre-glacial retreat of the sea as well as the post-glacial advance. However, we make no claim to have studied our data exhaustively, and indeed our second major objective is to draw attention to the existence of a wealth of material from Devil's Lair which could be studied from different angles or in greater detail.

Bone from the 1974, 1975 and 1976 excavations is that covered by the 12 116 Western Australian Museum fossil vertebrate catalogue entries 75.3.1-1024, 75.4.1-986, 75.5.1-891, 76.6.57-999, 76.7.1-999, 76.8.1-999. 76.9.1-383, 77.1.1-999, 77.2.1-999, 77.3.1-999, 77.4.1-999, 77.5.1-1000 and 77.6.1-890 inclusive. Excavation was continued in 1977, but the relatively small quantity of bone recovered from layers deeper than those mentioned herein (see Fig. 3) has not been examined in detail at the time of writing.

Devil's Lair (34°9'S, 115°4'E) is listed as W1.61 in the Western Australian Cave Nomenclature list (Bridge and Shoosmith 1975). It has been the subject of several published studies, and others are in preparation; these studies are cited in their appropriate contexts.

The 1974, 1975 and 1976 excavations

Excavations have been made in various parts of the cave floor, but from 1973 have been concentrated in one small area about central in the length (approximately the north-south axis) of the cave, but much closer to the eastern than to the western wall. Plans of the cave showing this area are given by Dortch and Merrilees (1973), Shackley (1978) and Clarke *et al.* (in press). For convenience in excavation, the area was subdivided, and the adjacent trenches so produced were numbered separately as shown in Figure 1.

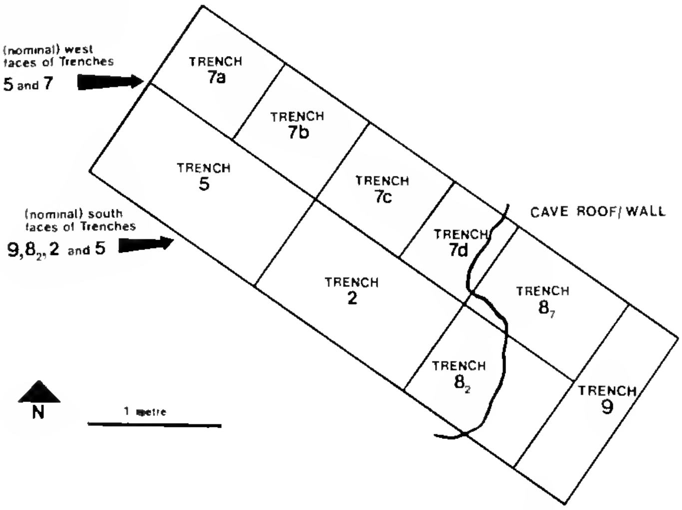

Figure 1.—Plan of trenches 2, 5, 7, 8 and 9.

By 1974, Trenches 7a, b, c and d had been excavated to a depth of about 1½ m below the cave floor surface, Trenches 5 and 8_2 to nearly 2 m, Trench 8_7 about ½ m, and Trench 2 just over 2½ m, while Trench 9 had not been begun. Progress in subsequent years was somewhat more even from trench to trench, but the volumes of sediment yielding the bone material described herein are by no means uniform. It is partly to report a more uniform sampling from layer to layer that we have included some of the 1973 material. Thus the material discussed is that excavated from Trenches 7a, b, and c to a depth of about 1½ m, Trench 2 from about 2½ m to about 4 m, and Trenches 7d, 8_7, 8_2 and 9 to depths of about 4 m below the surface.

However, depths were measured not from the surface of the deposit but from the same arbitrary cave datum level, marked on the wall of the cave near our excavations. (It is a little higher than the highest point on the sloping and rather uneven surface of the area excavated). Thus depths may be compared directly, and unless otherwise specified, a "depth" is to be taken as a depth below this arbitrary datum, and can be regarded as having an accuracy of ± 2 cm.

Stratigraphy

The Devil's Lair deposit consists mainly of siliceous sand rendered coherent to varying degrees by calcareous cement, and with interbedded flowstones and other predominantly calcareous masses (Shackley 1978). Where the calcareous component is dominant, the colour of the sediment is dirty white. Where siliceous sand is predominant, as is the general rule, the colours are brown or orange. Disseminated charcoal and humic material render two layers almost black. Layering in both siliceous and calcareous components is more obvious in some parts of the excavations than in others.

Bedding is fairly uniform over the excavated area, with a dip of about 8° towards the south, consistent with the interpretation made by Clarke *et al.* (in press) that an intermediate position in a broad cone of sediments has been sampled. The (dominant) siliceous component of these sediments appears to have entered the cave through a restricted shaft, now buried and largely concealed by the sediments both inside and outside the cave. The calcareous component appears to have been deposited from solutions dripping or oozing from the roof and walls of the cave, which is in a sandy dune limestone.

In excavations made in 1972, it proved difficult to distinguish bedding planes (especially in Trench 5) in as fine detail as was possible later. Dortch and Merrilees (1973) described artifacts found in 1972 in terms of relatively coarse stratigraphic subdivisions (one over 1 m thick, divided into arbitrary 10 cm "spits"), and Baynes *et al.* (1976), in describing the fauna represented in the 1972 and 1973 excavations, retained these coarse subdivisions. However, from 1973 on, very much finer stratigraphic subdivisions were recognized, averaging about 5 cm thick, and these smaller subdivisions, designated by letter or number, are the ones reported herein. A partial correlation of these smaller subdivisions of the upper parts of the deposit with the coarser subdivisions reported earlier, is made by Baynes *et al.* (1976).

It was not always possible to trace a given layer over the whole area excavated, and this and gradations in colour or (less often) texture from one layer to the next or laterally within the same layer often led to the recovery of interface mixtures. Mixed samples of this kind have been treated as if they were from discrete layers in the compilation of Table 3 and the bar charts (Figs. 5, 6, 7 and 8). With these provisos, the representative section drawings of Figures 2, 3 and 4 can be related to Table 3 and Figures 5, 6, 7 and 8.

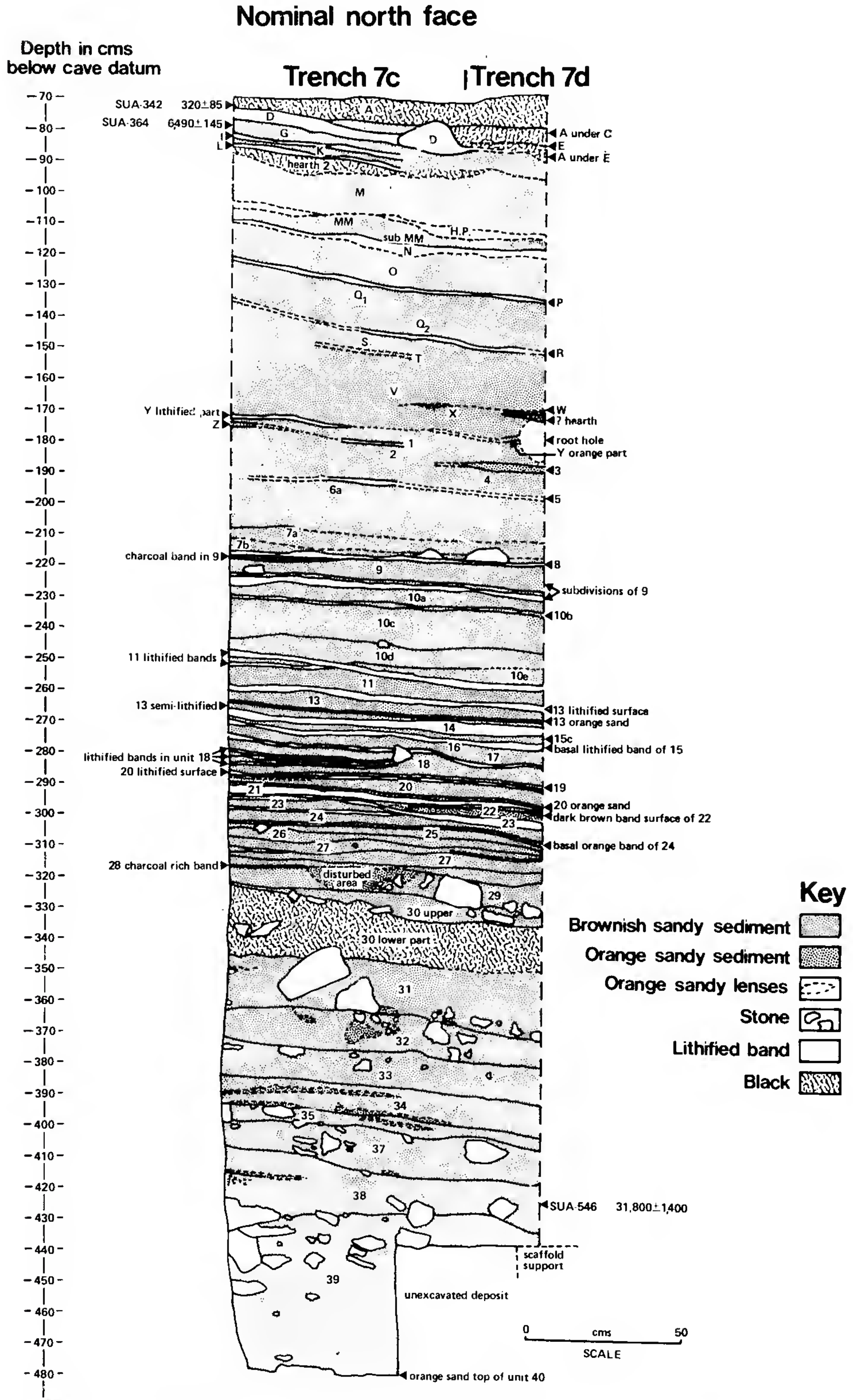

Figure 2.—Section, nominal north face of Trench 7c and part of Trench 7d.

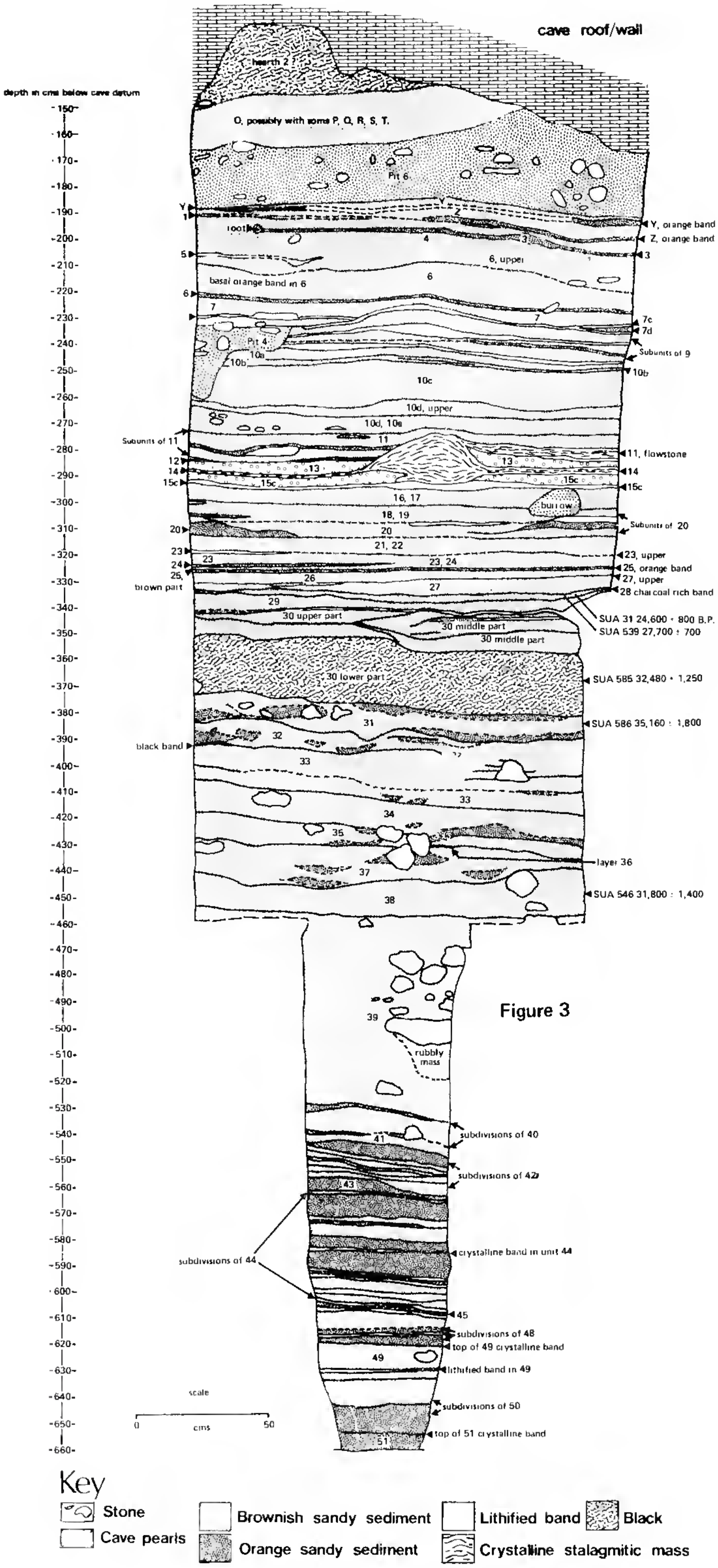

Figure 3.—Section, nominal east face of Trench 9.

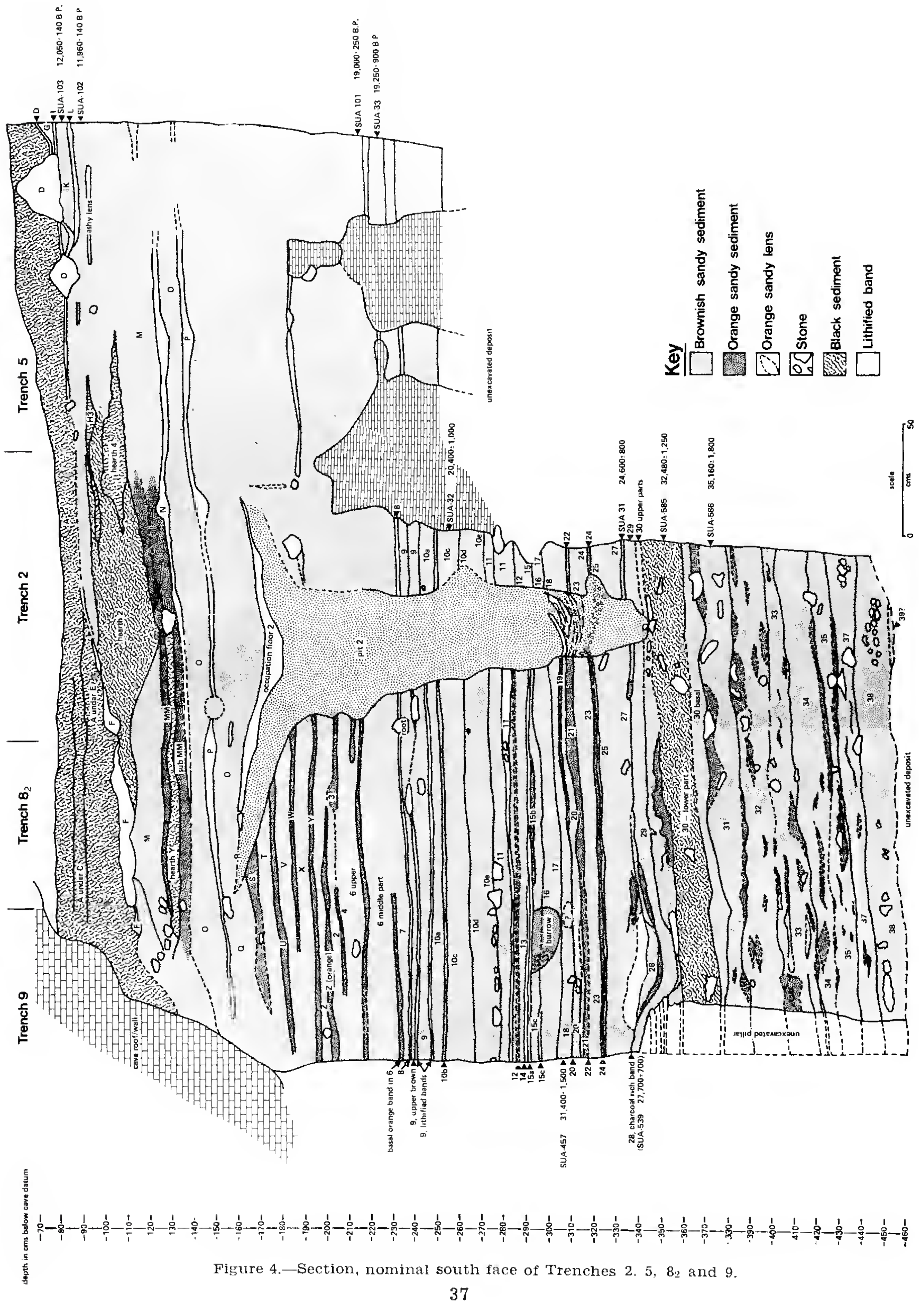

Figure 4.—Section, nominal south face of Trenches 2, 5, 8₂ and 9.

The slow average rate of deposition (much less than 1 mm per year) has been noted previously (Lundelius 1960, Shackley 1978) and shown to involve lengthy pauses in the actual accretion of sediment (Dortch and Merrilees 1972). Thus one must envisage a succession of sandy floors in the cave, each exposed for years, decades or even centuries, to the effects of sporadic visits by small groups of human beings (Dortch and Merrilees 1973, Dortch 1974, Baynes *et al.* 1976), and perhaps more frequent visits by other animals of various kinds, including "Tasmanian" devils and owls. Even without any actual digging or burrowing by such visitors, there must have been extensive disturbance of the cave floor surfaces before the next burst of sedimentation buried and to some extent protected them.

From layer 31 down, there are indications of a much faster sedimentation rate. The small orange lenses shown in section in Figures 3 and 4 in these horizons often appeared in plan as long, sinuous sand masses which we interpret as filled water-cut channels. We have attempted to take this higher energy sedimentation into account by recognizing thicker stratigraphic units.

We do not claim that each of our layers represents a single relatively short term event in the sedimentary history of the cave. Some (perhaps the orange bands) may represent short, discrete episodes, others (probably the crystalline flowstones) may represent discrete episodes of long duration, and others (perhaps most of the brown layers) represent a summation of many episodes extending over relatively long periods.

There is clear evidence of disturbance of this general stratigraphic succession in various places at various times, both ancient and modern (Baynes *et al.* 1976). We have made allowance for this by omitting certain material from stratigraphic consideration. Thus we omit most of the topmost layer (A), because of the signs of modern disturbance noted by Baynes *et al.* (1976, p. 102). We also omit material possibly containing spoil dug from Pits 2 and 6 in ancient times.

Pit 2 is shown in Figure 4. It is now thought to be part of the same structure as first detected in the northern part of Trench 2 and designated as Pit 1 (Dortch and Merrilees 1973, p. 97). The full extent of this pit was not at first appreciated, and its boundaries, especially towards its top, were difficult to determine, but we are now confident about the section shown in Figure 4 as Pit 2, and confident also that Pit 2 includes Pit 1. Pit 2 must have been dug from an ancient surface close to our layer S, and material brought up from layers as deep as 29, transected by it, may have been spread about on this surface. We have omitted material from layer S altogether from our considerations, and also material from R because the lithification of this layer may have extended its lower boundary into what was properly S. Layers down to 29 in Trench 2 are not included because these had not been established when this part of Trench 2 was being excavated, and their omission serves to exclude possible confusions due to the upper margins of Pit 2 being difficult to distinguish.

Pit 6, shown in Figure 3, completely obscures the stratigraphy in Trench 9 from layers Q to X, which are therefore excluded. Some material from layers O and P from Trench 9 is included in our considerations, but nothing from above these because the layering is either not now discernible, or else was disturbed in ancient times.

During the excavation of what we would now recognise as layers S to X in Trench 7a, arbitrary horizontal "spits" were removed which are difficult to correlate with the gently dipping "natural" layers. Therefore we omit material at these levels from Trench 7a.

As in other excavations, ours produced substantial quantities of material accidentally dislodged from crumbling edges, deliberately dislodged in cleaning sections preparatory to drawing or photographing them or to straighten the walls of the trenches. Some of this material is localized, and could be included in coarsely subdivided stratigraphic arrangements, as for example, by Baynes *et al.* (1976, p. 122). However, we have excluded all such material except the interface mixtures previously mentioned.

Age of the deposit

Numerous radiocarbon age estimates have been made on charcoal from various places and layers. Attempts have been made to verify these with other methods and materials, but all such attempts have been abortive. This is unfortunate in view of the findings of Archer (1974) that charcoal may be associated with bone of much greater age in a depositional environment not unlike that of Devil's Lair.

Radiocarbon dates on charcoal samples in or immediately adjacent to the layers and trenches discussed are as follows:—

Date no. SUA–342	Trench 7b	Layer A under B	320 ± 85 yr B.P.
Date no. SUA–364	Trench 7c	Layer G (perhaps with some D and H)	6 490 ± 145 yr B.P.
Date no. SUA–103	Trench 5	Layer K	12 050 ± 140 yr B.P.
Date no. SUA–102	Trench 5	Layer M	11 960 ± 140 yr B.P.
Date no. SUA–101	Trench 5	Layer 7	19 000 ± 250 yr B.P.
Date no. SUA–33	Trench 5	Layer 9	19 250 ± 900 yr B.P.
Date no. SUA–32	Trench 2	Layer 10	20 400 ± 1 000 yr B.P.
Date no. SUA–457	Trench 8_7 and 9	Hearth in layer 18	31 400 ± 1 500 yr B.P.
Date no. SUA–31	Trench 2	Layer 28	24 600 ± 1 500 yr B.P.
Date no. SUA–539	Trench 8_2 and 8_7	Layer 28	27 700 ± 700 yr B.P.
Date no. SUA–585	Trench 2, 8_2 and 9-South	Layer 30-lower part	32 480 ± 1 250 yr B.P.
Date no. SUA–586	Trench 2, 8_2. 9-South and 7d	Layer 31	35 160 ± 1 800 yr B.P.
Date no. SUA–546	Trench 8_2, 8_7, 9-South and 9-North	Layer 38	31 800 ± 1 400 yr B.P.

In addition, date SUA-34 (17 400 ± 350 yr B.P.) from Trench 6 is discussed by Dortch and Merrilees (1973) and dates 0-654 (8 500 ± 160 yr B.P.) and 0-658 (12 175 ± 275 yr B.P.) from what is now designated Trench A1 are discussed by Lundelius (1960) and by Dortch and Merrilees (1972). These three dates are not yet linked stratigraphically with the 1974, 1975 and 1976 excavations.

Date SUA-342 (320±85 yr B.P.) can be interpreted as supporting the suggestion made by Dortch and Merrilees (1973, p. 93, 94) that the uppermost layer in the deposit entered the cave in a different manner from the rest, since it is now shown to be of a different order of age from the rest.

Date SUA-364 (6 490±145 yr B.P.) is based on a sample from what Dortch and Merrilees (1973) called "flowstone complex with pockets and bands of earth". It shows, contrary to the belief of Baynes *et al.* (1976) that sedimentation through the original (now buried) entrance continued from terminal Pleistocene well into Holocene time. It leaves open the questions of when the thick flowstone D sealed the older sediments in the cave (and presumably also sealed the original entrance), and how long an interval elapsed before the lithologically very dissimilar layer A, entered from another, presumably newly made, opening. Provisionally we regard flowstone D as about 5 000 years old.

The charcoal samples for dates SUA-103, 102, 101, 33, 32 and 31 were collected from Trenches 5 and 2 prior to the establishment of the stratigraphic subdivisions used herein. There must be an element of doubt about our subsequent assignation of them to the layers shown, though we believe such doubt is minimal. SUA-103 and 102 and SUA-101, 33 and 32 are so close to one another as to inspire some confidence that the set of events they bracket are of the order of 12 000 and 19 000 years old respectively.

SUA-31 (24 600±1 500 yr B.P.) and SUA-539 (27 700±700 yr B.P.) date the same "event" (or summation of events in the sense discussed previously). The stratigraphic expression of this event or summation is a thin but laterally extensive layer so rich in disseminated charcoal as to appear nearly black in section in some trenches. It is the "charcoal rich band" shown low in Trench 2 in Figure 2 of Baynes *et al.* (1976 p. 99). It may contain redistributed charcoal, and the samples dated may represent different events between 24 000 and 28 000 years ago approximately.

Dates SUA-585, 586 and 546 are not significantly different and give a "pooled mean age" of 33 150±840 yr B.P. (R. Gillespie, pers. comm.) This "pooled" age should be considered in conjunction with our stratigraphic conclusion that layers 31-39 represent more rapid, higher energy sedimentation than the upper layers.

All the radiocarbon dates so far discussed are stratigraphically consistent, but SUA-457 (31 400±1 500 yr B.P.) is not. The charcoal sample concerned came from a small lenticular body encountered in the adjacent Trenches 8_7 and 9 on separate dates in 1975. None of the field notes mentioning the occurrence expresses any reservations about interpreting it as a hearth, implying a single short term event. We cannot account for the stratigraphic inconsistency of this date and for the time being disregard it.

Thus, taking the radiocarbon dates (except SUA-457) at face value, we assume our material to represent a time span from about 35 000 to about 5 000 years ago.

Methods of recovery, identification and quantification of material studied

The material excavated by brush or trowel was passed through one or more sieves of standard mesh in the field. Material remaining on the sieves was cursorily examined, except for large pieces of stone, which were subjected to careful scrutiny for signs of working, and accepted for further study or rejected on the spot. The remainder was bagged and taken to the Western Australian Museum for sorting and study. Our methods, and the material studied, were as described by Baynes *et al.* (1976) with an exception which we believe to be significant, namely in our method of recording "minimum number of individuals" of each taxon in each layer.

In their Appendix 3, Baynes *et al.* (1976) show that estimation of minimum numbers of individuals made by considering each trench separately and then adding the numbers so estimated leads to exaggeration, especially with larger animals. They also point out exaggeration of such minimum numbers of individuals attendant on adding results from small stratigraphic subdivisions to produce estimates for larger divisions.

We sorted, identified and catalogued material trench by trench as usual. But when we had decided, on stratigraphic grounds, what samples were admissible to represent a given layer, we then assembled all the identified material, one taxon at a time, for that layer. We then estimated a "minimum number of individuals" for that layer for each taxon, irrespective of trench divisions, but otherwise according to the procedures described by Baynes, *et al.* (1976). The difference between the two kinds of estimates is substantial, as illustrated by the examples of taxa showing a range of body size (Table 1).

We have adopted this procedure because we believe the estimates so obtained approximate more closely the actual number of individuals represented in a particular layer. It is not practicable in most cases to estimate this actual number in Devil's Lair because of the high degree of fragmentation of the bones. However, in the case of the largest mammal (*Macropus fuliginosus*, the western grey kangaroo) present (apart from man) it is clear from studies made by Balme (in press) that each first upper incisor and each deciduous or permanent premolar, whether right or left, represents a separate individual. Since the teeth of this species are rather sparsely represented, and few layers have yielded both right and left first upper incisors (the most commonly represented anatomical

Table 1

Comparison of former and present methods of estimating minimum number of individuals in given layer. Layers 11 (*upper*). 21 (*middle*) *and* 25 (*lower*). *All from Trenches* 7d, 8_2, 8_7 *and* 9.

	Addition of trench totals	Ignoring trench divisions
Sminthopsis (mouse-sized)	14	8
Rattus (rat-sized)	43	38
Trichosurus (possum)	7	4
Petrogale (small wallaby)	5	2
Macropus fuliginosus (large kangaroo)	5	2
lizards (mainly small)	11	7
Sminthopsis	10	8
Rattus	11	10
Trichosurus	1	1
Petrogale	4	3
Macropus fuliginosus	2	2
frogs	4	2
Sminthopsis	19	13
Rattus	38	33
Isoodon (bandicoot)	6	3
Pseudocheirus (ringtail possum)	3	2
Setonix (small wallaby)	7	4
Macropus fuliginosus	2	2
birds (mainly small)	6	3
lizards (mainly small)	8	5

element diagnostic of the species), the "minimum number of individuals" as we estimate it, probably underestimates the actual number of animals involved, but not greatly.

We have not made the time-consuming effort necessary to estimate actual numbers of individuals for any of the other species present in Devil's Lair. However, the statistical considerations set out in Table 2 to some extent support a claim that our "minimum numbers of individuals" might approximate actual numbers in the case of some, perhaps all, these species. The kind of data presented in Table 2, if subjected to appropriate statistical examination, could be expected to clarify the extent of lateral scattering of bones or bone fragments representing each animal taken into the cave, and the extent to which our excavations have sampled this lateral scatter. Coupled with minutely detailed anatomical scrutiny and cross comparison among the bone fragments studied, this would throw some light on the actual number of animals involved.

A study of such magnitude is beyond our present means, but such random observations and minor studies as we have been able to make suggest to us that the "minimum numbers of individuals" reported herein are underestimates of the actual numbers of animals involved, but only by some relatively small fraction, not by whole orders of magnitude, and that this fraction does not vary greatly from species to species nor layer to layer.

For example, layer 30-lower contained a minimum number of 3 individuals of *Potorous* (Gilbert's potoroo, a rat-kangaroo about the size of a rabbit). Two of these were juveniles. The left dentary of one of these, distinctive because of its extreme youth, was recovered from Trench 2 and the right dentary of what can be readily accepted as the same animal was recovered from Trench 9 more than a metre away. The area we sampled probably exceeded the area of lateral scattering of the parts of this particular animal. By extrapolation, we probably recovered identifiable fragments of all the potoroos brought into this part of the cave at that particular time, over 30 000 years ago. Similarly, the data presented in Table 2, though not supported by anatomical comparisons, do suggest a reasonably adequate sampling of laterally scattered material; the more discrepant the representation of right and left or upper and lower parts of paired anatomical elements, the less adequate the sampling can be assumed to be.

Table 2

Comparison of the representation of paired anatomical structures from certain mammal species in specified layers.

1. *Bettongia penicillata* (a rat-kangaroo) in Layer M, Trenches 7a, b, c, d and 8_2:—		
First upper incisor	11 left	24 right
Upper deciduous premolar	8 left	3 right
Upper permanent premolar	16 left	16 right
Maxillary fragment with first or second molars or their alveoli	14 left	19 right
Lower deciduous premolar	10 left	9 right
Lower permanent premolar	15 left	9 right
Dentary fragment with first or second molars or their alveoli	19 left	13 right
2. *Bettongia lesueur* (a rat-kangaroo) in Layer M, Trenches 7a, b, c. d and 8_2:—		
Upper deciduous premolar	2 left	1 right
Upper milk molar	4 left	0 right
Upper permanent premolar	4 left	1 right
Maxillary fragment with first molar or alveolus	10 left	3 right
Lower deciduous premolar	0 left	2 right
Lower milk molar	0 left	3 right
Lower permanent premolar	1 left	4 right
Dentary fragment with first molar or alveolus	2 left	3 right
3. *Pseudomys albocinereus* (a small native mouse) in Layer O, Trenches 7a, b, c. d, 8_7, 8_2 and 9:—		
Maxillary fragment with first molar or alveolus	18 left	11 right
Dentary fragment with first molar or alveolus	22 left	15 right
4. *Pseudomys shortridgei* (a large native mouse) in Layer O, Trenches 7a, b, c, d, 8_7, 8_2 and 9:—		
Maxillary fragment with first molar or alveolus	3 left	4 right
Dentary fragment with first molar or alveolus	4 left	3 right
5. *Tarsipes spencerae* (the mouse-sized honey possum) in Layer 30—lower, Trench 9—North half:—		
Humerus or distal end	51 left	52 right
Femur	40 left	51 right
6. *Tarsipes spencerae* in Layer 30—lower (deeper half), Trench 9—South half:—		
Humerus	11 left	7 right
Scapula	8 left	7 right
Femur	18 left	15 right
Innominate	8 left	6 right
Dentary (an extremely fragile structure)	5 left	3 right
7. *Tarsipes spencerae* in Layer 30—lower, Trenches 2, 7d, 8_7, 8_2, 9—North and 9—South:—		
Humerus	117 left	148 right
Femur	104 left	117 right
8. *Antechinus flavipes* (a carnivorous marsupial about the size of a young house rat) in Layer 30—lower, Trenches 2, 7d, 8_7, 8_2, 9—North and 9—South:—		
Maxillary fragment	21 left	17 right
Dentary	26 left	21 right
9. *Sminthopsis murina* (a mouse-sized carnivorous marsupial) in Layer 30—lower, Trenches 2, 7d, 8_7, 8_2, 9—North and 9—South:—		
Maxillary fragment	21 left	17 right
Dentary	21 left	27 right

Laboratory sorting of material recovered from the excavations included separation of some anatomical structures for detailed study from the bulk of fragmented bone. The present paper is based only on this selected material. It included isolated teeth or tooth-bearing structures of any vertebrate, recognizable fragments of scapula, humerus, pelvis, femur or calcaneum of any marsupial or bat (but not of murids), any recognizable limb-bone fragment of birds, lizards or frogs, and vertebrae of birds, lizards, snakes and fish.

Snakes were recorded only as present or absent in a given layer, but "minimum numbers of individuals" were estimated for all other vertebrates. Because of differences in the material studied, and differences in our expertise from taxon to taxon, our estimates are not strictly comparable with one another. For example, the minimum number of individuals of *Pseudomys shortridgei* in layer 11 was 2, as also for *Macropus fuliginosus*. But postcranial elements as well as teeth were used to estimate the latter which in any case is conspicuous by reason of size, and also likely to have received more careful attention because it was the sole subject of a parallel study by one of us (J.B.). We suggest it is legitimate to compare minimum numbers of *P. shortridgei* from layer to layer, or with other murids in the same layer, but less reliable to compare them with any marsupial taxon either in the same layer or from taxon to taxon. Bird numbers may have been overestimated because the anatomical structures identified were not restricted to a few as with mammals. On the other hand, underestimation may have resulted from our inability to distinguish bird species.

At least two of us have concurred in the identification of each of the fragments on which this paper is based. There may be errors of identification in spite of this, but we have no present means of judging the extent of such errors. The material would be amenable to detailed studies of many kinds, and indeed we have a few such studies in hand, though only a very small proportion of what can be envisaged. As such studies proceed, and the material is re-examined section by section, the degree of error in identification should become clearer. We hope to publish or otherwise record details of our identification procedures in due course. We have been unable to agree on the identities of about 50 specimens; they are widely dispersed stratigraphically, and it seems unlikely that agreement on them would require much revision of our conclusions.

All bone fragments recovered have been stored and are readily accessible for further study, even when not anatomically or taxonomically identified. Unidentified material has been labelled and stored with an identified, catalogued specimen (usually of *Bettongia penicillata* or *Rattus fuscipes)* from the layer and trench concerned. We have usually made a catalogue entry and hence given a number to each of the specimens upon which our "minimum number of individuals" of a particular taxon, layer and trench is based. But this practice has varied in that sometimes we have catalogued additional specimens of particular interest (e.g. identifiable charred specimens, or exceptionally complete ones), and in the case of section cleaning or other unlocalized samples, have catalogued only one example of each taxon. Thus the total number of catalogue entries may not be very close to the total of minimum numbers of individuals estimated on a trench by trench basis.

Taxa present

A summary of the vertebrate taxa present in contexts we consider to be stratigraphically secure is given in Table 3. For extant mammals, we have followed the names and species concepts of Ride (1970) who in his Appendix II lists authorship of names, but for extinct mammals we have had to follow various authors. Some notes on the taxa present follow with an indication of whether they fall into the "forest" or "non-forest" categories of Baynes *et al.* (1976).

Dasyurus. D. geoffroii only, the chuditch or western native cat; forest.

Phascogale. P. tapoatafa, the tuan or common wambenger; forest.

Antechinus. probably all *A. flavipes,* the mardo; forest.

Sminthopsis. probably all *S. murina,* the common dunnart or marsupial mouse; forest.

Sarcophilus. S. harrisii only, the Tasmanian devil; forest.

Thylacinus. T. cynocephalus only, the Tasmanian wolf or tiger; forest. Very sparsely represented; only 7 teeth (5 individuals) from all sources in Devil's Lair so far, and 3 of these teeth from uncertain stratigraphic position and 2 from Trench 6.

Isoodon. probably all *I. obesulus,* the short-nosed bandicoot or quenda; forest.

Perameles. Specific identity still in doubt—certainly a member of the "*P. bougainville* group" (Tate 1948) and closely resembling if not identical with *P. bougainville,* the barred bandicoot, marl or little marl (one of the long-nosed bandicoot group of species); non-forest.

Trichosurus. probably all *T. vulpecula,* the brush or brush-tailed or common possum; forest.

Pseudocheirus. probably all *P. peregrinus,* the common ringtail; forest.

Cercartetus. probably all *C. concinnus,* the south-western pigmy possum or mundarda; forest.

Tarsipes. T. spencerae only, the honey possum or noolbenger; non-forest. Presence in upper parts of deposit was not detected initially (Baynes *et al.* 1976 p. 107) but re-examination of material has shown that a few postcranial specimens were present but had been confused with *Sminthopsis.*

Phascolarctos. presumably *P. cinereus,* the koala or native bear; forest. Up to 1976 represented by one tooth isolated from its jaw, but confirmed by a specimen recovered in 1977.

Vombatus. Presumably *V. hacketti* (Glauert 1910), which appears to be distinct from the extant common wombat of eastern Australia. Preferred habitat unknown. Represented by an isolated upper molar enamel cap, probably never erupted, of an extremely young animal.

Potorous. May all represent the south-western form (previously known as *P. gilberti*) of the potoroo or long-nosed rat-kangaroo *P. tridactylus,* but if so, some small individuals included; forest.

Bettongia. two species present: *B. penicillata,* the brush-tailed bettong or rat-kangaroo or woylie; forest. *B. lesueur,* the burrowing rat-kangaroo, boodie, or tungoo; non-forest.

Lagorchestes. A doubtful inclusion here; record depending mainly on a small fragment of dentary found in Trench A1 in 1970, and then thought to represent *L. leporides*, although on biogeographical grounds, *L. hirsutus* would be more likely (Baynes *et al.* 1976 p. 109); non-forest.

Petrogale. Specific identity uncertain because of close similarities among named modern "species". Probably all *P. penicillata* as conceived by Ride (1970); non-forest.

Macropus. three extant species present; all in "forest" group. *M. eugenii*, the tammar or scrub wallaby; probably all Devil's Lair specimens resembling the eastern Australian pademelons (*Thylogale* spp.) can be referred to *M. eugenii*. *M. irma*, the western brush wallaby. *M. fuliginosus*, the western grey kangaroo (presumably; possibility of *M. giganteus* also being present has not been explored).

Setonix. S. brachyurus only, the quokka; forest.

Sthenurus. two species present, habitat preferences unknown. Extinct, hence no vernacular names. *S. brownei* Merrilees 1968a (see Fig. 9). *S. occidentalis* (Glauert 1910 as revised by Merrilees 1968a).

Protemnodon. Probably *P. brehus* (Owen 1874 as revised by Bartholomai 1973); habitat preferences unknown. Extinct, no vernacular name.

Zygomaturus. A doubtful record, based on a single very fragile enamel cap, perhaps never erupted, interpreted by us as an upper first incisor of *Zygomaturus* (See Fig. 10). We have not been able to obtain comparative specimens of *Zygomaturus* or any other diprotodontid upper incisors showing the unworn tip of the tooth. Some incisors of very young animals are available from Mammoth Cave, ascribed to *Z. trilobus* by Merrilees (1968b), and these match the Devil's Lair specimen in most discernible respects. Habitat preferences of *Zygomaturus* not known. Extinct, no vernacular name.

Hydromys. H. chrysogaster only, a native rodent of different sub-family ranking from the other native rodents listed below; the water rat, highly specialized for a largely aquatic life; forest.

Pseudomys. Four species of native mice present, all non-forest. *P. albocinereus*, the grey or ashy-grey mouse. *P. occidentalis*, the western mouse. *P. shortridgei*, the blunt-faced rat or Shortridge's native mouse. *P. praeconis*, the Shark Bay mouse.

Notomys. Specific identity still in doubt, but considered by Baynes *et al.* (1976 p. 109) on biogeographical grounds most likely to be *N. mitchellii*, Mitchell's hopping-mouse; non-forest.

Rattus. probably all *R. fuscipes*, the southern bush-rat; forest.

Homo. two deciduous human incisors, one permanent incisor and a pelvic fragment have been recovered (Davies 1968 and Appendix in Dortch and Merrilees 1973, Freedman 1976 and Allbrook 1976); not discussed further here.

Bats. No attempt made to distinguish species except to note: (1) more than one species present; (ii) *Macroderma gigas*, the ghost bat, or false vampire. Not present in 1974, 1975 or 1976 material, though recorded by Baynes et *al.* (1976) from layers G or H and Hearth 2, Trench 7c, recovered in 1973 and by Cook (1960) from early excavations in Devil's Lair. Non-forest. On assumption that bat species other than *Macroderma* are as listed by Baynes *et al.* (1976 Table 7, p. 109)), "bats" have been taken herein to be forest species.

Birds. No attempt made to distinguish species, and therefore habitats unknown. Predominantly small passerines. Fragments of emu egg shell common, but no emu bone, a puzzling absence if man was the major predator, in view of reports of emu flesh being a favoured food among modern south-western Aborigines (Meagher 1974).

Lizards. No attempt made to distinguish species and therefore habitats unknown. Predominantly very small skinks, and hence probably taken into cave by a predator active during day.

Snakes. No attempt made to distinguish species. Because diagnosed only on vertebrae, and these not diagnosed for anatomical position, no attempt made to estimate numbers of individuals. All small.

Frogs. No attempt made to distinguish species, and therefore habitats unknown.

Fish. Very uncommon. No attempt made to distinguish species. Indicate presence of free water in neighbourhood, but not whether river or sea.

The faunal succession

An attempt has been made in Figure 5 to show fluctuations in time among the major vertebrate groups included in Table 3. We have expressed the minimum numbers of individuals representing each taxon as percentages of the total vertebrates for the layer concerned. It is clear from Table 3 and from Figure 5 that mammals, birds, lizards, frogs and snakes occur throughout the deposit, usually with a marked preponderance of mammals. However, in layers 0, 0 and P mixed, P and Q, all involving substantial numbers of animals, lizard numbers exceed or are comparable with mammal numbers. Also, making due allowance for the larger samples probably being statistically more reliable than the smaller samples, Figure 5 suggests that lizard proportions (relative to mammals) increased in terminal Pleistocene (post-glacial maximum) time to a peak in layer P, and then more rapidly declined into early Holocene time.

At present we have no direct age estimate for layer P. On the assumption that average sedimentation rates remained constant between 19 000 and 11 960 years ago (the approximate ages of layer 7 and M respectively) the age of P would be about 14 000 years.

Figure 5 is intended to draw attention incidentally to the need to make allowance for sample size. Such an allowance has been made in Figures 6 and 7, dealing with relative proportions among the mammal taxa only. Samples in which the total number of vertebrate individuals of all kinds exceeds 50 have been considered reliable enough to warrant expressing the relative proportions of the constituent mammal taxa as percentages of the total mammals present in the layer concerned. Superimposed on this consideration, however, has been the consideration that certain mammal taxa are so sparsely represented throughout the deposit that reasons for their presence may be different from those for mammal taxa which are more abundant. We have made an attempt to allow for this "sparseness factor" by treating separately all mammal taxa in which the total representation throughout the deposit (in the stratigraphically secure contexts summed up in Table 3) does not exceed 10 individuals.

Thus we have shown a "sparsely represented" group of mammals in Figure 7 merely as being present in a given stratigraphic sample, without making any attempt to quantify such presence. Similarly, throughout Figures 6 and 7, we have recorded even the abundantly represented mammals simply as being present in any stratigraphic sample involving less than 50 vertebrate individuals. Only in larger samples have we quantified the presence of the abundantly represented mammals by showing each taxon as a percentage of the total mammals.

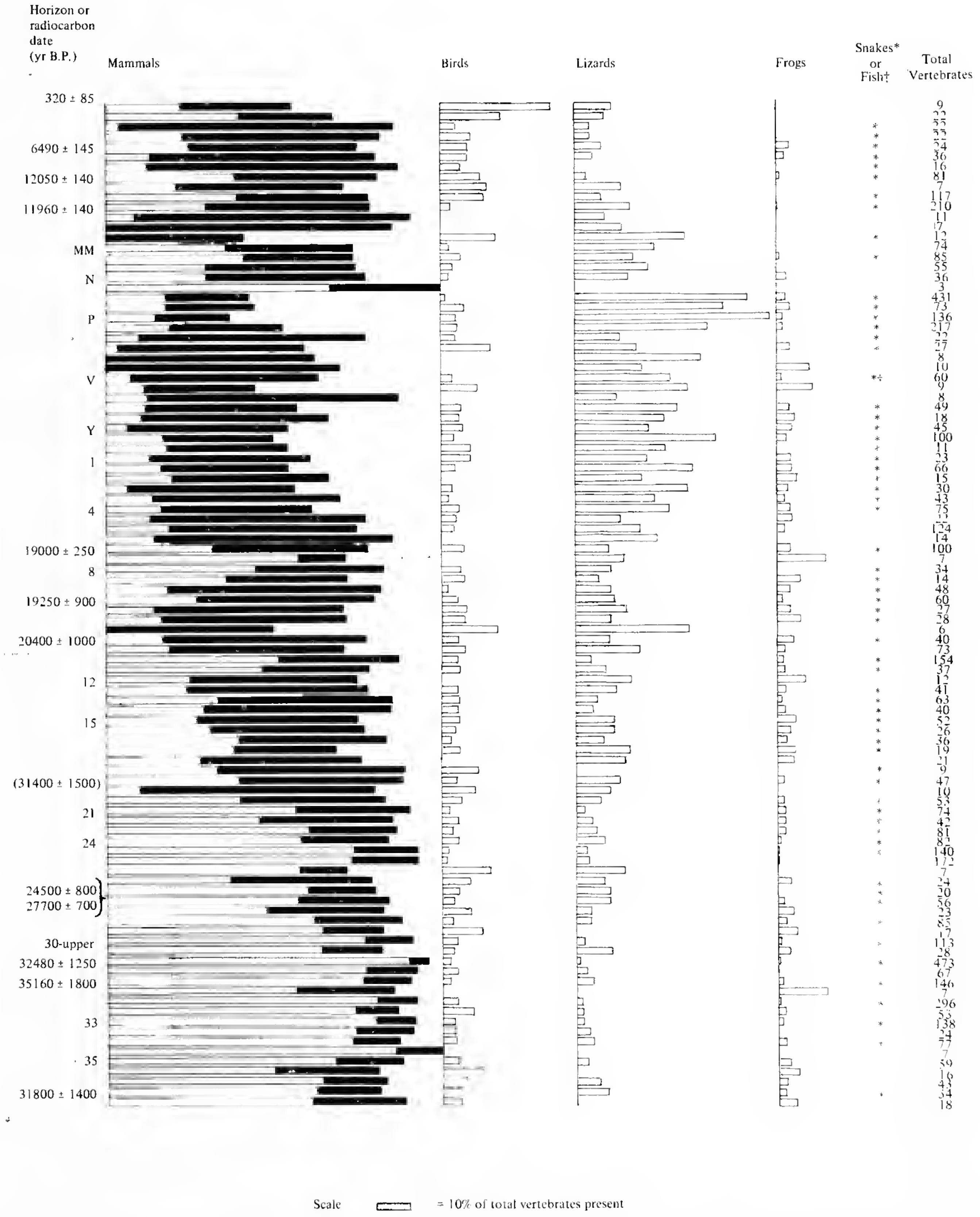

Figure 5.— Small mammals, large mammals (in black), birds, lizards and frogs as percentages of total vertebrates. "Small mammals"=*Phascogale*, *Antechinus*, *Sminthopsis*, *Cercartetus*, *Tarsipes* and all murids and bats. * snake present; † fish present.

Table 3

TABLE 3 – Minimum numbers of individuals of vertebrate taxa in stratigraphically reliable context, 1973-1976 excavations, Devil's Lair

Trench	Stratigraphic layer	Depth of top of layer below cave datum at NW corner of Tr 8_7 cm		Radiocarbon date yr BP	*Dasyurus*	*Phascogale*	*Antechinus*	*Sminthopsis*	*Sarcophilus*	*Thylacinus*	*Isoodon*	*Perameles*	*Trichosurus*	*Pseudocheirus*	*Cercartetus*	*Tarsipes*	*Phascolarctos*
	Present floor of cave	79															
	A under B			320													
7c, d; 8	**A under C**	87	T								1			1			
7d; 8	**A under E**	92	T				2				1	1	2				
7a, b, c	**D**		T		1						2		2	2			
8	**F**	c 109			1						1		1	1			
7b, c	**G**			6490	1		2				1		1	1			
7a, b, c	**H**				1						2		3	3			
7a, b, c	**I**						1				1		1	2			
7b, c, d; 8_7; 8_2	**K (incl. occupation floor)**			12050	2		8	3			2	1	4	5	4		
7a, b, c	**L**							1					2	1			
7c, d; 8_7; 8_2	**Hearth 2**				3		8	11	1		3	2	4	6	2		
7a, b, c, d; 8_2	**M (incl. orange & brown mottling)**		T	11960	5	1	7	10	2		16	5	10	12	1		
7b	**Hearth z**		T		1						2			1			
7a	**H.P.**										1		1	1			
7a	**"below H.P."**				1						1			1			
7b, c, d: 8_2	**MM**		T		3			4	1		4	2	3	2	1	1	
7d; 8_2	**Hearth y**				2		4	2			3	3	3	2	5		
7c, d; 8_2	**Sub MM**				3			3			3	2	2	2	1	1	
7a, b, c, d	**N**				1			1			2	1	2	1	1		
8_7	**N with small amounts of O**	135						1									
7a, b, c, d; 8_7; 8_2; 9	**O**	136	T		6	1	2	11	1		20	8	6	9	4	2	
8_7	**O and P mixed**	142			2			4			3	2	2	1	1	1	
7a, b, c, d; 8_7; 8_2; 9	P	142			3			2			7	3	2	2	3		
7a, b, c, d; 8_7; 8_2	Q	143	T		6		1	10	2		11	8	5	3	3	1	
7c, d; 8_2	T				1			1			1	1	2	1			
8_7	T and U mixed	167			1						2	1	2	1			
8_2	U										1		1	1			
7b	U and V mixed				1						2			1			
7c; 8_7; 8_2	V	171	T		3			2			2	3	3	3	1		
8_2	W										1						
7c, d	W and X mixed								1		1			1			
7c, d; 8_7; 8_2	X	176	T		2			2			3	2	3	1			
8_7	X and Y mixed	180			2						1	1					
7a, b, c, d: 8_2; 9	Y				1			1			2	1	2	1			
7a, b, c, d; 8_7; 8_2; 9	Z	185			2			4			3	2	2	3	2	1	
8_7	Z, 1 and 2 mixed	186						1			1		1				
7a, b, c, d; 8_7; 8_2; 9	1	188			1			1			2	1	1	1			
7a, b, c, d; 8_7; 8_2; 9	2	188			2			4			3	1	2	2	1		
8_7	2 and 3 mixed	191						1			2		1				
7c, d; 8_2; 9	3				1			1			2	1	2	2			
7a, b	3 and 4 mixed				2			1			4	2	2	2	1		
7a, b, c, d; 8_7; 8_2; 9	4	192			3			5			5	3	2	2			
7a, b, c, d; 8_7; 8_2; 9	5				2			2			1	1	2	2			
7a, b, c, d; 8_7; 8_2; 9	6	209	T		5			8	2		8	4	7	8	2		
8_7	6 and 7 mixed	219			1						2		1	1			
7a, b, c, d; 8_7; 8_2; 9	7	220	T	19000	5	1		6	1		5	3	6	6	2		
8_7	7 and 8 mixed							1			1						
7d; 8_7; 8_2	8				1	1		2			2	1	2	1	2	1	
9	8 and 9 mixed							3			1			1		1	
7d; 8_7; 8_2; 9	9-upper brown part	229			2	2		3			3		3	5	1		
7d; 8_7; 8_2; 9	9-lower	233	T	19250	2	1	1	2	1		4	1	3	6			
7d; 8_7; 8_2; 9	10a	240			1	1					2		2	4			
8_7; 8_2; 9	10b	244			2			1			2	1	2	2	1		
7d	10b and 10c mixed				[illegible]									1			
7d; 8_7; 8_2; 9	10c	250	T	20400	[illegible]	1		2			3		2	3	[illegible]		
7d; 8_7; 8_2; 9	10d and e	257	T		4		1	5			4	1	4	6	[illegible]		
7d; 8_7; 8_2; 9	11	265	T		2		4	8	1		3	3	[illegible]	11	9	3	
8_7; 8_2; 9	11 and 12 mixed	274			1			1			1		3	3	1		
7d; 8_2	12				1			1			1		1	[illegible]			
8_7; 9	11, 12 and 13 mixed	276			2			3			2	1	1	5	1		
7d; 8_7; 8_2; 9	13	277	T		3		1	5	1		2		2	6	1	1	
8_7; 8_2; 9	14	282			[illegible]	1	1	[illegible]			1		3	5			
7d; 8_7; 8_2; 9	15	285			2			3			2	1	1	4			
7d; 8_7; 8_2; 9	14, 15 and 16 mixed				[illegible]			2			1		1	1			

Table 3—Continued

Vombatus	*Potorous*	*Bettongia penicillata*	*Bettongia lesueur*	*Lagorchestes*	*Petrogale*	*Macropus eugenii*	*Macropus irma*	*Macropus fuliginosus*	*Setonix*	*Sthenurus brownei*	*Sthenurus occidentalis*	*Protemnodon*	*Zygomaturus*	*Hydromys*	*Pseudomys albocinereus*	*Pseudomys occidentalis*	*Pseudomys shortridgei*	*Pseudomys praeconis*	*Notomys*	*Rattus*	bat	Total Mammals	bird	lizard	snake	frog	fish	Total Vertebrates	Volume – cu m (* estimate only)	Incidence of Vertebrates Individuals/cu m	
	1																			2		5	3	1				9	0.16 *	60	l
		1							1						1					6		15	4	2		1		22	0.13 *	170	l
	2	2	1		2			1	3											1		19	1	1	p			22	0.09 *	240	
	1	1			2		1	1	3								1			4		18	2	1	p			22	0.05 *	440	
	1	1			1		1	1	3											4		18	2	2	p	1		24	0.10 *	740	
	2	5	1		1			1	5						1					4	1	29	3	2	p	1		36			
	1	2			1			1	3											1		14	1		p			16			
	3	5	2		1	1	1	2	5						3		1		1	12		66	10	3	p	1		81	0.06 *	1380	
		1																				5	1	1				7	0.04 *	180	l
	3	5	3		2	2	2	2	7						6		3		3	14	1	92	15	9	p			117	0.06 *	1940	
	3	24	10		4	3	3	3	3						12		2		10	20		166	7	35	p	1		210	0.45 *	470	
	1	1			1			1	1											1		10		1				11	<0.01 *		
		1			1			1														6		1				7	<0.01 *		
		1			1																	5	2	4	p			12	<0.01 *		
		4	3		1	1	1	1	2						8		1		6	6		55	2	17				74	0.12 *	620	
	1	3	1		2	3	1	1	2						9		1		9	6		63	5	15	p	1		85	0.02 *	4350	h
	1	2	2		2	1	1	1	2						7				2	4		42	2	12				55	0.05 *	1190	
	1	3			2	1		1	2						4		1		2	2		28	1	6		1		36	0.05	680	
									1										1			3						3	<0.01		
	2	20	9		11	2	3	6	3					1	22		4	1	11	20	2	187	6	223	p	14		431	0.33 *	1290	h
	1	1	2		2	1		1	1						1		1		3	2		32	5	32	p	3		73			
		3	1		2		2	1	3					1	7		1		2	4		49	3	80	p	3		136	0.04 *	3496	h
	2	11	10		7	1	1	3	2					1	7		2		5	11	1	114	11	86	p	5		217	0.44 *	500	
		3	1		1		1	2	1						1							17	1	3	p			22	0.02	1100	
		3	1		3		1								1							16	4	5	p	1		27	0.01		
			1		1																	5		3				8	<0.01		
	1		1		1																	7		2		1		10	0.09		
		5	5		4	1	1	1	2						1				1			38	2	17	p	1	1	60	0.12	480	
		1			1															1		4	1	3		1		9	0.01	750	
		1			1			1												1		7		1				8	0.02		
		3	1		3		1	1	2						2				1	1		28	3	15	p	2		49	0.10	480	
	1	2			1	1		1											2			12	1	3	p	1		18	0.02		
	2	6	3		2		1	1							2				1	3		29	3	10	p	2		45	0.07 *	650	
		9	3		3	1	1	3	1						4				1	5		50	4	42	p	3		100	0.20	490	
			1		1															1		6	1	3	p			11	<0.01		
	1	1	1		1	1									2							14	2	5	p	1		23	0.04	620	
	1	5	2		2	1		2	2						2				1	3		36	3	23	p	3		66	0.15	450	
		2			1	1									1					1		10		3	p	1		15	0.03		
		2	1		2	1			1											1		17	1	10	p	1		30	0.06	490	
	1	3	2		3		1	1	1						3		1					30	1	10	p	1		43	0.07		
	1	7	3		3			3	2						4					3		46	4	21	p	3		75			
		3	1		2										1							17	1	3		1		22	0.04	580	
	2	15	6		4		1	3	3						5		2		1	5	2	93	5	24		2		124	0.69	180	l
		2	1		1				1						1					1		12		2				14	0.01		
	3	4	4		4		1	2	3						11		1		1	8	1	78	7	10	p	4		100	0.28	360	
															2					1		5		1		1		7	0.02 *		
		2	1			1	1	1							2		1			5	1	28	2	3	p			34	0.05 *	740	
	1	1					1								1							10	1	1	p	1		14	0.01		
	2	4	1		2		2	4	2						1					2		39	1	5	p	2		48	0.12	410	
	1	4	2		1	1	2	2	2						2		1			9		48	3	7	p	1		60	0.16	370	
		2			1		1	1	1											3		19	2	4	p	1		27	0.09	290	
		2	1		2				1						2					1		20	2	3	p	2		28	0.07	400	
					1																	3	1	2				6	<0.01		
		4	3		3	1		2	2											3		31	2	4	p	2		40	0.30	130	l
	3	6	2		4		1	1	2						2					5		52	5	14		2		73	0.26	280	
	4	10	5		2	1	2	2	5						14		2		1	38	1	135	8	7	p	3		154	0.26	590	
	2	2			1	1		1	3						1					8		29	2	4	p	1		37	0.06		
		1							1											2		9		2		1		12	<0.01		
	3	2			1	1	1	1	2						2					4		32	2	5	p	1		41	0.04		
	3	3	1		2	1	1	2	6						4		1		1	7		54	3	4	p	1		63	0.09	720	
	1	2	2		1	2	1	1	2						2		1		1	4		34	2	2	p	1		40	0.05	890	
	2	5	1		1	1	1	1	3						4		1			6		39	3	6	p	3		52	0.10	540	
		2	1		1		1	1	2						2		1		1	2		20	1	3	p	1		26	0.06 *		

Table 3—Continued

TABLE 3 – Minimum numbers of individuals of vertebrate taxa in stratigraphically reliable context, 1973-1976 excavations, Devil's Lair

Trench	Stratigraphic layer	Depth of top of layer below cave datum at NW corner of Tr 8_7 cm		Radiocarbon date yr BP	*Dasyurus*	*Phascogale*	*Antechinus*	*Sminthopsis*	*Sarcophilus*	*Thylacinus*	*Isoodon*	*Perameles*	*Trichosurus*	*Pseudocheirus*	*Cercartetus*	*Tarsipes*	*Phascolarctos*
8_7; 8_2; 9	16	289			1			1	1		2	2				1	
7d; 9	16 and 17 mixed							2				1				1	
8_7; 8_2; 9	17	292			1			1			1		1	1		1	
9	16, 17 and 18 mixed							2			1			1			
8_7; 8_2; 9	18 (incl. hearth)	293	T	(31400)	2			3			3	1	1	3		2	
8_2; 9	19										1			1			
7d; 8_7; 8_2; 9	20	298	T		1		2	2			2	1		1		1	
7d; 8_7; 8_2; 9	21	306			1		1	8	1		1	2	1	1		4	
7d; 8_7; 8_2; 9	22	308			1		1	3			1	3		1		2	1
7d; 8_7; 8_2; 9	23	309			2			8			1	2	1	1		6	
7d; 8_7; 8_2; 9	24	313			1		1	8	1		2	2	1	1		6	
7d; 8_7; 8_2; 9	25	317			1		1	13			3	3	1	2	1	10	
7d; 8_7; 8_2; 9	26	321			1	2	3	22	1		6	3		2	1	7	
7d	26 and 27 mixed				1											1	
7d; 8_7; 8_2; 9	27 (incl. hearth)	325			1		1				1	2				2	
8_2; 9	27 and 28 mixed						1	1				1				1	
8_7; 8_2; 9	28 (incl. hearth)	328		24600	1		1	4	1		1	1	1	1		5	
8_7; 8_2	28 and 29 mixed	330		27700	1		1	2			1	1			1	2	
7d; 8_7; 8_2; 9	29	331	T			1	1	7	1		2	2		2	2	12	
2; 8_7	29 and 30-upper, mixed						2	1				1		1		2	
7d; 8_7; 8_2; 9-N; 9-S	30-upper	342	T		1	2	7	8			2	3		2	6	25	
2	30-upper and 30-lower mixed					1	1	2			1	1		1	1	4	
2; 7d; 8_7; 8_2; 9-N; 9-S	30-lower		T	32480	2	6	26	27			5	6		6	32	148	
2; 7d; 8_7; 8_2	30-lower and 31, mixed				1	1	1	4			2	2		1	4	17	
2; 7d; 8_7; 8_2; 9-N; 9-S	31	c.356	T	35160	1	1	2	15	1		6	3		3	6	39	
8_2	31 and 32 mixed										1					2	
2; 7d; 8_7; 8_2; 9-N; 9-S	32	372	T		2	3	8	20	1	2	5	9		4	6	85	
8_7	32 and 33 mixed				1	1	1	2			2	1		1	2	15	
2; 7d; 8_7; 8_2; 9-N; 9-S	33	390	T *		1	1	1	7			4	4		2	3	51	
2; 7d; 8_7; 8_2;9-N;9-S	33 and 34 mixed				1		1	1			1	1				8	
2; 7d; 8_7; 8_2; 9-N; 9-S	34	399	T			1	3	5			3	3		2	2	23	
8_7; 8_2	34 and 35 mixed							1			1				1	3	
2; 7d; 8_7; 8_2; 9-N; 9-S	35	414	T		1	1	2	3			3	2		2	2	20	
8_7; 9-N; 9-S	35 and 36 mixed							1			1	1		1		4	
2; 7d; 8_7; 8_2; 9-N; 9-S	37	427	T		1		1	3			1	2		2		9	
2; 7d; 8_7; 8_2; 9-N; 9-S	38	436	T	31800		1	2	3			1	2		1	2	9	
7d; 8_7; 8_2; 9-N; 9-S	38 and 39 mixed					1	1				1	1		1		3	
TOTAL					132	33	116	337	22	2	245	143	139	211	123	543	1

T = 5cm thick or more over most of area

* pooled mean 33150

We have grouped "forest mammals" in Figure 6, using the criteria of Baynes *et al.* (1976), i.e. recognizing a taxon as in the forest group if its known modern distribution included the sclerophyllous and mesophytic forest regions of Gardner (1944), even though many such mammals ranged far beyond these forest regions. "Non-forest mammals" (Figure 7) are those not known to have ranged into the sclerophyllous and mesophytic forest regions. *Sarcophilus* and *Thylacinus* are regarded as "forest mammals" by analogy with their known distribution pattern in Tasmania in historic time. *Tarsipes*, a "non-forest mammal" is shown separately because of its distinctive distribution in the Devil's Lair deposit. The data on which Figures 5, 6 and 7 are based are given in Table 3.

Figures 6 and 7 suggest that some mammal taxa are consistently present throughout the deposit, in contrast with others which at times are present and at other times not. Ignoring all considerations of sample reliability, *Isoodon* turns out to be the mammal most consistently present (in 93 of the 100 stratigraphic samples listed in Table 3), followed by *Pseudocheirus* (in 84 samples), *Rattus* (in 83), *Sminthopsis* (in 77), and *Pseudomys albocinereus* and *Dasyurus* (each 75).

The concept of consistency of presence has more meaning with large than with small samples. Some samples are of such size that one would expect them to include any taxon at all likely to be present. Furthermore, one would expect that taxa present in many layers would be

Table 3—Continued

Vombatus	*Potorous*	*Bettongia penicillata*	*Bettongia lesueur*	*Lagorchestes*	*Petrogale*	*Macropus eugenii*	*Macropus irma*	*Macropus fuliginosus*	*Setonix*	*Sthenurus brownei*	*Sthenurus occidentalis*	*Protemnodon*	*Zygomaturus*	*Hydromys*	*Pseudomys albocinereus*	*Pseudomys occidentalis*	*Pseudomys shortridgei*	*Pseudomys praeconis*	*Notomys*	*Rattus*	bat	Total Mammals	bird	lizard	snake	frog	fish	Total Vertebrates	Volume – cu m (* estimate only)	Incidence of Vertebrates Individuals/cu m
	2	1			1	1	1	1	3						6		1		2	3		30	1	3	p	1		36	0.07	490
	1	2						1	1						2		2					13	1	3	p	1		19	0.02	
					1	1		2	2						1		1		1	1		16		3	p	1		21	0.04	550
		1			1				1											1		8	1					9	<0.01	
	1	2			2	1	2	2	3						2		2		1	4		37	2	6	p	1		47	0.11	440
					1	1		1	2						1							8	1	1				10	0.02	630
	1	1			2	4	2	2	6						6		2		1	7		44	3	4	p	1		53	0.18 *	290
	3	1			3	3	2	2	4			1			9	1	5		2	10	1	67	2	2	p	2		74	0.08	990
	2	1				2	1	1	3						6		2		1	4		36	2	2	p	1		42	0.04	1200
	3	2			1	2	1	1	4						9		4		4	17	1	70	3	5	p	2		81	0.08	980
	2	2			1	2	2	1	3					1	15		3		5	9		69	4	7	p	1		82	0.08	1010
	3	2			1	3	2	2	4					1	22	1	17		3	33	1	130	3	5	p	1		140	0.10	1440
	4	2			2	3	2	3	5					1	17	7	20		5	40	1	160	3	7	p	1		172	0.11	1620
															2					1		5	1	1				7		
	1	1				1	1	1	1						2		1			3		19	2	2		1		24	0.03	750
						1	1	1							2	1	2		1	3		16	1	2	p			20	0.02	
	1				2	1	1	1	3						6	1	5		1	8	1	47	2	5	p	1		56	0.07	770
	1				1	1		1	1						1		1			3		19	2	1		1		23	0.03	
	2	2			1	2	3	1	3	1					8		4			18		75	3	4	p	2		85	0.15	560
									1						2				1	3		14	2			1		17	0.02	
	2	1							5						6		3			29	1	103	5	3	p	1		113	0.15	760
	1								1					1	1		1			6		23	1	3		1		28	0.04	
	3	1							4			1			15	1	25		2	139	5	454	11	4	p	3		473	0.51 *	920
	1						1		2						2		4			19	1	62	3	2				67	0.08	
	3			1				1	1	1					6		11			30	1	132	4	7	p	2		146	0.23	650
	1																1			1		6				1		7	0.01	
	3			1					1	3	2		1		28	1	12		1	71	3	273	14	5	p	2		295	0.53	550
	2														5		4			9		46	5	1		1		53	0.02	
1	2								1		1	1			11		8			27	1	127	5	3	p	2		138	0.24	590
	1														2					5	1	22	1	1				24	0.05	
	2								1						4		4			13	1	67	3	4	p	2		77	0.51	150 l
																				1		7						7	0.04	
	1								2			1			3		2			6	1	52	3	2		2		59		
	1						1								1					1	1	13	2			1		16	0.03	
	1								1						2		2			10	1	36	3	3		1		43	0.25	170 l
	2					1	1	1	1						4		2			10	1	44	3	5	p	1		54	0.43	130 l
	1								1								1			5		16	1			1		18	0.06	
1	115	244	104	2	136	63	66	96	176	5	3	4	1	7	376	13	182	1	99	808	32	4585	273	935	64	125	1	5980		

p = present

h = conspicuously high
l = conspicuously low
– see text

more likely to turn up in all samples of substantial size if they were available at the time concerned than taxa generally only sporadically present.

Table 4 represents our attempt to take these considerations into account. It is based on samples containing 20 or more mammal individuals, and on those 12 mammal taxa which occur in more than 60 of the 101 stratigraphic samples listed in Table 3.

The distributions (shown in Figures 6 and 7) of the 10 taxa ranked highest on the consistency scale used for Table 4 do indeed suggest consistent presence throughout the deposit. These—*Isoodon, Pseudomys albocinereus, Sminthopsis, Pseudocheirus, Setonix, Rattus, Dasyurus, Perameles, Potorous* and *Macropus fuliginosus*—must be regarded as the characteristic mammals of the Devil's Lair deposit. But *Bettongia penicillata* and *Petrogale* cannot be accepted as consistently present throughout. They make their first appearances a little over 30 000 and a little under 30 000 years ago respectively, and are consistently present only after these dates.

The examples of *Bettongia penicillata* and *Petrogale* raise the question of what weight to attach to the absence from parts of the deposit of mammals which elsewhere are present in some abundance. Absence from a small stratigraphic sample clearly does not have the same significance as absence from a large sample, and absence from one large sample sandwiched between two other large samples containing the

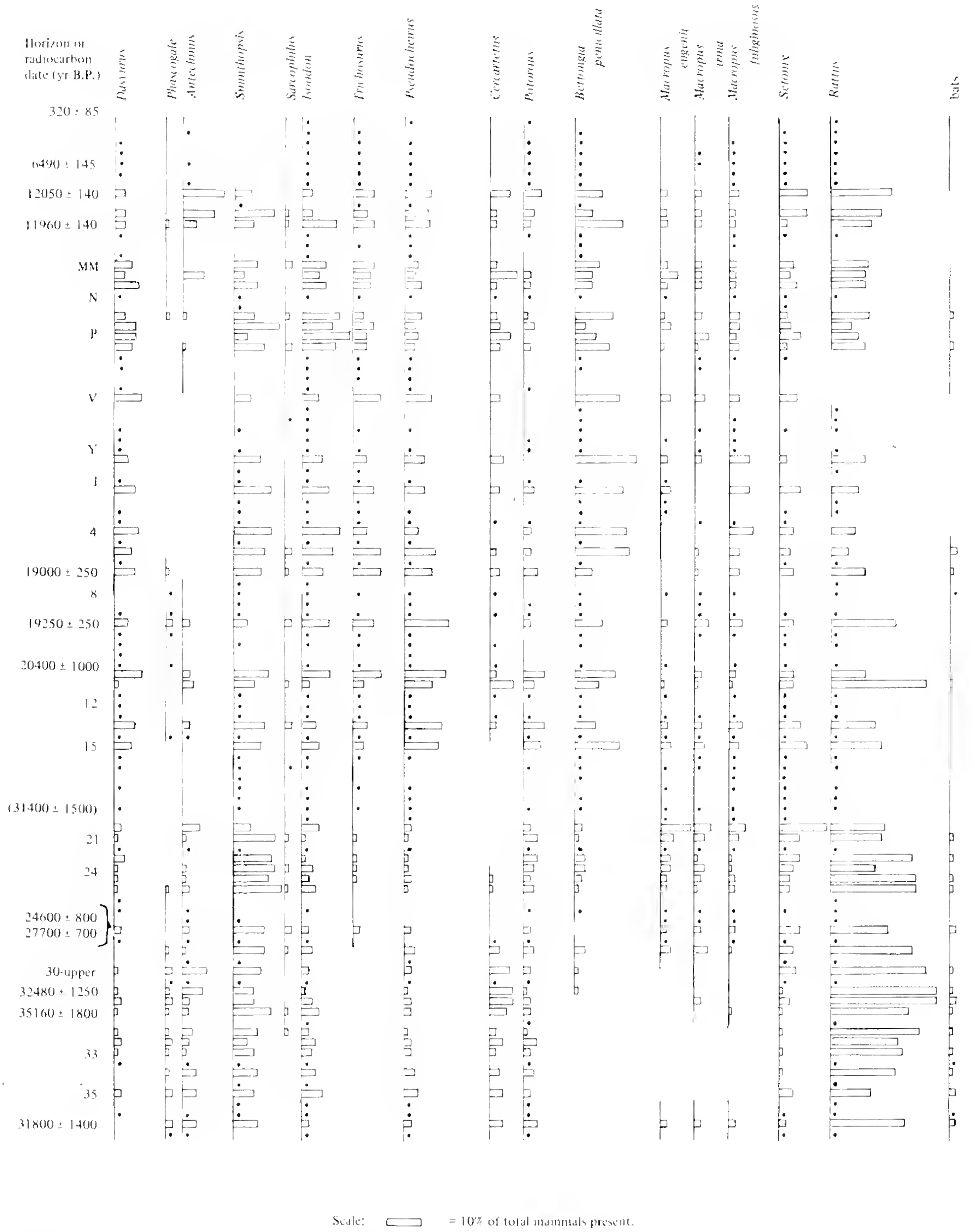

Figure 6.—Stratigraphic distribution of "forest mammals" (see text). In layers with more than 50 vertebrate individuals, mammal individuals shown as percentages of total mammals; in other layers, taxon present (●) or not. A gap in a vertical line indicates a "notable absence" (see text). A line indicates that taxon was probably present, whether or not represented in our sample.

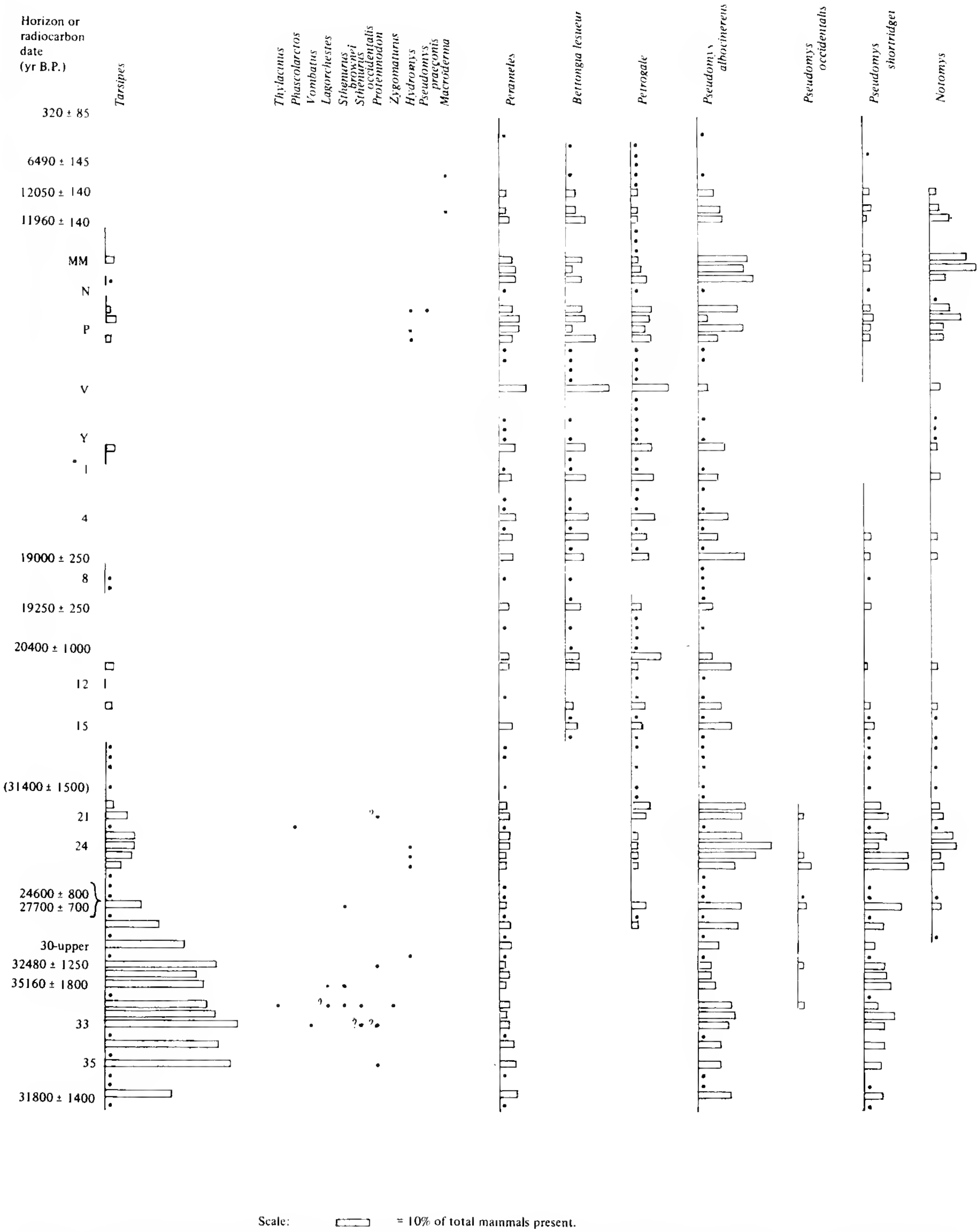

Figure 7.—Stratigraphic distribution of "non-forest" and "sparsely-represented" mammals (see text). In layers with more than 50 vertebrate individuals, mammal individuals shown as percentages of total mammals; in other layers, taxon present (●) or not. A gap in a vertical line indicates a "notable absence" (see text). A line indicates that the taxon was probably present, whether or not represented in our sample.

Table 4

Mammal taxa consistently present throughout deposit. Number of appearances in those 58 stratigraphic samples containing 20 mammal individuals or more.

Forest		Non-forest	
Isoodon	58	*Pseudomys albocinereus*	58
Pseudocheirus	57	*Perameles*	55
Sminthopsis	57	*Petrogale* (see text)	49
Rattus	56		
Setonix	56		
Dasyurus	55		
Potorous	50		
Macropus fuliginosus	50		
Bettongia penicillata (see text)	49		

taxon in question does not have the same significance as absence from two or more successive large samples plus the intervening small ones. Absence of a taxon elsewhere present in large total numbers is presumably more significant than absence of a taxon elsewhere present in only small numbers. We have attempted to take these factors into account in Table 5, which recognizes four arbitrary classes among the mammal taxa, based on overall abundance as set out in Table 3. Arbitrary criteria of what is to be regarded as a "notable absence" are set out for each class, becoming more stringent as the overall abundance becomes less. (Table 5 also incidentally draws attention to the great differences in overall abundance among the various mammal taxa, and in conjunction with Table 4, shows that the taxa most consistently present are not identical with those of greatest overall abundance).

With the reservations about the large totally extinct taxa discussed below, we are confident that the presence of any taxon shown in Table 3 in a given layer means not only that that taxon was present in the deposit but also that the animals concerned lived in the vicinity of Devil's Lair at about the time estimated for that layer. Not so for the "notable absences" listed in Table 5. Our criteria for absence are arbitrary, but even if they are well-based statistically, they are only criteria for "real" absence *from the deposit*. It is quite conceivable that the predator(s) responsible for the Devil's Lair bone accumulation at the time concerned did not or could not take individuals from populations of various mammals flourishing in the vicinity of the cave. As usual with faunal samples, a "presence" can carry much more weight of inference than an "absence".

Trends in the mammal fauna

Considering only trends within the deposit, and ignoring for the time being any relationships between the faunal sample left in the cave and the fauna living in the vicinity of the cave at any particular time, accepting the "notable absences" recorded in Table 5 as valid, and accepting the proportions calculated for the larger samples as giving some guide, even if only rough, to real fluctuations from layer to layer within the deposit, the following trends can be noted from Figures 6 and 7 (in time sequence, i.e. earliest first).

Dasyurus. Present throughout, but better represented from about layers 15 to MM than at the bottom or top.

Phascogale. Consistently present (in low numbers) only near the bottom of the deposit.

Table 5

"Notable absences" in Figures 6 and 7 (Refers only to mammal taxa recovered from secure stratigraphic context, listed in Table 3, and not shown as "sparsely represented" in Figure 7).

Class 1. Mammals present in total numbers of individuals exceeding 500. Absence from any stratigraphic sample involving more than 20 vertebrate individuals regarded as notable.

Rattus—absent, Layers T to V inclusive, 1, 3 and 4 mixed, 5.

Tarsipes—absent Layers A to M inclusive, Hearth y, N, P, T to Y inclusive, 1-7 inclusive, 9 and 10 (including subdivisions), 11 and 12 mixed, 11, 12 and 13 mixed, 14, 15 and 14, 15 and 16 mixed.

Class 2. Mammals present in total numbers exceeding 200, but with "minimum number of individuals" totalling less than 500. Absence from any stratigraphic sample involving more than 50 vertebrate animals regarded as notable.

Sminthopsis—no notable absences.

Isoodon—no notable absences.

Pseudocheirus—no notable absences.

Bettongia penicillata—absent Layers 30 - lower and 31 mixed to 38 and 39 mixed (inclusive).

Pseudomys albocinereus—no notable absences.

Class 3. Mammals present in total numbers exceeding 100, but with "minimum number of individuals" totalling less than 200. Absence regarded as notable if missing from two successive stratigraphic samples each involving more than 50 vertebrate individuals plus any intervening smaller samples.

Dasyurus—no notable absences.

Antechinus—absent, Layers O & P mixed and P, V - 7 inclusive.

Perameles—no notable absences.

Trichosurus—absent, Layers 29 to 38 and 39 mixed (inclusive).

Cercartetus—absent, Layers 15-23 inclusive.

Potorous—no notable absences.

Bettongia lesueur—absent, Layers 20 to 38 and 39 mixed (inclusive).

Petrogale—absent, Layers 30-upper to 38 inclusive.

Setonix—no notable absences.

Pseudomys shortridgei—absent, Layers V-2 inclusive.

Class 4. Mammals present in total numbers exceeding 10, but with "minimum numbers of individuals" totalling less than 100. Absence not regarded as notable unless missing from four successive stratigraphic samples each involving more than 50 vertebrate individuals plus all intervening smaller samples.

Phascogale—absent, Layers O and P mixed-6 inclusive, 15-25 inclusive.

Sarcophilus—absent, Layers 32 and 33 mixed - 38 and 39 mixed (inclusive).

Macropus eugenii—absent, Layer 30 upper to 35 inclusive.

Macropus irma—absent, Layers 31-35 inclusive.

Macropus fuliginosus—absent, Layers 32-35 inclusive.

Pseudomys occidentalis—absent, Layers K-20 inclusive, 32 and 33 mixed to 38 and 39 mixed (inclusive).

Notomys—absent, Layers 32 and 33 mixed to 38 and 39 mixed (inclusive).

Bats (not including *Macroderma*)—absent, Layers K-Sub MM, V-4 inclusive.

Antechinus. Consistently present from about layers 38 to 20, consistently absent 7 to V and rises to peak in K.

Sminthopsis. No notable absences. Trends, if any, not marked.

Sarcophilus. Notably absent from the lowest layers, and only sporadically present from layer 32 upward.

Isoodon. Present throughout, but less abundant low in the deposit than from about layer 10c upward. Peak representation in layer P.

Trichosurus. Notably absent from the bottom of the deposit, present from layer 28 upward, well and fairly constantly represented from layer 10d and e upward.

Pseudocheirus. Present throughout. Best represented in the middle, about layers 16 to 6.

Cercartetus. Consistently present near the bottom of the deposit, absent from layers 24 to 15 (or possibly 14), then sporadically present near the top.

Potorous. Present throughout in low numbers with no marked trends.

Bettongia penicillata. Absent from the bottom of the deposit. A minor component (if present at all) from layers 30—lower to about 16, and thereafter consistently present as a major component with a peak at about layer Z.

Macropus eugenii. Missing from layers 37 to 30 upper (most of this a "notable absence"). Thereafter sporadically present in low numbers with a peak in layer 20.

Macropus irma. Note similarity to *M. eugenii*, except for a shorter period of notable absence near the bottom of the deposit.

Macropus fuliginosus. Note similarity to *M. irma* and *M. eugenii*, except for higher peak (layer 4) and more consistent presence.

Setonix. No notable absences. Increasingly abundant from bottom to peak in layer 20, followed by slow decline and then increase towards top of deposit.

Rattus. Relatively more important and more consistently present at lower than upper levels. Increases to peak in layer 30—lower, then decreases slowly to about layer 16. Rises to second peak in 11, then declines, and is even sporadically absent, notably from layers V to T. Then rises to a third peak in layer K.

Bats. Consistently present, although in low numbers from the bottom of the deposit to layer 21. Then very sporadic, with long absences, above.

Tarsipes. Consistently present as a major component from the bottom of the deposit to about layer 29, then as a minor component to layer 20. Peak in layer 33. Above layer 20, present only very sporadically, with long absences.

Perameles. No notable absences, though numbers never great. Declines slightly from bottom of deposit to minimum about layer 9, then increases slightly to peak in layer V, and thereafter declines slightly to top of deposit.

Bettongia lesueur. Notably absent from lower half of deposit. Appears in layer 15 (not counting "14, 15 and 16 mixed") and is not significantly absent above this. Increases to peak in V and then declines to top.

Petrogale. Notably absent from bottom of deposit to layer 30—upper. No notable absences above this. Like *Bettongia lesueur*, increases to peak in layer V and then declines to top of deposit.

Pseudomys albocinereus. No notable absences, but more consistently present in lower than upper half of deposit. From bottom, increases to peak in 24, then declines to minimum about U. Increases to second peak in Sub MM and then declines to top of deposit.

Pseudomys occidentalis. Notably absent from bottom of deposit, present sporadically in low numbers from layers 32 to 21, then absent thereafter.

Pseudomys shortridgei. Consistently present in some abundance in lower half of deposit, increasing from bottom to peak in layers 25 and 24 and then declining until notably absent from 2 to V. Present in low numbers at top of deposit.

Notomys. Notably absent from bottom of deposit to layer 33 (not counting "32 and 33 mixed"). Appears in 32, increases to peak in 24, declines to minimum about layer 8, increases again to its main peak in Hearth y and then decreases.

Source of the bone

Fluctuations in relative proportions of mammals through the deposit do not necessarily reflect fluctuations in local mammal populations. The processes by which these populations were sampled may have varied with time. For example, if human beings were the major sampling agents, their tastes may have altered. Modern south-western Aborigines are said to have favoured *Bettongia penicillata* and disfavoured *Pseudocheirus* as food (Gilbert 1843, Bignell 1971 p. 9-12, Meagher 1974). There may have been fluctuating fashions in preferences like these which may have biassed our samples in unknown ways. Other kinds of bias have been discussed by Baynes *et al.* (1976).

Assemblages of bones in caves are usually taken (e.g. Lundelius 1966, Hirschfeld 1968) to result either from the cave concerned acting as a pit trap or from its use by predators. It is possible that Devil's Lair had a chimney-like entrance for most of its history (Clarke *et al.* in press) and could have acted as a pit trap. But if so, the vertical drop is not likely to have exceeded 11 m at any of the times under discussion. Pit trap deposits of similar magnitude are known—e.g. Skull Cave (Porter, in press) and Thylacine Hole (Lowry and Lowry 1967). Some of these contain large accumulations of bone, but individual bones are rarely broken, whereas in Devil's Lair most larger bones have been broken in more than one place. We infer that any pit trap effect in Devil's Lair was minor. Some bones may have come from rats, bats, frogs or other animals which lived in the cave.

On the other hand, many kinds of predators could have inhabited or used the cave—man, dingo, thylacine, Tasmanian devil, native cat, smaller carnivorous marsupials, water rat, hawks, falcons, owls, herons, cormorants, crows, kingfishers, butcher bird, currawong, magpie, monitor lizards, large skink lizards, fresh water turtles, pythons, large venomous snakes, and large frogs.

Some of these possibilities seem very remote in view of the habits of the species concerned. Perhaps most of the birds, except hawks, falcons and owls, can be dismissed, and also species with special requirements not likely to be met in or near the cave—water rat or turtles. Predators of small size may have contributed a component of the smallest prey remains, but cannot have contributed the larger pieces. Nevertheless there remains a substantial list of possibilities, together with the further disconcerting possibility (mentioned by Dortch & Merrilees 1972) that a scavenger like the devil could have worked over remains left by one or more other predators, superimposing its own characteristics and masking the characteristics of the primary predator's leavings.

At first, attention was concentrated on *Sarcophilus* as the primary predator (Lundelius 1960, 1966)—hence the name of the cave. Later, with the recognition of a human component, man was seen as the primary predator (Dortch & Merrilees 1972 and 1973, Baynes *et al.* 1976). We support the suggestion made by Dortch & Merrilees (1972) that at least one other predator was involved over some or all of the time spanned by the deposit, namely one or more species of owl or falcon or both. This would account for some of the striking differences between the bone samples from the upper and lower parts of the deposit.

The case for man rather than Tasmanian devil as the main predator has been presented by Dortch & Merrilees (1972) and Baynes *et al.* (1976), and need not be repeated in detail here. It rests on the very wide range of prey species, including birds, bats, fresh-water mussels, marine molluscs and fish, presumably marine, taken in conjunction with strong evidence of human occupation of the cave, in the form of emu eggshell (some charred), charring of much of the bone, other indications of hearths, stone and bone artifacts, and at least one deep, narrow pit. There appears also to be a selective bias in the western grey kangaroo and perhaps other macropod bone samples, at present under investigation (Balme, in press). An attempt is also being made to determine the origin of coprolites found in the deposit at various levels and we now have evidence of charring of *Sarcophilus* (specimen 77.3.399 from layer Q in Trench 8_7). A more detailed study of the whole subject of charring is being made (Balme, in preparation).

Field observations made by J. E. Stanton (pers. comm.) support a suggestion made by Baynes *et al.* (1976 p. 102) that bone might be extensively chewed and fragmented by human beings as well as by devils:—"Western Desert Aborigines at the present day commonly crack up and chew quite large bones such as those of kangaroos, emus and goats, and seem to swallow quite large pieces (perhaps up to 3 cm long and 1.5 cm wide). Bones of small animals such as rabbits or goannas are commonly chewed into small pieces and swallowed with the meat."

Characteristics of bone accumulated by *Sarcophilus* were studied by Douglas *et al* (1966), and on this basis, a deposit near Perth was interpreted by them as a *Sarcophilus* accumulation. But they commented on the presence of fresh-water mussel shell, and subsequent to the publication of their paper, a limestone artifact was recognized in this deposit (Merrilees 1973 p. 45—Dunstan's Quarry), so that it is now debatable whether this is primarily a human or a Tasmanian devil accumulation. Other sites under investigation (Merrilees, in preparation) show similar mixtures of devil and human characteristics, and we reiterate the suggestion made by Dortch and Merrilees (1972) that men and devils may have lived in close proximity, and both regularly impressed their special characteristics on bone accumulations.

The case for a contribution to the Devil's Lair bone accumulation by owls (or falcons or perhaps hawks), made by Dortch and Merrilees (1972) rests on the high relative proportions of small to medium sized and large animals in some layers and on the lesser degree of fragmentation of bones in these layers, together with certain other pointers discussed below. Figure 8 shows variations in the relative proportions of small mammals through the deposit, and Table 5 compares the bone breakage pattern in two layers from the upper part of the deposit and two in the lower, containing comparable total numbers of mammals. In both Figure 8 and Table 6, the "small mammal" group comprises *Phascogale, Antechinus, Sminthopsis, Cercartetus, Tarsipes* and all murids and bats. In Figure 8, there are no absences of larger mammals, but small mammals are missing from layers HP, Below HP, U, and U and V mixed. In view of the preponderance of small over larger mammals in natural populations, of the fact that the likely predators (other than man) would draw preferentially on small mammals, and of the likelihood of small mammals being voluntarily present in the cave, we suggest that all the absences in Figure 8 should be regarded as "notable".

In conjunction, Tables 3 and 6 and Figures 5 and 8 show that, in the lower parts of the Devil's Lair deposit, there is a great preponderance of mammals over lizards, of small mammals over larger mammals, and of unbroken over broken limb bones. This is what would be expected if the bone accumulation was the work of a predatory nocturnal bird rather than of a medium-sized or large predatory mammal such as devil

Table 6

Breakage in limb bones: comparison of upper with lower parts of deposit (Presence or absence of epiphyses ignored and only shafts scored. No account taken of side, hence numbers can exceed total of "minimum numbers of individuals." "Small mammals" = Phascogale, Antechinus, Sminthopsis, Cercartetus, Tarsipes *and all murids and bats).*

Layer	Trenches	Total of minimum numbers of mammal individuals, all species (in brackets, "small" and "larger")	Small mammals				Larger mammals			
			Humerus		Femur		Humerus		Femur	
			Unbroken	Distal end	Unbroken	Proximal end	Unbroken	Distal end	Unbroken	Proximal end
Sub MM	7c, 7d. 8_2	42 (18. 24)	5	1	3	2	0	8	1	3
9—lower	7d, 8_7, 8_2. 9	48 (16. 32)	1	3	0	1	0	3	0	1
35	2. 7d. 8_7. 8_2. 9=N, 9=S	52 (40. 12)	38	18	35	15	3	5	0	0
38	2. 7d. 8_7. 8_2. 9=N. 9=S	44 (34. 10)	20	10	19	5	1	1	1	1

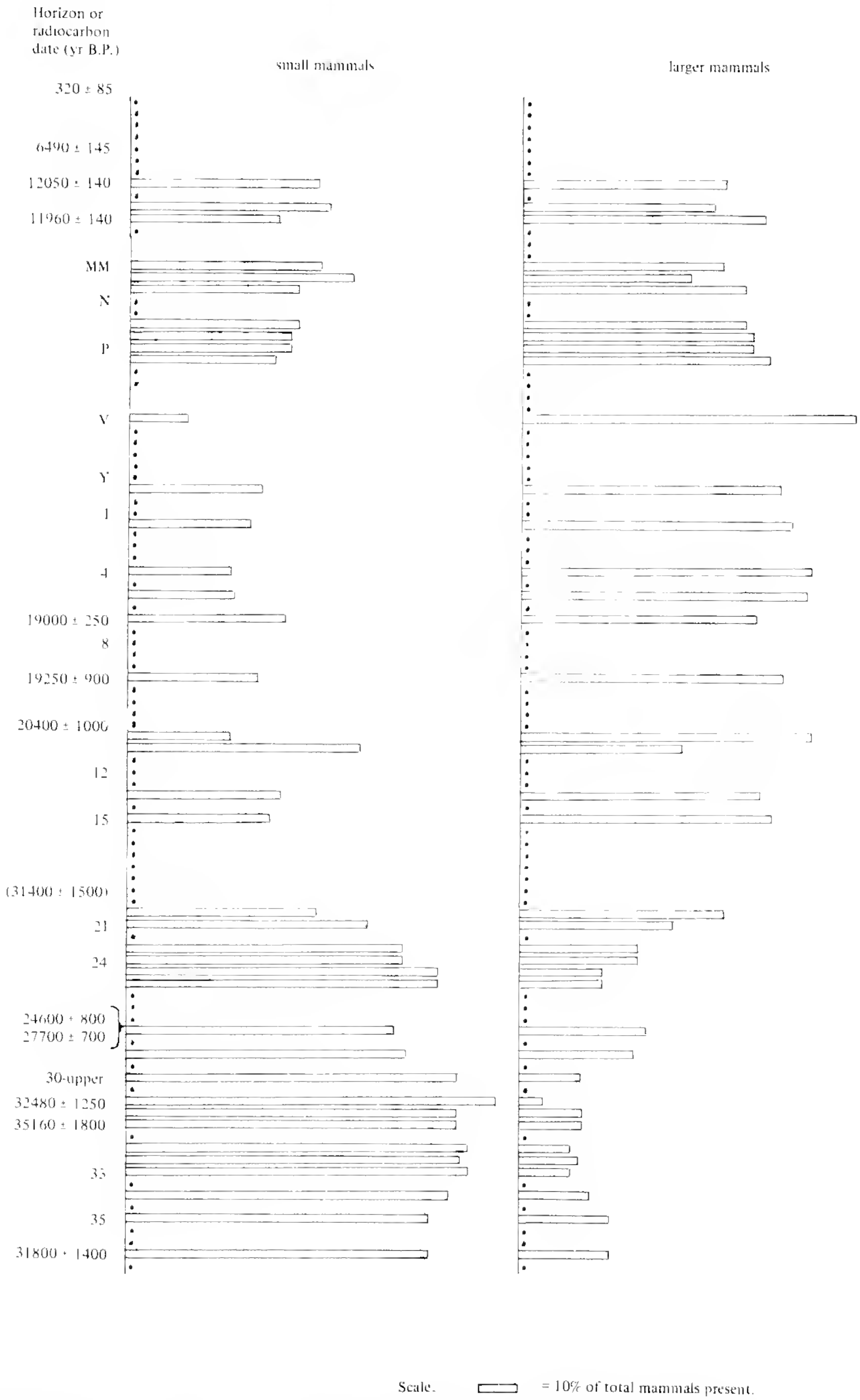

Figure 8.—Stratigraphic distribution of small (see Fig. 5) and larger mammals. In layers with more than 50 vertebrate individuals, mammal individuals shown as percentages of total mammals; in other layers, taxon present (●) or not.

or man. It would seem also that there was no secondary scavenger working over the leavings of the primary predator, as has been suggested for devils in the later stages of accumulation. It is possible that the very small representation of limb bones in the upper parts of the deposit, shown in Table 6, can be interpreted as disintegration of such bones into fragments too small to be identifiable, and such thorough distintegration might well be the work of devils.

If the only agents accumulating bone in the early history of the cave were birds, the presence of larger mammal species at all would require explanation. We suggest that two factors operated together to produce the representation of larger mammals. One is that juveniles of quite large mammals might be taken by owls or other birds, the other (amplified below) is that bones of large species secondarily derived from a pre-existing deposit have become mixed with the owls' leavings.

Our provisional assumption is that man and Tasmanian devils have been the major sources of bone in the upper parts of the deposit, and owls in the lower. It is possible that other predators contributed remains of their prey from time to time, but we have been able to think of no ways to assess their significance. The uncertainties may be illustrated from the two largest carnivorous species (other than man) which must be considered, namely the thylacine and dingo. Even the upper parts of the deposit may be too old to have received a contribution from dingoes, and there are no dingo remains in the deposit. However, we have pointed out that absence from the deposit does not necessarily mean absence of the species concerned from the district when the deposit was being accumulated. Attention has been drawn by Baynes *et al.* (1976 p. 107) to the scarcity of positive evidence of thylacines, comparable in size with dingoes, in the Devil's Lair deposit, and subsequent finds have not greatly enlarged the thylacine sample. It is possible that the factor responsible for an apparently unduly poor representation of thylacines operated also against dingoes, so that these are not represented at all—yet both species may have flourished in the district and contributed to the deposit. Similar uncertainty surrounds the more remote possibility of other large carnivores having contributed—for example the so-called marsupial lion (*Thylacoleo*) or the very large python known from the Mammoth Cave deposit not far away from Devil's Lair (Merrilees 1968b) or even the giant monitor lizard *Megalania prisca* (described by Hecht 1975), not known from anywhere near Devil's Lair at present.

Richness of the deposit

Dortch and Merrilees (1972) report substantial variation from layer to layer in the excavation made in 1970 (Trench A1). We also note such variation in the last two columns of Table 3, by giving data on volumes excavated and numbers of individuals found per unit volume, in our excavations.

Prior to 1974, volumes were estimated from field records of thicknesses of layers excavated and areas of trenches concerned. Such estimates are subject to considerable error related mainly to (unmeasured) variations in thickness. From 1974 onward, direct volume measurements were made in the field by filling buckets (up to 6 litre marks) with excavated material and keeping bucket by bucket records. It is to be expected that volumes estimated before excavation, and volumes measured after excavation, would differ, and that the latter would be greater because of the disturbance and loosening produced by our excavation methods. Thus caution is required in comparing estimates made by the two methods.

To give an indication of the magnitude of such differences, we show in Table 7 a comparison of measured and estimated volumes for layers 20-25 inclusive in Trenches 7_d, 8_7, 8_2 and 9. These were chosen because the stratigraphic boundaries were clear and no mixed interface samples were involved. The table shows that in most cases "bucket volumes" do indeed exceed estimated volumes, but to varying degrees. In Table 3 we have distinguished estimated volumes or volumes based partly on estimation and partly on bucket measurement, with an asterisk.

In the compilation of this part of Table 3, we noticed that mixed interface samples frequently showed much higher incidences of vertebrate animals per m^3 than the adjacent unmixed samples. We assumed this effect to be a special case of the exaggeration of individual number estimates inherent in considering thin layers, discussed in Appendix 3 of Baynes *et al.* (1976). Consequently we have omitted such mixed samples from the incidence column in Table 3, and also any other sample of very small volume (less than 0.01 m^3), as these too appeared to give unduly inflated incidence figures. But there still remain in Table 3 incidences based on layers of varying thicknesses, and some of the variation in incidence may be spurious, related to the exaggeration effect in thin layers.

We have drawn attention to conspicuously low incidences (under 200 vertebrate individuals per m^3, irrespective of layer thickness) by marking them "1" in Table 3. Conspicuously high incidences are marked "h", and we have attempted

Table 7

Order of accuracy of volume estimates and measurements. All samples from Trenches 7d, 8_7, 8_2 *and* 9.

Layer	Thickness at NW corner of trench—cm				Total "bucket volume" after excavation cm³	Volume estimated from trench geometry cm³
	Tr 7d*	Tr 8_7†	Tr 8_2†	Tr 9†		
20	6	8	5	5	180 000	131 000
21	1	2	2	4	75 000	69 000
22	3	1	2	3	35 000	29 000
23	2	4	6	1	83 000	83 000
24	3	4	2	3	81 000	60 000
25	3	4	5	4	97 000	61 000

* from section † from trench records

to take the thin layer exaggeration effect into account by scoring as "h" either samples with more than 2 000 individuals per m^3 from layers less than 5 cm thick, or samples with more than 1 000 individuals per m^3 from layers 5 cm or more thick (marked "T" in the depth column of Table 3).

We interpret the conspicuously low incidence figures for layer A as due partly to a sudden irruption of a great deal of sediment into the cave with the opening of the present entrance by collapse of a section of the roof as explained in more detail by Clarke *et al.* (in press). Prior to this sudden development of a new entrance, the cave may have been wholly or partly sealed by the development of flowstone D over sediment choking the old entrance. Thus there may have been little or no bone debris lying on the D surface, to be incorporated with the newly arriving sediment A.

Conspicuously low incidences in layers 34, 37 and 38 are consistent with rapid sedimentation, indicated both by the radiocarbon dates and the signs of channel cutting and filling. But it is possible that slow contribution of bone by the predator responsible also has an effect on the incidence figures.

Layer L is a flowstone and the conspicuously low incidence in it may be related to this fact in ways which we do not at present understand. We are also unable to interpret the conspicuously low incidences in layers 6 and 10c. Making due allowance for differences in estimating volume between Trench A1 and Trenches 7, 8 and 9, there are comparably low incidences reported by Dortch and Merrilees (1972, Table 1), but we do not know whether there is any stratigraphic correlation between these low incidence layers in different parts of the deposit.

It seems likely that the conspicuously high incidences in layers O and P are related to their conspicuously abundant lizard components, while that of Hearth Y is related to the human occupation implied by "hearth". But whether low sedimentation rates or high bone contribution rates or both are involved and in precisely what ways, we do not know.

Some of the other incidences recorded in Table 3 must be regarded as high (in spite of any thin-layer exaggeration effect) by comparison with those recorded by Dortch and Merrilees (1972) for Trench A1, though they do not meet our arbitrary criterion of conspicuousness. Some of these (K, Hearth 2 and possibly Sub MM) show evidence of human occupation of the cave (see Dortch 1974 for K), and we believe provisionally that great richness in the deposit is a sign of human presence, if not actual occupation of the cave.

Other signs of human presence such as incidence of artifacts or *débitage*, and incidence of charring, have not yet been studied in detail. In general (C. E. Dortch, pers. comm.), it appears that stone and bone artifacts, though nowhere conspicuously abundant, are markedly more so in layers G to 29 inclusive. Artifacts are rare below layer 29 and so far only about 20 unequivocal specimens have been identified.

Possibility that some specimens are reworked

Like Gill (1973), Milham and Thompson (1976) and others, we have been aware of the possibility that specimens from a pre-existing deposit have been dislodged and mixed with younger material entering the cave at any given time. Certain field observations lead us to suggest that such reworking has indeed taken place in Devil's Lair.

While excavating layers 31 and down, we recovered specimens from the sinuous, irregular masses of orange sand interpreted above as channel fillings, without at first recognizing that such specimens were more than just lumps of matrix. Only by close inspection in the daylight did it become clear that some of these lumps were bone fragments coated with sand grains made coherent by calcareous cement. *Sthenurus* specimen 76.5.12 (Fig. 9) is an example.

In subsequent laboratory examination of the material excavated we distinguished a "possibly reworked" class in each layer using as our criterion the presence of a coherent coating of relatively large, rounded, orange-coloured sand grains of uniform size over most of the surface. Minimum numbers of individuals were estimated for taxa represented in this "possibly reworked" class, and these are summarized in Table 8.

We show the numbers of "possibly reworked" specimens in Table 8 from the highest layer which includes a totally extinct species. The proportion of such specimens is always low but is higher for the larger than the small mammals.

Our criterion of "reworking" is arbitrary and to some extent subjective. Some specimens are more or less obscured by coatings of matrix, and yet are not included in our "possibly reworked" class. In some of these, the coating is of flowstone or other largely calcareous formation, for example the specimens mentioned by Baynes *et al.* (1976) as forming the nuclei of cave pearls. In others, the coating is granular, but the grains are of colours other than orange, or material other than rounded grains of sand, or of a very wide range of sizes, or all these together, as is the common case. We also recognize that the size and shape of a specimen would have some bearing on the likelihood of its becoming encased in a granular matrix at all. For example it seems unlikely that limb bones of very small animals like *Tarsipes* would acquire coatings of grains of diameter comparable with the diameter of the bone. Thus some of the uncoated or incompletely coated specimens in a given layer should really be included in the "possibly reworked" class. It is even possible that specimens of comparable size, shape and age lying side by side in a similar orange sand would acquire granular coatings differentially, perhaps according to the nature of any organic material left on the exposed surfaces. Some would then be included in the "possibly reworked" class and others not. If there has been any reworking at all, it is quite conceivable that material of primary and secondary origin has been lumped together in Table 3.

Table 8

Minimum numbers of individuals represented by specimens possibly re-worked (i.e. secondarily derived from a pre-existing deposit—see text) in the lower parts of the Devil's Lair deposit. Same samples as in Table 3. "Small" and "larger" mammals as in Table 6 and Figure 8. "Totally extinct" mammals = Vombatus hacketti, Sthenurus brownei, S. occidentalis Protemnodon brehus *and* Zygomaturus trilobus.

Layer	Larger mammals totally extinct		Other larger mammals		Small mammals	
	Total	Possibly re-worked	Total	Possibly re-worked	Total	Possibly re-worked
21 (includes *Protemnodon*)	1	1	149	2	41	0
22 (includes *Phascolarctos**)	0	0	26	4	19	0
23	0	0	18	9	49	2
24	0	0	21	8	48	0
25	0	0	27	5	93	1
26	0	0	16	1	97	26
26 and 27 mixed	0	0	1	1	4	2
27 (includes hearth)	0	0	10	6	10	2
27 and 28 mixed	0	0	4	2	12	1
28 (includes hearth)	0	0	15	3	32	3
28 and 29 mixed	0	0	8	4	11	2
29 (includes *Sthenurus brownei*)	1	0	22	7	49	5
29 and 30—upper mixed	0	0	3	2	11	0
30—upper	0	0	16	1	88	3
30—upper and 30—lower mixed	0	0	5	0	18	0
30—lower	1	1	27	1	426	3
30—lower and 31 mixed	0	0	9	2	53	6
31	1	0	20	3	111	16
31 and 32 mixed	0	0	4	0	2	0
32	6	5	29	1	238	15
32 and 33 mixed	0	0	7	0	39	2
33	3	2	14	1	110	2
33 and 34 mixed	0	0	4	0	18	2
34	0	0	11	1	56	2
34 and 35 mixed	0	0	1	0	6	1
35	1	0	11	1	40	3
35 and 36 mixed	0	0	5	1	8	0
37	0	0	8	1	28	4
38	0	0	10	2	34	3
38 and 39 mixed	0	0	5	0	11	0

* Not included in "possibly re-worked" class

Study of certain chemical characteristics of the bone is in progress, comparable with those of Gill and Sinnott (1973), Gill (1973) or Milham and Thompson (1976). Results of this study are to be reported independently in due course, and may throw light on the contemporaneity or otherwise of bone specimens in a given layer. Meantime it is our provisional belief that most if not all specimens of *Sthenurus* and *Protemnodon* are older than many of those of the extant taxa with which they are apparently associated in the lower parts of the deposit. By extrapolation, we suggest that all specimens of other totally extinct taxa, together with some unknown proportion of those of locally extinct or extant taxa, provisionally should be regarded as older than the remaining specimens in each layer, pending some clear demonstration otherwise.

Artifacts are present in apparent association with remains of extinct mammal species in some layers. These artifacts are relatively few below layer 29, just where remains of totally extinct species are relatively abundant. It is possible that some or all of these artifacts are reworked, or that they were washed into the cave from outside and fortuitously associated with reworked remains of extinct species. The Devil's Lair artifacts are also the subjects of independent study which might throw light on the reality of their association with extinct fauna. For the time being, we regard such association, with its corollary that man once coexisted with various mammal species long extinct, as not proven by the Devil's Lair deposit (see below).

Table 8 shows layer 21 as its youngest entry because of the occurrence in layer 21 of a fragment of enamel cap of an upper molar of *Protemnodon* (specimen 77.4.777). This fragment is shown as "possibly reworked" in Table 7, but only by a loose application of our criteria, for the coating of granular matrix is far from complete. A few scattered specimens above layer 21, at least as high in the sequence as layer 16, have been recorded as "possibly reworked". For example, in layer 16, fragments representing *Setonix,* "possibly reworked", were recovered from Trenches 8_2, 8_7, and 9. These are somewhat doubtful because the coating of granular matrix, though more or less complete, shows more cement and a higher proportion of very small grains, than typical of material so recorded in, say, layer 32.

There is considerable subjectivity in our criteria of reworking, to the extent that they would require rigorous re-examination before any important inference was made from our data. For example, the highest layer including "possibly reworked" material presumably is topographically below, but not far below, the hypothetical deposit from which the material was derived. It would be useful to determine this topographic level accurately as part of any attempt to locate the hypothetical primary deposit by excavation, and such a determination would require more stringent criteria of "reworking" than ours.


Figure 9.—Fragment of left maxilla of *Sthenurus brownei* (specimen 76.5.12, Trench 8_2, layer 32, Devil's Lair) showing granular coating.

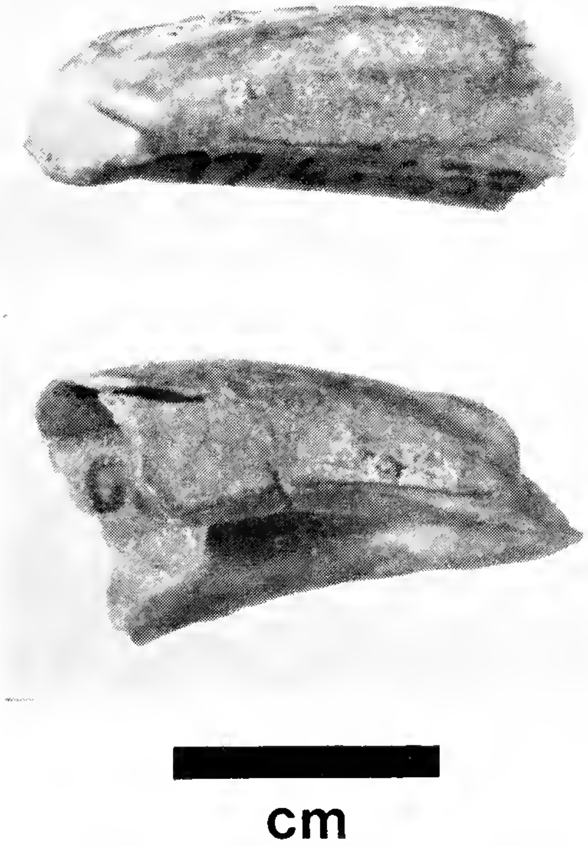
Figure 10.—Unerupted enamel cap, thought to be upper first incisor of *Zygomaturus* (specimen 77.4.630. Trench 8_2, layer 32, Devil's Lair).

Other deposits near Devil's Lair

The same belt of dune limestone as contains Devil's Lair also contains many other caves, and two in particular have influenced our concepts on Devil's Lair. These are Mammoth Cave, about 11 km north west and Skull Cave about 14 km south of Devil's Lair. Two radiocarbon dates on charcoal from the Mammoth Cave deposit (0-657, > 37 000 and Tx-31, > 31 500 yr. BP) and two from the Skull Cave deposit (SUA 227, 2 900 ± 80 and SUA-228, 7 875 ± 100) suggest that they extend the range of the Devil's Lair deposit at both upper and lower limits.

Mammoth Cave was excavated in the early years of the present century and yielded an abundance of *Vombatus hacketti, Zygomaturus trilobus, Sthenurus brownei* and *Sthenurus occidentalis* material, together with smaller quantities of a variety of other totally extinct mammals, and similarly for other "larger mammals" (in the sense used above). No comprehensive account of the Mammoth Cave material has been published, but a summary has been given by Merrilees (1968b). It does not include *Petrogale, Bettongia penicillata* or *Bettongia lesueur* in the same deposit as *Vombatus, Sthenurus* etc., although *B. pencillata* does occur in superficial deposits elsewhere in Mammoth Cave. Certain aspects of the Mammoth Cave deposit suggest that its bone component was accumulated by a predator, and some aspects of the bone suggest that the predator was man (Archer *et al.* in preparation).

If there is or was in Devil's Lair a deposit rich in *Sthenurus brownei* and *Sthenurus occidentalis* remains, and also containing *Zygomaturus trilobus, Protemnodon brehus, Vombatus hacketti, Phascolarctos cinereus* and other species, it may have been approximately contemporaneous with the Mammoth Cave deposit, and older than the bulk (the non-"possibly reworked" component) of the Devil's Lair material. In this case, it may have been the source of some or all the artifacts found below layer 29, as well as of the "possibly reworked" class of bone fragments.

Skull Cave consists mainly of a very steep-sided collapse doline, and has acted as a pit trap, although predatory birds might also have used it. An excavation has yielded a rich assortment of bones of both small and larger mammals, spanning Holocene time (Porter, in press). *Petrogale, Bettongia lesueur, Macropus eugenii, Macropus irma, Pseudomys occidentalis* and *Notomys* are absent.

Vegetation

Existing vegetation in the district has been described and mapped by Smith (1973) and further discussed by Baynes *et al.* (1976). A crest just over 1 km west of Devil's Lair marks a sharp boundary between high open karri forest on the eastern leeward slopes round Devil's Lair, and low open shrub heath on the western windward slopes, extending to the coast. This crest probably determines the boundary between heath and forest. There is no reason to postulate any major physiographic change in the time under consideration, and hence the crest may have acted in a protective way throughout. However, the boundary may not always have been between karri forest (or any other kind of forest) to the east and heath to the west.

Three eucalypt species are prominent in forest in the district, karri *(E. diversicolor)*, marri *(E. calophylla)*, and jarrah *(E. marginata)*. In some circumstances, jarrah and marri are co-dominant (Smith 1973). A study of the climatic determinants of these three species has been made by Churchill (1968), who suggests that rainfall is of far greater importance than temperature. The boundaries of areas of more or less contiguous occurrence seem to be set in each case by a (different) balance between total annual rainfall and intensity of the wet and dry seasons, together with various soil requirements. In general karri requires the wettest and jarrah will tolerate the driest conditions, with marri intermediate.

Interpretation of the sequence of events in Devil's Lair

In the light of evidence presented or cited above, we conceive the following sequence of events, beginning 35 000 years ago or more in a cave very much longer and deeper than the present Devil's Lair. This cave had an opening to the surface (which may have been substantially higher than it is now) about 16 m north of the site of our excavations.

The entrance was probably shaft-like, not easily negotiable by human beings, but wide enough for owls to fly through. It must have opened from a depression in the surface, and have been capable of receiving an in-wash of sand, perhaps only occasionally during exceptionally heavy rain. At some still-earlier time, it may have acted as a pit trap, sampling the contemporary fauna through individuals falling into it and being unable to get out. Alternatively, it may have functioned as a rubbish disposal chute for bands of human beings camped near it. For these or other reasons, a deposit accumulated near this old entrance which contained remains of *Sthenurus brownei*, *S. occidentalis* and other mammal species which were also represented in the Mammoth Cave deposit.

We visualize owls bringing predominantly small mammal prey into this cave, occasionally with juveniles of larger mammal species, and regurgitating pellets containing predominantly unbroken bones of these small or juvenile mammals. From time to time, relatively large quantities of sand were washed into the cave, enveloping and redistributing the owl pellets, and building up a talus cone extending radially from the entrance into the deeper recesses of the cave. The successive surfaces of this cone were extensively channelled and filled with sand of a brighter orange colour than the main mass. The water movement responsible for the channel cutting was sufficiently energetic to move material from the old *Sthenurus* deposit down the talus cone so that such material came to lie side by side with younger bone from the owl pellets. Artifacts derived either from the *Sthenurus* deposit or from the surface outside were also washed into juxtaposition with this mixture of older and younger bone from time to time. In this way we visualize the accumulation about 33 000 years ago of what we have called layers 39-31.

Layer 30-lower is lithologically very distinctive and presumably marks some unusual event. By analogy with layer A, we take this to be associated with some major change in the nature of the entrance, allowing the sudden ingress of large quantities of unmodified dark humic soil from the surface. Meantime, the owl pellets had continued to accumulate inside the cave, and the *Sthenurus* deposit to contribute small quantities of the coated bone fragments we have described as "possibly reworked".

This "layer 30-lower event" of about 32 000 years ago, possibly related to the end of channelling, was followed by a resumption of sedimentation producing layer 30-upper, with little contribution from the *Sthenurus* deposit. However, the *Sthenurus* deposit was not yet buried and continued to supply very small quantities of old bone to the developing talus cone over the next few thousand years.

A new phase in the history of the cave begins with layer 29. This may relate to the alteration in the character of the entrance denoted by layer 30-lower. It may have become possible or easy for human beings to enter the cave, and they appear to have done so from time to time, beginning some 30 000 years ago and continuing for the next 22 000 years or so. It is possible that small bands or family groups lived in the cave for a few days or a few weeks at a time at more or less regular intervals, or only sporadically, or that larger groups used the cave very sporadically. The bones of their prey, sometimes charred, and sometimes fashioned roughly or more carefully into implements, together with stone implements, fine chips resulting from the fashioning of stone implements, and occasional items of adornment, were left lying on successive surfaces of the talus cone. Deep and shallow pits were dug and fires were lit.

In the intervals between human occupancy of the cave, or possibly more or less continuously, owls and devils and perhaps other small carnivores visited or lived in the cave, contributing broken or unbroken bones of their prey species to the scatter left by the human occupants. It is possible that devils were attracted by only partly eaten carcases left by human visitors, and converted initially largely unbroken bones into small fragments. It is equally possible that the human visitors broke up the bones of their prey species, including devils, as part of the cooking or eating process.

In any case, we visualize sandy surfaces in the cave littered with bone fragments, and from time to time receiving accessions of fresh sand or of carbonate deposited in irregular masses from solutions dripping from the roof and walls, or in more regular sheets from surface films of solution or in the interstices of the sand from percolating solutions. Calcareous deposition may have been continuous, if seasonal, but deposition of sand seems to have been sporadic. Thus the bone litter on a given surface may have received contributions from many episodes of human occupation before becoming buried by sand. Some of our narrower layers may represent single episodes of sand deposition but multiple episodes of bone deposition.

From about layer L up to and including layer D, deposition of carbonate matched or exceeded deposition of sand, and the thick flowstone D, formed later than about 7 000 years ago, probably represents a more or less complete sealing of the entrance to the cave as well as of the deposit in it. The cave may have remained unoccupied, through lack of access, for several thousand years.

Then, only a few hundred years ago, a large segment of the roof and central west wall of the cave collapsed, forming the existing doline and the present entrances to Devil's Lair and Nannup Cave. What we now call Devil's Lair was left by this collapse as a small remnant of what was once a much more extensive cave. This event is marked in the depositional succession by layer A. This seems to be largely unmodified, black humic soil from the forest floor which suddenly fell into the cave following the opening of the new entrance. Human and animal use of the cave remnant would again have been possible, but seems to have been minimal.

Discussion and conclusions

While the succession of events inside the cave was unfolding, the environment outside the cave presumably also was changing. The local expression of two world-wide processes, glacio-eustatic fluctuation in sea level and fluctuations in climate, induced by glaciation or by the mechanisms themselves inducing glaciation, presumably had effects inside the cave.

We have attempted in Figure 11 to reconstruct the local expression of sea-level changes by showing probable migrations of the coastline west of Devil's Lair. We assume that the magnitude and timing of sea-level changes was as shown by Chappell and Thom (in Allen, *et al.* 1977) and Chappell (in Kirk and Thorne 1976) and that the topography of the sea floor shown by Lowry (1967) does not differ markedly from that of the late Pleistocene and early Holocene period we discuss. In at least one respect, such assumptions might over-simplify the reality. The present coastline is marked by cliffs cut in the aeolian calcarenites and related rocks of the Tamala Limestone, suggesting that one of the phases of marine transgression which followed the accumulation and lithification of these aeolianites was a phase of cliff cutting. Only in subsequent transgressions can the sea be envisaged as rising unimpeded over a relatively low, flat coastal plain. Presumably in the cliffing phase, there would be some time lag, possibly quite substantial, between the attainment of glacio-eustatic sea level and the attainment of an actual coastline appropriate to that level. We have assumed that there was no such lag during the last two phases of marine transgression considered in Figure 11. We know of no evidence for minor tectonic movement in the region and Lowry (1967) suggests that there has been no major movement since the Cretaceous, hence we ignore possible tectonic effects.

In our attempt, shown in Figure 12, to reconstruct the local expression of world-wide climatic change just preceding, during and succeeding the last glacial maximum, we have followed those authors who have dealt in most detail with southern Australian events, principally Bowler (1976), Wyrwoll and Milton (1976) and Rognon and Williams (1977). We have also in Figure 12 reproduced some of the data shown in Figures 5, 6 and 7, but in the form of smoothed curves. The "non-forest" mammals appear to be a more or less homogenous group as far as their incidence in Devil's Lair is concerned, with the exception of *Tarsipes*, which we have excluded for the purposes of Figure 12, and which is shown separately in Figure 7. The "forest mammals" appear less homogenous, and for the purposes of Figure 12, we have included only those two species most characteristic of the wetter, more densely vegetated habitats suggested by "forest" (Baynes *et al.* 1976 p. 108), namely *Setonix brachyurus* and *Potorous tridactylus.*

In their interpretation of the upper parts of the deposit, above Layer 9, Baynes *et al.* (1976) adopted a model of a band of human hunters occasionally using Devil's Lair as a base, and bringing back prey within a radius of about 10 km. (Date SUA-364, 6 490 ± 145 yr B P., was not available when their paper was written and their model covered only terminal Pleistocene time, whereas we now know it should cover early Holocene time as well.)

Such bands of hunters might have operated from much earlier times, probably about the time of deposition of Layer 29, some 30 000 years ago. Prior to that, it would seem that human hunters did not use the cave itself, though they might have camped at or near its chimney-like entrance. But owls did use the cave at this stage, about 35 000 years ago, and they continued to do so. When the cave became easily accessible to humans about 30 000 years ago, it also became accessible to devils, and they used the cave perhaps more continuously thereafter than did the human visitors.

We next proceed to test this modified and extended model against the internal trends shown by our excavations, and the external trends shown in Figures 11 and 12.

We have suggested that the present boundary between coastal heath and forest (Fig. 11) is in part topographically determined, with heath on the windward and forest on the lee slopes of the ridge. Under any regime windier than the present, as envisaged for the glacial maximum (Fig. 12), this ridge could be expected to remain as a boundary. But if precipitation was then substantially less than at present, this boundary might have been between heath and a woodland of different floral composition from the modern forest.

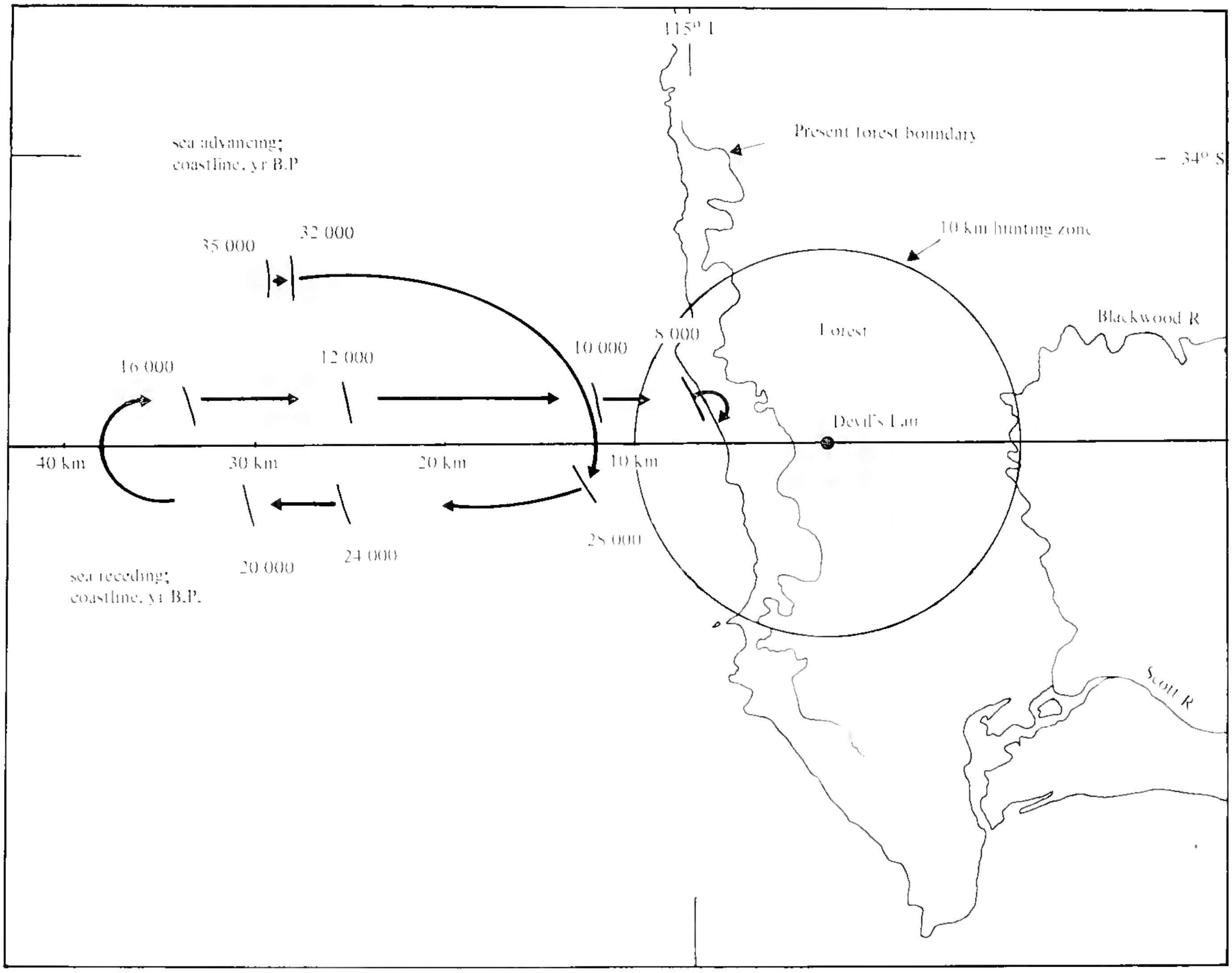

Figure 11.—Late Quaternary migrations of the coast near Devil's Lair.

The presence of a variety of "forest" and "non-forest" mammals throughout the Pleistocene record in Devil's Lair suggests to us that forests, woodland, heath and perhaps other plant formations were present continuously. Our "forest" group of mammals includes species of wide tolerances, and a continuous record in Devil's Lair could be consistent with quite substantial vegetational changes. As we suggest below, the Pleistocene "forest" in the district might have been a jarrah-marri association which was only replaced by karri in the Holocene.

But it may be that the continuous presence of *Potorous* and *Setonix* (Fig. 12) implies continuous presence of thickly vegetated watercourses, and the presence of the aquatic murid *Hydromys* during the most likely period of intense aridity (Figs. 7, 12) as well as at other times shows that free water was present throughout.

However far marine regression may have extended the coastal strip, this could never have been wholly colonized by forest or woodland. However marked the post-glacial phase of aridity may have been in other parts of southern Australia, it was not so devastating in this maritime southwestern corner as to extinguish forest and forest-dwelling mammals.

The record of *Tarsipes* (Fig. 7) suggests to us that there were indeed substantial changes in the character of the vegetation. *Tarsipes* is present in greatest abundance in the lowest layers to which owls may have been the main contributors of bone. But owls seem to have continued as major contributors long after *Tarsipes* began to decline relative to other small mammals, even to the time of its disappearance from the deposit, perhaps "notably" in our arbitrary meaning (Figs. 7 and 8). Since it seems likely that low sea levels (Fig. 11) would have left a belt of coastal heath considerably wider than 10 km during this period of decline of *Tarsipes*, it seems correspondingly likely that the decline can be attributed to some vegetational (and hence climatic) change.

It may be that a shrub or other open plant formation surrounded Devil's Lair about 35 000 years ago, gradually replaced by open woodland and then by forest about 20 000 years ago. Such

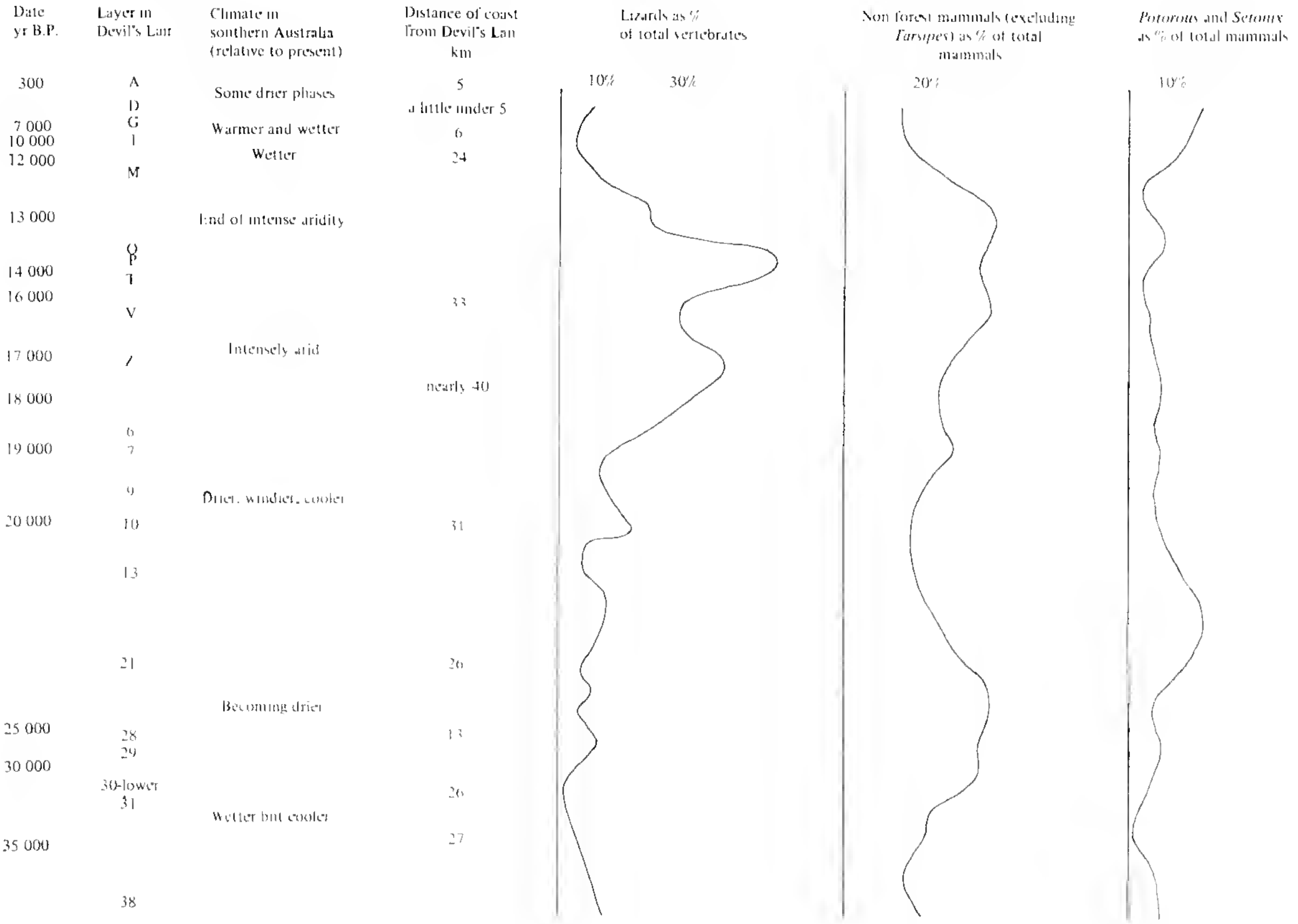

Figure 12.—Coastal migrations, climate and faunistic trends in Devil's Lair.

a sequence might account for the *Tarsipes* decline, while still allowing for a constantly high relative abundance of *Rattus* (which, though a "forest mammal" in our arbitrary sence, is not confined to forest). It may be that the "forest" of 20 000 years ago was a jarrah-marri association, which was not replaced by karri forest before about 10 000 years ago. We cannot at present differentiate suites of mammal species characteristic of different kinds of forest.

There is evidence of migration into and local extinction in or migration out of the region. Thus there is no record of the echidna *(Tachyglossus aculeatus)* anywhere in the Cape Leeuwin-Cape Naturaliste region in historic time (A. Baynes, pers. comm.), and no echidna remains have been found in Devil's Lair. Yet echidnas are known from Mammoth Cave (Merrilees 1968 b) and Labyrinth Cave (specimen 69.8.102, a hitherto unpublished record, cf. Merrilees 1969). The Mammoth Cave deposit, indeed, includes three echidna species, at least one of which is totally extinct.

On the other hand, the Mammoth Cave deposit containing echidnas, *Zygomaturus* and other extinct taxa, does not contain *Bettongia penicillata, Petrogale* or *B. lesueur,* although it does contain other macropods in abundance. We suggest therefore that the earliest appearances of these taxa in the Devil's Lair deposit approximately 32 000, 30 000 and 23 000 years ago respectively reflect their earliest appearances in the district. Once established, all three became incorporated in the Devil's Lair deposit as major components (Figs. 6, 7).

Bettongia penicillata persisted into historic time in the region, but *Petrogale* and *B. lesueur,* like most other "non-forest mammals" recorded from Devil's Lair, did not. It is unfortunate that samples from the various Holocene layers in Devil's Lair are too small to give any insight into the rate of change in the disappearing species. They may have dwindled gradually, as suggested by Figures 6 and 7. The absence of *B. lesueur, Petrogale* and *Notomys* from Skull Cave (Porter in press) suggests that they had disappeared from the region in quite early Holocene time. The relatively brief appearance of *Pseudomys occidentalis* (Fig. 7) in the Devil's Lair deposit may also reflect a short-lived invasion of the region. But the first appearance of *Trichosurus* in the Devil's Lair deposit between 24 000 and 28 000 yr. B.P. may be related to a change in predator, although it could represent a reinvasion of the region. *Trichosurus* is recorded from the Mammoth Cave deposit.

The increase in *Potorous* and *Setonix* in Devil's Lair in terminal Pleistocene and early Holocene time (Figs. 6, 12) and possibly the increases in *Antechinus*, *Cercartetus* and *Rattus* at this time (Fig. 6) are consistent with the views summarized in Figure 12 of the Pleistocene-Holocene transition as one of increasing temperature and rainfall.

A conspicuous feature of the Holocene sediments in Devil's Lair (Layers I and upward) is the high proportion of crystalline flowstone. Accretion of sandy sediment, always sporadic and at a low average rate, seems to have become even slower during the Holocene. We suggest this in itself is an index of warmer, wetter conditions during the early Holocene (ending with layer D, laid down some time after 6 490 yr. B.P.) than during the late Pleistocene. With an overall increase in the density of plant cover round the cave entrance, and a corresponding increase of floor litter and soil micro-organisms, there would be an increase in the production of soil carbon dioxide and hence speleothem formation in the cave, and a minimum of water transport of sand from exposed surfaces into the cave (cf. Franke 1965, Shackley 1978).

The terminal Pleistocene and early Holocene decline in the "non-forest mammals" (Figs. 7, 12) could be interpreted as a sea-level effect if one can envisage a hunting range rather geater than the 10 km envisaged in the Baynes *et al.* (1976) model. Marine transgression between 12 000 and 10 000 years B.P. seems to have been extremely rapid (Fig. 11) and contractions in range of the populations of the larger non-forest mammals may have been detectable even within the lifetimes of individual animals. But it is difficult to conceive later contractions in range as producing stress. We accept that marine transgression may be reflected in the declining proportion of non-forest mammals relative to forest mammals in the Devil's Lair deposit, beginning perhaps as early as the time of Layer M. But this decline culminated in the local extinction of five of the non-forest species which had persisted into the Holocene, and after about 7 000 yr. B.P., this cannot be attributed to continued contraction of range (Fig. 11). Thus we suggest that the local extinction of the non-forest mammals *Perameles*, *Bettongia lesueur*, *Petrogale*, *Pseudomys albocinereus* and *Notomys* was a climatic or human effect, not an effect of marine transgression.

We can see no reason to postulate direct effects of marine transgression or regression on the composition of the Devil's Lair mammal assemblage at any other time than terminal Pleistocene and earliest Holocene. On the other hand, the effects of human predation, habitat modification by intensified use of fire (Hallam 1975) or other human effects would appear to require consideration throughout the period studied, and require to be weighed against the possible effects of climatic change on the mammal fauna. Similarity in the vegetational trends at different sites studied by Churchill (1968) shows that climate rather than man had the major vegetational influence during the Holocene, and so by extrapolation we offer climatic interpretations of some of the trends observable in our data during the Pleistocene.

Perhaps the most striking of such trends is the rise to dominance in Layers P and O and then decrease in proportion of lizards relative to mammals (Figs. 5, 12). This might mean no more than that women and children rather than men occupied the cave for a period during which the tradition was for women and children to gather small lizards and bring them back to the cave to eat. (Most of the lizard remains do represent small skinks, as implied in this model.) Or, possibly a lizard-hunting bird species, active by day, replaced the hitherto normal mammal-hunting bird occupants for a period. But perhaps the predator pattern remained constant and the environment changed, and in this "lizard maximum" we see a local expression of the intense aridity registered elsewhere by quite different signs (cf. Bowler 1976, Rognon and Williams 1977 and others). Both "forest" and "heath", while still maintaining their relative positions round Devil's Lair, may have become much more open, with a corresponding flourishing of lizard populations relative to mammals. For lack of a comprehensive comparative osteological collection, we have been able to make no taxonomic analysis of the quite abundant lizard remains in Devil's Lair (Table 3), and so for the time being this equation of the "lizard maximum" with aridity must remain speculative.

If it could be substantiated, it would suggest that maximum aridity in this southwestern maritime climatic province was not quite in phase with the more interior continental climatic provinces described by Bowler (1976) or Rognon and Williams (1977) or the more northerly maritime province described by Wyrwoll and Milton (1976). As shown in Figure 12, the maximum terminal Pleistocene flourishing of the non-forest mammals and the minimum representation of *Potorous* and *Setonix* fall even later than the "lizard maximum", consistent with the concept of a rather late, almost terminal, Pleistocene arid episode.

The post-glacial increase in lizard and non-forest mammal proportions toward their respective maxima and the persistently low proportions of *Setonix* and *Potorous* are consistent with the climatic pattern suggested in Figure 12, allowing for a phase difference as just discussed.

Further, there are some "notable absences" during this post-glacial arid period which may be significant—*Phascogale, Antechinus,* bats and even *Rattus fuscipcs* (Fig. 6). But along with these "notable absences" from the suite of forest mammals are "notable absences" of *Tarsipes* and *Pseudomys shortridgei* among the non-forest mammals. These might have been expected to persist, and so indeed might *Pseudomys occidentalis* which seems to have vanished before the onset of any marked aridity.

There is a pre-glacial increase to a maximum of non-forest mammals (Fig. 12), which may represent increasing aridity and thinning out of plant cover, or landward retreat of the forest boundary. Either would be consistent with the climatic scheme suggested in Figure 12. But this non-forest mammal maximum (of immediately pre-glacial-maximum time) is not accompanied by any marked lizard maximum, and is followed by a marked decline in the non-forest mammals and a rise in *Potorous* and *Setonix* proportions which have no counterpart in any climatic scheme known to us.

Thus there are trends in mammal proportions in the deposit for which we cannot account at present. Of all the major groups of animals represented, mammals are perhaps best buffered against climatic fluctuations, best able to tolerate climatic extremes, and hence liable to misinterpretation. An informative example is given by Aitken (1977) in reporting the occurrence of *Cercartetus lepidus* living in a hot, dry shrubland environment near Pinnaroo, South Australia. Until 1964, this species was thought to have survived only in Tasmania, and on this belief, fossil occurrences at Wombeyan (N.S.W.) and Buchan (Victoria) had been taken as indicating wetter conditions in the past at these localities (Ride 1960, Wakefield 1963). Indeed, when *C. lepidus* was first reported living in relatively dry conditions on Kangaroo Island (Aitken 1967), the (single) relevant specimen was suggested by Wakefield (1970) to have been transported from Tasmania. However the subsequent discovery of additional specimens on Kangaroo Island and later on the mainland (Aitken 1974, 1977) indicates that the species does indeed persist in South Australia, and has a very much wider climatic tolerance than it was believed to have even after Aitken (1974) re-examined the Tasmanian records and found them to be climatically similar to those of Kangaroo Island.

To summarize, we suggest that the deposit establishes the presence of a much richer mammal fauna in late Pleistocene and early Holocen than in historic time, that it included taxa with habitat preferences or tolerances for both wet and dry microclimatic conditions for the whole time represented, and that some late Holocene changes not documented in Devil's Lair were responsible for the removal or severe reduction in the "non-forest" mammals. The climatic implications of our findings are that while the climate need not have differed greatly from the present regime, such differences as there were must have been in the direction of lower or more markedly seasonal rainfall during late Pleistocene time than now, and there is a possibility that such differences were substantial.

Thus we give qualified support to the many authors, such as Rognon and Williams (1977), Bowler (in Kirk and Thorne 1976) or Street and Grove (1976) who postulate greater aridity in the middle latitudes during the time of high latitude glaciation than now. A climatic mechanism which could apply to the region including Devil's Lair has been described by Wyrwoll and Milton (1976). Other parts of Australia (Bowler 1976, Dodson 1974 a and b, 1975, 1977, Kershaw 1974, McPhail 1975, Coventry 1976, Wyrwoll 1977) and neighbouring regions (Verstappen 1974) have been shown to have been more arid during the glacial maximum and for some time afterwards than they are now.

In the face of manifest uncertainties in our data, we have adopted some arbitrary statistical procedures. Attempts to refine these procedures are being made, and will be reported separately if fruitful. In the meantime, we hope we have reported our data in sufficient detail and sufficiently drawn attention to its shortcomings to permit independent studies to be made, revealing trends among the mammals which we have been unable to detect and perhaps throwing more light on climatic fluctuations in the Devil's Lair district. But we have suggested above that there is more to be expected in this direction from studies of plant micro/fossils or lower vertebrates or invertebrates than from mammals.

Two questions of considerable topical interest, possibly related, remain unanswered by our data, namely when, or over what period, did *Sthenurus*, *Zygomaturus* and other large marsupial taxa (represented abundantly in Mammoth Cave but sparsely in other caves in the district) become extinct, and were these taxa ever co-existent with man in the Devil's Lair district?

Work in hand may prove us wrong in our provisional belief that remains of the large totally extinct mammals, sparsely present in the lower layers in Devil's Lair, are older than remains of extant taxa with which they are apparently associated. That is, it is possible that Table 3 can be taken at face value. If so, and if the very small samples of *Sthenurus* have any statistical validity, it is possible that *S. occidentalis* became extinct some time before *S. brownei*, and that the latter did not survive long past the time of deposition of layer 29, perhaps dating from about 30 000 yr. B.P. (On similarly tenuous evidence, this same suggestion that *S. brownei* survived *S. occidentalis* has been made by Merrilees 1968b p. 18). Where very small numbers of individuals are involved, as in Devil's Lair, it would seem inadvisable to infer very much from an absence, such as the absence of *S. occidentalis* from layers 31-29, or of *S. brownei* above layer 29 (Table 3, Figure 7). Very small "minimum numbers of individuals" do not necessarily imply similarly small numbers of specimens, as shown indirectly by Table 2, but it so happens that all the large totally-extinct taxa are represented by very small numbers of specimens as well as of individuals in the layers in which they occur at all. Thus even if Table 3 could be taken at face value, it would show merely that *Sthenurus occidentalis*, *Zygomaturus* and *Vombatus* were still extant in the Devil's Lair district about 33 000 years ago, *S. brownei* about 30 000 years ago, and *Protemnodon* and *Phascolarctos* between 25 000 and 20 000 years ago, not when they became extinct.

On the other hand, if the specimens representing the large totally-extinct taxa in Devil's Lair really are secondarily derived from an older deposit, we cannot yet estimate the age of such a deposit. Even if we could, we still could not be certain that the taxa represented in it did not survive for a long time. They might still have been flourishing when owls were the sole or main predators taking carcases into the cave. But in this case, it would seem unlikely that they were flourishing when human beings began to use the cave, unless we accept the hypothesis of Bowdler (in Allen *et al.* 1977) that early Australian human groups were not hunters of big game. If they were, we could probably infer that *Sthenurus brownei* and *S. occidentalis* were both extinct by about 30 000 yr B.P., and *Protemnodon* between 25 000 and 20 000 yr. B.P.

If the specimens of totally extinct mammal taxa are re-worked, the small number of artifacts apparently associated with them below layer 29 may be re-worked from the same pre-existing deposit. That is, the association is likely to be genuine, but to date from some unknown time prior to the deposition of layers 39 to 30-upper. Alternatively, the artifacts could be contemporaneous with the remains of *Tarsipes* and other owl prey, and could represent material washed or thrown into the cave from the outside surface. The question of the contemporaneity of man with the large totally extinct mammals would then remain unanswered. We could be reasonably confident about the association of man with extinct mammals but not about the date, or confident about the date but not about the association. The main hope would seem to be of finding a bone or tooth artifact clearly referable to an extinct species.

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