# Vertebrate Taphonomy of Late Permian Floodplain Deposits in the Southwestern Karoo Basin of South Africa

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The predominantly fluvial strata of the Late Permian Beaufort Group in the southwestern Karoo Basin contain numerous fossils of therapsid reptiles. This study investigates the taphonomy of these fossils and the sedimentology of the floodplain deposits in which they are most commonly preserved.

Taphonomic assessment of 329 in situ fossils along 3 cliff exposures included data on disarticulation, bone weathering, attitude of skulls, bone color, type of perimineralization and degree of pre-fossilization damage. This led to the recognition of 6 "taphonomic pathways" along which bones entered the rock record.

Three floodplain facies, channel-bank, proximal floodplain and distal floodplain, that were previously defined on sedimentological and pedological criteria also have taphonomically discrete attritional bone assemblages. Localized concentrations of fossil bones are interpreted as evidence for the presence of waterholes on the inner-bank levees and playa margins. Taphonomically anomalous, fully-articulated and paired Diictodon skeletons are preserved in burrow casts.

A major influence on the taphonomic signature of each floodplain facies was the proximity of the burial site to the main channel, especially during episodes of channel avulsion, and the effect this had on the frequency and intensity of flooding and the overall rate of floodplain accretion. The former influenced disarticulation, transport and embedding of the bones whereas the latter determined their "residence time" on the floodplain before burial

Attritional fossil assemblages in the proximal floodplain mudrocks probably accumulated over 100–1000 years during which time floodplain accretion was more than 5.5 mm/y. However, paleosols superimposed on these strata record periods of floodplain stasis lasting from 5000–10,000 years, when sediment accumulation was considerably less, more in the order of 0.4 mm/y.

This study demonstrates the value of vertebrate taphonomy in providing additional information to support or contradict the paleoenvironmental interpretation of fluvial facies.

## INTRODUCTION

This study is primarily concerned with vertebrate fossils and sediments that contain them and is aimed at reconstructing, from all available clues, the post-mortem/pre-burial history of these fossils. Efremov (1940) used the term "biostratinomy" to describe this particular avenue of research, which by virtue of its concern for the transition from "the Biosphere into the Lithosphere," has to be an amalgamation of both biological and geological sciences (Behrensmeyer and Kidwell, 1985).

Similar studies have been carried out on North American dinosaurs of the Cretaceous Oldman Formation (Dodson, 1971) and Judith River Formation (Wood et al., 1988; Eberth, 1990) and the Jurassic Morrison Formation (Dodson et al., 1980) as well as on fossil mammals of the Miocene Siwalik Group in Northern Pakistan (Behrensmeyer, 1987, 1988; Badgely and Behrensmeyer, 1980).

Behrensmeyer (1987) demonstrated how 2-dimensional panel sections of the laterally continuous exposures of the Siwalik strata can facilitate the integration of taphonomic and facies data, a method which has been adopted for this study of therapsid fossils in the Beaufort Group.

The paleontological wealth of the Beaufort Group is perhaps its most important claim to fame. Skeletal fossils of reptiles, especially therapsids ("mammal-like reptiles") amphibians and freshwater fishes are well preserved in all stages of disarticulation. For the past 150 years paleontologists such as, Owen (1876), Broom (1907), Haughton (1919), and Boonstra (1969) have studied this abundance of vertebrate fossils mainly from a taxonomic angle, paying little attention to geological descriptions of their host rocks and rarely recording enough information to pinpoint localities.

To date there have been very few taphonomic studies of the Karoo vertebrate faunas. Colbert (1963) was perhaps
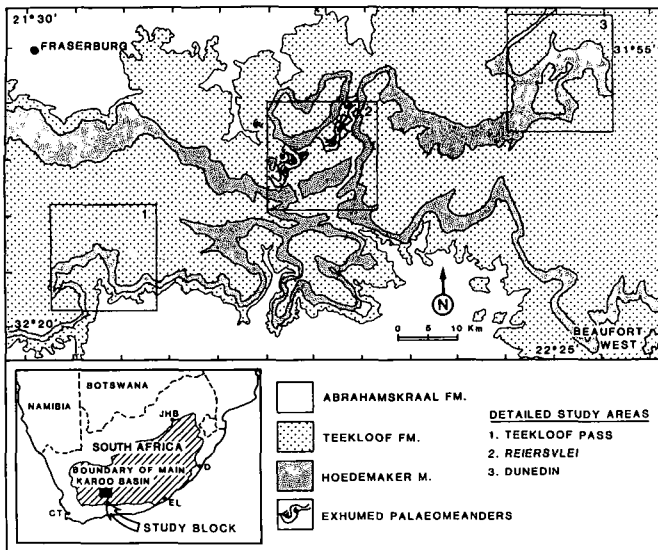
**FIGURE 1**—Lithostratigraphic map of the study block showing the extent of the Hoedemaker outcrop and the 3 study areas.

the first to use paleontological evidence from the Lower Beaufort in paleoclimatic interpretation. Hotton (1967) recognized some fundamental taphonomic differences including the "skull only" occurrences described here. Boonstra (1969) noted that some fully-articulated pareiasaurian fossils that were preserved in an upright "head-up" attitude were possibly mired in a floodplain pond. He also observed that the scarcity of articulated remains of dinocephalians was an indication that they lived in upland areas.

Because the transition from living to fossilized states is so complicated, there are several ways in which it may be studied, each concerned with different stages in the passage from living community through death, decomposition, disarticulation, embedding, burial, diagenesis and distortion, to exposure and recovery. This study uses field observations of *in situ* therapsid fossils to reconstruct the various "taphonomic pathways" that these fossils followed between death and final burial. This information is then combined with sedimentological and paleopedological studies to reconstruct the regional climate, geomorphic processes and habitats of this part of the Lower Beaufort landscape during their accumulation some 250 Ma.

## GEOLOGICAL SETTING

The Karoo Basin was one of several large intracontinental foreland basins that developed to the north of the Gondwanide Mountains in southern Gondwana during the late Paleozoic. The extensive mountain chain was caused by uplift and thrusting along the subduction of the Paleo-Pacific plate beneath the Gondwanan plate. Crustal loading and resultant downwarping was probably the major control over subsidence of the foreland trough, up to 1000 km wide, in which clastic sediments of the Karoo Sequence accumulated.

Over the 100 million years of basin infilling, from Permo-Carboniferous to early Jurassic (300–190 Ma), this part of the supercontinent drifted out of polar climes (75° S), through temperate to near tropical latitudes (35° S) resulting in a concomitant aridification of climate (Visser, 1991).

The Beaufort Group lies about halfway up the Karoo Sequence and comprises a 2000 m thick fluvio-lacustrine succession of late Permian age. This study is based on the Teekloof Formation, a 400 m thick argillaceous unit in the lower part of the Beaufort succession that outcrops mainly in the Beaufort West and Fraserburg districts of Cape Province (Fig. 1).

During deposition of the Teekloof Formation the southern Karoo trough was drained by three large drainage nets, a southeasterly, southwesterly and west-northwesterly (Cole et al., 1990) which originated in the Gondwanides some 1500 km to the south. These Mississippi-sized rivers meandered across a wide, flat alluvial plain before issuing into a shallow lake (Smith, 1987a). Melt-out from the snow-capped Gondwanides (Rust, 1975) probably provided enough summer discharge to maintain perennial flow in the trunk rivers which resulted in several large meander-belt ridges traversing an area that was for the most part drained by second and third order ephemeral streams and playa lakes (Stear, 1980, 1983, 1985). Paleopedological evidence from the Teekloof floodplain deposits confirms that a semi-arid climate prevailed in this part of the basin with mean annual temperatures between 16 and 20° C and highly seasonal rainfall of 50–70 cm/y (Smith, 1990).

Paleosol features suggest that vegetation flourished along river banks and abandoned channel furrows and consisted of *Glossopteris* trees, horsetails, ferns and clubmosses. This supported a stable terrestrial vertebrate fauna dominated by a variety of therapsid reptiles the fossils of which provide the basis of this study.

The study block covers part of a northeasterly flowing paleodrainage system which deposited several fining upward megacycles (Visser and Dukas, 1979) consisting of 50–100 m thick "packages" of clustered channel sandstones at the base passing up into a 100–350 m succession of floodplain mudrocks with only isolated channel sandstones (Fig. 2). There is no change in sandstone grain size through these sequences, it remains fine grained and none of these cycles have basinwide expression even though their lateral dimensions are in the order of 200–300 km.

An obvious, albeit crude, correlation exists between the vertebrate fossil assemblage zones (Smith, 1981) and this first order cyclicity. Each biozone contains one of the basal sandy units which is lateral to one of the argillaceous units (Fig. 2).

Thus it appears that the first order cyclicity that is observed at any section within the Beaufort Group of the southern Karoo trough may be made up of the proximal and distal equivalents of major loci of channelization (Smith, 1981). Even though the basin was entirely intracontinental, the eustatic effect of lake-level fluctuations on base levels may explain some of the major differences in channel sandstone geometry and connectedness (Gard-

ner, 1991). However, lateral shifts in the position of large distributary channel-nets were possibly caused by increased alluviation rates in areas with high channel density compared to adjacent low density areas and their subsequent abandonment in favor of more advantageous gradients (Turner, 1986; Smith, 1990). Such major shifts in drainage nets were probably the result of differential subsidence rather than source area tectonism. A similar intrabasinal control over major fluvial cycles is interpreted for the Permian Gondwana basins of peninsular India (Kahn and Tewari, 1991).

Following the discovery of uraniferous sandstones in the Beaufort West area the components of some first order cycles within the Teekloof Formation have been allocated an informal stratigraphic nomenclature (Fig. 2). The outcrops studied here are confined to the argillaceous Hoedemaker member that overlies the uranium bearing sand-
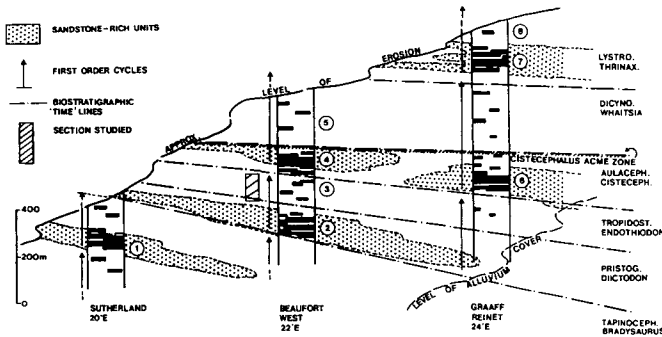


FIGURE 2—Large scale fluvial architecture of the Teekloof Formation, west of 24° E, showing the relationship between biozones and the first-order cycles. The density and connectedness of sandstones are schematically indicated in the columns. Most of the sandstone packages have been given an informal stratigraphic nomenclature. 1 = Verlatenkloof member, 2 = Poortjie Sandstone Member, 3 = Hoedemaker member, 4 = Oukloof member, 5 = Steenkampsberg member, 6 = Ouderberg sandstone Member, 7 = Katberg Sandstone Member, 8 = Burgersdorp Formation. Informal members in lower case.

stones of the Poortjie Sandstone Member and is erosively topped by the Oukloof sandstone member.

## SEDIMENTARY FACIES OF THE HOEDEMAKER MEMBER

Vertical and lateral variations in the volumetric proportions and packing of the different rock types that make up the Teekloof succession were ultimately controlled by pulses of basin subsidence (Bridge and Leeder, 1979; Allen, 1974a, b; Smith, 1980) through their effect on: 1) local sedimentation rates and gradients, 2) regional floodplain accretion rates, and 3) the size and migration behavior of drainage nets and fluvial channels.

These three geomorphic variables had a profound influence on the landscape, its topography, its soils and the flora and fauna which they supported. Following is a summary of the information gathered to date on sedimentary environments and paleosols of the Hoedemaker mudrocks and their usefulness in interpreting major landscape features, the dominant geomorphic processes and the prevailing climate during accumulation.

Figure 3 is a summary of the various sedimentary facies that comprise the Hoedemaker member taken from previous studies (Smith, 1980, 1981). The facies nomenclature is interpretive, summarizing the environment of deposition of a certain rock unit. Facies that consistently occur in juxtaposition or close association are grouped under larger scale "facies associations." Smaller scale features within the facies may warrant recognition as discrete "sub-facies."

Detailed descriptions of the channel facies are not included here because this study is based on vertebrate fossils that are preserved in the interchannel facies association. Nevertheless, the channel facies are important in that they most accurately reflect the fluvial style and flood hydrology of the paleo-rivers. Factors which must have influenced sedimentation on the flanking floodplains and are worth summarizing here.

Extensive planimetric exposures of a single meandering channel sandstone, "the Reiersvlei sandstone," in the study
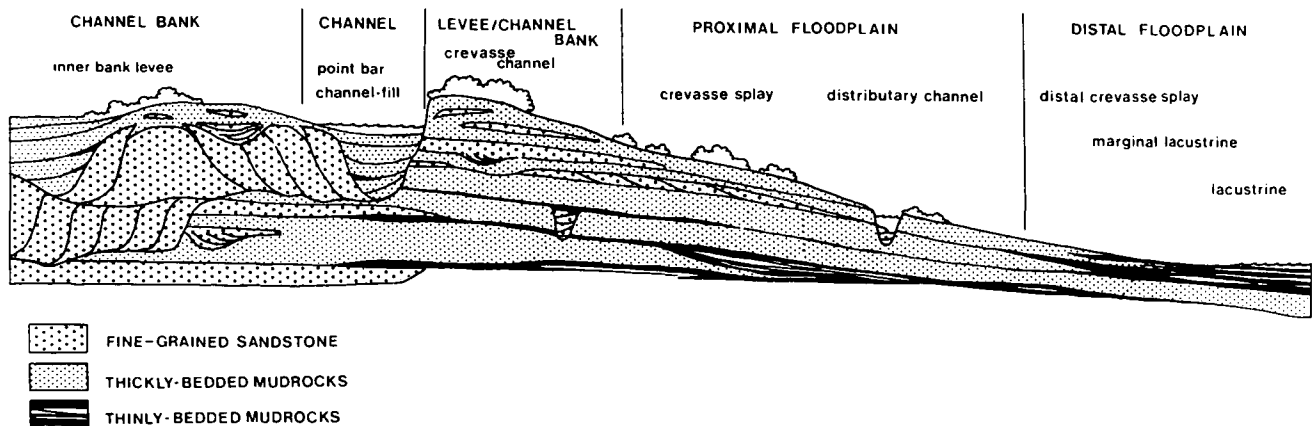


FIGURE 3—Generalized cross-section of a Hoedemaker floodplain showing the various depositional environments and their sedimentary facies.

area demonstrate the fluvial style of the major rivers. Detailed field mapping and measurement of paleomorphological features on the exhumed points bars allowed accurate reconstruction of the dimensions of the original system (Smith, 1987a).

At bankfull discharge the river was in the order of 350 m wide and 11 m deep with 2–3 km wide sandy point bars inside relatively tight meander loops (sinuosity ratio 1:6). Irregular lateral accretion topography and the dominance of upper-flow-regime structures suggest fluctuating, possibly ephemeral, discharge. Substituting the measurable paleomorphological values into equations derived from the study of modern rivers (Schumm, 1972) gives an estimated mean annual discharge of around 850 m$^3$/sec and mean annual flood of 12,000 m$^3$/sec. The well-vegetated and pedogenically cemented floodplain alluvium provided relatively stable banks, but they were susceptible to undercutting and collapse during rising floods. Such cut-bank failures caused sudden shifts in the thalweg, resulting in sporadic inner-bank accretion and an irregular expansion of the meanders. Despite being larger, the flood hydrology and migration behavior of the lower reaches of the Ganges River (Sehgal and Stoops, 1972) is considered to be a reasonable modern analog to the ancient Reiersvlei River.

The interchannel facies association includes deposits from a suite of depositional environments that existed on the floodplains between meanderbelt ridges. These strata are predominantly vertically stacked beds of drab-colored mudrock with occasional thin (<1 m thick) sheets of fine-grained sandstone and narrow shoestring-shaped sandstone strips. Differences in sandstone/mudrock ratio, geometry and bedding characteristics of sandstone bodies, paleosol maturity and vertebrate taphonomy all contribute to the distinction of interchannel facies. These include channel-bank facies made up of inner- and outer-bank levee deposits, proximal floodplain facies, including crevasse splay and distributary channel sub-facies and distal floodplain/playa deposits with marginal playa and offshore sub-facies (Smith, 1989; Fig. 3).

Channel-bank deposits comprise 1–3 m thick sequences of sandstone/siltstone couplets or bedsets (Bridge, 1984), each in the order of 5–10 cm thick. The sequences as a whole have a general fining-upward trend as the siltstone component becomes dominant over the sandier portion. The nature of internal discontinuity surfaces within these sequences as well as their stratigraphic relationship with respect to channel facies are used to distinguish between the inner- and outer-bank levee deposits. Inner-bank deposits overlie point-bar sandstones and have characteristic undulating or "swaley" bedding planes and, in places, prominent high angle internal erosion surfaces with terraced or stepped topography. The undulating bedding is a direct reflection of the underlying point-bar topography. Outer-bank levee subfacies do not display swaley bedding and their internal erosion surfaces are much smoother and non-terraced. They do, however, contain isolated channel-shaped scours up to 10 m wide and 2 m deep conformably filled with sandstone/siltstone couplets and interpreted as crevasse channel fills. Paleosols in the channel-bank de-

posits are weakly developed comprising vertical calcareous rhizocretions (Klappa, 1980), clay-lined root channels and horizons of smooth-surfaced calcareous glaebules. Vertebrate fossils, although generally scarce in this lithofacies, are sometimes found in abundance in restricted mudrock filled channels eroded into the top of a point-bar sandstone. These are interpreted as swale or chute channel accumulations and will be discussed more fully later.

Proximal floodplain deposits make up the bulk of the interchannel facies association. They consist of 2–8 m sequences of grey, greenish-grey and dark reddish-brown siltstone beds. Individual bed thicknesses range from 0.3–0.75 m, each capped with a thin silty mudstone veneer. Tabular crevasse splay sandstones up to 2 m thick commonly occur in the proximal floodplain facies. These have flat, non-erosive bases and either sharp or transitional upper contacts and are interpreted as a discrete sub-facies deposited mainly during floods by floodwaters emerging from narrow crevasses cut into the natural levees. The lithologies and sedimentary sequences of the proximal floodplain facies are comparable to avulsion-controlled wetland deposits of stage II splay complexes described by Smith et al. (1989) from Cumberland Marshes, Saskatchewan.

Despite their rapid sedimentation, the most mature paleosols are hosted by siltstones of the proximal floodplain facies indicating that sedimentation in these areas was highly episodic. Horizons of coalescing calcareous glaebules, accretionary sheets, slickensided "skew planes" (Brewer, 1964), root molds and pervasive encrustation of fossil bone with micrite are similar to features of modern calcic vertisols developed on semi-arid alluvial plains (Sehgal and Stoops, 1972; Butler, 1958). Therapsid fossils are generally more common in the proximal floodplain than in the other interchannel facies. They occur in abundance in some outcrops apparently associated with scoured surfaces and mature paleosols.

Distal floodplain deposits are 0.5–1.5 m thick sequences of thinly-bedded sandstone/mudrock couplets interbedded with sharply bounded, tabular fine-grained sandstones, many of which have preserved paleosurfaces. These mudstone veneered surfaces display an array of sedimentary and biogenic structures, including vertebrate tracks, which record shallow water sedimentation followed by stillstand, exposure and desiccation (Smith, in press). Vertebrate fossils are generally rare in distal floodplain deposits comprising mostly disarticulated individual elements.

Mudrock colors are generally darker than in the proximal floodplain deposits commonly alternating between dark bluish-grey, greenish grey and dark brown. Color mottling, involving green and maroon tints is interpreted as evidence of hydromorphic gleying. Hydromorphic textures suggest that the distal floodplains were frequently saturated and, for part of the year at least, water tables intersected the landsurface. Calcite pseudomorphs after gypsum "desert rose" clusters and siliceous septarian nodules are interpreted as having precipitated on the margins of playa lakes in the axial floodbasin between meanderbelt
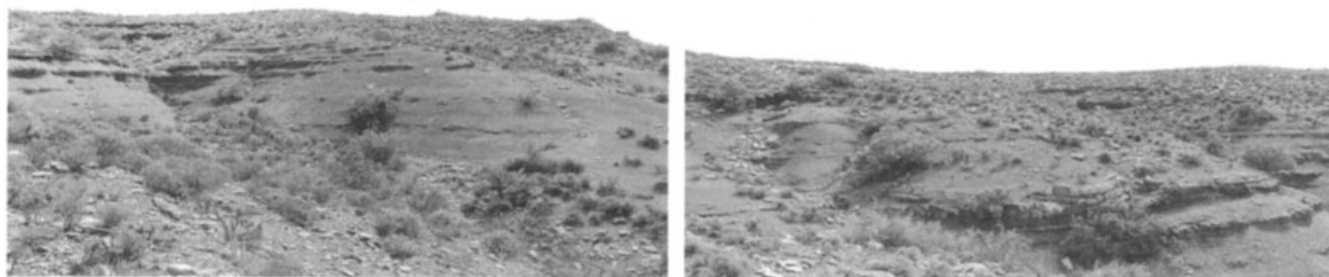
**FIGURE 4**—A portion of the Dunedin cliff exposure between 850 and 900 m (see Fig. 5)

ridges. Following brief episodes of flooding, these inter-fluve lowlands were converted into playa lakes (Stear, 1980) producing diagenetic reddening, calcification of mudcrack fills (Smith, 1990) and precipitation of evaporites. Ex-humed shoestring sandstones are evidence that low sinu-osity distributary channels, similar in size and style to Stage III splays described by Smith (1989), carried flood-water across the proximal floodplain and discharged into the playas (Smith, 1989). This paper presents evidence that the distributary channels caused embayments in the playa margins which became sites for bone accumulation.

The overriding factor that determined the sedimentary and pedogenic characteristics of any part of the floodplain was its proximity to the major rivers and the effect that this had on the periodicity and magnitude of floods in that area. This directly influenced the local rates of sedimen-tation, the overall rate of floodplain accretion and conse-quently the degree of soil maturity (Bown and Kraus, 1987; Kraus, 1987; Smith, 1990). This study attempts to quantify some of these geomorphic factors through their influence on the transportation, burial and fossilization of vertebrate skeletons on various parts of the ancient floodplains.

## VERTEBRATE TAPHONOMY OF HOEDEMAKER FLOODPLAIN FACIES

### Field Procedures

Within each study area shown in Figure 1, three con-tinuous cliff section exposures of Hoedemaker mudrocks were selected for detailed taphonomic investigation. These exposures are named Wilgerboschkloof (WBK), Leeukloof (LK) and Dunedin (DN) after the farms on which they occur. Despite being widely spaced within the study block, all three localities occur at roughly the same stratigraphic level, some 60 m above the base of the 200 m thick Hoe-demaker member.

Field procedures for gathering taphonomic data differ from the normal fossil collecting methods in that the cov-erage and scrutiny of the exposed rock surface is much more intense and more controlled so as to apply an even "collecting pressure" to the entire outcrop. To complete a full taphonomic analysis of an outcrop may take up to

three weeks depending on the number of fossils and extent of exposure. For the first week or so the positions of all *in situ* fossil bones, as well as coprolites, plant impressions and vertebrate burrow-fills, are marked with white beacons made from a boulder wrapped in tissue paper. Before re-cording taphonomic data from each fossil, the entire out-crop is photographed from a distance making sure that major bounding surfaces and the fossil beacons are visible. Care is taken to ensure sufficient overlap between succes-sive frames to compile a photomosaic that can be used as a reference section and to check the positional accuracy of the panel sections (Fig. 4).

Scaled panel sections are then drawn up. These are 2-dimensional graphic representations of the outcrop used to record the lithologies and major bedding planes and the exact stratigraphic and spatial position of each embedded fossil with reference to a datum level. Loose fossils are much more commonly encountered than those *in situ*, but unless they can be repositioned in the rock they are of no value for this taphonomic analysis.

As each embedded fossil is being uncovered, details of its field identification, disarticulation ratio (taphonomic class), attitude, compaction, peri-mineralization, color, host matrix, skull dimensions and the pre-fossilization damage are recorded on taphonomic data sheets. The fossils are then excavated using geological picks and chisels. Some of the small delicate fossils and most of the larger articulated skeletons are protected with a Plaster of Paris jacket before lifting. Factors that determine whether a fossil is worth recovering include its rarity, completeness, type of pres-ervation and degree of weathering. Only about 30% of the taphonomically assessed fossils found along the 3 sections were collected, amounting to 100 specimens. To complete the fieldwork on each cliff section, the vertical succession was logged in detail at roughly 100 m intervals. These columnar logs record sedimentological and paleopedologi-cal features to an accuracy of 5 cm.

### Vertical and Lateral Distribution of Vertebrate Fossils

The 2-dimensional distribution of major lithologies and the positions of all *in situ* fossils exposed in a 1300 m long
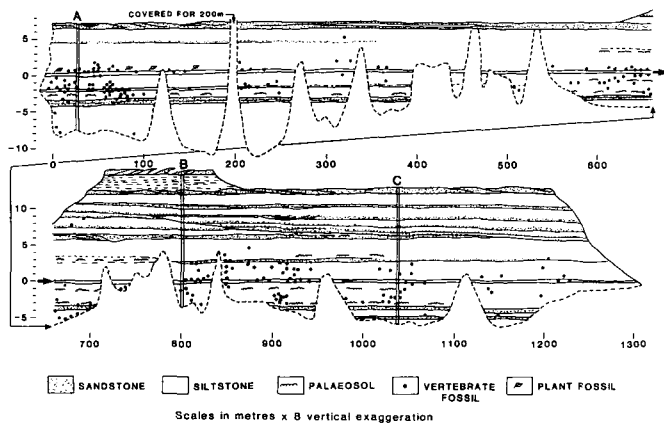
**FIGURE 5**—Microstratigraphic panel section of the Dunedin cliff exposure showing the distribution of *in situ* fossils that were taphonomically assessed in this study.

cliff section on Dunedin are shown in Figure 5. Detailed sedimentological logs of three vertical sections through this exposure are given in Figure 6 along with the facies distribution and fossil abundance. Microstratigraphic panel sections of the Wilgerboschkloof and Leeukloof exposures are shown in Figures 7 and 8. All 3 outcrops are typical of the Interchannel Facies Association of the Hoedemaker member and illustrate portions of the common facies sequence: channel/channel bank/proximal floodplain/distal floodplain/proximal floodplain/channel bank/channel. It can also be seen that fossils are not evenly distributed between or within these facies.

The Dunedin cliff section is a 1300 m wide exposure of floodplain mudrocks up to 25 m thick. It contains a single fossiliferous "horizon" hosted by proximal floodplain siltstone which occurs above and below a prominent, thin, distal crevasse splay sandstone (Figs. 5, 6 and 9). The overall impression is that the fossils occur in clusters within this 8 m interval. Repeated searches of the entire outcrop ensured that these clusters were not due to collecting bias. The strata above and below contained only rare body fossils but bone-bearing coprolites were relatively more common in the overlying channel-bank deposits. Three main paleosol profiles occur in this cliff section, two of which are superimposed on the fossiliferous interval.

In the Leeukloof exposure, which is only 42 m wide by 14 m high, there are 3 fossiliferous "horizons" within proximal floodplain sediments. The outcrop is not wide enough to demonstrate if th? fossils are clustered within these fossiliferous intervals but their distribution along the limited outcrop is similar to that of Dunedin. The lowermost fossil accumulation is in grey siltstone containing lenses and pods of fine-grained sandstone overlying a low relief scour surface. All three fossil-rich intervals have been affected by pedogenesis, but not all the paleosols in this section host fossils.

On Wilgerboschkloof, fossils are again most abundant in fine-grained sandstone and siltstone beds of the prox-
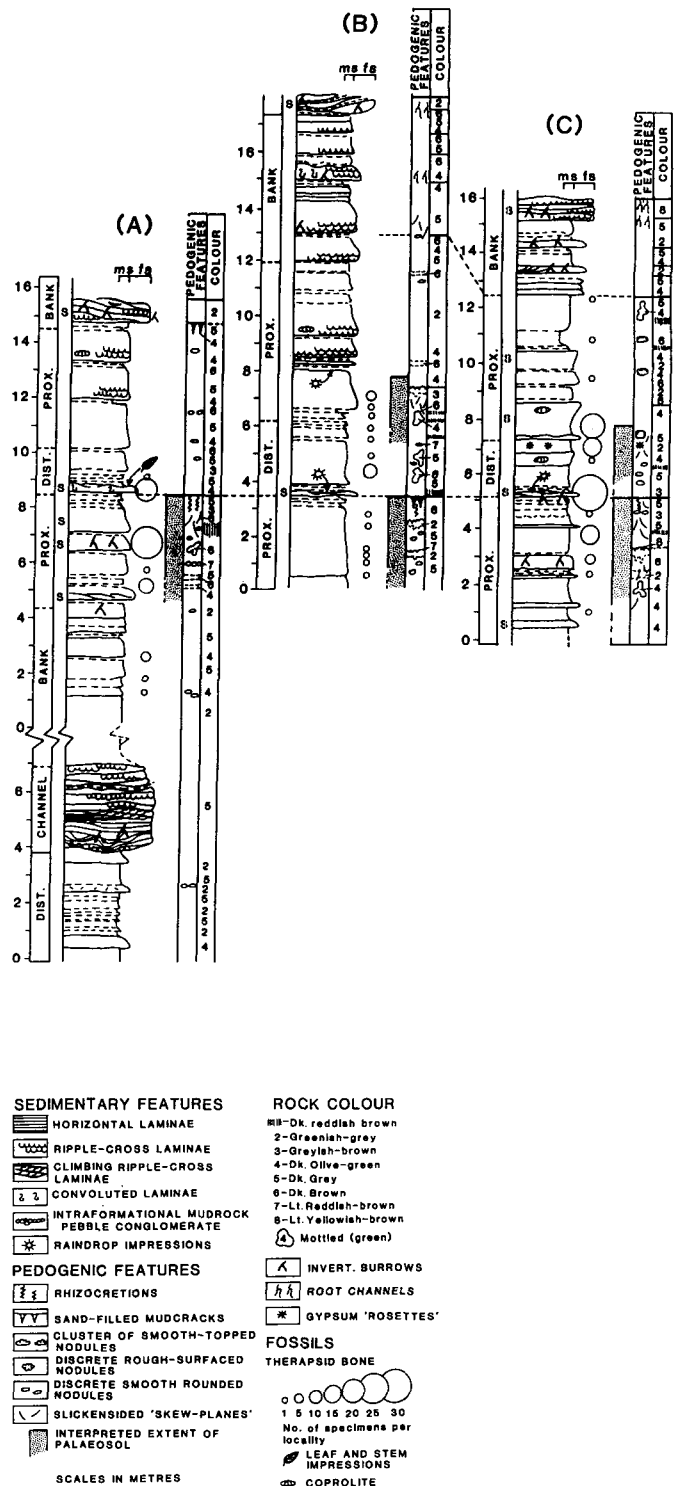
**SEDIMENTARY FEATURES**

HORIZONTAL LAMINAE
RIPPLE-CROSS LAMINAE
CLIMBING RIPPLE-CROSS LAMINAE
CONVOLUTED LAMINAE
INTRAFORMATIONAL MUDROCK PEBBLE CONGLOMERATE
RAINDROP IMPRESSIONS

**PEDOGENIC FEATURES**

RHIZOCRETIONS
SAND-FILLED MUDCRACKS
CLUSTER OF SMOOTH-TOPPED NODULES
DISCRETE ROUGH-SURFACED NODULES
DISCRETE SMOOTH ROUNDED NODULES
SLICKENSIDED 'SKEW-PLANES'
INTERPRETED EXTENT OF PALAEOSOL

SCALES IN METRES

**ROCK COLOUR**

MB-Dk. reddish brown
2-Greenish-grey
3-Greyish-brown
4-Dk. Olive-green
5-Dk. Grey
6-Dk. Brown
7-Lt. Reddish-brown
8-Lt. Yellowish-brown
Mottled (green)

INVERT. BURROWS
ROOT CHANNELS
GYPSUM 'ROSETTES'

**FOSSILS**

THERAPSID BONE

1 5 10 15 20 25 30
No. of specimens per locality
LEAF AND STEM IMPRESSIONS
COPROLITE



**FIGURE 6**—Columnar logs of the Dunedin cliff section showing the lithologies, sedimentary features and paleosols of the various floodplain facies and the relative abundance of vertebrate fossils. Abbreviations for rock texture—m = mudstone, s = siltstone, fs = fine-grained sandstone.
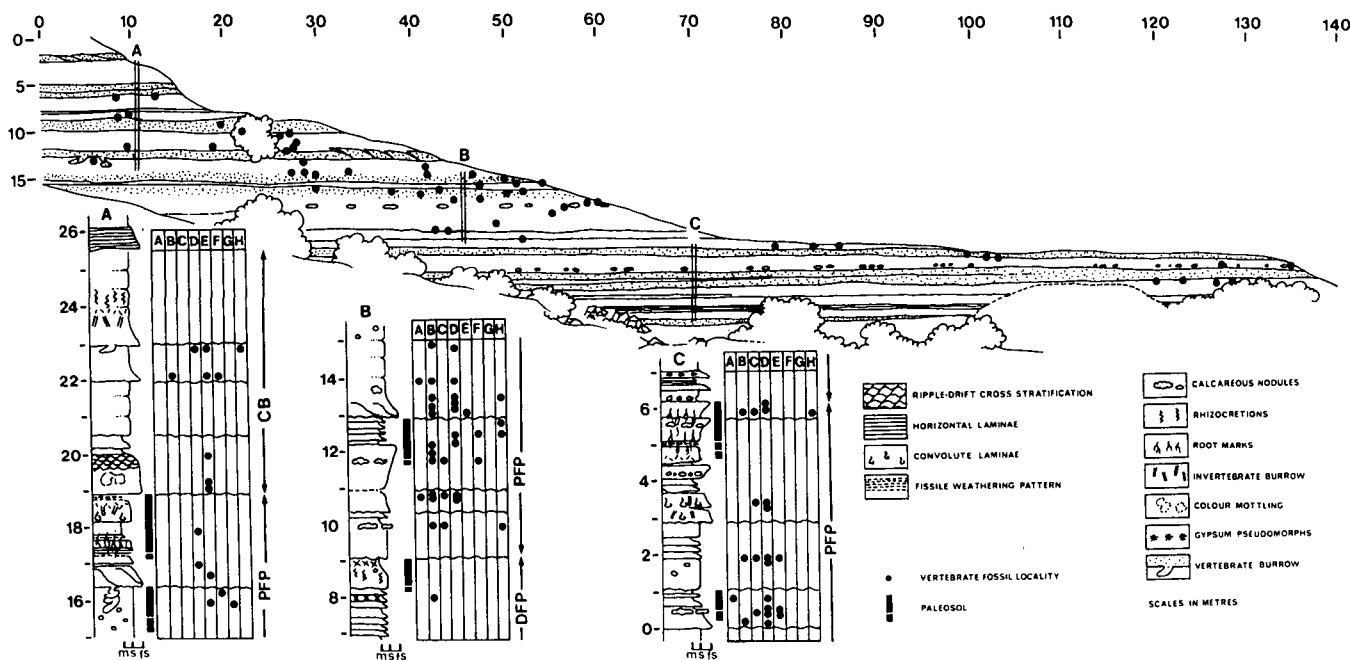
FIGURE 7—Microstratigraphic panel section and columnar logs of the Wilgerboschkloof cliff exposure showing bedding, paleosols and the taphonomic classes of all *in situ* vertebrate fossils. Refer to Table 2 for description of taphonomic classes A–H. Abbreviations for facies nomenclature—DFP = Distal floodplain facies, PFP = Proximal floodplain facies, C = Channel-bank facies.

imal floodplain facies although a few fossils occur scattered throughout the channel bank deposits. A cluster of 12 fossils occurs between 25 and 30 m along the section covering a 2.0 m interval from 13–15 m above base. Paleosols are again a common occurrence in these strata.

Semi-arid denudation of the horizontally bedded Hoedemaker mudrocks along these cliff sections has produced a dissected topography of V-shaped gulleys separated by convex bluffs. In consequence, the actual area of clean exposure is roughly 30% more than the 2-D projections of Figures 5, 7, 8 and 12. Table 1 is a compilation of data illustrating the relative abundance of vertebrate fossils in each of the three floodplain facies. To compensate for the tangential nature of the section and topographic irregularities, the areas of outcrop measured on the panel sections have been increased by 33%.

Proximal floodplain facies outcrop over 54% of the exposure and contain 90% of the fossils, giving an average density of 1 fossil every 67 $m^2$ (a fossil being anything from a single skeletal element to a group of complete skeletons). The distal floodplain deposits occupy only 8% of the exposure and yielded 6% of the fossils with an average density of 1 every 160 $m^2$, whereas the channel bank yielded only 4% of the fossils despite occupying 38% of the exposure with a very low density of 1 fossil every 1135 $m^2$. Combining the results of the three study sections, a total of 329 *in situ* fossils were taphonomically assessed from 36 637 $m^2$ of Hoedemaker strata giving an overall vertebrate fossil density of 1 fossil per 111 $m^2$.
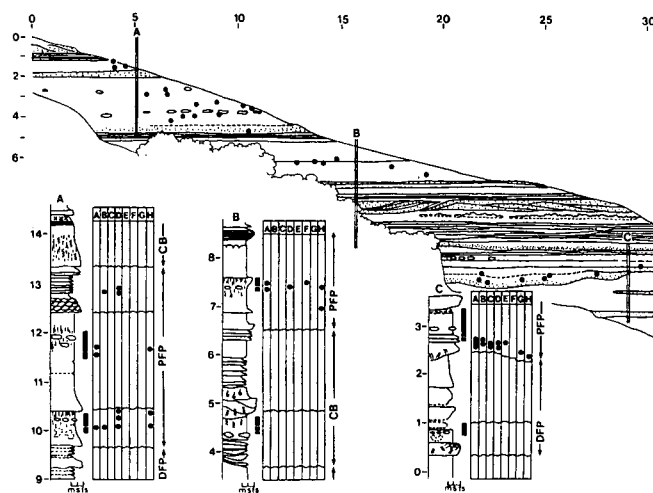
The vertebrate fossils of the Hoedemaker member are



FIGURE 8—Microstratigraphic panel section and columnar logs of a cliff exposure of floodplain rocks on Leeukloof showing the bedding characteristics, paleosols and taphonomic classes of *in situ* vertebrate fossils. Refer to Figure 7 for legend and Table 2 for description of taphonomic classes A–H. Abbreviations for facies nomenclature—DFP = Distal floodplain facies, PFP = Proximal floodplain facies, CB = Channel-bank facies.

representative of the *Tropidostoma-Endothiodon* Assemblage Zone (Keyser and Smith, 1979). The relative abundance of genera among the 329 fossils assessed in this study are shown in Figure 10. Fossils of the small and medium-

**FIGURE 9**—A distinct ledge-forming distal crevasse splay sandstone used as a base-line for the Dunedin cliff section. Most of the vertebrate fossils were found in strata immediately above and below this bed.

sized herbivores such as *Diictodon, Pristerodon* and *Oudenodon* clearly outnumber the predatory gorgonopsians and therocephalians by around 60:1. Although there are many taphonomic factors that could bias this ratio, it is accepted that this broadly reflects differences in their original abundances.

Using the different sources of taphonomic evidence presented below, it is possible to gain a better understanding of the post-mortem/pre-burial history of each of these specimens. Statistical analysis of these data allows an assessment of the taphonomic bias in the fossil fauna of various floodplain facies.

### Degree of Skeletal Disarticulation
### (Taphonomic Class)

Prior to this study, field observations of some 2500 *in situ* therapsid fossils in the Teekloof strata surrounding the study sections (Smith, 1980) made it possible to identify regularly occurring patterns of skeletal disarticulation that could be grouped into 8 taphonomic classes (A–H of Table 2). These classes range from fully-articulated curled-up specimens through articulated skeletons with straight or reflexed spinal curvature, isolated skulls, with or without attached lower jaws, to individual post-cranial elements.

The relative abundance of the various taphonomic classes among all the fossils assessed in this study is shown in Figure 11 and it clearly demonstrates the dominance of isolated skulls (taphonomic classes D and E). The absence of animals with dentition capable of crushing long bones suggests that carnivory was not a major factor causing the disarticulation and scattering of larger skeletons. However, the presence of bone shards in some coprolites indicates that some bones were being ingested (Smith, 1989). These may have been accidentally ingested while scavenging a larger prey but more likely these shards originated from smaller infant and juvenile prey.

Ruling out carnivory as a major factor in the progressive disarticulation from classes A to H, it is possible that this broadly reflects increasing "residence time" that skeletons remained exposed on the floodplain surface before being buried. Ignoring special circumstances such as trampling

**TABLE 1**—Vertebrate fossil abundance data for the three study sections. The area of outcrop is measured from the 2-D panel sections with a correction factor of an additional 33% to account for the 3-D irregularities of the outcrop

| Floodplain facies | Area of outcrop (m²) | No. of in situ fossil bones | Density of vert. foss (1:m²) | % of total outcrop area | % of total fossils |
|---|---|---|---|---|---|
| Channel bank | 13,629 | 12 | 1:1135 | 37.2 | 4.0 |
| Proximal floodplain | 19,968 | 296 | 1:67 | 54.5 | 90.0 |
| Distal floodplain | 3030 | 19 | 1:160 | 8.3 | 6.0 |
| Overbank deposits | 36,637 | 329 | 1:111 | — | — |

(Behrensmeyer et al., 1986) or miring (Weigelt, 1989), the time taken to completely bury a skeleton or any part thereof is a function of its size and the episodicity of local sedimentation events. The averaged floodplain accretion rates decrease with increasing distance from the main channel and are generally too slow to preserve bone. However, areas of the proximal floodplain that are affected by avulsions of the main channel have significantly higher aggradation
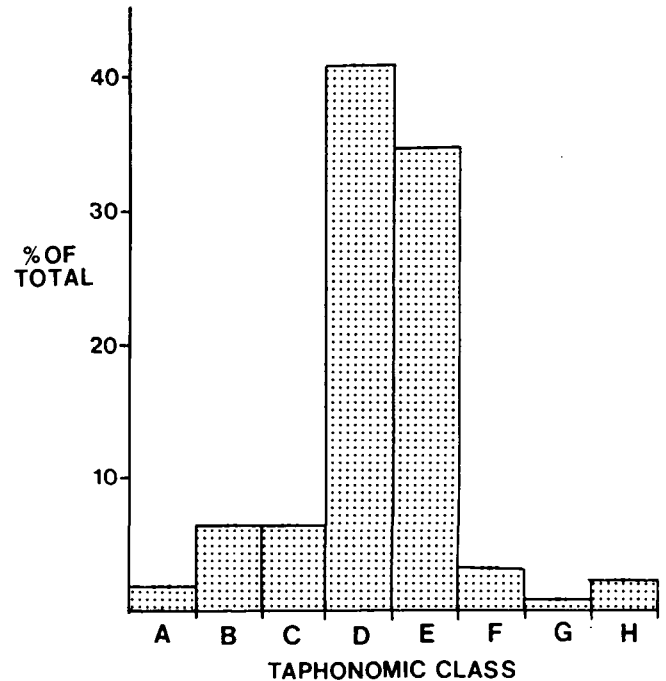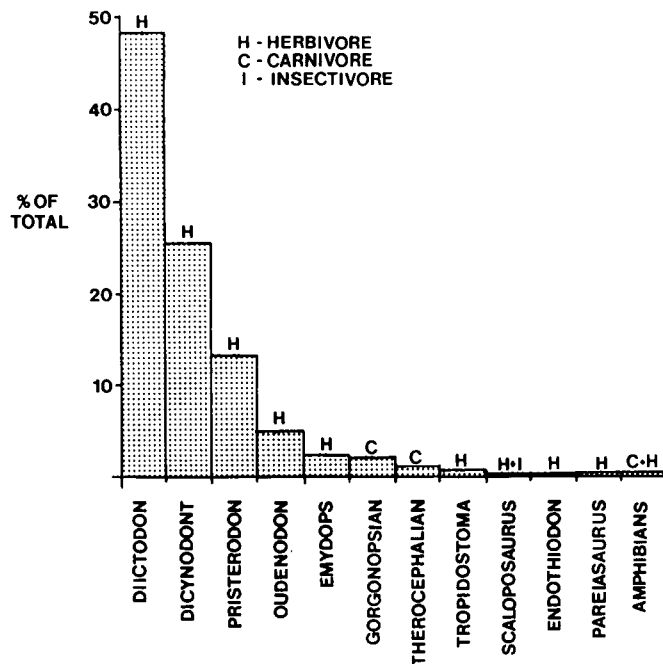


FIGURE 10—Relative abundance of vertebrate genera amongst the 329 fossils that were taphonomically assessed in this study highlighting the dominance of the small herbivorous dicynodont *Diictodon*.

FIGURE 11—Relative abundance of taphonomic classes amongst all fossils found in the study sections. Note the dominance of isolated skulls and the overall paucity of individual post-cranial elements.

TABLE 2—Taphonomic classes of *Diictodon* based on the degree of disarticulation of the skeleton.

|  |  | Taphonomic class | Transportation | Duration of post mortem/ preburial period |
|---|---|---|---|---|
| Preserved at site of death | A | Complete articulated skeleton in "curled up" attitude—sometimes paired | No transportation (preserved in burrow) | V. short |
|  | B | Complete or near complete skeleton with straight or reflexed spinal curvature—sometimes paired | Slightly rolled (preserved in burrow) | Short |
| Preserved near site of death | C | Skull with articulating cervical vertebrae and lower jaw |  | Short |
|  | D | Skull with displaced lower jaw | Lag—short distance transport | Long |
|  | E | Skull without lower jaw |  | Long |
|  | F | Lower jaw |  | Long |
| Preserved far from site of death | G | Accumulation of variety of small post-cranial elements into "bone bed" | Long distance transport reworked & winnowed & sorted | V. long |
|  | H | Isolated and/or fragmented ribs, limb bones and vertebrae | Long distance transport | V. long |
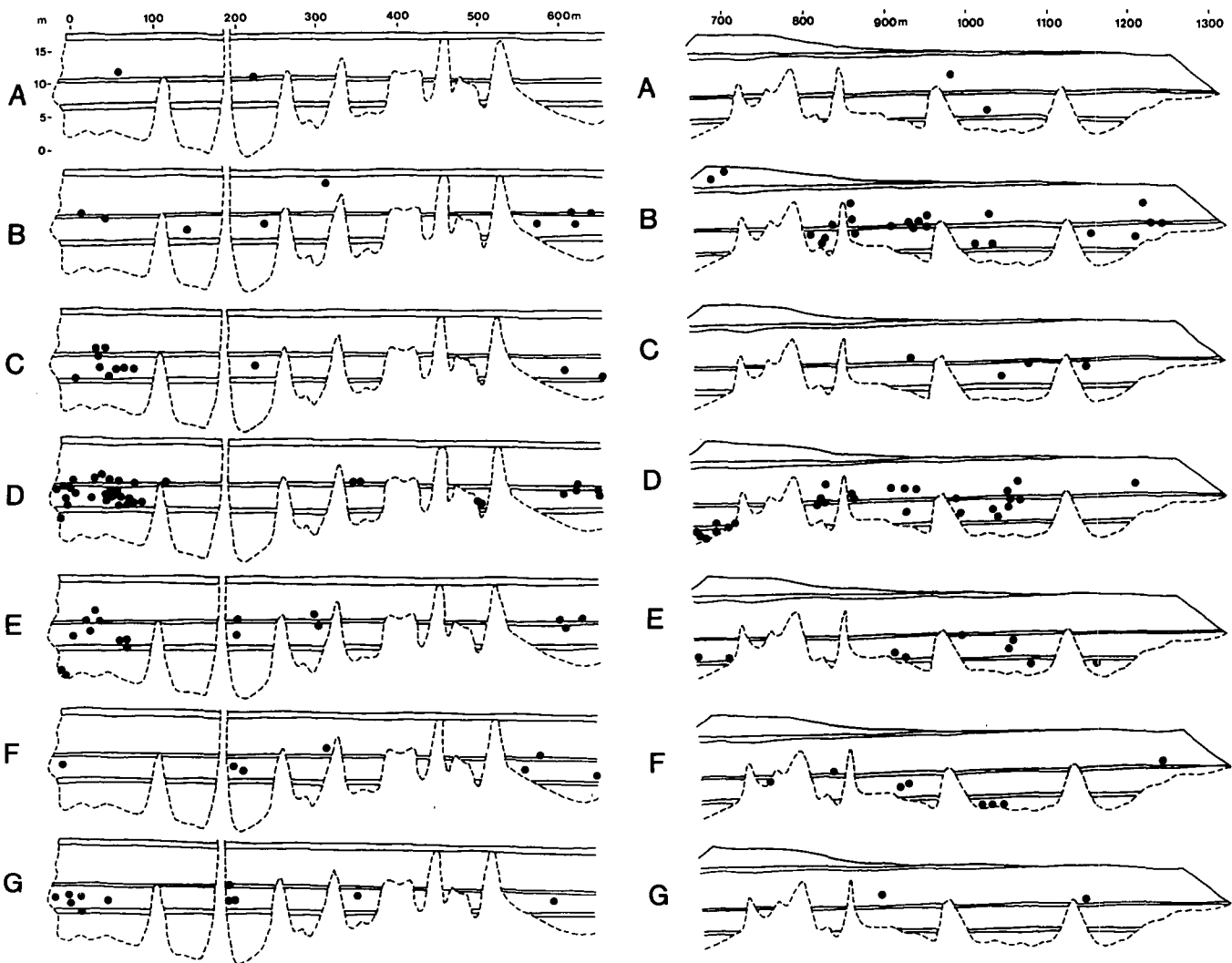
**FIGURE 12**—Distribution of taphonomic classes amongst the *in situ* therapsid fossils found on the Dunedin cliff exposure showing that they occur in "clusters" within a fairly narrow interval rather than evenly spaced throughout the outcrop. No fossils of taphonomic class H, normally associated with channel lag conglomerates, were found in this section.

rates (Smith et al., 1989). It follows that if the "residence time" of a particular element is longer than that needed to reach late stage weathering then the bone has little chance of preservation. Thus it may be predicted that the distal floodplain facies with the slowest accretion rates should contain fewer, more disarticulated and more highly weathered fossils than the other overbank facies. This is the case in many but not all exposures of distal floodplain facies in the Hoedemaker member.

The 2-dimensional distribution of the various taphonomic classes of fossils in the Dunedin cliff section is shown in Figure 12. It demonstrates that the fossils are clustered rather than evenly scattered along the section and they are not confined to a single bed or bedding plane although they mostly occur in the interval of proximal floodplain strata between +4 m and −4 m. This distribution also demonstrates that these clusters are of mixed taxa and taphonomic classes. The cluster of 56 fossils around meter 50 contains mostly isolated skulls with articulated lower jaws (36) along with 10 skulls without lower jaws. Three near-complete and only one complete skeleton occurred in this cluster. Another cluster of 27 fossils around meter 650 again contains mostly isolated skulls of which 14 are with and 5 are without lower jaws. Between meter 800 and 900 there is a cluster of some 53 fossils that contains more near-complete skeletons than the equivalent-sized cluster at meter 50 (16 as opposed to 4) and fewer isolated skulls (28 compared to 46).

The distribution of fossils along the 1300 m Dunedin exposure reflects the high "preservation potential" for therapsid skeletons buried in the alluvium of the proximal floodplain between crevasse splay sand sheets. It also dem-

onstrates that the "preservation potential" of certain patches of the floodplain was considerably higher than the rest for extended periods of time resulting in clusters of fossils preserved in the successive layers of alluvium. This implies that the physical conditions in these areas were favorable for preservation of bone but does not indicate whether there were any additional biological concentrating mechanisms. Sequences with increased "preservation potential" of bones may represent preservation of avulsion deposits (Smith et al., 1989) which reflect high sedimentation rates and rapid vertical accretion in localized parts of the proximal floodplain.

A cluster of 14 fossils in the Wilgerboschkloof section around meter 30 (Fig. 7) contains 7 articulated skeletons (6 class B and 1 class A) and 5 isolated skulls of *Diictodon*. This anomalously high degree of articulation is possibly caused by their preservation within burrows, casts of which occur in the vicinity.

In the Leeukloof section an interval containing 12 articulated skeletons occurs 2.5 meters above base in a silty sandstone bed directly overlying a scour surface (see Fig. 8). These specimens contain 3 curled-up skeletons (class A, see Fig. 20), 2 reflexed-spine skeletons (class B) and some isolated post-cranial elements. With no evidence of burrows in the host sediments it appears that the high degree of articulation may be due to catastrophic inundation of the proximal floodplain resulting in death and burial in the same event.

To facilitate direct comparison of the taphonomic characteristics of different facies, a single common genus was selected for detailed analysis. *Diictodon* (see Fig. 13) is the obvious candidate being of medium size, occurring in all floodplain facies, and by far the most common genus in all three study sections (Fig. 10). The taphonomic class distribution of *Diictodon* within the three interchannel facies (Fig. 13) shows the proximal floodplain facies contains most of the fully-articulated specimens and the channel bank deposits the least.

During the course of this study it was found that fully-articulated *Diictodon* skeletons of taphonomic classes A and B are, in some cases, the result of the animal having died within underground burrows (Smith, 1987b). At least 50 helical burrow casts have been located to date, mainly in siltstones of proximal floodplain facies, two of which contain "curled-up" *Diictodon* skeletons. These skeletons were not subjected to the same taphonomic processes as those that lay exposed on the floodplain surface and consequently their high degree of completeness and articulation does not necessarily reflect a short post-mortem/pre-burial period.

Taphonomic classes C to F reflect the disarticulation of isolated skulls that were separated from the rest of the skeleton. Being some of the largest bones on the Hoedemaker floodplains they were subjected to the destructive effects of trampling, transportation, weathering and reworking before final burial. Nevertheless they appear to have survived better than the smaller post-cranial elements (Weigelt, 1989). The dominance of "skull-only" occurrences (classes C, D and E) over all other taphonomic
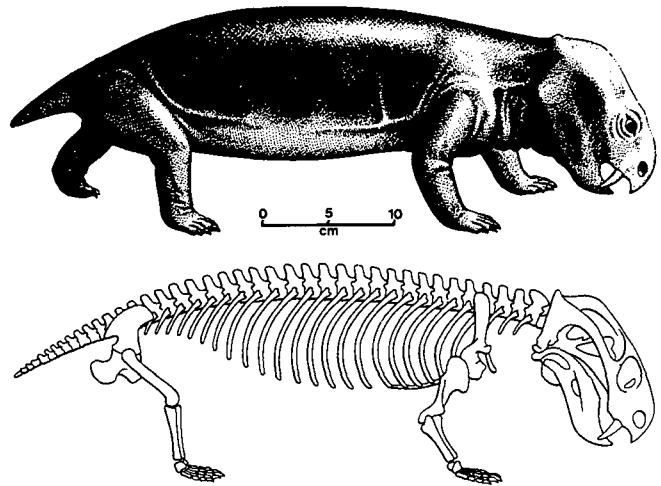


FIGURE 13—Reconstruction of the skeleton and a fleshed-up carcass of *Diictodon* (from Cluver, 1978). Note how much larger the skull and lower jaw are in relation to the individual elements of the post-cranial skeleton.

classes of *Diictodon* has been noted previously from the Lower Beaufort (Boonstra, 1969; Hotton, 1967; Smith, 1980) and is well demonstrated by this study (Fig. 14).

*Diictodon* skulls are the largest and heaviest single element of the skeleton (see Fig. 13) especially if the lower jaw remains articulated (class D) as it has done in the majority of isolated skulls found during this study (Fig. 14, taphonomic class D). This meant that of all the disarticulated elements, the skull was the least likely to become entrained and transported and possibly remained at or close to the site of death. Voorhies (1969) studied the mechanisms of transport and patterns of dispersal of modern disarticulated mammal skeletons under controlled current velocities. He established three bone dispersal groups for sheep and coyote skeletons of which the least transported members (lag) were always the skull and mandible. Even though adult *Diictodon* skeletons are only half the size of coyote, their basic anatomy is similar so it is likely that their skulls were the least transportable element of the skeleton.

It is improbable that carnivore activity is solely responsible for "head-only" occurrences but if, as in many modern predators, the neck was the target of attack, this would have accelerated the decomposition of ligaments that attach the skull to the post-cranial skeleton. Thus, relatively soon after death the combination of carnivore, scavenger, insect and bacterial action, enhanced by shrinkage and desiccation of skin and ligaments, would have led to the separation of the head from the rest of the body. Upon inundation by fast-flowing floodwaters, the skull would resist entrainment while the post-crania would either float away as a whole within a mummified skin or be transported as individual elements in the bedload.

Hill (1979) noted that desiccation of the skin covering the carcasses of small savanna mammals causes it to become mummified and hold the disarticulated bones in close
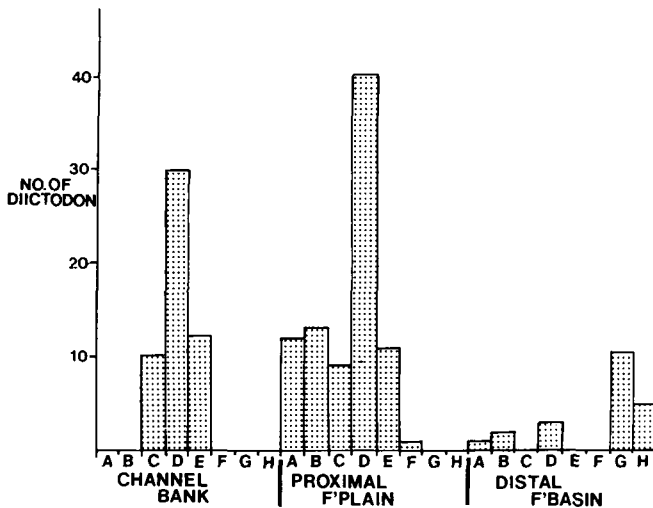
**FIGURE 14**—Taphonomic class distribution of 158 *Diictodon* fossils found within the floodplain facies of all three study sections. Note that the proximal floodplain facies contains the more highly articulated specimens (classes A and B).

association indefinitely. It has been speculated that the therapsids had a leathery skin without scales or hair (Romer, 1966; Chudinov, 1970). Under semi-arid climatic conditions *Diictodon* unshaded carcasses lying on the floodplain would have dried fairly rapidly so that mummification of the skin may well have played an important role in the preservation of near complete skeletons with straight or reflexed spinal curvature (taphonomic class B).

Desiccation and shrinkage of the jaw ligaments and the fibrous cheek tissue ("mundplatt" of Crompton and Hotton, 1967) of *Diictodon* (see Fig. 13) would have effectively clamped the jaws keeping them closed long after the adductor musculature had decomposed. The toothless jaws and curved snout of *Diictodon* closely resemble the "beak" of modern tortoises (see Fig. 13) and are interpreted as having been horn-covered (King, 1990). Tortoise carcasses observed in the semi-arid Karoo regions today have their jaws held tight closed by desiccated ligaments across the jaw articulation, causing the curved horny beak to remain wedged firmly closed. It is likely that a similar combination of ligament desiccation and "beak wedging" in *Diictodon* accounted for the high proportion of isolated skulls with articulated lower jaws (Fig. 14, taphonomic class D).

## Attitude of Skulls

The attitude of isolated skulls is a measure of their spatial orientation within the rock relative to surrounding bedding planes. This may be expected to vary according to sizes and shapes of skulls influencing their hydrodynamic, aerodynamic and gravitational stability.

In this study the attitudes of 158 *in situ Diictodon* skulls from the three study sections in the Hoedemaker member were measured (Fig. 15a). The majority are lying on their

sides, with dorsal-up and ventral-up being the next most common groups. A few were preserved in anterior-up, posterior-up, dorsolateral-up and ventrolateral-up attitudes. Figure 15b, c shows that the presence of an articulated lower jaw strongly influences the burial attitude. Skulls with lower jaws are much more likely to be embedded lying on their sides (Fig. 16), whereas those without are most commonly buried dorsal-up although a considerable number were found lying lateral-up. These reflect the attitudes of maximum gravitational and hydrodynamic stability of isolated *Diictodon* skulls and suggest that they were initially embedded by shallow competent flows and buried incrementally during subsequent flood events. This is consistent with the sedimentological interpretation of periodic flooding of the proximal floodplain areas with shallow sheetflows that were competent enough to topple and orientate *Diictodon* skulls. Smith et al. (1989) showed that this style of sedimentation occurs around crevasse splay lobes that are involved in channel avulsion.

Anomalous skull attitudes are possibly caused by the "self-burial" mechanism described by Behrensmeyer (1975) whereby the skull topples into a scour pit excavated by turbulent eddies flowing around the stationary skull. Trampling is another effective embedding mechanism (Behrensmeyer et al., 1986) that may have resulted in the skull lying tangentially to bedding. Burial within burrows also results in some anomalous skull attitudes although these normally involve articulated skeletons (Smith, 1987b).

## Bone Weathering

Most of the vertebrate fossils in the Hoedemaker member have some evidence of pre-fossilization weathering, which may be used as a rough indicator of their "residence" time on the floodplain surface. In this study, the degree of pre-fossilization weathering is reflected by 5 weathering states (1–5) which are roughly comparable to the 6 weathering stages (0–6) of modern bones exposed to semi-arid climatic conditions (Behrensmeyer, 1978). Although there are differences in bone histology between therapsids and mammals (De Riqueles, 1969), they are similar enough in overall structure and composition to have comparable weathering characteristics.

The following weathering states of Karoo therapsids are based on macroscopic features that are distinguishable on unprepared material from the Hoedemaker member.

STATE 1 (Stage 0 of Behrensmeyer, 1978)
Long bones: Smooth "fresh-looking" bone surface without longitudinal cracks or fissures. Articular surfaces are still moderately well-rounded.
Skulls: "Fresh-looking" bone surface. Sutures between individual elements of skull roof are tightly closed and almost invisible. Sclerotic plates sometimes preserved inside the orbit.

STATE 2 (Stages 1 & 2 of Behrensmeyer, 1978)
Long bones: Some cracking and flaking of periosteal laminae and a few longitudinal fractures parallel to the
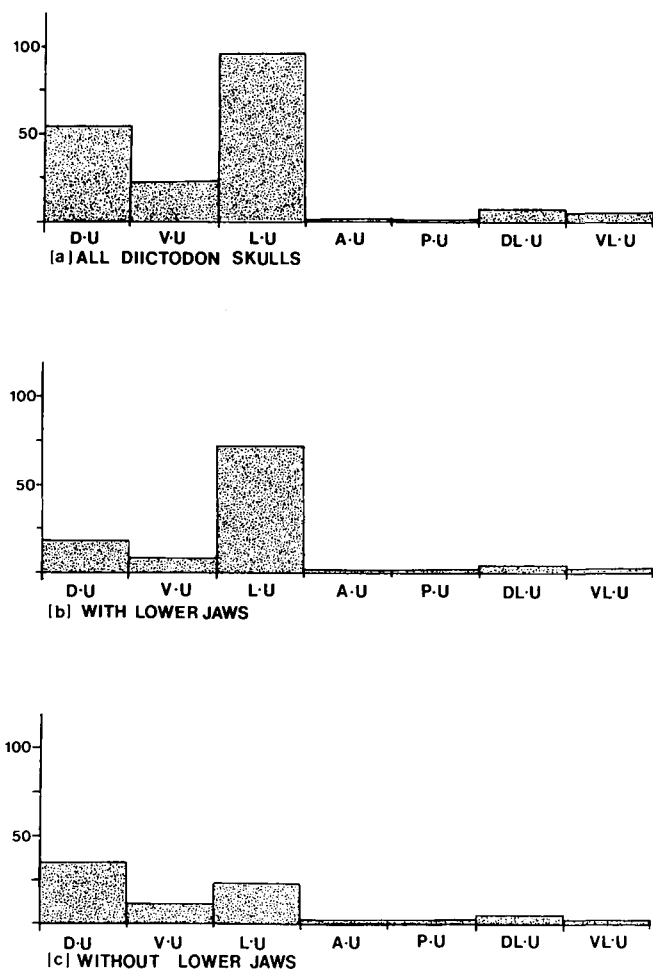
FIGURE 15—Attitude of 158 in situ Diictodon skulls collected from the study sections, (a) all skulls (b) skulls with articulated lower jaws, (c) skulls without lower jaws. Abbreviations D-U = Dorsal-up, V-U = Ventral-up, L-U = Lateral-up, A-U = Anterior-up, P-U = Posterior-up, DL-U = Dorso-lateral-up, VL-U = Ventro-lateral-up.



FIGURE 16—An embedded Diictodon skull with articulated lower jaw lying lateral-up in mudrocks of the Dunedin cliff section.

shaft, closing towards each end. Articular surfaces are still rounded with cancellous bone exposed.

Skulls: Some cracks along the outer rim of the squamosals and areas, especially around the snout, where periosteal bone has flaked off. Sutures of the skull roof are visibly open. Tusks and teeth intact and uncracked.

STATE 3 (Stage 3 of Behrensmeyer, 1978)

Long bones: Flaking of bone along the edge of longitudinal fissures. Articular surfaces flat and cancellous.

Skulls: Longitudinal cracks in squamosals, post-orbitals and parietal bones. Flaking of rugosities on nasals and pre-maxillae. Gaping of nasal and frontal sutures. Tusks intact and uncracked.

STATE 4 (Stage 4 of Behrensmeyer, 1978)

Long bones: Covered in longitudinal and radial cracks with almost complete loss of periosteal bone and a crazed

pattern of cracks in sub-periosteum. Cancellous bone may be visible in places along the shaft.

Skulls: Most bones are cracked and fissured, post-orbitals and tusks are often missing. Caniniform processes and edges of squamosals are rough and splintered.

STATE 5 (Stages 5 & 6 of Behrensmeyer, 1978)

Long bones: The dense periosteal bone has completely flaked-off. Inner cancellous bone is worn so that the original bone shape is barely recognizable.

Skulls: The bone/matrix contact is indistinct due to the penetration of silt into the cracked and crumbling bone during burial. Extensive marginal erosion of squamosal and pre-maxilla bones.

Figure 17 shows the distribution of weathering states among the fossils found in the three study sections. It clearly demonstrates that over half the fossils are relatively fresh (states 1 & 2), an observation that has been made
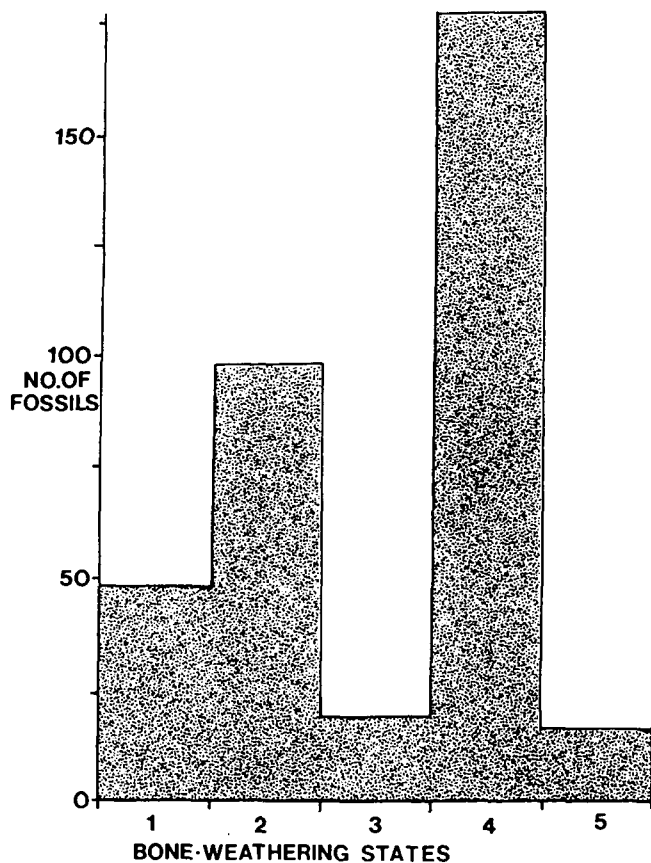
FIGURE 17—Distribution of weathering stages of all fossils recovered from the three study sections.



FIGURE 18—Distribution of bone-weathering stages amongst *Diic-todon* skulls recovered from the three floodplain facies.

by many paleontologists over the years and is the hallmark of Hoedemaker fossils.

A breakdown of bone weathering states among the fossils within the three floodplain facies (Fig. 18) shows that the more weathered fossils are relatively more common in the distal floodplain areas, and the fresher bone is generally associated with channel bank and proximal floodplain deposits. The proximal floodplain deposits contain the widest range of weathering states in a bimodal distribution with states 2 and 4 being most abundant and a paucity of state 3. This may be an artifact of the definition of this particular weathered state, but it is also possible that bones exposed on the semi-arid floodplains spent less time in state 3 than states 2 and 4 and were therefore underrepresented in the buried sample.

Despite this, it is clear that proximal floodplain deposits contain both fresh and weathered bones in roughly equal quantities. This is discussed later as evidence for differential burial provinces on the proximal floodplain caused by avulsion controlled aggradation (Smith et al., 1989)

The patterns of weathering of therapsid bones in the Teekloof Formation are broadly similar to those of modern mammal bones on semi-arid alluvial plains of Amboseli National Park, Kenya, where medium-sized mammal bones
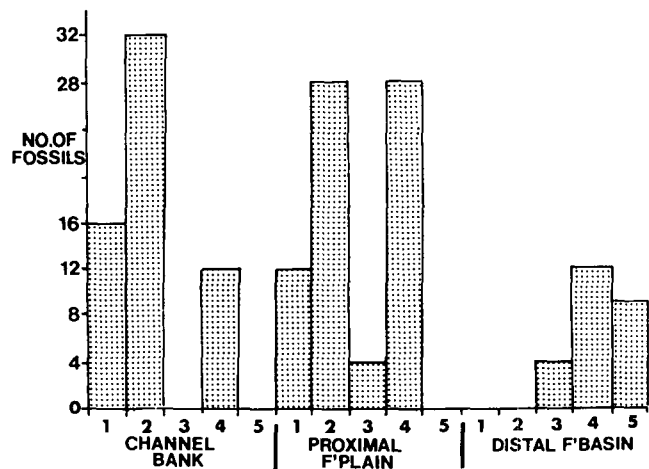
take up to 15 years to reach stage 5 weathering (Behrens-meyer, 1978). The most significant changes in weathering textures occur around three years after death when, in exposed situations, the bones lose their surficial perios-teum and with it their fresh appearance.

There are many other factors that can influence the degree of bone weathering apart from the size of the bone and its residence time on the floodplain surface; for instance, shading by vegetation, insect borings, trampling and the displacive growth of evaporite crystals. Nevertheless it is felt that the lack of fresh bones recorded in the distal floodplain facies of the Hoedemaker mudrocks is a reflection of a decreased rate of floodplain accretion on the margins of the axial playa lake.

## Peri-Mineralization

Most of the fossil bones in the Teekloof Formation are completely or partly encrusted by a thin layer of micritic siltstone. This peri-mineralization ranges in thickness from 2–20 mm and is sharply contacted with the surrounding sediment, a feature that makes their excavation much easier than non-encrusted specimens. The texture and composition of the crust is identical to the numerous pedogenic calcareous nodules that occur in horizons throughout the succession (Smith, 1990) and is interpreted to be of similar origin. Only very rarely are fossils so thickly encased in nodular material that the original shape is masked.

Skulls that have been moderately peri-mineralized are only slightly compressed compared to those without peri-mineralization which are flattened. This suggests that calcite was deposited in the sediment immediately surrounding the bone before compaction and possibly before complete mineral replacement of the bone.

Slickensided surfaces commonly occur in the host mud-rocks around peri-mineralized fossils and calcareous nodules. These were formed by differential compaction of the
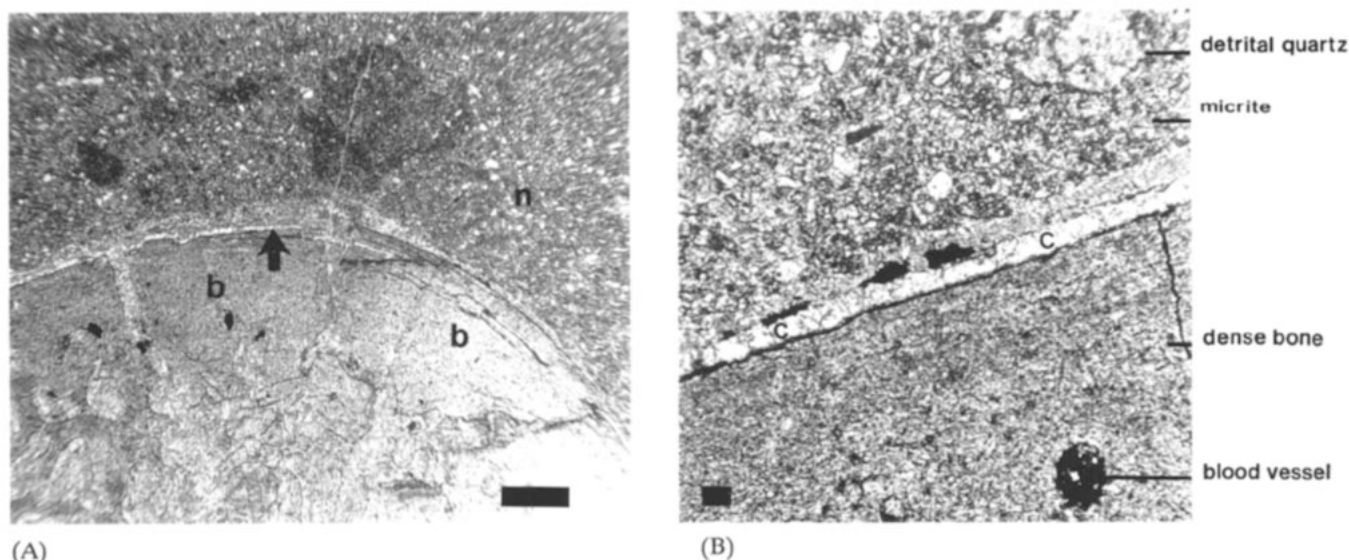
**FIGURE 19**—(**A**) Photomicrograph of the contact between a fossilized therapsid bone (b) and its encrusting micrite nodule (n). Note the narrow laminar calcite layer (arrowed) between the two. Scale bar = 5 mm. (**B**) Closer view of calcite layer (c) showing it to be made up of equant calcite crystals oriented normal to the bone surface. Note the detrital quartz in the micritic groundmass of the encrusting nodular material. Scale bar = 1 mm.

mudrocks around rigid objects and they are another indication that early diagenetic consolidation has taken place. The presence of slickensides in the overbank mudrocks is therefore ultimately determined by the rates of floodplain accretion versus soil maturation.

Thin sections of peri-mineralized therapsid bones reveal the presence of a narrow zone of equant calcite crystals, oriented normal to the bone surface which separates the bone from the micrite cemented siltstone (Fig. 19). Similar calcite laminae occur in the mudrocks surrounding many of the fossils including those without peri-mineralization. They appear to have formed after compaction because they occupy gaps between the bedding planes that were opened up by differential compaction around the consolidated bone.

### Bone Color

The color of bone in the Lower Beaufort fossil assemblages varies considerably from dark bluish-grey, black and purple in the lowest strata becoming grey, light reddish-brown and white higher in the succession. This may reflect a metamorphic gradient related to depth of burial. There is no consistent relationship between the color of fossil bone and the color of the host matrix nor are any colors specific to any taxonomic group.

Locally, bone colors are influenced by the degree of contact metamorphism in the vicinity of dolerite sills and dykes. The proximity of an intrusive body may be visually assessed by the "whiteness" of fossil bone. Nearing the dyke margin the bone becomes gradually whiter and more brittle until a "porcelain-like" state is reached. Closer still, the bone begins to disintegrate and within a few meters of the dyke margin, empty molds from which the bone has been completely "baked-out" are common.

### VERTEBRATE TAPHONOMY OF CHANNEL-BANK DEPOSITS

Fossils in the channel-bank deposits are generally rare, consisting of skulls and isolated post-cranial elements such as ribs and limb bones, with a density in the order of 1 every 1135 m² of dissected cliff section outcrop. Bone-bearing coprolites are often found in these deposits and are generally more common than bone fossils. There are, however, important exceptions to this general paucity of bone, where linear patches of outcrop yield 1 specimen every 50 m². These fossiliferous patches are invariably found in 2–3 m thick inner-bank levee deposits directly overlying a high sinuosity channel sandstone (Fig. 21). The host rocks are massively-bedded, greenish-grey, fine-grained sandstone or siltstone and all the fossils are completely encrusted with smooth-surfaced calcareous nodular material, some to such thicknesses that the bone shape is no longer discernable.

One such fossil-rich occurrence within the Hoedemaker member in study area 2 (Fig. 1) on Brandywyns Gat in the Beaufort West district has yielded numerous skeletons and skulls of *Diictodon*. Among the 52 fossils collected from this locality during this study there are 43 *Diictodon*, 2 *Tropidostoma*, 4 *Pristerodon* and 3 gorgonopsians. The *Diictodon* fossils are mostly isolated skulls both with and without lower jaws (classes D and E), a few with articulated cervical vertebrae (class C) and one fully articulated class

B skeleton. The bone surfaces are relatively unweathered (states 2 and 3) and light-grey or yellowish-brown in color.

The geometry and position of the fossil-rich levee deposits in relation to the underlying point bar suggests that they may be swale fills or possibly the fine-grained infilling of a chute channel. Similar floodplain channels are interpreted as the main depository for localized mammal bone accumulations in the Miocene Siwaliks of northern Pakistan (Behrensmeyer, 1987) and the reptile bone-beds of the Permian "red beds" of Texas (Behrensmeyer, 1988; Sander, 1989). However, the bone densities in the Lower Beaufort strata never approach those of the bone-bed occurrences mentioned above although the degree of articulation is generally higher.

After a major overbank flood, swales, chutes and crevasse channels would have provided watering holes for much of the year. In taking advantage of the increased density of prey species, carnivores would have contributed more than the "background" number of small and medium-sized herbivore skeletons to the death assemblage (Behrensmeyer, 1987; Badgley, 1986; Conybeare and Haynes, 1984). In such a setting, trampling may have been an important taphonomic agent in disarticulating, breaking and embedding bones that lay around the waterhole (Behrensmeyer et al., 1986).

Being close to the main channel, overbank flows would have had the competence to lift and transport smaller non-embedded, disarticulated skeletal elements, as well as infant and juvenile skeletons and larger mummified carcasses (Hill, 1979). The larger elements such as skulls and lower jaws were toppled and perhaps oriented to attitude of least hydraulic resistance. Thus, although the initial abundance of *Diictodon* cadavers on the channel banks may have been due to biological factors, the composition of the fossil assemblage in these deposits was mainly determined by the hydrodynamic stability of individual skeletal elements and the buoyancy of mummified carcasses.

## VERTEBRATE TAPHONOMY OF PROXIMAL FLOODPLAIN DEPOSITS

Proximal floodplain sequences of the Hoedemaker Member are the most fossiliferous, having an average bone density of 1 specimen every 67 m² of dissected cliff section exposure with patches where the incidence of bone increases to 1 fossil every 10 m² (e.g., Fig. 5, 50–75 m and 800–825 m). It is significant that the clusters of fossils are not confined to a single bed. They appear to be vertically rather than horizontally clustered on more than one stratigraphic level and involve a considerable time span rather than a single catastrophic event. These fossils cover a wider range of taphonomic classes than those of the channel bank (Fig. 12) and it is apparent that bone accumulating mechanisms on this part of the floodplain were slightly different (Fig. 2). These data demonstrate the relatively high proportion of articulated *Diictodon* skeletons along with numerous isolated skulls with articulated lower jaws in the proximal floodplain deposits compared to the channel-bank fossils.

The high preservation potential of bones and the enclosing proximal floodplain deposits may reflect the later stages of channel avulsion processes described by Smith et al. (1989) with high rates of vertical accretion on the floodplain that would be necessary to entomb the entire attritional accumulation of bones.

Preservation of *Diictodon* skeletons in underground burrows, casts of which have been found at 2 of the logged outcrops, certainly accounts for some of these highly articulated specimens (Smith, 1987b). The burrows were excavated into proximal floodplain soils, possibly as a mechanism to keep cool nearer the water table, and were sometimes occupied by more than one individual. It is possible that these animals had fixed burrow sites that were occupied year after year, thus accounting for the 3-D clustering of bones in the proximal floodplain. Catastrophic crevasse splay progradation infilled many of the burrows with fine-grained sand and silt and occasionally entombed an aestivating *Diictodon* (Fig. 20).

The greater maturity of paleosols in the proximal floodplain deposits suggests that pedogenic processes affected the early diagenesis of these fossils to a greater degree than in the channel-bank soils (Smith, 1990). The occurrence of these bones in mature paleosols suggests that they are mainly autochthonous attritional accumulations (Bown and Kraus, 1981b) on non-deposition surfaces rather than biogenic or hydraulic placer concentrations. It is therefore likely that the increased bone density in these paleosols basically reflects an extended period of time during which that area of the floodplain was not affected by major floods.

The low periodicity of major floods allowed time for the skeletons that were exposed on the proximal floodplain surface to completely disarticulate and reach late stage weathering. During this period the floodplain accretion rates were minimal, possibly as a result of regional drought but more likely due to migration of the main channel away from that part of the floodplain (Leeder, 1975; Allen, 1978). The next major sheet flood, which probably heralded the arrival of an avulsed channel back into the area, was of sufficient competence to scour the floodplain surface and transport the smaller post-cranial elements away from the site, leaving skulls and lower jaws to be buried by traction load fines. Thus, in effect, these bones are hydrodynamically sorted beds rather than simply attritional accumulations.

The Dunedin exposure clearly demonstrates that the transitional strata between proximal and distal floodplain facies are the most fossiliferous (Fig. 4) of all the interchannel facies in this area. This is interpreted as being primarily indicative of an "optimal burial environment" for the preservation of small and medium-sized dicynodonts but there may have been some biologically controlled concentration in this part of the floodplain in that drought stricken animals may have congregated here before dying (Weigelt, 1989; Rogers, 1990). The strip of floodplain bordering the axial floodbasin playas appears to have had the optimal balance between bone accumulation and bone burial mechanisms. The floodplain accretion rates were fast enough to bury bones before they disintegrated through

exposure yet the flow velocities were small enough to avoid entrainment. For most of the time there was normal attritional accumulation of skeletons on surface but during periods of drought many more mummified carcasses were added to the bone assemblage.

Subsequent inundation by sheet flows effectively buried the embedded skeletons where they lay. Thus a combination of physical and biological accumulation mechanisms around embayments in the playa margins resulted in an abundance of vertebrate fossils in the transitional strata between proximal and distal floodplain facies of the Hoedemaker member.

## VERTEBRATE TAPHONOMY OF DISTAL FLOODPLAIN DEPOSITS

Vertebrate fossils in the distal floodplain deposits are scarce, in the order of 1 specimen every 160 m² of dissected cliff section exposure, and relatively poorly preserved. They are mainly scattered post-cranial elements such as vertebrae, ribs, humeri and pelvic girdles (taphonomic class G). Skulls are rare and generally extremely compressed, strongly weathered and poorly peri-mineralized. Amphibian remains occur in these rocks as disarticulated but associated skeletons where individual elements lie in close proximity.

Plant fossils are relatively more common in the distal floodplain deposits than in other interchannel facies. They occur in thin (1–2 cm) mudstone beds that continue for up to 100 m along strike and often form a veneer on the upper surface of distal crevasse splay sandstones. The most common plant fossils in these beds are impressions of small *Glossopteris* leaves (max. length 10 cm), equisetalian stem fragments (*Schizoneura*) and leaf whorls (*Phyllotheca*). Their distribution and preservation is attributed to strandline accumulation of seasonal leaf-falls on the downwind margin of a floodbasin lake. However the seasonally saturated soils and saline groundwaters along the playa margins would not have supported a particularly flourishing vegetation.

Vertebrate footprints are preserved on the upper surface of distal crevasse splay sandstones at several localities in the vicinity of the study area (Smith, in press). Their preservation is largely a function of the sequence and style of sedimentation in this environment whereby sand deposited around the mouths of distributary channels was briefly exposed, imprinted and then gently inundated as the lake level rose during the inflow of floodwater. At the Leeu River trackway site the imprinted sandstone has a surface texture similar to the underside of matted filamentous algae; thus it is possible that the footprints were preserved as underprints. Another trackway site near Fraserburg (De Beer, 1987) is on a distal crevasse splay that shows obvious evidence of sub-aerial exposure and desiccation. The paleosurface consists of numerous shallow troughs with narrow intervening ridges. Detailed ichnological mapping has shown that the animals preferentially walked along the ridges probably because the substrate was firmer and drier than in the pools. The troughs are fringed with falling



**FIGURE 20**—Fully-articulated curled-up *Diictodon* skeleton in a siltstone-filled burrow cast in the Leeukloof section.

water-level marks, wind induced adhesion warts and run-off rills attesting to slow infiltration of ponded water.

The sedimentology and taphonomy of distal floodplain deposits are indicative of very slow rates of sediment accretion on the shore and floor of ponds and lakes. Although the sedimentation was essentially episodic and therefore similar to the channel-bank and proximal floodplain, the paucity of bone indicates firstly that there were no biological bone-concentrating mechanisms operating (e.g., waterholes, middens, etc.), in fact the environment may have been inhospitable to many of the therapsids, and secondly that the long periods of unshaded exposure of bones in a saline environment caused severe weathering (Behrensmeyer, 1978). It is also possible that the bones were buried but failed to become fossilized because the soils in this part of the floodplain were for the most part too alkaline for the narrow range of pH conditions necessary for bone preservation (Pate et al., 1989).

## SUMMARY AND DISCUSSION

### Taphonomic Pathways

This study is aimed at reconstructing the post-mortem/ pre-burial history of the Hoedemaker fossils and gaining some insight into the physical and biological processes that affected them during this period. Detailed observations of some 329 *in situ* fossils and their host sediments has led to the recognition of 6 "taphonomic pathways" that bones took on their way to becoming fossilized (Fig. 21). These are summarized in Table 3 and below.

### *Taphonomic Pathway 1*

For most of the time the expansive Hoedemaker floodplains were dry. This allowed ample time for a scattering of skeletons of animals that died of sickness, old age or predation to decompose, disarticulate and start weathering. Mummified carcasses with straight or reflexed spinal

FIGURE 21—Taphonomic model for bone input into the Hoedemaker fluvial deposits. 1 = Disarticulated skeletons of animals that died of natural causes (i.e., old age, sickness and predation) and were embedded at death site to be subsequently buried by fluvial/aeolian deposits. 2 = Articulated and disarticulated but associated skeletons preserved in hibernation/estivation burrows. 3 = Sheet flood transportation of small post-cranial elements onto marginal playa area. Embayments in the lowstand lake margin becomes sites of bone accumulation under drought conditions. 4 = Recently drowned and previously mummified carcasses floating in the Mississippi-sized meandering rivers dropped bones into the thalweg gravels where they were broken and strongly abraded. 5 = Partially fossilized bones reworked from cut-bank collapses. 6 = Waterhole accumulation of predated and mired skeletons in and around swales and chute channels.

curvature commonly occurred on the surface, with desiccated skin and ligaments holding the ribs and lower jaw firmly in position. Periodically, the channel banks were overtopped or breached by floodwaters that were heavily laden with fine sand and silt. These sheet floods flowed off the meanderbelt rise, across the proximal floodplain into the distal playa lake. The smaller skeletal elements were entrained and transported further into the floodbasin whereas heavier and partially embedded bones were draped with a layer of fine sand and silt. Isolated skulls of *Diictodon,* being the largest single element of the skeleton and heavy enough to resist entrainment, are consequently commonly preserved in the proximal floodplain deposits.

### Taphonomic Pathway 2

Some of the *Diictodon* skeletons were buried inside their underground burrows. Very rarely a pair of fully-articulated intercurled or intertwined skeletons were entombed alive. A few of the burrow casts contain disarticulated but associated skeletons, more contain isolated and weathered bones but most are devoid of bone. Helical burrow casts of *Diamonelix* geometry are mostly hosted by proximal floodplain sediments and owe their preservation to being plugged by crevasse splay sands.

### Taphonomic Pathway 3

In the axial floodplain areas accretion rates were generally very slow except during unusually large overbank events where crevasse splays and distributary channels issued into the lake and dumped their traction load as small sub-lacustrine deltas. Individual post-cranial elements and a few mummified limbs were brought in by sheet floods and dropped on the lake margin. During the dry season the lake margin migrated to the level at which the water-table intersected the surface. At this stage shallow embayments in the saline lake margin were used as watering holes and became a focus of predation. They were also the site of death of the sick, the aged, and in drought periods, the thirsty. Some of these skeletons were trampled into the muddy substrate, others were held half-embedded in a desiccated salt crust. Subsequent highstands over a number of years gradually buried these skeletons but not before they had undergone considerable weathering.

Thus bones accumulated and were buried in the same embayments year after year. In the stratigraphic record these embayments would lie at the transition between proximal and distal floodplain deposits. This situation could account for the "clusters" of fossils in the transitional beds between proximal and distal floodplain facies of the Dunedin section.

## Taphonomic Pathway 4

Some of the animals that foraged on mid-channel sandbars in the major rivers were drowned during rising flood as the islands were inundated. Others died on the channel margins through normal attrition and their desiccated carcasses were picked up in the turbulent flow. As these carcasses were transported downstream they slowly disarticulated, dropping bones into the gravel lag that lined scour pools on the channel bed. After multiple winnowing and abrasion events these gravels, which mainly consisted of compacted and pedogenically cemented clay pebbles and calcareous glaebules derived from the bank alluvium, were buried beneath point-bar sands. The intraformational conglomerates of the Hoedemaker channels contain scattered broken and abraded bones (taphonomic class H) but no mass accumulations like those of the dinosaur-bearing Judith River Formation (Wood et al., 1988) and the Morrison Formation (Dodson et al., 1980).

## Taphonomic Pathway 5

Partially fossilized bones were reworked from collapsed cutbank alluvium as the meanders expanded and migrated. These bone fragments were added to the gravel lag accumulation along with rounded clods of compacted alluvium and calcareous glaebules winnowed out of the soil profiles in the collapsed bank material.

## Taphonomic Pathway 6

Fossils are very scarce in the bulk of the point-bar and levee deposits of the Hoedemaker meanderbelts, however some swales and chute channels in the upper point-bar and inner-bank levees of the Hoedemaker meanderbelts were sites of bone accumulation. The water in these ditch-like depressions was only replenished during flood events and was therefore susceptible to drying-up. Numerous disarticulated *Diictodon* skeletons accumulated in the muddy sediments in and around the shrinking waterhole, probably through predation. Their burial was possibly accelerated by larger animals trampling the skeletons into the soft substrate.

Behrensmeyer (1982) proposed a similar model for taphonomic processes of bone burial and reworking in fluvial channels. Her model is based on observations of carcasses in the East Fork River of Wyoming and Amboseli National Park in Kenya. Bone enters the East Fork River mainly through erosion of the banks which contain an attritional accumulation of vertebrate bones. Additional bones entered the river through overland transport off the banks and carcasses that died in the upstream channel. Bone input into the Hoedemaker fluvial system is essentially similar but with a different emphasis in that channel lag bone accumulations are not as common, or as rich, as those hosted by floodplain strata. Although bank erosion (5) and drifting carcasses (4) were certainly in operation to produce channel lags, they were not the main bone-concentrating mechanisms. These were on the flanking floodplains where attritional accumulations in calcic soils (1)

**TABLE 3**—Summary of bone input into the various Hoedemaker facies. Size of circle denotes the relative importance of each taphonomic pathway in generating the fossil assemblage of each facies.

| Facies | Taphonomic pathways |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Channel | | | | ● | ● | |
| | | | | | | ⬤ |
| Channel bank | ● | ● | | | | |
| Proximal floodplain | ⬤ | ● | | | | |
| | | | ⬤ | | | |
| Distal floodplain | ● | | | | | |

1—Disarticulated skeletons embedded at site of death, buried by vertically accreted alluvium.

2—Articulated and disarticulated skeletons preserved in underground burrows.

3—Articulated, disarticulated and transported small postcranial elements accumulated in embayments of the low-stand lake margin.

4—Carcasses of animals that died in the channel furrow, disarticulated during transport downstream and bones added to thalweg gravels.

5—Caliche encrusted bone reworked from cut bank collapse.

6—Waterhole accumulation in and around swales and chute channels.

and soil-hosted burrows (2) were buried by prograding crevasse splays. More restricted, predation derived accumulations occurred around waterholes on the margins of playas (3), and swales on top of point bars (6).

## Estimates of Floodplain Accretion Rates

Each of the 6 taphonomic pathways resulted in fossil suites that are taxonomically similar but taphonomically distinguishable by their relative abundance, disarticulation ratios, bone weathering ratios and sedimentology of the host sediments. Apart from indicating various floodplain environments the taphonomic suites each represent a time interval during which the bones accumulated on surface, became embedded, and finally buried.

Time resolution in alluvial sequences hinges on the ability to quantify the duration of breaks or "gaps" in the stratigraphic record. This has been successfully approached through the study of paleosols that formed during extended periods of non-deposition and therefore record time that is not otherwise represented in the rock record. Paleosol studies have led to the quantification of floodplain accretion rates (Allen, 1974a, b; Leeder, 1975; Bown and Kraus, 1981a; Atkinson, 1986) as well as the recognition of time-equivalent sedimentation (Behrensmeyer and Tauxe, 1982; Kraus and Bown, 1986). Combin-

ing pedogenic and taphonomic data from vertebrate-bearing alluvial paleosols enhances the environmental interpretation but does little to improve time resolution, which remains in the 1000–10,000 year interval (Bown and Kraus, 1981b; Behrensmeyer, 1982; Retallack, 1986). It appears that neither approach can confidently quantify periods of floodplain stasis of less than 5000 years (Behrensmeyer, 1982).

The present study is no exception. Although temporal information has been interpreted from sediments, paleosols and fossils, its resolution is still in the range of 1500–10,000 year time resolution. Taphonomic pathway 1 is the most useful fossil suite for these studies because it represents steady attritional accumulation of bones over a wide area of the floodplain. On this surface vertebrate skeletons are typically widely dispersed with a low density scattering of isolated bones in between (Behrensmeyer, 1978). At any one time, depending on weathering and burial rates, the surface bones may represent as little as a few years or as much as 100 years. If these bones are then buried by rapid sedimentation such as lacustrine transgression (taphonomic pathway 3) or crevasse splay progradation (taphonomic pathway 2) the resulting fossil suites may represent the shorter time intervals. However the normal floodplain accretion rates are slower and the resultant strata contain a liberal scattering of vertebrate bones but without any foci of concentration. The fact that such an attritional fossil suite is preserved in the proximal floodplain facies of the Hoedemaker member means that, at least locally, sedimentation rates were sufficient to curtail the bone-weathering processes before complete disintegration. Although there are many variables that can shorten the residence time of medium-sized bones on semiarid floodplains before they disintegrate, current research has shown that 15 years is a reasonable estimate (Behrensmeyer, 1978). Thus, an adult *Diictodon* skull lying unshaded on the proximal floodplain surface could not have withstood more than 15 years exposure and still remain intact.

The depth of sediment needed to completely bury an adult *Diictodon* skull depends on the attitude of the skull. Lateral-up skulls protrude on average 85 mm above the surface whereas the average height of dorsal-up skulls without lower jaws is only 42 mm. Thus the presence alone of numerous lateral-up *Diictodon* skulls in the proximal floodplain attritional assemblage would indicate a minimum rate of floodplain sedimentation of 5.6 mm/y. This is only averaged over 15 years and is therefore not necessarily the average rate of floodplain accretion.

In fact, within the proximal floodplain facies the lateral-up adult *Diictodon* skulls are either fairly "fresh" (weathering stages 1 and 2) or relatively weathered (stage 4, see Fig. 18) which suggests that there were two burial provinces, the former with an overall accretion rate of 14 mm/y and the latter with an accretion rate of 9 mm/y. Avulsion and crevasse splay progradation could have accounted for an increase in floodplain accretion in some parts of the proximal floodplain, especially in depressions flanking the meanderbelt rise (Smith et al., 1989).

Behrensmeyer (1982) demonstrated that there are methods of embedding bones during non-aggradational periods. These include litter accumulation, arthropod activity and vertebrate trampling into wetted soil. Locally, especially around waterholes, these were probably important but on most of the Hoedemaker floodplains incremental sedimentation was the major burial process.

The presence of mature calcic paleosols in the proximal floodplain strata of the Hoedemaker member (Smith, 1990) is a contradiction to the attritional fossil assemblages contained in them. Pedological interpretation of stasis-corrected floodplain accretion rates for 45 m Hoedemaker strata are in the order of 0.35 mm/y (Smith, 1989). This is based on an average of 10,000 years of non-deposition for each of 17 mature paleosol profiles (Reeves, 1970; Williams and Polach, 1971) and a compaction factor of 33% (Allen, 1986) during lithification of the original 60 m of alluvium. Although there are many sources of error in such calculations it is significant that the two methods should yield such different estimates. The favored explanation is that the Hoedemaker paleosols not only record a gradual reduction in floodplain accretion leading to preservation of an attritional fossil assemblage but they also represent long periods of floodplain stasis during which accretion rates were less than 5.6 mm/y which allowed time for bones to disintegrate before they could become buried.

Thus it seems that the Hoedemaker vertebrate fossils record variations in floodplain accretion rates down to a minimum of approximately 5.5 mm/y and that with lower accretion rates, at least in the proximal floodplain facies, paleosols are a better source of information regarding much longer periods of negligible deposition that punctuated the depositional history of the Hoedemaker member.

## CONCLUSIONS

This study has shown that each of the 3 floodplain facies that had been previously identified on sedimentological and pedological criteria within the Hoedemaker member can also be distinguished on taphonomic characteristics of their vertebrate fossils.

### CHANNEL BANK

Vertebrate fossils generally rare, 1 per 1135 m².

Skulls and isolated post-crania most common.

Mostly fresh (States 1–2) or slightly weathered (State 3).

Chute and swale fills contain more fully articulated skeletons and higher density of bone, 1 per 50 m².

Bone-bearing coprolites common.

### PROXIMAL FLOODPLAIN

Vertebrate fossils common, 1 per 67 m².

Wide range of taphonomic classes with relatively more articulated specimens.

Wide range of weathering stages although most are either fresh (State 2) or moderately weathered (State 4).

Transitional beds with distal floodplain characterized by clusters of *Diictodon* skulls with some articulated post-crania.

Rare fully-articulated curled-up and paired skeletons associated with burrows.

DISTAL FLOODPLAIN

Vertebrate fossils rare, 1 per 160 m².

Plant impressions relatively more common.

Mostly isolated post-cranial elements especially ribs and vertebrae.

Moderately weathered bone (States 3 and 4).

Vertebrate footprints rarely preserved.

The controlling factor influencing the taphonomic signature of each floodplain facies was the proximity of the burial site to the main channel and the effect this had on the frequency and intensity of floods and the local rate of sediment accretion. The former influenced disarticulation, transport and embedding whereas the latter determined "residence time" before burial.

Localized taphonomically anomalous fossil occurrences yield valuable paleoecological detail that is not evident in the sedimentary record. For example, there is evidence for the former presence of waterholes situated on inner bank levees, embayments in the distal playa margins, and underground burrows in the proximal floodplain areas.

Attritional assemblages of vertebrate fossils in the proximal floodplain mudrocks probably accumulated over 100–1000 year periods during which floodplain accretion rates rarely dropped below approximately 5.5 mm/y. The high preservation potential of these deposits suggests that they were laid down during avulsion events when vertical accretion was strongly enhanced as the fluvial system aggraded to re-attain its regional gradient.

Paleosols are commonly superimposed onto strata containing attritional assemblages. They record periods of floodplain stasis lasting from 5000–10,000 years when sediment accumulation in that part of the floodplain was considerably less than 5.5 mm/y, more in the order of 0.4 mm/y.

In conclusion, this study demonstrates the value of taphonomic analysis in providing corroborative or contradictory evidence to support or question the paleoenvironmental interpretation of fluvial facies and paleosols.

## ACKNOWLEDGMENTS

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