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TAPHONOMY AND PRESERVATION OF A MONOSPECIFIC TITANOTHERE ASSEMBLAGE FROM THE WASHAKIE FORMATION (LATE EOCENE), SOUTHERN WYOMING. AN ECOLOGICAL ACCIDENT IN THE FOSSIL RECORD

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Abstract

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More than twenty partial skeletons, all cf. *Mesatirhinus* sp., were discovered in overbank deposits associated with sandstone channels within the Adobe Town Member of the Washakie Formation (Washakie Basin, southwest Wyoming). Taphonomic and sedimentologic data indicate a mass mortality event with reduced post-mortem transport of the carcasses. Such a mass-death assemblage of a large mammal taxon is a rare occurrence for the Paleogene record. Accordingly, position and orientation of all the bones were recorded to make possible an accurate detailed map of the deposit. The remains principally include disarticulated skeletons of both sexes, from juveniles to old adult. Some axial portions and limbs remained articulated; others suggest partial articulation. The collected remains were scattered in loose associations within an area of about 7.5 × 9 m. Recent erosion (sheetwash) has destroyed an unknown extent of the original mass burial to the east and south of the excavation, but the 68 oriented bonebearing blocks collected represent about 50% of the exposed site.

The skeletal remains occurred within a single unit of poorly sorted but generally upward-fining quartz grit with a basal mudflake conglomerate. The bones are not abraded, but have suffered from severe compaction damage and recent freeze-thaw action. The sediment represents a mass flow accumulation deposited during the waning stages of a flash flood.

The large number of individuals of a single taxon suggests that part of a herd of titanotheres was killed in a single mass mortality event. The cause of death is not known, but it is likely that the accumulation represents a small fraction of a large herd that was crossing a flooded river. The carcasses drifted downstream to be left as a carcass jam on the flood plain as the floodwaters withdrew.

It follows that the assemblage represents a close approach to a single taxon slice from a terrestrial biocoenosis, and allows interpretations to be made about the autecology (social behavior, age composition and community structure) of titanotheres. Decomposition of the integument and other tissues of partially buried carcasses may have been a factor contributing to the "pockety" nature of the sediment.

Introduction

Large concentrations of vertebrate remains occur relatively frequently in the fossil record, but such concentrations can usually be attributed to reworking and other time condensing processes (Behrensmeyer, 1978; Damuth, 1982; Reif, 1982). Less frequently mass mortalities representing geologically instantaneous

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Attachment 31

events can also be represented by high concentrations of vertebrate remains but these may be difficult to recognize and their causes may be varied. Probably the most common vertebrate mass mortalities are those in which entire bedding planes are covered by fish, some of which may extend for many square meters, or even kilometers (McGrew, 1975; Grande, 1984). Such deposits may contain many millions of individuals, and are relatively easy to recognize as mass mortalities, although the cause of the event may not be obvious. Mass mortalities (mass death vs. mass accumulation) in terrestrial environments are rare occurrences in the first place, and are made rarer in the fossil record due to the generally erosive processes operating on land, and the continual reworking of fluvial sedimentary systems. Furthermore, when mass mortalities do occur on land, taphonomic processes such as scavenging (Voorhies, 1969; Coe, 1980), trampling (Behrensmeyer et al., 1979), weathering (Behrensmeyer, 1978) and other destructive processes (Toots, 1965) operate to obscure the event. Only in a few rapid depositional settings can mass deaths be preserved. On Africa's grassland plains mass mortalities of large herding vertebrates such as wildebeest are known to occur (Talbot and Talbot, 1963), but it is unlikely that such an event will be recorded as a true biocoenosis due to the action of the processes discussed above. It is possible that certain autochthonous bone accumulations may indicate a mass mortality.

It is important to be able to recognize mass death assemblages as they have the potential to yield information about community structure, herd composition, parental care, migration habits, and age structure of communities. Such behavioral activities cannot confidently be derived from single specimen or time averaged data sets.

The recognition of a mass mortality event should be based on sedimentologic and taphonomic criteria, as each on their own may be unreliable. It is essential that the degree of autochthony of the accumulation is confirmed. Monospecific accumulations, while not necessarily confirming mass mortality, are often an indication that little or no time condensing has taken place if the age composition of the assemblage comprises individuals of a range of ages. Taphonomic evidence such as the degree of articulation, and presence or absence of scavenging may also be important criteria.

Sedimentological criteria indicating rapidity of deposition are important. Mudflake conglomerates, poorly sorted sediment, armored clay balls and turbiditic sequences with basal scour marks may be used to indicate rapid sedimentation, and if found overlying bone accumulations may imply mass mortality. A general lack of reworked material including worn bones, teeth and shells is desirable. Bone accumulations in the bottoms of channels which lack articulation should be treated with caution when inferring mass mortality events. Accumulations of bones due to predator activity can usually be distinguished very readily by the variety of prey taxa and the presence of tooth marks and broken nature of the bones.

During the field season of 1970, a member of the field crew working with Turnbull discovered the partially disarticulated remains of part of a group of titanotheres (Mammalia, Perissodactyla), in badland topography of the central Washakie Basin (Fig.1A). The remains were excavated by Field Museum crews during the summers of 1970–1973 (Fig.1B).

Sufficient field data were collected with the specimens (position of bones, degree of articulation, sediment samples and associated fauna) for a taphonomic study of the site. This preliminary study covers the sedimentological and some of the biological aspects of the titanothere assemblage. The authors revisited the site in 1986 to check details of the microstratigraphy and collect further sediment samples. Criteria for recognizing rapid mass mortality events in terrestrial vertebrates will be discussed with respect to fluviatile sedimentary regimes.

Locality and stratigraphy

The Washakie Basin is both a topographic and structural basin situated in southwestern

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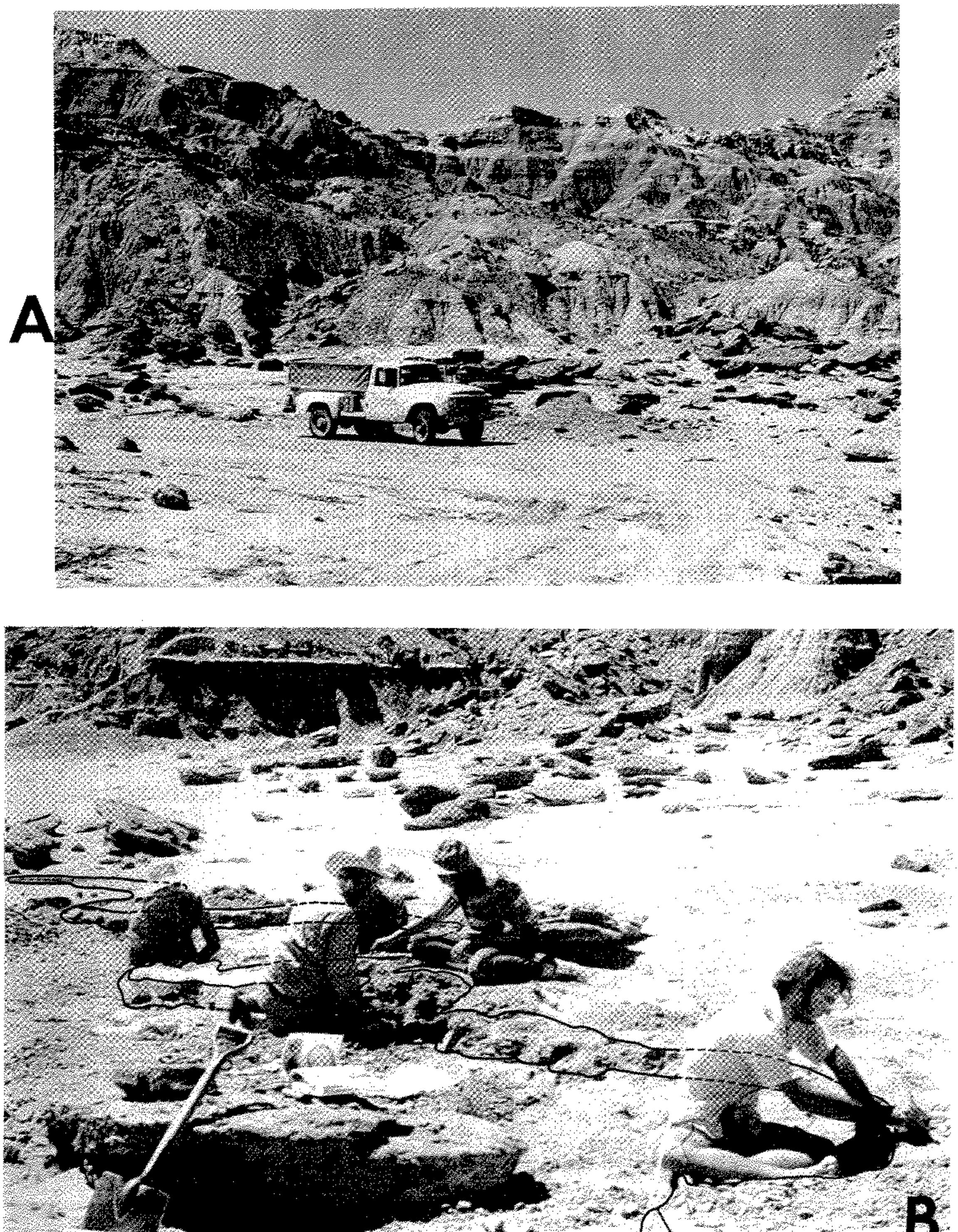

Fig.1A. Photograph of the titanothere site excavated in 1970–1973. B. Photograph of one of the field crews at work. Note the marked upper and lower limits of the unit containing the fossils.

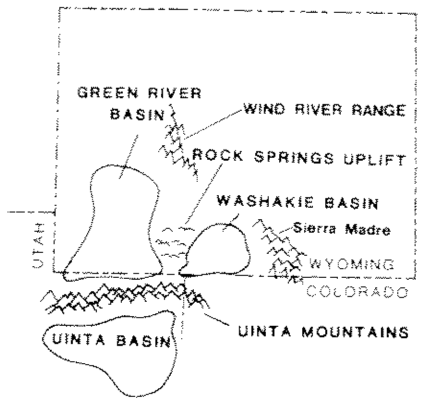

Fig.2. Sketch map of Wyoming outlining the position of the Washakie basin.

Wyoming, close to the Colorado state line, south of I-80, between Rock Springs and Rawlins (Fig.2). It comprises an area of approximately 6450 km^2 with elevations of between 1860–2650 m above sea level (Roehler, 1973a). The Washakie Basin is an intermontane basin with faulted boundaries between highs of the Uinta Mountains to the southwest, the Sierra Madres to the east and southeast, the Wind Rivers to the north-northwest, and the Rock Springs uplift to the west. (The Rock Springs uplift may not have been a positive block during Eocene times.) The basin received coarse clastic sediments from these structural highs, and also volcaniclastics from beyond the margins of the basin (Roehler, 1972).

During some of its history the basin was occupied by a freshwater lake (Lake Gosiute) in which wide deposition of oil shales took place. Most of these sediments comprise the Laney Member of the Green River Formation, but the dominant late Middle Eocene to Late Eocene sediments are of fluviatile and fault scarp fan facies type.

A complex lithostratigraphy of the terrestrial sediments in the basin has been established which essentially distinguishes fluviatile sequences from lacustrine deposits (Roehler, 1969, 1972, 1973a, b; Turnbull, 1978). The oldest Tertiary rocks in the basin, the Paleocene Fort Union Formation, outcrop near the margins. The great majority of the approximately 3660 m of Tertiary strata are of Eocene age. Rocks spanning the Early to Late Eocene are exposed on concentric rock-rims, the youngest located in the central portion of the basin.

There are two important terrestrial sedimentary sequences: the Washakie Formation above and the Wasatch Formation below, separated by the dominantly lacustrine Green River Formation (Fig.3). The Washakie Formation is divided into two members, a lower Kinney Rim Member (Twkk — 275 m), overlain with slight unconformity by the Adobe Town Member (Twka — 700 m), the latter comprising three subdivisions ($Twka_1$ = old Lower Washakie, $Twka_2$ = old Upper Washakie, and $Twka_3$, a previously unrecognized uppermost unit (Turnbull, 1978). The titanothere assemblage was discovered in the basal $Twka_2$ subdivision of the Adobe Town Member (Fig.3).

The precise age of the various members of the Washakie Formation is difficult to establish due to the lack of stratigraphically diagnostic fossils. However, paleomagnetic detail is beginning to improve this situation (Flynn, 1986). Systematic collecting of vertebrates by various workers (Turnbull, 1972; West et al., 1987) indicates a Middle to Late Eocene age for the Washakie Formation as a whole. The two members span the late Middle Eocene to Late Eocene and incorporate part of the Bridgerian (part of Bridger A–B and all of Bridger C–D), Uintan B and possibly Uintan C. The disconfirmity between the Kinney Rim and Adobe Town Members is thought to lie within Bridger C–D. The titanothere assemblage is therefore early Uintan in age (Late Eocene).

Vertebrate paleontology

By far the most abundant vertebrate macrofossils in the Washakie Formation are turtles, which at some horizons form an appreciable amount of the sediment. They may have been surpassed in number by fishes, whose remains are abundant but much less noticeable. Among the large mammals, titanotheres appear to be most common, several taxa being present, but screen washing of some horizons shows that rodents, condylarths, insectivores, primates,

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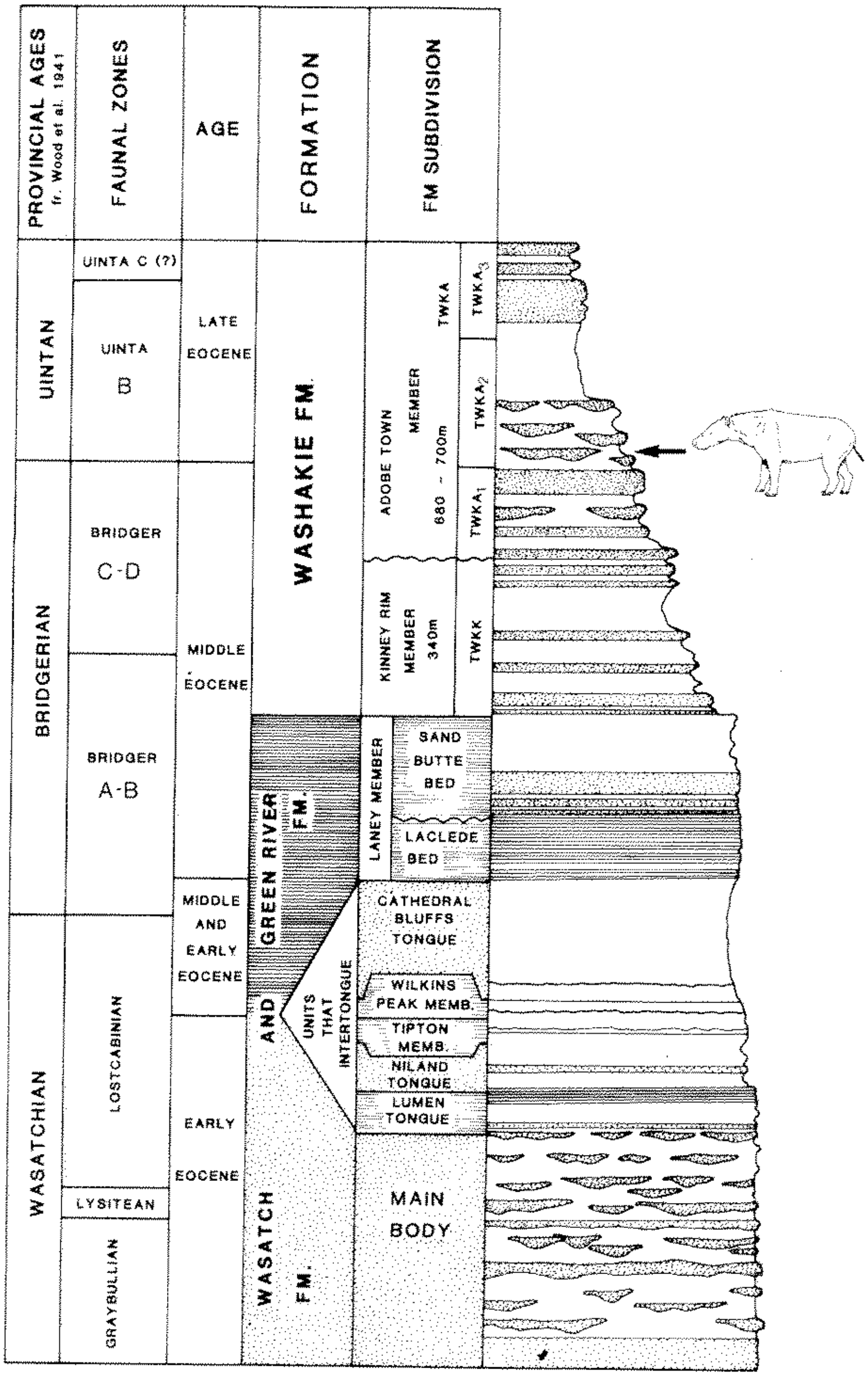

Fig.3. Stratigraphic section through the Tertiary sediments of the southwest portion of the Washakie basin, showing the estimated position of the titanothere site in the Adobe Town Member. Section after Roehler (1972).

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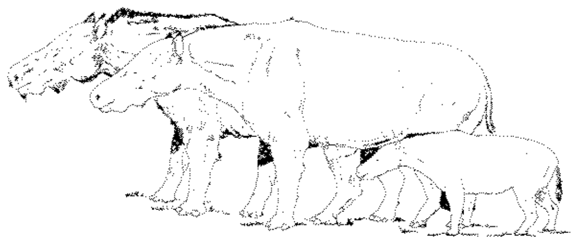


Fig.4. Reconstruction of the titanothere *Mesatirhinus* sp. based on Osborn (1929) illustrating yearling with mother and old individual.

carnivores and marsupials are also well represented. The apparent abundance of the titanotheres can be attributed to the greater visibility of their large remains. An extensive faunal list is given by Turnbull (1972) who lists no fewer than 35 mammalian taxa from the Washakie Formation from over 75 sites within the basin.

At the titanothere site reported here (loc. FM 12-70 WDT) the remains of some 24 (MNI, minimum number of individuals) titanotheres approximating to the genus *Mesatirhinus* Osborne (1929) were discovered in varying states of disarticulation (Fig.4). All of the remains come from within a single depositional horizon, a unit that varied in thickness from 10 to 30 cm at its thickest part (Fig.1B). No other taxa of the many known from the formation are represented, except for three isolated fragmentary specimens[1] of mammals, which we consider to have been deposited before the arrival of the titanotheres, and reworked during a flood event. One other associated specimen[2] clearly was float from a bed above the titanothere horizon.

Composition of the titanothere assemblage

The titanothere sample from the titanothere quarry falls within the expected range of morphological variation for a single taxon. To illustrate the point, we show bivariate plots for each of the lower cheek teeth. These include all specimens for which tooth position could be ascertained with certainty and excludes all others. Therefore the sample can be considered a monospecific assemblage (Fig.5).

Over 500 recognizable skeletal elements and thousands of bone and teeth fragments were recovered belonging to this one species, cf. *Mesatirhinus* sp.[3] As noted above, the sample includes 25 specimens of mandibles representing no fewer than 24 individuals. No other single element has a greater MNI count (Table I), but skulls and most postcranial elements are also well represented.

It is important to note that even though no fully articulated skeletons were found, a considerable proportion of the postcranial elements showed a degree of association (or even were in articulation) with one or more other element(s) (Table I). This means that there were sinew connections at the time of burial. In light of this we have not presented rose diagrams of bone orientation, since we do not believe that they would be meaningful with such a large proportion of the bones "tied together", and not able to orient freely and independently in response to the dynamics of the stream.

Age determination

The titanotheres, an extinct perissodactyl lineage, were similar in many ways to their living rhinocerotoid and equoid relatives. All have similar basic morphology and all tend to herd. *Mesatirhinus*, a small titanothere compared to its giant Oligocene horned relatives, was a hornless animal comparable in size and habitus to a small modern horse. It is well known that ungulate populations tend to have similar age structure, "with differences reflect-

[1]The recovered fragments are from an unidentified condylarth (PM 36008), a possible uintathere (PM 36023), and a paramyid rodent (uncatalogued). They are relatively more fragmented and rounded, and thus probably had been transported as isolated bones rather than carcasses.

[2]A tapir jaw (PM 28365) with P4–M-3 was found lying on the surface. It exhibits a style of preservation distinct from that of the titanotheres.

[3]No modern systematic treatment of the titanotheres exists. Assignment even to genus is uncertain since the types of many of the taxa are inadequate. Regardless of how the taxonomy is ultimately resolved, this species will be known from well defined and narrow dental and skeletal parameters.

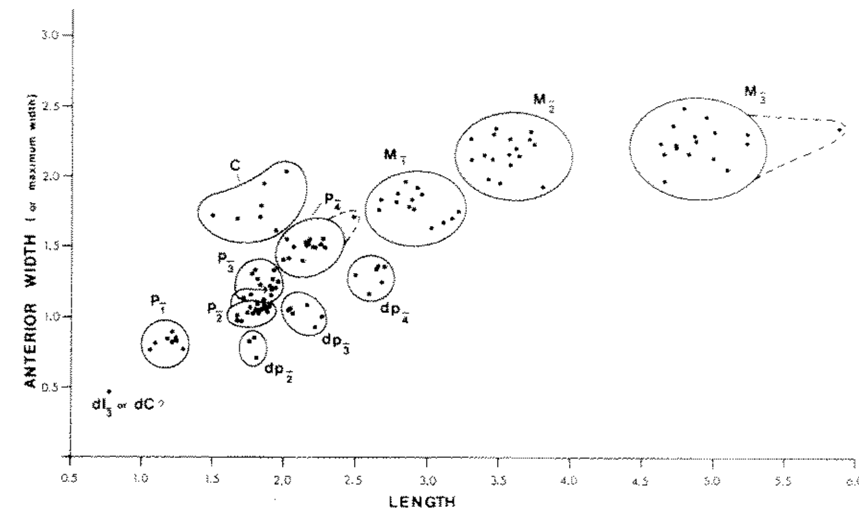


Fig.5. Plot of length/anterior width measurements in cm for teeth of lower jaws cf. *Mesatirhinus* sp. from the titanothere site. Most of the data group within the accepted range of variation for a biological species. One specimen accounts for the three exceptions (arrow for P/2, dashed extensions of the clouds of points for P/4 and M/3); its other teeth are all within their respective point clusters.

ing differences in body size" (Voorhies, 1969). Hence, the domestic horse model was chosen for the dental age-stage comparisons since it is well documented (Sisson and Grossman, 1975), and because there did not appear to be a reason for using the zebra model (Spinage, 1972) since it was not based upon known-age animals, nor did its crown-height measure of hypsodont teeth seem appropriate. We had considered using a rhino model (Goddard, 1970), but rejected it for several reasons: (1) size difference between the taxa are too great, (2) the rhinos Goddard studied have a reduced anterior dentition relative to that of *Mesatirhinus*, and (3) that sample had only a few known-age animals. We share the desire to achieve "even a rough approximation to a true chronological age-scale which can later be refined", this being more useful than relative ages. We have tried to determine age as closely as possible, based upon eruption, loss, and wear sequences as known for the domestic horse, with dentine exposure of crown cusps and crests being used for the advanced stages rather than to try to adapt the scale for hypsodont teeth to that for our low-crowned Mesatirhinus form.

All age classes beyond those with relatively firm markers such as eruption or replacement times are more or less arbitrary since they are based solely on dental wear, which with more time tends to produce more aberrant examples as well as simply more advanced overall wear (Fig.6). Detailed dental data are presented in Table II, and age-stage tabulations in Table III.

0–1 year old

Of the five young of the year animals, judged primarily by the degree of wear on the deciduous premolars, PM 35931 is at the youngest age stage, followed by PM 35928"B". Both were but a month or two old at most. PM 28359"A" has slightly more heavily worn dP/3-4's and was perhaps 3–4 or even 5 months old at death, as were PM 28014 (Fig.6A) and PM 30434 which have the P/1 formed, unerupted within their crypts. The latter specimen also preserves the left and right dI/3 (unerupted) and the right dI/1 (?) which apparently was erupted.

1–2 year old

No specimens in the one to two year old stage are represented by jaws with dentition.

TABLE I

Composition of the titanothere assemblage

Skulls:	7 complete + 6–8 palate, mx, pmx pieces and 8–10 cranial pieces	Total: 25 *MNI* ~ *20* individuals
Jaws:	25 that could be segregated as distinct specimens and 4 ramus/fgts, 1 coronoid fgt (and 1 hyoid)	Total: 30 *MNI* = *24* individuals

	Total	Isolated	Articulated or closely associated	% of total in association
vertebrae:				
atlas	5	3	2	40
axis	6	3	3	50
C^3–C^7	3	2	1	33
thoracics	36+	12	12 strings of 2–11 vert.	33+
lumbars	3	2	1	
sacrals	7	3	4 assoc. w/pelvis	57
caudals	3	3	—	0
indet.	22	11	11 assoc. w/humerus or ulna	50
ribs	70+	46	12 assoc. w/ 2–16 vertebrae	17+
scapulae	13	11	2 assoc. w/humerus or ulna	15
humerus	15	9	6 assoc. w/humerus and ulna or scapula	40
radius	20	6	14 assoc. w/humerus and ulna, or ulna	70
ulna	17	3	14 assoc. w/scapula, or humerus and radius, or radius	82
bones of carpus and manus	3	0	3 assoc. w/radius–ulna	100
pelvis (ilium, ischium, pubis)	9	6	3 assoc. w/sacrum or femur	33
femur	24	19	5 assoc. w/pelvis or tibia–fibula, also astragalus, sometimes patella and calc.	21
tibia	21	11	10 assoc. w/femur, fibula, etc. or w/fibula and patella or w/astrag. and calc., or w/fibula only	48
patella	24	20	4 assoc. w/femur and/or tibia and/or fibula, and/or astrag. and calc	16
astragalus	19	5	4 assoc. w/femur, tibia, fibula and calc., and 10 assoc. w/calc.	74
calcaneum	15	2	3 assoc. w/femur, tibia, fibula, etc. and 10 assoc. w/astragalus	87
bones of tarsus and pes	7	6	1 assoc. w/astrag. and calc.	14
indet. podials and metapodials and phalanges	54	35	19 in assoc. w/others	35

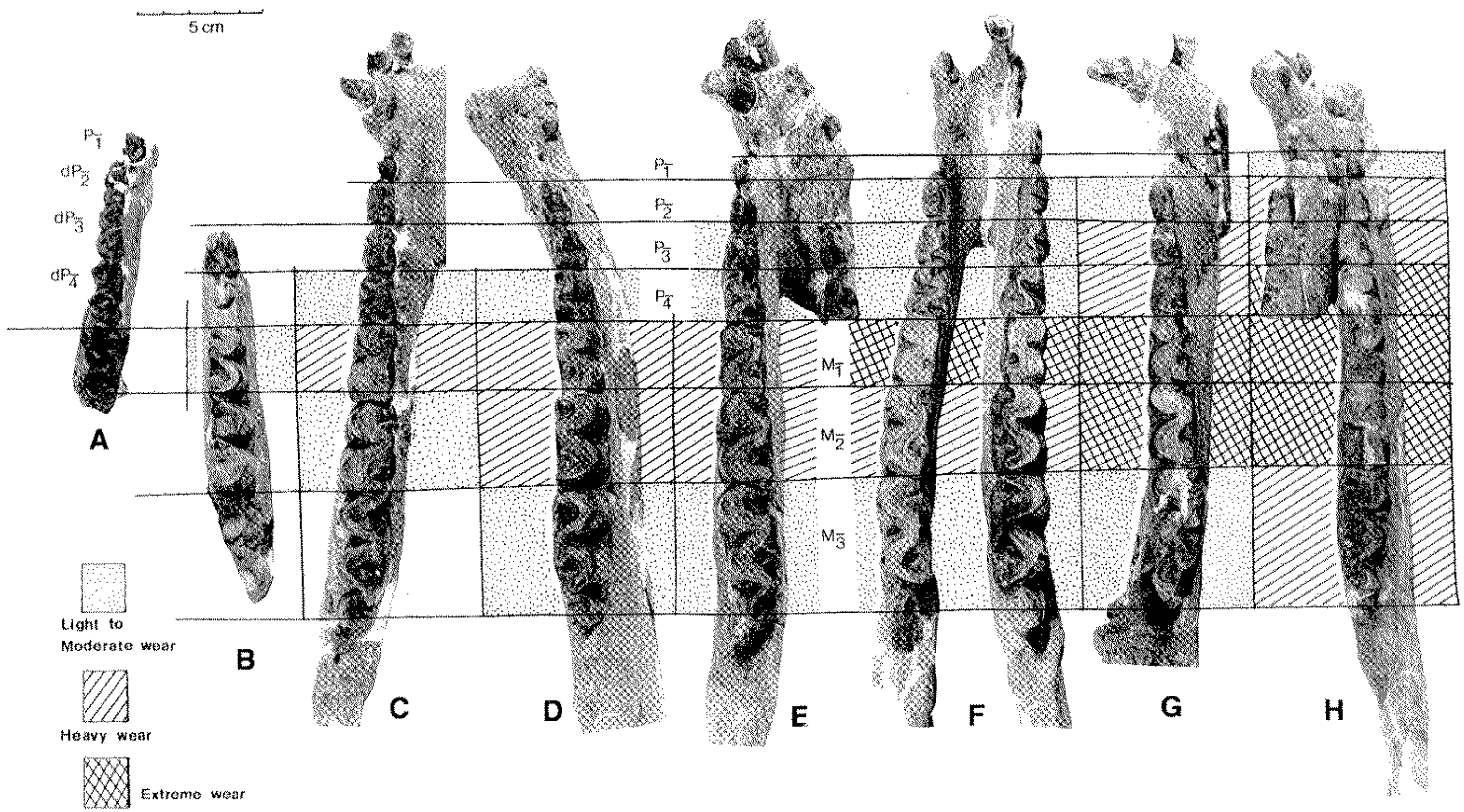


Fig.6. Wear pattern on cheek teeth of cf. *Mesatirhinus* sp. demonstrating the increasing degree of wear with age. A. PM 28014, one of the young of the year specimens. B. PM 35928A, a 2–3 year old. C. PM 28001, a 4–5 year old. D. PM 28007/PM 28359"C", a 6–7 year old. E. PM 28002, a 7–8 year old. F. PM 30422, an 8–10 year old. G. PM 35970, an 11–14 year old. H. PM 28004, a 15+ year old.

TABLE II

Characterization of age classes by dental eruption and wear, specimen by specimen

Specimen no.	Criteria and age estimate
PM 35931	M/1 formed, lying deep within crypt: no wear on dP/4; (P/4 formed within crypt beneath dP/4), only very slight wear on dP/2–3. Age 0–1 year (~2 months).
PM 35928"B"	M/1 in crypt; slight wear on dP/4; moderate wear on dP/2–3; L. dC (? or dI/3) in crypt. Age 0–1 year (~2 months).
PM 28014	M/1 deep within its crypt; slight wear on dP/4 (moderate on anterior lophid); dP/2–3 with moderate wear; P/1 within crypt Age 0–1 (3, 4 or 5 months).
PM 30434	M/1 in crypt; dP/4 with slight wear; dP/2–3 with moderate wear; P/1 in crypt; L. and R. dI/3 in crypts; R. I/1 (? or I/2) in crypt ? Age 0–1 (~3, 4 or 5 months).
PM 28359"A"	dP/4 with slight wear; dP/3 with moderate wear. Age 0–1 (~3, 4 or 5 months).
PM 35928"A"	M/1 with moderate wear; M/2 with slight wear; M/3 deep within crypt; dP/4 shed; P/4 beginning to erupt but still deep within crypt; P/3 nearly fully erupted and unworn. Age 2–3 years.
PM 28009/ 28359"B"	M/1 broken away; M/2 with slight to moderate wear; M/3 PM/2–4 erupted, trigonid with slight wear; P/2–4 in place, P/2–3 show beginning of wear and P/4 has slight wear. Age 3–4 years.
PM 30435	M/1 worn; M/2 moderate wear; M/3 slight wear; P/3–4 slight wear; P/2 and P/1 erupted, nearly unworn; dC shed, but no sign of C; R. and L. I/3 with slight wear; I/2 beginning wear; I/1s not preserved. Age 3–4 years.
PM 28359"D"	M/2 with moderate wear; M/3 slight wear. Age 4–5years.
PM 28001	M/1 worn; M/2 moderate wear to worn; M/3 slight wear; P/3–4 slight wear; P/1 unworn, P/2 slight wear; C erupting, already worn at tip; L. I/3 and L. and R. I/2 with slight wear. Age 4–5 years
PM 28010	M/1 worn; M/2 moderate wear to worn; M/3 slight wear; P/4 slight to moderate wear. Age 4–5 years.
PM 28343	M/1–2 worn; M/3 slight wear (but more than PM 28010); P/3–4 slight to moderate wear; P/2 slight wear. Age 5–6 years.
PM 28007/ 28359"C"	M/1–2 worn; M/3 moderate wear; P/3–4 moderate wear; P/2 PM slight to moderate wear; P/1 slight wear. Age 7–8 years.
PM 28003	M/1–2 worn; M/3 moderate wear; P/3–4 moderate wear; P/2 slight to moderate wear; P/1 shed. Age 7–8 years.
PM 28002	M/1 with heavy wear; M/2–3 worn; P/2–4 moderately worn to worn; P/1 slight wear; C worn. Age 7–8 years.
PM 28006	M/1 heavy wear; M/2–3 worn; P/2–4 moderate wear; C very worn (perhaps broken in life with subsequent wear). Age 8–10 years.
PM 28008	M/2–3 worn. Age 8–10 years.
PM 28342	M/1–2 with heavy wear; M/3 worn; P/3–4 worn; P/1–2 moderate wear. L. P/4 and M/1 have been shed, and the jaw appears to have been diseased. Age 8–10 years.

TABLE II (*continued*)

Specimen no.	Criteria and age estimate
PM 30422	M/1–2 with heavy wear; M/3 worn; P/2–4 worn; P/1 slight wear; I/1 worn. Age 8–10 years.
PM 28344	M/1–2 heavy wear; M/3 worn; P/2–4 worn; P/1 shed; C with long anterior and posterior wear facets. Age 8–10 years.
PM 35970	M/1 worn out (lingual side of trigonid breaking off); M/2–3 heavy wear; P/2–4 heavy wear; C with long deep anterior facet. Age 11–14 years.
PM 35996	M/1 nearly worn out; M/2–3 heavy wear (M/3 has abnormally heavy wear on the posterior lophid which is worn down into the root portion of the tooth); P/3–4 heavy wear; L. and R. P/2's are each worn, but in different manner; I/2–3 worn. Age 11–14 years
PM 35933	M/1–2 nearly worn out; M/3 heavy wear; P/2–4 heavy wear. Age 15+ years (~15 years).
PM 28004	M/1 worn out (lingual side of trigonid broken off); M/2–3 heavy wear; P/2–4 heavy wear; P/1 Moderate wear; C worn out (posterior facet truncated by the nearly flat horizontal anterior facet which is aligned with the I/3 crown remnant); I/2–3 worn out (crowns worn through). Age 15+.

2–3 year old

A single specimen. PM 35928"A" (Fig.6B) is the fragmentary jaw of a colt at age stage 2–3 years (on the horse scale) as indicated on the basis of eruption of M/2 which had functioned long enough to become slightly worn, and on the nearly complete eruption of P/3.

3–4 year old

Two specimens (PM 28009, PM 28359"B") probably from the same individual (therefore counted as one), and PM 30435 represent the 3–4 year old age stage. The premolars show increasing wear from P/2 to P/4. (This is distinct from the pattern in horses where P/4 is the last to erupt and the wear sequence decreases from P/2 to P/4.) However the eruption sequence is the same as in the horse (from front to rear) as can be seen in part from PM 35928"A" which has P/3 nearly fully erupted and P/4 still deep within its crypt. The M/3, which in *Equus* erupts at 3.5–4 years, had been in place long enough for slight wear to have developed on the crests. PM 30435 had I/2-3 functioning for long enough to show some wear, but although the dC had been shed, no permanent canine had appeared at the time of the animal's death.

4–5 year old

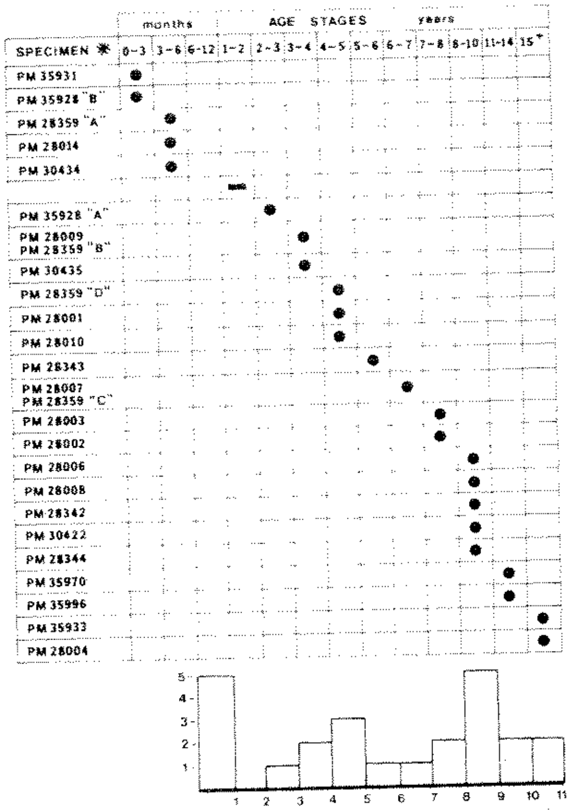
PM 28359"D", PM 28001 (Fig.6C) and PM 28010 represent three individuals in this age stage. Wear, especially on M/2, is moderate, with exposed dentin of trigonid and talonid connected on the labial sides of the metaconids. In PM 28001 the I/2-3 show slight wear, and the canines are nearly fully erupted with wear facets at their tips. In PM 28010 the right M/1 shows aberrant wear in that its labial side is nearly entirely worn away.

5–6 year old

One specimen, PM 28343, is arbitrarily placed in this group. Its general dental wear is

TABLE III

Age-stage tabulation for the mandibles upon which the MNI count is based. In the histogram summary the vertical axis gives number of individuals. Ages 0–8 are annular, 8–15+ lump several years together.



more advanced than that of the 4–5 year old age stage, yet is not as advanced as any of the rest of the individuals in the sample.

6–7 year old

This age stage is represented by a single individual, PM 28007/PM 28359"C" (Fig.6D), with a complete right mandibular ramus. The left ramus had disintegrated due to weathering leaving only broken tooth fragments. Assignment to this age stage is based on the greater degree of wear seen on P/2-M/3 than that seen on the specimen in the 5–6 year old age stage, and less than that seen on specimens assigned to the 7–8 year old age stage.

7–8 year old

Two specimens, PM 28003 and PM 28002 (Fig.6E), are from individuals with nearly equally worn cheek teeth. The first is slightly less worn than the latter and is perhaps a little younger, but for such minor differences considering the individual variation, it seems unnecessary to create a distinct age category.

8–10 year old

Five specimens are considered to fall within this age stage, PM 28006, PM 28008, PM 28342, PM 30422 (Fig.6F) and PM 28344. All have M/1-2 showing heavy wear with little of the original crown features remaining. There are noteworthy differences in the way the posterior lophid of M/3 wears, which can begin to be seen at this age stage. Usually there is an oblique facet inclined at about 45° on the antero-labial side. With increased age this often becomes more horizontal, and in PM 28342 the condition differs from side to side, the left remaining oblique, the right becoming more horizontal.

11–14 year old

Two specimens, PM 35970 (Fig.6G) and PM 35996, are assigned to this age stage. Their M/1's are worn to the gumline, or nearly so, and the M/3's are heavily worn. The latter specimen has its M/3's with differing degrees of advanced oblique wear on the posterior lophid. On the left side it was so extreme that a portion of the crown has worn away completely and the wear facet is deeply incised into the root of the tooth.

15+ year old

Two specimens, PM 35933 and PM 28004 (Fig.6H), are considered to be the oldest individuals and are categorized by having all teeth except P/1 very heavily worn so that the crown pattern has disappeared on M/1-2; lophids are recognizable, but deeply truncated on other teeth.

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Skeleton distribution

The excavated remains (those that can be considered in-situ) occur as dense groups of bones representing several individuals (Fig.7). Parts of the axial skeleton and some limb bones are associated, and show true bone to bone relationships, but no individual skeleton is entire. Most of the skeletons are disarticulated, and represent scattered skeletal elements. Transport has been in the order of only a few meters, and is probably attributable to scavenging. The general lack of abrasion of bone and the presence of articulated skeletal portions indicates that transport by fluvial agencies after or during decomposition has been minimal.

It is clear however that the bones have been scattered. Almost certainly this is due to the activities of scavengers, although there are no obvious signs of tooth marks on the bones, or evidence of crunched bone. The only

Fig.7. Plan of titanothere site showing distribution of the skeletal remains of at least 24 individuals of cf. *Mesatirhinus* sp. Cranial material is shaded black. The dotted area represents a sandstone body, the exact relationship of which remains uncertain.

significant post-mortem damage suffered by the bones is due to compaction caused by overburden pressure (we considered that this might be due to trampling, but it is restricted to less dense, non-permineralized bone). Hill (1980) has discussed post-mortem damage in Recent mammals and has demonstrated that under certain conditions carcasses may become stripped of flesh in a matter of days, and that bones are scattered due to the agencies of scavengers over a wide area. At the titanothere site bones are widely scattered, and only those elements that would have had strong ligaments during life retain any degree of articulation (e.g. vertebral column, limbs).

Sedimentology

The upper part of the Adobe Town Member ($Twka_2$ of Roehler, 1972) consists of gray, green, pink and lilac lacustrine and overbank clays with numerous fine- to coarse-grained fluviatile sandstone. Most of the sandstones were deposited in channels only a few tens of meters across, although some larger sandstone bodies occur. The majority of the channels have gently sloping margins and the downcutting relationship with the beds below is obvious. The titanothere assemblage occurs in a coarse clastic unit that is laterally impersistent, thinning out completely some one hundred meters from the fossil site. Down-

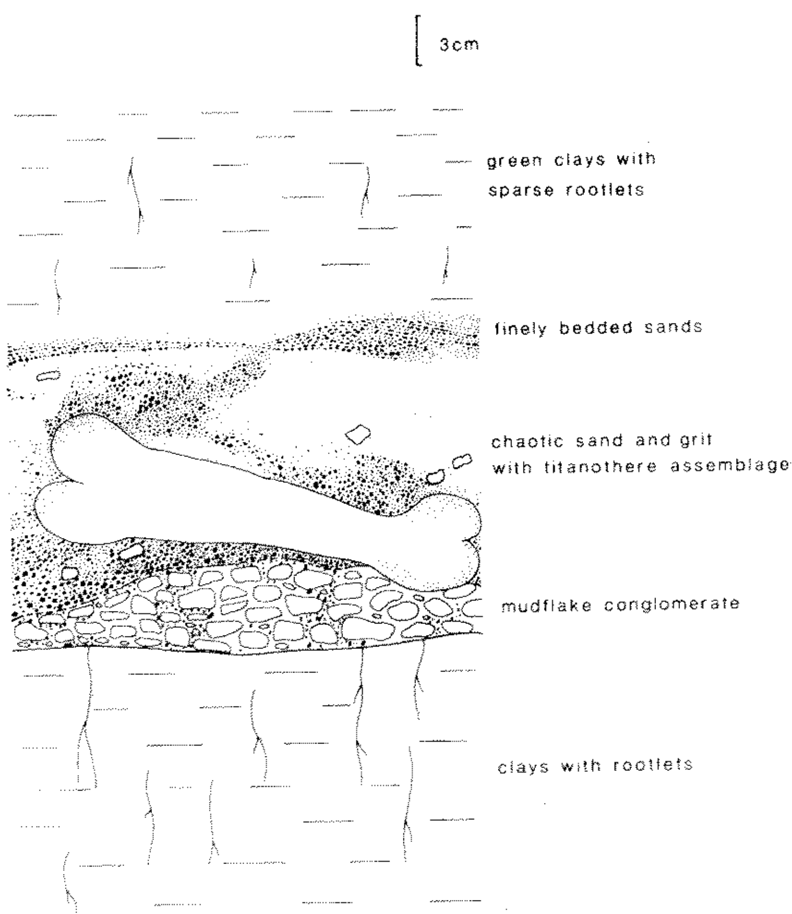

Fig.8. Schematic representation of the micro-stratigraphy of the titanothere site. Of particular note is the basal mudflake conglomerate, and the chaotic nature of the sands and grits enclosing the titanothere bones.

cutting of this unit is not obvious, although the base of the unit is erosive. This unit is distinct from all other coarse clastic units in the sequence in this respect, and in its complex internal sedimentary features.

The titanothere assemblage occurs towards the base of a thin lens of poorly sorted sand and grit lying on and partly within gray/green overbank mudstones (Fig.8). Oxidized rootlets are abundant in the mudstones of the unit below the lens, but are sparse in the bed above.

The sand lens is light purple and stands out conspicuously at the foot of a nearby butte. The interface of the sand lens with the bed below is sharp, and marked by the presence of a mudflake conglomerate of bright green mudstone clasts derived from the bed below (Fig.8). The mudflake conglomerate is 3–5 cm thick with subrounded and angular mudclasts generally 0.5–2 cm in diameter. The grit is rich in quartz and feldspar with lesser amounts of epidote. There is considerable iron staining towards the top of the lens. In some places limonite has cemented the grit, but in many areas the sand and grit are supported by a clay matrix. Generally the sand appears to fine upwards, but in the region of the titanotheres the sediment is a chaotic mixture of sand, grit and green and purple clays.

The poorly sorted nature of these sands and gravels is indicative of a flood deposit, but the chaotic nature might be explained as intense bioturbation caused by scavenging animals walking through wet sediment.

In one direction a thick unit (up to 50 cm seen) of medium to coarse current bedded sand represents the course of a (?) former channel (Fig.7). Due to obscure field relationships it is not possible to accurately determine whether this channel preceeded, or was coeval with the titanothere bed, or whether it cuts down through it.

Very little mineralization has taken place in cavities within the bone, resulting in many of the more trabecular bones such as limb bone articulations and vertebral centra being highly crushed due to compaction. The degree of compaction suggests that the unit may have been a great deal thicker than its present 30 cm maximum.

The sharp contact at the base of the unit and the presence of an angular mudflake conglomerate indicates rapid deposition from a high energy system, which in an intermontane basin is most likely to be a river in flood.

Taphonomic summary

Proposed sequence of events leading to present assemblage.

(1) Live herd comprising adults with yearlings, juveniles and old individuals of both sexes.

(2) Flood due to intense rain? in surrounding highlands.

(3) Accidental death of large number of titanotheres while crossing flooded stream.

(4) Drowned carcasses drift downstream in flood waters.

(5) Bloated carcasses drift onto inundated flood plain.

(6) Flood waters retreat leaving carcasses in chaotic pile, partly embedded in mud and sand mixture.

(7) Growth of vegetation around skeletons preventing further scattering and drying of bones in intense sun.

(8) Burial of skeletal elements by later flood plain deposits.

(9) Compaction of sediment with severe crushing of highly trabecular skeletal elements.

Discussion

Sedimentological data from the titanothere site shows that the titanothere sample was in a deposit representing an isolated event significantly different from that of the background environment. The remains occur in a flood deposit. The abundance and age range of the assemblage indicates that a herd or part of a herd of titanotheres containing young, juvenile, adult and old adult individuals were killed in a single event.

We propose that the herd was attempting to cross a stream in flood. Individuals of all ages, except two year olds, possibly foundered on slippery banks, either while leaving the flooded stream or due to pressure from other members of the herd while standing in close proximity to the bank. The presence of a mudflake conglomerate at the base of the flood deposit is possibly an indicator of widespread bank erosion and possibly failure. There is little evidence that the mudflakes are from dessicated ground. There are no large mudclasts to indicate local bank collapse, suggesting that if bank collapse was a contributing factor, it took place some distance upstream.

The floundering titanotheres drifted downstream until the channel became too shallow to carry them, and their carcasses were dumped. The carcasses may have formed a barrier in the river allowing sediment to build up around them, thus trapping them on the flood plain. As the carcasses decomposed and presumably were scavenged, the sediment was remobilized producing a chaotic mixture of sand, gravel and skeletal remains.

The absence of two year olds in the assemblage may reflect the vigor of young animals that were capable of escaping the flooded river, but could indicate a bad breeding year due to environmental factors, or may just be due to chance.

A mass death of many individuals of a herd, as opposed to the sporadic deaths of solitary individuals, is considered most likely based on the number of individuals of a single taxon, the lack of other large or small mammalian taxa or any other vertebrates, even though they are known to be present in the Adobe Town Member, and the generally associated nature of the assemblage. Although the assemblage represents a thanatocoenosis, we consider that a true biocoenosis of large terrestrial vertebrates is an exceptionally rare occurrence in the fossil record. The accumulation of large numbers of vertebrates killed in a single event and subject to minimal transport and reworking can be considered in the context of a biocoenosis and used to examine population structure and behavior in fossil vertebrates.

Ecological and evolutionary significance

One of the most important aims of paleontology is to construct the autecology of extinct organisms using whatever data are available. In many cases a lack of fossil material and of sedimentological data make this task difficult, resulting in very tentative conclusions. In this paper we conclude that *Mesatirhinus* was a herding animal that undertook journeys of unknown length as a herd. The herd was composed of most age stages from the very young to very old. This behavioral pattern is not uncommon among herd mammals today, but it is of evolutionary significance that this strategy appeared at least 45 million years ago, or even longer if the several similar monospecific assemblages of *Coryphodon* remains can be interpreted in this way. This raises the question whether this type of behavior evolved independently in several mammalian orders, or only once in a group of very early ungulates, perhaps as far back as the late Cretaceous, but was lost in some later groups.

In this case study we have examined the autecology of a monospecific assemblage using sedimentological and taphonomic criteria. Nevertheless, many of the conclusions remain tentative. Is this the best that the fossil record can offer? We have tried to think of geological mechanisms that can "freeze fram" life in the fossil record and leave a life history preserved. Only catastrophic events are able to do this in terrestrial environments. By far the most likely events are volcanic eruptions, which instantly bury populations of organisms in ash, or cave collapses, which may bury all or part of a family unit of cave dwellers (see discussion on bones in caves by Brain, 1980). In this situation ash or other material falls from above and transport of the population does not take place. But in most other geological situations transport of sediment is horizontal to sub-horizontal and often involves the transportation of any engulfed populations. As soon as transport takes place the record of community structure beings to erode, destroying the levels of confidence at which conclusions can be made about life histories.

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References

Behrensmeyer, A. K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4(2): 150–162.

Behrensmeyer, A. K., Western, D. and Dechant Boaz, D. E., 1979. New perspectives in vertebrate paleoecology from a Recent bone assemblage. Paleobiology, 5(1): 12–21.

Brain, C. K., 1980. Some criteria for recognition of bone-collecting agencies in African caves. In: A. K. Behrensmeyer and A. P. Hill (Editors), fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago, Ill., pp. 108–130.

Coe, M., 1980. The role of modern ecological studies in the reconstruction of paleoenvironments in sub-Saharan Africa. In: A. K. Behrensmeyer and A. P. Hill (Editors), Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago, Ill., pp. 59–71.

Damuth, J., 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology, 8(4): 434–446.

Flynn, J. J., 1986. Correlation and geochronology of Middle Eocene strata from the western United States. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 55: 335–406.

Goddard, J., 1970. Age criteria and vital statistics of a black rhinoceros population. *East Afr. Wildl. J.*, 8: 105–121.

Grande, L., 1984. Paleontology of the Green River Formation, with a review of the fish fauna. *Geol. Surv. Wyo., Bull.*, 63, 333 pp. (2nd ed.).

Hill, A. P., 1980. Early post-mortem damage to the remains of some contemporary East African mammals. In: A. K. Behrensmeyer and A. P. Hill (Editors), Fossils in the Making, Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press, Chicago, Ill., pp. 131–155.

McGrew, P. O., 1975. Taphonomy of Eocene fish from Fossil Basin, Wyoming. *Fieldiana*, 33(14): 257–270.

Osborne, H. F., 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geol. Surv. Monogr., 55, 953 pp. (2 vols.).

Reif, W.-E., 1982. Muschelkalk/Keuper bone-beds (Middle Triassic, SW-Germany) — storm condensation in a regressive cycle. In: G. Einsele and A. Seilacher (Editors), *Cyclic and Event Stratification*. Springer, Berlin, pp. 299–325.

Roehler, H. W., 1969. Stratigraphy and oil shale deposits of Eocene rocks in the Washakie Basin, Wyoming. In: *21st Field Conf. Tertiary Rocks of Wyoming, Wyo. Geol. Assoc. Guidebook*, pp. 197–206.

Roehler, H. W., 1972. A review of Eocene stratigraphy in the Washakie Basin. In: *Field Conf. Tertiary Biostratigr. Southern and Western Wyoming*, Garden City, N.Y., pp. 3–19.

Roehler, H. W., 1973a. Stratigraphy of the Washakie Formation in the Washakie Basin. Wyo. Geol. Surv. Bull., 1369: 1–40.

Roehler, H. W., 1973b. Stratigraphic divisions and geologic history of the Laney Member of the Green River Formation in the Washakie Basin in southwestern Wyoming. *Contrib. Stratigr. U.S. Geol. Surv. Bull.*, 1372E: E1–E28.

Sisson, S. and Grossman, J. D., 1975. The Anatomy of the Domestic Animals. Saunders, Philadelphia, 2 vols., pp. 1–2095 (5th ed. with R. Getty).

Spinage, C. A., 1972. Age estimation of the zebra. *East Afr. Wildl. J.*, 10: 273–277.

Talbot, L. M. and Talbot, M. H., 1963. The wildebeest in Western Masailand, East Africa. Wildl. Monogr., (12): 5–88.

Toots, H., 1965. Sequence of disarticulation in mammalian skeletons. Contrib. Geol., U. Wyo., 4(1): 37–39.

Turnbull, W. D., 1972. The Washakie Formation of Bridgerian-Uintan ages, and the related faunas. In: *Field Conf. Tertiary Biostratigr. Southern and Western Wyoming*, Garden City, N.Y., pp. 20–31.

Turnbull, W. D., 1978. The mammalian faunas of the Washakie formation, Eocene age, of southern Wyoming.