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TAPHONOMY OF A MIDDLE PENNSYLVANIAN MARINE VERTEBRATE ASSEMBLAGE AND AN ACTUALISTIC MODEL FOR MARINE ABRASION OF TEETH

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ABSTRACT

The taphonomy of assemblages of disarticulated remains of marine vertebrates is not well studied. Examination of a Middle Pennsylvanian chondrichthyan assemblage from Kohl's Ranch, Naco Formation, central Arizona, contributes to knowledge of such assemblages and reveals a complex taphonomic history. This vertebrate assemblage is restricted to two thin horizons associated with a concentration of disarticulated and tightly packed invertebrates. The vertebrate specimens are associated with phosphatic internal molds of molluscs and bryozoans. Most vertebrate specimens show abrasion. Several lines of evidence suggest that the specimens were abraded in a nearshore wave environment and subsequently transported offshore by a storm surge, where they were incorporated into an environmentally condensed assemblage. In particular, the presence of abrasion, a concentrated skeletal assemblage, significant amounts of siliciclastic sand, presence of intraclasts, phosphatic molds, and a basal lithologic discontinuity support this hypothesis; similar characteristics are found in many bone beds in the fossil record.

To test whether wave-dominated nearshore marine environments are capable of abrading vertebrate teeth, modern elasmobranch teeth (*Odontaspis* and *Myliobatis*) were placed in an experimentally simulated abrasive environment of fine siliciclastic sand. Results indicate that progressive degradation of specimens by abrasion and cracking occurs as the duration of abrasion increases. Abrasion occurs along the edges of both the crown and root, and cracking proliferates across the surface of the crown. These data confirm that wave-dominated marine environments can progressively abrade vertebrate teeth, and are consistent with the taphonomic hypothesis presented for the Kohl's Ranch vertebrate assemblage.

INTRODUCTION

A recently described Carboniferous (Moscovian stage, Middle Pennsylvanian) marine chondrichthyan assemblage from central Arizona (Elliott et al., 2004) represents an excellent case for studying marine vertebrate taphonomy of isolated remains. The Kohl's Ranch site preserves a diverse fauna represented predominantly by isolated teeth within a highly restricted stratigraphic sequence. This research describes the taphonomy of this assemblage and compares it to experimental results of abrasion of modern elasmobranch teeth. All specimens in this study (both fossil and modern) are deposited in the collections of the Museum of Northern Arizona (MNA), Flagstaff, Arizona.

The systematic study of taphonomic environments has blossomed in recent years. Nevertheless, large gaps in taphonomic knowledge remain, especially with respect to accumulations of marine vertebrates. Although significant attention has been paid to vertebrate preservation within marine fossil-Lagerstätten (e.g., Maples and Schultze, 1988; Schultze and Chorn, 1988; Schultze and Maples, 1992; Schultze et al., 1994; Schultze, 1995; Emslie et al., 1996; Kemp and Unwin, 1997; Brand et al., 2004) and bone beds (e.g., Wells, 1944; Conkin et al., 1973, 1976; Sykes, 1977; Antia and Whitaker, 1978; Antia, 1979; Reif, 1982; MacQuaker, 1994; Trueman and Benton, 1997; Martill, 1999), only isolated studies have investigated the taphonomy of more typical assemblages of disarticulated remains (e.g., Martill, 1985, 1991; Becker et al., 1996, 1998; Burris, 2001). Schäfer's pioneering work (1972) still remains the only study to develop actualistic models for marine vertebrate taphonomy.

GEOLOGY

The Kohl's Ranch site (Fig. 1) lies within the informally designated "Beta Member" of the Naco Formation in central Arizona (Brew, 1970; Brew and Beus, 1976). The locality is assigned a Desmoinesian (Moscovian) age on the basis of both fusulinid Foraminifera (Brew, 1970; Brew and Beus, 1976; Brew, 1979) and ostracodes (Lundin and Sumrall, 1999). The macrofaunal assemblages are also consistent with this assignment (Brew, 1979). At this locality, the Naco Formation is represented by interbedded fissile marine mudstones and limestones which are evidence for fluctuation of siliciclastic sedimentation rates, as recognized by Lundin and Sumrall (1999). Brew and Beus (1976) interpreted the paleoenvironment at Kohl's Ranch as being a quiet marine setting no more than 15–20 meters deep with some turbidity. A number of factors, including the alternation between carbonate and mudstone deposition, suggest that the environment was variable. In particular, there must have been periods of rapid siliciclastic sedimentation to preserve the articulated echinoderms at the site (Lundin and Sumrall, 1999). The ostracode record supports an interpretation of a periodically fluctuating, marine offshore depositional environment with possible storm events (Lundin and Sumrall, 1999).

The majority of the invertebrate macrofauna most closely resembles Taphofacies 5 of Speyer and Brett (1988), which suggests an environment with moderately high sedimentation, moderate turbulence, and oxic to dysoxic conditions. This interpretation is independently supported by the conspicuous absence of corals from Kohl's Ranch because corals generally do not tolerate environments with a high sediment load. It is also consistent with that seen for other marine shale environments in the Pennsylvanian mid-continent (Malinky and Heckel, 1998). Invertebrate specimens from the mudstones include both articulated and disarticulated echinoderms (e.g., Brew and Beus, 1976; Webster, 1981; Sumrall, 1992; Webster and Elliott, 2004), articulated brachiopods (Brew and Beus, 1976), well-preserved branching and fenestrate bryozoans, and articulated specimens of the bivalve *Myalina* (Brew and Beus, 1976). Thin carbonate lenses, similar to those described by Kreisa (1981) and interpreted to be minor storm deposits, contain abundant articulated brachiopods and *Myalina* bivalves. The thicker limestone sequences include a mix of disarticulated and articulated echinoderms and brachiopods. Although much of the invertebrate fauna indicates a turbulent, oxic to dysoxic environment with high sedimentation, the vertebrate assemblage provides a different taphonomic signal. Most vertebrate specimens, predominantly chondrichthyan teeth, display abrasion and breakage that suggests signif-

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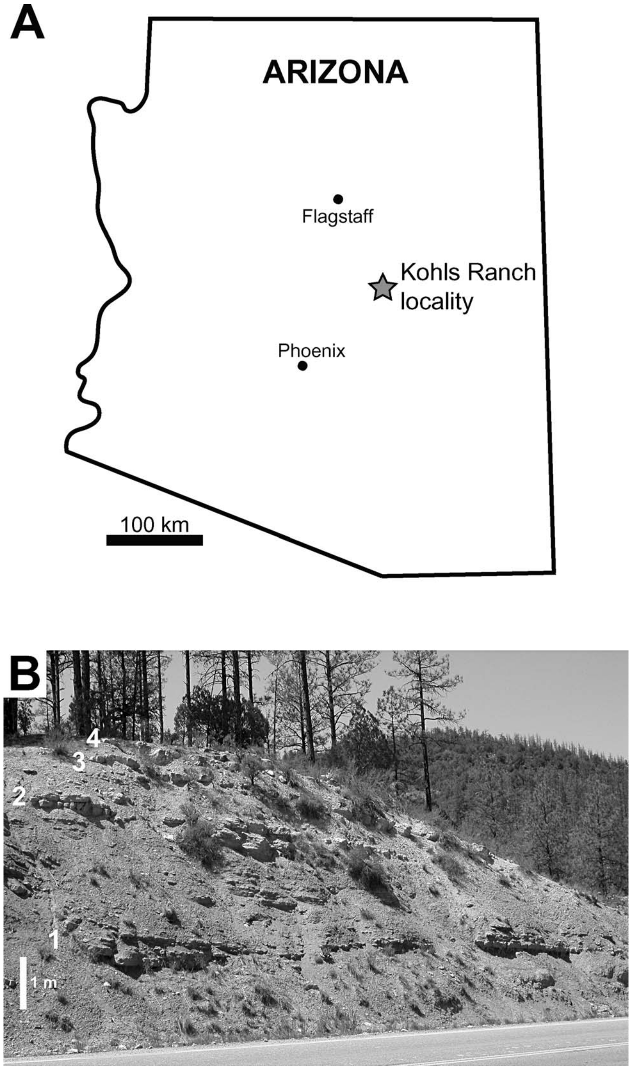

FIGURE 1—The Kohl's Ranch fossil locality. (A) Map displaying the location of the site in Arizona. (B) Photograph of the main outcrop of Naco Formation at the locality. Beds are numbered according to the sequence used in Figure 2. Scale bar equals 1 meter.

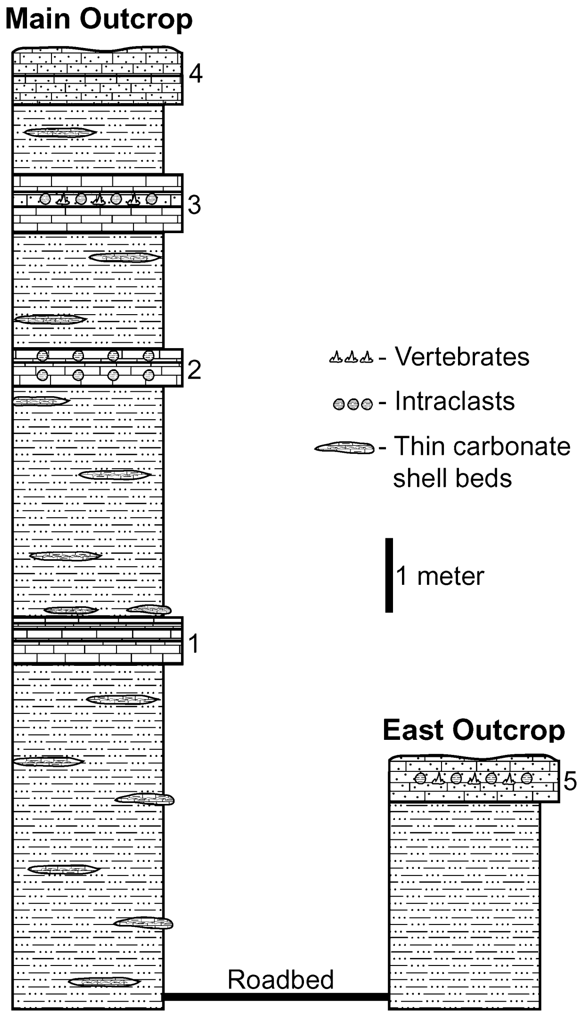

FIGURE 2—Geologic section of strata exposed at Kohl's Ranch.

icant transport prior to burial. Invertebrates associated with the vertebrate specimens include crinoids, brachiopods, and bryozoans, which are always disarticulated and tightly packed, sometimes broken, but not abraded, and have no consistent orientation. Additionally, phosphatic internal molds of a variety of gastropod and bivalve molluscs are very common, despite their absence from non-vertebrate-bearing layers. Together, the taphonomy and sedimentology of the vertebrate-bearing deposits supports a separate taphonomic history for the vertebrates.

Sedimentology

Two main outcrops exist on either side of State Highway 260. The main exposure, on the west side of the road (Figs. 1B and 2), crops out over 10 m of strata, with four exposed major limestone beds, informally referred to as limestones 1–4 in stratigraphic order, separated by thicker sequences of fissile mudstone. East of the road is a low exposure of mudstone capped by a single limestone designated as limestone 5 (Fig. 2). Vertebrate remains are found exclusively within and eroding out of limestones 3 and 5. These limestones are persistent throughout the outcrop, although they can change thickness, and it is unclear how laterally extensive they are. Thin, laterally restricted fossiliferous limestone layers containing articulated brachiopods, bivalves, and bryozoans that may be related to storm deposits (Kreisa, 1981) are also found within the mudstone units; however, these do not compare with the five major limestone beds mentioned earlier. Edrioasteroid specimens preserved on limestone surfaces and described from the Kohl's Ranch locality by Sumrall (1992) also probably derive from this facies. These thin layers are generally 2–3 cm thick and extend only 10–20 cm laterally. The brachiopods and bivalves are concentrated and generally show the same convex-up orientation. These thin limestones are interspersed within the mudstone units, and they are often common just above the major limestone beds. The mudstone units (Figs. 1 and 2) are nearly uniform in lithology; they are purple to gray, split into small shaly fragments 0.5–1 cm thick, and are often fossiliferous, containing abundant disarticulated echinoderms, articulated brachiopods, and less common articulated crinoid calices. No evidence of sedimentary structures such as burrows or flow indicators has been observed in the mudstone facies.

The sedimentology of the limestones 1–5 at the Kohl's Ranch site is of particular interest, because vertebrate remains have been recovered only from this lithology. To better understand the taphonomy of these vertebrates, the five limestones were examined petrographically (Fig. 3) to determine differences in sedimentology and depositional setting. It is notable that all limestones exhibited extensive diagenesis. All lithologies are classified using the schemes of both Folk (1959) and Dunham (1962).

Limestone 1.—This unit is 61 cm thick and displays internal bedding planes that get progressively closer together stratigraphically up section (Fig. 1). This bed is a fossiliferous micrite/wackestone (Fig. 3A). Skeletal allochems include abundant molluscs (mostly gastropods), fusulinid

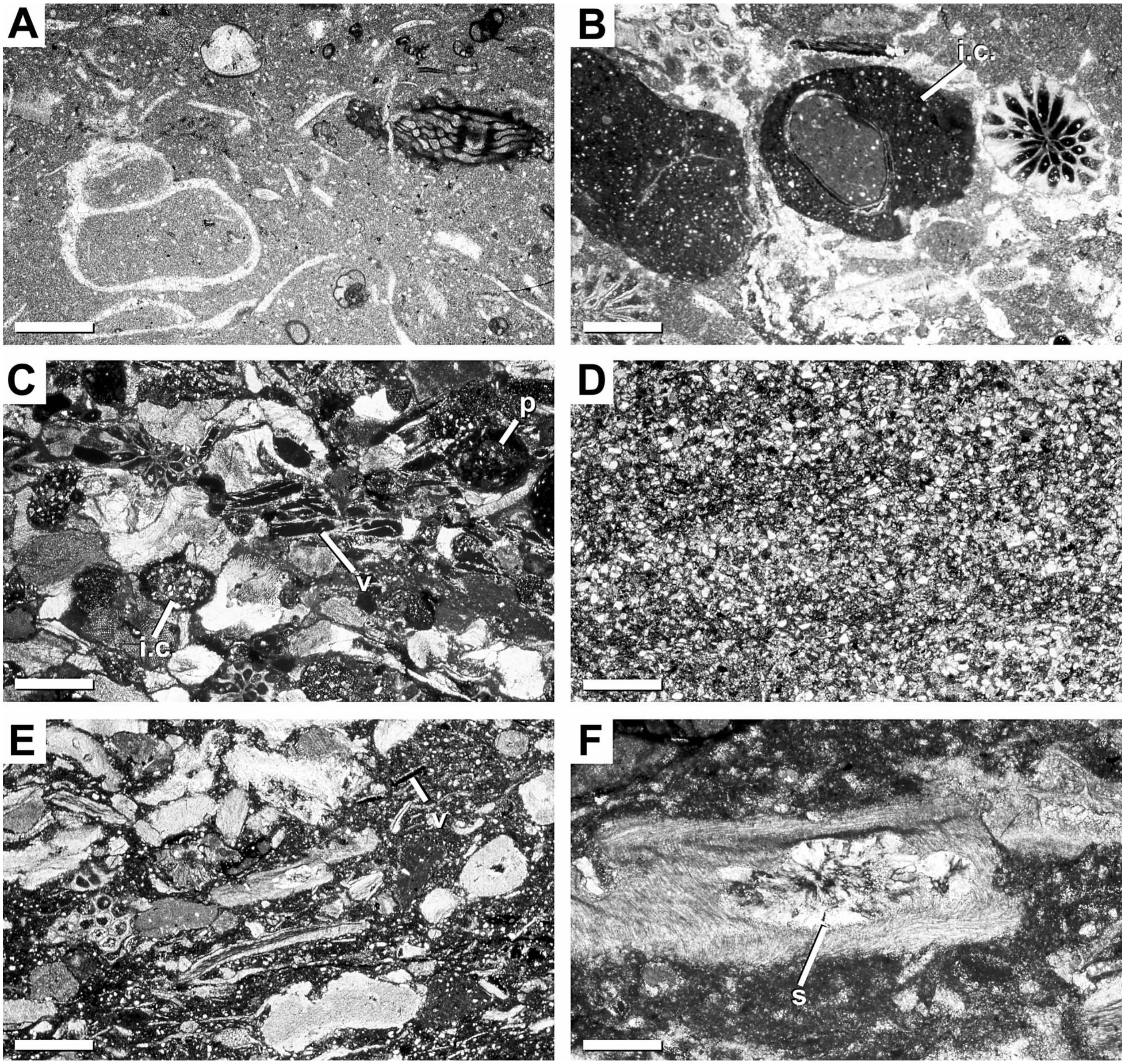

FIGURE 3—Thin sections of limestones from Kohl's Ranch locality. (A) Limestone 1. (B) Limestone 2; note brachiopod within micrite intraclast. (C) Limestone 3. (D) Limestone 4. (E) Limestone 5. (F) Partially silicified brachiopod in Limestone 5. All photos taken with crossed polars. Scale bars: A, B, E = 1000 μm; C, D = 500 μm; F = 200 μm. Abbreviations: i.c., intraclast; p, phosphate infilling; s, silicification; v, vertebrate remains.

Foraminifera, and less common brachiopods and echinoderms. The molluscan fossils are poorly defined; they are composed of recrystallized neomorphic blocky calcite spar (Fig. 3A). Echinoderm elements generally show an indistinct boundary with the surrounding cement and tend to exist in a patchy distribution of concentrated fossil lenses throughout the sample. Nonskeletal allochems are restricted to silt- to very fine sand-size angular to subangular monocrystalline quartz grains representing ~5% of the total composition. The carbonate matrix is micrite mud. On the whole, very little of the micrite has been diagenetically altered to neomorphic spar; however, some infillings of the fusulinids contain neomorphic textures.

Limestone 2.—Two main subhorizons of this layer, 30 cm and 16 cm thick, are separated by a distinct bedding plane at the outcrop scale (Fig. 1); both layers are lithologically identical. The lithology of this bed varies from a packed biomicrite/packstone to a micrite/mudstone because the distribution of allochems is not even and is concentrated in lenses, like limestone 1 (Fig. 3B). Skeletal allochems include brachiopods, molluscs, echinoderms, and both branching and fenestrate bryozoans. Nonskeletal allochems are represented by silt- to very fine sand-size, angular to subangular monocrystalline quartz grains, and micrite intraclasts that contain the same quartz grains (Fig. 3B). Thus, the intraclasts appear to have been derived from a local source. The matrix is micrite, which shows some diagenetic neomorphic spar. This sequence was compacted, and some fossils were fractured prior to cementation. Some brachiopod specimens show small areas of silicification. The morphology of silicification, concentric chalcedonic disks, conforms to Pattern IV of Schmitt and Boyd (1981), which suggests void-filling silicification. This implies that partial dissolution of the brachiopods occurred before deposition of silica.

Limestone 3.—This sequence is the sole vertebrate-bearing layer in the main outcrop. The complete bed is 76 cm thick; however, the vertebrates are concentrated within a 15 to 20 cm interval whose base is 30 cm from the top of the unit. This horizon is lithologically distinct from the rest of the limestone and is described here separately. It is classified as a fossiliferous packed biomicrite/packstone (Fig. 3C) with fossils aligned subparallel to bedding, except for the basal 6–7 mm of the unit, which is much less fossiliferous. Skeletal allochems are very dense and include echinoderms, bryozoans, brachiopods, phosphatic internal molds of molluscs (both bivalves and gastropods) and bryozoans, and vertebrates (Fig. 3C). Monocrystalline angular to subangular quartz grains and small amounts of mica, of silt to very fine sand size, constitute around 5% of the total composition. They are also included within the phosphatic mollusc and bryozoan internal molds. Micrite intraclasts are also present and appear to be derived from the underlying sediment lithology. The matrix is micrite mud. Extensive diagenesis is apparent, with dissolution textures on some echinoderms, and void-filling blocky calcite spar that sometimes forms syntaxial overgrowths on the echinoderms. Such diagenesis may indicate a movement from the stagnant zone to the active zone in the marine phreatic environment (Longman, 1980). The molluscs are represented only by the internal mold itself; dissolution has destroyed any trace of the original shells. A small amount of Pattern IV silicification also exists within brachiopods.

The other lithology found in limestone 3 is a virtually unfossiliferous micrite/mudstone occurring both above and below the vertebrate concentration. It does not contain vertebrates except for immediately adjacent to the vertebrate bearing layer, where some specimens are found, probably as a result of bioturbation. The contact with the vertebrate horizon is always sharp and distinct. What few skeletal allochems do exist include disarticulated brachiopods and echinoderms. The limestone is dominated by a micrite matrix, with some neomorphic diagenetic calcite spar.

Limestone 4.—This is the stratigraphically highest bed in the main outcrop and is 76 cm thick with a distinct bedding plane dividing the bed in half (Fig. 1). This unit is distinct in containing absolutely no fossils, and is a well-bedded micrite/wackestone (Fig. 3D). Nearly 40% of its composition is very fine sand-size angular to subangular monocrystalline quartz grains. Less common (~5%) are angular silt-size mica grains, with rare grains of angular plagioclase feldspar. Up to 10% of the rock is dark opaque grains that may be organics. The matrix is micrite, although much of that is now neomorphic calcite spar due to extensive diagenetic recrystallization.

Limestone 5.—This is the only exposed limestone in the eastern outcrop, and it is also the only other bed to contain vertebrates. Limestone 5 is 61 cm thick, but the top of the bed is also the top of the section and is truncated by modern erosion. Vertebrates are found in a restricted stratigraphic interval in the thin-section sample. The lower boundary of this vertebrate-bearing interval is distinct and marks a change in concentration of allochems, although it is unclear what the distribution of vertebrates is throughout the entire limestone bed. This limestone is a packed biomicrite/packstone. Skeletal allochems observed are brachiopods, molluscs, crinoids, bryozoans, and vertebrates (Fig. 3E). Again, subangular to subrounded silt to very fine sand-size monocrystalline quartz grains are present. The matrix is composed of micrite and shows some neomorphic spar. Many of the skeletal allochems are fractured and some show dissolution textures, indicating that compaction occurred before lithification. A small amount of Pattern IV silicification occurs in association with the brachiopods (Fig. 3F).

Discussion.—The relationship that exists between limestone 3 and limestone 5 is unclear. The two beds display similar lithologic textures, but are vertically disjunct. Both units contain vertebrates in a dense concentration of skeletal allochems with a fraction of quartz silt. The faunal composition of both the vertebrate and invertebrate assemblages for each of the limestones is identical. Shared diagenetic features include minor pattern IV silicification; however, limestone 5 does not display the same dissolution-reprecipitation diagenesis that is seen in limestone 3. Also, limestone 5 lacks mica grains and intraclasts. The lithologic and faunal similarities may indicate that the limestones are laterally equivalent but vertically displaced because many small faults exist in the area, and other workers have postulated that such a displacement occurs between the two outcrops (Lundin and Sumrall, 1999). Alternatively, and equally parsimonious, is that both beds share a similar depositional setting but are stratigraphically distinct and are not separated by any faulting.

Although each limestone bed is lithologically distinct, certain trends can be seen across all horizons. The most conspicuous commonality is the presence of silt- to sand-size quartz grains. These siliciclastics are sometimes associated with mica and even feldspar. It is certainly possible that their presence is due to subaqueous transport. The mica and quartz grains are highly angular, suggesting a local source during higher-energy regimes of subaqueous transport. Alternatively, the grains could be wind blown; early Permian loess deposits from Colorado display very similar qualities (Tramp et al., 2004). The base of this unit interfingers with the Minturn Formation, which is the same age as the Naco Formation and contains similar vertebrate and invertebrate faunas. Furthermore, paleowind data for western North America suggests predominantly northeast winds during the Desmoinesian, which would be ideal for blowing silt offshore from exposed granitic plutons (Soreghan et al., 2002). Given the size of the quartz and mica grains, long distance wind-blown transport of more than one or two kilometers seems unlikely. Therefore, it is more likely that these grains are a result of normal marine deposition.

Another feature found in all the limestones is extensive diagenesis, a common occurrence in shallow marine carbonates. The presence of neomorphic calcite spar most likely represents alteration of the micrite matrix from compaction and burial. Dissolution textures are observed in some of the beds, and this represents a momentary shift in water chemistry from deposition to dissolution, although the cause is unknown. The limited silicification observed in some limestones was probably associated with this shift because dissolution provides voids for silica infilling.

TAPHONOMIC OBSERVATIONS

Vertebrates are found only within a small thickness of limestones 3 and 5. Phosphatic internal molds of bivalve and gastropod molluscs and bryozoans are also restricted to only the vertebrate-bearing levels. The vertebrates and phosphatic molds are contained within a concentrated invertebrate hash composed predominantly of disarticulated crinoid debris. Vertebrate material recovered ranges in size from microscopic remains up to specimens with a maximum diameter of 2 cm, with very rare larger specimens of teeth of the holocephalian chondrichthyan *Deltodus*. Specimens are often missing their tooth bases, and are frequently broken and incomplete. For example, teeth of *Petalodus ohioensis* are found only as small fragments of the crown, although this may be due in large part to recent weathering, whereas complete specimens are known from elsewhere in the Naco Formation (Elliott et al., 2004). Although the majority of the studied specimens were recovered from screenwashing and surface collection of weathered sediment, examination of *in situ* specimens in thin section confirms that the incomplete nature of the vertebrates was present before recent weathering. Figure 4 shows a tooth of *Deltodus angularis* in thin section displaying an incomplete base and abraded edges. Acid dissolution of *in situ* blocks of vertebrate-bearing limestone with dilute acetic acid was unsuccessful because most of the vertebrate specimens fractured into unidentifiable fragments; however, specimens found *in situ* on the surface of the limestones and in thin section (Fig. 4) have abrasion patterns consistent with those collected loose.

The most striking feature of this vertebrate assemblage is the predominance of abrasion (Figs. 5 and 6), in contrast to the lack of observable abrasion on specimens from the invertebrate hash and phosphatic internal molds. All vertebrate specimens show some sort of wear; some are so abraded that they are now subspherical bone pebbles that preclude identification (e.g., Fig. 5B). In many areas, the enameloid has been removed, exposing the underlying dentine tubules (Fig. 6B, C). The effects observed clearly represent abrasion as opposed to corrosion, inasmuch as rounded surfaces are polished and do not correspond to the observed effects of corrosion (e.g., Denys, 2001: fig. 3.1.8.5). To quantify the state of abrasion, the collection of *Glikmanius occidentalis* (Ginter et al., 2005) from the site was classified using the abrasion stages of Fiorillo (1988) as modified by Cook (1995). *Glikmanius occidentalis* was selected because it is a common vertebrate species from Kohl's Ranch and has

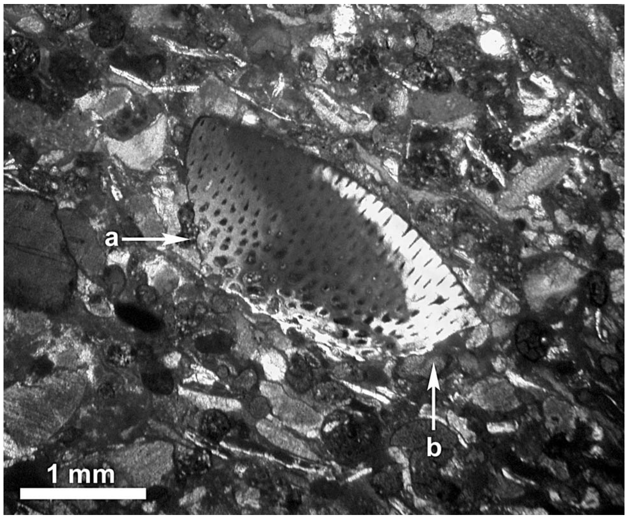

FIGURE 4—Specimen of *Deltodus angularis* in thin section showing abraded (a) and broken (b) surfaces. Photographed under crossed polars.

several cusps and processes that make it straightforward to evaluate abrasion. Also, it is generally easily identifiable from incomplete and highly abraded specimens. Although more common, *Deltodus angularis* was not used because its naturally rounded morphology makes it difficult to quantify abrasion. It is possible that a slight collection bias exists in favor of larger and more complete specimens because part of this collection was accumulated via surface collection. This should not seriously skew the abrasion data because it produces conservative results in favor of the null hypothesis of no abrasion.

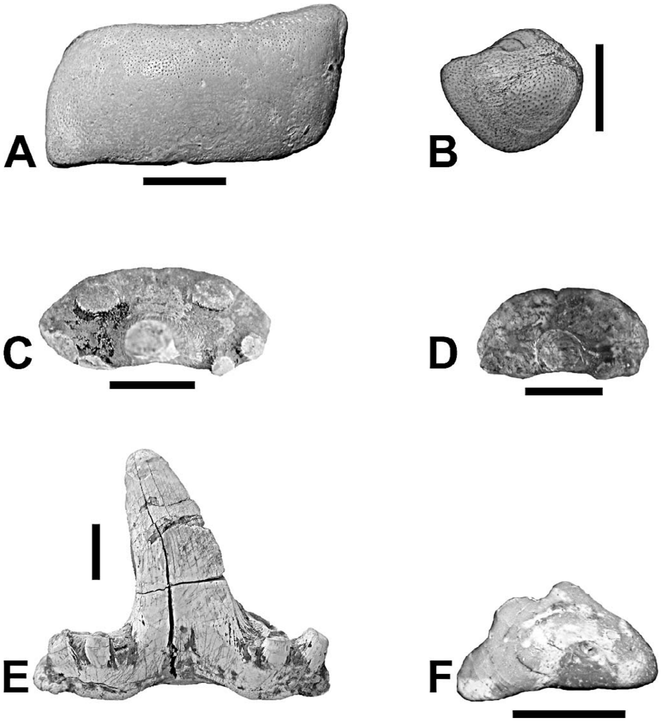

FIGURE 5—Examples of natural abrasion exhibited by chondrichthyan teeth from Kohl's Ranch. (A–B) *Lagarodus angustus*; (C–F) *Glikmanius occidentalis*. (A) Occlusal view (MNA V9404); (B) occlusal view (MNA V9940); (C) occlusal view (MNA V9416); (D) occlusal view (MNA V9941); (E) labial view (MNA V4714); (F) labial view (MNA V9942). A, C, and E are relatively unabraded and complete, whereas B, D, and F are severely abraded. Scale bars = 0.5 cm.

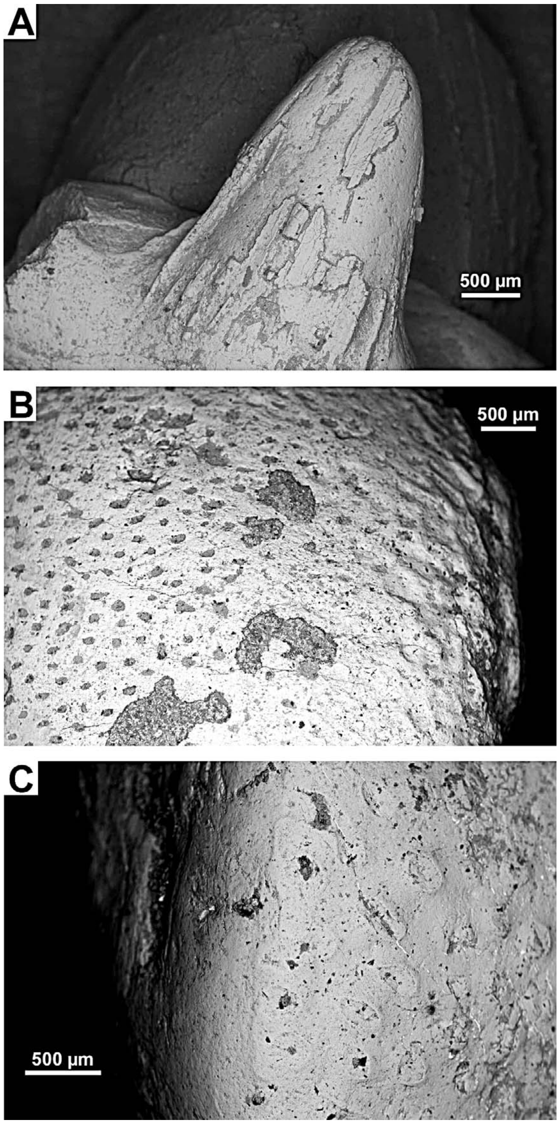

FIGURE 6—Abrasion on chondrichthyan teeth under scanning electron microscopy. (A) Main cusp of *Glikmanius occidentalis* (MNA V10118); (B) occlusal surface of *Lagarodus angustus* (MNA V4715) with exposed dentine tubules; (C) edge of *L. angustus* "bone pebble" (MNA V9940) displaying rounded and abraded surface, and exposed dentine tubules.

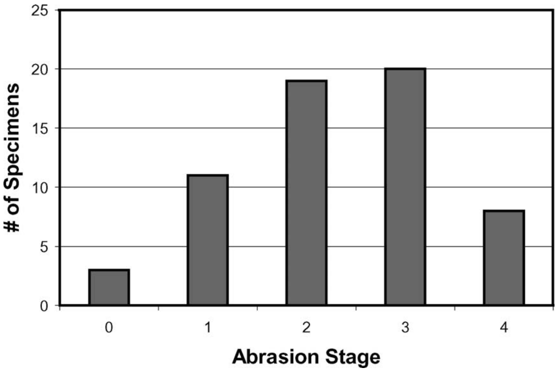

FIGURE 7—Graph showing distribution of abrasion stages (Fiorillo, 1988) in specimens of *Glikmanius occidentalis*.

It is clear from the abrasion data (Fig. 7) that a majority of the teeth (73%) show significant abrasion (Stages 2, 3, or 4). In fact, these data are probably conservative, because many extremely rounded specimens that form bone pebbles (Stage 4) are not identifiable as any particular taxon and cannot be included, although some most likely belong to *G. occidentalis*. This distribution of abraded specimens from Kohl's Ranch matches distributions seen for other vertebrate assemblages that reflect allochthonous transport signals (Cook, 1995).

The vertebrate specimens from Kohl's Ranch display significant abrasion that is not observed in the invertebrate assemblages from the site. Therefore, it is probable that their taphonomic history is different from that of the invertebrate assemblage. In particular, it is hypothesized that vertebrates were transported from a nearshore environment and deposited at the Kohl's Ranch site, on the basis of the extensive tooth abrasion and stratigraphically and sedimentologically restricted occurrence of the chondrichthyan specimens. Physical weathering from subaerial exposure or chemical weathering from prolonged exposure on the sea floor could also affect the rates of abrasion of these teeth, potentially allowing them to be abraded in place rather than through transport. Preliminary experimental work suggests that weathered bone abrades much more quickly than fresh bone (Fernández-Jalvo and Andrews, 2003). Geochemical diagenesis begins soon after deposition of vertebrate specimens (Trueman et al., 2003) and could structurally weaken the vertebrate remains to abrasion. It is difficult to directly assess if either of these possibilities occurred in the case of the Kohl's Ranch specimens. Nevertheless, the fact that all the vertebrate specimens are found in only two sedimentologically unique and stratigraphically thin layers supports a separate taphonomic history for the vertebrates.

In addition to abrasion, bioerosion is often a significant cause of taphonomic damage to specimens prior to burial. Endobionts remove material from specimens pre-, peri-, and post-mortem. Not only does bioerosion directly destroy material, but it also weakens the structural integrity of the fossil, causing accelerated rates of abrasion (Davis, 1996). Although a broad survey of fossil vertebrate specimens suggests that the level of bioerosion is generally low in the fossil record (Trueman and Martill, 2002), bioerosion of marine vertebrate specimens is often significant (Antia, 1979; Davis, 1997; Underwood et al., 1999a). Bioerosion of fossil marine vertebrate specimens is known at least as far back as the Silurian (Antia and Whitaker, 1978; Antia, 1979) and throughout the later Paleozoic (Bystrov, 1956, 1959; Goujet and Locquin, 1979), and is very common in Mesozoic marine vertebrate assemblages (e.g., Bystrov, 1956; Martill, 1989; Underwood et al., 1999a, 1999b; Underwood and Rees, 2002; Underwood, 2004; Underwood and Ward, 2004a, 2004b); it is also known from Neogene marine assemblages (Underwood and Mitchell, 2003). Therefore, it would not be surprising to observe bioerosion of the vertebrate specimens from Kohl's Ranch. Examination of vertebrates in hand sample, thin section, under stereomicroscope, and using scanning electron microscopy (SEM) yielded no evidence of bioerosion (Fig. 6). This was unexpected because invertebrates from the site, especially brachiopods, display a wide diversity of epibionts and endobionts that colonized their hosts both during life and after death (Sumrall, 1992; Lescinsky, 1997; Dyer and Elliott, 2003). Some of the endobiont traces on Kohl's Ranch brachiopods include ramifying networks of borings (Dyer and Elliott, 2003) very similar to those described for Mesozoic marine vertebrate teeth (Martill, 1989; Underwood et al., 1999a), yet they are absent from the chondrichthyan teeth. The lack of evidence for bioerosion of vertebrate specimens and the common bioerosion of invertebrate assemblages is additional evidence for a separate taphonomic history for the vertebrates.

EXPERIMENTAL ABRASION OF MODERN TEETH

To test the effect of nearshore marine abrasion on chondrichthyan teeth, an experiment was devised that approximates these conditions. Most previous studies of vertebrate abrasion have focused on the fluvial environment. Argast et al. (1987) abraded fossil theropod dinosaur teeth in a tumbler with sand and concluded that significant transport did not have a measurable effect on the teeth. The results of Argast et al.'s (1987) experiment are limited in their applicability because fossil teeth rather than modern examples were used, and a tumbler is not the preferred analogue for a river system. In response to Argast et al. (1987), Ely and Rigby (1989) and Ely (1995) placed modern crocodylian teeth in a racetrack flume with traction and saltation loads of sand. They found that progressive abrasion and degradation of the teeth was apparent, indicating that it is possible to abrade teeth in a fluvial setting. Unfortunately, these studies are published only as abstracts, and the data have yet to be published. Fernández-Jalvo and Andrews (2003) abraded both modern and fossil bone in a tumbler under a variety of initial conditions and using a variety of sediment sizes. They concluded that abrasion was always observed but that its extent depended on the initial condition of the bone (fresh, dry, weathered, or fossil) and sediment size. Generally, larger grain size increased abrasion intensity, and weathered and fossil bone abraded more quickly than fresh or dry bone. This study did not consider vertebrate teeth. Furthermore, all of these studies focused on fluvial environments, an inappropriate analogue for vertebrates from a marine setting. Therefore, an experiment was conducted targeting the taphonomy of vertebrate teeth in a marine wave-dominated setting to determine whether prolonged abrasion left identifiable characteristics on tooth specimens.

Experimental Materials and Methods

Modern elasmobranch teeth were selected for abrasion because they are the closest living relatives to fossil chondrichthyans and therefore have a similar dental composition. Modern specimens were used because diagenesis (especially permineralization) could alter the mechanical properties and thus reaction to abrasion of fossil specimens. Secondly, the two specific taxa used in this study have morphologies that are analogous to those from Kohl's Ranch. Two dried modern teeth from *Odontaspis ferox* (MNA V9951–9952) (Compagno, 2001) and seven teeth from *Myliobatis* sp. (MNA V9944–9950) were used for the experiment. The general shape of the *Odontaspis* teeth is very similar to that of *Glikmanius occidentalis*, a common taxon from the study site (Elliott et al., 2004). The *Myliobatis* teeth represented two morphologies: elongate symphysial teeth very similar to those of *Lagarodus angustus*, and small polygonal lateral teeth that are reasonable analogues for a variety of smaller teeth from Kohl's Ranch.

A fixed-speed Eberbach 6010 reciprocal shaker was used for the experiment because its back-and-forth movement approximates that of waves in a shallow marine environment. The tub placed in the agitator was filled with 1350 ml of fine arkosic sand that is analogous to nearshore sand in the Pennsylvanian of Arizona (R. Blakey, personal communication, 2004) and 900 ml of marine saltwater. The mixture, including teeth, was covered with plastic wrap to prevent evaporation, and the experiment run in 100-hour cycles at a speed of 180 agitations per minute for a total of 1000 hours. After each cycle, the teeth were removed from the mixture, rinsed with fresh water to remove sand, and dried on a hotplate at 38°C for 24 hours. The teeth were then weighed using an electronic scale and digitally photographed in several views. Typically, before restarting the experiment, 75–200 mL of fresh water was added to compensate for unpreventable evaporation so that the consistency of the mixture remained constant.

Argast et al. (1987) also weighed their teeth at specific intervals; however, they noted no significant change in weight. They postulated that this was partially a result of sand lodging in cracks and crevices within the teeth. Although the weights of the teeth in this study generally show a downward trend (Table 1), large fluctuations are noticeable, and it is hypothesized that this results from a variety of factors, including lodging of sand grains within crevices, deposition of salt crystals within the teeth, and changes in the outside environment such as humidity. With such small teeth, these variables can have a large impact on the measured

TABLE 1—Mass of modern elasmobranch teeth throughout experimental abrasion study.

Tooth #	Hours											Percent Loss
	0	100	200	300	400	500	600	700	800	900	1000	
MNA V9944	0.73788	0.73096	0.73336	0.73703	0.72714	0.74787	0.73077	0.72875	0.73627	0.74752	0.75736	−2.64
MNA V9945	0.81482	0.79880	0.79859	0.80639	0.79317	0.81273	0.79555	0.79310	0.79614	0.79613	0.81725	−0.30
MNA V9946	0.08370	0.08286	0.08370	0.08442	0.08318	0.08591	0.08355	0.08384	0.08429	0.08466	0.08673	−3.62
MNA V9947	0.02310	0.02237	0.02152	0.01923	0.01781	0.01568	0.01553	0.01520	0.01303	0.01346	0.01486	35.67
MNA V9948	0.05864	0.05862	0.05999	0.06072	0.05934	0.06139	0.06053	0.06054	0.06115	0.06184	0.06349	−8.27
MNA V9949	0.09326	0.09176	0.09208	0.09287	0.09175	0.09441	0.09208	0.09220	0.09324	0.09308	0.09500	−1.87
MNA V9950	0.09363	0.09230	0.09261	0.09376	0.09279	0.09532	0.09267	0.09305	0.09349	0.09404	0.09600	−2.53
MNA V9951	0.20611	0.20532	0.20703	0.20956	0.20678	0.21182	0.20827	0.20608	0.20770	0.20701	0.21142	−2.58
MNA V9952	0.43760	0.43310	0.43673	0.43930	0.43469	0.44300	0.43373	0.43241	0.43244	0.40385	0.43757	0.01

mass in grams

weight of the teeth. Weight is probably not a reliable measure of the amount of material lost from the teeth because clear abrasion that would result in weight loss was observed.

RESULTS

Although weight was determined not to be a reliable indicator of material loss, an overall decrease in weight was seen over the course of the experiment (Table 1). Despite such a trend, it is clear that these data do not represent the true loss of mass.

Each tooth displayed slightly different abrasion effects (Figs. 7 and 8). MNA V9951, a specimen of *Odontaspis ferox*, first displayed abrasion at 200 hours, with slight blunting and reduction in size of the lateral cusps and a chisel effect developing on the tip of the central cusp (Fig. 8B, E). At 300 hours, these effects continued with the addition of noticeable abrasion of the tips of the root. Also, the interface between the root and the crown on the labial side of the tooth began retreating underneath the cusp. All of these abrasion characteristics were exacerbated throughout the duration of the study (Fig. 8C, F), and an additional wear facet began developing on the central process of the lingual side of the base at 400 hours (Fig. 8B, E). The chisel effect of abrasion at the tip of the main cusp is clearly visible under SEM when compared with unworn specimens (Fig. 10). The abrasion has also removed enough enameloid and dentine to expose the dentine tubules at the tip of the cusp (Fig. 10).

MNA V9952 is also a specimen of *Odontaspis ferox*. It displayed abrasion similar to that of MNA V9951, although abrasion of the tips of the root did not occur (Fig. 8K, L). Onset of the abrasion of the lingual side of the root occurred much earlier, at 100 hours. Also at 100 hours, longitudinal cracking of the crown developed near the root (Fig. 8H), an effect not seen in MNA V9951. This continued throughout the study until at 800 hours small flakes of the crown started to delaminate, which progressed until the end of the study (Fig. 8I). This longitudinal cracking is very similar to weathering stage 1 of Behrensmeyer (1978).

MNA V9944 is a symphysial tooth of *Myliobatis*. Already at 100 hours, several mesio-distal cracks developed in the crown. These cracks deepened and increased in number throughout the study (Figs. 9B, 9C, 9E, 9F). Smaller anastomosing surface cracks appeared on the crown at 200 hours (Fig. 9B). Again, both of these sets of cracks are similar to weathering stage 1 of Behrensmeyer (1978). During the duration of the experiment, the tips of the finger-like projections of the root were progressively worn down (Figs. 9E and 9F). Starting at 400 hours, the mesial side of the root developed an abrasion facet in the central portion of the tooth (Fig. 9E, F). Throughout the abrasion study the edges of the crown were progressively polished and worn.

MNA V9945, also a symphysial *Myliobatis* tooth, showed similar effects, although fewer anterior-posterior cracks developed in the crown. The progressive wetting and drying in this experiment required for weighing and photographing may have exacerbated the widening of cracks; however, it was obvious that they did in fact develop while immersed in the actively abrading sand-saltwater mixture. It is also likely that teeth in natural wave environments are periodically subaerially exposed.

The small lateral *Myliobatis* teeth showed little abrasion to the unaided eye. MNA V9948 showed some degradation of the finger-like projections of the base, however, MNA V9946, MNA V9949, and MNA V9950 show no visible wear, although the data show some small weight loss. Examination by SEM indicates significant wear on the edges of the crown and extensive cracking on the occlusal surface of the crown (Fig. 10). MNA V9947 is a notable exception. At the start of the experiment it was much smaller than the other teeth, and its root was much more porous (Fig. 9G). Clear degradation of the root began at 200 hours, with abrasion clearly noticeable on the distal edge. At 300 hours, the exterior surface of the distal side of the crown started to be abraded. These effects continued until the base was completely removed by 500 hours (Fig. 9H). From this time onwards, abrasion progressively attacked the distal and

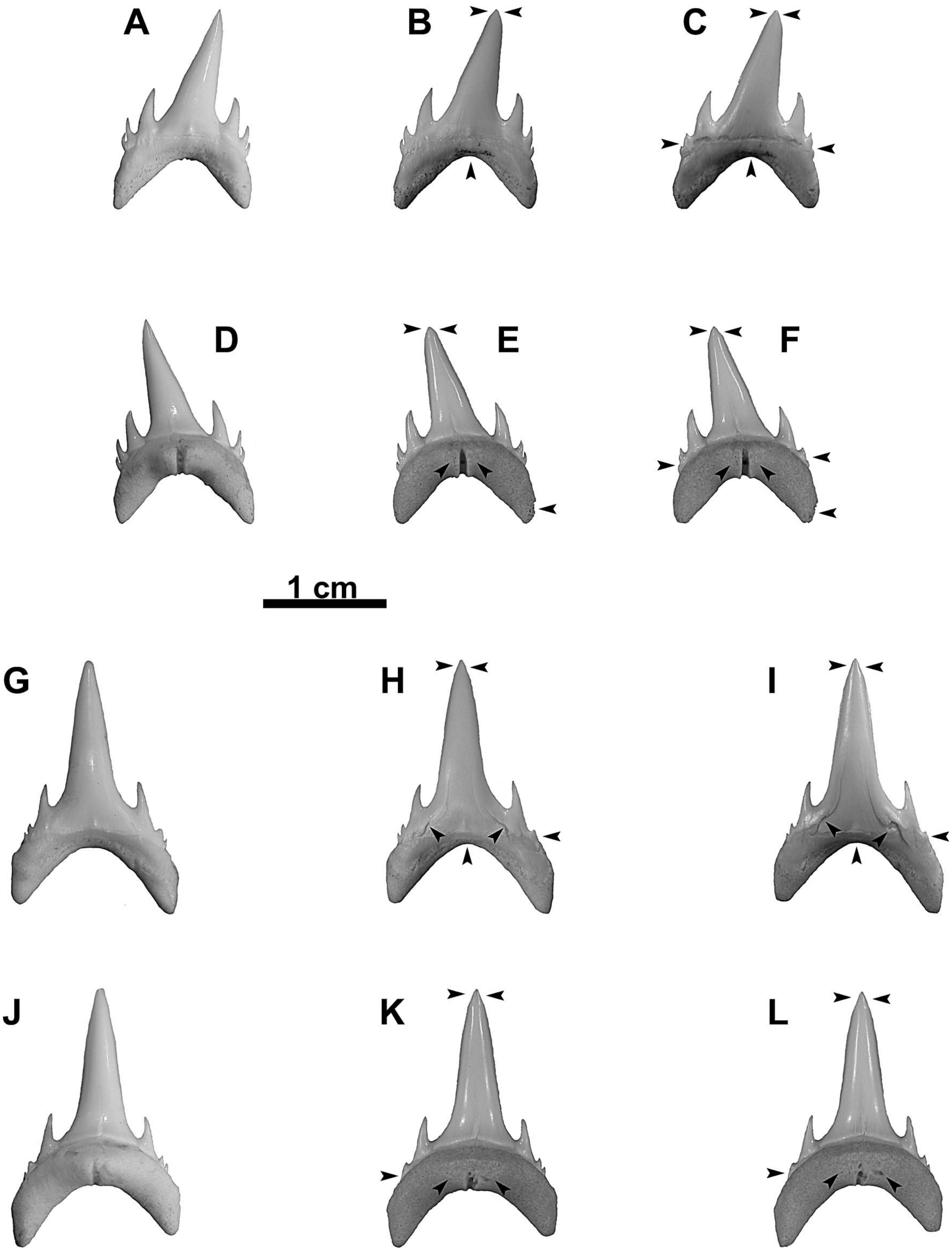

FIGURE 8—Teeth of modern *Odontaspis ferox*. Arrows indicate abrasion effects. A–C and G–H, lingual views; D–F and J–L, labial views. A–F, MNA V9951; G–L MNA V9952. (A) 0 hrs; (B) 500 hrs; (C) 1000 hrs; (D) 0 hrs; (E) 500 hrs; (F) 1000 hrs; (G) 0 hrs; (H) 500 hrs; (I) 1000 hrs; (J) 0 hrs; (K) 500 hrs; (L) 1000 hrs.

basal portions of the crown, reducing the tooth to about half of its original size (Fig. 9I).

Contra Argast et al. (1987) and in agreement with Ely and Rigby (1989) and Ely (1995), progressive development of abrasion and other degradation features do occur when vertebrate teeth are placed in an experimental abrading environment. If these experiments were run long enough (probably over 10,000 hours), it is conceivable that highly abraded and rounded bone pebbles could have been produced. Extrapolating the time required in a natural environment to produce the effects seen in this study is impossible at this stage. Too many variables (e.g., wave base, wave intensity, wave frequency, grain size, etc.) exist to produce any kind of reliable estimate. In addition, each tooth morphology produces its own unique abrasion characteristics, so that timing and production of particular wear in the fossil record cannot always be correlated with experiments on modern teeth. Nonetheless, such studies are valuable in determining what types of abrasion are possible, and whether they

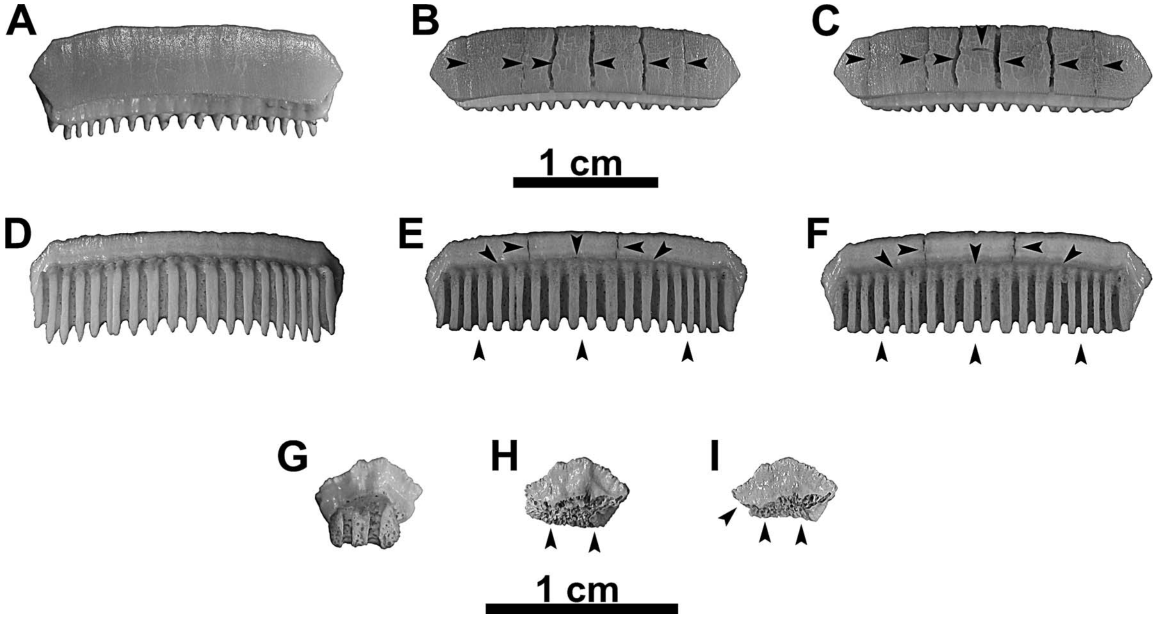

FIGURE 9—Teeth of modern *Myliobatis* sp. Arrows indicate abrasion effects. A–C, occlusal views; D–I, basal views. A–F, MNA V9944; G–I, MNA V9947. (A) 0 hrs; (B) 500 hrs; (C) 1000 hrs; (D) 0 hrs; (E) 500 hrs; (F) 1000 hrs; (G) 0 hrs; (H) 500 hrs; (I) 1000 hrs.

conform to hypotheses for taphonomic assemblages. The use of only nine specimens limits the statistical power of this study, but it represents a beginning for understanding the abrasion of vertebrate remains. Future studies should incorporate a greater number of specimens and taxa, be run for longer durations, and test the effects of different sediment size and composition, ratios of seawater to sediment, salinities, and types of agitation. A recent study testing these variables in a terrestrial experimental setting suggests they significantly impact the degree of abrasion observed (Fernández-Jalvo and Andrews, 2003).

TAPHONOMIC INTERPRETATIONS

The experimental results are consistent with the hypothesis that the vertebrate specimens were abraded in a nearshore marine environment and not in the marine environment where they were buried, which lacks suitable abrasive material. Similarities between the modern experimental evidence and the assemblage at Kohl's Ranch include blunt wear on cusps and extensive erosion and abrasion of the roots of teeth. The anterior-posterior cracking seen in the symphysial *Myliobatis* teeth may eventually lead to breakage of the tooth into several pieces. Subsequent rounding of these sections could eventually form the equant bone pebbles seen in some specimens of *Lagarodus angustus* from Kohl's Ranch (Figs. 5B and 6C). Similar breakage has been observed in at least one specimen of *Lagarodus* from Kohl's Ranch (Fig. 11). Chave (1964) experimentally simulated wave-induced abrasion of a variety of calcium carbonate skeletal elements and noted significant degradation of both size and shape, and this was subsequently demonstrated in natural field experiments by Driscoll (1967), although neither abraded vertebrate tissues. Nevertheless, Kuenen (1964) demonstrated that wave environments were quite successful at abrading even the hardest of siliciclastic materials, which provides further evidence that a nearshore environment would be effective in abrading teeth.

Several lines of evidence suggest strongly that the isolated vertebrate elements (mostly teeth) represent a transported assemblage. First, they show extensive abrasion. This abrasion varies in intensity (Fig. 7), which suggests an assemblage that accumulated over time in the abrading environment before being transported together. Furthermore, there is a distinct lack of sufficient clastic material in the limestones to cause such major abrasion (see results of Driscoll, 1967 on sediment size versus abrasion). The fact that the vertebrates are found only in a maximum of two (possibly one) very restricted limestone sequences also suggests transport. If the animals were living in the area, a much less dense concentration of vertebrate material distributed evenly throughout the section would be expected. In fact, this pattern is observed at another vertebrate-bearing locality in the Naco Formation, near Pine (Elliott et al., 2004), which also produces more complete and less abraded specimens.

The distinct lithology of each limestone bed demonstrates that different environmental conditions existed throughout the deposition of the Kohl's Ranch sequence, so it is not improbable to see only one or two episodes of transport of vertebrate material into the area. Anderson (2001) listed four criteria to differentiate local and transported elements of an assemblage. The local segment of the assemblage should have: (1) specimens with different transport potential; (2) different hydraulic potential from the surrounding matrix; (3) specimens not associated with sedimentary structures that are evidence for transport; and (4) specimens in life position or randomly distributed. The Kohl's Ranch sequences containing vertebrates fail all of these criteria: (1) the vertebrates and associated invertebrate hash are of similar size and density, suggesting they have similar transport potential; (2) micrite mud has a greater transportation potential than the bioclasts, and this is consistent with the potential for transport of either or both the matrix and bioclasts; (3) the vertebrate sequences show an abrupt base with the concentration of bioclasts decreasing up section, associated with intraclasts; and (4) specimens are disarticulated, not in life position, and sometimes exhibit breakage. Together, these characteristics of the vertebrate assemblage are strong evidence for transport. Recently, Trueman and Benton (1997; also Trueman et al., 2003) used rare-earth-element signatures to suggest that the Rhaetian bone beds of the United Kingdom were transported assemblages. This is a promising new technique; unfortunately, it cannot be applied to the Kohl's Ranch assemblage because there are no known nontransported parent assemblages with which to compare it.

Although many authors have suggested that the impact of transport on fossil marine assemblages is minimal (e.g., Kidwell and Bosence, 1991; Parsons and Brett, 1991; Martill, 1991; Kidwell and Flessa, 1996; Meldahl, 2001; Allmon, 2001), there is a growing recognition (Donovan, 2002) that transport can have a significant impact on the composition of marine assemblages, especially in outer shelf and slope environments. Experimental placement of mollusc shells in a variety of marine environments has indicated that there is high potential for reworking and

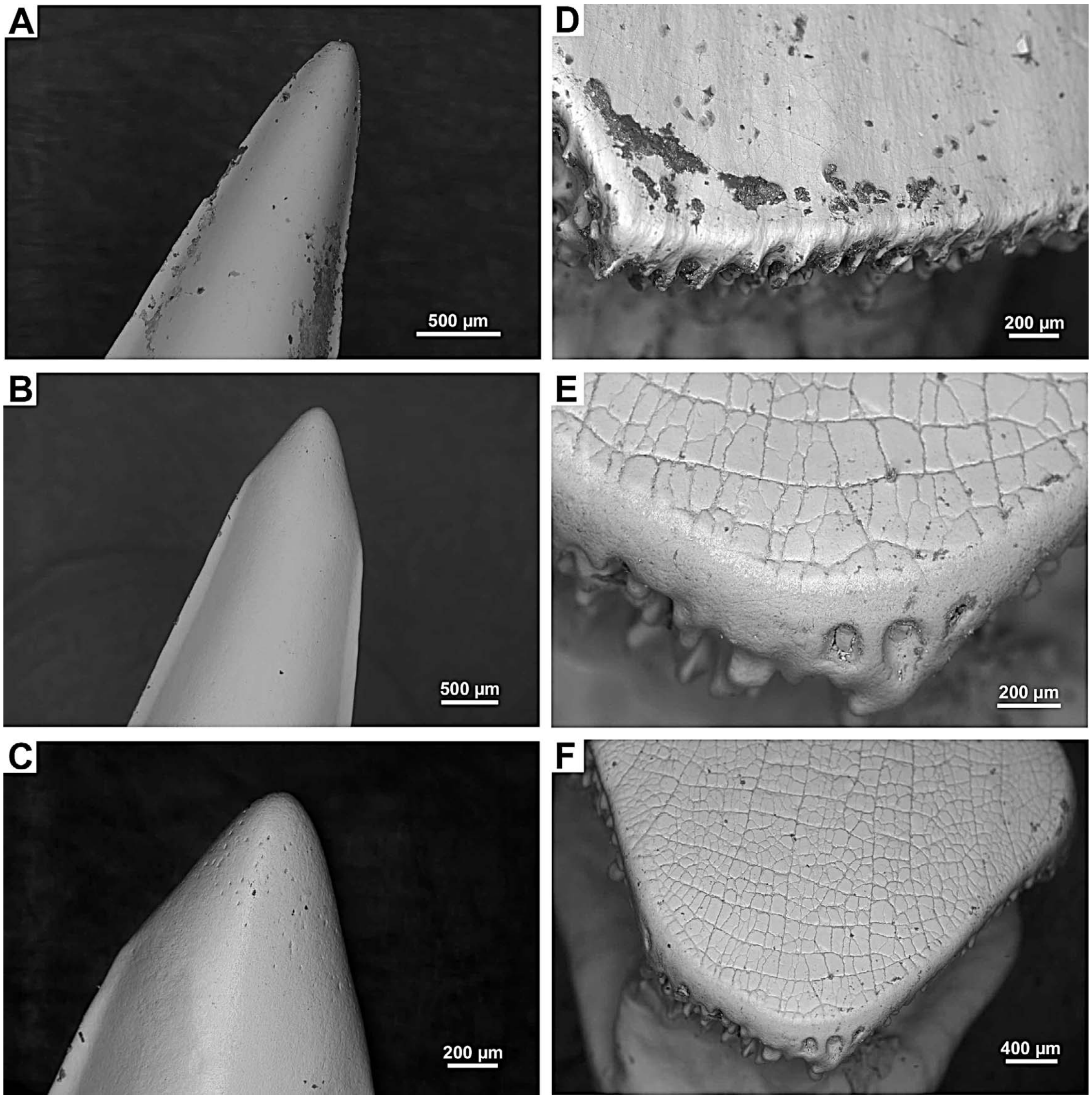

FIGURE 10—Comparison of unworn and abraded modern elasmobranch teeth. A–C, *Odontaspis ferox*; D–F, *Myliobatis* sp. A) Tip of main cusp of unworn tooth (MNA V10119); (B) tip of main cusp of abraded tooth (MNA V9951); (C) close-up of tooth in Fig. 10B displaying exposed dentine tubules; (D) edge of unworn lateral tooth (MNA V10120); (E) edge of abraded lateral tooth (MNA V9948); (F) oblique view of tooth in Fig. 10E displaying edge abrasion and network of cracks on the occlusal surface of the crown.

transport in outer-shelf and slope environments with low sedimentation rates (Parsons-Hubbard et al., 1999). Study of the modern Georgia coast (USA) suggests that reworking and transport are major processes affecting mollusc and vertebrate assemblages; fossils dating back to the Miocene are routinely reworked into modern depositional environments (Frey et al., 1975). An actualistic study of mollusc assemblages in the Caribbean demonstrated that storm transport has a significant effect on the composition of assemblages, potentially increasing measured species richness (Miller et al., 1992).

The Kohl's Ranch locality is interpreted to have been below wave base, and the sediment from background allochthonous sedimentation is very fine grained (mud). It is unlikely that regular sediment transport conditions would be of high enough energy to transport the larger vertebrate specimens. Thus, the best hypothesis for transport of the vertebrate material is occasional storms. Although many storm deposits are found in shallow marine sands, several studies have documented storm deposits in mixed siliciclastic mud and carbonate facies very similar to those found at Kohl's Ranch. Kreisa (1981) and Kreisa and Bambach (1982) described Ordovician marine shelf deposits from Virginia that are interpreted to be storm generated. These strata are very similar to those at Kohl's Ranch. The sections studied by Kreisa (1981) consist of layers of mudstone (shale) alternating with packstones (sometimes sandy) capped by laminated sand and silt. The packstones contain a concentration of skeletal elements with common intraclasts and sometimes sand (Kreisa, 1981). The skeletal fauna is dominated by shells that show convex-up orientation and shelter structures (Kreisa, 1981). This facies is nearly identical to the Kohl's Ranch limestones, and it is interpreted to be the result of storms that affected conditions below the normal wave base (Kreisa, 1981; Kreisa and Bambach, 1982). The Kohl's Ranch limestones lack the convex-up orientation of shells, but this is due mainly to the dominance of echinoderms in the limestones rather than brachiopods. The other major difference between the Kohl's Ranch section and those described by Kreisa (1981) is the lack of laminated silts and sands above the packstones at Kohl's Ranch. A possibility for this difference may be that the Kohl's Ranch section is a more distal storm facies, so it lacks large deposits of coarser siliciclastic material. This interpretation is consistent with the common presence at Kohl's Ranch of thin skeletal beds of articulated convex-up specimens in the mudstone sections (Fig. 2). Kreisa (1981)

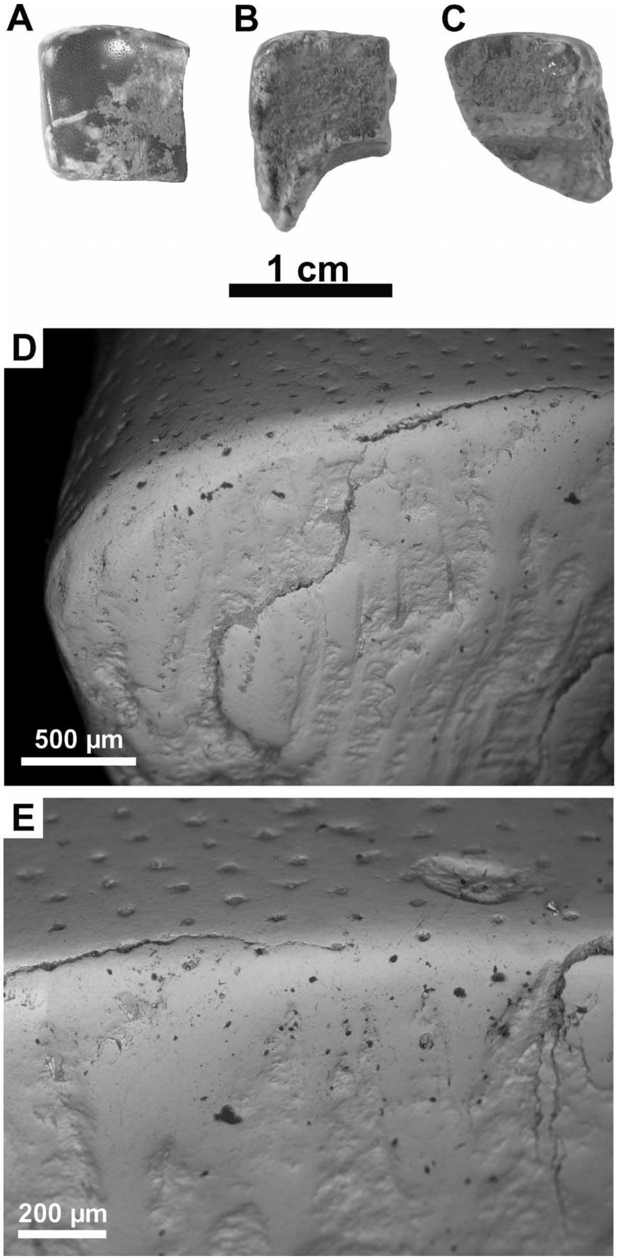

FIGURE 11—Tooth of *Lagarodus angustus* (MNA V9943) displaying breakage and subsequent abrasion. (A) Occlusal view; (B) labial view; (C) broken surface in distal view; (D) close-up of broken surface in oblique distal view showing abrasion; (E) close-up of edge of broken surface displaying abrasion.

noted that this facies was rare in most of his sections but more common in the deeper-water settings, and he interpreted them to be minor storm-event deposits in a distal shelf setting. Facies similar to those described by Kreisa (1981) and those from Kohl's Ranch were also described by MacDonald and Byers (1988) from the Cretaceous Greenhorn Formation of Wyoming. These deposits also displayed alternating mudstone and skeletal packstone layers that were described as storm deposits (MacDonald and Byers, 1988). Additionally, a diverse marine vertebrate fauna was recently described from equivalent limestone layers in Colorado (Shimada et al., 2006). Deposits from the Middle Devonian of New York state are consistent with the above examples, and they have also been interpreted as storm deposits (Brett et al., 1986). As with the previous examples, facies included sandy limestones and skeletal packstones (mainly shell beds) interspersed in thicker mudstone layers (Brett et al., 1986). Also similar to the other storm deposits, these sections contained thin, fossiliferous carbonate layers in the mudstone facies that were interpreted as further evidence for storm deposits (Brett et al., 1986). Given that the sedimentology and facies associations are consistent with other examples of marine-shelf storm deposits, this provides strong evidence for a storm-related genesis of the Kohl's Ranch vertebrate-bearing deposits that is independently corroborated by the abrasion evidence from the vertebrates.

The restricted sequence containing vertebrates in limestone 3, and possibly limestone 5, is strongly suggestive of an environmentally condensed assemblage. These assemblages represent intensely time-averaged sequences that accumulate faunas from different habitats. Kidwell and Bosence (1991) described several criteria that characterize environmentally condensed assemblages: they lie along facies boundaries or discontinuities; occur as dense concentrations; have infills that differ from the surrounding matrix; and can include a wide variety of preservational states. Concentrations of bone (lags) have long been recognized as being associated with depositional hiatuses (Krumbein, 1942; Kidwell, 1989; Brett and Baird, 1993; Becker et al., 1996, 1998); however, Rogers and Kidwell (2000) demonstrated that this relationship is not systematic. Limestone 3 conforms to all of Kidwell and Bosence's (1991) criteria: (1) A distinct lithologic change occurs at the lower boundary with intraclasts found in the condensed zone; (2) skeletal allochems are very dense; (3) mollusc and bryozoan infills are phosphate rather than micrite; and (4) a variety of preservational states occur in the invertebrates and vertebrates. The presence of phosphatic infillings is one of the most characteristic of these criteria, because it has been repeatedly mentioned as strong evidence for little or no net sedimentation (e.g., Speyer and Brett, 1988; Lucas and Prévôt, 1991). Brett and Baird (1993) specifically mentioned internal infillings of phosphate-impregnated mud (exactly what is seen at Kohl's Ranch) as being common in environmentally condensed sequences.

The association of a transported assemblage as part of a condensed assemblage is not unique; this relationship is common among well-studied bone beds (e.g., Wells, 1944; Antia, 1979; Reif, 1982; MacQuaker, 1994; Trueman and Benton, 1997). Whether or not the Kohl's Ranch assemblage can be classified as a bone bed is a matter of definition (see Antia, 1979 and Martill, 1999) and has little bearing on genetic interpretations. Although the surrounding matrix varies (micrite, mudstone, sand, etc.), there appears to be a suite of characters that are systematically associated with bone beds that are also transported and condensed assemblages, including the assemblage at Kohl's Ranch. First, vertebrate specimens show significant, but varying, amounts of abrasion. This obvious feature has been observed in numerous assemblages, including the Silurian Ludlow bone bed (Antia and Whitaker, 1978), Middle Devonian bone beds of the central United States (e.g., Wells, 1944, 1947; Conkin et al., 1973, 1976), Middle Triassic bone beds of Germany (Reif, 1982), the latest Triassic Rhaetian bone beds of England (Sykes et al., 1970; Sykes, 1977; Antia, 1979; MacQuaker, 1994; Trueman and Benton, 1997; Martill, 1999), Middle Jurassic bone beds of Scotland (Hudson, 1966; Antia, 1979), Late Cretaceous assemblages in eastern North America (Becker et al., 1996, 1998), and the Pliocene bone bed of Suffolk, England (Reid, 1890; Boswell, 1928, 1929; Antia, 1979). A second characteristic is that the vertebrate specimens are part of a tightly packed facies with additional non-vertebrate skeletal components. When the matrix is limestone, this generally results in a skeletal packstone. Regardless of matrix composition, siliciclastic sand grains are usually common, and intraclasts are also present (e.g., Wells, 1944; Antia and Whitaker, 1978; Antia, 1979). Concentrated assemblages are characteristic of all bone beds and are especially notable in the Ludlow (Antia and Whitaker, 1978), Middle Devonian (Wells, 1944), German Middle Triassic (Reif, 1982), and Rhaetian (Sykes, 1977; Antia, 1979; MacQuaker, 1994) bone beds. Most condensed bone beds have large amounts of phosphate external to the vertebrate specimens (Antia, 1979), generally as nodules or internal molds. Phosphate is especially common in the Middle Devonian, German Middle Triassic, Rhaetian, and Suffolk (Reid, 1890; Antia, 1979) assemblages. This property results at least in part from the fact that phosphate deposition is favored by low net sedimentation (Manheim et al., 1975), an environment also required for formation of condensed assemblages. Finally, these bone beds always display basal lithologic discontinuities (unconformities or other erosional boundaries), a characteristic of all environmentally condensed assemblages.

Although environmentally condensed assemblages are clearly the result of intensive time averaging, it is unclear exactly how long it takes for them to develop (Kidwell and Bosence, 1991; Brett and Baird, 1993). Phosphatization has traditionally been considered a slow process; however, rates can be variable (Lucas and Prévôt, 1991). In the case of the vertebrate horizon at Kohl's Ranch, some relative constraints are evident. First, the basal discontinuity and the presence of intraclasts derived from underlying carbonate strata suggests that partial lithification of the previous carbonate surface had already occurred, indicating a significant amount of time prior to deposition of the vertebrate bearing unit. Although it is unclear how long it took to accumulate the non-vertebrate portion of the assemblage, the simplest hypothesis is that vertebrates were transported in as one event.

Phosphatization can be constrained to early diagenesis. The presence of quartz grains within the phosphatized skeletal allochems suggests that the matrix and cement had already been deposited by the onset of phosphate deposition. This hypothesis is supported by evidence that high levels of calcium carbonate in solution inhibit phosphate deposition (D'Anglejan, 1968; Manheim et al., 1975; Lucas and Prévôt, 1991). Additionally, phosphatization requires high phosphate levels in pore waters (MacQuaker, 1994), something that would be more difficult if the assemblage were exposed on the seafloor. This is consistent with phosphate deposition in modern environments, where nodules grow in place after being covered with sediment (Burnett et al., 1982) and into early diagenesis (D'Anglejan, 1968). Examples of modern phosphate deposition also display deposition in pore waters between sediment (Burnett, 1977). The phosphate must have originated from the vertebrates, inasmuch as phosphatic molds are found only in association with the vertebrates and there is no other apparent source for phosphate. Shark teeth from phosphorite beds in North Africa are often missing their roots (Lucas and Prévôt, 1991), suggesting preferential dissolution of the roots because they are not covered by a layer of protective enamel. This condition is also seen in some of the Kohl's Ranch teeth, although loss of the roots probably also results from abrasion.

It is most likely that phosphatization occurred during the period of carbonate dissolution but before the deposition of blocky spar and compaction because phosphate is typically deposited within pores (Burnett, 1977; Lucas and Prévôt, 1991). Additionally, MacQuaker (1994) suggested that carbonate dissolution should be expected in association with phosphate deposition because the organic decay that releases phosphate also increases pore-water acidity. In the case of the Kohl's Ranch assemblage, phosphate deposition occurred during early diagenesis, so it is probably not advisable to use the presence of phosphate to hypothesize a long period of exposure prior to cementation.

CONCLUSIONS

The evidence presented in this study suggests the following taphonomic sequence for the vertebrate assemblage at Kohl's Ranch. Chondrichthyans lived and died in a nearshore marine environment. Teeth and spines accumulated through time in this environment and were abraded by wave action. At some point, a storm transported the vertebrate accumulation to a site below the wave base to the Kohl's Ranch locality. Here, the specimens were extensively time-averaged and accumulated within an environmentally condensed assemblage. Deposition of micrite mud preserved the sequence and, after a period of selective carbonate dissolution, phosphate from the vertebrates infilled molluscs and bryozoans. Diagenetic infilling of other pores by blocky calcite spar followed along with compaction and burial.

Based on this and other studies (e.g., Trueman and Benton, 1997; Becker et al., 1996, 1998; Staron et al., 2001), assemblages of isolated specimens of marine vertebrates in many cases have much more complex taphonomic histories than previously recognized. Detailed investigation of the sedimentology and microstratigraphy of vertebrate-bearing horizons provides much information to build strong taphonomic hypotheses regarding marine vertebrate assemblages.

Experimental abrasion of modern elasmobranch teeth displays the value of actualistic experiments in evaluating ancient taphonomy. This study demonstrates that progressive degradation of vertebrate teeth can occur through abrasion in wave-dominated environments. The results of the experimental work corroborate other studies suggesting that bone is progressively modified through abrasion in aqueous environments, and are also consistent with the hypothesis that the vertebrate teeth were transported prior to final burial. Although the limitations of the present experiment are recognized, it represents a first step towards developing actualistic models for marine abrasion of vertebrate elements. Further studies are needed that include a greater number of specimens, longer duration of abrasion, and a test for the effects of variation in the amount of sediment, saltwater, and fluid movement.

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