



# Evidence for gregarious behavior and age segregation in sauropod dinosaurs

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## ABSTRACT

Both body fossil and ichnofossil evidence for gregarious behavior in sauropod dinosaurs is examined. Some localities suggest that herds were partitioned on the basis of age, whereas other sites reveal groups consisting of both adult and juvenile/subadult individuals. Two skeletal accumulations showing evidence of age segregation are examined in detail. The Mother's Day Quarry in the Upper Jurassic Morrison Formation of Montana contains the remains of several immature diplodocoid sauropods. An assemblage in the Upper Cretaceous Javelina Formation of Big Bend National Park in Texas consists entirely of juvenile *Alamosaurus*. Both the Mother's Day and Big Bend assemblages are interpreted here as remnants of age-segregated herds. The differences between skeletal accumulations composed entirely of immature animals and mixed-age ichnological assemblages imply that herd composition was variable. When age segregation is recognized, in both fossil and modern taxa, it is thought to minimize the fitness costs related to behavioral synchronization within social groups. Age segregation of herds also contraindicates extended parental care as typical of at least some sauropod taxa.

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## 1. Introduction

Gregarious behavior has been postulated for a number of dinosaur taxa, including ceratopsids, ornithopods, theropods, and sauropods. This behavioral model is supported by multiple examples of skeletal evidence in the Ceratopsia (Currie and Dodson, 1984; Davies and Lehman, 1989; Ryan et al., 2001; Qi et al., 2007), Ornithopoda (Horner, 1982; Hooker, 1987; Davies and Lehman, 1989; Winkler and Murray, 1989; Forster, 1990; Rogers, 1990), and Theropoda (Schwartz and Gillette, 1994; Currie, 1998; Kobayashi and Lu, 2003; Currie et al., 2005; Coria and Currie, 2006). A number of mass accumulations of sauropod skeletal material are also known (Jain, 1980; Xia et al., 1984; Dong, 1990; Coria, 1994; Heinrich, 1999; Winkler et al., 2000; Yadagiri, 2001; Bandyopadhyay et al., 2002; Sander et al., 2006), but most reports of these assemblages do not include the taphonomic data necessary for behavioral interpretations, with some exceptions (e.g., Coria, 1994; Winkler et al., 2000; Bandyopadhyay et al., 2002). The best evidence of gregarious behavior in sauropods currently comes from the ichnological record (Ostrom, 1985; Pittman and Gillette, 1989; Barnes and Lockley, 1994; Lockley et al., 1994; Day et al., 2004). Trackway accumulations can provide much information about herds that is not available in the body fossil record, including speed, direction of travel, and herd structure, the spatial organization of individuals within a group (e.g., Bakker, 1968; Lockley, 1995). Potential complicating factors in the interpretation of ichnological assemblages include uncertainties in identification of lower-level taxonomic

affinities and age estimates of trackmakers. Body fossil assemblages provide complimentary information to ichnological evidence of gregarious behavior, allowing a clear picture of the age and taxonomic affinities of individuals within a herd, in contrast to the spatial and contextual data produced by trackway studies. Use of body fossils mitigates problems related to trackmaker identification, but both track and skeletal accumulations are susceptible to subtle biasing factors. Prior to use in behavioral interpretations, each skeletal assemblage must be evaluated for taphonomic biases related to cause of death, time-averaging, and postmortem transport.

Two sites, the Mother's Day Quarry (MDQ) in the Upper Jurassic Morrison Formation of Montana (Myers and Storrs, 2007) and a locality in the Upper Cretaceous Javelina Formation of Texas (Fiorillo, 1998a), reveal unique details of herd composition. Both the MDQ and Big Bend assemblages consist entirely of juvenile sauropods, implying social partitioning of individuals by age. Age segregation of sauropod herds has been suggested based on available trackway data (Lockley et al., 1986, 1994, 2002b), but has not been reported in the sauropod body fossil record as it has for other dinosaurian groups (Coombs, 1982; Forster, 1990; Varricchio and Horner, 1993). Here we explore the implications of the MDQ and the Big Bend site for our understanding of sauropod herd composition and parental care.

## 2. Evidence for gregarious behavior

### 2.1. Ichnological evidence

Typically, the passage of a herd is inferred when several trackways are oriented subparallel to one another, intertrackway spacing is small,

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and individual trackways produce similar speed estimates and exhibit little overlap (Ostrom, 1972; Lockley et al., 1986). Excellent examples of sauropod herd ichnocoenoses are known from the Jurassic of Portugal (Lockley et al., 1994), China (Lockley et al., 2002b), and the United Kingdom (Day et al., 2004), as well as from the Cretaceous of Brazil (Leonardi, 1989) and Bolivia (Leonardi, 1989; Lockley et al., 2002a). Within the United States, herd trackways of Jurassic age have been reported from Colorado (Lockley et al., 1986) and Utah (Barnes and Lockley, 1994); Cretaceous sites occur in Texas (Farlow, 1987; Hawthorne, 1990) and Arkansas (Pittman and Gillette, 1989). This global sample of tracksites offers conflicting evidence of herd composition, some localities showing commingling of immature and adult individuals, and others containing prints from a single age class. The different age profiles documented at these sites suggest either undiagnosed time-averaging of some assemblages or variability in sauropod herd composition.

Absence of adult tracks implies that herds may have been partitioned on the basis of age, with young animals forming groups separate from those composed of mature, adult animals. However, absence of juvenile tracks in an assemblage is not necessarily evidence of age segregation because formation of adult herds does not always correlate with occurrence of exclusive juvenile or subadult herds. For example, modern taxa that segregate by sex, but not age, form bachelor groups of adult males that are separate from groups containing both females and juveniles (e.g., Côté et al., 1997; Bender and Haufler, 1999). Of the 13 sauropod trackway accumulations showing indications of gregarious behavior, nine contain tracks belonging to a single age class. Five sites record the passage of distinct juvenile or subadult groups, while four localities preserve only adult tracks and therefore are uninformative with regard to age segregation (Table 1).

## 2.2. Differences between ichnological and body fossil data

Like body fossil assemblages, ichnological interpretations of gregarious behavior require careful consideration of possible sources of bias. Time-averaging in ichnological assemblages may be constrained using criteria such as comparative track depth or track preservation (Lockley, 1991; Day et al., 2004). Regardless of constraints on time-averaging, tracks cannot be matched with lower-level taxonomic groups based on body-fossils due to the effects of substrate variability on print shape and conservative pes morphology that may not reflect diagnostic differences between genera or species (Farlow, 2001; Day et al., 2004). Consequently, when herd trackways are identified, the taxonomic composition of the herd may remain unknown.

Tracksites are assumed to be time-averaged when trackways frequently intersect and overprint one another; adjacent, similar-sized tracks differ in depth; or tracks show signs of exposure such as erosion or slumping around track margins (Lockley, 1991; Day et al., 2004). An assemblage that lacks all these indications of time-averaging likely represents a census accumulation of coeval trackways. However, firm sedimentary substrates may mitigate the effects of erosion; and subparallel trackways may be produced by topographic constraints, such as shorelines, that limit the number of possible directions of travel, condensing trackways along certain routes (Lockley and Hunt, 1995) (Fig. 1). The presence of topographic barriers may be ruled out at sites containing trackways with perpendicular orientations (Ostrom, 1972), but time-averaging again becomes a concern for sites with many non-parallel trackways.

Time-averaging in a skeletal assemblage is typically estimated by comparing degrees of disarticulation and bone modification of different elements. Bone modification features typically begin to accumulate shortly after death and continue to develop for several years before a bone fully decays (Behrensmeyer, 1978). Since tracks are more susceptible to destruction, tracksites typically represent brief periods of accumulation relative to skeletal assemblages, but are less likely to exhibit a continuum of modification features that could be used to estimate exposure time prior to burial. Though lesser potential for time-averaging is an obvious benefit of ichnological data, tracksites are sensitive to even small amounts of time-averaging that may skew interpretations of herd behavior. For example, several solitary individuals traveling in a common direction and passing the same point within hours of one another could produce a set of subparallel trackways that creates the false impression of a herd. Many skeletal accumulations have similar problems with time-averaging, but distinct temporal subsets in an assemblage are often identifiable as different taphonomic modes, usually defined by differing degrees of bone modification.

Identification of trackmakers is difficult because ichnotaxa do not correspond to taxonomic classifications based on skeletal material, and the two taxonomies cannot be linked directly at lower levels. In some instances, even consistent identification of ichnotaxa may be complicated by the impacts of substrate characteristics and quality of preservation on track appearance and clarity, respectively (Nadon, 2001 and references therein). Conservative pes morphology renders identification of sauropod trackmakers especially complicated (Farlow, 1992). Issues with taxonomic identification also affect the ability to determine precise ages of individuals from tracks. Track size correlates well with overall size within many modern animal populations (Lockley, 1996); however, body size, estimated from tracks or skeletal elements, is not always a reliable indicator of age

**Table 1**

Table showing localities with potential ichnological evidence of gregarious behavior in sauropods<sup>a</sup>

| Map # | Location       | Geologic age           | Age classes present | Estimated # of individuals | References  |
|-------|----------------|------------------------|---------------------|----------------------------|---|
| 1     | United Kingdom | Bathonian              | Adult               | ~40                        | Day et al., 2002; Day et al., 2004                                |
| 2a    | Colorado, USA  | Kimmeridgian?          | Juvenile            | 5                          | Lockley et al., 1986  |
| 2b    | Colorado, USA  | Kimmeridgian?          | Adult               | 6                          | Lockley et al., 1986  |
| 3     | Utah, USA      | Kimmeridgian           | Juvenile            | 3                          | Barnes & Lockley, 1994  |
| 4     | Portugal       | Portlandian            | Subadult            | 7                          | Lockley et al., 1994  |
| 5     | Brazil         | Berriasian – Barremian | Adult and juvenile? | 5                          | Leonardi, 1989  |
| 6     | Brazil         | Berriasian – Barremian | Unknown             | 6                          | Leonardi, 1989  |
| 7     | China          | Barremian – Aptian     | Juvenile            | 4                          | Lockley et al., 2002b   |
| 8     | Texas, USA     | Albian                 | Adult               | ~10                        | Bird, 1939, 1941, 1954; Farlow, 1987; Farlow et al., 1989         |
| 9     | Texas, USA     | Albian                 | Adult and juvenile  | 23                         | Bird, 1944, 1954; Ostrom, 1985; Farlow, 1987; Farlow et al., 1989 |
| 10    | Arkansas, USA  | Albian                 | Adult               | 10                         | Pittman & Gillette, 1989  |
| 11    | Bolivia        | Campanian              | Adult and juvenile  | 8                          | Leonardi, 1989  |
| 12    | Bolivia        | Campanian              | Subadult            | 11                         | Lockley et al., 2002a   |

<sup>a</sup> Sites with strong evidence for age segregation are indicated by italicized text. Map numbers correspond to those in Fig. 4. Data from Bird, 1939, 1941, 1944, 1954; Ostrom, 1985; Lockley et al., 1986; Farlow, 1987; Farlow et al., 1989; Leonardi, 1989; Pittman & Gillette, 1989; Barnes & Lockley, 1994; Lockley et al., 1994, 2002a,b; Day et al., 2002, 2004.





**Fig. 1.** Human footprints adjacent to those left by a grizzly bear (*Ursus arctos*). These tracks, which were made along a beach in southwestern Alaska, were not made simultaneously; rather, the activity of the two trackmakers was separated by several hours. The human trackmaker was utilizing the firmness of the sand substrate that lies along the beach. Presumably the grizzly bear was employing a similar strategy.

since size varies within and between taxa (Brinkman, 1988). Size-independent criteria for estimating age – such as degree of skeletal ossification (Brinkman, 1988), fusion of neurocentral sutures (Brochu,

1996; Irmis, 2007), and bone histology (Sander et al., 2006) – allow more precise determination of age for skeletal material. Ambiguities in taxonomic identification and age estimation of trackmakers create uncertainty in determining if conflicting behavioral evidence is the result of inter- or intraspecific variation. While body fossil evidence circumvents problems related to trackmaker identification, a skeletal assemblage must meet certain taphonomic criteria before it may be used in behavioral interpretations. If a site is not thoroughly analyzed, bias generated by post-mortem processes may distort or obscure behavioral characteristics of the initial biocoenose.

Low taxonomic diversity within a skeletal assemblage, the primary indicator of a herd, may result from taphonomic processes instead. Selective agents of mortality, such as miring of large animals, may produce monospecific or paucispecific skeletal accumulations (e.g. Agenbroad, 1984; Sander, 1992; Hungerbühler, 1998). Thereby, a single locality may amass a number of non-contemporaneous skeletal elements, creating a time-averaged assemblage that has no bearing on gregarious behavior. Selective agents of mortality may preferentially sample a subsection of individuals in a group (Lyman, 2001), providing a biased view of herd composition. Consequently, a deposit containing only juvenile individuals may simply record the aftermath of a mortality in which survival was directly tied to physical robustness and ability to withstand environmental stress. In order to avoid misinterpretations, a detailed taphonomic history must be constructed before proceeding with any behavioral interpretation.

### 2.3. Body fossil evidence

Currently, several monospecific or paucispecific sauropod-dominated sites are known from the body fossil record (Table 2). Most of these assemblages are composed entirely of adult individuals and consequently are uninformative with regard to age segregation. In addition to the MDQ and Big Bend localities, one other site reportedly contains only juvenile individuals, potentially representing an age-segregated herd. The locality, in the Middle Jurassic Wucaiwai Formation of northwestern China, contains the remains of 17 small sauropods that provide the holotype material of *Bellusaurus sui* (Dong, 1990, 1992). The *Bellusaurus* specimens are of consistently small size and most vertebrae recovered have unfused neurocentral sutures (James Clark, pers. comm.), suggesting that all individuals in the assemblage are either juvenile or subadult. Given that neurocentral sutures close semi-sequentially in most archosaurs rather than all at once (Brochu, 1996; Irmis, 2007), some fused sutures are not unexpected in a large assemblage of immature individuals. Although this assemblage may have derived from an age-segregated herd,

**Table 2**  
Table showing localities with potential skeletal evidence of gregarious behavior in sauropods<sup>a</sup>

| Map # | Taxon   | Location     | Geologic age                    | Age classes present | Estimated # of individuals | References  |
|-------|---|--------------|---------------------------------|---------------------|----------------------------|---|
| 1     | <i>Barapasaurus</i>   | India        | Early Jurassic                  | Adult               | ≥6                         | Jain et al., 1975; Jain, 1980; Bandyopadhyay et al., 2002 |
| 2     | <i>Kotasaurus</i>   | India        | Early Jurassic                  | Adult               | ≥12                        | Yadagiri et al., 1979; Yadagiri, 1988; Yadagiri, 2001     |
| 3     | <i>Patagosaurus</i>   | Argentina    | Middle Jurassic                 | Adult and juvenile  | 5                          | Coria, 1994   |
| 4     | <i>Bellusaurus</i>  | China        | Middle Jurassic                 | Juvenile            | ≥17                        | Dong, 1990, 1992  |
| 5     | <i>Diplodocoidea</i>  | Montana, USA | Late Jurassic (Kimmeridgian)    | Juvenile            | 8                          | Myers & Storrs, 2007; this paper                          |
| 6     | <i>Europasaurus</i>   | Germany      | Late Jurassic (Kimmeridgian)    | Adult and juvenile  | ≥11                        | Sander et al., 2006                                       |
| 7     | <i>Brachiosaurus</i> ,<br><i>Janenschia</i> ,<br><i>Dicraeosaurus</i> | Tanzania     | Late Jurassic                   | Variable            | ≥2 to ≥5                   | Heinrich, 1999  |
| 8     | <i>Paluxysaurus</i>   | Texas, USA   | Early Cretaceous                | Adult               | ≥4                         | Winkler et al., 2000; Rose, 2007                          |
| 9     | <i>Alamosaurus</i>  | Texas, USA   | Late Cretaceous (Maastrichtian) | Juvenile            | ≥3                         | Fiorillo, 1998a; this paper                               |

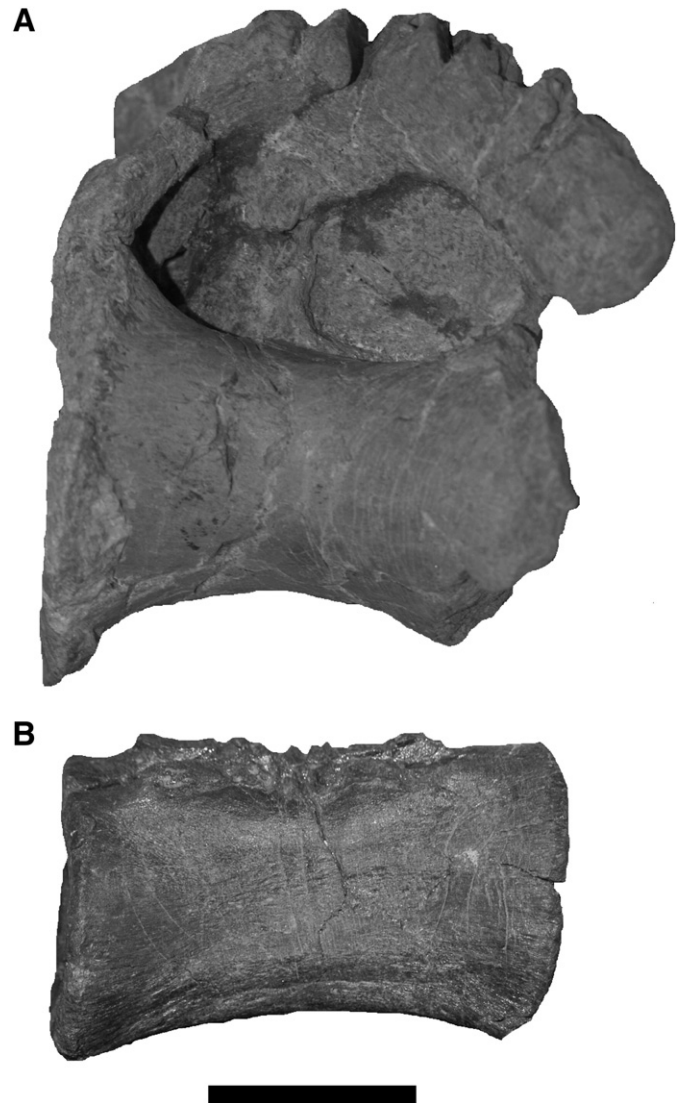
<sup>a</sup> Sites with strong evidence for age segregation are indicated by italicized text. Map numbers correspond to those in Fig. 4. Data from Jain et al., 1975; Yadagiri et al., 1979; Jain, 1980; Yadagiri, 1988; Dong, 1990, 1992; Coria, 1994; Fiorillo, 1998a; Heinrich, 1999; Winkler et al., 2000; Yadagiri, 2001; Bandyopadhyay et al., 2002; Sander et al., 2006; Myers & Storrs, 2007; Rose, 2007; this paper.

preservation of only juvenile individuals may also be attributable to taphonomic bias. Time-averaging may have influenced the composition of the assemblage since the bonebed contains the remains of theropods, ornithopods, and fish in addition to the sauropod material (Dong, 1990), suggesting some degree of post-mortem mixing. Selective mortality of juveniles also cannot be discounted. A thorough investigation of the taphonomic history of the site is needed to determine whether the 17 sauropods collected at the Wucuiwan locality represent the remnants of an age-segregated social group.

In contrast to the Wucuiwan locality, two other sites preserve the remains of both juvenile and adult sauropods, implying a different mode of gregarious behavior than age-segregated groups. These potential mixed-age herd assemblages are found in the Middle Jurassic of Argentina (Coria, 1994) and the Late Jurassic of Germany (Sander et al., 2006). At the Middle Jurassic Patagonian locality, portions of five skeletons of the cetiosaurid *Patagosaurus fariasi* were recovered, belonging to two adults and three juveniles (Coria, 1994). This co-occurrence of mature and immature individuals was construed as evidence of extended parental care in sauropods (Coria, 1994). The remains were disarticulated, with little cranial material present, and lack of significant variation in weathering stages between specimens was interpreted as an indication of little time-averaging (Coria, 1994). More recently, an assemblage containing at least 11 individuals belonging to the new sauropod taxon *Europasaurus holgeri* was reported from the Kimmeridgian of northern Germany (Sander et al., 2006). The site contains juvenile, subadult, and adult specimens, ranging in length from 1.7 m to 6.2 m (Sander et al., 2006). Buried in shallow marine carbonates, the sauropod material consists of partially articulated skeletons as well as isolated bones; most specimens are disarticulated, but remain associated (Sander et al., 2006). Though bones of fishes, crocodiles, turtles, and pterosaurs are also present in the bonebed, the assemblage is dominated by *Europasaurus* (Sander et al., 2006). Variable bed thickness, a relatively depauperate marine fauna, and preservation of delicate skeletal elements were interpreted as evidence for minimal transport (Sander et al., 2006). This site is an excellent candidate for a herd assemblage, but still requires better taphonomic constraints.

### 3. Mother's Day Quarry

The MDQ is located in the Morrison Formation along the north-western rim of the Bighorn Basin in south-central Montana. The assemblage has been interpreted as the remnant of a drought mortality, interred by a high-density sediment flow (Myers and Storrs, 2007). The quarry has a strikingly low taxonomic diversity, with one sauropod taxon and one theropod taxon present. However, the relative abundance of elements from these taxa is so uneven – diplodocoid sauropod material comprises 99% of the recovered bones – that the quarry is effectively monospecific (Myers and Storrs, 2007). The theropod material consists of isolated teeth only and is probably related to scavenging of the sauropod carcasses. All identifiable sauropod elements belong to either juvenile or subadult individuals (Fig. 2); none is attributable to a fully-adult individual (Myers and Storrs, 2007). The sauropod material in the assemblage is well preserved, with some elements remaining articulated or associated (Myers and Storrs, 2007). Skin impressions indicate soft tissues were still present at the time of burial, and there is little evidence of pre-burial bone modification in the assemblage (Myers and Storrs, 2007). The bones apparently underwent little, if any, transport from the site of death; there are no size-dependent trends in the vertical distribution of elements that would suggest a transport-induced taphonomic bias toward large or small bones (Myers and Storrs, 2007). Although the MDQ meets the initial criterion for a potential herd assemblage in that it is paucispecific, it must be determined whether this diversity pattern and the unusual age profile of the deposit are taphonomic artifacts or accurate reflections of the original

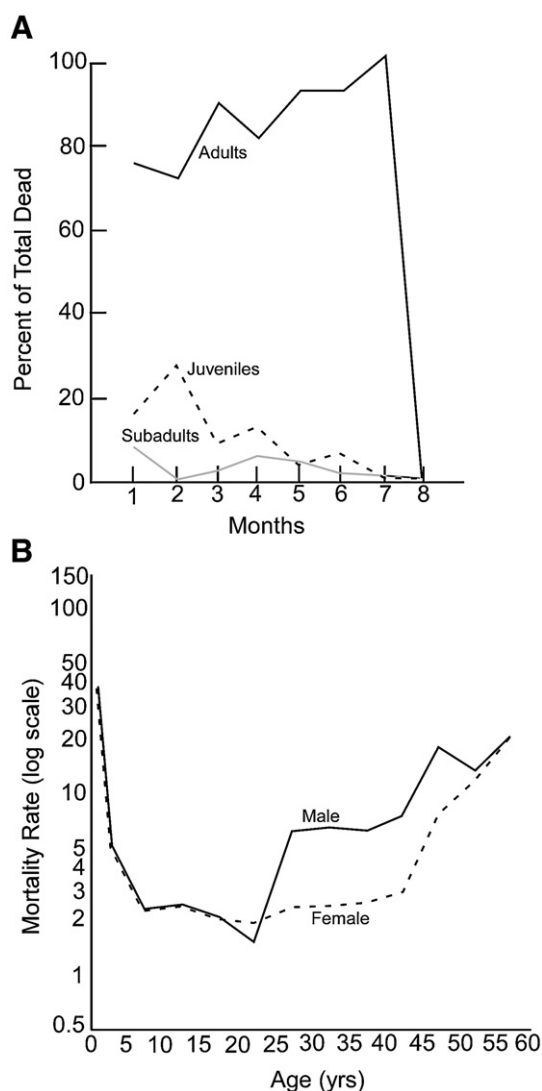


**Fig. 2.** Vertebrae with unfused neurocentral sutures. Neural arches separated from centra post-mortem. Lack of fusion of neurocentral sutures in dorsal and caudal vertebrae is characteristic of immature archosaurs (Brochu, 1996). (A) Dorsal vertebra (CMC VP7913). (B) Caudal vertebra (CMC VP7929). Scale bar equals 5 cm.

biologic assemblage. Possible biasing factors that are relevant to this study include a selective agent of mortality, an attritional mode of death, and transport processes that are either age-specific or taxon-specific.

If the MDQ sauropods died during a drought, immature animals may have been sampled selectively from a larger herd containing both juveniles and adults. Droughts induce higher rates of mortality among the weaker individuals of a population, especially young individuals that are more vulnerable to environmental stress (Corfield, 1973; Barnes, 1982; Dudley et al., 2001; Oba, 2001) (Fig. 3A). However, adult animals comprise a large percent of any population, and they will always represent a portion of the drought death assemblage if they were present in the initial biological group (Hillman and Hillman, 1977; Dudley et al., 2001) (Fig. 3B). Drought assemblages will not accurately reflect the age ratios within the affected population, but all age groups in the sampled population should appear in the assemblage, even if they are represented by relatively few individuals. Age profiles of fossil drought assemblages typically contain animals from a broad spectrum of age classes and do not exhibit juvenile-only preservation patterns as would be expected if drought conditions affected young animals exclusively (Rogers, 1990; Varricchio and





**Fig. 3.** Graphs of drought mortality. (A) Percent of death assemblage represented by each age class for a population of African ungulates. Modified from Hillman and Hillman (1977). (B) Mortality rates as a function of age in a population of African elephants. Modified from Corfield (1973).

Horner, 1995; Evanoff and Carpenter, 1998; Richmond and Morris, 1998; Fiorillo et al., 2000).

Mode of death (catastrophic vs. attritional) also has the potential to significantly bias a fossil assemblage. Herds are ephemeral entities in terms of both time and space, so an assemblage that accumulates through attritional processes does not represent an aggregate of gregarious individuals. Since the MDQ assemblage is interpreted as an accumulation of bones resulting from drought, the total interval of potential carcass accumulation was likely on the order of months. Dearth of pre-fossilization bone modification indicates that the sauropod carcasses were amassed and buried relatively quickly because subaerial weathering in arid conditions can cause extensive surficial damage after less than one year of exposure (Coe, 1978). Remnants of soft tissue in the assemblage also suggest rapid burial.

The final source of potential bias to consider for the MDQ is post-mortem transport. In many cases, significant taphonomic bias may be introduced into fossil assemblages as they are transported prior to their final burial. Fluvial currents have been shown to mix disparate skeletal elements from different environments and sort elements based on size and density differences that may be either taxon-specific or age-specific (Behrensmeyer, 1975, 1982; Aslan and Behrensmeyer, 1996). Even if the initial death accumulation was an accurate

reflection of the herd from which it was sampled, transport could sufficiently alter the assemblage so that it was no longer representative of the original biological entity. For example, juvenile bones, characterized by lower density and smaller size than adult elements, could be transported preferentially or winnowed from a broader assemblage, leaving a deposit composed of a single age group. Since the MDQ bones at the MDQ underwent little transport, no transport biases are expected. The MDQ assemblage was not subjected to significant taphonomic biasing as a result of either selective mortality, long-term attritional accumulation, or differential transport mechanism, so the skeletal material contained therein should be an accurate reflection of the composition of the biological group from which the assemblage was derived.

#### 4. Big Bend locality

The Big Bend *Alamosaurus* site, in the Upper Cretaceous Javelina Formation of west Texas, contains multiple juvenile titanosaurs (Fiorillo, 1998a). Streams and rivers depositing the Javelina Formation generally flowed in a southeastwardly direction on an alluvial plain (Lehman, 1986). Precise stratigraphic position of the quarry within this rock unit is difficult to discern because the outcrop exposure is sporadic. The quarry is comprised of two basic lithologies (Fiorillo, 1998a). The lower unit is a light to medium gray to greenish-gray siltstone, generally massive in appearance. The upper contact is sharp and irregular. The overlying unit is also a siltstone, but maroon in color. Based on the fine-grained nature of both of these units, the general depositional setting for this bonebed is interpreted as part of the floodplain facies (Fiorillo, 1998a; Fiorillo and Montgomery, 2001). The fine-grained matrix and the presence of charophytes suggest the presence of a non-ephemeral lake margin (Fiorillo and Montgomery, 2001).

Recovered elements compare well with those described by Gilmore (1922, 1946), so it can be determined confidently that the assemblage contains the remains of *Alamosaurus sanjuanensis*. The minimum number of individuals at this site (three) is determined by the number of left femora (Fiorillo, 1998a). These individuals are considered juveniles because the femora are approximately 50%–60% the size of those of an adult femur of this taxon and the neurocentral sutures are unfused on all vertebrae recovered (cervicals and dorsals). The weathering stage of the bones is minimal. The occurrence of a few steeply plunging bones ( $>30^\circ$ , *sensu* Fiorillo, 1988) and an irregular contact between the two lithologic units that is suggestive of sauropod footprints in cross section imply that the accumulation of bones underwent significant bioturbation following deposition (Fiorillo, 1998a).

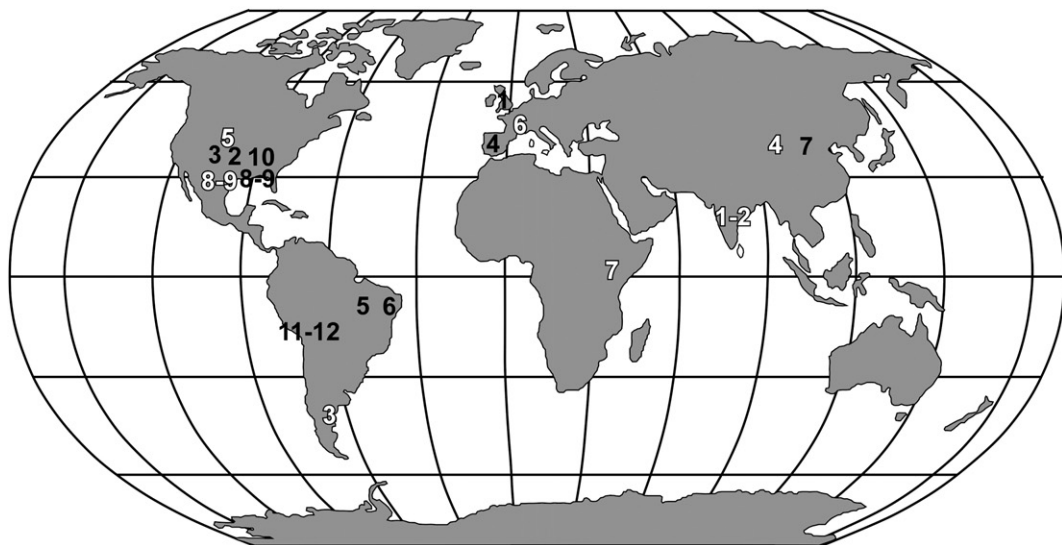
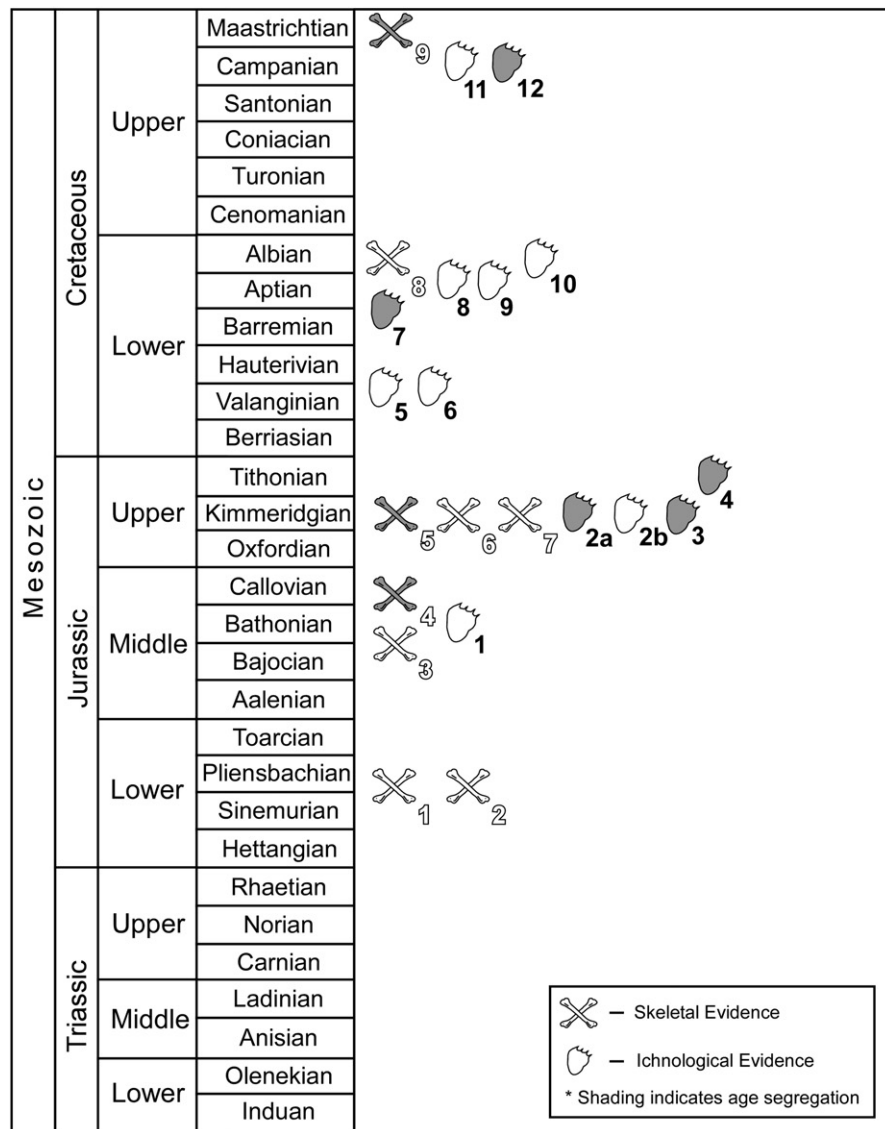
Minimal weathering of the bones in the assemblage indicates that all three individuals died in a single event and were buried together rather than accumulated attritionally. The juvenile *Alamosaurus* quarry stands in direct contrast to other occurrences of sauropod remains in the Javelina Formation (Table 3). All other sites are solitary accumulations of single individuals. Based on the size of the elements found, the majority of occurrences may be attributed to adults, with uncommon occurrences of isolated juvenile remains. We suggest that

**Table 3**

Table showing frequency of modes of preservation for sauropod remains from the Javelina Formation (Late Cretaceous) in west Texas

| Mode of preservation                | Number of localities |
|-------------------------------------|----------------------|
| Isolated adult skeletal elements    | 23                   |
| Isolated juvenile skeletal elements | 4                    |
| Multiple juvenile individuals       | 1                    |

This table was derived from observations in the field and in the collections housed at the Texas Memorial Museum by ARF. Based on comparison with adult forms, all juveniles were all two-thirds adult size or smaller. Note there were no observations of multiple individuals of adults.



**Fig. 4.** Temporal/geographic distribution of skeletal and ichnological accumulations showing evidence of gregarious behavior in sauropods. Numbers correspond to localities in Tables 1 and 2.

this mode of preservation is a function of a behavioral phenomenon in *Alamosaurus* that relates to ontogenetic age. In addition to the data in Table 3, the lack of discovery of a bonebed containing adult *Alamosaurus* nearly 100 years after this taxon was first recognized implies that adult forms of these animals were solitary, while immature forms existed for part of the year in small herds or pods.

Individual animals today die by disease, accident, or some form of biological defect. Further, it is common for isolated juveniles to have higher mortality than adults. Therefore, the isolated occurrences of juvenile *Alamosaurus* remains may reflect a higher mortality amongst this age group. In contrast, the Big Bend quarry accumulation represents an ecological snapshot of a mortality event, thereby providing data that allow for a behavioral interpretation. Thus, the occurrence of isolated juvenile individuals of *Alamosaurus* does not impact the behavioral conclusions below.

## 5. Modern age segregation

Gregarious behavior is thought to have evolved because it increases the fitness of individuals within a group, relative to solitary living (Alexander, 1974). Formation of social groups will be favored by natural selection when associated fitness benefits, such as decreased risk of predation and increased foraging efficiency, outweigh costs, such as increased competition for resources and increased transmission of diseases and parasites (Alexander, 1974). In order to maintain group cohesion, individuals within a group must synchronize their behavior in terms of time spent resting, foraging, and moving (Conradt, 1998). Intraspecific differences in individual activity budgets and movement rates of modern ungulates are largely a function of body size, so fitness costs related to synchronization of these behaviors are minimized when groups consist of animals of similar body size (Ruckstuhl, 1999). For gregarious taxa with pronounced sexual dimorphism, reduction of fitness costs related to synchronization would favor the formation of groups based on sex or age (Ruckstuhl and Neuhaus, 2000; Ruckstuhl and Neuhaus, 2001). Indeed, ungulate taxa with pronounced sexual dimorphism show a higher frequency of sexual segregation (Mysterud, 2000). Sexual differences in predation risk and forage selection are secondary contributing factors to segregation of populations by sex (Ruckstuhl and Neuhaus, 2002). Segregation of groups by sex or age is influenced further by reproductive cycles, population size, resource distribution, and environmental conditions (Main et al., 1996).

Based on patterns of gregarious behavior in modern taxa, it is probable that dinosaurian herds were highly variable in composition. The composition and size of modern herds vary between taxa and often change seasonally, depending on the timing of reproductive cycles or the availability of forage (e.g., Western and Lindsay, 1984; Bender and Haufler, 1999). Some animals, such as elk, show extreme variation in group size and composition within a single geographically-defined population. Although certain aspects of elk social behavior follow a seasonal schedule, at any given point in the year some herds are segregated by age and/or sex, other groups are mixed, and some individuals remain solitary (Bender and Haufler, 1999). The variation in herd composition observed in this modern population, irrespective of predictable seasonal cycles, suggests caution is warranted for attempts to generalize aspects of gregarious behavior in extinct taxa.

## 6. Implications for sauropod behavior

If interpretations of age segregation based on the MDQ and Big Bend evidence are correct, these sites confirm a unique aspect of sauropod behavior that has few other supporting examples in the fossil record. le Loeuff (2005) suggested that overrepresentation of young individuals in collections of sauropod material from the Late Cretaceous of Romania was the consequence of sampling bias related to age partitioning of sauropod communities and invoked resource

partitioning as an explanation for the separation of adults and juveniles into distinct herds. In fact, utilization of different types of forage by mature and immature sauropods has been indicated by studies of dental microwear (Fiorillo, 1998b). Given dietary differences and the extreme size difference between immature and adult sauropods, individuals in a mixed-age group would incur significant fitness costs from behavioral synchronization, perhaps rendering mixed-age herds less beneficial than age-segregated groups under certain conditions. If ontogenetic difference in body size was a controlling factor in the development of age-segregated herds, sauropod taxa that reached greater adult size would be expected to demonstrate age segregation more frequently than taxa of smaller size. Examination of the sauropod fossil record supports this conclusion. Though no adult specimens are known for the MDQ diplodocoid taxon or *Bellusaurus*, *Alamosaurus* grew to a very large size (Lehman and Coulson, 2002) resulting in a significant difference in body size between immature individuals and fully mature adults.

Recognition of age segregation of sauropod herds may have implications for our understanding of parental care as well. If juveniles formed groups separate from adults, parental care must not have lasted far beyond the hatchling stage of development, if sauropods exhibited parental care at all. This conclusion contrasts notably with the findings of Coria (1994), who suggested, based on the mixed-age sauropod assemblage in the Middle Jurassic of Patagonia, that sauropod behavior was characterized by extended parental care. These contrasting inferences imply a diversity of behavioral strategies within the Sauropoda. The sauropod taxa discussed here constitute too small a sample of skeletal material to delineate taxonomic trends in behavior, and known tracksites lack the taxonomic resolution necessary to integrate them accurately into a behavioral analysis. Temporal and geographic trends in modes of gregarious behavior are also not apparent, even considering both skeletal and ichnological data (Fig. 4). While it is possible that age segregation evolved multiple times within the Sauropoda, a more likely explanation for the lack of patterning in the data is behavioral flexibility within taxa. Given the variation in herd composition observed in modern analogues, such variability is not unexpected for sauropods, though the existence of multiple juvenile-only sauropod assemblages indicates recurring behavioral strategies.

## 7. Conclusions

The MDQ contains the remains of a herd of diplodocoid sauropods that succumbed to drought conditions and were entombed by a high-density sediment flow. The Big Bend locality contains the remains of a herd of *Alamosaurus* that died near an ancient lake margin. In both cases, the group from which the death assemblage was derived consisted of immature individuals only. These two sites represent the first well constrained skeletal evidence of age segregation of sauropod herds and suggest that parental care was either minimal or non-existent in some sauropod taxa. The identification of age segregation in an array of tracksites indicates that age-partitioned herds were present in different sauropod groups at different times. Development of age-segregated herds in large sauropods such as *Alamosaurus* suggests that this behavioral strategy may be the result of increased costs of behavioral synchronization related to ontogenetic difference in body size. Although both the body fossil and ichnofossil records contain evidence of age-segregated herds, sauropods likely exhibited a wide variety of gregarious behaviors. Based on the range of variation observed in modern gregarious taxa, herd composition may have varied according to seasonal or reproductive cycles. The MDQ and Big Bend localities are important test cases because investigations of other monospecific and paucispecific sites thought to contain herds may allow delineation of evolutionary trends in gregarious behavior and age segregation, as well as determination of the extent of variation in gregarious behavior within certain groups of herbivorous dinosaurs.

Developing a detailed taphonomic history for each site is a necessary first step in this process, for without an understanding of the processes responsible for site formation, biases with the potential to affect behavioral interpretations cannot be identified adequately.

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