Geology

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Geology 2009;37;843-846
doi: 10.1130/G30188A.1

Notes

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ABSTRACT

An unusually high proportion of large-bodied carnivorous theropod dinosaurs has been reported from the Moroccan Late Cretaceous Kem Kem Formation, a well-known package of North Africa vertebrate fossil–bearing sediments. We investigate whether recorded proportions of predator and prey taxa in Kem Kem sediments are real, or an artifact generated by collecting biases, by comparing field data to counts of fossil vertebrates from Moroccan fossil shops. The application of common techniques for standardizing ecological survey data confirms that previous workers have been misled by the acquisition by museums of specimens from commercial collectors rather than from detailed field surveying. Claims that an unusual number of theropod dinosaurs were present in North Africa Late Cretaceous ecosystems are likely the result of biases due to both commercial activity and collectorship biases.

INTRODUCTION

Vertebrate fossils have been known from the Kem Kem Formation in the Moroccan Sahara of North Africa for more than 50 years (Lavocat, 1954). This intensively collected sequence (i.e., the Kem Kem beds of Sereno et al., 1996) comprises Late Cretaceous (Albian–Cenomanian) fluvial and shallow-marine sediments exposed in southeastern Morocco (Province d'Errachidia) around Erfoud (e.g., Hamada du Guir and Tafilalt) that are part of the "continental intercalaire" (Lavocat, 1954) that extended across much of North Africa during the late Mesozoic. In terms of described taxa, taking fossil records at face value, large theropod dinosaurs were disproportionately abundant in Kem Kem Formation sediments (e.g., Russell, 1996; Sereno et al., 1996; Amiot et al., 2004; Weishampel et al., 2004), even though such a preponderance of carnivores defies what we know about modern ecosystems (Farlow, 1993). How could ecosystems like those that composed the Kem Kem have supported so many predators at the apex of the food chain, while relatively fewer potential prey taxa (e.g., herbivorous dinosaurs, smaller vertebrates) are known from the same sequence? We dub this paradox Stromer's Riddle, after Ernst Stromer, who worked on fossil vertebrates from North Africa during the 1930s, describing some of the key taxa of large theropods (Stromer, 1936; Russell, 1996; Nothdurft, 2002). Understanding Stromer's Riddle has wide implications for vertebrate paleoecology: is it valid to use vertebrate fossil records, either published or housed in museum collections, to reconstruct ancient ecosystems?

Paleoecological studies based on Moroccan material are further complicated because of the widespread commercial fossil trade: many vertebrates described from the Kem Kem Formation were obtained from dealers rather than field collected (e.g., Novas et al., 2005). Such collections have a positive effect on our knowledge of taxonomic richness, as they sample rare taxa in the right tail of the specimens:taxa curve discussed by Koch (1998), yet biased sampling of rare taxa can produce a distorted picture of ecosystems (Goldwasser and Roughgarden, 1997). We hypothesize that this collectorship effect is strongly biasing understanding of the relative proportions of taxa in Kem Kem Formation vertebrate faunas.

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COLLECTORSHIP BIASES

Similar collectorship biases have already been identified in museum data: Davis and Pyenson (2007) performed a comparative analysis of rarefaction curves of North American Paleocene mammal faunas from museums and field collections and reported a tendency for collector curves based on museum data to have steeper initial trajectories because of preferential sampling of rare taxa. Museums tend not to accumulate large numbers of common taxa, while rare taxa are biased in collections toward "trophy specimens" (Davis and Pyenson, 2007). Guralnick and Van Cleve (2005) demonstrated the importance of museum collections for capturing records of rare taxa, increasing species-richness estimates for extant birds in southern Colorado.

Here we examine Stromer's Riddle by comparing field-counted vertebrate abundance data from a single stratigraphically well correlated site within the Kem Kem Formation to counts of fossils from Moroccan fossil shops. We suspect that data from fossil shops are analogous to museum collections in that they are unlikely to accurately sample true faunal proportions at a particular place and time, simply providing data about the presence of taxa. Biases identified by Guralnick and Van Cleve (2005) and Davis and Pyenson (2007) would be magnified in shop data because the rarity, or aesthetic appeal, of a fossil will augment its economic value, irrespective of its scientific worth. Thus we address two questions. (1) How comparable are field and fossil shop-based surveys? (2) Were there really too many theropods in the Kem Kem Formation, or are collecting biases the source of reports of an unusual predator:prey ratio?

MATERIALS AND METHODS

Field data come from the Kem Kem Formation locality of Gara Sba (e.g., Lavocat, 1954; Sereno et al., 1996) (030°30.879N, 004°50.224W) in southeastern Morocco (Table 1). Field data were compared with averaged counts of vertebrate fossils recorded in six Moroccan fossil dealerships (Table 1). Using rarefaction and resampling techniques, we tested

TABLE 1. COUNTS OF INDIVIDUAL KEM KEM FORMATION FOSSILS AND ASSIGNMENTS TO BROAD VERTEBRATE TAXA

	Shops* (counts)	Shops (percentages)	Field (counts)	Field (percentages)
Crocodilians	256	35.3	140	36.8
Pterosaurs†	24	3.3	12	3.2
Nonavian theropods	178	24.5	57	15.0
Sauropods	58	8.0	2	0.5
Ornithischians	14	1.9	5	1.3
Chelonians	158	21.8	194	51.1
Birds§	2	0.3	6	1.6

Note: Fossils comprise bones, teeth, and carapace fragments.
*Some fossils counted in the field were not retained; no fossils were purchased as part of this study.
†Fragmentary pterosaur bones and teeth from the Kem Kem Formation are referable to Ornithocheiridae, Pteranodontidae, Tapejaridae, and Azdarchidae (Barrett et al., 2009).
§Fossil birds remain undescribed. An isolated vertebra reported by Riff et al. (2004) from the Kem Kem Formation exhibits no avian synapomorphies.

whether the observed relative proportions of higher taxa in shop and field data sets are drawn from the same distribution.

Rarefaction was used to generate collectorship curves for the two faunas ("field" versus "shop") using Analytic Rarefaction 1.4 (Holland, 2003). To test whether the two collections sample from the same pool of taxa, a resampling program was written by one of us (McGowan; available upon request). Resampling with replacement was used, with sampling probabilities derived from the combined pool of specimens from shop and field (Table 1). We generated two distributions, based on 1000 replications in each case: one of n = 416 (number of individuals in field sample) and the other with n = 690 (number of individuals in shop samples). Results were expressed as proportions of the total sample for comparison with observed proportions.

RESULTS

Comparison of Proportions of Higher Taxa Between Shop and Field Samples

To determine whether the two data sources are converging on common proportions of each higher taxon, field and shop samples were plotted as histograms (Fig. 1A). Even this simple analysis highlights taxa being sampled in similar proportions from each data set: when sampling is equivalent the bars should be ~50:50, although divergence is expected when sample size is small (Raup, 1976). However, in the shop sample all major nonavian dinosaur taxa are overrepresented (Fig. 1A). Figure 1B emphasizes the increased proportions of theropod and sauropod dinosaur material in the shop sample, while our field sample contains a higher proportion of turtles and birds.

Rarefaction and Resampling Results

Rarefaction curves for the shop and field samples have markedly different equations and shapes (Fig. 2A). It is surprising that our field sample captures high diversity with fewer specimens. Note that in the central section of these curves, the shop samples provide higher diversity estimates, but at higher sample sizes the field collection performs better (Fig. 2A). Rarefaction results indicate that field data are more consistent at recovering the full suite of higher taxa present when samples with more than 100 specimens are taken.

Resampling results are shown in Figure 2B; significant differences between the two groups are observed within the shop and field samples for turtles, theropod, and sauropod dinosaurs. The dinosaur taxa compose a significantly higher proportion of the shop sample than would be expected from the combined pool, while chelonians make up a significantly higher proportion of our field sample and a significantly lower proportion of our shop sample (scraps of fossil turtle shell don't sell well). Fossil birds compose a significantly higher proportion of the field sample than predicted:

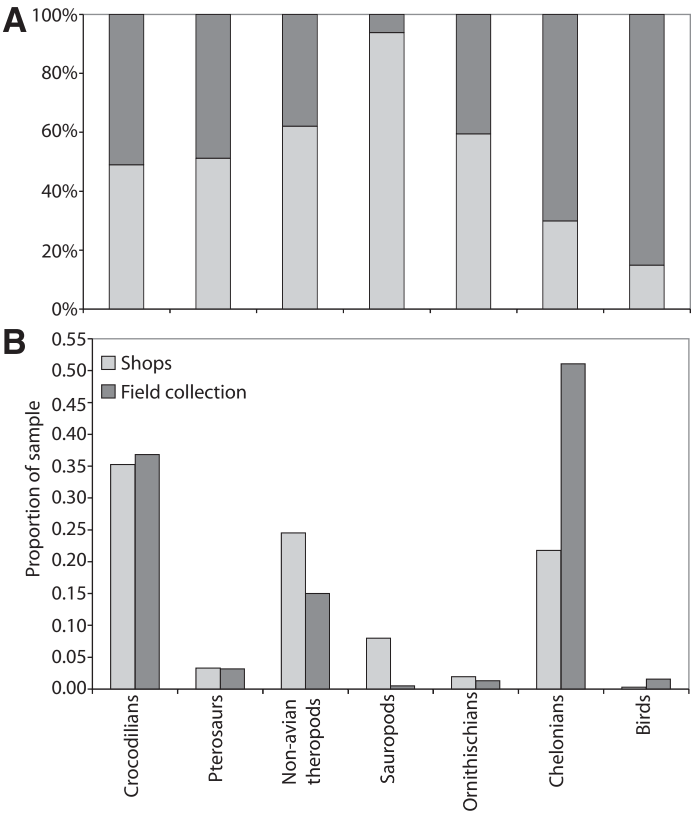

Figure 1. Counts of Kem Kem Formation fossils and referrals to higher vertebrate taxa as percentages: A: Proportions as stacked columns. If shop and field samples are similar, then proportions should be ~50:50 (with scope for variation at low sample sizes). B: Bars stacked side by side to emphasize departures from 50:50 ratio. Three dinosaurian higher taxa are all overrepresented in shop samples, while birds and chelonians are overrepresented in field samples.

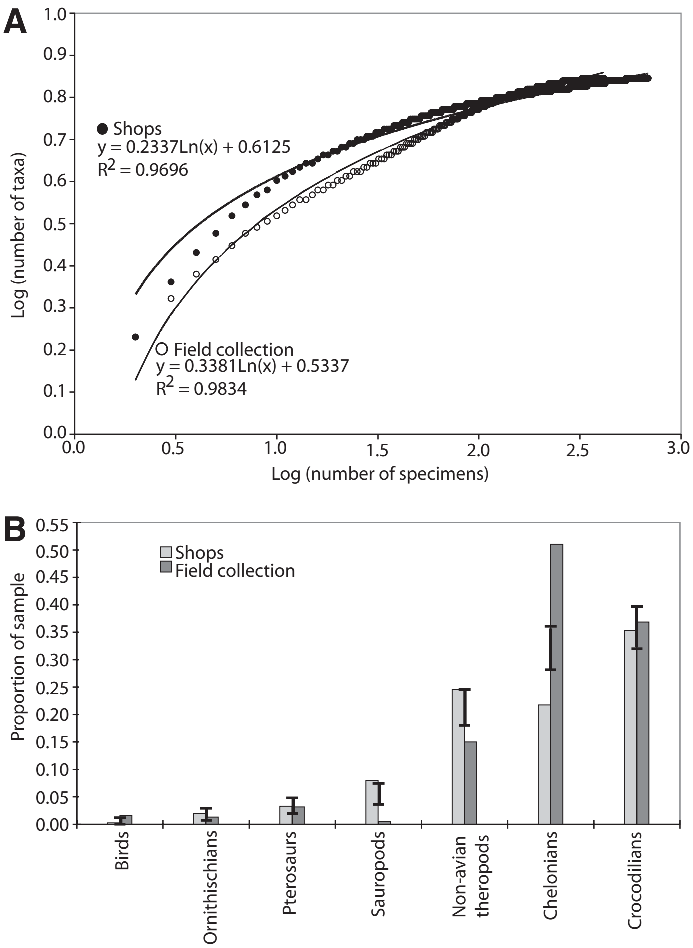

Figure 2. Rarefaction and resampling results. A: Plots of shop and field samples with logistic models fitted. Our shop samples, just like museum collections, tend to capture more diversity at lower numbers of specimens, although crossover occurs at ~100 specimens, when field sample begins to sample more of the diversity. B: Comparison of observed proportions higher taxa between shop and field samples with 95% confidence limits derived from resampling model.

these taxa are represented by small, morphologically cryptic bones that are easily overlooked in the field.

DISCUSSION

Need for Collection Protocols and Education of Commercial Collectors

Our results highlight the clear potential for differences in data collection and surveying methodologies to bias estimates of taxon abundance, richness, and spatio-temporal distributions. Such biases are especially prevalent in vertebrate paleontology where small numbers of taxa from individual localities or geological units (e.g., Kem Kem Formation) are often used to build paleoecological scenarios or even to model food webs (Farlow, 1976, 1993; Béland and Russell, 1980; Farlow and Pianka, 2002; Nothdurft, 2002). This has wide-ranging implications: that such simplistic models continue to be applied in vertebrate paleontology is surprising, given that sampling effects are well known to ecologists. Significant effort goes into designing biological surveys to avoid bias and to control the quality of survey data (Sutherland, 2005), while the use of predator:prey ratios was used as one cornerstone in debates over dinosaur metabolism (e.g., Béland and Russell, 1980). Of even more concern, fossil vertebrate collections often completely lack stratigraphic control. It is clear that broad proportions of taxa from a thick sedimentary unit cannot be used to build a model for local paleoecology (i.e., taxa known from the full 100 m thickness of the Kem Kem Formation cannot used to reconstruct faunal ecology).

More generally, given the element of serendipity involved in fossil collecting, the biases we have identified are unsurprising. What is less forgivable is the filtering of collections, or uneven search effort in the field, for particular taxa or trophy specimens. Selection of material that is eventually accessioned into museum collections is another bias that has been noted for collections of extant (Guralnick and Van Cleve, 2005) and fossil taxa (Raup, 1976; Guralnick and Van Cleve, 2005). When rarefaction to small sample sizes is carried out with museum collection data, it is possible for a low specimen:species ratio to create a false impression of high diversity in samples that do not record abundance data with high fidelity and thus disproportionately sample rare taxa (Koch, 1998).

It is well known that commercial collectors operate in Morocco by accumulating large volumes of disarticulated Kem Kem Formation material (individual teeth and skeletal elements). Predatory taxa, whether extinct or extant, have an allure in many human cultures that makes these trophy specimens more attractive even than complete skeletons or skulls of other, less enigmatic, animals, and means that they have a high economic value. This bias is due to commercial, rather than scientific, priorities; M. Dale, a fossil dealer in Edinburgh, Scotland, indicated that this explanation was feasible, based on his own experiences of selling Kem Kem Formation specimens. Equally, although our field sample only represents a small collection effort, it nevertheless provides important baseline data on the differences likely to emerge between field surveys that record all data rather than those than recover a selective, filtered subset of the fauna.

Abundance data are extremely valuable, and Alroy et al. (2008) demonstrated their potential for improving understanding of diversity fluctuations through time. We urge field collectors to at least record all material at a given site, even if it cannot all be collected, to increase the amount of data available for abundance-based analyses.

Relative Proportions of Dinosaur Higher Taxa Reanalyzed

Statistical comparison of the relative proportions of the three major dinosaur groups known from the Moroccan Late Cretaceous indicates that theropods and sauropods are significantly overrepresented in fossil shop samples. While reports of theropods are common in the literature, sauropods have much less frequently been described, restricted to one genus (*Rebbachisaurus*; see Weishampel et al., 2004).

Comparison of proportions of carnivores and herbivores between the Kem Kem Formation (71% carnivore, 29% herbivore based on shop data), the intensively sampled Late Cretaceous Hell Creek Formation of North America (7% carnivores, 93% herbivores; Pearson et al., 2002), and a similar 10:1 herbivore:carnivore ratio for several Early Cretaceous East Asia basins (Matsukawa et al., 2006) highlights the apparent oddity of the Kem Kem Formation proportions; ecological theory would lead us to expect proportions more similar to those of Hell Creek and the East Asia beds. Our resampling study indicates that differences between shop and field samples could be adding 5%–10% to the relative number of theropods in collections in the range of 400–500 specimens.

This still leaves an apparently unusually high number of theropods in the Kem Kem Formation (relative to other Cretaceous basins, if counts are representative of actual populations), perhaps explained by relaxing assumptions about food webs based on hypercarnivory. Such assumptions have been shown to create the false impressions that Australian marsupial mammal diversity and abundance patterns are driven by low productivity (Wroe et al., 2004); with this in mind, high abundance in the Kem Kem Formation of the large fish-eating theropod *Spinosaurus* seems reasonable in an ecosystem famous for its fossil fish. Theropod dinosaurs also regularly shed their teeth, and these have formed the basis for some descriptive studies (Amiot et al., 2004). More broadly, other factors could be responsible for the low numbers of sauropods and ornithischians. The latter group, despite a difference in proportions (Fig. 1), was recorded extremely rarely in both shop and field samples (Table 1). Skeletal remains of these dinosaurs have yet to be formally described from the Kem Kem Formation, although their footprints (alongside those of theropods) characterize a bed that caps the Gara Sba sequence (Sereno et al., 1996); counts reported here are tentative, based on fragmentary limb elements and broken teeth observed in the field (Table 1). Fastovsky and Sheehan (2005) discussed the potential for taphonomy and variable preservation of individuals to skew the North American dinosaur record, and such biases need further study in the Kem Kem Formation. Another issue that relates to all three groups is the lack of studies of the minimum number of individuals represented by the remains recovered from the Kem Kem Formation. Given the large amounts of disarticulated material involved, this could be a significant source of overestimates of theropod numbers.

CONCLUSIONS

We know that major biases exist in the marine fossil record; they are taken seriously and are the subject of considerable research effort (e.g., Alroy et al., 2008). We also know that vertebrate paleontological data include a number of significant biases that can compromise analyses (e.g., Davis and Pyenson, 2007). Our findings examine just one aspect of human bias in an important North Africa Late Cretaceous unit, and clearly show that the vagaries of fossil collecting, rather than unusual community assembly dynamics, are a credible source of the odd proportions of dinosaurian higher taxa reported from the Kem Kem Formation.

Analysis of counts from shops compared to field data indicates that fossil shops have a higher proportion of dinosaurian taxa for sale, particularly large-bodied theropods, than other fossil vertebrates. Such obvious biases must be accounted for before building scenarios that invoke non-analogue communities based on data that have not been vetted and statistically analyzed. Hutton's (1795) remark about geological processes, "the present is the key to the past," remains extremely pertinent to vertebrate paleoecology.

ACKNOWLEDGMENTS

We are profoundly grateful to Nour-Eddine Jalil, Fouad Ouanaimi, Remmert Schouten, and Julia Sigwart for their support. Paolo Viscardi and Matt Dale assisted with commercial aspects and Mike Benton, Eric Buffetaut, Lionel Cavin, Steve Cumbaa, Alex Kellner, Paul Upchurch, David Varricchio, Ian Somerville, and two anonymous reviewers provided access to specimens, advice, and comments on earlier drafts. This study was supported by an Alexander von Humboldt Foundation Fellowship to McGowan. Dyke was supported by University College Dublin and Chris and Clare Leonard.

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Manuscript received 3 March 2009
Revised manuscript received 14 April 2009
Manuscript accepted 28 April 2009

Printed in USA