GIS and Paleoanthropology: Incorporating New Approaches from the Geospatial Sciences in the Analysis of Primate and Human Evolution.

By: R.L. Anemone, G.C. Conroy, and C.W. Emerson

Link to published version with set statement: This is the pre-peer reviewed version of the following article:

RL Anemone, GC Conroy, CW Emerson (2011) GIS and Paleoanthropology: Incorporating New Approaches from the Geospatial Sciences in the Analysis of Primate and Human Evolution. *Yearbook of Physical Anthropology (Supplement to the American Journal of Physical Anthropology),* 146, Suppl 53:19-46.

which has been published in final form at http://onlinelibrary.wiley.com/doi/10.1002/ajpa.21609/abstract.

Abstract:

The incorporation of research tools and analytical approaches from the geospatial sciences is a welcome trend for the study of primate and human evolution. The use of remote sensing (RS) imagery and geographic information systems (GIS) allows vertebrate paleontologists, paleoanthropologists, and functional morphologists to study fossil localities, landscapes, and individual specimens in new and innovative ways that recognize and analyze the spatial nature of much paleoanthropological data. Whether one is interested in locating and mapping fossiliferous rock units in the field, creating a searchable and georeferenced database to catalog fossil localities and specimens, or studying the functional morphology of fossil teeth, bones, or artifacts, the new geospatial sciences provide an essential element in modern paleoanthropological inquiry. In this article we review recent successful applications of RS and GIS within paleoanthropology and related fields and argue for the importance of these methods for the study of human evolution in the twenty first century. We argue that the time has come for inclusion of geospatial specialists in all interdisciplinary field research in paleoanthropology, and suggest some promising areas of development and application of the methods of geospatial science to the science of human evolution. Yrbk Phys Anthropol 54:19–46, 2011.

Keywords: paleoanthropology | spatial analysis | remote sensing | geographic information systems | anthropology

Article:

Paleoanthropology, the search for and analysis of human and nonhuman primate fossil remains, is today a highly interdisciplinary science with a long history of appropriation of methods and techniques of analysis from related scientific fields. But it was not always this way. The earliest paleoanthropologists were mostly trained as archaeologists or medical doctors and early fieldwork was typically carried out by individual workers or small teams who would excavate fossil sites and publish their results without significant input from other specialists (Dart, 1925, 1948; Broom, 1938, 1949). Fragmentary fossils were reconstructed by the knowing hand and discerning eye of experienced anatomists, with liberal amounts of plaster of Paris to fill in the missing pieces, and evolutionary relationships were determined by phenetic comparisons with modern taxa. Fossil localities were often identified in a serendipitous and/or haphazard fashion, for example as the result of mining operations in the case of the famous australopithecine-bearing caves of South Africa (Broom, 1950; Dart, 1959), or as the result of initial exploratory work by geologists such as in the case of Ethiopia's Middle Awash Valley (Taieb et al., 1972), or even by a lepidopterist such as in the case of Olduvai Gorge (Morell, 1995)! More recently, paleoanthropologists have sought their training in such diverse fields as biological anthropology, prehistoric archaeology, geology, vertebrate paleontology, paleoecology, functional morphology, and genetics (among others).

Modern paleoanthropological research typically involves collaborations, both in the field and in the laboratory, with specialists in such areas as geochronology, palynology, vertebrate paleontology, taphonomy, genomics, computer imaging, and stratigraphy. This new, interdisciplinary approach has revolutionized the field in many ways. For example, it is now almost routine to digitize and CT scan fossils in three-dimensions, allowing previously hidden internal features to be revealed and missing parts to be virtually reconstructed—a technique first introduced to paleoanthropology only two decades ago (Conroy and Vannier, 1984, 1987, 1991; Vannier et al., 1985; Conroy et al., 1990). In addition, phylogenetic relationships of fossil taxa can now be studied by comparative genomics (Krings et al., 1997; Green et al., 2008), and recent advances in the recovery and analysis of ancient DNA hold great promise for creating a single, comprehensive “tree of life” (Hofreiter et al., 2001; Delsuc et al., 2005; Letunic and Bork, 2007).

The history of fieldwork in Africa is informative in illustrating the existence of at least three different stages in the evolution of paleoanthropological inquiry and analysis. The earliest stage can be called the single-investigator approach, and it is exemplified by the work of Robert Broom (op. cit.) and Raymond Dart (op. cit.) in the South African caves that yielded the first evidence of Plio-Pleistocene hominins in Africa. Broom and Dart were both medical doctors who worked independently on human evolutionary studies in the field and the lab from the 1920s through the 1950s. Continuing mostly in the single-investigator mode, Louis and Mary Leakey worked for much of the 1950s and 60s at Olduvai Gorge, with the able help of their crew of African fossil collectors (Leakey, 1958, 1959, 1961). Discoveries of fossil hominins at Olduvai led to successful collaborations between the Leakeys and anatomists Philip Tobias and John Napier (Leakey et al., 1964), geologist Richard Hay (1976), and geochronologists Garniss Curtis and Jack Evernden (Leakey et al., 1961). This body of work set the stage for further development of the interdisciplinary approach in the 1970s and 80s on the eastern side of Lake Turkana by Richard Leakey (Leakey and Walker, 1976, 1985, 1988) and along the Lower Omo River by F. Clark Howell (Coppens et al., 1976; Howell 1978a, b; Howell et al., 1987). Howell is generally recognized as the major intellectual force to first fully implement the interdisciplinary and integrative approach in African paleoanthropology that brought together teams of specialists in different areas including stratigraphy, radiometric dating, archaeology, vertebrate and invertebrate paleontology, and palynology (Corruccini and Ciochon, 1994; Pope, 1994). The latest stage in this developmental sequence of paleoanthropological inquiry can be seen in much of the research currently underway in East and South Africa. While still highly interdisciplinary in the manner developed by Howell and Leakey, much recent paleoanthropological work includes the latest developments in imaging, scanning and 3-D reconstruction of specimens that have been called Virtual Anthropology (Weber, 2001; Weber et al., 2001), as well as the use of remote sensing techniques and geographic information systems for identifying suitable fossil exposures (Njau and Hlusko, 2010).

Increasingly, paleoanthropologists are collaborating with geographers, cartographers, and remote sensing specialists to apply the tools of the geospatial sciences to a variety of research questions that share a spatial component in paleontological studies (Conroy, 2006; Conroy et al., 2008). Here we review the application of some of these tools and analytical methods, specifically the use of geographic information systems (GIS) and remote sensing (RS) to the study of human and primate paleontology, and suggest some promising avenues for further collaborative research between anthropologists and geospatial scientists. We suggest that the application of new methods and analytical approaches from the geospatial sciences can provide exciting insights to numerous paleoanthropological investigations, as well as many other anthropological questions that involve a spatial component. While the application of these new techniques to vertebrate paleontology and human evolutionary studies is still in its infancy, the potential for significant new insights, and perhaps even paradigm shifts, is great.

THE NEW GEOSPATIAL SCIENCES

A geographic information system (GIS) is a set of hardware and software tools for collecting, managing, analyzing, querying, and displaying nearly any kind of data that have a spatial component (Marble, 1990). GIS allows researchers to organize and interrogate geographically referenced information in a multitude of innovative ways that can illuminate patterns and relationships within the data. GIS software is but one part of an emerging discipline known as geographical information science (Goodchild, 1992). GIScience includes the rapidly evolving theory, techniques, and applications that underpin the GIS software itself, as well as the processes of characterizing, measuring, storing, and analyzing all types of spatial phenomena. Two key technologies-global navigational satellite systems such as the Navstar Global Positioning System (GPS) operated by the US Department of Defense, and aircraft or satellite borne digital remote sensing scanners, such as can be found on the Landsat series of satellites, provide the means to both locate existing phenomena and to search for items of interest over the entire earth's surface.

Modern geospatial technologies such as geographic information systems, satellite and airborne remote sensing, and global navigational satellite systems enhance our ability to collect, store, analyze and represent geographical data. This process presents unique challenges, since geographical phenomena are inherently complex since they have spatial, descriptive, and temporal components. One must use Cartesian or other types of spatial coordinates to locate features. Describing features or phenomena involves a systematic method of recording, organizing, and retrieving quantitative and qualitative measurements (including locations), typically in the form of a database management system: such database systems are typically used by modern museums in cataloguing and georeferencing their collections. Because geographical phenomena often change over time, some means of recording or representing temporal changes is necessary for understanding dynamic phenomena and processes.

GIS data models

We can represent complex geographical phenomena utilizing one of three available data models: vector, raster or triangulated irregular networks (TINs). Discrete phenomena can be characterized using the vector model, where the locations of small objects are represented as (x,y) or (x,y,z) coordinates. Features with length, but (conceptually) no width are represented as vector lines, or strings of coordinates. Area features are represented as linear boundaries that reconnect to enclose the feature. In a typical vector GIS, each discrete point, line, or area feature is linked to a single record in a database management system that contains descriptive quantitative or qualitative attribute information.

Some phenomena, such as temperature, vary continuously over an area and do not necessarily have sharp boundaries. These types of phenomena are represented in a GIS as surfaces or fields, where each (x,y) location in a mapped area has a unique z value. Fields may be discontinuous, in that they have void areas; they may be piecewise continuous, with sharp changes in measured z value and rate of change of z; they may be once differentiable, in which value changes slowly from one location to the next, but the slope can change abruptly; or they may be twice differentiable, or smoothly continuous.

The raster data model is one way of representing continuous phenomena. A raster consists of rows and columns of identically sized grid cells or pixels. Each cell is assigned a measured value such as barometric pressure or brightness (in the case of imagery). If the measured value is assumed to represent the entire area of the cell or pixel, the raster is termed a grid. A lattice, by contrast, is a regular row and column arrangement of spot measurements that are not assumed to represent areas in between the lattice mesh points. In practice, lattices are handled in a similar fashion to grids in most GIS applications. Many types of manipulations, such as interpolation, resampling to different spatial resolutions, extraction, and projection can be performed on raster data sets. Specialized tools such as surface analysis (described briefly below), hydrological modeling, and spatial statistics are based on the raster model. Map algebra (Tomlin, 1991), a “language” for analyzing raster data sets, includes tools such as local functions that operate on a cell by cell basis, zonal functions that operate on groups of cells that share some characteristic, global functions that derive characteristics such as cost functions, and focal functions that operate on groups of neighboring cells in a moving window.

The TIN data model incorporates some of the advantages of both the vector and raster data model. TINs are a series of linked triangles, where the heights of the corners of the triangles correspond to the z value of the surface. The triangles form “facets” that show the overall form of the surface. Unlike the raster model, which is restricted to the row/column arrangement, the corners of the TIN triangles can be at any (x,y) location, thus the form of objects such as ridges, valleys, and void areas is not restricted to the blocky, stair-step arrangement of a raster. In GIS applications, TINS are most often used to represent topography, in finite element models, to interpolate surface z-values and to derive vector contour lines.

History of GIS

The dim beginnings of GIS can be traced back to the work of John Snow, a medical doctor in Victorian England, who is often considered a founding father of two different medical disciplines, anesthesiology and epidemiology (Johnson, 2006). His pioneering epidemiological work involved the suggestion that the London cholera epidemic of 1853–54 was spread primarily by a sewage-contaminated water pump on Broad Street. In the crude hand-drawn map that Snow created, we can see the humble beginnings of GIS. Snow used vertical bars to represent the number of cholera deaths in individual households in South London. The clustering of these fatalities near the Broad Street pump, which supplied drinking water to the neighborhood, suggested to Snow that cholera was a water-borne microbial disease. Although the number of cases had already peaked and was in decline, he convinced the local authorities to remove the pump handle on the Broad Street pump. This was done on, September 8, 1854, and the cholera epidemic was soon over.

The first modern computerized GIS was developed in the mid- 1960s by Roger Tomlinson to maintain an inventory of Canada's land resources and was known as the Canada geographic information system (CGIS; Tomlinson, 1998). At around the same time, Howard Fisher established the laboratory for computer graphics and spatial analysis at the Harvard graduate school of design and developed the SYMAP raster GIS and the ODYSSEY vector GIS (Chrisman, 2006). The US Census Bureau developed the dual independent map encoding-geographic database files (DIME-GBF) system for use in the 1970 decennial census (Cooke, 1998), and expanded and refined this street-address database for later censuses as the topologically integrated geographic encoding and referencing (TIGER). The development of relatively inexpensive minicomputers in the late 1970s and 1980s led to the adoption of GIS technology by several large governmental agencies (Foresman, 1998), while smaller agencies and businesses adopted GIS in the 1990s when UNIX workstations and Windows microcomputers became sufficiently powerful to run commercial software packages such as Arc/INFO, ArcView, Intergraph GeoMedia, and MapInfo.

Today GIS is used by researchers in many different fields to solve numerous and diverse spatially related problems. It has become a staple of government, commerce, and industry, ranging from land use and environmental planning to cartography and the national census. Its value for intelligence gathering is obvious as its use in the hunt for Osama bin Laden suggests (Gillespie et al., 2009). The tools and techniques of GIS have increasingly become an important component of many scientific research programs in a wide variety of different disciplines, including anthropology, geology, biology, paleontology, and environmental science. Several commercial software applications exist for GIS (e.g., MAPINFO, IDRISI), as does at least one free application (GRASS), but the clear-cut industry leader is ArcGIS from environmental systems research institute (ESRI) of Redlands, California.

Remote sensing

Remotely sensed imagery and maps are an important source of data for GIS-based investigations. Remote sensing is the measurement or acquisition of information by a recording device that is not in physical contact with the object or phenomenon under study. In most cases, the information being measured is electromagnetic radiation. Measurements of the interactions of electromagnetic radiation with the earth's surface are recorded by either a film camera or digital scanner that is typically mounted on an airplane or satellite platform. It can be argued that remote sensing-based mapping began with Gaspard-Félix Tournachon, an early French photographer and journalist, who, in 1855 obtained a patent for drawing maps from aerial photographs. “Nadar,” as Tournachon was known, is generally credited with obtaining the first aerial photographs from a balloon in 1858 (Newhall, 1964). The obvious military applications of this new technology were immediately recognized, and aerial photography has been used in every conflict since the American civil war. The use of film persisted even into the space age, when the early military remote sensing satellites ejected spent film canisters via parachute into the earth's atmosphere, where they were picked up by specially equipped aircraft for processing and analysis.

Civilian digital earth imaging was first employed in the early 1960s in meteorological satellites such as TIROS (television infrared observation satellite). In the mid to late 1960s this technology was extended to imaging the earth's surface itself using the visible and near-infrared parts of the electromagnetic spectrum. The first of a series of civilian remote sensing satellites that eventually became known as Landsat was launched in 1972. Landsat 5 and 7 are currently active, and today France, China, and many other countries as well as private firms operate earth observation satellites.

The original Landsat multispectral scanner (MSS) imagery had pixels that were roughly 80 m on a side. The MSS had four bands in the visible light and near infrared parts of the electromagnetic spectrum. When Landsat 4 became operational in 1982, the technology had improved so that the pixels for the Thematic Mapper (TM) scanner were nominally 30 m in size and included two additional bands (in the blue–green and infrared range) and one lower resolution thermal IR band. Landsat 7 carries the Enhanced Thematic Mapper+ (ETM+) sensor, which has the same multispectral bands as the earlier TM sensor, plus a 15-m panchromatic (gray scale) band for a total of eight available bands (Table 1).

Table 1. Spectral and spatial characteristics and applications of the Landsat 7 ETM+ Sensor

Band	Sensitivity (μm)	Spectrum	Spatial resolution (m)	Applications
1	0.45–0.52	Blue	30	Water penetration
2	0.52–0.60	Green	30	Green vegetation
3	0.63–0.69	Red	30	Chlorophyll absorption, cultural features
4	0.76–0.90	Near IR	30	Vegetation health, soil moisture
5	1.55–1.75	Mid IR	30	Vegetation, soil moisture, snow/clouds
6	10.4–12.5	Thermal IR	120	Vegetation, soil moisture, thermal

7	2.08–2.35	Mid IR	30	Minerals
8	0.52–0.90	Panchromatic	15	Gray scale image/pan sharpening

The Landsat program spurred the rapid development of digital image processing and analytical techniques in the civilian sector. Application software packages such as ERDAS and ENVI (ITT Technologies) allow users to georeference imagery so that it is registered to other spatial data sets, convert the digital brightness measurements to physical units such as W m^{-2}, statistically classify images to yield thematic land cover maps, and export images into other formats for use in GIS, word processing and presentation software. By 2009, the entire Landsat archive was available free of charge from the US geological survey (edc.usgs.gov). Other sources of mid- to high-resolution imagery, such as the French SPOT (systeme pour l'observation de la terre) and the commercial IKONOS and Quickbird satellites charge from $0.40 to ∼ $60.00 per square kilometer, depending on the source, age and amount of preprocessing of the data.

In addition to analog aerial photography and digital scanners that use reflected solar radiation to produce images in the visible and near infrared portions of the electromagnetic spectrum, other technologies such as radar and lidar (light detection and ranging), use their own sources of energy to produce images or measure surface elevations. A digital elevation model (DEM) is a lattice of spot elevation measurements that can be used to derive a number of indices that characterize topographic surfaces (Moore et al., 1991). The slope and aspect of the surface can be computed at each pixel in a DEM to determine the rate and direction of overland flow and erosional processes. Curvature, the second derivative of the changes in elevation (slope of the slope) indicates the rate of change in flow along and across a surface (Zeverbergen and Thorne, 1987). Curvature can be computed in both plan and profile directions. Profile curvature affects the acceleration and deceleration of flow down slope, while plan curvature influences horizontal convergence and divergence of flow.

For visualization purposes, a DEM can be converted to a hillshade layer, which uses a solar light source (usually in the northwest at an elevation of 45 degrees) to add shadows that fall toward the viewer. In a GIS visualization, overlays such as aerial or satellite photos or maps of surface geology are made semi-transparent and draped over the hillshade layer to create a 3-D effect that allows one to relate mapped features to topographical features (see Fig. 1).

Figure 1. Four different images of the northwestern part of the Great Divide Basin demonstrate how imagery derived from remote sensing can reveal overlapping aspects of local topography and surficial geology. Black dots are fossil-bearing localities. (A) geological map of Wyoming.

(B) Digital orthophoto (DOQ). (C) Digital elevation model (DEM). (D) Geological map and DOQ draped over DEM with hillshade applied. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Global navigational satellite systems (GNSS), such as the American NAVSTAR global positioning system (GPS), the Russian GLONASS, and the European Galileo system, have become widely available and today are routinely used by most field workers in anthropology. Although GPS and GLONASS were initially developed for military purposes, the civilian applications have revolutionized car, truck, and ship navigation, air traffic control, and have made accurate field measurements by paleontologists and paleoanthropologists much easier to obtain than they were in the days of traditional optical surveying methods and paper map reading.

Practical use of GPS for site surveys necessitates higher accuracy than that provided by simple standalone receivers. Atmospheric conditions, satellite and receiver clock drift, and uncertainties in the orbital position of satellites require corrections obtained via the use of multiple frequencies or multiple receivers, one of which is a base station at a known location. Differential correction (Parkinson and Enge, 1996) improves the root mean square error of GPS measurements from approximately roughly 40 m to between 2 and 5 m. Surveying applications generally set up a base station over a benchmark or other known monument and obtain field measurements using a separate roving receiver. Postprocessing software corrects the field measurements and reformats the observations into GIS compatible formats. For nautical navigation, the US Coast Guard, Army Corps of Engineers, and other entities concerned with shipping have a network of GPS base stations broadcasting on VHF, allowing suitably equipped receivers to obtain real time corrections. In North America, Western Europe and parts of east Asia, satellite-based systems such as the Wide Area Augmentation System (WAAS) extend differential correction to aircraft navigation (Kee, 1996). These systems receive information from ground base stations and rebroadcast the corrections over large areas. Today, even simple, consumer level GPS receivers employ this technology to enhance accuracy, making post-processing unnecessary.

REMOTE MAPPING AND IDENTIFICATION OF ROCK UNITS

Paleontologists and paleoanthropologists require knowledge of the geology of their field areas to successfully locate fossil-bearing deposits, and this knowledge is often gained through examining geological maps that, at various scales, depict the surface geology of the region. While large scale geological maps (1:24,000 or greater) may provide detailed information on exposures of and contacts between different rock units, many parts of the world have not yet been mapped at this level of detail by field geologists. Experience suggests that lithological contacts drawn on small scale geological maps (1:100,000 or less) often involve a large degree of interpretation and interpolation, resulting in less than precise information on the availability and location of outcrops of particular units on the ground. Advances in geospatial science now allow investigators to determine rock types and environments of deposition, as well as identify known geological units (e.g., formations and members), through examination and analysis of data and images derived from a variety of remote sensing techniques and instruments.

GIS and RS are by now well-accepted tools that geologists routinely use for mapping surface geology and for identifying land forms and structural elements in a landscape (An et al., 1995; Bilotti et al., 2000; Pederson et al., 2002; Belt and Paxton, 2005). While much of this work is oriented towards the location of mineral deposits (Kaczmarek et al., 2010) and seemingly of little interest to the paleoanthropologist, a closer look at this literature suggests otherwise. in fact, many of the geospatial approaches used to remotely identify geological features are directly applicable to the search for hominin or primate fossils, as more and more paleontologists are coming to realize (Stucky et al., 1989, 1990; Stucky and Krishtalka, 1991; Conroy, 2006; Conroy et al., 2008; Njau and Hlusko, 2010). In particular, the geological literature utilizing GIS and RS establishes that each of the following geological features can be identified and distinguished one from another by their characteristic signatures in RS images

- major and minor lithological units (e.g., formations, members, tongues, beds),
- different facies, representing different depositional environments (e.g., fluvial, lacustrine, deltaic)
- structural features (e.g., faults and folds, anticlines and synclines, strikes and dips).

Like the petroleum geologist, paleontologists want to know where certain resources can be found. If fossils are preferentially located in certain lithologies or facies, or in association with certain structural features, then our search can be optimized by the use of remote sensing (to locate the features) and geographic information systems (to analyze their spatial relations). The real strength of GIS is that it allows us to combine and overlay multiple layers of spatial information to identify patterns that can lead to new insights, better understanding, and ultimately predictive models.

One approach to remotely mapping the extent of known geological units has been applied to the search for Paleogene fossil mammals in the Wind River Basin of central Wyoming by researchers from the Carnegie Museum of Natural History and the Denver Museum of Nature and Science (Stucky et al., 1989, 1990; Stucky and Krishtalka, 1991), in collaboration with NASA scientists from the Jet Propulsion Laboratory (Conel et al., 1985; Lang et al., 1987). The Wind River Basin is famous among vertebrate paleontologists for its rich early Eocene fossil mammal deposits from near the towns of Lysite and Lost Cabin, WY (Granger, 1910; Robinson et al., 2004). It has also been well mapped geologically (Tourtelot, 1957; Keefer, 1965, 1970; Korth, 1982), allowing a close comparison of traditional geological maps with the results from the remote sensing analysis. Stucky and coworkers (op. cit.) used data from the Landsat 5 Thematic Mapper (TM) spectral scanner to differentiate between members of the Wind River formation, the main terrestrial sedimentary unit of early Eocene age in the Wind River Basin (see Fig. 2). Remote sensing data included six of the seven available bands of electromagnetic information derived from the visible and near infrared spectrum. Principal components analysis (PCA) was applied to the TM data, and false color images were derived from the first six eigenvectors derived from the analysis. The resulting images could then be compared to published geological maps and checked on the ground. The results indicated that the Lysite and Lost Cabin members of the Wind River formation could be just as easily distinguished on the RS images as on the ground. Red mudstones, lenticular sandstone bodies, and conglomerates with clasts derived from Paleozoic and Mesozoic rocks predominate in the Lysite member, while the Lost Cabin member includes drab to variegated mudstones, channel sandstones, and conglomerates with clasts derived from Precambrian rocks (Stucky and Krishtalka, 1991). Precambrian and Mesozoic strata in the Wind River Basin could also be easily differentiated on the basis of these false color images (ibid).

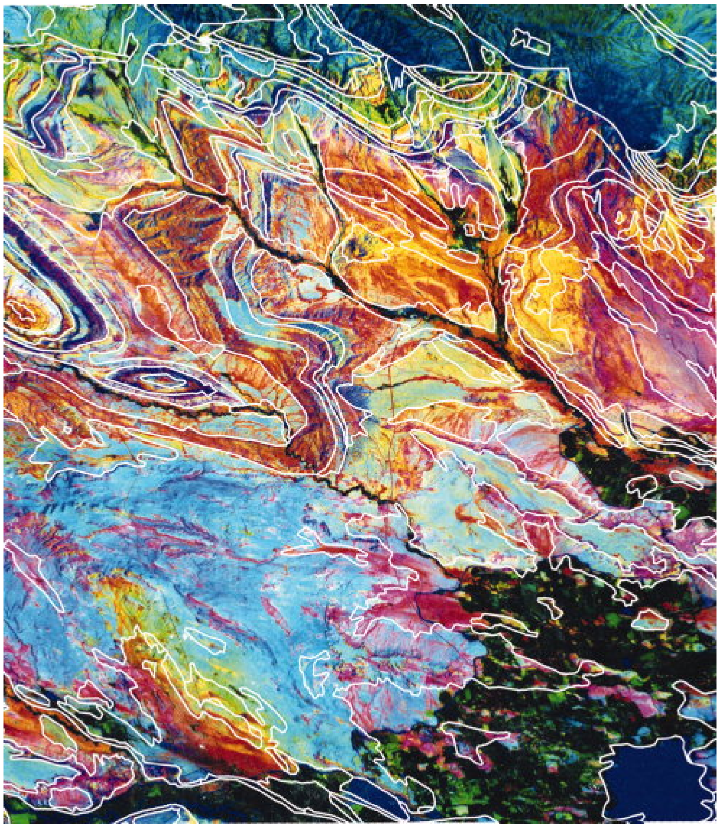

Figure 2. Principal components image of the northwestern part of the Wind River Basin, Wyoming. This image is a color composite of the 1st, 2nd, and 3rd principal components of all seven Landsat ETM+ bands displayed as red, blue and green, respectively.

We can demonstrate this approach to remote geological mapping in our own research area of the Great Divide Basin of southwestern Wyoming, where several intertonguing members of the early Eocene Green River and the Wasatch formations crop out between the Fort Union formation of Paleocene age and the Bridger formation of middle Eocene age. Figure 3 shows a classified Landsat image of the western Great Divide Basin in Wyoming. The ISODATA unsupervised classification image analysis algorithm (Tou and Gonzalez, 1974) statistically clustered the brightness values for the visible and near infrared bands of a Landsat 7 ETM+ mosaic of the Great Divide Basin, Wyoming. The statistical clusters were related to ground cover in an inductive process, so that vegetated (mostly sagebrush) areas are shown in green, sparse grass areas are yellow, bare soil or rock is brown, and sand is white. The red polygons are from the Wyoming bedrock geology map, digitized at a scale of 1:500,000 (Love and Christianson, 1985). In the upper left of this figure, the Tipton Shale member of the Green River formation (Tgt) intertongues with the main body of the Wasatch formation (Twm). Several fossil-bearing localities (indicated by black points) were found in this area. These localities were associated with sandstone outcrops in the main body of the Wasatch (Twm) just north of a large, east–west trending sand dune deposit (Qs) marked by intermittent bright white areas of very reflective sand dunes. The correlation between the different types of land cover in the classified Landsat image and the geological map are evident in this figure.

Figure 3. Classified Landsat image of the western Great Divide Basin, Wyoming with overlay of digital Geological Map of Wyoming. Black dots indicate fossil localities. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Spectral data from the Landsat 7 Enhanced Thematic Mapper + (ETM+) sensor have recently been used to remotely map lithological facies on a series of six different carbonate platforms and coral reefs ranging from the West Indies to the Persian Gulf (Kaczmarek et al., 2010). In this analysis, facies maps were generated on the basis of an unsupervised classification of seven visible and infrared spectral bands with a spectral resolution of 28.5 m, derived from the ETM+ sensor. The classification of sediments and depositional environments or facies that resulted from the remote sensing data analysis were compared to sediment maps derived from sampling on the ground. In all four areas where sufficient data were available, ∼ 85% agreement was found between sedimentary deposits identified from the remote sensing analysis at points where sediments were collected and identified on the ground (ibid). In addition to this excellent agreement at a macro scale (e.g., at a spatial resolution of nearly 30 m), the authors suggest that at a more detailed scale, the “Landsat facies maps exhibit significant improvements over published maps in the dimensions of individual facies bodies. Landsat facies maps capture more of the natural architectural complexity and internal heterogeneity with facies belts than conventional mapping techniques… (which are) created at far lower resolution than what Landsat provides and therefore offer a fairly unrealistic representation of aerial facies distributions” (Kaczmarek et al., 2010; p 1604).

The usefulness to the paleoanthropologist of this approach to mapping environments of deposition and lithological facies via analysis of remote sensing images should be obvious. Fossils of different kinds of organisms tend to be found preferentially in certain lithological facies and not in others because of the associations between environments of deposition and the locations where these organisms tended to be found while living (in open grasslands or in woodlands, near rivers or lakes), and where they tended to die. This is as true of Eocene primates as it is of Plio-Pleistocene hominins, and much of the work of paleontologists in the field is to determine these associations and to search for the lithologies that tend to be more productive for the taxa they are interested in finding. An Eocene example can be found in the work of Roehler and coworkers in the Vermillion Creek area of southwestern Wyoming (Roehler and Martin, 1987). Here, close to the common border of Wyoming, Colorado and Utah, detailed geological work indicated the presence of seven different depositional environments during the early Eocene deposition of the Niland tongue of the Wasatch formation. These different facies ranged from alluvial fans and conglomeratic sandstones deposited on the Uinta mountain front, through upland and lowland flood plains, paludal and peat bog deposits, to onshore delta and beach deposits and offshore lacustrine oil shales and carbonates (Roehler, 1987). Characteristic mammalian fossils of early Eocene (Wasatchian) age have been recovered from many localities in the Niland Tongue, typically and most frequently in flood plain deposits, while fish remains are, not surprisingly, found in lacustrine deposits (Roehler, 1987). In our own work in the Great Divide Basin of Wyoming, some 60 miles north of Vermillion Creek, mammalian fossils are most frequently found in river channel and overbank deposits of the Wasatch formation whose remote sensing signature is currently being explored by a variety of techniques and approaches (Emerson and Anemone, in press). The ability to remotely identify different environments of deposition can also aid in the search for fossil hominins in the African Plio-Pleistocene. In their discussion of the paleoenvironmental context of the Hadar site in Ethiopia, Campisano and Feibel (2008) suggested that the great majority of fossil hominins and other vertebrates come from fluvial channel sands and silty overbank deposits in the Hadar formation, rather than from the multiple levels of lacustrine deposits or other paleoenvironmental settings present in the vicinity.

A variety of innovative approaches have been used by geospatial scientists to remotely map lithological units in three dimensions and evaluate geological structures and processes. For example, Pederson et al. (2002) were able to determine maximum values of uplift and erosion on the Colorado Plateau since it was positioned at sea level during the Late Cretaceous, between about 90 and 65 million years ago. Utilizing 100 points of known elevation in the region today, the authors used a raster-based GIS model with a cell size of 1 km to develop a tensional spline algorithm for interpolating a continuous topographic surface across the region (ibid). This model used the elevations of the five nearest cells to interpolate the elevation of a given cell, and was successfully tested for accuracy against the actual topography as revealed by a digital elevation model (DEM). The same algorithm was then used to recreate the landscape topography at the Eocene-Oligocene boundary (ca. 30 million years ago), a time when the plateau landscape is thought to have undergone a transition from a predominantly depositional to a predominantly erosional state and when Laramide orogeny had been completed. Data points for the paleo-landscape model came from measured elevations of 69 points where the Eocene-Oligocene stratigraphic boundary is preserved and exposed today (ibid). With these three landscape models in hand (i.e., Late Cretaceous, Eocene-Oligocene boundary, and present day); the authors were able to estimate the total amount of erosional exhumation of the Colorado Plateau over the past 30 million years (nearly 1 km). This allowed them to estimate the total amount of uplift resulting from the isostatic rebound in response to post-Eocene erosion (ca. 600 m) and from early Cenozoic Laramide uplift (ca. 2 km). The elevation estimates for the Eocene–Oligocene boundary landscape derived from this GIS-based model were consistent with a variety of independent geological and paleontological estimates, thus increasing confidence in the model (Pederson et al., 2002).

Advanced analytical methods have been used with a variety of different remote sensing technologies, including satellite based multispectral scanners like SPOT, Landsat TM and ETM+, and airplane based approaches like digital orthophoto quadrangles (DOQs). These approaches allow researchers to develop complex three dimensional models of surface geology and structure. For example, Bilotti et al. (2000) demonstrated an elegant numerical method for measuring strike and dip of complexly folded beds by applying stereoscopic methods to Landsat TM images from several different regions of the North American and Andean cordilleras. In all cases, the calculated strikes and dips were within four degrees of the field measured values, in spite of the fact that a series of anticlines, synclines, and thrust faults provided complex structures and relationships. Belt and Paxton (2005) explored the relationship between bedrock geology and surface topography in a GIS by draping the mapped bedrock geology over a 30 m resolution DEM for a region in north central Oklahoma characterized by “subtle topography.” By creating map layers of slope and relief and overlaying these on the DEM, the authors were able to find associations between erosional patterns that influence the overall topography of the region and locally exposed bedrock types. The presence and thickness of sandstone units were found to be significantly related to erosional and topographic patterns evident in slope and relief.

One final approach to remote geological mapping involves the creation of scaled three dimensional images by draping geological maps and georectified aerial photos on top of a digital elevation model (DEM) in a GIS database (Banerjee and Mitra, 2004). By integrating topographic and geologic data for the Sheep Mountain anticline in the Bighorn Basin of northwestern Wyoming, Banerjee and Mitra (op. cit.) were able to accurately map formational contacts and measure strikes and dips that were comparable to data obtained in the field. In its four panels, Figure 1 illustrates how we have used a similar approach to mapping formational contacts and topography in our work in the Great Divide Basin of southwestern Wyoming. The three elements that are overlain to create the final composite image (Fig. 1D) include the bedrock geology of the region (Fig. 1A), a digital orthophoto (DOQ, Fig. 1B), and a digital elevation model (DEM, Fig. 1C). We then applied a hillshade to the DEM and draped the geology and DOQ over it to create the composite image seen in Figure 1D. This image nicely reveals the close fit between mapped geological units and the images derived from remote sensing and geospatial manipulation within a GIS.

REMOTE SENSING AND THE SEARCH FOR FOSSIL HOMININS

The use of remote sensing to explore sedimentary and volcanic deposits in search of new early hominin sites was pioneered in eastern Africa in the late 1980s by Ethiopian paleoanthropologists involved in a project sponsored by the Ethiopian government's Ministry of Culture. Developed in 1988 by Berhane Asfaw in collaboration with Tim White and several NASA space scientists, the “Paleoanthropological Inventory of Ethiopia” sought to assess the geological, paleontological and paleoanthropological resources of the mostly unexplored Main Ethiopian Rift and Afar depression (Asfaw et al., 1990). Recognizing that the areas of interest were vast, remote, and difficult to survey on the ground, Asfaw et al. took advantage of the availability of satellite, space shuttle, and airplane-borne multispectral scanners and other remote sensing instruments to visualize and differentiate lithologies (e.g., fluvial and lacustrine sediments, datable tephras, recent alluvium, basalt flows) and geological structures (e.g., fault escarpments and other features associated with rifting) of paleoanthropological interest. The initial Ethiopian work utilized standard aerial photo coverage on a scale of 1: 30,000, photographs taken by the space shuttle's large format camera (LFC) at a scale of 1:50,000, and the Landsat Thematic Mapper (TM) multispectral scanner, whose spatial resolution in each of its seven different bands was 30 m (ibid). False color mosaic images were produced from the TM data, and these images were used to distinguish between different lithologies on the ground and to identify unexplored areas that exhibited similar geological features to those with known fossil deposits. In our opinion, the “Paleoanthropological Inventory of Ethiopia” created a new research paradigm for paleoanthropology which was to yield great successes through the 1990s and into the first decade of the current century (see Fig. 4).

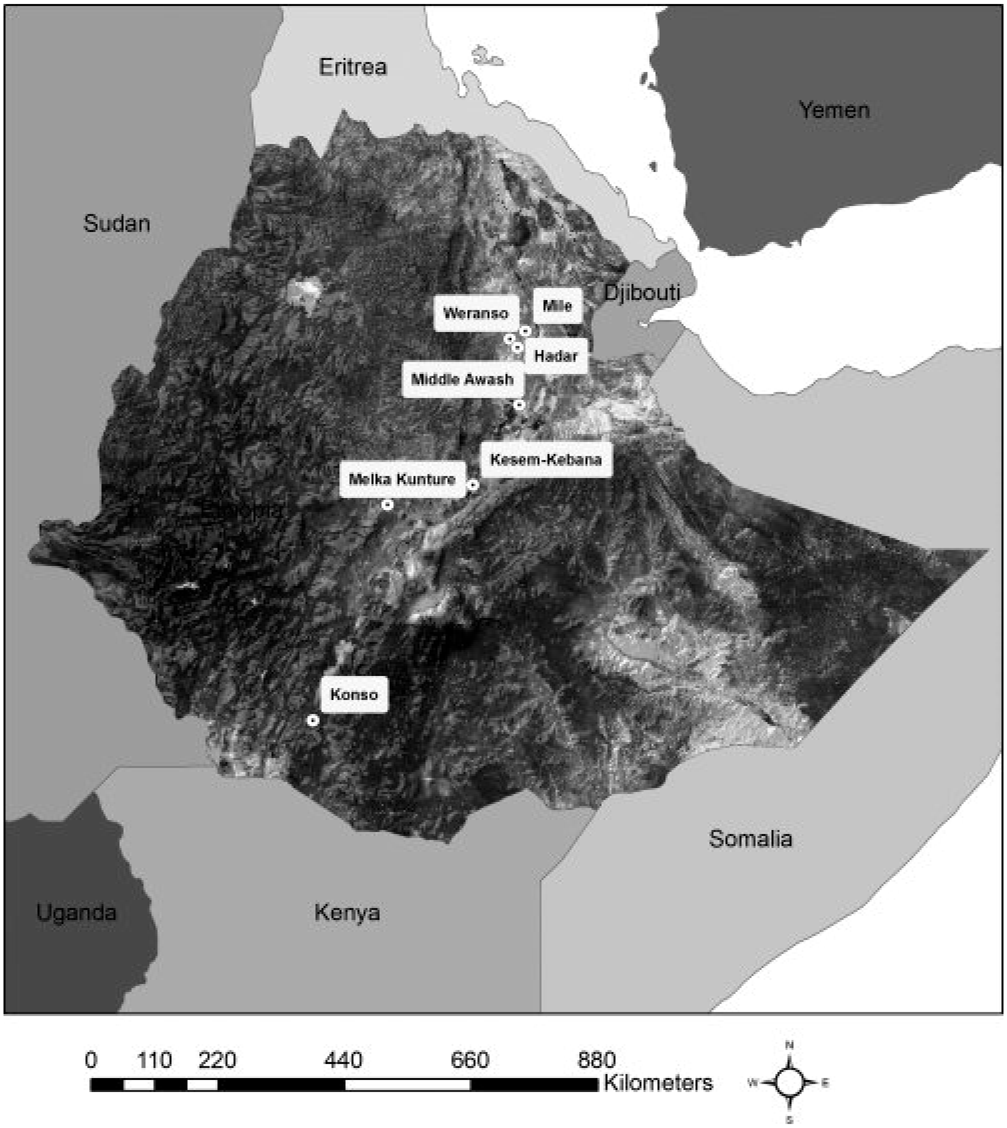

Figure 4. A cloud-free composite panchromatic image of Ethiopia obtained by the MODIS (MODerate resolution Imaging Spectroradiometer) sensor carried aboard NASA's Terra satellite. This image is distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (http://lpdaac.usgs.gov). 500 meter cloud-free pixels obtained during an eight day period in late December, 2010 were reassembled into a composite image. A gray-scale panchromatic image was created by taking the first principal component of the red, green and blue surface reflectance bands. This image was draped over a digital elevation model derived from the Global 30-arc second digital elevation dataset (GTOPO30), which is a global raster Digital Elevation Model (DEM) with a horizontal grid spacing of 30 arc seconds (approximately 1 kilometer) (http://edc.usgs.gov).

The first marked success of the approach developed by Asfaw et al. was the identification of potentially fossil-bearing sedimentary deposits ranging in age from Oligocene to Pliocene in the

Fejej area of southern Ethiopia (Gibbons, 1991; Wood, 1992). Described in 1991 as "the last major paleoanthropologically unexplored quadrant of the Omo River-Lake Turkana Basin" (Asfaw et al., 1991; p 137), Fejej lies just east of the exposures of the Usno and Shungura formations of the Lower Omo region made famous in the 1970s and 1980s (Coppens et al., 1976; Howell, 1978a, b; Howell et al., 1987). When the initial analysis of remote sensing images in 1988 indicated the presence of suitable deposits, an Ethiopian expedition to the area in 1989 provided the ground-truth for the presence of paleoanthropologically significant deposits that warranted further detailed exploration (Asfaw et al., 1991). At the suggestion of members of the Ethiopian research team, John Fleagle led a crew to Fejej in the Fall of 1990. Although they found no fossil vertebrates in the Oligocene aged deposits of the Langaria formation, Fleagle's team recovered middle Miocene vertebrates from the Bakate formation and Pliocene mammals, including 3.7-million-year-old dental remains from the Fj-4 locality identified at the time as among the oldest known fossil hominins (Fleagle et al., 1991). The hominin remains comprised seven teeth from at least two individuals, and most closely resemble teeth from Hadar and Laetoli attributed to Australopithecus afarensis. With an antiquity of at least 3.6 and potentially more than 4.0 million years, the Fejej hominin remains indicated that A. afarensis was present in the Lower Omo-Turkana Basin at about the same time as they occur at Laetoli (Johanson et al., 1978)

The success achieved by the "Paleoanthropological Inventory of Ethiopia" during the 1990s is best exemplified by the work of Asfaw, WoldeGabriel and their collaborators in the Kesem-Kebena region (Asfaw et al., 1990; WoldeGabriel et al., 1992). The methodology employed at Kesem-Kebena was an iterative one combining field surveys with analysis of remote sensing images, informed throughout by detailed geological knowledge of the mechanics and structural correlates of East African rifting. Landsat images from the Thematic Mapper instrument allowed the geologists to determine the main features of each rift segment (e.g., presence of boundary faults and escarpments) and to identify the spectral characteristics of surficial geological deposits, including those known to be fossiliferous. With this knowledge in hand, field surveys were then accomplished via a series of transects on foot and in four-wheel drive vehicles to sample the geological, paleontological and archaeological resources of each visited area. Geological samples of volcanic materials were collected for chronometric dating and mineralogical "fingerprinting" (WoldeGabriel et al., 1990), which allow regional correlation with the well characterized sections from the Turkana Basin (Brown et al., 2006) and even offshore (Sarna-Wojcicki et al., 1985), and the development of a local time scale and biochronology.

The Kesem-Kebena area lies west of the Awash River near the northern terminus of the Main Ethiopian Rift, far upstream of the Middle Awash and Hadar field areas to the north. This area had never been visited by geological or paleoanthropological field crews prior to its sediments being identified on Landsat TM images as potentially fossiliferous in 1988 (WoldeGabriel et al., 1992). Field surveys in 1989 quickly confirmed the presence of extensive "Pliocene and Pleistocene deposits of the Kesem-Kebena area, with their interstratified volcanics, well-preserved vertebrate fossils, and extensive archaeological evidence" (WoldeGabriel et al., 1992; p 490). In addition to a diverse Pliocene vertebrate fauna dating between 2.5 and 3.0 million years that included one primate (Theropithecus brumpti), Kesem-Kebena included a rich Middle Pleistocene (ca. 1.0 million years) vertebrate fauna and numerous Acheulean bifaces, as well as a Later Stone Age assemblage. The work at Kesem-Kebena demonstrated a clear "proof of principle" that the search for fossil and archaeological remains of early hominins could be facilitated through the application of new remote sensing techniques from the geospatial sciences. Further successes would come in the succeeding years, notably with the recovery of rich Acheulean deposits and Homo erectus remains from the early Pleistocene at Konso in the southern Main Ethiopian Rift (Asfaw et al., 1992; Suwa et al., 2007), and more recently, Pliocene hominins (Australopithecus sp.) and a rich vertebrate fauna from 3.5- to 3.7-million-year-old deposits in the Woranso-Mille area in the northern Afar region (Haille-Selassie et al., 2007).

The "Paleoanthropological Inventory of Ethiopia" represents the first, and still most successful, attempt to apply state-of-the-art remote sensing approaches to the search for early hominins and their archaeological remains. In spite of the demonstrated success and outstanding potential of the approach to paleoanthropological survey and exploration developed by Asfaw and his collaborators (Gibbons, 1991; Wood, 1992), very few other paleoanthropologists have utilized remote-sensing to aid in their search for fossil hominins in the more than 20 years that have passed since the original publications of the "Paleoanthropological Inventory of Ethiopia" team. More recently, however, high resolution satellite imagery (HRSI) using Google Earth (www.earth.google.com) and IKONOS satellite imagery has been successfully employed to locate small sedimentary units of paleontological/archeological interest in Tanzania that otherwise might have escaped detection and investigation (Njau and Hlusko, 2010). In contradistinction to the spatial resolution limitations of the earlier East African studies, some of this newer HRSI has spatial resolutions approaching 1 m. Using a combination of freely available (Google Earth) and commercial (IKONOS) high resolution satellite imagery, Njau and Hlusko (2010) were able to locate 28 new fossil/archeological localities in Tanzania by first identifying sedimentary units of potential interest based on erosional patterns and spectral reflectance "signatures" of sedimentary rock and then assessing the degree of vegetative cover and ease of access. Once potential sedimentary targets were identified, ground surveys were initiated to assess the paleontological/archeological significance of sites in essentially the same iterative fashion that had been developed earlier in Ethiopia. Njau and Hlusko (2010: see Supporting Information Online) also discuss the importance of ground truth for verifying interpretations derived from remote sensing imagery. They demonstrate that metamorphic rocks sometimes mimic sediments in having high reflectance and appearing white or very bright in false color-coded images derived from satellite data. These “false positives” may result from similarities in mineral or moisture composition or particle size of the rocks, and can only be identified through field surveys which allow testing of the interpretations derived from the analysis of remote sensing data.

GIS AND RS IN PALEONTOLOGICAL DATABASES

Much of the work in vertebrate paleontology in the American West occurs on federal lands administered by the Bureau of Land Management (BLM). The BLM's governmental mandate is to “regulate the collection, preservation, and curation of vertebrate and other fossils deemed to be significant” (Matthews et al., 2006; p 119), and since the 1990s they have been the leading advocates and early adopters of geospatial technologies in American vertebrate paleontology (Bryant and Matthews, 1998; DeBlieux et al., 2003; Matthews et al., 2005a, b; Foss et al., 2009). Matthews et al. (2006) review the many geospatial tools and techniques available to vertebrate paleontologists that can aid in the location, collection, curation, and preservation of fossil resources, many of which have been pioneered by BLM scientists, often in collaboration with academic paleontologists and geologists. Perhaps the most interesting examples they discuss, and the most relevant to students of human evolution, involve the use of remote sensing and photogrammetric approaches to document the spectacular dinosaur tracksites at Red Gulch in the Bighorn Basin of Wyoming (Breithaupt and Matthews, 2001; Breithaupt et al., 2001) and at Twentymile Wash in Utah's Grand Staircase-Escalante National Monument (Matthews et al., 2005a, b). A combination of data and images derived from close-range photography, standard aerial photos taken on blimps and Ultra-light aircraft, digital terrain models derived from satellite borne instruments, and even subsurface geophysical imaging techniques like Ground Penetrating Radar (GPR) were analyzed in a GIS environment. The use of integrated approaches like those utilized at these and other paleontological sites on BLM land hold much promise for the documentation and preservation of trace fossil resources like tracks, and would seem to be equally valuable if applied to sites yielding hominin footprints, for example Laetoli (Leakey and Harris, 1987) or Langebaan Lagoon (Berger and Hilton-Barber, 2000).

Another public agency at the lead in developing new geospatial approaches to geological and paleontological research is the Utah Geological Survey (UGS) (DeBlieux et al., 2003, 2004). The UGS has for some years been developing a comprehensive, searchable digital database of all known paleontological localities in the state of Utah. Incorporating this database with the digital version of the geological map of Utah allowed paleontologists at the UGS to produce a paleontological sensitivity map for the entire state of Utah (Kirkland et al., 2006). Each mapped rock unit was rated on a six-point scale from 5 ("Significant fossils are abundant and widespread; e.g., Morrison and Uinta formations") to 0 ("Map units represent rocks in which fossils are not preserved, such as igneous and high-grade metamorphic rocks"; Kirkland et al., 2006; p 77). While the usefulness of this map for both paleontologists and land managers is limited by the small scale of the base geologic map (1:500,000), work is underway at the UGS to develop larger scale (1:100,000) geologic base maps, which would greatly enhance the utility of these paleontological sensitivity maps.

GIS provide a powerful set of tools to the paleoanthropologist for the storage, retrieval, mapping, querying, and analysis of spatial data encoded in most fossil databases. Fossil locality coordinates in, for example, latitude/longitude or UTM units can be associated with paleontological data sets (specimen numbers, fossil descriptions, geologic/stratigraphic information, etc.) in spreadsheet form and then layered together to create interactive, unique maps for further analysis. Here we provide some examples from our work in several early Tertiary basins in Utah and Wyoming of how GIS can be used to create and display interactive maps of paleoanthropological interest; create custom maps based on any combination of fossil locality attributes (e.g., stratigraphic level, sedimentological characteristics, faunal composition); plan field logistics by mapping the accessibility of fossil localities using spatial (proximity) analysis; characterize topographic features of potential fossiliferous areas such as degree and/or aspect (direction) of slope on both regional and/or local scales, and share these data with other researchers by combining GIS with Google Earth (Conroy, 2006; Conroy et al., 2008). This kind of data sharing with professional colleagues and other interested scientists is increasingly a requirement of funding agencies and journals, and the approach described here can fulfill these requirements.

Since 1994, teams from Washington University (WU) under the direction of D. T. Rasmussen, and Western Michigan University (WMU) under the direction of Anemone, have been working in early Tertiary sediments of the Uinta Basin (Utah) and Great Divide Basin (Wyoming), respectively. The WU project has identified more than 200 fossil vertebrate localities within the Middle Eocene sediments exposed in the Uinta Basin (Rasmussen et al., 1999; Townsend et al., 2006) and the WMU project has identified nearly 100 localities in the Paleocene/Eocene deposits exposed in the Great Divide Basin (Anemone et al., 2007; Anemone and Dirks, 2009). Both of these sedimentary basins have played an important role in documenting trends in primate and early mammalian evolution during the early Tertiary, and their careful curation and georeferenced databases allow a number of interesting geospatial analyses.

Creating interactive maps: An example from the Uinta basin

The first layer of our interactive Uinta Basin map (Conroy, 2006) was created from digital terrain data accessed from the USGS seamless data distribution system (SDDS; seamless.usgs.gov). From these data, Digital Elevation Models (DEMs) were created that merged high-resolution best-quality elevation data into a seamless raster format. Shaded relief maps (see Fig. 5) were created from these same DEMs using a hillshade technique in which illumination is from northwest to southeast (hillshade parameters: 315 degrees azimuth, 45 degrees elevation). DEMs consist of terrain elevation data for ground positions at regularly spaced horizontal intervals, 10-m intervals being the ones used in the Uinta study. The scale of our DEM maps could be interactively changed, with acceptable results down to scales approaching 1:10,000. User defined elevation contours were also calculated and displayed on the DEMs using the spatial analysis extension of ArcGIS.

Figure 5. Digital elevation model (DEM) with hillshade of Washington University (WU) fossil localities (dots) in the Uinta Basin, Utah. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

The next layer added to our Uinta map was the WU fossil catalog data itself. The fossil catalog data was first saved as an Excel spreadsheet in comma delimited (csv) format and then layered onto the DEM map using the “Add XY data” command. In this way, the spatial relationship of each fossil locality was automatically registered to the digital elevation map and could subsequently be visualized at any user-defined scale. This Excel spreadsheet included a number of user-defined “attributes” for each fossil specimen: locality name, universal transverse mercator (UTM) coordinates, stratigraphic level (in meters), taxonomic identification, dental or skeletal element, etc. This WU locality “layer” was always kept as the topmost layer in the ArcMap table of contents so that it could be displayed over any of the other map layers since ArcMap always displays layers from the bottom layer to the top layer in the ArcMap table of content.

When it was desirable to have higher-resolution views of fossiliferous areas, new, higher-resolution map layers were created using Black and White Digital Orthophoto Quads (DOQs) of Uinta County retrieved from the Utah Automated Geographic Reference Center (agrc.utah.gov). These aerial photographs were exposed at a flying height of 20,000 feet above mean terrain and each DOQ used in the Uinta study covered 3.75 min of both longitude and latitude. Therefore, each 7.5 Quad consisted of four DOQ images and each pixel represented one square meter on the ground. Because DOQs are referenced to the North American Datum of 1983 and the universal transverse mercator (UTM) projection, the Uinta DOQs could be easily registered to our previously created DEM layers. By simply clicking on the WU fossil site covered in each DOQ, a complete list of the fossils recovered from that site, and all the information about those fossils recorded in the fossil catalog, is immediately displayed. In the same way, many additional AGRC shape-files (e.g., roads, place names, geologic maps, and contour intervals) were added as individual map layers to perform some of the analyses discussed below.

Querying the attribute table

Once all the map layers of interest are in place in the ArcMap table of contents, it becomes relatively simple to “query” the attribute table associated with the fossil catalog data. Here we discuss just some of the many possibilities. Let's imagine that a paleontologist wishes to query the Uinta Basin fossil catalog to see if, for example, any stratophenetic patterns emerge in a particular taxon of interest (in this example, the artiodactyl genus Protoreodon). By definition, such patterns of change can only emerge if putative ancestral taxa are lower in the stratigraphic section than their putative descendants. Thus, the first necessary step in such an analysis is to determine the relative stratigraphic relationships among the many hundreds of fossil Protoreodon specimens in the fossil catalog. This is easily done with GIS by simply querying the attribute tables of the various map layers using any combination of attributes relevant to the analysis and displaying the results as a new map layer. In this example, we might want to query the attribute tables to create a new map layer showing only those sites that have Protoreodon in the lower 50 m of the stratigraphic section, then another map layer showing only those sites that have Protoreodon in the next 50–150 m of the stratigraphic section, etc. By querying the attribute table (i.e., fossil database) to “select by attribute” (in this case by genus and stratigraphic level), only those fossil sites that meet both conditions of the query are identified in the newly created map layer. Once particular fossil localities of interest have been identified, hyperlinks can be created to relevant pdf and/or URL files thereby providing immediate access to further details about the locality and/or specimens of interest.

Paleoanthropological surveys in remote badland areas can be expensive, time-consuming, and logistically challenging. GIS provides valuable tools for planning and directing such field projects. Spatial (proximity) analysis tools in ArcGIS can be used to first create user-defined “buffers” around each fossil localities and then query the attribute data to find other attributes of interest lying within those buffer zone. For example, we first created a 100-yard buffer zone around each WU fossil locality, then created and layered a second map layer of existing oil and gas company roads on top of this WU fossil site layer. A new map layer was then created from the “intersection” of these two layers, thereby identifying only those WU fossil localities situated within 100 yards of a road accessible by a 4 WD vehicle (see Fig. 6). Such maps are helpful when “strategizing” about the logistical preparations needed to reach any particular fossil locality, or when heavy, plaster-jacketed specimens need to be carried out to the nearest road.

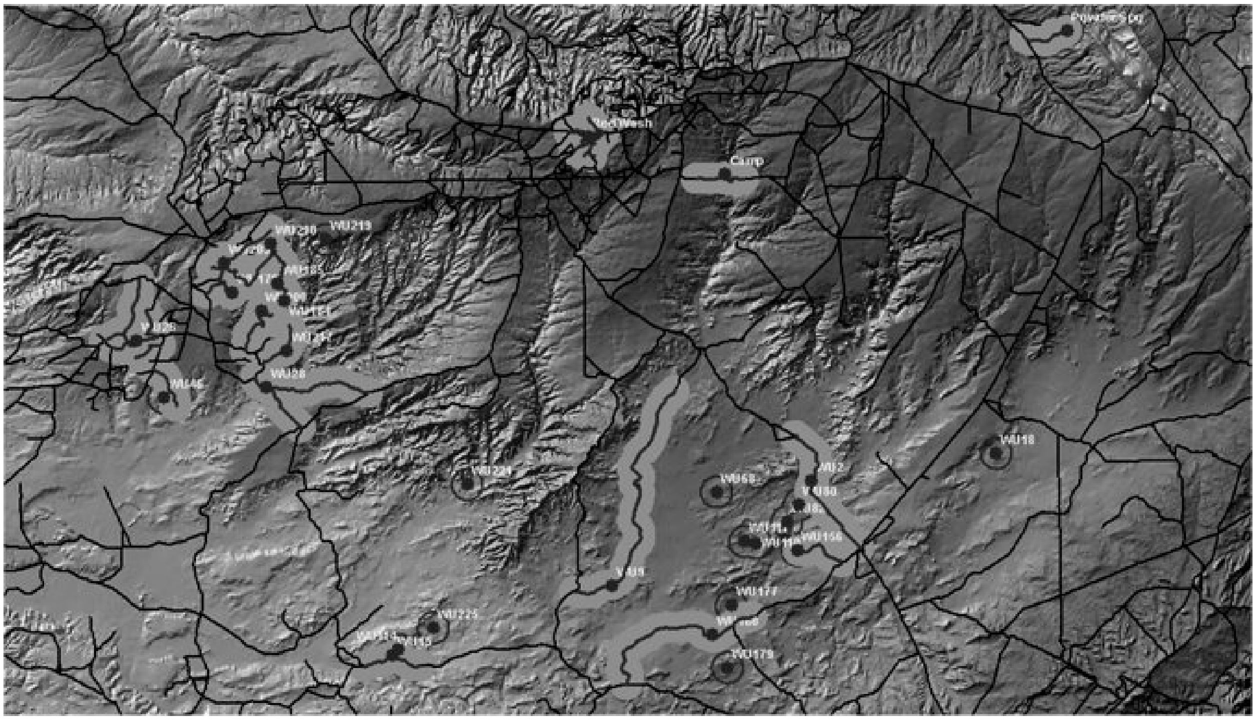

Figure 6. Spatial Proximity Analysis: A 100 yard circular “buffer zone” is created around each WU fossil locality (black dots). Only those fossil localities beyond 100 yards of any 4WD access route still have the circular “buffer zone” displayed; all the others are within the 100 yard “buffer zone”.

survey areas. We illustrate here two such methods—slope and aspect analyses. Slope is a measure of the steepest downhill slope for a location on a surface, the lower the slope value, the flatter the terrain; the higher the slope value, the steeper the terrain (slope is a directionless value). Slope can be calculated as percent or degree of slope. In our Uinta study, degree of slope is calculated. Aspect is a directional measure of slope and can be thought of as the compass direction a hill faces (e.g., southwest, northeast). The value of each cell in an aspect dataset indicates the direction the cell's slope faces. Aspect is measured clockwise in degrees from 0 (due north) to 360. By combining Aspect and Slope maps, investigators can create maps that provide excellent visualization of the surface landscape of fossil survey areas (see Figs. 7 and 8). The slope map (in degrees of slope) is derived from the national elevation dataset (NED) map layer covering the WU permit area. Note that the majority of WU localities are found on surfaces having a slope of less than 10°. The aspect of slope map of the same area suggests that the sediments generally dip in a west northwesterly direction. This is confirmed by combining an elevation profile line with stratigraphic level data through the same region (see Fig. 8). Fossil localities get younger (that is, are higher in the section) from southeast to northwest, indicating that stratigraphic horizons in this region of the Uinta Basin generally dip toward the west-northwest. Slope and aspect information can also be determined at the level of individual sites, leading to more refined characterizations of each fossil locality. One may wish to keep these landscape features in mind when planning future paleontological explorations in the region. For example, one can query the various map layers to find the “intersection” of layers showing only those WU fossil localities within 10 m of SW dipping slopes of less than 10°. Finally, as a further add to visualizing access routes to potential fossiliferous areas, 2D landscapes can be rotated and tilted for 3D analysis.

Figure 7. Slope map (in degrees) of WU fossil localities (dots) within the Uinta Basin. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 8. Aspect map (direction of slope) of WU fossil localities (red dots) within the Uinta Basin. By combining information from the slope map, aspect map, and the profile line (black line), it is clear that the sediments are dipping (i.e., getting younger) from the Southeast to the Northwest. This is verified by the increasing height of the stratigraphic levels (brown vertical boxes, in meters) of several WU fossil localities as one moves from SE to NW along the landscape. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Sharing paleoanthropological data: GIS and Google Earth

We have shown that GIS is an extraordinarily powerful tool for many aspects of (geo)spatial analyses; however, there are still certain obstacles to its broader adoption in paleoanthropology. Part of the problem is that GIS software is expensive and very few paleoanthropologists are trained in its use. We have attempted to address some of these issues by showing how at least some paleontological data derived from GIS analyses can be easily displayed and communicated to others by “wedding” certain GIS functions to Google Earth displays (Conroy et al., 2008). In many cases, GIS map layers of paleontological interest, including their associated attribute tables (e.g., field catalog data); can be freely and easily transmitted to anyone with Internet access and familiarity with Google Earth. Data organized as GIS map layer attachments can be simply emailed to recipients and “dragged and dropped” by the recipient onto their own desktop Google Earth display. The GIS map layers will then immediately appear “draped” over the recipients Google Earth landscape where the recipient has access to all the graphics and attributes of each map layer that has been exported from GIS as well as to all Google Earth tools [e.g., ability to adjust map layer transparencies, labeling, latitude/longitude (or UTM determinations), spatial measurements, and “tilting” of landscapes for enhanced 3D views (Conroy et al., 2008)]. We demonstrate the power and ease of this process by using data derived from The Great Divide Basin Project currently underway by Anemone et al. (2007) and Anemone and Dirks (2009).

We first created six map layers in ArcGIS from the Great Divide Basin field catalog: 1) LOCALITIES (latitude and longitude of each fossil locality); 2) FAUNA (faunal list from each fossil locality including taxonomic and skeletal identification information); 3) PRIMATES (localities yielding primates, including national elevation dataset (available online at:

ned.usgs.gov); 4) SLOPE (landscape slope, in degrees, derived from the DEMs); and 5) GEOLOGICAL MAP (1:500,000 scale geologic map of the region accessed through the USGS and the Wyoming GIS center (available online at: www.sdvc.uwyo.edu). Using simple drop-down commands in ArcToolbox (ArcToolbox >3D analyst tools > conversion > to KML > layer to KML), each of these layers was converted and saved into a Keyhole Markup Language (KML) file and then compressed using zip compression. The resulting six files, each having a ".KMZ" extension, could be read by any KML client, including Google Earth. Each of these resulting KML layer files could be sent as an email attachment to any recipient. Upon receiving such an attachment, the recipient need only open their own version of Google Earth and simply "drag and drop" the attached files onto their own Google Earth display. Each map layer now appears draped over the Google Earth landscape and can be turned on/off and/or rendered more/less transparent (using Google Earth tools) to reveal underlying map layers. The underlying data base (attribute table), or field catalog information in this case, is available in the Google Earth display as well. All of Google Earth's built-in tools, for example "tilting" of the landscape for three-dimensional viewing, geographic coordinate data for each locality, and distance measurements between localities are functional and automatic. The "drag and drop" files initially appear under "temporary places" in the recipient's Google Earth display and can be moved by the user into "my places" for permanent display at any time.

After "dragging and dropping" the .KMZ files into Google Earth, the recipient first selects the "LOCALITIES" layer. All fossil localities are displayed and labeled with a red "balloon." Clicking on each red "balloon" automatically displays all the available field catalog information about that site (see Fig. 9). Next, the "FAUNA" layer is selected (green "balloons" appear over each of the red "balloons" for which there is faunal information). Clicking on each green/red "balloon" brings up a starburst of lines; clicking on the line leading to the red "balloon" gives fossil site information (as in Step 1 above), while clicking on those leading to each green "balloon" gives information about every fossil specimen from that site that is recorded in the field catalog (see Fig. 10). Next, the "PRIMATES" layer is turned on ("FAUNA" is turned off). This results in another starburst with the red "balloons" again providing locality data and the yellow "balloons" providing field catalog data about every fossil primate from that locality (see Fig. 11). If one keeps the "FAUNA" layer turned on, the starburst will consist of red, green, and yellow "balloons" denoting locality data, faunal data, and primate data, respectively. The other layers created in GIS, such as SLOPE, GEOLOGICAL MAP, and ELEVATION, can also be opened and "draped" over the Google Earth landscape. The transparency slider in Google Earth can be used to change the transparency of any of these layers so that underlying layers can still be seen.

Figure 9. Locality layer displayed within Google Earth for fossil localities from Western Michigan University's Great Divide Basin Project. Field catalog data can be displayed for each

locality by clicking on the marker. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 10. Locality and Fauna layers displayed within Google Earth. Starburst pattern includes green “balloons”, which provide field catalog data for fossil specimens from that locality, and red “balloon”, which provides site data as in the previous figure. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 11. Locality, Fauna, and Primates layers displayed within Google Earth. Starburst pattern in which yellow “balloons” provide field catalog data for each fossil primate at each locality, green “balloons” provide field catalog data for other fossils from the site, and red “balloon” provides field catalog data for the site. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

By combining the power of GIS and Google Earth, uniquely created maps of paleontological interest originally created in ArcGIS can be shared with colleagues having no experience with, or access to, GIS as simply and easily as sending an email attachment. Google Earth, as a powerful and freely downloadable geographic visualization tool, opens up enormous possibilities for paleoanthropologists to freely and easily disseminate paleontological data in a visually meaningful and stimulating way to students, colleagues, and the interested general public around the world (Conroy et al., 2008).

SPATIAL TECHNOLOGIES IN ARCHAEOLOGY

Unlike paleoanthropologists and vertebrate paleontologists, archaeologists have long recognized the value of the new geospatial technologies (Gibbons, 1991; Kvamme, 1999), many of which have become routine items in the toolkit of many archaeologists (see recent review by McCoy and Ladefoged, 2009). Rather than attempt to exhaustively describe the many innovative uses of GIS and RS within archaeology, we will briefly highlight three approaches that should be of interest to paleoanthropologists and biological anthropologists: prospecting for new sites, developing predictive models for site location, and spatial analysis of artifacts within a single site.

Archaeologists have been using spatial technologies like aerial photography for prospecting new localities, particularly in forested or mountainous areas where ground survey is difficult. In the early 1980s, NASA archaeologist Tom Sever began working with remote sensing specialists at NASA's Stennis space center to explore the use of Landsat imagery for archaeological prospecting. A landmark conference held in 1984 (Sever and Wiseman, 1985) brought together remote sensing specialists and archaeologists to discuss possible applications of remote sensing to archaeological analysis Giardino (2011). Over the next decade a number of successful collaborations were forged in which Landsat thematic mapper (TM) and thermal infrared multispectral scanner (TIMS) imagery was used to locate and map Anasazi roads in Chaco Canyon (Sever and Wagner, 1991), prehistoric sites in Mississippi (Johnson et al., 1988), and forest paths and villages in the Arenal region of Costa Rica (Sheets and McKee, 1994). In recent years, satellite imagery has been used to great effect in archaeological prospecting and mapping of hidden features in the Maya region of Mesoamerica (Saturno et al., 2007), at Angkor Wat in Cambodia (Evans et al., 2007), and at ancient Harappan sites in the Indus basin and Thar desert of India (Rajani and Rajawat, 2011). Perhaps the most spectacular recent success of remote sensing in archaeological prospecting has been the use of airborne LIDAR (light detecting and ranging) at the Mayan site of Caracol in Belize (Chase et al., 2011). At this important Classic Mayan site in the heavily forested southern Mayan lowlands, LIDAR was used to penetrate the forest canopy and create a DEM that portrays major and minor features (with relief on the order of 5–30 cm) of the site and landscape including structures, terraces and causeways over an area of 200 km2. The authors demonstrate that their methods are far more cost-effective and time-efficient than traditional large-scale mapping of archaeological sites, although as always, interpretations based on remote sensing imagery need to be verified on the ground.

One of the major uses of geospatial technologies in modern American archaeology has been in developing predictive models for the location of sites, often referred to as archaeological site location modeling (Mehrer and Westcott, 2006). Typically, a GIS is used to determine which set of environmental characteristics characterize known archaeological sites, and then to use the presence of these characteristics to predict the presence of similar sites in areas that have not been prospected. Being firmly grounded in processual archaeology (Kvamme, 2006), it comes as no surprise that this approach has been criticized by postprocessual archaeologists for environmental determinism (Wheatley and Gillings, 2002) and "overgeneralizing, deterministic, and dehumanized" (Wheatley, 2004: 1). The features that predictive modelers use to characterize known archaeological sites typically include standard GIS-derived features like slope, aspect, viewshed, as well as a series of buffered calculations (e.g., distance to water, distance to roads, etc.). Typically, a multiple logistic regression analysis is performed on a raster grid to determine the loadings of the various predictor variables (e.g., slope, aspect, elevation, etc.) on the dependent variable (presence or absence of site). For example, a GIS-based study of Paleoindian sites in the Pine Bluffs area of southeastern Wyoming determined that site location was best predicted by distance to the escarpment, distance to hydrology, and elevation (Jaime, 2006). The

GIS can then identify other areas that share these traits, and create a map that reflects the potential for locating other Paleoindian sites.

Similar approaches have been used to predict the location of paleontological sites and are equally applicable to hominin sites. Working in the late Cretaceous (Campanian) Two Medicine formation of north-central Montana, Oheim (2007) developed and ground-tested a GIS-based predictive model for locating dinosaur-bearing fossil localities. Her simple model included four variables (geology, elevation, vegetation cover, and distance to roads) whose attributes were ranked from 0 (lowest probability of bearing fossils) to 4 (highest probability of bearing fossils) for each raster cell in the study area. The four variables were weighted from most important (geology) to least important (distance to roads), and a suitability analysis was calculated for each raster cell. The result was a data layer in which each grid cell had a score derived from the suitability analysis that predicted its likelihood to bear fossils. Field testing of the model was performed by systematically prospecting the areas of high and low probability for new fossil sites. A measure of fossil density was calculated based on the number of fossil sites found per km2, and this was determined to be highly correlated with the predictive score calculated from the suitability analysis (R2 = 0. 9053; Oheim, 2007; p 363). While Oheim's model was based on only four predictor variables, one of which (distance to roads) concerns ease of access rather than likelihood of finding fossils, the results are promising and the development of more detailed predictive models should be a high priority for paleontologists and paleoanthropologists (Emerson and Anemone, in press).

The third approach used by archaeologists involves the spatial analysis of artifacts or features within a site, or of sites within a landscape, to better understand aspects of the behavior of the people that resulted in the formation of these assemblages or sites. Two notable examples exist of GIS-based intrasite analysis of artifacts and fossils at African hominin sites by Paleolithic archaeologists. Nigro et al. (2002, 2003) developed a three dimensional model of the South African cave site at Swartkrans (based on 14,500 survey points captured by theodolite) including all the artifacts and fossils (ca. 60,000 items) collected there by C.K. Brain between 1979 and 1986. Since 1999, an Italian team has been working at the prehistoric site of Melka Kunture in Ethiopia, following in the footsteps of and collaborating with a French team that had worked there for more than 20 years (Chavaillon et al., 1979). Piperno et al. digitized the spatial location of thousands of lithic artifacts and bones (including several hominins) from multiple Oldowan, Acheulean, and Middle Stone Age layers at Melka Kunture to study taphonomic aspects of site formation and human activity (D'Andrea et al., 2002; Galloti and Piperno, 2003).

The development of a GIS-based model of the spatial distribution of artifacts, fossils, and fauna at multiple levels within a single site allows researchers to explore taphonomic aspects of the archaeological assemblage. Because of the limitations of GIS software which restricts data collection to only a single z-coordinate for any x,y pair, developing a fully three dimensional model is usually not possible: what can be achieved is called by some researchers a 2.5-dimensional model (Nigro et al., 2003; Chase et al., 2011). Even so, the GIS model allows researchers to interrogate the spatial distribution of the assemblage at a complex cave site like Swartkrans or at the multiple levels of Melka Kunture in a variety of ways that can lead to new insights concerning aspects of site formation and other taphonomic issues. Many different queries can be quickly and efficiently performed to reveal patterns of distribution of different bone and artifact types. Thematic maps can then be created to explore the spatial distribution of lithics, fauna, and various skeletal elements in both horizontal and vertical layers of the site. While the amount of time and labor required to digitize the spatial position of thousands of bones and artifacts is enormous, the digital database that results provides an elegant solution to the dilemma that is inherent in many archaeological excavations: as a site is excavated, it is, in a sense, destroyed. Further development of the (nearly) three dimensional model developed at Swartkrans (Nigro et al., 2002, 2003), perhaps in association with virtual reality and 3D modeling software, may one day provide a permanent record of excavations that would allow future generations of scholars to apply new methods and analytical techniques to virtually reexcavate sites.

Vertebrate paleontologists have also explored the use of GIS in exploring taphonomic biases that influence the formation of fossil assemblages. Jennings and Hasiotis (2006) applied GIS to a Jurassic site in the Morrison formation of northern Wyoming to test the hypothesis that the locality documents a site where allosaurs repeatedly fed upon sauropod dinosaurs. Finding a high ratio of juvenile to adult allosaur teeth associated with sauropod bones at several different levels in the site suggested that at most one or two adult allosaurs along with several juveniles preyed upon sauropods at different times. The intrasite analysis at this quarry site thus revealed interesting and unexpected aspects of social and feeding behavior of these predatory dinosaurs (Jennings and Hasiotis, op. cit.). Chew and Oheim (2009) were mainly interested in testing the relationship between the sampling area and species diversity recovered from individual localities. By digitizing polygons on paper maps representing fossil localities in Ken Rose's research area in the Eocene Willwood formation of the southern Bighorn Basin, the authors were able to compare the area of localities with the number of different species recovered. They calculated the density of species per unit area, and found a strong taphonomic signal indicating that the size of the area sampled strongly and positively influences the number of species found there. While rarefaction analysis is typically used by paleontologists to standardize species diversity in relation to area (Foote, 1992), Chew and Oheim (op. cit.) demonstrate that rarefaction successfully standardizes species richness against area only on small scales where the magnitude of area variation was less than about one square kilometer. At larger scales, for example basin-wide analyses, species richness was heavily influenced by sampling area and rarefaction failed to successfully standardize these comparisons. These studies indicate that, while applications of GIS to taphonomic analyses of archaeological and paleontological sites are few in number and small in scope, they hold great potential for future insights and new analytical approaches to some very important questions concerning the formation of site assemblages and different kinds of sampling bias.

GIS IN FUNCTIONAL MORPHOLOGY

Since the 1990s,a small number of biological anthropologists and paleontologists have recognized the value that GIS software tools can provide for the analysis of morphology, and this has been one of the most exciting areas of application of the geospatial sciences to our field. Much of this research has involved the study of teeth, mostly focusing on the documentation, analysis, and interpretation of occlusal topography, changes to that topography resulting from attritional wear during mastication, and the relationships of tooth morphology and microwear to diet. The study of dental morphology and microwear has a long and rich history that will be well known to many biological anthropologists. Typically, this work starts with the development of a model based on living animals, whose diets can be studied in nature or controlled in the lab (Ryan, 1979; Gordon, 1982; Teaford and Glander, 1991, 1996; Daegling and Grine, 1999). After one determines the morphological features or characteristic wear patterns seen on the teeth of living animals with different diets (e.g., folivores, insectivores, and frugivores), the next step is generally to explore the morphology or wear patterns seen on the teeth of fossil organisms. Reasoning by analogy with living, closely related animals, the dietary behavior of fossil organisms can then be reconstructed (Grine, 1986; Grine and Kay, 1988; Ryan and Johanson, 1989; Teaford and Ungar, 2000).

Rich Kay's (1975, 1984) classic work on quantifying shearing crests on primate molars demonstrated that folivores and insectivores had more of their occlusal surfaces devoted to shear than is seen in frugivores. Kay (op. cit.) also demonstrated that, in spite of their similar shearing quotients, folivorous and insectivorous primates could be distinguished on the basis of body size, with folivores typically being larger than and insectivores smaller than 500 g. Gingerich (1980; p 128) later formalized this 500 g body size threshold as “Kay's Threshold,” and many biological anthropologists have successfully applied this technique to a variety of different living and fossil primates (Kay and Covert, 1984; Conroy, 1987; Strait, 1993; Williams and Covert, 1994; Ungar and Kay, 1995). One drawback of Kay's shearing quotient approach is that it can only be used on unworn teeth since, with attrition, the lengths of the shearing crests are quickly reduced and become impossible to measure in heavily worn teeth (Ungar and M'Kirera, 2003). The scanning electron microscope (SEM) allowed anthropologists to explore the microscopic traces of attritional wear on primate teeth as an alternative approach to the problem of inferring diet from dental morphology (Teaford, 1988, 1991, 1994, 2007). In spite of the successes of this approach (Grine, 1981, 1986; Grine and Kay, 1988; Teaford and Ungar, 2000), identifying and counting scratches and pits on high magnification micrographs is a long and tedious process that is highly prone to interobserver errors and subjective interpretations that are often difficult to replicate (Teaford, 1994; Ungar et al., 2003). In combination with new and improved microscopic and scanning methods for the analysis of three dimensional coordinate data for tooth occlusal surfaces, the use of GIS has revolutionized the study of dental microwear and morphology.

The basic research design seen in much of the GIS-based work on dental morphology and microwear involves the collection of either landmark data or a point cloud of three dimensional data points along the occlusal surface of the tooth (Zuccotti et al., 1998; Jernvall and Selanne, 1999). These data are then interpolated to create a smoothed model of the occlusal surface that is essentially a DEM or digital elevation model (Ungar and Williamson, 2000). The DEM can then be analyzed by all of the available GIS functions, allowing the researcher to easily calculate areas and volumes of cusps and basins, lengths and angles of crests, slope and aspect, and other spatial quantities or parameters (Ungar and M'Kirera, 2003). As in the earlier work summarized above, the goal of these analyses is generally to determine how dental morphology and/or dental microwear correlate with different patterns of diet in extant and extinct taxa.

The first explicit use of GIS in the analysis of dental morphology was by Reed (1997), who used a reflex microscope to describe the three dimensional surface of primate molar teeth and GIS software to map the resulting contours and to analyze the occlusal morphology. His method suggested differences in the proportion of the tooth surface devoted to crests, cusps, and basins between folivorous (i.e., Lepilemur) and faunivorous (i.e., Galago) prosimian primates. Jernvall and Selanne (1999) demonstrated a method for creating high resolution DEMs of the occlusal surface of small mammal teeth with laser confocal microscopy and NIH-image software, followed by analysis using GIS. They suggested that this method could be used to document the three dimensional morphology of small mammalian teeth, allowing web-based study of dental morphology. In further work that utilizes the GIS approach, Jernvall's research team has studied the relationship between patterns of gene expression and resultant occlusal morphology in rodents (Jernvall et al., 2000) and identified surprising dental similarities between the teeth of rodents and carnivorans (Evans et al., 2007). Suzanne Strait's NSF-funded PaleoView 3D project at Marshall University (paleoview3d.marshall.edu/) uses a high resolution laser scanner to bring this vision to fruition, at least for small North American mammals from the Paleocene and Eocene.

But the worker most responsible for advances in the use of GIS software in the analysis of dental morphology and microwear is Peter Ungar of the University of Arkansas. Beginning in the late 1990s and in collaboration with numerous colleagues and students, Ungar has continually advanced the state-of-the-art for the application of the geospatial sciences to the analysis of dental functional morphology (Zuccotti et al., 1998; Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; Ungar et al., 2003; Ungar, 2004; Scott et al., 2005, 2006; Scott et al., 2009). Ungar's group has used a variety of different approaches to digitize the occlusal surface of primate molar teeth, beginning with an electromagnetic tablet and stylus digitizer (Zuccotti et al., 1998) and later using a laser scanner (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; Ungar, 2004) to create their DEMs. The major advance of Ungar's new analytical approach to “dental topographic analysis” (Ungar, 2004) is the ability to compare the occlusal morphology of worn teeth (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003). Recall that the shearing quotient comparisons made popular by Kay (op. cit.), like all landmark-based morphological comparisons of teeth, require the use of unworn specimens (because with wear, dental landmarks disappear). Ungar's GIS-based solution to the “worn tooth conundrum in primate functional anatomy” succeeds because it allows the complex three dimensional occlusal surface of teeth to be compared and statistically analyzed without the use of transient landmarks (Teaford, 2003; Ungar and M'Kirera, 2003). Evolutionary theory predicts that, even as they wear, teeth must maintain the mechanical ability to fracture specific foods and to perform this function efficiently throughout the life of an individual. In their study of gorilla and chimpanzee second lower molars, Ungar and M'Kirera (2003) found that shape differences between these two taxa remain consistent from the unworn condition through the various stages of wear. This result suggests that primate teeth do indeed maintain their mechanical ability to perform efficiently as they wear. Because unworn teeth are quite rare in the primate fossil record, “the ability to include worn specimens in analyses opens the door to reconstructing the diets of many more extinct primate groups, allowing us to better understand the adaptive radiation of our order” (Ungar and M'Kirera, 2003; p 3874). Shortly after establishing this proof-of-principle, Ungar (2004) applied this new method to the long-standing question of dietary differences between fossil hominin taxa. He determined that the differences in average cusp slope and occlusal relief seen between chimps and gorillas were matched or exceeded in a comparison of Australopithecus afarensis and early Homo. The higher amount of occlusal relief through all wear stages seen in early Homo suggested that they were “capable of more efficiently consuming tough, elastic foods than are chimpanzees or than was A. afarensis” (Ungar, 2004; p 618). With the lowest amount of occlusal relief among the four taxa studied, A. afarensis was thought to be “well-suited to crushing hard, brittle foods” (ibid).

Although not strictly a GIS-based approach, a new method for studying dental microwear that has recently been developed by Ungar's group warrants mention here. Rather than using the

SEM, these researchers have begun to use the tandem scanning confocal microscope (Boyde and Fortellius, 1991) to represent the occlusal surface in three dimensions, and then apply scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2006) to quantitatively characterize and compare evidence of microwear on the imaged surfaces. Because this technique does not rely on landmark data, it too can be applied to teeth in any stage of wear, and since it doesn't utilize subjective identifications of scratches and pits, the potential for generating reproducible results with lower error rates is high. Rather, three-dimensional occlusal surface models are characterized with respect to textural parameters like complexity, anisotropy, heterogeneity, and textural fill volume (Scott et al., 2006), and early results are promising. This approach has already been successfully applied to the analysis of dietary differences between fossil hominins (Scott et al., 2005) and between two families of subfossil lemurs (Scott et al., 2009).

FUTURE RESEARCH DIRECTIONS

It has become clear to us in the writing of this article that the geospatial sciences can now claim a central place in the modern, multidisciplinary study of primate and human evolution. But it is also clear that the tools and techniques of geospatial analysis remain underutilized by paleoanthropologists, in spite of clear evidence of their utility and promise. In the same way that fieldwork in paleoanthropology routinely requires the participation of geologists and geochronologists, we suggest that geospatial specialists must now also be included in these research teams, and that our students need to be trained in the use of GIS and RS. In this final section, we turn our attention to future directions in paleoanthropological research that, in our opinion, hold the greatest potential for fruitful and productive collaborations between geospatial scientists and paleoanthropologists. We consider the use and utility of new approaches from the geospatial sciences in several areas of paleoanthropological inquiry, including the sharing of paleoanthropological data, modeling migrations and landscapes in the past, developing predictive models, and in the analysis of postcranial form and function.

Georeferenced databases

Like much of the rest of the scientific world (Nelson, 2009), paleoanthropologists are beginning to recognize the importance of making available to the wider scientific community and even to the public, the data that forms the foundation of our science (Delson et al., 2007). With the wealth of new geospatial approaches and datasets that paleoanthropologists are creating, the need for web-based archival systems is critical (Schofield et al., 2009). Paleoanthropologists can greatly benefit from the foundational work done in this area by many geologists and vertebrate paleontologists, especially those working for federal (e.g., US Geological Survey, Bureau of

Land Management) and state agencies (e.g., Utah Geological Survey) whose work has been discussed earlier in this article. In addition, several online and georeferenced paleontological databases have been developed to make available to the scientific community taxonomic and occurrence data from a large portion of the paleontological literature, along with statistical tools to analyze these large datasets. The Paleobiology Database (www.paleodb.org), developed largely by analytical paleontologist John Alroy, is certainly the most ambitious of these. Based on over one hundred thousand individual collections representing nearly a million separate fossil occurrences from around the world and through all of geological time, the Paleobiology Database includes taxonomic, chronological, bibliographical, and geographical information for terrestrial plants and animals, including fossil primates and hominins. All localities included in the database have geographic coordinates attached, and a mapping tool is provided that allows users to draw maps (at varying scales) describing the geographic and temporal ranges of any included taxa. The kinds of analyses that can be performed with the Paleobiology Database are only limited by the ingenuity of the investigator, and have included studies of biodiversity (Alroy, 2000, 2010), rates of origination and extinction (Alroy, 2001; Foote, 2003), and evolutionary dynamics (Alroy, 1998, 1999).

Several other online paleontological databases are available for more limited sets of taxa and periods of geological time. Like the Paleobiology Database, they too provide georeferenced (hence, mappable) data that may be of interest to paleoanthropologists and that may stimulate the development of similar approaches by paleoanthropologists or other biological anthropologists. The Neogene Mammal Mapping Portal (www.ucmp.berkeley.edu/neomap/) provides access to two important databases for the analysis of all published occurrences of Oligocene through Holocene North American mammals: MIOMAP is the Miocene mammal mapping project coordinated by Anthony Barnosky and Marc Carrasco, and FAUNMAP is the quaternary faunal mapping Project developed by Russell Graham and Ernest Lundelius. In addition to a common portal, these databases share a thematic focus on how mammalian communities have responded to changing climates and environments during the Neogene. As the titles suggest, these databases are focused on the distribution of Neogene mammals across North American space. A broader taxonomic and ecological focus is attained in the Neotoma paleoecology database (www.neotomadb.org), which was developed by some of the same individuals associated with FAUNMAP and MIOMAP and which includes invertebrates, pollen, and plant macrofossil data. Each of these databases provide a very sophisticated interactive mapping interface that allows users to create customized maps of plant and animal distributions at different points in time or in different environments, or explore the faunal or floral lists and other features of any published Neogene mammal locality in North America, as well as many Quaternary localities in Canada. This is clearly an underutilized but very promising resource for paleoanthropologists. Henry Gilbert has made a substantial contribution to the development of paleoanthropological geodatabases with his Fossilized.org site, which focuses on the sites and specimens that make up the record of human evolution over the past seven million years (www.fossilized.org). The development of similar databases for the Neogene paleontological record of the Old World could illuminate many questions relating to the environments that were utilized by early hominins, or the paths they took in their migrations (Carbonell et al., 1999; Holmes, 2007) out of Africa.

Developing predictive models

The classified image in Figure 3 is the first step toward developing a model that uses multispectral Landsat imagery together with topographic parameters such as slope, aspect and curvature, geological maps, maps of roads and trails, and other digitized inputs to pick localities with a high likelihood of being productive sites. This would involve using the previously visited sites (both productive and sterile) to train and calibrate a model in a deductive, supervised, fashion. Statistical approaches such as k-means, Gaussian maximum likelihood (Richards, 1999), and spectral angle mapping (Kruse et al., 1993) are commonly used methods of matching pixels to spectral signatures derived from the brightness values at a set of training (or “ground truth”) sites. Artificial neural networks (An et al., 1995; Atkinson and Tatnall, 1997) are a flexible modeling method that avoids some of the assumptions (such as normal distributions) required in many statistical approaches, and we are currently developing such a predictive model as part of ongoing work in the Great Divide Basin of Wyoming (Anemone et al., in press; Emerson and Anemone, in press). Neural networks simulate the neurons that connect brain cells, by using a set of input nodes, one or more hidden layers of nodes, and a set of output nodes. In the training process, connections and weights between the different node layers are established using a set of known output nodes.

Multilayer perceptrons with training through back-propagation (Rumelhart et al., 1986) are the most common form of artificial neural network model used in image analysis. A perceptron element is a single node that receives weighted inputs from nodes in the preceding neural network layer. The sum of the weighted inputs is transformed to an output using a sigmoid (s-shaped) activation function such as a logistic or hyperbolic transformation equation. In a crisp image classification where pixels are assigned to one class only, the output of a node that corresponds to the chosen class is set to one and all other node outputs are set to zero. In a fuzzy classification, the outputs may be scaled probabilistically, so that the output classes may blend into one another, rather than having crisp boundaries between land cover types (see Fig. 12).

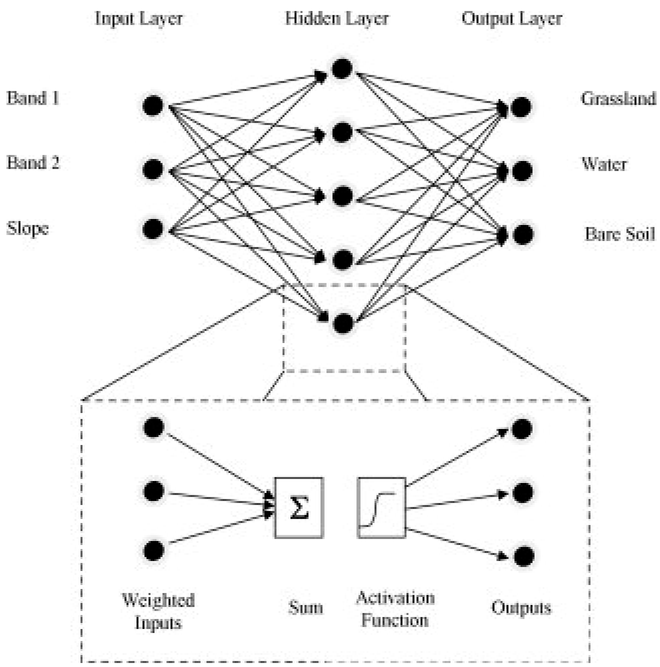

Figure 12. Schematic Diagram of a Simple Artificial Neural Network with Structure of a Single Neuron.

Input nodes can consist of the brightness values from the spectral bands, slope, aspect, curvature, and other quantitative or categorical inputs such as geological or soil parameters. The hidden layers are nodes that receive weighted inputs, become activated according to a sigmoid function and generate values that are fed to layer of output nodes, which in the case of image classification are the land cover classes.

Training is performed by identifying groups of pixels in an input image according to their known land cover type, such as forest, bare soil, grassland, built-up, water bodies, and different types of rock outcrops. The input image is fed forward through the multilayer perceptron process, with the weights initially set to random values, and the result is compared to the known land covers. The error is then iteratively back-propagated through the network and the weights are readjusted until the output nodes match the training site classifications to a specified degree.

In addition to an input image that contains defined training sites, the inputs to a neural network classifier include the number of hidden layers of nodes, the activation function type, (logistic or hyperbolic), the training threshold contribution, the training rate, the training momentum, the maximum number of iterations, and the exit root mean squared error exit criterion. The training threshold contribution determines the size of the contribution of the internal weight with respect to the activation level of the node (Kanellopoulos and Wilkinson, 1997). The training algorithm interactively adjusts the weights between nodes and optionally the node thresholds to minimize the error between the output layer and the desired response. Adjustments of the node internal weights could lead to better classifications but too many weights could also lead to poor generalizations. The training rate determines the magnitude of the adjustment of the weights at each iteration. A higher rate will speed up the training, but will also increase the risk of oscillations or nonconvergence of the training result. A higher momentum rate trains with larger steps than a lower momentum rate, while encouraging weight changes along the current direction.

Once the artificial neural network classifier is trained with a sufficiently low error, a different input is run through the process to generate a classified image. Although, neural network-based classifiers have been shown to be superior to other types of supervised classification (Paola and Schowengerdt, 1995), they can be over-trained so that while they have low error as compared to the training data, they are not generalizable to other input sources. Conversely, an undertrained classifier will yield high rates of classification error. Kanellopoulous, and Wilkinson (1997) have identified several best practice strategies for setting up a neural network classifier. For example, a user could specify multiple hidden layers, but for most classification efforts with fewer than 20 output classes, little additional accuracy is gained and processing time is increased if more than one hidden layer of nodes is used.

Several other issues impact the success or failure of a model for predicting the location of productive localities. In a practical sense, the cost of imagery and other input data must be considered, and this, in part, determines the available spatial and spectral resolution, as well as the areal extent that can be considered. Commercial remote sensing satellites offer spatial resolutions of 1 m or less, but this imagery is very expensive, and it generally only offers four spectral bands in the visible and near-infrared parts of the spectrum. Digital aerial photographs that has been rectified to map coordinates and corrected for elevation distortions, have high spatial resolutions, but generally include only red, green, and blue, or red, green, near-infrared bands. Large file sizes also limit the spatial extent of areas that can be efficiently stored and analyzed using high resolution imagery.

Landsat imagery has a lower spatial resolution (~ 30 m), but it does have seven spectral bands and is available for free download (ned.usgs.gov). The larger pixel size; however does mean that in complex landscapes, most pixels are a combination of several types of ground cover. Several techniques have been developed to spectrally “unmix” these mixed pixels so that an analyst can infer that a particular pixel is, for example, 20% barren, 65% grassland, and 15% shrubland. Linear mixture models (Adams et al., 1995) use “pure” spectral response patterns (called endmembers) from pixels that contain only one type of land cover to estimate the percentages of land covers in mixed pixels. A disadvantage of these models is that they require homogeneous pixels to determine the endmembers, and the assumption that a mixed pixel is a simple linear combination of endmembers is not always correct. Foody et al. (1997) used an artificial neural network approach to estimate the composition of mixed pixels in a coarse resolution satellite image, using higher resolution imagery to train the classifier, and this technique might show promise in the development of a model for prioritizing fossil localities. This is particularly important for this application in the Great Divide Basin of Wyoming (Anemone et al., in press; Emerson and Anemone, in press), because many of the productive localities there are associated with small sandstone outcrops that would not occupy a large group of Landsat pixels.

The analysis of skeletal form and function

In spite of the success of GIS-based analyses of dental form and function cited above, functional morphologists have been slow to utilize these same techniques in the analysis of the morphology of primate postcranial skeletal elements. Measuring areas of joint surfaces or muscle attachments, studying conjoint surfaces of complex articulations, and other parameters of interest to functional morphologists have always been difficult to study by traditional anatomical approaches. With laser scanners and even micro CT scanners being routinely used by many researchers, we clearly have the ability to accurately and precisely scan the complex three-dimensional shapes of bones and create virtual models of these elements. We suggest that GIS can allow new and innovative approaches to analyzing form-function correlates of musculo-skeletal anatomy that may contribute to long-standing debates and unsolved anatomical controversies. Joints with complex shapes (e.g., subtalar joint) or that allow multiple axes of motion (e.g., trapezium-metacarpal 1 joint) may be compared between taxa in new and quantifiable ways by using some of the standard GIS functions, for example slope and aspect.

Arizona State University archaeologist Curtis Marean's work in zooarchaeology has utilized GIS in some very creative ways to study both lithics and skeletal remains from archaeological sites. Unsatisfied with manual methods for determining the minimum number of elements (MNE) in an archaeofauna that involved determining overlap for individual skeletal elements by drawing all fragments on 2D templates of each bony element and counting how many overlapping layers were present, Marean et al. (2001) developed a GIS-based approach that was a substantial improvement over the earlier approaches. Now, rather than tracing all bone fragments on separate layers of paper, they draw separate polygons representing each bone fragment on a digital bone template in a GIS. They later convert the polygons to a raster grid, and calculate the number of overlapping pixels: this simple calculation yields the MNE. Marean and coworkers also developed a GIS-based approach to quantifying cutmarks on archaeofauna (Abe et al., 2002). Because the frequency of cutmarks on a butchered bone fragment must be related to the amount of surface area preserved on the fragment, they utilized GIS to control for the available surface area preserved on all cutmarked bones, thus controlling for the degree of fragmentation in an archaeofaunal assemblage. In a related approach, they utilized GIS to document edgewear on a Middle Stone Age lithic assemblage to analyze details of usewear and retouch (Bird et al., 2007). These three innovative uses developed for GIS by this one archaeological research team suggest the untapped potential of these methods for paleoanthropology and prehistoric archaeology.

Final thoughts

While researchers in many different fields of inquiry have utilized the tools and techniques of geospatial analysis for a long time and in many innovative ways, biological anthropologists and paleoanthropologists have been slow to incorporate GIS and RS into their analytical toolkits. This situation is now rapidly changing, and we predict that in the not too distant future, the geospatial sciences will play a much more central role in much paleoanthropological research. We are encouraged to see paleoanthropologists beginning to demonstrate the utility of GIScience for building models of human behavior and particularly note the innovative work of Holmes (2007) on modeling the route taken by Plio-Pleistocene hominins out of Africa. In a similar vein, Bailey et al. (2011) have recently developed a fascinating model that incorporates paleoenvironmental reconstructions and evidence of active tectonism to explore aspects of human behavior in the landscapes of eastern and southern Africa during the Pleistocene. Our science is clearly headed in the direction of developing testable models to explain human behavior in the past, and GIS will play an increasingly important role in this and many other aspects of our science that rely on understanding the distribution within space of living and fossil humans and their artifacts.

Acknowledgements

The authors thank Bob Sussman for his invitation to contribute this article to the Yearbook. RLA acknowledges the contributions of all the members of his Great Divide Basin field crews, especially Brett Nachman, Wendy Dirks, Ron Watkins, Bill Moore, John Van Regenmorter, and Ed Johnson. RLA also acknowledges the FRACAA program in the office of the Vice President for Research at Western Michigan University for funding. GCC thanks Aaron Addison for GIS support and advice, and Tab Rasmussen and Beth Townsend for Uinta Basin data. Special thanks to Richard Stucky for the RS image of the Wind River Basin shown in Figure 2 and for his careful reading of the manuscript and insightful review. The comments of two other, anonymous reviewers also helped to make this a better article, and they thank them. All Great Divide Basin fossils have been collected by WMU field parties under Wyoming Bureau of Land Management permit 287-WY- PA95 to Robert L. Anemone (PI). The permanent repository for these fossils is the Carnegie Museum of Natural History in Pittsburgh, PA.

LITERATURE CITED

Abe Y,Marean CW,Nilssen PJ,Assefa Z,Stone EC. 2002. The analysis of cutmarks on archaeofauna: a review and critique of quantification procedures, and a new image-analysis GIS approach. Am Antiq 67: 643–663.

Aldenderfer MS,Maschner HDG, editors. 1996. Anthropology, space, and geographic information systems. New York: Oxford University Press.

Alroy J. 1998. Cope's rule and the dynamics of body mass evolution in North American mammals. Science 280: 731–734.

Alroy J. 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. Syst Biol 48: 107–118.

Alroy J. 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26: 707–733.

Alroy J. 2001. A multi-species overkill simulation of the end-Pleistocene megafaunal mass extinction. Science 292: 1893–1896.

Alroy J. 2010. The shifting balance of diversity among major marine animal groups. Science 329: 1191–1194.

An P,Chung C,Rencz A. 1995. Digital lithology mapping from airborne geophysical and remote sensing data in the Melville Peninsula, northern Canada, using a neural network approach. Remote Sens Environ 53: 76–84.

Anemone RL,Dirks W. 2009. An anachronistic mammal fauna from the Paleocene Fort union formation (Great Divide Basin, Wyoming, USA). Geol Acta 7: 113–124.

Anemone RL,Dirks W,Watkins R,Nachman B,Van Regenmorter J. 2007. A late Wasatchian mammalian fauna from the Steamboat Mountain-Freighter Gap area, Great Divide basin, southwestern Wyoming. J Vert Paleo 27(Suppl 3): 40A.

Anemone R,Emerson C,Conroy G. Finding fossils in new ways: An artificial neural network approach to predicting the location of productive fossil localities. Evol. Anthro. in press.

Asfaw B,Beyene Y,Semaw S,Suwa G,White T,WoldeGabriel G. 1991. Fejej: a new paleoanthropological research area in Ethiopia. J Hum Evol 21: 137–143.

Asfaw B,Beyene Y,Suwa G,Walter R,White T,WoldeGabriel G,Yemane T. 1992. The earliest Acheulean from Konso-Gardula. Nature 360: 732–735.

Asfaw B,Ebinger C,Harding D,White T,WoldeGabriel G. 1990. Space-based imagery in paleoanthropological research: an Ethiopian example. Natl Geogr Res 6: 418–434.

Atkinson P,Tatnall A. 1997. Introduction to neural networks in remote sensing. Int J Remote Sens 18: 699–709.

Bailey GN,Reynolds SC,King GCP. 2011. Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. J Hum Evol 60: 257–280.

Banerjee S,Mitra S. 2004. Remote surface mapping using orthophotos and geologic maps draped over digital elevation models: application to the Sheep Mountain anticline, Wyoming. Am Assoc Pet Geol Bull 88: 1227–1237.

Belt K,Paxton S. 2005. GIS as an aid to visualizing and mapping geology and rock properties in regions of subtle topography. Geol Soc Am Bull 117: 149–160.

Berger L,Hilton-Barber B. 2000. In the footsteps of eve: the mystery of human origins. Washington, DC: National Geographic Adventure Press.

Bewley R,Rączkowski W, editors. 2002. Aerial archaeology: developing future practice. Amsterdam: IOS Press.

Bilotti F,Shaw J,Brennan P. 2000. Quantitative structural analysis with stereoscopic remote sensing imagery. Am Assoc Pet Geol Bull 84: 727–740.

Bird C,Minichillo T,Marean CW. 2007. Edge damage distribution at the assemblage level on Middle Stone Age lithics: an image-based GIS approach. J Archaeol Sci 34: 771–780.

Boyde A,Fortelius M. 1991. New confocal LM method for studying local relative microrelief, with special reference to wear studies. Scanning 13: 429–430.

Breithaupt B,Matthews N. 2001. Preserving paleontological resources using photogrammetry and geographic information systems. In: Harmon D, editor. Crossing boundaries in park management. Hancock, MI: The George Wright Society. p 62–70.

Breithaupt B,Southwell E,Adams T,Matthews N. 2001. Innovative documentation methodologies in the study of the most extensive dinosaur tracksite. In: Santucci V, McClelland

L, editors. Proceedings of the 6th fossil resource conference: National Park Service Geological Resource Division Technical Report NPS/NRGRD/GRDTR-01/01, p 113–122.

Broom R. 1938. The Pleistocene anthropoid apes of South Africa. Nature 142: 377–379.

Broom R. 1949. Another new type of fossil ape-man. Nature 163: 57.

Broom R. 1950. Finding the Missing Link. London: Watts and Co.

Brown F,Haileab B,McDougall I. 2006. Sequence of tuffs between the KBS tuff and the Chari tuff in the Turkana Basin, Kenya and Ethiopia. J Geol Soc London 63: 185–204.

Bryant L,Matthews N. 1998. GIS—What'll we do with it next? J Vert Paleo 18: 30A.

Campisano C,Feibel C. 2008. Depositional environments and stratigraphic summary of the Pliocene Hadar formation at Hadar, Afar depression, Ethiopia. In: Quade J,Wynn J, editors. The geology of early humans in the horn of Africa. Boulder, CO: The Geological Society of America. p 179–202.

Carbonell E,Mosquera M,Rodriguez XP,Sala R. 1999. Out of Africa: the dispersal of the earliest technical systems reconsidered. J Anthropol Arch 18: 119–136.

Chase AF,Chase DZ,Weishampel JF,Drake JB,Shrestha RL,Slatton KC,Awe JJ,Carter WE. 2011. Airborne LiDAR, archaeology, and the ancient Maya landscape at Caracol, Belize. J Archaeol Sci 38: 387–398.

Chavaillon J,Chavaillon N,Hours F,Piperno M. 1979. From the oldowan to the middle stone age at Melka-Kunture (Ethiopia). Understanding cultural changes. Quaternaria 21: 87–114.

Chew A,Oheim K. 2009. Using GIS to determine the effects of two common taphonomic biases on vertebrate fossil assemblages. Palaios 24: 367–376.

Chrisman N. 2006. Charting the unknown: how computer mapping at Harvard became GIS. Redlands, CA: ESRI Press.

Conel J,Lang H,Paylor E,Alley R. 1985. Preliminary spectral and geologic analysis of Landsat-4 thematic mapper data. Wind River Basin area, Wyoming. IEEE Trans Geosci Remote Sens 23: 562–573.

Conolly J. 2006. Geographical information systems in archaeology. Cambridge, UK: Cambridge University Press.

Conroy G. 2006. Creating, displaying, and querying interactive paleoanthropological maps using GIS: an example from the Uinta Basin, Utah. Evol Anthropol 15: 217–223.

Conroy G,Anemone R,Van Regenmorter J,Addison A. 2008. Google Earth, GIS, and the Great Divide: a new and simple method for sharing paleontological data. J Hum Evol 55: 751–755.

Conroy G,Vannier M. 1984. Noninvasive three dimensional computer imaging of matrix-filled fossil skulls using high resolution computed tomography. Science 226: 456–458.

Conroy G,Vannier M. 1987. Dental development of the Taung skull from computerized tomography. Nature 329: 625–627.

Conroy G,Vannier M. 1991. Dental development in South African australopithecines. Part 2: dental stage assessment. Am J Phys Anthropol 86: 137–156.

Conroy G,Vannier M,Tobias P. 1990. Endocranial features of Australopithecus africanus revealed by 2 and 3 D computed tomography. Science 247: 838–841.

Cooke D. 1998. Topology and TIGER, the Census Bureau's contribution. In: Foresman T, editor. The history of geographic information systems. Upper Saddle River, NJ: Prentice Hall. p 45–58.

Coppens Y,Howell F,Isaac G,Leakey R, editors. 1976. Earliest man and environments in the Lake Rudolf Basin. Stratigraphy, paleoecology, and evolution. Chicago: University of Chicago Press.

Corruccini R,Ciochon R, editors. 1994. Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell. Englewood Cliffs, NJ:Prentice Hall.

Daegling D,Grine F. 1999. Terrestrial foraging and dental microwear in Papio ursinus. Primates 40: 559–572.

D'Andrea A,Gallotti R,Piperno M. 2002. Taphonomic interpretation of the developed Oldowan site of Garba IV (Melka Kunture. Ethiopia) through a GIS application. Antiquity 76: 991–1001.

Dart R. 1925. Australopithecus africanus: The man-ape of South Africa. Nature 115: 195–199.

Dart R. 1948. The Makapansgat proto-human Australopithecus prometheus. Am J Phys Anthrop 5: 259–284.

Dart R. 1959. Adventures with the missing Link. New York: Harper.

DeBlieux D,Kirkland J,Butler M,Hayden M,Titus A. 2004. Developing research and management tools for paleontology at grand staircase-escalante national monument (GSENM) and other public lands in Utah: using computers to manage data and explore patterns in the distribution of fossils and paleoenvironments. J Vert Paleo 24: 51A.

DeBlieux D,Smith J,McGuire J,Santucci V,Kirkland J,Butler M. 2003. A paleontological inventory of Zion National Park, Utah, and the use of GIS technology to create paleontological sensitivity maps for use in resource management. J Vert Paleo 23: 45A.

Delson E,Harcourt-Smith W,Frost S,Norris C. 2007. Databases, data access, and data sharing in Paleoanthropology: first steps. Evol Anthropol 16: 161–163.

Delsuc F,Brinkmann H,Philippe H. 2005. Phylogenomics and the reconstruction of the tree of life. Nat Rev Genet 6: 361–375.

Dunn CW,Hejnol A,Matus DQ,Pang K,Browne WE,Smith SA,Seaver E,Rouse GW,Obst M,Edgecombe GD,Sorenson MV,Hadock SHD,Schmidt-Rhaesa A,Okusu A,Kristensen RM,Wheeler WC,Martindale MQ,Giribet G. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452: 745–749.

Emerson CW,Anemone RL. in press. An artificial neural network-based approach to identifying mammalian fossil localities in the Great Divide Basin, Wyoming. Remote Sensing Letters in press.

Evans AR,Wilson GE,Fortelius M,Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445: 78–81.

Evans D,Pottier C,Fletcher R,Hensley S,Tapley I,Milne A,Barbetti M. 2007. A comprehensive archaeological map of the world's largest preindustrial settlement complex at Angkor, Cambodia. Proc Natl Acad Sci USA 104: 14277–14282.

Evans TL,Daly PT, editors. 2006. Digital archaeology: bridging method and theory. London: Routledge.

Fleagle JG,Rasmussen DT,Yirga S,Bown TM,Grine FE. 1991. New hominid fossils from Fejej, Southern Ethiopia. J Hum Evol 21: 145–152.

Foody GM,Lucas RM,Curran PJ,Honzak, M. 1997. Non-linear mixture modeling without end-members using an artificial neural network. Int J Remote Sens 18: 937–953.

Foote M. 1992. Rarefaction analysis of morphological and taxonomic diversity. Paleobiology 18: 1–16.

Foote M. 2003. Origination and extinction through the Phanerozoic: a new approach. J Geol 111: 125–148.

Foresman T. 1998. GIS early years and the threads of evolution. In: Foresman T, editor. The history of geographic information systems. Upper Saddle River, NJ: Prentice Hall. p 3–17.

Forte M,Siliotti A, editors. 1997. Virtual archaeology: re-creating ancient worlds. New York: H.N. Abrams.

Foss S,Cavin J,Brown T,Kirtland J,Santucci V, editors. 2009. Proceedings of the eighth conference on fossil resources. Salt Lake City, UT: Bureau of Land Management.

Galloti R,Piperno M. 2003. Recent activities of the Italian archaeological mission at Melka Kunture (Ethiopia): the open air museum project and the GIS application to the study of the Oldowan sites. In: Moreno J,Torcal R,Sainz IdlT, editors. Oldowan: rather more than smashing stones. Bellaterra, Spain: Centre d'Estudis del Patrimoni Arqueologic de la Prehistoria. p 37–76.

Giardino MJ. 2011. A history of NASA remote sensing contributions to archaeology. J Archaeol Sci 38: 2003–2009.

Gibbons A. 1991. A “new look” for archaeology. Science 252: 918–920.

Gillespie T,Agnew J,Mariano E,Mossler S,Jones N,Braughton M,Gonzalez J. 2009. Finding Osama bin Laden: An application of biogeographic theories and satellite imagery. On-line working paper series. Los Angeles: California Center for Population Research (published as MIT International Review).

Gingerich P. 1980. Eocene Adapidae, paleobiogeography, and the origin of South American Platyrrhini. In: Ciochon R,Chiarelli A, editors. Evolutionary biology of the new world monkeys and continental drift. New York: Plenum. p 123–138.

Goodchild M. 1992. Geographical information science. Int J Geogr Inf Sci 6: 31–45.

Gordon K. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am J Phys Anthropol 59: 195–215.

Granger W. 1910. Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals. Bull Am Mus Nat Hist 28: 23–251.

Green RE,Malaspinas A-S,Krause J,Briggs AW,Johnson PLF,Uhler C,Meyer M,Good JM,Maricic T,Stenzel U,Prufer K,Siebauer M,Burbano HA,Ronan M,Rothberg JM,Egholm M,Rudan P,Brajkovic D,Kucan Z,Gusic I,Wikstrom M,Laakkonen L,Kelso J,Slatkin M,Paabo S. 2008. A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. Cell 134: 416–426.

Grine F. 1981. Trophic differences between “gracile andobust” australopithecines: a scanning electron microscope analysis of occlusal events. S Afr J Sci 77: 203–230.

Grine F. 1986. Dental evidence for dietary differences in Australopithecus and Paranthropus: a quantitative analysis of permanent molar microwear. J Hum Evol 15: 783–822.

Grine F,Kay R. 1988. Early hominid diets from quantitative image analysis of dental microwear. Nature 333: 765–768.

Haile-Selassie Y,Deino A,Saylor B,Umer M,Latimer B. 2007. Preliminary geology and paleontology of new hominid-bearing Pliocene localities in the central Afar region of Ethiopia. Anthropol Sci 115: 215–222.

Hay R. 1976. Geology of the Olduvai Gorge: a study of sedimentation in a semiarid basin. Berkeley: University of California Press.

Hofreiter M,Serre D,Poinar HN,Kuch M,Paabo S. 2001. Ancient DNA. Nat Rev Genet 2: 353–359.

Holmes K. 2007. GIS simulation of the earliest hominid colonisation of Eurasia. Oxford: Archaeopress. 154 p.

Howell F. 1978a. Hominidae. In: Maglio V,Cooke H, editors. Evolution of African mammals. Cambridge, MA: Harvard University Press. p 154–248.

Howell F. 1978b. Overview of the Pliocene and earlier Pleistocene of the lower Omo basin, southern Ethiopia. In: Jolly C, editor. Early Hominids of Africa. London: Duckworth. p 85–130.

Howell F,Haesaerts P,de Heinzelin J. 1987. Depositional environments, archaeological occurrences and hominids from Members E and F of the Shungura Formation (Omo Basin, Ethiopia). J Hum Evol 16: 665–700.

Jaime Z. 2006. Building a predictive model for Paleoindian archaeological site location using geographic information systems. MA thesis in Anthropology. Kalamazoo, MI: Western Michigan University. 130 p.

Jennings DS,Hasiotis ST. 2006. Taphonomic analysis of a dinosaur feeding site using geographic information systems (GIS). Morrison formation, southern Bighorn Basin, Wyoming, USA. Palaios 21: 480–492.

Jernvall J,Keranen S,Thesleff I. 2000. Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography. Proc Natl Acad Sci USA 97: 14444–14448.

Jernvall J,Selanne L. 1999. Laser confocal microscopy and geographic information systems in the study of dental morphology. Paleontol Electron 2: 18.

Johanson D,White T,Coppens Y. 1978. A new species of the genus Australopithecus (Primates: Hominidae) from the Pliocene of eastern Africa. Kirtlandia 28: 1–14.

Johnson J,Madry S,Sever T. 1988. Remote sensing and GIS analysis in large scale survey design in north Mississippi. SE Archaeol 7: 124–131.

Johnson JK. 2006. Remote sensing in archaeology: an explicitly North American perspective. Tuscaloosa: University of Alabama Press.

Kaczmarek S,Hicks M,Fullmer S,Steffen K,Bachtel S. 2010. Mapping facies distributions on modern carbonate platforms through integration of multispectral Landsat data, statistics-based unsupervised classifications, and surface sediment data. Am Assoc Pet Geol Bull 94: 1581–1606.

Kanellopoulos I,Wilkinson GG. 1997. Strategies and best practices for neural network image classification. Int J Remote Sens 18: 711–725.

Kay R. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 42: 192–215.

Kay R. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman P,Cant J, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 21–53.

Kay R,Covert H. 1984. Anatomy and behavior of extinct primates. In: Chivers D,Wood B,Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum. p 467–508.

Kee C. 1996. Wide area differential GPS. In: Parkinson B,Spilker J, editors. The global positioning system: theory and applications. Reston, VA: American Institute of Aeronautics and Astronautics. p 81–116.

Keefer W. 1965. Stratigraphy and geologic history of the uppermost Cretaceous, Paleocene, and lower Eocene rocks in the Wind River Basin, Wyoming. US Geol Surv Prof Pap 495-A: 1–76.

Keefer W. 1970. Structural geology of the Wind River Basin, Wyoming. US Geol Surv Prof Pap 495-D: 1–35.

Kirkland J,Deblieux D,Hayden M,Willis G. 2006. Utah geological survey: a valuable partner in the management of federal fossil resources. In: Lucas S,Spielmann J,Hester P,Kenworthy J,Santucci V, editors. America's antiquities: 100 years of managing fossils on federal lands. Albuquerque, NM: New Mexico Museum of Natural History and Science Bulletin. p 77–80.

Korth WW. 1982. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 2. Geologic setting. Ann Carnegie Mus 51: 57–78.

Krings M,Stone A,Schmitz RW,Krainitzki H,Stoneking M,Pääbo S. 1997. Neandertal DNA sequences and the origin of modern humans. Cell 90: 19–30.

Kruse F,Lefkoff A,Boardman J,Heidebrecht K,Shapiro A,Barloon P,Goetz A. 1993. The spectral imaging processing system (SIPS)—Interactive visualization and analysis of imaging spectrometer data. Remote Sens Environ 44: 145–163.

Kvamme K. 1999. Recent directions and developments in geographic information systems. J Archaeol Res 7: 153–201.

Kvamme K. 2006. There and back again: revisiting archaeological location modeling. In: Mehrer M,Westcott K, editors. GIS and archaeological site location modeling. Boca Raton, FL: Taylor and Francis. p 3–38.

Lang H,Adams S,Conel J,McGuffie B,Paylor E,Walker R. 1987. Multuispectral remote sensing as stratigraphic and structural tool. Wind River Basin and Big Horn Basin areas, Wyoming. Am Assoc Pet Geol Bull 71: 389–402.

Leakey L. 1958. Recent discoveries at Olduvai Gorge. Nature 181: 1099–1103.

Leakey L. 1959. A new fossil skull from Olduvai. Nature 184: 491–493.

Leakey L. 1961. New finds at Olduvai Gorge. Nature 189: 649–650.

Leakey L,Evernden J,Curtis G. 1961. Age of Bed 1. Olduvai Gorge, Tanzania. Nature 191: 478.

Leakey L,Tobias P,Napier J. 1964. A new species of the genusHomo from Olduvai Gorge, Tanzania. Nature 202: 308–312.

Leakey M,Harris J, editors. 1987. Laetoli: a Pliocene site in Northern Tanzania. Oxford: Oxford University Press.

Leakey R,Walker A. 1976. Australopithecus, Homo erectus, and the single species hypothesis. Nature 261: 572–574.

Leakey R,Walker A. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. Am J Phys Anthropol 67: 135–163.

Leakey R,Walker A. 1988. New Australopithecus boisei specimens from east and west Lake Turkana, Kenya. Am J Phys Anthropol 76: 1–24.

Letunic I,Bork P. 2007. Interactive tree of life (iTOL): an online tool for phylogenetic tree display and annotation. Bioinformatics 23: 127–128.

Lin Z,Oguchi T. 2009. Longitudinal and transverse profiles of hilly and mountainous watersheds in Japan. Geomorphology 111: 17–26.

Lock GR,Stanc?ic? Z, editors. 1995. Archaeology and geographical information systems: a European perspective. London: Taylor & Francis.

Love J,Christianson A. 1985. Geological map of Wyoming. US Geological Survey, State Geologic Map, scale 1:500,000, 3 sheets.

Marble D. 1990. Geographic information systems: an overview. In: Peuquet D,Marble D, editors. Introductory readings in geographic information systems. London: Taylor and Francis. p 8–17.

Marean CW,Abe Y,Nilssen PJ,Stone EC. 2001. Estimating the minimum number of skeletal elements (MNE) in zooarchaeology: a review and a new image-analysis GIS approach. Am Antiq 66: 333–348.

Marzolff I,Poesen J. 2009. The potential of 3D gully monitoring with GIS using high-resolution aerial photography and a digital photogrammetry system. Geomorphology 111: 48–60.

Matthews N,Noble T,Breithaupt B. 2006. The application of photogrammetry, remote sensing and geographic information systems (GIS) to fossil resource management. In: LucasS,Spielman J,Hester P,Kenworthy J,Santucci V, editors. Fossils from federal lands. Albuquerque: New Mexico Museum of Natural History and Science. p 119–131.

Matthews N,Noble T,Breithaupt B,Titus A,Smith J. 2005. A geospatial look at the morphological variation of tracks at the Twentymile Wash Dinosaur Tracksite, Grand Staircase-Escalante National Monument, Utah. J Vert Paleo 25: 90A.

Matthews N,Noble T,Titus A,Smith J,Breithaupt B. 2005. Digital dinosaur tracking: using GIS to analyze the twentymile wash dinosaur tracksite. Grand staircase-escalante national monument, Utah. Geol Soc Am 37: 114 (abstracts with programs).

McCoy M,Ladefoged T. 2009. New developments in the use of spatial technology in archaeology. J Archaeol Res 17: 263–295.

Mehrer M,Westcott K, editors. 2006. GIS and archaeological site location modeling. Boca Raton, FL: CRC Press.

Moore I,Grayson R,Landson A. 1991. Digital terrain modeling: a review of hydrological, geomorphological, and biological applications. Hydrol Process 5: 3–30.

Morell V. 1995. Ancestral passions. The Leakey family and the quest for humankind's beginnings. New York: Simon and Schuster.

Nelson B. 2009. Empty archives. Nature 461: 160–163.

Newhall B. 1964. The history of photography. New York: The Museum of Modern Art.

Nigro J,Limp W,Kvamme K,de Ruiter D,Berger L. 2002. The creation and potential applications of a 3-dimensional GIS for the early hominin site of Swartkrans, South Africa. In: Burenhult G, Arvidsson J, editors.Archaeological informatics: pushing the envelope CAA 2001. Proceedings of the 29th conference, Gotland, April 2001 ed. Oxford: Archaeopress. p 113–124.

Nigro J,Ungar P,de Ruiter D,LR B. 2003. Developing a geographic information system (GIS) for mapping and analyzing fossil deposits at Swartkrans, Gauteng Province, South Africa. J Archaeol Sci 30: 317–324.

Njau J,Hlusko L. 2010. Fine-tuning paleoanthropological reconnaissance with high resolution satellite imagery: the discovery of 28 new sites in Tanzania. J Hum Evol 59: 680–684.

Oheim KB. 2007. Fossil site prediction using geographic information systems (GIS) and suitability analysis: the two medicine formation. MT, a test case. Palaeogeogr Palaeoclimatol Palaeoecol 251: 354–365.

Paola JD,Schowengerdt RA. 1995. A review and analysis of back-propagation neural networks for classification of remotely-sensed multi-spectral imagery. Int J Remote Sens 16: 3033–3058.

Parkinson B,Enge P. 1996. Differential GPS. In: Parkinson B,Spilker J, editors. The global positioning system: theory and applications, Vol. 2. Reston, VA: American Institute of Aeronautics and Astronautics. p 3–30.

Pederson J,Mackley R,Eddleman J. 2002. Colorado Plateau uplift and erosion evaluated using GIS. GSA Today 12: 4–10.

Pope G. 1994. The Howellian perspective: its development and influence on the study of human evolution and behavior. In: Corruccini R,Ciochon R, editors. Integrative paths to the past paleoanthropological advances in honor of F Clark Howell. Englewood Cliffs, NJ: Prentice-Hall. p 1–15.

Rajani MB,Rajawat AS. 2011. Potential of satellite based sensors for studying distribution of archaeological sites along palaeo channels: Harappan sites a case study. J Archaeol Sci 38: 2010–2016.

Rasmussen D,Conroy G,Friscia A,Townsend K,Kinkel M. 1999. Mammals of the Middle Eocene Uinta formation. In: Gillette D, editor. Vertebrate paleontology in Utah. Salt Lake City, UT:Utah Geological Society. p 401–420.

Reed D. 1997. Contour mapping as a new method for interpreting diet from tooth morphology. Am J Phys Anthropol Supp 24: 194.

Reid BA, editor. 2008. Archaeology and geoinformatics: case studies from the Caribbean. Tuscaloosa: University of Alabama Press.

Go here for SFX

Richards J. 1999. Remote sensing digital imaging analysis. Berlin: Springer-Verlag.

Robertson EC, editor. 2006. Space and spatial analysis in archaeology. Calgary: University of Calgary Press.

Robinson P,Gunnell G,Walsh S,Clyde W,Storer J,Stucky R,Froehlich D,Ferrusquia-Villafranca I,McKenna M. 2004. Wasatchian through Duchesnean biochronology. In: Woodburne M, editor.

Late Cretaceous and Cenozoic mammals of North America: biostratigraphy and geochronology. New York: Columbia University Press. p 106–155.

Roehler H. 1987. Paleoenvironments and sedimentation. US Geol Surv Prof Pap 1314-C: 25–45.

Roehler H,Martin P. 1987. Geological investigations of the Vermillion creek coal bed in the Eocene Niland tongue of the wasatch formation, Sweetwater County, Wyoming. US Geol Surv Prof Pap 1314 A-L: 1–202.

Rumelhart DE,Hinton GE,Williams RJ. 1986. Learning internal representations by error propagation. In: Rumelhart D,McClelland J,the PDP Research Group, editors. Parallel distributed processing: explorations in the microstructure of cognition, Vol. 1: Foundations, Cambridge, MA: MIT Press. p 318–362.

Ryan A. 1979. Wear striation direction on primate teeth: a scanning electron microscope examination. Am J Phys Anthropol 50: 155–168.

Ryan A,Johanson D. 1989. Anterior dental microwear in Australopithecus afarensis: comparisons with human and nonhuman primates. J Hum Evol 18: 235–268.

Sarna-Wojcicki A,Meyer C,Roth P,Brown F. 1985. Ages of tuff beds at East African early hominid sites and sediments in the Gulf of Aden. Nature 313: 306–309.

Saturno W,Sever T,Irwin D,Howell B,Garrison T. 2007. Putting us on the map. In: Wiseman J,El-Baz F, editors. Remote sensing in archaeology. New York: Springer. p 137–160.

Schofield P,Bubela T,Weaver T,Portilla L,Brown S,Hancock J,Einhorn D,Tocchini-Valentini G,Hrabe de Angelis M,Rosenthal N. 2009. Post-publication sharing of data and tools. Nature 461: 171–173.

Scott J,Godfrey L,Jungers W,Scott R,Simons E,Teaford M,Ungar P,Walker A. 2009. Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. J Hum Evol 56: 405–416.

Scott R,Ungar P,Bergstrom T,Brown C,Childs B,Teaford M,Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51: 339–349.

Scott R,Ungar P,Bergstrom T,Brown C,Grine F,Teaford M,Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436: 693–695.

Sever T,Wagner D. 1991. Analysis of prehistoric roadways in Chaco Canyon using remotely sensed digital data. In: Trombold C, editor. Ancient road networks and settlement hierarchies in the New World. Cambridge: Cambridge University Press. p 42–52.

Sever T,Wiseman J. 1985. Conference on remote sensing: potential for the future. MS: NASA Earth Resources Laboratory, NSTL.

Sheets P,McKee B, editors. 1994. Archaeology, volcanism and remote sensing in the arenal region, Costa Rica. Austin, TX: University of Texas Press.

Strait S. 1993. Molar microwear in extant small-bodied faunivorous mammals: an analysis of feature density and pit frequency. Am J Phys Anthropol 92: 63–79.

Stucky R,Krishtalka L. 1991. The application of geologic remote sensing to vertebrate biostratigraphy: general results from the Wind River basin, Wyoming. Mount Geol 28: 75–82.

Stucky R,Krishtalka L,Dawson MR. 1989. Paleontology, geology and remote sensing of Paleocene rocks in the northeastern Wind River basin. Wyoming, USA. Guidebook: Int Geol Congr T 322: 34–44.

Stucky RK,Krishtalka L,Redline A. 1990. Geology, vertebrate faunas, and paleoecology of the Buck Spring quarries (early Eocene, Wind River formation), Wyoming. In: Bown T,Rose K, editors. Dawn of the age of mammals in the northern part of the Rocky mountain interior, North America. Boulder, CO: Geological Society of America. p 169–186.

Suwa G,Asfaw B,Haile-Selassie Y,White T,Katoh S,WoldeGabriel G,Hart W,Nakaya H,Beyene Y. 2007. Early Pleistocene Homo erectus fossils from Konso, southern Ethiopia. Anthropol Sci 115: 133–151.

Taieb M,Coppens Y,Johanson D,Kalb J. 1972. Depots sedimentaires et faunes du Plio-Pleistocene de la basse vallee de l'Awash (Afar central. Ethiopie). C R Acad Sci 281: 1297–1300.

Teaford M. 1988. A review of dental microwear and diet in modern mammals. Scanning Microsc 2: 1149–1166.

Teaford M. 1991. Dental microwear. What can it tell us about diet and dental function? In: Kelley M,Larsen C, editors. Advances in dental anthropology. New York: Alan R. Liss. p 341–356.

Teaford M. 1994. Dental microwear and dental function. Evol Anthropol 3: 17–30.

Teaford M. 2003. Looking at teeth in a new light. Proc Natl Acad Sci USA 100: 3560–3561.

Teaford M. 2007. What do we know and not know about dental microwear and diet? In: Ungar P, editor. Evolution of the human diet. The known, the unknown, and the unknowable. Oxford: Oxford University Press. p 106–131.

Teaford M,Glander K. 1991. Dental microwear in live, wild-trapped Alouatta palliata from Costa Rica. Am J Phys Anthropol 85: 313–319.

Teaford M,Glander K. 1996. Dental microwear and diet in a wild population of mantled howlers (Alouatta palliata). In: Norconk M,Rosenberger A,Garber P, editors. Adaptive radiations of neotropical primates. New York: Plenum. p 433–449.

Teaford M,Ungar P. 2000. Diet and the evolution of the earliest human ancestors. Proc Natl Acad Sci USA 97: 13506–13511.

Tomlin C. 1991. Cartographic modeling. In: Goodchild M,Maguire D,Rhind D, editors. Geographical information systems: principles and applications. Harlow, UK: Longman. p 361–364.

Tomlinson R. 1998. The Canada geographic information system. In: Foresman T, editor. The history of geographic information systems. Upper Saddle River, NJ: Prentice Hall. p 21–32.

Tou J,Gonzalez R. 1974. Pattern recognition principles. Reading, MA: Addison-Wesley.

Tourtelot HA. 1957. Geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin. Wyoming. Part 1: Geology. Smithson Misc Colls 134: 1–27.

Townsend K,Friscia A,Rasmussen D. 2006. Stratigraphic distribution of upper Middle Eocene fossil vertebrate localities in the eastern Uinta Basin, Utah, with comments on Uintan biostratigraphy. Mount Geol 43: 115–134.

Ungar P. 2004. Dental topography and diets of Australopithecus afarensis and early Homo. J Hum Evol 46: 605–622.

Ungar P,Brown C,Bergstrom T,Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analysis. Scanning 25: 185–193.

Ungar P,Kay R. 1995. The dietary adaptations of European Miocene catarrhines. Proc Natl Acad Sci USA 92: 5479–5481.

Ungar P,M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional morphology. Proc Natl Acad Sci USA 100: 3874–3877.

Ungar P,Williamson M. 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. Paleontol Electron 3: 18.

Vannier MW,Conroy GC,Marsh JL,Knapp RH. 1985. Three-dimensional cranial surface reconstructions using high-resolution computed tomography. Am J Phys Anthropol 67: 299–311.

Weber GW. 2001. Virtual anthropology (VA): a call for Glasnost in paleoanthropology. Anat Rec 265: 193–201.

Weber GW,Schafer K,Prossinger H,Gunz P,Mitterocker P,Seidler H. 2001. Virtual anthropology: the digital evolution in anthropological sciences. J Physiol Anthropol Appl Hum Sci 20: 69–80.

Wheatley D. 2002. Spatial technology and archaeology: the archaeological applications of GIS. London: Taylor & Francis.

Wheatley D. 2004. Making space for an archaeology of place. Internet Archaeol. Available at: http://intarch.ac.uk/journal/issue15/wheatley_toc.html.

Wheatley D,Gillings M, editors. 2002. Spatial technology and archaeology: the archaeological applications of GIS. London: Taylor and Francis.

Williams B,Covert H. 1994. New early Eocene anaptomorphine primate (Omomyidae) from the Washakie Basin, Wyoming, with comments on the phylogeny and paleobiology of Anaptomorphines. Am J Phys Anthropol 93: 323–340.

WoldeGabriel G,Aronson J,Walter R. 1990. Geology, geochronology, and rift basin development in the central sector of the Main Ethiopian Rift. Geol Soc Am Bull 102: 439–458.

WoldeGabriel G,White T,Suwa G,Semaw S,Beyene Y,Asfaw B,Walter R. 1992. Kesem-Kebena: a newly discovered paleoanthropological research area in Ethiopia. J Field Archaeol 19: 471–493.

Wood B. 1992. A remote sense for fossils. Nature 355: 397–398.

Zeverbergen L,Thorne C. 1987. Quantitative analysis of land surface topography. Earth Surf Proc Land 12: 47–56.

Zuccotti L,Williamson M,Limp W,Ungar P. 1998. Modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107: 137–142.