

## Estimating soil $p\text{CO}_2$ using paleosol carbonates: implications for the relationship between primary productivity and faunal richness in ancient terrestrial ecosystems

Timothy S. Myers, Neil J. Tabor, Louis L. Jacobs, and Octávio Mateus

**Abstract.**—In this paper we present a method for estimating soil  $p\text{CO}_2$  in ancient environments using the measured carbon-isotope values of pedogenic carbonates and plant-derived organic matter. The validity of soil  $p\text{CO}_2$  estimates proves to be highly dependent on the organic  $\delta^{13}\text{C}$  values used in the calculations. Organic matter should be sourced from the same paleosol profiles as sampled carbonates to yield the most reliable estimates of soil  $p\text{CO}_2$ . In order to demonstrate the potential use of soil  $p\text{CO}_2$  estimates in paleoecological and paleoenvironmental studies, we compare samples from three Upper Jurassic localities. Soil  $p\text{CO}_2$  estimates, interpreted as a qualitative indicator of primary paleoproductivity, are used to rank the Late Jurassic terrestrial environments represented by the Morrison Formation in western North America, the informally named Lourinhã formation in Western Europe, and the Stanleyville Group in Central Africa. Because modern terrestrial environments show a positive correlation between primary productivity and faunal richness, a similar relationship is expected in ancient ecosystems. When the relative paleoproductivity levels inferred for each study area are compared with estimates of dinosaur generic richness, a positive correlation emerges. Both the Morrison and Lourinhã formations have high inferred productivity levels and high estimated faunal richness. In contrast, the Stanleyville Group appears to have had low primary productivity and low faunal richness. Paleoclimatic data available for each study area indicate that both productivity and faunal richness are positively linked to water availability, as observed in modern terrestrial ecosystems.

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### Introduction

Pedogenic carbonates have been used for over 20 years to produce quantitative estimates of atmospheric  $p\text{CO}_2$  (e.g., Cerling 1991; Mora et al. 1991; Ekart et al. 1999; Quast et al. 2006); however, the realization that geochemical analysis of carbonates may also be used to estimate soil  $p\text{CO}_2$  is relatively recent (Sheldon and Tabor 2009). In order to demonstrate one of the potential paleoecological applications of this technique, soil  $p\text{CO}_2$  estimates are interpreted here as a qualitative indicator of primary productivity so that the linkage between productivity and faunal richness in ancient terrestrial ecosystems may be evaluated. The relationship between faunal richness and various environmental factors such as climate and primary productivity is a topic of much interest and debate in modern ecology (Currie 1991; Waide et al. 1999; Mittelbach et al. 2001; Chase and Leibold 2002). Considering

that estimation of primary productivity in modern environments is no simple task (Clark et al. 2001; Scurlock et al. 2002), estimating productivity in ancient environments presents an even greater challenge. Geochemical analysis of paleosols provides a basis for qualitative evaluation of paleoproductivity levels using estimates of soil  $\text{CO}_2$  concentration. Retallack (2008, 2009) produced equations relating soil  $p\text{CO}_2$  to the depth to calcic and gypsic horizons within soil profiles; however, these soil  $p\text{CO}_2$  estimates were used to refine geochemical estimates of atmospheric  $\text{CO}_2$  concentrations derived from pedogenic carbonates (sensu Cerling 1991; Ekart et al. 1999), rather than to assess primary productivity. The geochemical technique used here to estimate soil  $p\text{CO}_2$  is based on carbon isotopic differences between coexisting paleosol calcite and organic matter. This approach has not been widely employed (Milleson and Tabor 2008; Sheldon and Tabor



(Fig. 2) and represent similar depositional environments.

The predominantly fluvio-lacustrine deposits of the Morrison Formation (Kimmeridgian–Tithonian) crop out over a large portion of the western United States (Kowallis et al. 1998; Foster 2003) and were deposited between 30°N and 35°N paleolatitude (Smith et al. 1994). Although some basal beds in the Morrison Formation show evidence of marine influence (O’Sullivan 1992; Peterson 1994), the sequence as a whole comprises mostly continental deposits, and all of the samples analyzed here are derived from fully continental paleoenvironments (Myers 2009). Most of the Morrison Formation is thought to have formed under semiarid to arid conditions with seasonal rainfall (Demko and Parrish 1998; Demko et al. 2004; Dunagan and Turner 2004; Parrish et al. 2004). Samples were collected from outcrops near Ghost Ranch, New Mexico; Shell, Wyoming; and Bridger, Montana (Fig. 1A).

The informally named Lourinhã formation (Kimmeridgian–Berriasian) was deposited in the Lusitanian Basin of western Portugal (Hill 1989). During the Late Jurassic, Portugal was one of a series of small, scattered, European landmasses that were separated intermittently by shallow seas (Smith et al. 1994). Fluvio-deltaic deposits of the Lourinhã formation prograded from the western basin margin toward the southeast, gradually filling an embayment of the early North Atlantic (Hill 1989; Mohr 1989). The Lourinhã formation was deposited at paleolatitudes equivalent to those of the Morrison Formation (Smith et al. 1994), but it reflects greater marine influence due to its close proximity to the proto–North Atlantic (Hill 1989). Paleoclimatic reconstruction of Lourinhã formation environments indicates warm and subhumid conditions with seasonal precipitation (Myers et al. in press). The sampling area within the Lourinhã formation is restricted to Upper Jurassic coastal outcrops between the towns of São Bernardino and Porto Novo (Fig. 1B). Lower Cretaceous strata in the Lusitanian Basin were not sampled and are not discussed here.

The Stanleyville Group (Kimmeridgian–?Barremian) consists of fluvio-lacustrine strata deposited in present-day Democratic Republic

of Congo (DRC) (Cahen et al. 1959; Cahen 1983), located near the center of Gondwana in the Late Jurassic (Smith et al. 1994). Stanleyville strata crop out in the eastern Congo Basin, just east of Kisangani (Fig. 1C), and extend westward into the subsurface as far as Kinshasa (Egoroff and Lombard 1962; Lepersonne 1974; Cahen 1983). These deposits differ from those of both the Morrison and Lourinhã formations in that they represent low-latitude environments (10°S to 15°S) that developed deep in the interior of Gondwana (Smith et al., 1994). Paleoenvironments of the Stanleyville Group were hot and arid with only a small amount of seasonal precipitation (Myers et al. 2011). The Stanleyville Group samples analyzed here were collected from a core drilled near Samba in the center of the Congo Basin (Fig. 1C) (Cahen et al. 1959).

The age of the Stanleyville Group is a subject of considerable debate. Numerous biostratigraphic studies, including analyses of fishes (Saint-Seine et al. 1952; Cahen and Lepersonne 1955; Saint-Seine 1955; Saint-Seine and Casier 1962), ostracodes (Grekoﬀ 1957), conchostracans (Defréтин-Lefranc 1967), and bivalves (Cox 1953, 1960), all support assignment to the Upper Jurassic. Further refinement of the biostratigraphy suggests that the Stanleyville Group extends from the lower Kimmeridgian to the Barremian or Aptian (Cahen 1983). Most recently, Colin (1994) reinterpreted the biostratigraphic evidence in favor of a Middle Jurassic (Aalenian–Bathonian) age, largely based on aspects of the fish and ostracode assemblages. Subsequently, an entirely Middle Jurassic age assignment has been adopted by some (Arratia et al. 2002; López-Arbarello et al. 2008; Rauhut and López-Arbarello 2009), but not all (Yanbin et al. 2004; Giresse 2005; Kadima et al. 2011) researchers. The ostracode assemblage from the Stanleyville Group does not resemble those of the Upper Jurassic Morrison or Tendaguru Formations (Colin 1994), but the conchostracan fauna is similar to that of the Upper Jurassic Tacuarembó Formation of Uruguay (Yanbin et al. 2004). Although more work is needed to resolve the precise age of the Stanleyville Group, this study adheres to the stratigraphic chronology presented by Cahen (1983).

*Productivity and Faunal Richness in Modern Environments.*—In modern terrestrial environments, the relationship between primary productivity and faunal richness is complex and variable. Most studies conclude that the productivity-richness relationship is either unimodal, where maximum richness is reached at intermediate productivity levels, or positive linear, where richness increases monotonically with increasing productivity (Waide et al. 1999; Mittelbach et al. 2001). Increasing evidence indicates that the nature of this relationship is dependent on a number of factors, primary among them the spatial scale at which data are collected (Currie 1991; Chase and Leibold 2002). Positive linear patterns are observed more frequently at larger regional to global scales than at smaller local scales (Chase and Leibold 2002). Given the general paucity of data and larger spatial scales that necessarily characterize studies of terrestrial faunal richness in ancient environments, the productivity-richness relationship in Late Jurassic terrestrial ecosystems is expected to follow a positive monotonic pattern.

Modern terrestrial ecosystems also reflect positive relationships among soil CO<sub>2</sub> concentration, primary productivity, and water availability. Soil CO<sub>2</sub> production in modern terrestrial environments is a function of both temperature and soil moisture conditions (Witkamp 1966; Garrett and Cox 1973; Edwards 1975; Buyanovsky and Wagner 1983; Kiefer 1990). High soil moisture levels decrease diffusion rates, reducing the surface CO<sub>2</sub> flux from the soil (Edwards 1975) and increasing the subsurface concentration of soil CO<sub>2</sub> (Buyanovsky and Wagner 1983). High productivity environments—typically characterized by large plant litter input and elevated rates of microbial respiration (Amundson 2001; Joffre and Ågren 2001)—possess high soil CO<sub>2</sub> concentrations (Brook et al. 1983) and high levels of water availability (Lieth 1975; Churkina and Running 1998; Loustau et al. 2001; Nemani et al. 2003; Bradford et al. 2006). Experimental studies demonstrate that elevated atmospheric pCO<sub>2</sub> induces increased soil respiration and higher soil pCO<sub>2</sub> (Johnson et al. 1994; Andrews and Schlesinger 2001; King

et al. 2001; Karberg et al. 2005), as well as increases in primary productivity (DeLucia et al. 1999), indicating that soil pCO<sub>2</sub> and productivity are positively linked. The positive relationship between soil pCO<sub>2</sub> and productivity indicators such as root biomass has also been documented in modern environments (Johnson et al. 1994; King et al. 2001). Therefore, terrestrial environments with elevated levels of soil CO<sub>2</sub> may be expected to also have high productivity levels and high water availability, and because ancient terrestrial ecosystems are assumed to have operated under the same basic principles as modern ecosystems, they should display similar relationships among soil pCO<sub>2</sub>, soil moisture, and productivity.

## Methods

*Field Sampling.*—Paleosol carbonates were collected from each of the three study areas and analyzed. Samples from the Lourinhã formation were collected from two composite, correlative stratigraphic sections adjacent to the coastal town of Areia Branca, one located north of the town and the other located to the south. The northern stratigraphic section is 415 m thick, and the southern section measures 314 m (Supplementary Fig. 1). A total of 164 paleosol profiles were identified and described in the Lourinhã formation, 100 profiles in the northern section and 64 profiles in the southern section. Paleosol carbonate samples were also collected from composite sections at three localities within the Morrison Formation, located near Ghost Ranch, New Mexico; Bridger, Montana; and Shell, Wyoming (Supplementary Fig. 2). The Ghost Ranch locality provides the longest section through the Morrison Formation, with a thickness of 167 m and 23 described paleosols. The sections measured near Bridger and Shell are 39 m and 76 m thick, respectively. The Shell locality yielded 21 paleosol profiles, but the stratigraphic section measured near Bridger contained only six paleosols. Seven carbonate samples were collected from the Stanleyville Group strata in the Samba core, although only two of these samples are potentially Jurassic in age, and only one is appropriate for use in soil pCO<sub>2</sub> calculations. The overall thickness of the

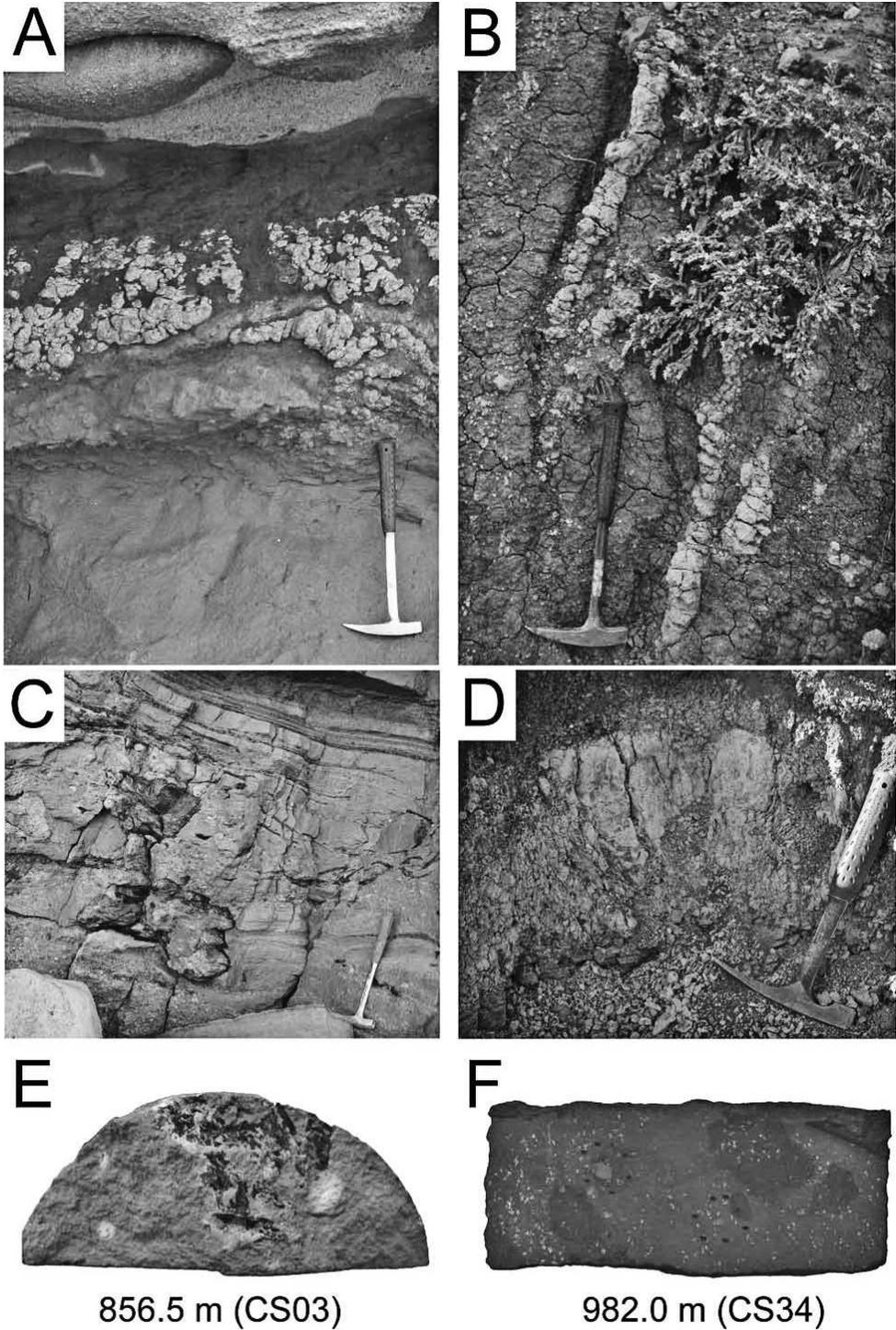


FIGURE 3. Photos showing carbonate morphologies and organic matter from each of the three study areas. A, Bk II carbonate accumulation in a Lourinhã paleosol. B, Calcareous rhizoliths in a Lourinhã paleosol. C, Carbonized logs and seams of fine particulate organic matter in the Lourinhã formation. D, Bk III carbonate accumulation in a Morrison Formation paleosol near Ghost Ranch, N.M. E, Woody organic matter from the Stanleyville Group in the Samba core. F, Small carbonate nodules from the Stanleyville Group in the Samba core. Hammer in photos A–C, 41 cm. Hammer in photo D, 28 cm. Scale bar, 5 cm.

Stanleyville Group in the Samba core is 323 m, with 16 identified paleosol profiles (Supplementary Fig. 3).

Organic matter samples derived from fossil vascular plant remains were collected from the same stratigraphic sections as the sampled carbonates. The Lourinhã formation contains an abundance of carbonized wood, varying in size from small fragments to large logs, as well as layers of concentrated organic particulate matter (Fig. 3). Organic matter was collected wherever it appeared in the stratigraphy, typically from fluvial deposits adjacent to the carbonate-bearing paleosol horizons. Organic matter is much less common in the Morrison Formation and the Stanleyville Group. Samples collected from these units typically consist of fine particles of disseminated plant matter (Fig. 3).

Carbonate samples consisting of discrete pedogenic nodules or calcareous rhizoliths (Fig. 3) were collected from depths at least 50 cm below the upper contact of each paleosol profile. At depths greater than 50 cm below surface in modern soil profiles, the concentration and isotopic composition of soil CO<sub>2</sub> are essentially constant; above 50 cm depth, mixing of atmospheric and soil CO<sub>2</sub> produces steep gradients in CO<sub>2</sub> concentration and isotopic composition (Cerling and Quade 1993; Ekart et al. 1999). Because all sampled carbonates are assumed to have formed at least 50 cm below the original soil surface, soil *p*CO<sub>2</sub> calculations based on these samples should reflect conditions of maximum CO<sub>2</sub> concentration within the soil profile at the time of calcite crystallization. Samples from fully cemented Bk III horizons were not used to estimate soil *p*CO<sub>2</sub>.

*Laboratory Analysis.*—Thin sections of carbonate nodules and rhizoliths from the Lourinhã and Morrison formations were examined petrographically to identify areas with fabrics of likely pedogenic origin. Observed samples resemble the alpha-type microfabric described by Wright (1990), with micritic or microsparitic groundmasses that may contain skeletal quartz grains, spar-filled veins, or glaeboles with circumgranular cracks (Fig. 4). We sampled both micritic and microsparitic fabrics with crystals <20

μm for δ<sup>13</sup>C analysis, avoiding spar-filled voids and veins. We avoided coarse sparry fabrics with crystals >20 μm, as these typically represent groundwater or diagenetic cements (Courty et al. 1987; Mora et al. 1993; Quast et al. 2006). For some samples, sparry fabrics that appeared to be non-pedogenic or diagenetically altered were sampled for comparison with areas of suspected pedogenic calcite. Although diagenetic alteration of primary isotopic values may not always be reflected by textural characteristics, δ<sup>13</sup>C values appear less susceptible to alteration than δ<sup>18</sup>O values (Cerling 1991; Mora et al. 1996; Leier et al. 2009). Nonetheless, in order to further constrain potential diagenetic alteration of samples, we assessed internal variability of δ<sup>13</sup>C values in addition to textural criteria. Samples were not used in soil *p*CO<sub>2</sub> calculations if apparently unaltered areas yielded δ<sup>13</sup>C values within 1.0‰ of co-occurring calcite spar.

Selected areas within the thin sections were drilled with a Merchantek Micromill in the Roy M. Huffington Department of Earth Sciences at Southern Methodist University (SMU). Sample powders from the Lourinhã and Morrison formations were analyzed at the University of California, Davis, where they were loaded into a GVI Optima Stable Isotope Ratio Mass Spectrometer equipped with an automated carbonate reaction device and reacted with 100% H<sub>3</sub>PO<sub>4</sub> at 90°C. The evolved gases were cryogenically purified to isolate pure CO<sub>2</sub>, which was subsequently moved into the mass spectrometer to determine δ<sup>13</sup>C and δ<sup>18</sup>O values. Samples from the Stanleyville Group were drilled from hand-sample and analyzed at SMU. These samples were reacted with 100% orthophosphoric acid at 25°C and cryogenically purified to isolate CO<sub>2</sub> (McCrea 1950). The carbon-isotope composition of the extracted CO<sub>2</sub> was then measured using a Finnigan MAT 252 isotope ratio mass spectrometer. Delta values (δ) for all carbonate samples are reported here in per mil (‰) units relative to the Peedee Belemnite (PDB) international standard.

Plant-derived organic matter samples collected from each of the study areas were soaked in dilute HCl for a minimum of four

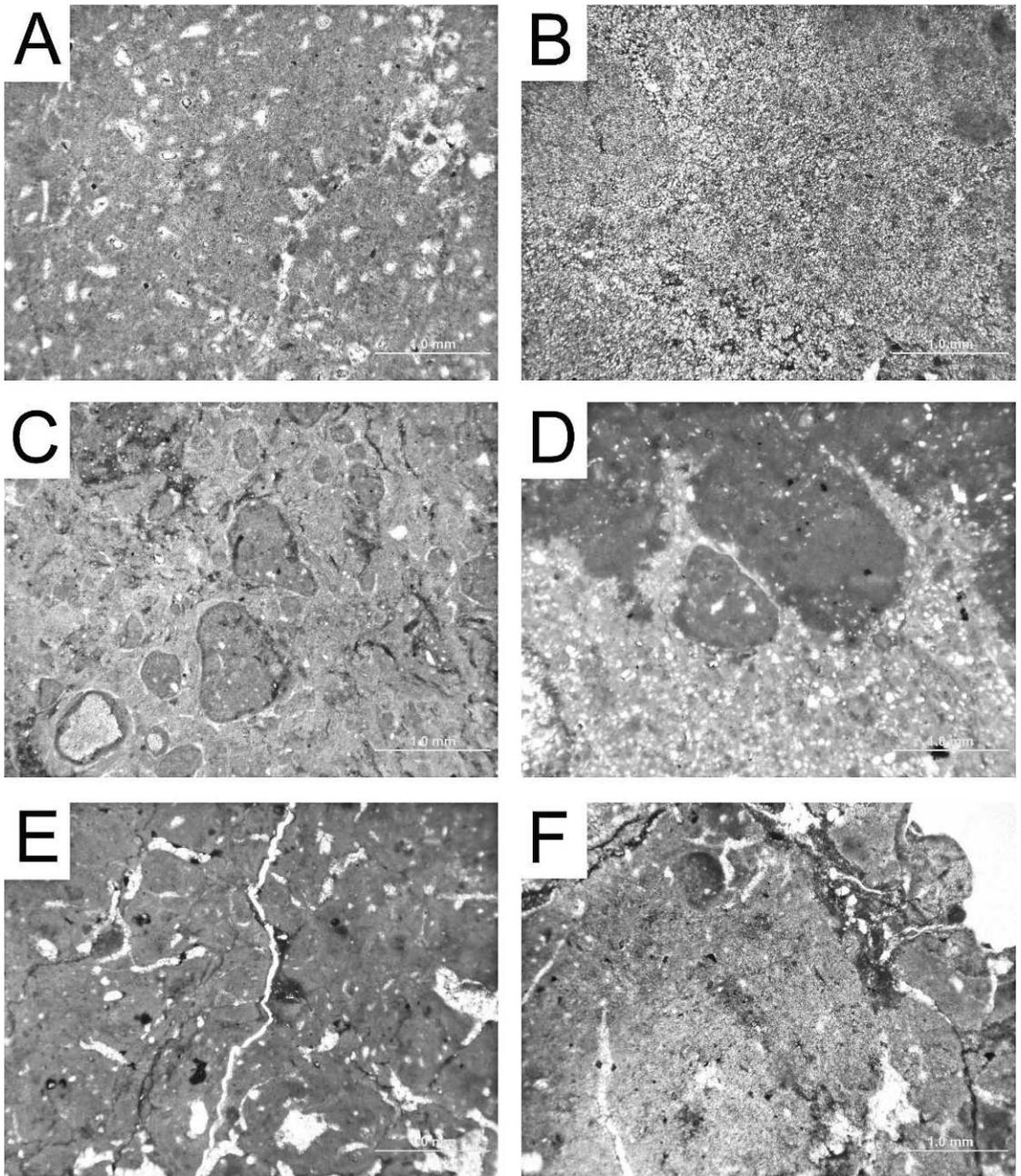


FIGURE 4. Thin section photomicrographs of calcite fabrics encountered in pedogenic carbonate samples. A, GR018 – micritic groundmass with skeletal quartz grains. B, GR024 – microspar. C, MD014 – micritic groundmass with glaebules and spar-filled circumgranular cracks. D, SH021 – micritic glaebules adjacent to micrite surrounding quartz grains. E, PL026 – micrite with spar-filled veins. F, PT011 – microspar with spar-filled veins.

hours to remove any carbonate material. Samples were then rinsed thoroughly with deionized water and air dried. Procedures for extraction of  $CO_2$  from organic samples for  $\delta^{13}C$  analysis were based on the methods

detailed by Boutton (1991). Each sample was sealed under vacuum in a Vycor tube containing 1 g copper oxide and 0.5 g native copper. Samples were then pyrolyzed at  $900^\circ C$  for two hours before the temperature was reduced

incrementally and maintained at 650°C for two hours. Gases evolved during pyrolysis were cryogenically purified to isolate CO<sub>2</sub>. The  $\delta^{13}\text{C}$  value of the CO<sub>2</sub> gas was measured and reported as described above for the carbonate samples.

*Faunal Richness Estimates.*—In order to compare faunal richness between Portugal and the western United States, we compiled data on occurrences of dinosaur genera from the literature. We selected the Dinosauria from among various groups of vertebrates because dinosaurs were restricted to terrestrial paleoenvironments and are relatively well sampled. The Stanleyville Group of Central Africa is devoid of terrestrial vertebrate remains, so its faunal richness is set as zero, and it is not included in the statistical comparison between the western United States and Portugal.

Dinosaur occurrences in the Morrison Formation ( $n = 863$ ) were compiled from Foster (2003), augmented with more recently published data (Harris and Dodson 2004; Carrano and Velez-Juarbe 2006). Occurrences from the Late Jurassic of Portugal ( $n = 79$ ), including specimens from both the Lourinhã formation and roughly contemporary strata in the nearby Guimarota coal mine, were tabulated from a variety of sources (Thulborn 1973; Zinke and Rauhut 1994; Weigert 1995; Zinke 1998; Rauhut 2000, 2001; Antunes and Mateus 2003; Rauhut 2003). Raw generic richness counts for the Morrison Formation and Portuguese localities are 29 and 19 genera, respectively. All taxa were checked against Weishampel et al. (2004) to determine current status and validity. The number of individual occurrences of each dinosaur taxon was estimated using the Minimum Number of Individuals (MNI) counting method. For cases in which a taxon was represented only by numerous, isolated teeth recovered at different localities (a problem for several Portuguese taxa), we counted all teeth as a single occurrence of the taxon unless the total number of tooth specimens exceeded the number typically present in a single individual. Each data set was rarefied using Analytic Rarefaction Ver. 1.3 (Holland 2003) in order to estimate richness at smaller sample sizes.

We then compared estimates of generic richness for eight different sample sizes using a two-tailed Wilcoxon rank sum test (equivalent to a Mann-Whitney *U*-test) to check for statistically significant difference. Implicit in use of the rarefaction technique are assumptions that the samples being compared are taxonomically similar, are derived from similar habitats, and were collected using comparable sampling methods (Tipper 1979). Rarefaction also assumes a random spatial distribution of individuals (Kobayashi 1982, 1983).

## Results

*Carbon Isotope Values of Pedogenic Carbonates.*—Of the 58 pedogenic carbonate samples from the Lourinhã formation that we analyzed for  $\delta^{13}\text{C}$  composition, 56 had no textural or geochemical evidence of diagenetic alteration and were used to estimate soil  $p\text{CO}_2$ . The  $\delta^{13}\text{C}$  values for these microsampled Lourinhã carbonates vary between  $-10.7\text{‰}$  and  $-5.3\text{‰}$ , with a mean of  $-8.3\text{‰}$  (Supplementary Table 1). The carbonate  $\delta^{13}\text{C}$  values from the northern and southern stratigraphic sections did not differ substantially. Average values are  $-8.2\text{‰} \pm 1.2\text{‰}$  ( $1\sigma$ ) for the northern section and  $-8.5\text{‰} \pm 0.8\text{‰}$  ( $1\sigma$ ) for the southern section (Supplementary Table 1). No pronounced stratigraphic trends in the carbonate  $\delta^{13}\text{C}$  values are discernible in either section, although variability appears to increase upsection (Supplementary Fig. 4A,B).

Thirty-two of the 34 microsampled, pedogenic carbonates from the Morrison Formation were judged suitable for use in soil  $p\text{CO}_2$  calculations: 19 samples from the Ghost Ranch locality, ten samples from the Shell locality, and three from the Bridger locality. Carbon-isotope values for all selected Morrison samples range from  $-7.0\text{‰}$  to  $-3.3\text{‰}$ , with a mean value of  $-5.7\text{‰}$  (Supplementary Table 2). The average  $\delta^{13}\text{C}$  values for carbonates from each sampling area are analytically indistinguishable from one another. Average values from each locality are  $-5.8\text{‰} \pm 0.9\text{‰}$  ( $1\sigma$ ) for Ghost Ranch,  $-5.6\text{‰} \pm 1.0\text{‰}$  ( $1\sigma$ ) for Shell, and  $-5.8\text{‰} \pm 1.4\text{‰}$  ( $1\sigma$ ) for Bridger (Supplemen-

TABLE 1. Soil pCO<sub>2</sub> estimates for the Lourinhã formation (*n* = 53), calculated using the average δ<sup>13</sup>C value of sampled organic matter, soil temperatures of 25°C and 30°C, and the fractionation equation derived by Romanek et al. (1992). δ<sup>13</sup>C<sub>Atm</sub> = -6.7‰ PDB, C<sub>A</sub> = 3200 ppmV. Dashes denote negative soil pCO<sub>2</sub> estimates (see discussion).

| Sample  | δ <sup>13</sup> C <sub>Sec</sub><br>(‰ PDB) | δ <sup>13</sup> C <sub>Org</sub><br>(‰ PDB) | δ <sup>13</sup> C <sub>Occ</sub><br>(‰ PDB) (25°C) | δ <sup>13</sup> C <sub>Occ</sub><br>(‰ PDB) (30°C) | C <sub>S</sub><br>(ppmV) (25°C) | C <sub>S</sub><br>(ppmV) (30°C) |
|---------|---|---|--|--|---------------------------------|---------------------------------|
| PT009   | -7.27                                       | -22.3                                       | -9.0   | -9.6   | 20921                           | 15529                           |
| PT011   | -7.64                                       | -22.3                                       | -9.0   | -9.6   | 26627                           | 18467                           |
| PT015   | -7.90                                       | -22.3                                       | -9.0   | -9.6   | 32924                           | 21291                           |
| PT032AB | -7.89                                       | -22.3                                       | -9.0   | -9.6   | 32626                           | 21166                           |
| PT048   | -8.36                                       | -22.3                                       | -9.0   | -9.6   | 56657                           | 29201                           |
| PT061AB | -7.11                                       | -22.3                                       | -9.0   | -9.6   | 19148                           | 14531                           |
| PT064AB | -7.36                                       | -22.3                                       | -9.0   | -9.6   | 22070                           | 16154                           |
| PT076   | -8.26                                       | -22.3                                       | -9.0   | -9.6   | 48937                           | 27005                           |
| PT079   | -6.20                                       | -22.3                                       | -9.0   | -9.6   | 12921                           | 10639                           |
| PT092   | -9.46                                       | -22.3                                       | -9.0   | -9.6   | —                               | 264052                          |
| PT094   | -8.52                                       | -22.3                                       | -9.0   | -9.6   | 75617                           | 33534                           |
| PT098   | -6.65                                       | -22.3                                       | -9.0   | -9.6   | 15397                           | 12263                           |
| PT107   | -9.56                                       | -22.3                                       | -9.0   | -9.6   | —                               | 948426                          |
| PT114   | -9.16                                       | -22.3                                       | -9.0   | -9.6   | —                               | 82768                           |
| PT121   | -9.20                                       | -22.3                                       | -9.0   | -9.6   | —                               | 90812                           |
| PT123   | -9.43                                       | -22.3                                       | -9.0   | -9.6   | —                               | 209832                          |
| PT128   | -7.63                                       | -22.3                                       | -9.0   | -9.6   | 26469                           | 18391                           |
| PT137A  | -8.15                                       | -22.3                                       | -9.0   | -9.6   | 42628                           | 24966                           |
| PT139A  | -9.06                                       | -22.3                                       | -9.0   | -9.6   | —                               | 67728                           |
| PT144AB | -8.12                                       | -22.3                                       | -9.0   | -9.6   | 41172                           | 24459                           |
| PT149A  | -8.14                                       | -22.3                                       | -9.0   | -9.6   | 42132                           | 24795                           |
| PT158A  | -9.34                                       | -22.3                                       | -9.0   | -9.6   | —                               | 139785                          |
| PT158B  | -8.74                                       | -22.3                                       | -9.0   | -9.6   | 140067                          | 42132                           |
| PT164   | -5.86                                       | -22.3                                       | -9.0   | -9.6   | 11539                           | 9685                            |
| PT180   | -5.31                                       | -22.3                                       | -9.0   | -9.6   | 9803                            | 8431                            |
| PT184   | -6.99                                       | -22.3                                       | -9.0   | -9.6   | 17964                           | 13839                           |
| PT187   | -8.51                                       | -22.3                                       | -9.0   | -9.6   | 74796                           | 33372                           |
| PL005A  | -9.00                                       | -22.3                                       | -9.0   | -9.6   | —                               | 60792                           |
| PL005B  | -8.61                                       | -22.3                                       | -9.0   | -9.6   | 93152                           | 36589                           |
| PL019   | -8.18                                       | -22.3                                       | -9.0   | -9.6   | 44138                           | 25477                           |
| PL025   | -8.79                                       | -22.3                                       | -9.0   | -9.6   | 173717                          | 44738                           |
| PL026   | -8.61                                       | -22.3                                       | -9.0   | -9.6   | 92168                           | 36436                           |
| PL028   | -8.55                                       | -22.3                                       | -9.0   | -9.6   | 80449                           | 34452                           |
| PL036   | -7.98                                       | -22.3                                       | -9.0   | -9.6   | 35358                           | 22283                           |
| PL039   | -9.39                                       | -22.3                                       | -9.0   | -9.6   | —                               | 171176                          |
| PL044   | -8.77                                       | -22.3                                       | -9.0   | -9.6   | 161792                          | 43905                           |
| PL050   | -8.72                                       | -22.3                                       | -9.0   | -9.6   | 128887                          | 41060                           |
| PL051   | -8.86                                       | -22.3                                       | -9.0   | -9.6   | 259020                          | 48884                           |
| PL052   | -7.74                                       | -22.3                                       | -9.0   | -9.6   | 28737                           | 19457                           |
| PL065   | -7.67                                       | -22.3                                       | -9.0   | -9.6   | 27267                           | 18772                           |
| PL067   | -8.57                                       | -22.3                                       | -9.0   | -9.6   | 83543                           | 35007                           |
| PL071   | -8.81                                       | -22.3                                       | -9.0   | -9.6   | 193970                          | 45975                           |
| PL074   | -7.54                                       | -22.3                                       | -9.0   | -9.6   | 24845                           | 17592                           |
| PL076   | -9.28                                       | -22.3                                       | -9.0   | -9.6   | —                               | 113020                          |
| PL081   | -8.46                                       | -22.3                                       | -9.0   | -9.6   | 67076                           | 31742                           |
| PL086   | -8.74                                       | -22.3                                       | -9.0   | -9.6   | 140382                          | 42160                           |
| PL087   | -8.43                                       | -22.3                                       | -9.0   | -9.6   | 64059                           | 31050                           |
| PL113   | -7.25                                       | -22.3                                       | -9.0   | -9.6   | 20664                           | 15387                           |
| PL115   | -8.24                                       | -22.3                                       | -9.0   | -9.6   | 47513                           | 26566                           |
| PL120   | -8.87                                       | -22.3                                       | -9.0   | -9.6   | 272449                          | 49344                           |
| PL131   | -6.26                                       | -22.3                                       | -9.0   | -9.6   | 13206                           | 10832                           |
| PL135   | -9.37                                       | -22.3                                       | -9.0   | -9.6   | —                               | 156058                          |
| PL139   | -8.02                                       | -22.3                                       | -9.0   | -9.6   | 36907                           | 22888                           |

tary Table 2). There is no discernible stratigraphic trend in the carbonate δ<sup>13</sup>C values in the Ghost Ranch section (Supplementary Fig. 4C). The Shell section shows a slight positive trend upsection, although the sam-

pled interval represents only about 20% of the total section thickness (Supplementary Fig. 4D). The Bridger section yielded too few samples to accurately assess any stratigraphic trends.

TABLE 2. Soil  $p\text{CO}_2$  estimates for the Morrison Formation ( $n = 32$ ), calculated using the average  $\delta^{13}\text{C}$  value of sampled organic matter, soil temperatures of 25°C and 30°C, and the fractionation equation derived by Romanek et al. (1992).  $\delta^{13}\text{C}_{\text{Atm}} = -6.7\text{‰ PDB}$ ,  $C_A = 3200 \text{ ppmV}$ . GR = Ghost Ranch, N.M.; SH = Shell, Wyo.; MD = Bridger, Mont.

| Sample | $\delta^{13}\text{C}_{\text{Sec}}$<br>(‰ PDB) | $\delta^{13}\text{C}_{\text{Org}}$<br>(‰ PDB) | $\delta^{13}\text{C}_{\text{Occ}}$<br>(‰ PDB) (25°C) | $\delta^{13}\text{C}_{\text{Occ}}$<br>(‰ PDB) (30°C) | $C_S$<br>(ppmV) (25°C) | $C_S$<br>(ppmV) (30°C) |
|--------|---|---|--|--|------------------------|------------------------|
| GR006A | -6.58   | -20.3   | -6.9   | -7.5   | 66417                  | 29451                  |
| GR006B | -6.77   | -20.3   | -6.9   | -7.5   | 115048                 | 36281                  |
| GR007  | -6.94   | -20.3   | -6.9   | -7.5   | 341482                 | 45926                  |
| GR010  | -5.60   | -20.3   | -6.9   | -7.5   | 20866                  | 14933                  |
| GR013  | -6.55   | -20.3   | -6.9   | -7.5   | 62016                  | 28549                  |
| GR018  | -6.71   | -20.3   | -6.9   | -7.5   | 92766                  | 33716                  |
| GR019  | -4.78   | -20.3   | -6.9   | -7.5   | 13291                  | 10594                  |
| GR020  | -6.48   | -20.3   | -6.9   | -7.5   | 54007                  | 26717                  |
| GR021  | -6.73   | -20.3   | -6.9   | -7.5   | 99288                  | 34544                  |
| GR023A | -4.97   | -20.3   | -6.9   | -7.5   | 14496                  | 11349                  |
| GR024  | -4.92   | -20.3   | -6.9   | -7.5   | 14185                  | 11157                  |
| GR025A | -4.67   | -20.3   | -6.9   | -7.5   | 12653                  | 10182                  |
| GR026  | -5.48   | -20.3   | -6.9   | -7.5   | 19316                  | 14119                  |
| GR028A | -5.07   | -20.3   | -6.9   | -7.5   | 15236                  | 11799                  |
| GR029A | -4.31   | -20.3   | -6.9   | -7.5   | 10978                  | 9065                   |
| GR030  | -5.10   | -20.3   | -6.9   | -7.5   | 15438                  | 11921                  |
| GR034  | -5.62   | -20.3   | -6.9   | -7.5   | 21124                  | 15066                  |
| GR035A | -5.24   | -20.3   | -6.9   | -7.5   | 16683                  | 12653                  |
| GR046B | -6.68   | -20.3   | -6.9   | -7.5   | 86293                  | 32818                  |
| SH008  | -6.96   | -22.3   | -8.9   | -9.5   | 17889                  | 13788                  |
| SH018  | -6.12   | -22.3   | -8.9   | -9.5   | 12623                  | 10433                  |
| SH020  | -6.67   | -22.3   | -8.9   | -9.5   | 15625                  | 12403                  |
| SH021  | -5.81   | -22.3   | -8.9   | -9.5   | 11392                  | 9578                   |
| SH023  | -5.93   | -22.3   | -8.9   | -9.5   | 11852                  | 9901                   |
| SH025  | -4.78   | -22.3   | -8.9   | -9.5   | 8593                   | 7519                   |
| SH027  | -5.41   | -22.3   | -8.9   | -9.5   | 10126                  | 8667                   |
| SH028  | -5.79   | -22.3   | -8.9   | -9.5   | 11325                  | 9531                   |
| SH029  | -5.40   | -22.3   | -8.9   | -9.5   | 10086                  | 8638                   |
| SH030  | -3.28   | -22.3   | -8.9   | -9.5   | 6329                   | 5726                   |
| MD010A | -4.18   | -21.2   | -7.8   | -8.4   | 8784                   | 7562                   |
| MD013A | -6.73   | -21.2   | -7.8   | -8.4   | 28040                  | 18499                  |
| MD014  | -6.35   | -20.2   | -6.8   | -7.4   | 21182                  | 15243                  |

Of the seven carbonate specimens sampled from the Samba core, only one proved suitable for estimating soil  $p\text{CO}_2$  (CS34). This nodule, collected from a pedogenically modified siltstone, has a  $\delta^{13}\text{C}$  value of  $-6.8\text{‰}$  (Supplementary Table 3). The other carbonate samples from the Stanleyville Group are derived from coarse-grained fluvial deposits, and although they were likely formed by pedogenic processes, they are detrital clasts and not appropriate for use in  $p\text{CO}_2$  calculations (Ekart et al. 1999; Sheldon and Tabor 2009).

*Carbon-Isotope Values of Plant-Derived Organic Matter.*—Plant-derived organic matter is common in the fluvial channel deposits of the Lourinhã formation. We collected 32 samples from the northern stratigraphic section near Lourinhã, and 34 were collected from the southern section. These samples are a mix of carbonized wood and disseminated particulate matter. Carbon-isotope analysis of these samples yielded values between  $-29.4\text{‰}$  and  $-20.2\text{‰}$ , with an average value of  $-22.3\text{‰}$  (Supplementary Table 4). As with the Lourinhã carbonate samples, there are no apparent

TABLE 3. Soil  $p\text{CO}_2$  estimates for the Stanleyville Group ( $n = 1$ ), calculated using the average  $\delta^{13}\text{C}$  value of sampled, potentially Upper Jurassic organic matter, soil temperatures of 25°C and 30°C, and the fractionation equation derived by Romanek et al. (1992).  $\delta^{13}\text{C}_{\text{Atm}} = -6.7\text{‰ PDB}$ ,  $C_A = 3200 \text{ ppmV}$ .

| Sample | $\delta^{13}\text{C}_{\text{Sec}}$<br>(‰ PDB) | $\delta^{13}\text{C}_{\text{Org}}$<br>(‰ PDB) | $\delta^{13}\text{C}_{\text{Occ}}$<br>(‰ PDB) (25°C) | $\delta^{13}\text{C}_{\text{Occ}}$<br>(‰ PDB) (30°C) | $C_S$<br>(ppmV) (25°C) | $C_S$<br>(ppmV) (30°C) |
|--------|---|---|--|--|------------------------|------------------------|
| CS34   | -6.8  | -24.4   | -11.0  | -11.6  | 9961                   | 8743                   |

stratigraphic trends in the  $\delta^{13}C$  values of the sampled organic matter (Supplementary Fig. 4E,F).

Carbonized plant material is much less common in the Morrison Formation, and despite careful inspection of over 1000 meters of section at several different localities, we recovered only four organic matter samples from three sites. One sample from Montana (MD020) consists of carbonized woody material, and the rest comprise disseminated particles of organic matter suspended in clastic matrix. The  $\delta^{13}C$  values of these samples range from  $-22.3\text{‰}$  to  $-18.7\text{‰}$ , with an average of  $-21.0\text{‰}$  (Supplementary Table 5).

We analyzed five organic samples collected from the Stanleyville Group to determine their  $\delta^{13}C$  values. Three of these samples are derived from Lower Cretaceous strata in the Stanleyville section, and two samples were collected from the Jurassic/Cretaceous boundary interval between 942 m and 1009 m depth (Cahen, 1983). One of the samples (CS03) is composed of carbonized wood, but the rest comprise disseminated particles of organic matter. Carbon-isotope values for these organics range from  $-24.8\text{‰}$  to  $-23.2\text{‰}$  PDB, with an average of  $-24.3\text{‰}$  (Supplementary Table 6).

*Estimates of Faunal Richness.*—The rarefaction curve for the Morrison Formation begins to plateau near a generic richness between 25 and 30, but the curve for the Portuguese data set has a very high slope, indicating inadequate sampling of this population (Fig. 5). A two-tailed *t*-test conducted for larger sample sizes of 50, 60, and 70 individuals, within the diverging portions of the rarefaction curves and beyond their intersection point, indicates that the richness of the parent populations is not significantly different at a confidence level of  $\alpha=0.10$ ; however, this apparent similarity is a product of insufficient sampling of the Portuguese fauna. Although the divergent trajectory of the Portuguese curve appears to suggest a higher overall richness relative to the sample for the Morrison Formation, a larger sample is required to justify such a conclusion. Consequently, to estimate the total generic richness of the Portuguese and Morri-

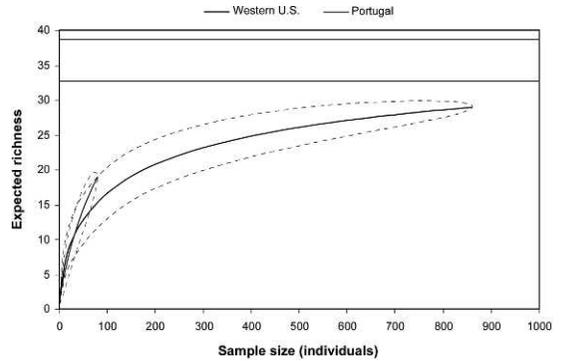


FIGURE 5. Rarefaction curves for Late Jurassic dinosaur genera from Portugal (Lourinhã formation and the Guimarota mine) and the Morrison Formation. Dashed-line envelopes indicate the 95% confidence interval for each curve. The horizontal lines near the top of the plot denote the estimated total generic richness for each sample, calculated using equation (1). The Lourinhã formation is undersampled, but yields a higher total richness estimate than the Morrison Formation.

son faunas we used the equation given by Chao (1984):

$$S = S_{obs} + a^2/2b \quad (1)$$

where  $S$  is the estimated total taxonomic richness of the sample,  $S_{obs}$  is the observed number of taxa,  $a$  is the number of observed taxa represented by a single individual, and  $b$  is the number of taxa in the sample represented by exactly two individuals. This equation yields an estimated total richness of 39 genera for Portugal and 33 genera for the Morrison Formation. This method of extrapolating total richness tends to underestimate the true richness of a population, especially at smaller sample sizes (Colwell and Coddington 1994). Therefore, each of these numbers should be considered a minimum estimate of true faunal richness.

## Discussion

*Estimating Soil  $pCO_2$ .*— Because soil  $pCO_2$  and primary productivity are positively correlated in modern ecosystems, we interpret soil  $CO_2$  concentration as a qualitative indicator of terrestrial paleoproductivity levels. The  $\delta^{13}C$  values of  $CO_2$  extracted from pedogenic calcite and plant-derived organic matter are used to calculate soil  $pCO_2$  with a two-endmember mixing equation (Yapp and Poths

1996) that describes the relative contributions of atmospheric CO<sub>2</sub> and soil-respired CO<sub>2</sub> derived from root respiration and in situ oxidation of organic matter in soils characterized by one-dimensional Fickian diffusion:

$$C_S = C_A \frac{\delta^{13}C_{Acc} - \delta^{13}C_{Occ}}{\delta^{13}C_{Scc} - \delta^{13}C_{Occ}} \quad (2)$$

C<sub>S</sub> is the concentration of CO<sub>2</sub> (ppmV) in the soil, whereas C<sub>A</sub> is the concentration of CO<sub>2</sub> (ppmV) in the atmosphere. δ<sup>13</sup>C<sub>Acc</sub> is the δ<sup>13</sup>C value of a calcite formed in equilibrium with atmospheric CO<sub>2</sub>, whereas δ<sup>13</sup>C<sub>Occ</sub> is the δ<sup>13</sup>C value of a calcite formed in equilibrium with soil-respired CO<sub>2</sub>. δ<sup>13</sup>C<sub>Scc</sub> is the measured δ<sup>13</sup>C value of pedogenic calcite that reflects a soil CO<sub>2</sub> mixture derived from both the atmosphere and in situ soil processes.

In addition to measured values of pedogenic calcite and organic matter, equation (2) requires assumptions for (1) soil temperature, which affects the carbon-isotope fractionation between CO<sub>2</sub> and calcite, as well as (2) the δ<sup>13</sup>C value and (3) concentration (in ppmV) of atmospheric CO<sub>2</sub> at the time of calcite crystallization. Pedogenic carbonate most likely forms during the driest and warmest times of year, when soil biota utilize and expend water stored in the soil profile (e.g., Breecker et al. 2009). According to the results of Late Jurassic general circulation models, as well as soil temperature estimates derived from the oxygen and hydrogen isotope composition of pedogenic phyllosilicates from the Lourinhã formation and the Stanleyville Group, summer surface air temperatures ranged from 25°C to 35°C (Rees et al. 2000; Sellwood and Valdes 2006, 2008; Myers 2009; Myers et al. 2011, in press). On the basis of this range of temperatures, we calculated carbon-isotope fractionation factors for CO<sub>2(g)</sub>—calcite at 25°C and 30°C, using the experimentally derived equation presented by Romanek et al. (1992):

$$\epsilon_{cc-CO_2} = 11.98 - 0.12 * T_{°C} \quad (3)$$

We used an atmospheric CO<sub>2</sub> δ<sup>13</sup>C value of -6.7‰ for calculations of soil pCO<sub>2</sub> because this value reflects the mean δ<sup>13</sup>C value of Upper Jurassic shallow marine carbonates

(Veizer et al. 1999), including a -8‰ offset between the oceanic and atmospheric reservoirs (Ekart et al. 1999).

Ancient atmospheric pCO<sub>2</sub> can be estimated using a variety of methods, including geochemical proxies and mass-flux models. Commonly used techniques for determining atmospheric paleo-pCO<sub>2</sub> include δ<sup>13</sup>C analysis of pedogenic carbonates (Cerling 1991; Ekart et al. 1999), pedogenic goethite (Yapp and Poths 1992, 1996), or phytoplankton remains (Freeman and Hayes 1992); analysis of stomatal density or stomatal index of fossil plants (Beerling and Chaloner 1992; McElwain and Chaloner 1995); and carbon mass-flux models of atmospheric composition (Berner 1990, 1994, 2006a,b, 2008; Berner and Kothavala 2001). Recent estimates of atmospheric pCO<sub>2</sub> for the Late Jurassic range from 900 ppmV (Berner 2008) to 3200 ppmV (Fig. 6) (Ekart et al. 1999). Results of the most recent carbon mass-flux models suggest Late Jurassic atmospheric pCO<sub>2</sub> levels near 2300 ppmV (Berner

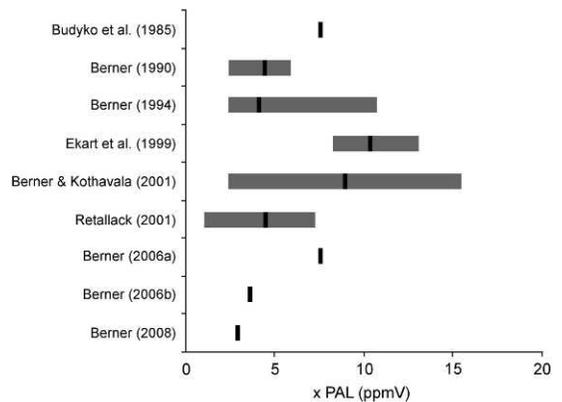


FIGURE 6. Comparison of Late Jurassic atmospheric pCO<sub>2</sub> estimates reported in the literature, represented as a function of present atmospheric levels (PAL), where PAL is the preindustrial concentration of 290 ppmV. Black vertical bars denote average estimates and horizontal bars indicate standard deviation or standard error. Estimates reported by Budyko (1985), Berner (1990, 1994, 2006a, 2006b, 2008), and Berner and Kothavala (2001) are derived from geochemical mass balance models. The estimate of Ekart et al. (1999) is derived from δ<sup>13</sup>C analysis of pedogenic carbonates, and that of Retallack (2001) is based on the stomatal index proxy. The average atmospheric pCO<sub>2</sub> value used for soil pCO<sub>2</sub> calculations in this study (3200 ppmV) is based on estimates generated using the pedogenic carbonate geochemical proxy of Ekart et al. (1999).

2006a) or as low as 1200 ppmV (Berner 2006b) or 900 ppmV (Berner 2008), depending upon the effects of volcanic weathering. Analysis of the stomatal index of fossil plant leaves also suggests relatively low atmospheric  $p\text{CO}_2$  for this period, with an estimated concentration of approximately 1300 ppmV (Retallack 2001). Expanding upon the method used by Cerling (1991, 1992), Ekart et al. (1999) provided the first long-term estimates of atmospheric paleo- $p\text{CO}_2$  based on the carbon-isotope composition of pedogenic carbonates. This geochemical approach is thought to provide the most accurate proxy-based estimates of past atmospheric  $p\text{CO}_2$  (Royer et al. 2001), especially when atmospheric  $p\text{CO}_2$  is relatively high (>1000 ppmV). Consequently, the 3200 ppmV value used here to represent Late Jurassic atmospheric  $p\text{CO}_2$  ( $C_A$ ) is based on published estimates derived from  $\delta^{13}\text{C}$  analysis of pedogenic carbonates from the Morrison Formation (Ekart et al. 1999).

The soil  $p\text{CO}_2$  estimates produced here are also dependent on the season during which pedogenic carbonates formed within the soil. Recent work by Breecker et al. (2009) suggests that pedogenic carbonates form during warm, dry periods in seasonal environments and do not record mean growing season conditions. As a result, the  $\delta^{13}\text{C}$  values of pedogenic carbonates would reflect conditions during periods of lower seasonal soil  $p\text{CO}_2$  because of relatively reduced productivity and in situ production of  $\text{CO}_2$  from oxidation of soil organic matter (Breecker et al. 2009), leading to underestimates of paleoproductivity. Therefore, the model used here may produce soil  $p\text{CO}_2$  estimates that reflect the lower soil  $\text{CO}_2$  concentrations typical of dry season conditions.

We used the average  $\delta^{13}\text{C}$  value of fossilized plant material from each locality to calculate the isotopic value of soil-respired  $\text{CO}_2$ , which is necessary to determine  $\delta^{13}\text{C}_{\text{OCC}}$ . To estimate the effect of diffusive enrichment, we used the following equation, simplified from equation 1b presented by Tabor et al. (2004):

$$\delta^{13}\text{C}_{\text{CO}_2} = 1.0044\delta^{13}\text{C}_{\text{org}} + 4.4 \quad (4)$$

We estimated the  $\delta^{13}\text{C}$  value of soil organic matter ( $\delta^{13}\text{C}_{\text{org}}$ ) from the measured  $\delta^{13}\text{C}$  values of fossil plant material collected from the same stratigraphic sections as the pedogenic carbonate samples and averaged for each locality. Organic matter and pedogenic carbonates do not physically co-occur in the examined stratigraphic sections, so most of the organic samples used here are derived from fluvial channel deposits interstratified with finer-grained paleosol-bearing strata. Consequently, there is only a loose temporal association between these allochthonous organic samples and the sampled pedogenic carbonates. Because there are no major shifts or stratigraphic trends in organic matter  $\delta^{13}\text{C}$  values at the study localities, the values from each locality may be averaged and used with the  $\delta^{13}\text{C}$  values of carbonate samples to produce estimates of soil  $p\text{CO}_2$ .

*Error and Sensitivity in the Soil  $p\text{CO}_2$  Model.*—Soil  $p\text{CO}_2$  in modern terrestrial environments ranges from atmospheric levels near the soil surface to values as high as 104,000 ppmV (Retallack 2009), although most carbonate-forming soils are characterized by substantially lower soil  $p\text{CO}_2$  values (e.g., Cerling and Quade 1993; Ekart et al. 1999; Sheldon and Tabor 2009; Breecker et al. 2009). Of the 89 coupled pedogenic carbonate-organic matter values from the three study areas, 86 provide soil  $p\text{CO}_2$  estimates that range from 5700 to 948,200 ppmV at soil temperatures of 25°C and 30°C (Tables 1–3, Fig. 7). The other three samples provide estimates of soil  $p\text{CO}_2$  with negative values for both temperatures. Negative values of  $p\text{CO}_2$  have no physical meaning and indicate that the coupled paleosol calcite and organic matter  $\delta^{13}\text{C}$  values of those samples are inconsistent with the two-component  $\text{CO}_2$  mixing model used here. These inconsistent values may reflect (1) diagenesis (Ekart et al. 1999; Sheldon and Tabor 2009), (2) coupling of inappropriate detrital organic matter samples with stratigraphically associated pedogenic carbonate (Tabor et al. 2004), (3) crystallization of carbonate under poorly drained, closed-system conditions (Tabor et al. 2007; Sheldon and Tabor 2009), or (4) assumed fractionation temperatures that do not accurately reflect

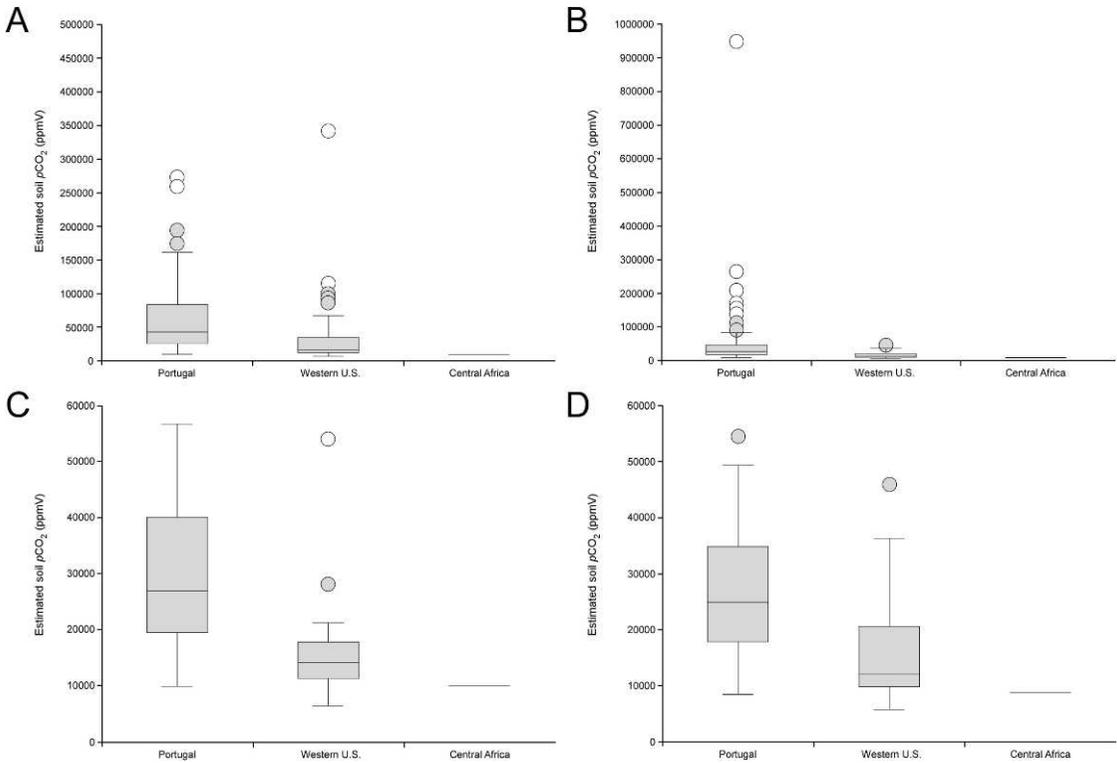


FIGURE 7. Box plots of soil  $p\text{CO}_2$  estimates for Portugal, the Western U.S., and Central Africa. A, Soil  $p\text{CO}_2$  estimates calculated assuming 25°C temperature of formation. Average values are 68,100 ppmV (Portugal), 39,500 ppmV (Western U.S.), and 10,000 ppmV (Central Africa). B, Soil  $p\text{CO}_2$  estimates calculated assuming 30°C temperature of formation. Average values are 64,600 ppmV (Portugal), 16,800 ppmV (Western U.S.), and 8700 ppmV (Central Africa). C, Box plots of soil  $p\text{CO}_2$  estimates calculated at 25°C with values greater than 60,000 ppmV removed. D, Box plots of soil  $p\text{CO}_2$  estimates calculated at 30°C with values above 60,000 ppmV removed. Relative rankings of the study areas do not change as different temperatures of formation are used.

the actual conditions of calcite crystallization. Petrographic analysis of carbonate samples provides reasonable constraints on potential diagenetic alteration, and there is little evidence of poorly drained conditions within the paleosol profiles sampled (Myers et al. 2011, in press). The assumed soil temperatures of 25°C and 30°C that are used in the soil  $p\text{CO}_2$  calculations are considered reasonable because they are based in part on quantitative paleotemperature estimates for the Lourinhã formation and Stanleyville Group derived from  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values of pedogenic phyllosilicates (Myers et al. 2011, in press). Formation temperatures in excess of 35°C are required to remove all negative values from the data set. Therefore, option (2), inappropriate  $\delta^{13}\text{C}_{\text{Occ}}$  values derived from detrital organic matter samples, provides the most

likely explanation of the inconsistent values encountered in this study.

Because the three samples that produce negative estimates of soil  $p\text{CO}_2$  are of little value for inferring relative paleoproductivity levels, we discarded them from the final data set (Tables 1–3). Also of concern are some of the exceptionally high soil  $p\text{CO}_2$  estimates produced here. Development of pedogenic carbonates usually occurs in seasonally dry environments that are characterized by lower soil  $\text{CO}_2$  concentrations (Breecker et al. 2009), so the validity of the higher soil  $p\text{CO}_2$  estimates presented here is suspect. Given the great variability of soil  $p\text{CO}_2$  values within a single locality and the occurrence of improbably large  $p\text{CO}_2$  values (>100,000 ppmV) within the data set, the estimates produced here should not be considered an accurate

indication of the quantitative concentration of ancient soil  $\text{CO}_2$ . Instead, these values reflect only qualitative differences among the study areas, but should still allow relative ranking of productivity levels in these areas. Soil  $p\text{CO}_2$  estimates derived from the remaining 86 samples indicate substantial differences among the study areas. Calculations based on an assumed soil temperature of  $25^\circ\text{C}$  yield average estimates of 68,100 ppmV for the Lourinhã formation, 39,500 ppmV for the Morrison Formation, and 10,000 ppmV for the Stanleyville Group. At assumed soil temperatures of  $30^\circ\text{C}$ , average soil  $p\text{CO}_2$  estimates are 64,600 ppmV for the Lourinhã formation, 16,800 ppmV for the Morrison Formation, and 8700 ppmV for the Stanleyville Group.

The precision of calcite ( $\delta^{13}\text{C}_{\text{Scc}}$ ) and organic matter ( $\delta^{13}\text{C}_{\text{org}}$ ) measurements presented here is approximately  $\pm 0.1\%$ . The value of the denominator in equation (2), which is a function of the  $\delta^{13}\text{C}$  values of sampled calcite and soil organic matter, is inversely related to soil  $p\text{CO}_2$  estimates, and the magnitude of change in soil  $p\text{CO}_2$  estimates produced by changes in the  $\delta^{13}\text{C}$  values of calcite and organic matter is dependent upon the size of the difference between these two measured values ( $\delta^{13}\text{C}_{\text{Scc-org}}$ ). A change of  $0.1\%$  in both  $\delta^{13}\text{C}_{\text{Scc}}$  and  $\delta^{13}\text{C}_{\text{org}}$  corresponds to only a small change in soil  $p\text{CO}_2$  estimates when  $\delta^{13}\text{C}_{\text{Scc-org}}$  is large and soil  $p\text{CO}_2$  is small; however, the same  $0.1\%$  change produces a very large shift in soil  $p\text{CO}_2$  estimates when  $\delta^{13}\text{C}_{\text{Scc-org}}$  is small and soil  $p\text{CO}_2$  is large. For example, sample SH030 is characterized by the largest  $\delta^{13}\text{C}_{\text{Scc-org}}$  in the data set ( $19.0\%$ ) and the lowest  $p\text{CO}_2$  estimate (5700 ppmV), and an uncertainty of  $\pm 0.1\%$  corresponds to a range of approximately 100 ppmV in the soil  $p\text{CO}_2$  estimates from this sample. In contrast, sample PT107 is associated with the smallest  $\delta^{13}\text{C}_{\text{Scc-org}}$  value ( $12.7\%$ ) and the highest  $p\text{CO}_2$  estimate (948,400 ppmV), and an uncertainty of  $\pm 0.1\%$  induces a change of approximately 5000 ppmV in the estimated soil  $p\text{CO}_2$ . The sensitivity of this method to small changes in the measured  $\delta^{13}\text{C}$  values of calcite and organic matter at low  $\delta^{13}\text{C}_{\text{Scc-org}}$  values indicates that soil  $p\text{CO}_2$  levels above 60,000 ppmV

are not resolvable with reasonable precision and should be treated with caution. If only the soil  $p\text{CO}_2$  estimates below 60,000 ppmV are considered, the relative ranking of the study areas does not change.

Although the samples compared here are roughly coeval, potential changes in atmospheric  $\text{CO}_2$  over time also have the potential to affect soil  $p\text{CO}_2$  estimates. Sensitivity to changes in  $C_A$ , like  $\delta^{13}\text{C}_{\text{Scc}}$  and  $\delta^{13}\text{C}_{\text{org}}$ , is directly correlated with the magnitude of estimated soil  $p\text{CO}_2$ . For the range of soil  $p\text{CO}_2$  estimates less than 60,000 ppmV, changes of  $\pm 100$  ppmV in  $C_A$  induce changes of approximately 400 ppmV to 3500 ppmV in estimated soil  $p\text{CO}_2$ .

*Inferred Paleoproductivity Levels.*—Because modern soil  $p\text{CO}_2$  and primary productivity levels are positively correlated with water availability, more productive environments with high soil  $p\text{CO}_2$  should be characterized by more humid conditions. Conversely, drier landscapes will be less productive, and their soil systems will have lower  $\text{CO}_2$  concentrations. The soil  $p\text{CO}_2$  estimates generated here imply that Portuguese terrestrial environments were characterized by higher productivity levels than western North America during the Late Jurassic. The soil  $p\text{CO}_2$  estimate from the Stanleyville Group corresponds to lower productivity levels than either the Lourinhã or Morrison formations, although this estimate is based on only a single sample and must be treated with caution. Nevertheless, this low soil  $p\text{CO}_2$  estimate may indicate a low-productivity ecosystem incapable of sustaining populations of large terrestrial animals.

*Comparison of Faunal Richness.*—Estimates of total generic richness produced using equation (1) (Chao 1984) indicate a higher richness for Portuguese paleoenvironments relative to the Morrison Formation (Fig. 5). Although both of the calculated values likely underestimate true faunal richness, the asymptotic behavior of the rarefaction curve for the Morrison Formation suggests that richness is unlikely to increase dramatically with further sampling. These results reinforce the paleoclimatic conditions and paleoproductivity levels inferred for the study areas. Late Jurassic Portuguese terres-

trial paleoenvironments show evidence of relatively moist conditions, higher soil CO<sub>2</sub> concentrations (implying higher primary productivity), and higher generic richness of dinosaurs. Contemporary paleoenvironments in the western United States reflect similar, but slightly more arid, paleoclimatic conditions, lower soil CO<sub>2</sub> concentrations (implying lower primary productivity), and lower faunal richness. Interpretation of the record from Central Africa is complicated by the small data set available, but the continental interior setting of the Congo Basin appears to have contributed to development of an arid, low-productivity ecosystem that was too inhospitable to support a rich terrestrial fauna (Myers et al. 2011).

### Conclusions

The highest average soil *p*CO<sub>2</sub> estimates presented here are derived from the Lourinhã formation, with the Morrison Formation and the Stanleyville Group yielding increasingly lower values. These soil *p*CO<sub>2</sub> estimates imply increasingly drier conditions moving from the Lourinhã formation, to the Morrison Formation, to the Stanleyville Group. Similar climatic trends among the study areas are supported by paleoclimate indicators such as paleosol morphology, clay mineralogy, and weathering indices (Myers 2009; Myers et al. 2011, in press). The Lourinhã formation yields both the highest inferred primary productivity levels and the highest estimate of faunal richness. The Morrison Formation produces a slightly lower average soil *p*CO<sub>2</sub> estimate (implying lower productivity) and a lower estimated faunal richness. Data for the Stanleyville Group are sparse, but this paleoenvironment appears to have been much more arid than either the Lourinhã or Morrison formations, with low levels of primary productivity. These results indicate that Late Jurassic terrestrial ecosystems with more abundant moisture were characterized by higher levels of primary productivity and richer faunas. Arid paleoenvironments, such as those deep in the interior of Gondwana, had much lower productivity levels and greatly reduced faunal richness. As in modern terrestrial environments, primary productivity,

water availability, and faunal richness seem to be positively correlated in Late Jurassic ecosystems.

Use of soil *p*CO<sub>2</sub> estimates as a qualitative indicator of paleoproductivity provides a powerful tool for examining relationships among the various components of ancient terrestrial ecosystems. Because it is dependent on the presence of pedogenic carbonates, this technique is not applicable to environments characterized by extremely high precipitation and productivity levels, although carbonates may persist in environments with mean annual precipitation as high as 1400 mm/yr (Nordt et al. 2006). It is also of the utmost importance that the carbonate and organic samples used for calculating soil *p*CO<sub>2</sub> are chosen carefully. Organic matter sampled from non-pedogenic strata may not accurately reflect the isotopic composition of soil organic matter, and its use in soil *p*CO<sub>2</sub> calculations is therefore inadvisable. Future studies should analyze in situ organic matter derived from the same paleosol profiles from which pedogenic carbonates are collected, as advocated by Bowen and Beerling (2004), rather than allochthonous material from adjacent units.

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