

Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California, and characterization of the Clarendonian mammal age (late Miocene) in California

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ABSTRACT

The Dove Spring Formation (DSF) is an 1,800-m-thick succession of fluvial, lacustrine, and volcanic rocks that contains a nearly continuous sequence of diverse vertebrate fossil assemblages. When the North American provincial mammalian ages were originally defined in 1941, the fossil fauna of the DSF (now part of the Ricardo Group) was one of four fossil assemblages named as principal correlatives of the Clarendonian mammal age. Early radiometric work yielded a maximum age of 10.0 Ma for this fossil assemblage, and by correlation to the Great Plains of the United States, this date was considered representative of Clarendonian time.

Detailed geologic mapping and precise stratigraphic control of fossils collected in the DSF permit the development of a biostratigraphy consisting of four mammalian fossil assemblage zones. The biologic characterization of the Clarendonian mammal age in California is expanded on the basis of this succession of assemblage zones.

Radiometric and paleomagnetic results provide a detailed chronologic framework that indicates a time span from at least 13.5 Ma to 7.3 Ma for the fossils of the DSF. Furthermore, the new sequence of assemblage zones helps to fill faunal gaps that appear to exist at the upper and lower boundaries of the Clarendonian faunal record in the Great Plains. On the basis of the biochronology developed in the DSF and on the faunal correlation with the Great Plains sequence, the Barstovian/Clarendonian boundary, as recently characterized by some workers, is dated at 12.5 Ma, and the Clarendonian/Hemphillian boundary is constrained to 8.9 Ma. This lower boundary is about 0.9 m.y. older than previously proposed, whereas the upper boundary is in close agreement with previous proposals.

INTRODUCTION

The Cenozoic time scale was originally founded on the European marine sequence; as a result, correlation with the North American terrestrial sequence has been particularly difficult. As a consequence, a series of ages for the North American sequence has been developed based primarily on mammalian evolution and dispersal events. The terrestrial chronology composed of North American land mammal ages (NALMA) proposed by the Wood Committee (Wood and others, 1941) has become the firmly established standard of terrestrial biochronology in North America (Woodburne and others, 1987), and similar systems have been forthcom-

ing on other continents (Savage and Russell, 1983). The characterization of the NMLMA has undergone continuous revision since 1941, but the first comprehensive redefinition was recently completed after a 12-year effort (Woodburne, 1987). Detailed studies of local successions, such as the Dove Spring Formation (DSF), provide the data needed for further refinement of the North American terrestrial biochronologic system.

Due to rapid rates of speciation in fossil mammals during Cenozoic time, it is possible to construct detailed biostratigraphic histories that often depict complex evolutionary patterns. Terrestrial vertebrates are influenced by tectonic barriers and local environmental factors, however, and these animals become isolated into regional zoogeographic provincial associations. The significance of biostratigraphies developed in localized basins thus cannot be fully evaluated in the absence of independent chronological control.

Radiometric-dating techniques provide a powerful tool for establishing the desired age control. Radioisotopic dates (Evernden and others, 1964) have yielded valuable insights into timing of evolutionary events, but these dates could only be applied to a limited number of fossil-bearing sequences, most found in the far-western United States. More recently, studies utilizing magnetic polarity stratigraphy, often in conjunction with radiometric dating, have been successfully applied to terrestrial sediments in order to generate temporal constraints for sedimentary sequences (for example, Johnson and others, 1975; Opdyke and others, 1977; MacFadden and others, 1979, 1990; Woodburne and others, 1990). Such studies, in combination with paleontologic data, provide one of the best available means to understand the timing and rates of evolutionary events (Barry and others, 1982).

The Dove Spring Formation (DSF) (formerly the Ricardo Formation of Dibblee, 1952; see Loomis and Burbank, 1988) in the western Mojave Desert of California comprises more than 1,800 m of fluvialite sediment and numerous interbedded air-fall and flow volcanic rocks (Figs. 1 and 2). Consequently, it is well suited for radiometric studies. During the first half of this century, studies of abundant fossils in the DSF led to its use as a standard of correlation for similarly aged faunas in western North America (Wood and others, 1941; Savage, 1955). Renewed collecting since the early 1960s has expanded the knowledge of the taxonomic diversity and has led to recognition of a faunal succession in the DSF (Tedford, 1965; Tedford and others, 1987; Whistler, 1969, 1982). Fossils have been collected from 800 localities, including 58 sites yielding small vertebrate concentrations, all precisely located within a stratigraphic context. Fossil-producing localities are fairly evenly spaced through the middle

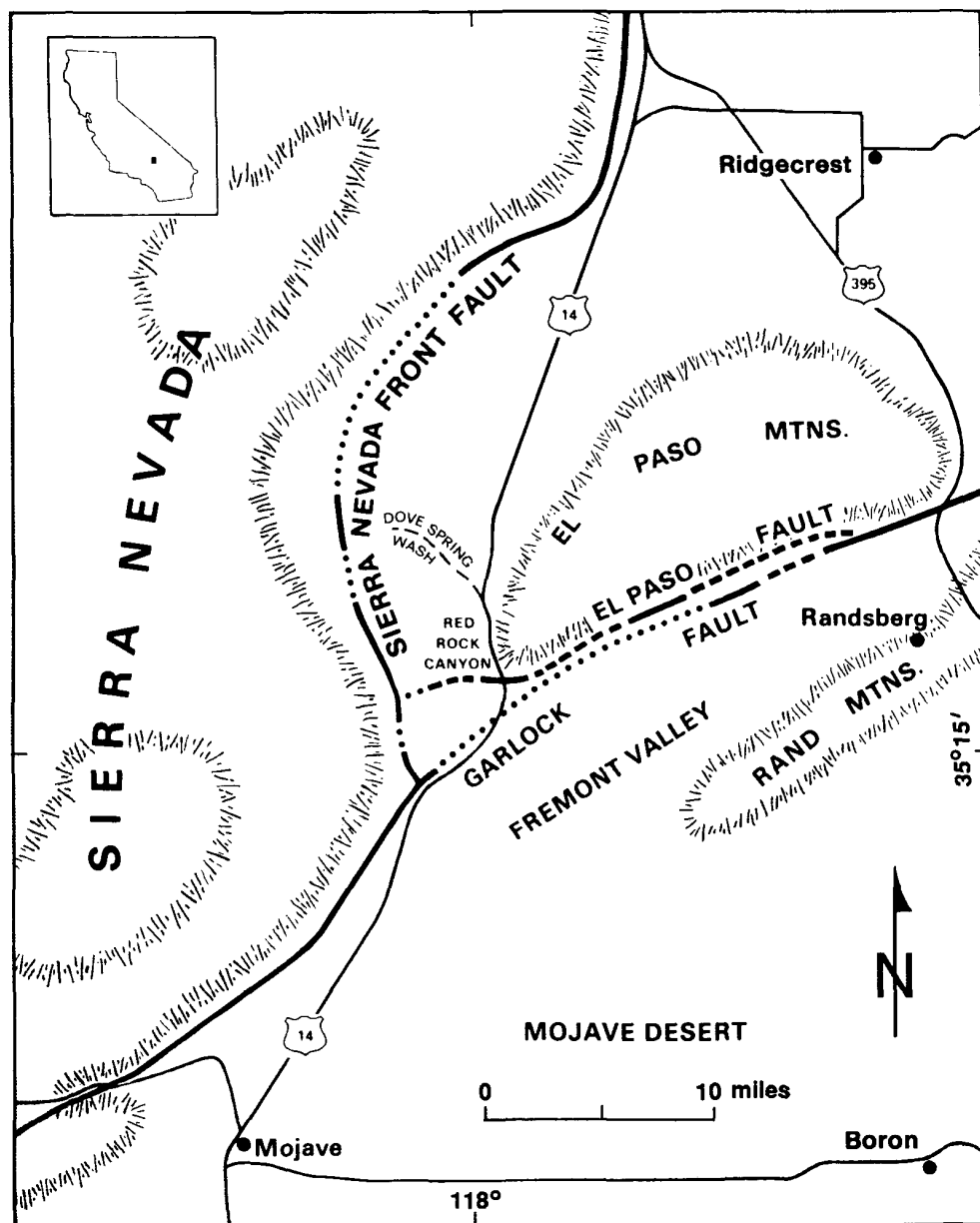


Figure 1. Index map showing general location of study area. Regional geology from Dibblee (1967).

1,500 m of the DSF. We have developed a detailed biostratigraphy for this interval and used a magnetic polarity stratigraphy in conjunction with fission-track and K-Ar dates to develop a chronology for this interval (Fig. 3).

The magnetic stratigraphy and radiometric chronology indicate that the fossils from the DSF span 13.4 Ma to 7.3 Ma. This temporal span and correlations with both the North American standard and the regional biostratigraphies developed in California (Savage, 1955) indicate that the fossil assemblages of the DSF encompass more than the entire Clarendonian interval. Faunal provincialism (Tedford and others, 1987) precludes using the fossil assemblages of the DSF to redefine the taxonomic characterization of the Clarendonian age that would be applicable for all of

North America. The DSF, however, provides an independent means for calibrating the biochronologic boundaries in California and the southern Great Basin and, by faunal correlation with the faunal succession in the Great Plains, the biochronologic boundaries of the Clarendonian age.

METHODS

R. Tedford and D. Whistler have mapped 70 km² of the DSF (Fig. 2) on air photos with a nominal scale of 1:15,840 and subsequently transferred them to a topographic base. Using an alidade and/or a Jacobs staff, six stratigraphic sections (Fig. 3) have been measured. More than 25 volcanic ashes and flows permit precise lithostratigraphic correlations be-

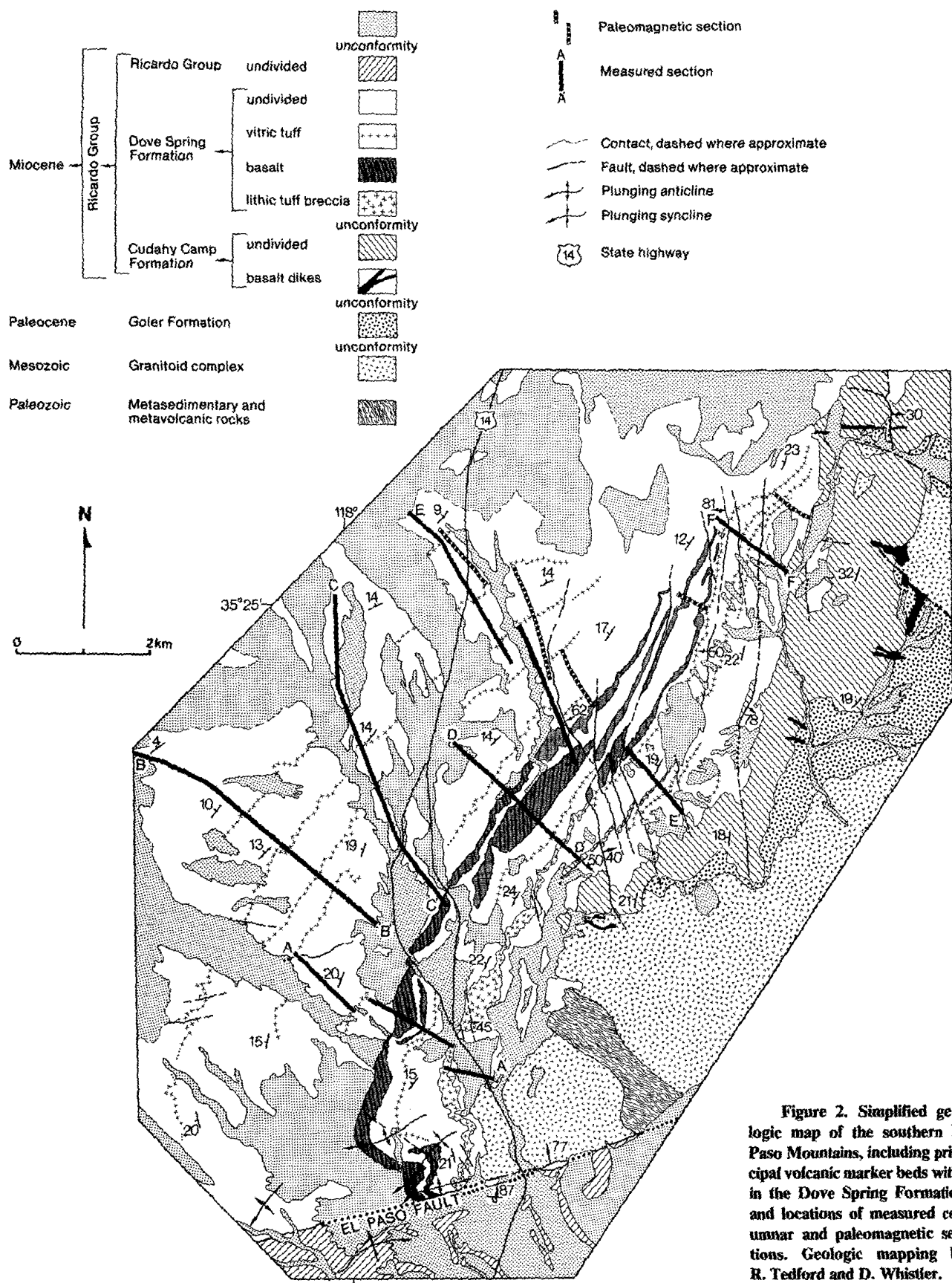


Figure 2. Simplified geologic map of the southern El Paso Mountains, including principal volcanic marker beds within the Dove Spring Formation and locations of measured columnar and paleomagnetic sections. Geologic mapping by R. Tedford and D. Whistler.

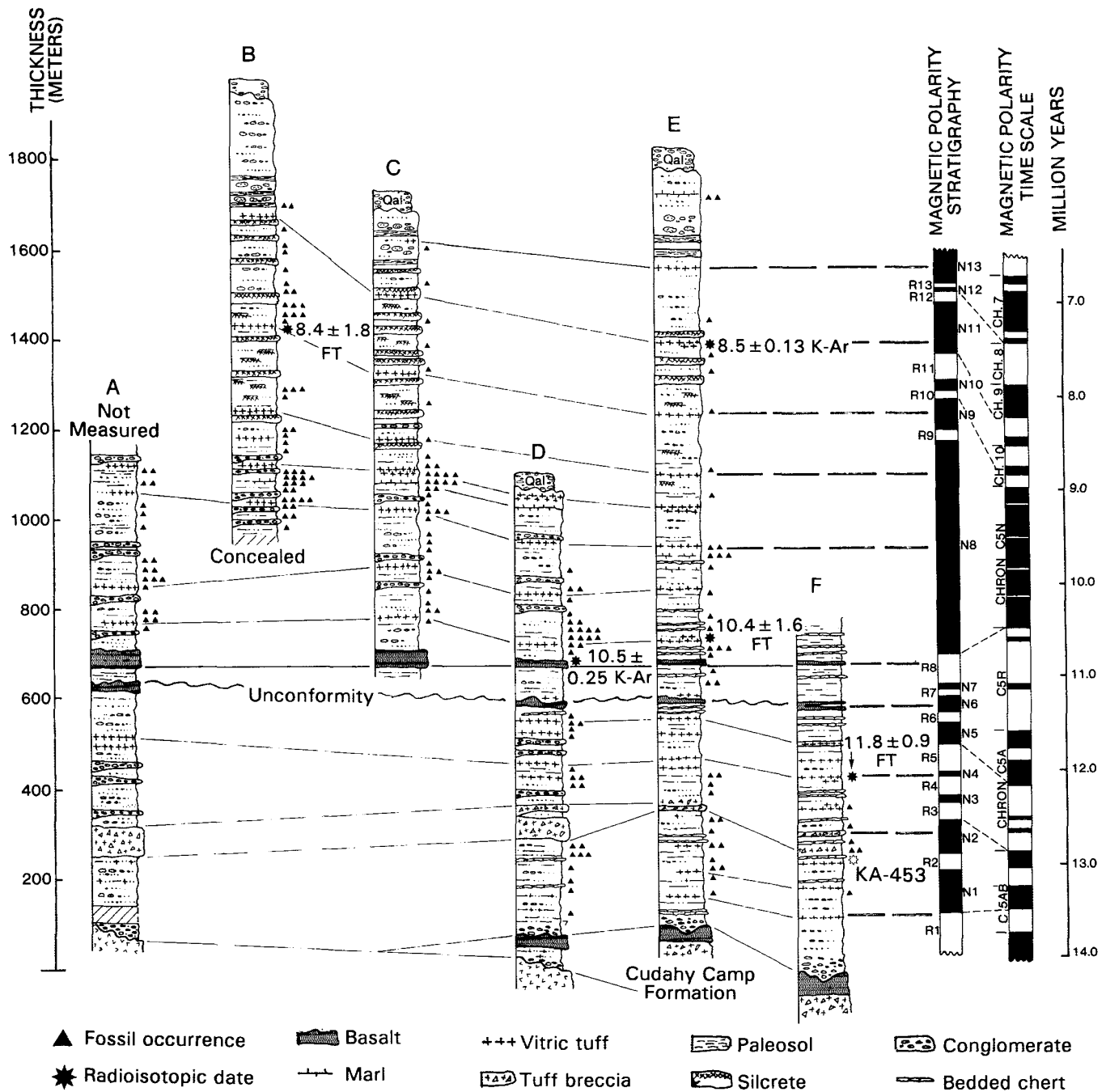


Figure 3. Columnar sections within the Dove Spring Formation, showing stratigraphic occurrence and correlation of major volcanic marker beds, general distribution of fossil occurrences, stratigraphic position of radiometrically dated samples, and the magnetic polarity stratigraphy. Magnetic polarity sections directly correlated with measured sections E-E' and F-F' (see Fig. 2). See text for sources of radiometric dates.

tween measured sections. Details of the magnetic sampling, demagnetization, and data analyses are given elsewhere (Loomis and Burbank, 1988). In brief, three or more specimens were collected at each sampling level (site), and following thermal demagnetization, the reliability of the mean vector from each site was assessed and classified using Fisher statistics

(Fisher, 1953). The polarity of each site was determined from the latitude of the virtual geomagnetic pole.

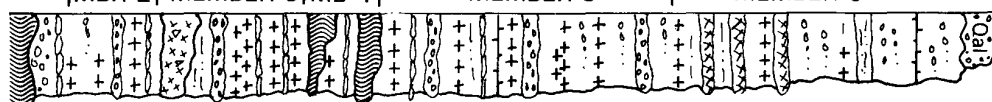
Samples for fission-track dating were collected from ashes at nine different stratigraphic levels and were processed at the University of Southern California fission-track laboratory. Due to high vitric content

DOVE SPRING FORMATION

|MBR 2| MEMBER 3|MB 4|

MEMBER 5

MEMBER 6



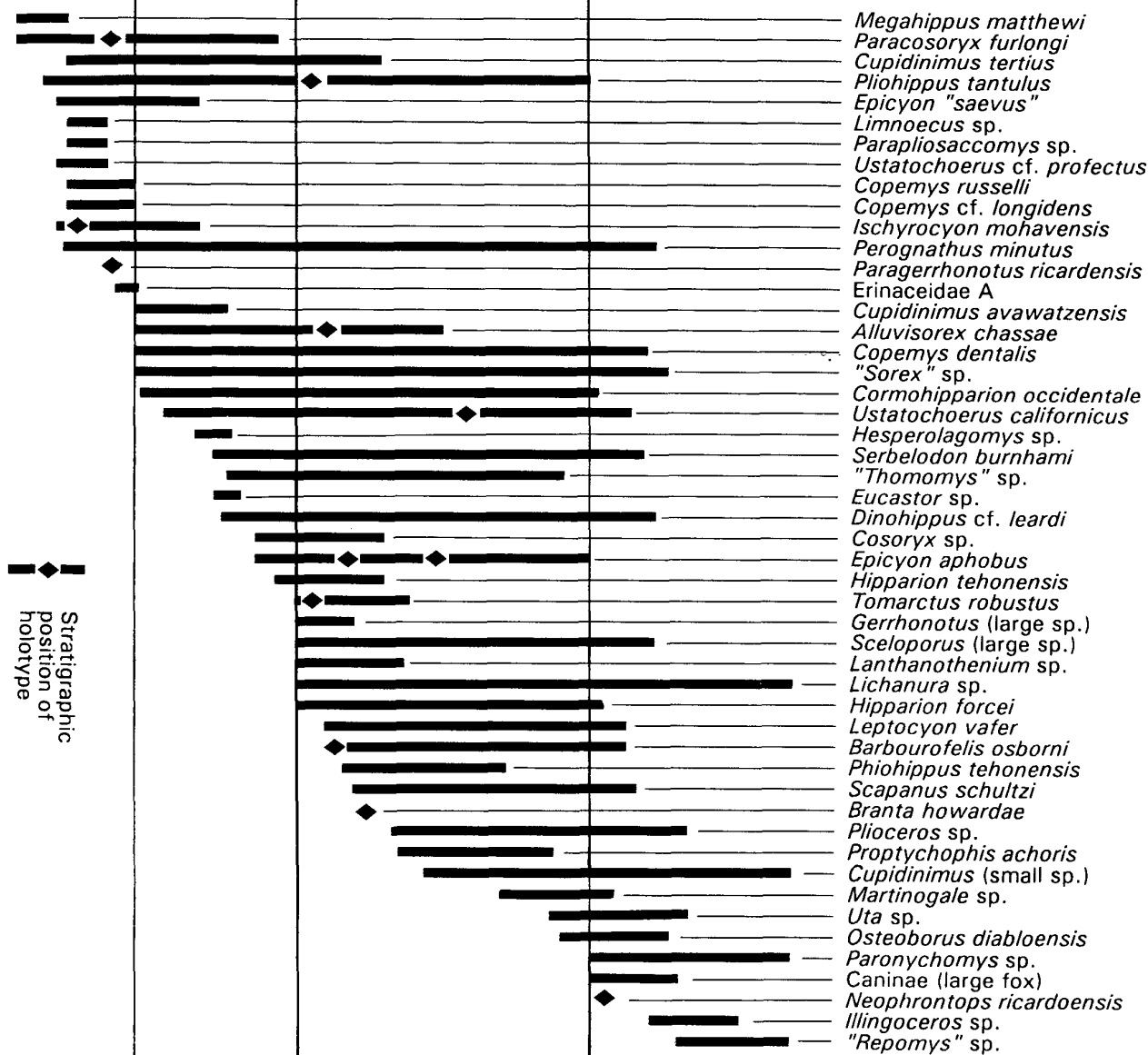
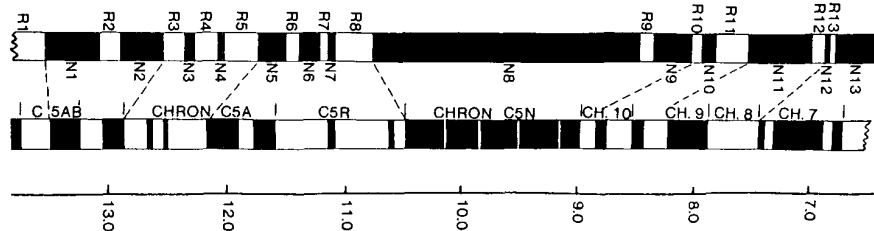
Iron Canyon Fauna

Ricardo F. Dove Spring Fauna

LOCAL FAUNAS ⁽¹⁾PROVINCIAL STAGES ⁽²⁾

ASSEMBLAGE ZONES

Cerrotejonian		Montediablan	
<i>U. profectus/ C. russelli</i>	<i>C. avawatz./ P. furlongi</i>	<i>E. aphobus/ H. forcei</i>	<i>Paronychomys/ O. diabloensis</i>

Stratigraphic
position of
holotypeMAGNETIC POLARITY
STRATIGRAPHYMAGNETIC POLARITY
TIME SCALE

MILLION YEARS

Figure 4. Teilzones of selected vertebrate taxa and assemblage zones correlated to the MPS and MPTS within the Dove Spring Formation (DSF). Taxa are those either with significant occurrences within the DSF, or those most commonly used in vertebrate biochronology. All taxa with type specimens from the DSF are shown, even when represented by single specimens. The two holotype occurrences within *E. aphobus* represent the type of this species and of *E. ricardoensis* (see Table 1). Members of the Dove Spring Formation after Loomis and Burbank (1988). (1) Local faunal subdivisions after Tedford (1965) and Tedford and others (1987). (2) Provincial stages after Savage (1955). Symbols in columnar section as in Figure 3.



and apparent contamination, only four ashes yielded sufficient pristine zircons for fission-track dating. These were processed using standard techniques (Naeser, 1978) and were calibrated against both NBS glass standards and the Fish Canyon Tuff. Samples from both volcanic ashes and basalts were collected with assistance from C. Swisher for K-Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ dating at the Berkeley Institute of Human Origins.

Significant fossil collections from the DSF are housed in the Natural History Museum of Los Angeles County (LACM); the University of California, Berkeley, Museum of Paleontology (UCMP); and the University of California, Riverside, Department of Earth Sciences (UCR). These collections have been reviewed in order to produce the biostratigraphy presented here. Faunal terminology follows Woodburne and others (1987), with the abbreviations F. = fauna and Lf. = local fauna.

GEOLOGY

The El Paso Mountains (Figs. 1 and 2) are composed of a core of Mesozoic crystalline rocks intruding Paleozoic metasedimentary rocks, both overlain with Paleocene (Goler Formation) and Miocene (Ricardo Group) epiclastic and volcanic rocks exposed on the western slopes of the range (Dibblee, 1952). Post-Miocene uplift of the El Paso Mountains along the El Paso fault has tilted these Cenozoic rocks into primarily westward-dipping homoclines (Fig. 2). Rocks of the Ricardo Group (Dibblee, 1952; Loomis and Burbank, 1988) were deposited in an elongate trough (the El Paso Basin) that is situated along the north side of the present-day trend of the Garlock fault (Fig. 1).

The mostly coarse, epiclastic rocks of the Goler Formation are unconformably overlain by Miocene volcanic rocks and sedimentary strata. These Miocene strata were initially included in the Rosamond Series (Baker, 1912) and later were described as the Ricardo Formation with eight members (Dibblee, 1952, 1967). Whistler (1969), Cox (1982), and Loomis (1984) all recognized that the Ricardo Formation of Dibblee was divisible into two lithostratigraphic units: a lower, dominantly volcanic unit (Members 1 and 2 of Dibblee, 1967) and an upper, dominantly sedimentary unit (Members 3 through 8 of Dibblee, 1967).

Magnetostratigraphic studies and radiometric dating (Cox and Diggle, 1986; Loomis and Burbank, 1988; this study) demonstrated that the unconformity between these two lithostratigraphic units represents a hiatus of at least 1.5 m.y. Loomis and Burbank (1988), therefore, defined two new formations within an elevated Ricardo Group: the Cudahy Camp Formation for the predominantly volcanic unit, and DSF for the overlying, predominantly sedimentary units. The Cudahy Camp Formation develops a maximum thickness in the vicinity of Last Chance Canyon (Figs. 2 and 3). Like the Goler Formation, it also onlaps and pinches out toward the southwestern end of the El Paso Mountains, an area that apparently represented a persistent topographic high along the southeastern margin of

the El Paso Basin. On the other hand, the overlying DSF thickens toward the southwest and is truncated by the El Paso fault.

Lithology of the Dove Spring Formation

The DSF comprises more than 1,800 m of fluviolacustrine sediment and volcanic and volcanoclastic rock (Dibblee, 1952; Loomis and Burbank, 1988; Whistler, 1969) that can be broadly separated into four lithofacies: (1) fine-grained lacustrine deposits (clay, silt, reworked ash, fresh-water limestone, and bedded chert); (2) fluvial deposits (channel sandstone, conglomerate, and finer-grained overbank and floodplain silt); (3) poorly sorted alluvial-fan deposits (mudflow conglomerate and breccia); and (4) paleosol, caliche, and silicified hardpan deposits (silcrete).

Air-fall vitric ashes (18) and 2 lithic tuff breccias have been traced throughout most of the exposed section (Figs. 2 and 3). The DSF also contains two basalt flow sequences (each comprising several individual flows) that thicken to the southwest (Figs. 2 and 3). No explicit source is known for these flows and ashes.

With one exception, deposition throughout the more than 1,800 m of the DSF is continuous except for local hiatuses typical of fluvial deposition and soil formation. A more pronounced unconformity at the top of the lower basalt flow sequence is demonstrated by an upper surface that is locally dissected by erosion channels that are infilled with finer-grained sediments. This flow sequence was removed by syndepositional erosion in several areas along strike before deposition of overlying, mostly fine sediments. This unconformity may represent a depositional hiatus of as much as 0.7 m.y., but there is no dramatic faunal break at this level (Fig. 4). No comparable unconformity is evident at the top of the upper-basalt-flow sequence.

MAGNETOSTRATIGRAPHY AND RADIOMETRIC CHRONOLOGY

More than 100 sites were collected at 15- to 20-m stratigraphic intervals along the main magnetic sampling traverse (Fig. 2) through the DSF (for a more detailed discussion, see Loomis and Burbank, 1988). The resulting magnetic-polarity stratigraphy (MPS) for the DSF (Fig. 3) can be correlated with the magnetic-polarity time scale (MPTS, Berggren and others, 1985) with confidence. This correlation indicates that the DSF ranges from ~ 13.6 Ma at its base to ~ 7.0 Ma at the top of the sampled sequence.

Because the correlation of the MPS to the MPTS provides the critical chronological context within which to interpret the faunal data, we have (1) stratigraphically linked (mainly through bed tracing) the MPS section with the fossil-producing sites in each of the sections, (2) replicated complex portions of the MPS in numerous other localities in order to verify the reversal pattern, (3) statistically analyzed the MPS data (Johnson and McGee, 1983) to assess the probability of the correlation, and (4) used key radiometric dates to guide aspects of the correlation. Although in the originally published MPS (Loomis and Burbank, 1988), several magnetozones, such as N4, were represented by single sites and might be considered unreliable, we have subsequently sampled much of the lower 500 m of the DSF strata in more than 15 other sections. In almost all of these supplementary sections, we have replicated the reversal pattern between N2 and N7. Consequently, the originally defined reversal pattern appears to be reliable.

The most remarkable aspect of the DSF MPS is the 500-m-thick, normal magnetozones (N8). Given the late Miocene age of the upper DSF strata, N8 should correlate to chron C5N, which spans 8.92 to 10.4 Ma (Berggren and others, 1985) and is the highly distinctive, normal-polarity

interval in the late Miocene MPTS (Fig. 3). This correlation is supported by the K-Ar date of 10.5 ± 0.25 Ma (Institute of Human Origins, 86CS-URB) and the fission-track date of 10.4 ± 1.6 Ma from the upper basalt (680 m, Fig. 3) and a nearby ash, respectively.

Given the correlation of magnetozones N8 with chron C5N (Fig. 3), it remains to correlate the underlying and overlying portions of the MPS with the MPTS. Figure 3 depicts the most logical correlation of the discovered reversal patterns and is the primary basis for the chronological control of the DSF. The correlation of the upper portion of the MPS with the MPTS is somewhat ambiguous, in part due to decreasing rate of sediment accumulation, paleosol development, and depositional hiatuses that become more widespread in the upper members of the DSF. The most reasonable correlation indicates that this portion of the MPS spans 8.92 Ma to ≈ 7.0 Ma. A K-Ar date of 8.5 ± 0.13 Ma for an ash at 1,400 m (Institute of Human Origins, 86CS-R4) supports this correlation, as does the fission-track date of 8.4 ± 1.8 Ma (Cox, 1987) at 1,420 m.

Given the prevalent perception within the paleontological community that the base of the DSF dates from ≈ 12 Ma (Tedford and others, 1987), it might be suggested that magnetozones N1 and N2 should be correlated with the normal subchrons at the top of the chron C5A (Fig. 3). This would require either (a) several of the DSF magnetozones between R3 and R8 to be unreliable or (b) the magnetic time scale actually to include many more magnetozones than are presently recognized in this time interval. We reject both of these possibilities, because the numerous replicate magnetic sections in the DSF confirm the magnetic zonation and because numerous detailed magnetic studies of this portion of the MPTS (for example, see Johnson and others, 1982, 1985; Tauxe and Opdyke, 1982) have failed to reveal significantly more complex reversal patterns.

The primary weakness in the MPS-MPTS correlation (Fig. 3) is that, despite repetitive sampling, only one of the normal subchrons in chron C5R is present in the MPS and that the apparent sediment-accumulation rate drops dramatically during this interval. This problem is likely explained, however, by the unconformity that is situated above the lower basalt between magnetozones N6 and N7. This unconformity appears to represent a gap of as much as 0.7 m.y. due to local uplift and/or base-level lowering during the early portion of chron C5R. Except for the normal subchron that is not represented due to this hiatus, all of the other recognized chron and subchrons of the MPTS between 10.4 Ma and 13.5 Ma (Berggren and others, 1985) are represented by magnetozones in the DSF.

Given what is known about the statistical character of the Miocene MPTS, it is possible to estimate the likely duration of the sampled interval below 700 m using the approach of Johnson and McGee (1983). Given a random sample distribution with respect to time, the discovery of 15 reversals among 41 sites indicates that the lower portion of the section should span 3.7 ± 1.0 m.y. This estimate is close to that predicted by our correlation to the MPTS and appears more reasonable than a correlation that would place the base of the section at 12.2 Ma and would require that the lower 700 m of the DSF span less than 2 m.y.

Because the new magnetic data indicate ages for the lower DSF strata that are at considerable variance with long-held perceptions regarding the age of the enclosed faunas (Tedford and others, 1987), a concerted attempt was made to date some of the volcanic units distributed throughout the section. Earlier attempts at fission-track dating in the DSF had yielded dates of 8.4 ± 1.8 Ma and 10.4 ± 1.6 Ma at 1,420 m and 720 m, respectively (Cox, 1987), that are essentially in agreement with our correlations. Despite our efforts to collect uncontaminated samples and to analyze pristine zircons, only one ash (at 410 m) yielded sufficient countable zircons (>10) to provide a reliable date (11.8 ± 0.9 Ma). The over-

TABLE 1. COMPOSITE FLORAL AND FAUNAL LIST OF THE DOVE SPRING FORMATION

Plants	
Palmaeae	<i>Palmyrodon mohavensis</i> Webber, 1933
Pinaceae	<i>Pinus kelloggii</i> Webber, 1933
Cupressaceae	<i>Cupressus</i> sp.
Fagaceae	<i>Quercus ricardensis</i> Webber, 1933
Rhamnaceae	<i>Ceanothus</i> sp.
Leguminosae	<i>Acacia</i> sp.
	<i>Lycium</i> sp.
	<i>Robinia alexanderi</i> Webber, 1933
Osteichthyes	
Cyprinodontidae	<i>Empetrichthys</i> sp.
Amphibia	
Plethodontidae	<i>Batrachoseps</i> sp.
	cf. <i>Ensatina</i> sp.
Bufoidea	Toads
Ranidae	Frogs
Reptilia	
Testudinidae	<i>Clemmys</i> sp.
	<i>Geochelone</i> sp.
	? <i>Gopherus</i> sp.
Iguanidae	<i>Sceloporus</i> sp. (large)
	? <i>Uta</i> sp.
	<i>Callisaurus</i> sp.
Xantusiidae	<i>Xantusia</i> sp.
Anguillidae	<i>Gerrhonotus</i> , cf. <i>G. kingi</i> (Gray)
	Genus indeterminate (very large)
	<i>Paragerrhonotus ricardensis</i> Estes, 1963
Boidae	<i>Lichanura</i> sp.
Colubridae	<i>Paracoluber</i> sp.
	<i>Paleoheterodon</i> sp.
	<i>Protyphlops achoris</i> Whistler and Wright, 1989
	" <i>Thamnophis</i> " sp.
Aves	
Anatidae	<i>Branta howardae</i> Miller, 1930
Accipitridae	<i>Neophronotops ricardensis</i> Rich, 1980
Mammalia	
Chiroptera	Genera and species not determined
Insectivora	
Erinaceidae	<i>Lanthanotus</i> sp.
	Erinaceidae "A"
Soricidae	<i>Alluvisorex chassenei</i> Tedford, 1961
	<i>Limnocetus</i> sp.
	" <i>Sorex</i> " sp.
Talpidae	<i>Scapanus (Xeroscapheus) shultzi</i> Tedford, 1961
Carnivora	
Canidae	<i>Epicyon aphobus</i> (Merriam, 1919) (= <i>Epicyon ricardensis</i> [Stirton and Vanderhoof, 1933])
	<i>Epicyon "saevus"</i>
	<i>Leptocyon vafer</i> (Leidy, 1858)
	<i>Osteoborus diabloensis</i> (Richey, 1938)
	<i>Tomarctus robustus</i> Green, 1948
	<i>Tomarctus</i> sp.
	" <i>Vulpes</i> " sp.

whelming vitric content of the ashes resulted in a paucity of zircons in other samples. Moreover, the individual crystal dates suggested that many ashes had been contaminated. For example, in the basal portions of the section, it was typical to find two of three groupings of zircon dates clustering around 12–13 Ma, 17–18 Ma, and >30 Ma.

The younger dates appear to represent approximate stratigraphic ages, the intermediate dates probably represent reworked detritus from the underlying, volcanoclastic-rich Cudahy Camp Formation dated at 15–18 Ma (Loomis and Burbank, 1988), and the older dates likely represent early Tertiary volcanism not represented in the area today. Several of the single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ analyses appear to reinforce the results from the fission-track dating regarding contamination. One of the lowest ashes in the section, for example, yielded two analyses with a mean date of 13.7 ± 0.5 Ma, three analyses with a mean date of 17.3 ± 0.3 Ma, and one analysis with a date of 34.2 ± 1.4 Ma (Institute of Human Origins, 86CS-R1).

In our analyses, we have used only apparently reliable dates from multiple analyses of ashes or basalt flows exhibiting little or no contamination. The relatively large errors on the fission-track dates (1–2 m.y.) make them useful only as general guides to correlation, whereas the more precise K-Ar dates serve to delineate specific ties between the MPS and the MPTS. Although many paleontologists put an emphasis on radiometric

TABLE 1. (Continued)

Amphicyonidae	<i>Ischyrocyon mohavensis</i> (Stock and Furlong, 1926)
Procyonidae	<i>Bassariscus</i> sp.
Mustelidae	<i>Martingale</i> sp. "Mephitis" sp. ? <i>Mustela burwaldi</i> Merriam, 1919 cf. <i>Eomellivora</i> sp. <i>Barbourofelis osborni</i> (Merriam, 1919) <i>Pseudaelurus</i> sp. "Felis" sp. (small)
Felidae	
Rodentia	
Sciuridae	<i>Ammospermophilus</i> sp. <i>Protospermophilus</i> sp. <i>Tamias ateles</i> (Hall, 1930) <i>Eucastor</i> sp.
Castoridae	<i>Cupidinimus awakwatensis</i> Barnesky, 1986 <i>Cupidinimus tertius</i> (Wilson, 1939) <i>Cupidinimus</i> sp. (small)
Heteromyidae	<i>Perognathus furlongi</i> Gazin, 1930 <i>Perognathus minutus</i> James, 1963 <i>Parapliosaccus</i> sp. "Thomomys" sp.
Geomyidae	<i>Lepidodomys</i> sp.
Eomyidae	<i>Copemys dentalis</i> (Hall, 1930) <i>Copemys</i> cf. <i>C. longidens</i> (Hall, 1930) <i>Copemys russelli</i> James, 1963 <i>Copemys</i> sp. <i>Paronychomys</i> spp. "Repomys" sp.
Cricetidae	
Lagomorpha	
Leporidae	<i>Hypolagus</i> sp.
Ochotonidae	<i>Hesperolagus</i> sp.
Proboscidea	
Gomphotheriidae	<i>Gomphotherium</i> sp. <i>Serbeldodon burnhami</i> Osborn, 1933
Perissodactyla	
Rhinocerotidae	<i>Aphelops</i> sp. <i>Peraceras</i> sp. <i>Teleoceras</i> cf. <i>T. meridianum</i> <i>Dinohippus</i> cf. <i>D. leardi</i> (Drescher, 1941) <i>Cormohipparion occidentale</i> (Leidy, 1856) (= <i>Hipparion mohavense</i> Merriam, 1919) <i>Hipparion forcei</i> Richey, 1948 <i>Hipparion tejonensis</i> (Merriam, 1916) <i>Megahippus</i> cf. <i>M. matthewi</i> (Barbour, 1914) <i>Pliohippus tejonensis</i> Merriam, 1915 <i>Pliohippus tantulus</i> Merriam, 1913 (= <i>P. fairbanksi</i> Merriam, 1915)
Artiodactyla	
Merycoidodontidae	<i>Ustatochoerus californicus</i> (Merriam, 1919) <i>Ustatochoerus</i> , cf. <i>U. profectus</i> (Mathew and Cook, 1909) ? <i>Prosthennops</i> sp. ? <i>Hemiachena</i> sp. ? <i>Michenia</i> sp. ? <i>Megatylopus</i> sp. ? <i>Procamelus</i> sp. <i>Cosoryx</i> sp. (? hornless) <i>Illingoceras</i> sp. <i>Paracosoryx furlongi</i> Frick, 1937 <i>Plioceras</i> sp.
Tayassuidae	
Camelidae	
Antilocapridae	

dates, or give them priority over magnetic data (for example, MacFadden and others, 1990; Tedford and others, 1987), the problems with contamination, the paucity of statistically reliable radiometric dates, and the good quality of the magnetic data dictate that the magnetochronology should have priority in this study. None of the available dates, with the exception of Evernden and others' (1964) date, contradicts our magnetic chronology, and several of them closely support our correlation.

PALEONTOLOGIC SETTING

Vertebrate fossils were first collected from the DSF in 1911 (Baker, 1912). Merriam (1919) provided the first comprehensive study and established the Ricardo fauna as the most diverse assemblage of this age from the southwestern United States. Studies during the next three decades expanded the fossil diversity (Stock and Furlong, 1926; Furlong, 1927; Stock, 1928; Miller, 1930; Osborn, 1933; Frick, 1937; Green, 1948; Richey, 1948; Tedford, 1961; Estes, 1963). Additional studies described fossil wood (Webber, 1933) and leaf floras (Axelrod, 1939). More recent

reviews have added taxonomic records and modified previous works (Whistler, 1969; Schultz and others, 1970; Baskin, 1980; Rich, 1980; MacFadden, 1980, 1984), but no single comprehensive study of the entire fossil assemblage has been produced since Merriam (1919). Such a study is in progress by one of us (Whistler), but detailed, species-level analyses are not required for the biostratigraphic results presented here.

The "Ricardo" fossil assemblage, as it was called prior to Tedford's work in 1965, was used as a standard of comparison in studies of assemblages of similar age in the Pacific Southwest. When the Wood Committee set out the original biochronological definitions of the North American land mammal ages, the "Ricardo Fauna" was used as one of four principal correlatives of their newly defined Clarendonian mammal age (Wood and others, 1941).

Based on correlation with his regionally defined Montediablan Stage, Savage (1955) suggested that the fossils of the DSF were all later Clarendonian in age. The late Clarendonian assignment was further reinforced by the early radiometric work of Evernden and others (1964) that reported a date of 10.0 Ma from low in the DSF. Although Tedford (1965) recognized a superposition of three faunal assemblages within the DSF, he still considered all to be late Clarendonian in age. Working with Tedford, Whistler (1969) suggested a correlation of the fossils from lower DSF with the earlier Clarendonian, Cerrotejonian Stage of Savage (1955) and the early Clarendonian, Burge F. from Nebraska (Webb, 1969). Both the biostratigraphic subdivisions of Savage and the Burge F. and overlying Minnecheduza F. of Webb (1969) were described in discontinuously fossiliferous successions, and Whistler (1969) concluded that the fossil record of the DSF represented a more continuous record filling these gaps. This conclusion is borne out by the biochronology presented below.

The composite fauna and flora of the DSF is presented in Table 1. Few groups have been studied in detail, and it is not the purpose of this paper to present a taxonomic review. Some animal groups have been reviewed recently (hipparionine horses: MacFadden, 1984) and others are currently under review (canids: R. Tedford and B. Taylor, American Museum of Natural History; proboscideans: C. Madden, Center for Mastodon and Elephant Research, Aurora, Colorado; oreodonts: B. Lander, Paleoenvironmental Associates, North Hollywood, California; antilocaprids: M. Ahern, University of Florida). Many of the microvertebrates represent new taxa, but they are assigned to the most closely related genus or species for purposes of the biochronology presented here.

BIOSTRATIGRAPHY

During the first 50 years of collecting in the DSF, the fossils were treated as a single assemblage, and the precise stratigraphic occurrences of specimens were not recorded. After a decade of collecting with precise stratigraphic controls, Tedford (1965) recognized three superimposed fossil faunas within the DSF. Whistler (1969, 1982) has continued detailed biostratigraphic work, including use of expanded taxonomic diversity provided by microvertebrate fossils. Detailed geologic mapping and precise stratigraphic controls applied since 1959 permit the expanded biostratigraphy of the DSF presented below (Fig. 4).

We have concentrated our analyses on those taxa that are most commonly used in vertebrate biostratigraphic analyses (horses, carnivores, antilocaprids, oreodonts, and rodents) and have included additional taxa (snakes, lizards, and insectivores) that are abundant in the DSF, even if their biochronologic significance has not been established elsewhere. The ranges of all taxa whose type specimens were recovered from the DSF are plotted in Figure 4, even if represented by single specimens. Sampling

biases may have influenced the teilzones of the less common taxa, but biases are unlikely for the more common ones because of the large number (>800) of collecting sites that are distributed fairly evenly throughout 1,500 m of the stratigraphic succession (Fig. 3). Although fossil occurrences may be influenced by paleoenvironmental factors, similar

lithofacies and similar inferred paleoenvironments are repeated throughout the lower two-thirds of the section. Consequently, the teilzones of most taxa in this part of the DSF are particularly well justified. For the taxa used to develop the biozonation in Figures 4 and 5, we have confidence that the sample sizes (typically in the range of 10 to 20 specimens for larger

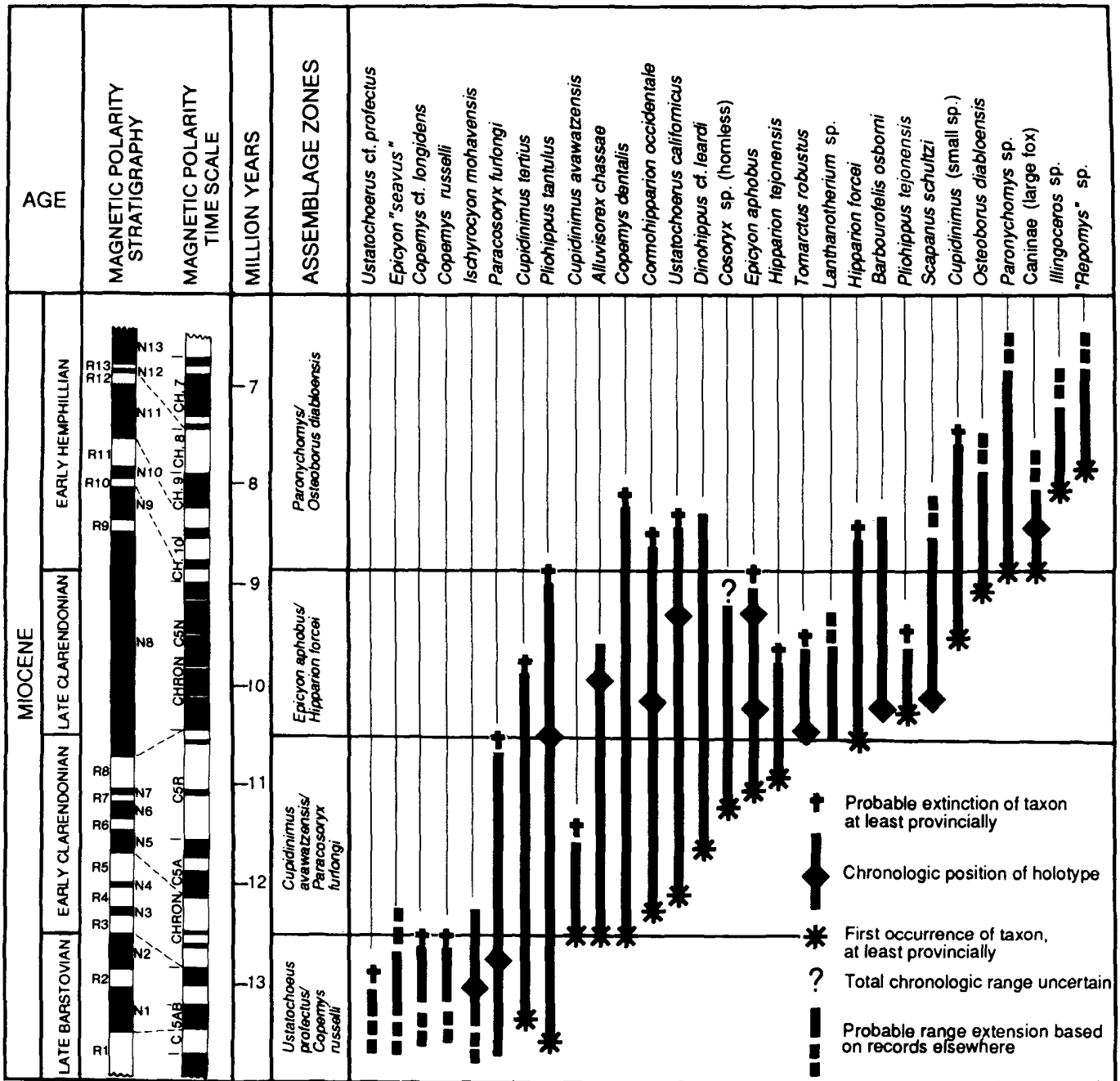


Figure 5. Biochronology of the Dove Spring Formation showing chronologic range of specific taxa used to characterize assemblage zones. Chronology based on magnetic polarity stratigraphy and radiometric dating.

animals, greater than 50 specimens for microvertebrates) are an accurate representation of the local stratigraphic range, except where otherwise noted.

The high frequency of fossil occurrences and the inclusion of microvertebrate taxa permit characterization of a precise biochronology within the DSF (Fig. 5). The taxa selected for this biozonation are those (1) with adequately determined species-level taxonomy, (2) abundantly represented within the DSF, (3) displaying limited biostratigraphic ranges within the DSF, and (4) having a potential for correlation with other Clarendonian assemblages due to a generalized occurrence, at least within the far-western United States.

Four assemblage zones (*sensu* North American Stratigraphic Code, Article 51, 1983) are delineated in Figures 4 and 5, although other subdivisions are possible. These assemblage zones (hereafter simply referred to as "zones") are of local importance for now, and their utility elsewhere is yet to be tested. The zone boundaries have been drawn primarily at one or more first occurrences of taxa. These first occurrences represent either (1) the first record of species that probably evolved in the southwestern United States (for example, *Cupidinimus avawatzensis*) or (2) the first appearance of allochthonous taxa into this area (for example, *Alluvisorex chassae*, *Paronychomys*, *Cormohipparion occidentale*). Several of the zone boundaries are further reinforced by last occurrences of taxa. In these instances, the zones may better be referred to as "concurrent range zones" (*sensu* North American Stratigraphic Code, Article 51(b)2, 1983). Some of the extinctions may be due to local ecological replacement by closely related species (for example, *Paracosoryx* replaced by *Cosoryx*). Others more likely represent direct evolutionary lineages (for example, *Copemys dentalis* derived from the form referred to as *C. cf. longidens*).

The lowest zone, the *Ustastocherus profectus*/*Copemys russelli* zone, is characterized by the restricted occurrence of the name bearers and other taxa shown in Figures 4 and 5. *Megahippus* cf. *M. matthewi*, *Epicyon* "saevus," *Ischyrocyon mohavensis*, and *Parapliosacomys* sp. are all limited to this zone in the DSF, but they have more extended ranges elsewhere. Noteworthy is the first occurrence of the grazing horse, *Pliohippus tantulus*. This is the only horse found within this interval, even though species of "Merychippus," *Hipparion*, and *Cormohipparion* are found in this time interval in the Great Plains (MacFadden, 1984). Notable by their absence are the common, late Barstovian horses of the "Merychippus" group.

The two deer mice restricted to the *U. profectus*/*C. russelli* zone, *Copemys* cf. *C. longidens* and *C. russelli*, are common in the youngest intervals of the Barstow Formation (Lindsay, 1972; Woodburne and others, 1990), and they provide the clearest link with these later Barstovian assemblages. It appears that the *C. russelli* zone of Lindsay (1972) may extend upward to about 12.5 Ma. Due to the absence of "Merychippus" species, however, it appears that the *U. profectus*/*C. russelli* zone represents an interval somewhat younger than the youngest assemblages found in the Barstow Formation, the latter dated at a minimum age of 13.2 Ma (Lapilli sandstone; MacFadden and others, 1990). In the far-western United States, horses referred to large species of "Merychippus" are accepted as indicators of terminal Barstovian time (Woodburne and others, 1990), and these horses are replaced by *Pliohippus* spp. in younger faunas. Based on the paleomagnetic correlation presented here, the lowest interval yielding *Pliohippus* within the DSF (Fig. 4) has an apparent age of 13.2 Ma, the same as the age of the upper intervals of the Barstow Formation that contain "Merychippus." The apparent contradiction can be accommodated by the error envelope surrounding both dates. A greater

contradiction exists in comparison with the Cronese Lf., a small assemblage with a "Barstovian character" (Tedford and others, 1987) with a reported date of 12.6 Ma (Evernden and others, 1964). This assemblage has not been described or adequately studied, however, and the volcanic rock samples used by Evernden and others (1964) for radiometric dating are separated from the fossil-producing sequence by a fault with an offset of undetermined magnitude (R. H. Tedford, 1990, personal commun.).

The *Cupidinimus avawatzensis*/*Paracosoryx furlongi* zone contains few restricted occurrences in addition to *C. avawatzensis*. The highly limited ranges of the ochotonids and beaver (Fig. 4) may be ecologically controlled as they occur in lacustrine beds representing the maximum lake development in the DSF. More significantly, the lower boundary of this zone can be characterized by the first occurrences of the abundantly represented *Alluvisorex chassae* and *C. dentalis*, the latter probably replacing the species of *Copemys* found in lower intervals. First occurring very near the lower boundary of this zone are *Cormohipparion occidentale* (formerly *Hipparion mohavensis*; MacFadden, 1984), the most common horse in the DSF, and *Ustastocherus californicus*. Many other taxa that become more common in younger intervals have first occurrences later in the *C. avawatzensis*/*P. furlongi* zone. No taxa become extinct at the upper boundary of this zone, but significantly, the very common *P. furlongi* (and all antilocaprids with dense, bony "horncores") drop out near the top of the zone.

The fossil assemblages of these lower two zones are those used by Tedford (1965) and Tedford and others (1987) to characterize their Iron Canyon F. Subsequent collecting in this interval has yielded three taxa used by Tedford and others (1987) to characterize their next younger fauna: *P. tantulus*, *C. occidentale*, and *U. californicus*.

The *Epicyon aphobus*/*Hipparion forcei* zone is characterized by the first occurrences of *T. robustus*, *H. forcei*, and *Lanthanotherium*, although the latter occurs in Barstovian-age assemblages elsewhere (Lindsay, 1972). Although neither of the name bearers is restricted to this zone, they are common only in this interval. Although present in the older, *C. avawatzensis*/*C. furlongi* zone, *H. tehonensis* and *D. cf. D. leardi* are most common in this zone. Noteworthy are the first occurrences of *Barbourofelis*, a taxon used by Tedford and others (1987) to define the beginning of the Clarendonian; and the first occurrence of the horse, *Pliohippus tehonensis*, a species used by Savage (1955) to characterize the earlier Clarendonian, Cerrotejonian Stage in California (see Fig. 6 and further discussion below). The first occurrence of *Barbourofelis* at ≈ 10.0 Ma could be interpreted as a delay in arrival of this taxon by as much as a million years relative to its arrival in the Great Plains. The dating of the first appearance of *Barbourofelis* in the Great Plains is poor, however, and the 10.0 Ma provided by the DSF may be an accurate estimate for the arrival of this taxon in North America. The upper boundary of the *E. aphobus*/*H. forcei* zone is characterized, in part, by the last occurrences of *P. tantulus* and *E. aphobus*.

The *E. aphobus*/*H. forcei* zone contains most of the elements used by Tedford and others (1987) to characterize the Ricardo F., but it also includes the taxa used to characterize their youngest, Dove Spring F. Expanded collecting within the upper part of the DSF has diminished the distinctions used by Tedford and others (1987).

We have also recognized a zone that represents an interval within the DSF from which fossils were previously unknown. The lower boundary of this youngest zone, the *Paronychomys*/*Osteoborus diabloensis* zone, is characterized by the first occurrence of one or more species of the cricetid genus *Paronychomys*. Although *C. dentalis* extends into the lower part of this zone, no small cricetines (for example, *Peromyscus*) have been found later in the interval. Fossil occurrences from paleosols and silcretes in the

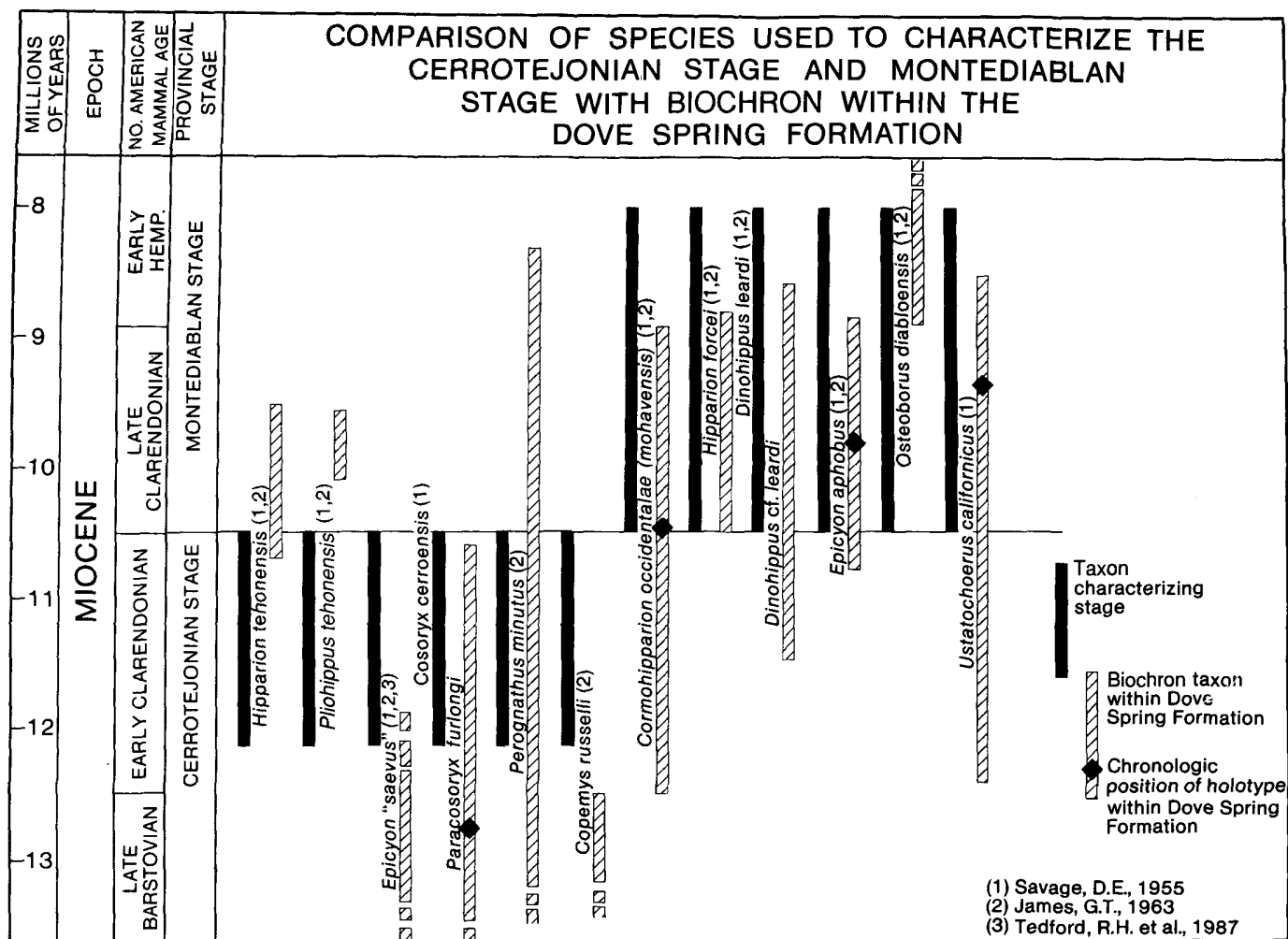


Figure 6. Comparison between the biochronologic ranges of mammalian species used to characterize the Cerrotejonian and Montediablan Stages (Savage, 1955) and their chronological ranges within the Dove Spring Formation. The boundary between the Cerrotejonian and Montediablan Stages was not originally defined but placed at the early/late Clarendonian boundary as proposed herein. The two merycodontine antelope species shown in third column are similar and probably represent ecomorphs; thus their biochrons are directly compared.

upper 200 m of the DSF are scarce, widely scattered, and poorly preserved; thus the characterization of the *Paronychomys*/*O. diabloensis* zone is less complete than the other zones. This zone is characterized further by first records of "*Repomys*" and *Illingoceros*. These taxa, and *Paronychomys*, are characteristic of Hemphillian-age assemblages; however, the immigrant taxa used by Tedford and others (1897) to define the beginning of the Hemphillian have not been found in the DSF. The earliest records of *Paronychomys* at about 8.9 Ma, well constrained by both radiometric dates and by paleomagnetic correlations, correspond closely with the 9.0 Ma Clarendonian/Hemphillian boundary proposed by Tedford and others (1987).

REGIONAL CORRELATIONS

Although correlation between west-coast fossil assemblages and those from the Great Plains is possible on a broad scale, there are many differ-

ences in detail due to regional provincialism. Provincialism is particularly evident in fossil assemblages west of the Rocky Mountains where pronounced tectonism led to the formation of disjunct basins. Savage (1955) attempted to deal with this provincialism by proposing a twofold local biostratigraphic subdivision of the Clarendonian interval in California based on superposed fossil assemblages in the southern San Joaquin Valley and San Francisco Bay area. The older, Cerrotejonian Stage was based on the fauna of the Santa Margarita Formation in the southern San Joaquin Valley; the younger, Montediablan Stage was based on the Black Hawk Ranch Lf. from the Green Valley Formation east of the San Francisco Bay. James (1963) expanded the faunal characterization of these stages based on the fossils in a Miocene succession within the Caliente Formation in the Transverse Ranges of California.

Figure 6 contrasts the biochrons of characterizing species from the Cerrotejonian and Montediablan Stages, with the biochronologic ranges from the same or closely related species in the DSF. Although many of the

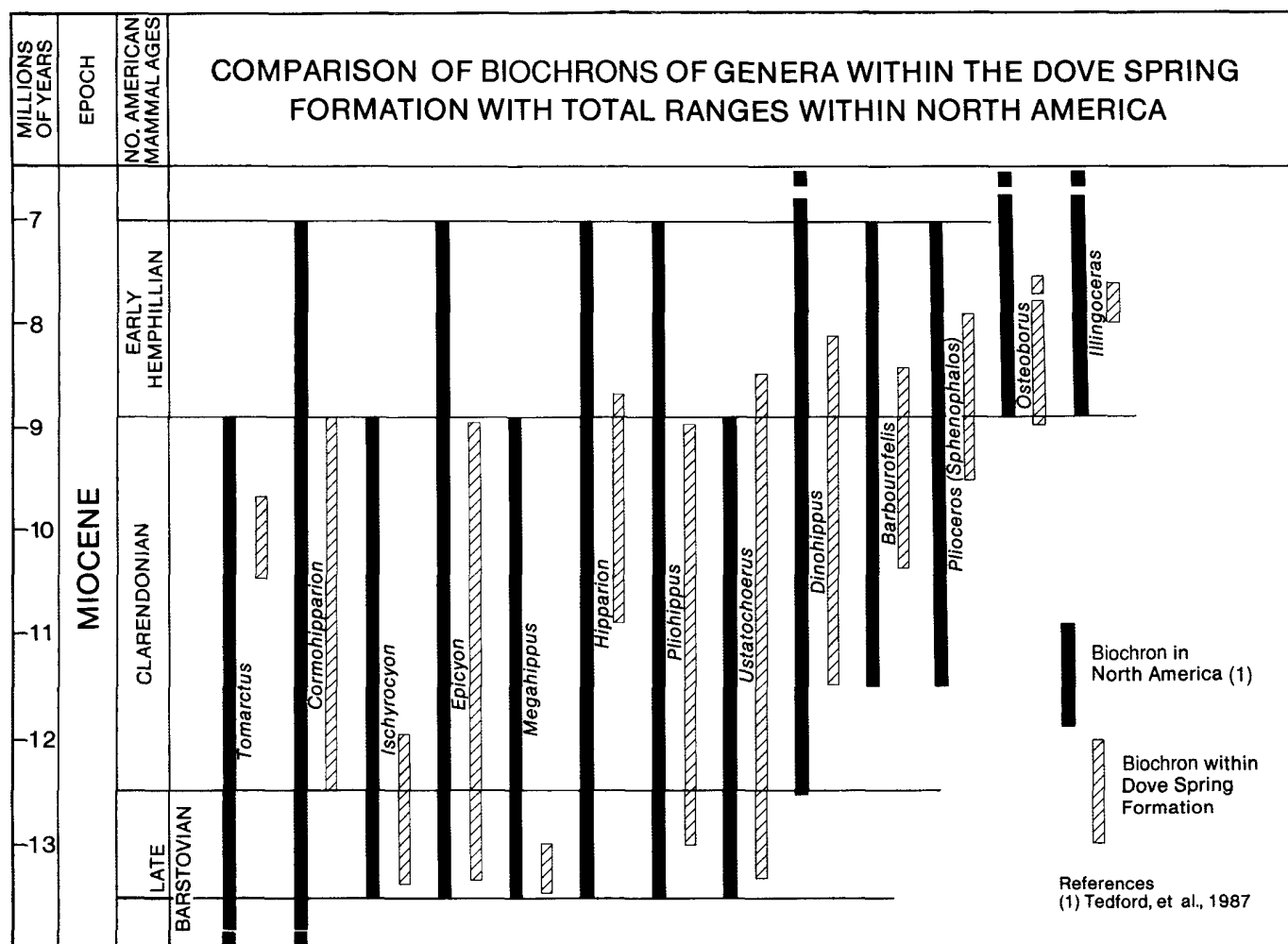


Figure 7. Comparison between the total chronologic range of fossil taxa used to define North American land mammalian chronology (from Tedford and others, 1987) and their biochrons within the Dove Spring Formation. Chronologic boundaries of North American land mammal ages are placed as proposed herein.

taxa have different or overlapping ranges within the DSF, the general superpositional relationships of the Cerrotejonian and Montediablan Stages remain evident. Noteworthy is an overlap in ranges of the type-Cerrotejonian horses, *H. tehonensis* and *P. tehonensis*, with the type-Montediablan horses, *C. occidentale* and *D. leardi*. The extended range of *U. californicus* into the Cerrotejonian interval in the DSF supports the similar findings of James (1963) in the Matthews Ranch Fauna. The taxa used to define both the Cerrotejonian and Montediablan Stages persist for longer time intervals within the DSF than in their type areas. There is a broad overlap of Cerrotejonian and Montediablan taxa within the *E. aphobus*/*H. forcei* zone. Retaining previous convention, the Cerrotejonian/Montediablan boundary is drawn corresponding to the early/late Clarendonian boundary at 10.5 Ma on Figures 4, 6; see also Figure 8 below.

The Black Hawk F. is placed at the boundary between the upper two zones in the DSF because of the late occurrence in the DSF of *O. diabloensis* (type from Black Hawk Ranch), and the presence at Black Hawk

Ranch of the large antilocaprid *Capromeryx*, a more derived genus not found in the DSF. The Matthews Ranch F. of James (1963) is considered a little older than the South Tejon Hills F. (type of the Cerrotejonian Stage) because of the presence of *Limnoecus tricuspidatus* (a species common in the Barstow fauna; Lindsay, 1972) and *Copemys russelli* and *Megahippus*, animals restricted to the late Barstovian *U. profectus*/*C. russelli* zone of the DSF. The Nettle Springs F. of James (1963) is considered older than the Black Hawk Ranch Lf. (type Montediablan Stage) because of the absence of *D. leardi* and the presence of *Cosoryx* cf. *C. cerroensis* instead of the larger *Capromeryx* sp. (or possibly *Plioceros*) at Black Hawk Ranch.

COMPARISON WITH NORTH AMERICAN STANDARD

Tedford and others (1987) have proposed modification in the limits and faunal characterizations of the Barstovian and Clarendonian mammal ages based predominantly on faunal assemblages from Nebraska and the Great Plains of the central United States. Figure 7 shows that genera

within the DSF display a pattern similar to that as redefined by Tedford and others (1987). In all cases but one (*Ustatochoerus*), genera within the DSF have more restricted local ranges than the total range of the genus in North America.

The *U. profectus*/*C. russelli* zone of the DSF compares most closely with the Burge F. of Nebraska (Webb, 1969), both containing *U. profectus*, *M. matthewi*, primitive protohippine horses (*Pliohippus supremus* in the Burge F., a horse close to *P. tantulus* of the DSF), and forked-horned antilocaprids, *Paracosoryx furlongi* in the DSF, *Cosoryx furcatus* in the Burge F. The *U. profectus*/*C. russelli* zone thus represents a western equivalent to the later Barstovian interval (as redefined by Tedford and

others, 1987). Except among rodent species whose upper biochronologic ranges were undetermined, however, the *U. profectus*/*C. russelli* zone contains more derived taxa than are found in the uppermost fossil assemblages of the *C. russelli* zone (Lindsay, 1972) of the type Barstow Formation, even though the two areas were separated by no more than 40 km at the time of deposition. A latest Barstovian interval thus appears to extend above the uppermost assemblages of the Barstow Formation.

A prominent change in taxonomic composition within the DSF occurs between the *U. profectus*/*C. russelli* zone and the overlying *C. avawatzensis*/*P. furlongi* zone (Figs. 4 and 5), including first occurrences of *C. avawatzensis*, *C. dentalis*, *C. occidentale*, and *U. californicus*. This

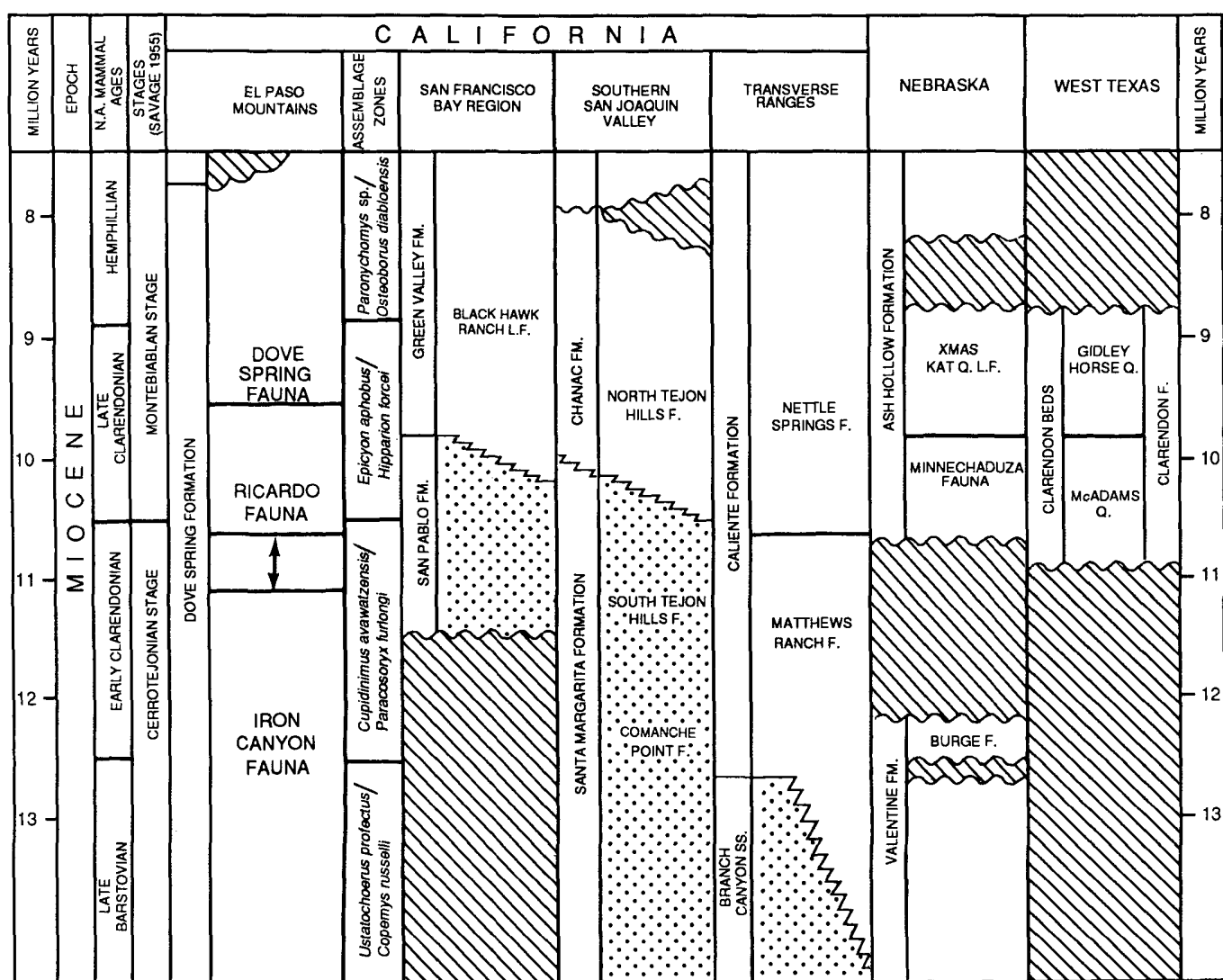


Figure 8. Comparison among biochronology in the Dove Spring Formation (DSF) and selected assemblages in California and the Great Plains. Stratigraphic positioning of faunas within the DSF after Tedford (1965). Nebraska and Texas columns taken, in part, from Tedford and others (1987). Chronologic positioning of the assemblages are based on faunal correlations with the continuous biochronological sequence in the DSF. Chronological boundaries between the North American land mammal ages are placed as proposed in this paper.

turnover represents a good point to recognize locally a boundary between Barstovian and Clarendonian. Paleomagnetic chronologic correlation within the DSF indicates this boundary falls at 12.5 Ma, 0.9 m.y. older than the 11.5 Ma suggested by Tedford and others (1987).

The *C. awawatzensis*/*P. furlongi* zone shares elements typical of both the late Barstovian Burge F. (*I. mohavensis*, *P. furlongi*) and the early Clarendonian Minnecheduza F. (large *Ustatochoerus*), and thus it probably represents an assemblage that fills the gap that exists between the two Great Plains faunas (Fig. 8). The *C. awawatzensis*/*P. furlongi* zone also contains first records of *C. occidentale*, a horse found in both the Burge F. and Minnecheduza F., further supporting an intermediate position for this zone.

The *E. aphobus*/*H. forcei* zone most closely resembles the Minnecheduza F. of Nebraska (Webb, 1969) and the Clarendon F. of Texas. The *E. aphobus*/*H. forcei* zone and the Minnecheduza F. both contain *Barbourofelis*, *Hipparion tehonensis*, *Cormohipparion occidentale*, a large oreodont (*Ustatochoerus major* in Nebraska and *U. californicus* in California), and *Plioceros*. It is more difficult to precisely tie assemblages from the DSF to later Clarendonian faunas of the Merrit Dam Member of the Ash Hollow Formation because only generic lists have been given (Skinner and Johnson, 1984). At this level of identification, similarities to the *E. aphobus*/*H. forcei* zone seem indicated.

The *Paronychomys*/*O. diabloensis* zone is too incomplete for meaningful comparisons with the Great Plains. It contains fossil mammals (*Paronychomys*, "*Repomys*," and *Illingoceros*) that are found in middle to late Hemphillian faunas of Arizona, California, and the Great Basin (Merriam, 1909; Furlong, 1943; Jacobs, 1977; May, 1981). The *Paronychomys*/*O. diabloensis* zone, however, lacks other characteristic Hemphillian taxa. There is a gap between Clarendonian and Hemphillian faunas in the Ash Hollow Formation in the Great Plains (Fig. 8). The *Paronychomys*/*O. diabloensis* zone probably lies in this hiatus in the Great Plains sequence, thus it lacks the defining taxa of Hemphillian (promethomine rodents and edentates) that occur in rocks younger than the DSF. Tedford and others (1987) noted that early Hemphillian faunas retain a chronofaunal affinity with Clarendonian faunas such that most differences are at the species level. The early Hemphillian assemblages of the southern Great Plains contain Clarendonian forms such as *Barbourofelis*, *Hipparion forcei*, *Cormohipparion occidentale*, and *Plioceros*. All of these taxa also occur in the lower part of the *Paronychomys*/*O. diabloensis* zone. The *Paronychomys*/*O. diabloensis* zone contains taxa with definite Hemphillian affinities, however, and the chronologic correlation of the lower boundary of this zone at 8.9 Ma corresponds closely with the Clarendonian/Hemphillian boundary proposed by Tedford and others (1987).

Based on the continuous succession of fossil faunas within the DSF, the fossil characterization of the Clarendonian mammal age in California can be refined as follows. (1) Early in the interval, first occurrences of *Cormohipparion occidentale* (= *Hipparion mohavense*), *Alluvisorex chassesei* (Eurasian immigrant), shoveltusk gomphotheres, *Copemys dentalis*, *C. awawatzensis*, and *Ustatochoerus californicus* appear. (2) All species in (1) except the serbelodont gomphotheres are restricted to the age. (3) Appearing later in the interval, and restricted to the age, are *Scapanus schultzi*, *Epicyon aphobus*, *Martinogale*, *Hipparion tehonensis*, *Plihippus tehonensis*, and *Cosoryx*. (4) Last occurrences of survivors from older assemblages, including *Ischyrocyon*, *Plihippus tantulus*, *Cupidinimus tertius*, *Copemys russelli*, and *Paracosoryx*, occur during this age. (5) Although not restricted to the interval, *Hipparion forcei*, *Hypolagus*, several species of *Perognathus*, and a diversity of camels are common.

CONCLUSIONS

We conclude the following from the preceding discussions. (1) The Dove Spring Formation (DSF) is characterized by nearly continuous deposition and yields a succession of fossil assemblages spanning a longer interval of the later Miocene than elsewhere in southwestern North America. (2) Radiometric and paleomagnetic correlations indicate that the DSF spans a time interval from at least 13.6 Ma to 7.0 Ma. (3) Four fossil assemblages are recognized within the DSF. (4) Correlation with other North American assemblages (Tedford and others, 1987) indicates that the DSF fossils span a time interval encompassing more than the Clarendonian mammal age. (5) Some of these assemblages help to fill the gaps that exist in the type areas between the Barstovian and Clarendonian and between the Clarendonian and Hemphillian mammal ages; thus a more precise chronology can be applied to these hiatuses. (6) The greatest change in the DSF is between the *U. profectus*/*C. russelli* zone and *C. awawatzensis*/*P. furlongi* zone, and this faunal change provides for a local definition of the boundary between the Barstovian and Clarendonian. (7) Less well-defined changes between the *E. aphobus*/*H. forcei* zone and the *Paronychomys*/*O. diabloensis* zone locally mark the boundary between the Clarendonian and Hemphillian. (8) The chronology developed in the DSF, and correlation with other fossil assemblages, permit a more precise chronologic definition of two of the North American mammal age boundaries: the late Barstovian/Clarendonian boundary lies at 12.5 Ma, and, whereas the Clarendonian/Hemphillian boundary is less clearly delineated, the transition occurs at 8.9 Ma. (9) Comparisons between the DSF fossil assemblages and those of the Cerrotejonian and Montediablan Stages (Savage, 1955) show more shared taxa than previously appreciated.

ACKNOWLEDGMENTS

R. H. Tedford began the biostratigraphic work that led to this ongoing study. His geologic mapping and stratigraphic data were graciously turned over to the senior author (Whistler), who wishes to acknowledge this pioneer work and the succeeding discussions which have enhanced this study. Discussions with D. Savage and M. Woodburne have also greatly enhanced this study. Fossil collections with biostratigraphic control have been made by many individuals over a 27-year period. Special recognition is due B. Chassé, the MacConnell family, H. Quinn, R. Kefauver, D. Spitzer, M. Stokes, S. Cox, and many volunteers of the George C. Page Museum. Many of the staff and families of Red Rock Canyon California State Park have provided assistance and amenities, particularly S. Alexander, M. Faull, B. Graham, C. Helton, J. McCummins, and A. Wilkinson. Fossil collecting has been done under permit from the California State Department of Parks and Recreation and the United States Department of Interior, Bureau of Land Management. Partial field support has been provided by the Annie Alexander Scholarship Fund of the University of California, Berkeley, Museum of Paleontology (1967), The Center for Field Research (Earthwatch) (1982), and the Natural History Museum of Los Angeles County Foundation. Funding for the paleomagnetic and fission-track studies was provided by National Science Foundation Grant EAR 8305874, the Shell Foundation, and the University of Southern California Faculty Research and Innovation Funds. Partial support for K-Ar dating was provided by C. Swisher at the Institute of Human Origins, Berkeley, California, and National Science Foundation Grant EAR 8618701. Additional support was provided by National Science Foundation Grants BSR 8218194 (1972–1977) and BSR 8202014 (1982–1985). The authors wish to thank L. Barnes, J. Harris,

C. Stevens, C. Swisher, R. Tedford, and M. Woodburne, who provided comments on drafts of this manuscript.

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MANUSCRIPT RECEIVED BY THE SOCIETY MAY 13, 1991

REVISED MANUSCRIPT RECEIVED OCTOBER 4, 1991

MANUSCRIPT ACCEPTED OCTOBER 16, 1991

Geological Society of America Bulletin

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Geological Society of America Bulletin 1992;104, no. 6;644-658
doi: 10.1130/0016-7606(1992)104<0644:MBABOT>2.3.CO;2

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