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Revised large mammal biostratigraphy and biochronology of the Barstow Formation (Middle Miocene), California

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A new biostratigraphic zonation for the middle Miocene Barstow Formation based on the mammalian megafauna is presented. Four biostratigraphic zones are outlined, two containing fossil assemblages of early Barstovian (Ba1) age, and two with late Barstovian (Ba2) assemblages. Recommendations are made for defining and characterizing the Barstovian North American Land Mammal Age (NALMA). The Ba1 biochron is defined based on the first occurrence of *Plithocyon*, and the base of the Ba2 biochron is revised based on the first appearance of the antilocaprid *Ramoceros*.

The ursid *Plithocyon* remains a valid defining taxon for the base of the Barstovian NALMA. The use of both gomphotheriid and mammutid proboscideans to define the base of the Ba1 or Ba2 is abandoned due to the diachrony of first appearances across North America. The Ba1 biochron is additionally characterized based on the first appearance of the equid *Scaphohippus*. The base of the Ba2 biochron is revised based on the first appearance of *Ramoceros*. The Ba2 can also be characterized by the first appearance of the borophagine canid *Protepicyon* and the anchitherine equid *Megahippus*.

INTRODUCTION

The Barstow Formation, with significant outcrops located within the Mud Hills region of the Mojave Desert (Fig. 1) approximately ten miles north of the town of Barstow, San Bernardino County, California, is renowned for its mammalian fossils. The Wood Committee on Stratigraphic Nomenclature (Wood et al. 1941) designated the fossil assemblage from the “fossiliferous tuff member” of the Barstow Formation as the type assemblage for the Barstovian North American Land Mammal Age. Subsequent workers (Tedford et al. 1987, Tedford et al. 2004) defined an early (Ba1) and late (Ba2) subdivision of the Barstovian NALMA. The Barstovian NALMA is recognized as encompassing a geochronologic time span from approximately 16.0–12.5 Ma (Tedford et al. 2004).

A revised systematic treatment of the megafaunal constituents (here defined as small mustelid or larger) has been accomplished by Pagnac (2005a, 2005b, 2006). Prior to these works, the mammalian megafauna from the Barstow Formation had not been subjected to a comprehensive description and review since that presented by Merriam (1919). In this study, revisions to the biostratigraphy of the Barstow Formation, based on these systematic reviews, are presented. These revisions include only the Barstovian taxa from the Barstow Formation, excluding the earlier Hemingfordian taxa. In the type area (Mud Hills), the Barstovian fauna occurs from the stratigraphic level of Steepside Quarry to several localities (e.g., RV 6126, UCMP V6447) which occur near the stratigraphic level of the Lapilli Tuff (approximately 120 meters above the Hemicyon Tuff), or within the upper half of the middle member and the upper member of the Barstow Formation (Figs. 1–3).

To date, three informal “faunal zones” have been recognized within the “Barstovian portion” (as outlined above)

of the Barstow Formation (Woodburne and Tedford 1982, Tedford et al. 1987, Woodburne et al. 1990, Tedford et al. 2004), the Third or “Green Hills” Division, the Second Division, and the First Division (Fig. 2). These zones are in reality lithologic subdivisions developed by field crews from the Frick Laboratory (see abbreviations). Because these lithologic subdivisions coincidentally contain relatively discrete fossil assemblages, subsequent researchers (Frick 1937, Schultz and Falkenbach 1940, 1941, 1947, 1949) utilized these Frick Lab lithologic subdivisions to denote relative stratigraphic relationships of fossil assemblages. As such, no formal biostratigraphic zonation based on established protocol has been presented for the mammalian megafauna of the Barstow Formation, although Lindsay (1972) proposed a fourfold biostratigraphic zonation based on mammalian microfossils (Fig. 2). Herein I present a revised biostratigraphy for the mammalian megafauna of the Barstow Formation as exposed in the Mud Hills (Figs. 2–3) and a revised biochronology for the Barstovian NALMA. The paper concludes with a brief consideration of the boundary between the Barstovian and Clarendonian NALMAs.

History of Study

The development of the modern lithostratigraphic subdivisions of the Barstow Formation is a complicated story that involves both lithostratigraphic and biostratigraphic interpretations. For a comprehensive and detailed review of interpretations prior to 1980, see Woodburne and Tedford (1982), Woodburne et al. (1990) and Pagnac (2005a).

The modern lithostratigraphic subdivisions of the Barstow Formation (Fig. 2) were developed by Woodburne and Tedford (1982), Tedford et al. (1987) and Woodburne et al. (1990). The basal member, the Owl Conglomerate (Fig. 2), consists of at least 200 m of granitic conglomerates. These basal conglomerate layers grade laterally into the granitic

breccia of the Pickhandle Formation (Ingersoll et al. 1996). The base of the Owl Conglomerate is demarcated by the Red Tuff. The top of the Owl Conglomerate is marked by the Rak Tuff.

Atop the Owl Conglomerate is the unnamed middle member (which begins with the Rak Tuff) which comprises

approximately 570 m of fluvial conglomerates, sandstones and clays. The top of the middle member is marked by the prominent Skyline Tuff, a 1-2 m thick detrital, ash-fall tuff bed.

The unnamed upper member (which begins with the Skyline Tuff) consists of about 270 m of lacustrine clays and mudstones, with limited occurrence of sandstone facies. The

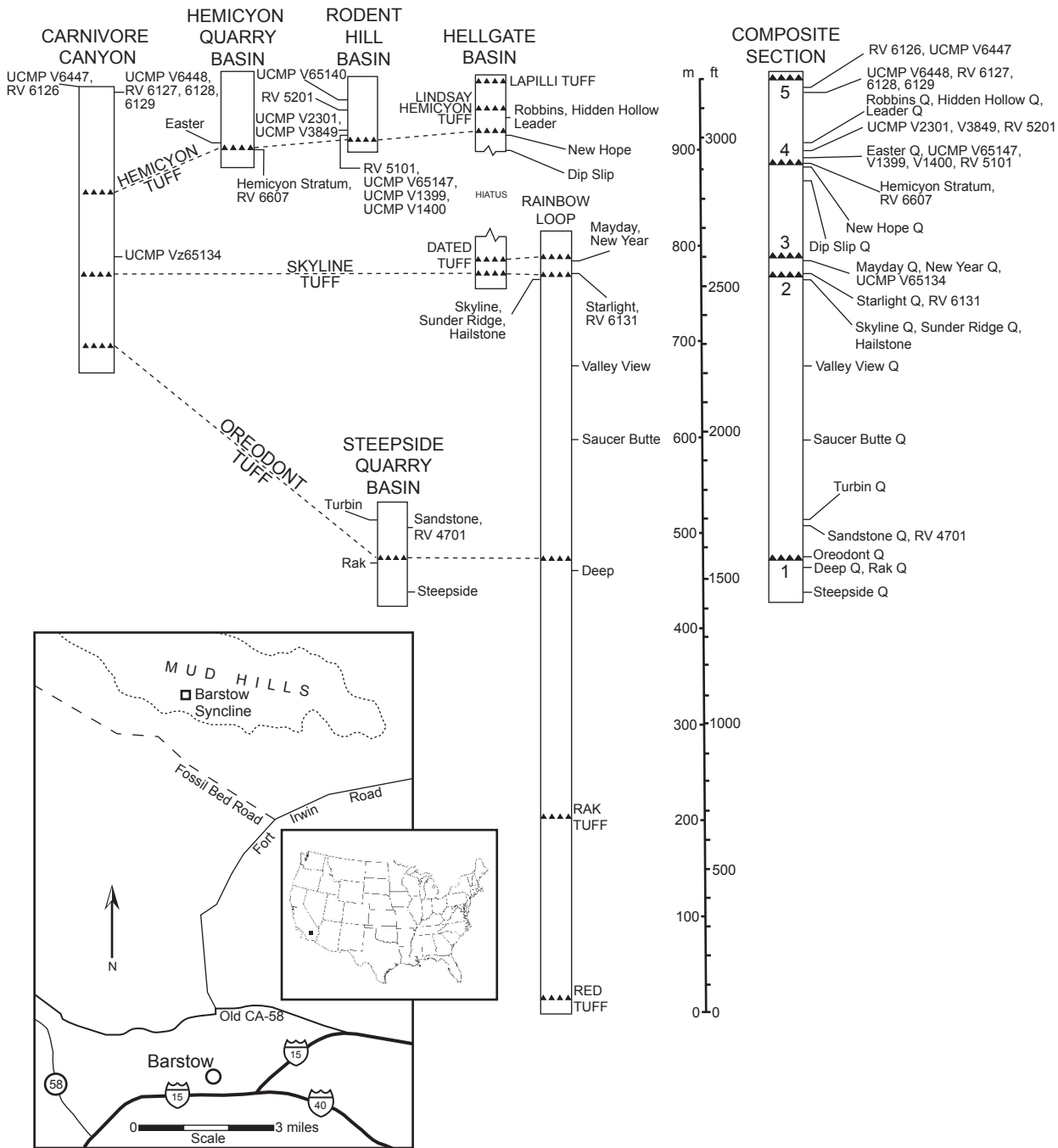


Figure 1. Stratigraphic sections from the Barstow Formation in the Mud Hills, CA, region (for specific geographic locations of sections refer to Woodburne et al. 1990 and MacFadden et al. 1990). Stratigraphic locations of vertebrate localities are also indicated. Numbers in composite section correspond to the following tuff beds: 1—Oreodont Tuff, 2—Skyline Tuff, 3—Dated Tuff, 4—Hemicyon Tuff, 5—Lapilli Tuff. Insert illustrates geographic location of Mud Hills region and Barstow Syncline area of the Mojave Desert where significant deposits of the Barstow Formation crop out.

upper member is capped unconformably by Quaternary alluvium. Each of the three members shares an interfingering relationship with a western fanglomerate facies of distinct lithology (Steinen 1966, Woodburne et al. 1990) that has never been recognized as a formal lithostratigraphic unit.

Frick field crews recognized five distinct lithostratigraphic intervals within the Barstow Formation (Fig. 2): the Fifth or Red Division, the Fourth or Rak Division, the Third or Green Hills Division, the Second Division and the First Division (Barstow Fauna of Woodburne et al. 1990). Frick field crews recognized relatively distinct fossil assemblages associated with each of these divisions, although these data were never formally published. Subsequent researchers (Frick 1937, Schultz and Falkenbach 1940, 1941, 1947, 1949) utilized these lithostratigraphic divisions to indicate the relative stratigraphic relationships of mammalian taxa as no formal biostratigraphic zonation was available. As a result, these lithostratigraphic divisions have been used continuously to describe discrete faunal assemblages within the Barstow Formation (Tedford 1966, Woodburne and Tedford 1982, Tedford et al. 1987, Woodburne et al. 1990, Tedford et al. 2004). Tedford (1966) compiled the stratigraphic ranges of fossil taxa from Frick Laboratory data and presented them in a brief report. Tedford's report is the only published megafaunal biostratigraphic data available from the Barstow Formation.

Wood et al. (1941) designated the fauna from the "fossiliferous tuff member" of the Barstow Formation (equivalent to the unnamed upper member of Woodburne et al. 1990) as the type assemblage for the Barstovian North American Land Mammal Age. The fossils from the "fossiliferous tuff member" of Merriam (1919) were considered equivalent to the assemblage from the First Division of the Frick Laboratory, thus limiting the original definition of the Barstovian to that zone. At this point, lithostratigraphy and biochronology became inter-mixed, resulting in a confusing characterization of the type Barstovian assemblage. The Frick zones were essentially lithostratigraphic units that coincidentally contained distinct fossil assemblages. Thus, the original definition of the Barstovian NALMA was based on fossil occurrences restricted to lithostratigraphic zones rather than a desired biostratigraphic zonation.

A revised biostratigraphic zonation is needed to provide a suitable basis for recognition of Barstovian NALMA aged assemblages. Lindsay (1972) developed a number of biostratigraphic zones within the upper member of the Barstow Formation based on microfossils (Fig. 2). Although Lindsay recognized four distinct biostratigraphic zones, three were limited to the upper member of the Barstow Formation. Additionally, the microfauna from the lower portions of the Barstow Formation, particularly the middle member, has not been adequately sampled to provide a basis for detailed biostratigraphy. It is for these reasons that the revised zonation presented here is limited to the macrofauna.

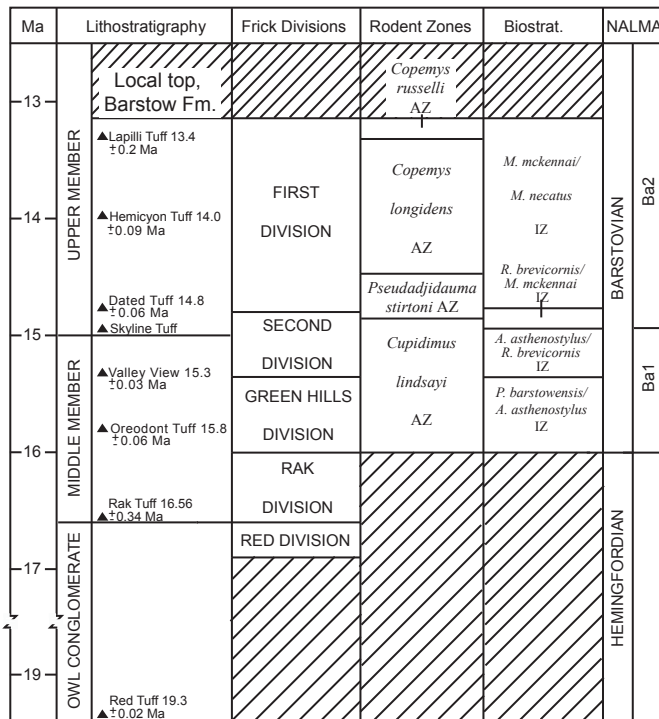


Figure 2. Lithostratigraphic and biostratigraphic subdivisions of the Barstow Formation. Triangles represent stratigraphic position and Ar⁴⁰/Ar³⁹ ages of tuff beds (Woodburne et al. 1990, Woodburne 1996). Rodent assemblage zones after Lindsay 1972. Macrofossil biostratigraphy from this paper.

Abbreviations in text

AMNH—American Museum of Natural History, New York, NY; F:AM—Frick American Mammals Collection. The late Childs Frick (Frick Laboratory) conducted extensive vertebrate collection programs throughout the United States. Upon his death in 1966, his collection of fossil vertebrates was donated to the American Museum, where they are currently housed. FOD—First occurrence datum (temporal) as defined by Aubry (1997); HO—Highest occurrence (stratigraphic) as defined by Aubry (1997); IZ—Interval Zone; LACM—Los Angeles County Museum, Los Angeles, CA; LO—Lowest occurrence (stratigraphic) as defined by Aubry (1995); LOD—Last occurrence datum (temporal) as defined by Aubry (1997); Ma—Mega-annum, or a point in the geochronologic timescale; m.y.—million years, or an interval in the temporal timescale; NALMA—North American Land Mammal Age; RAM—Raymond Alf Museum, Claremont, CA; RV—University of California, Riverside, CA, fossil locality. SBCM—San Bernardino County Museum, Redlands, CA; UCMP—University of California Museum of Paleontology, Berkeley, CA; UCR—University of California, Riverside (vertebrate paleontology collections now housed at UCMP)

Unless otherwise stated, the term Barstow Formation refers only to the outcrops of that formation in the Mud Hills, San Bernardino County, California.

MATERIALS AND METHODS

The data used in this study were obtained from surveying the fossil mammal collections at a number of institutions. The bulk of the data were collected from the F:AM collections at AMNH. Significant amounts of data were also collected from specimens at UCMP. The remaining data were compiled from specimens at LACM, SBCM, UCR, and RAM.

The stratigraphic ranges of each of the taxa were tabulated based on occurrences recorded from several localities. The occurrences were gathered from published references and documentation of specimens within collections (many of the key specimens utilized in defining biohorizons are listed in Appendix I). Localities were located in the field and correlated to the nearest previously published lithostratigraphic section (Fig. 1). See Woodburne et al. 1990 and MacFadden et al. 1990 for details as to the exact geographic location of each section in Figure 1. A composite section was produced and each locality was placed based on its relative position to key marker beds (Fig. 1). The composite section was arranged within a geochronologic framework based on radioisotopic dates from previously published results (Woodburne et al. 1990, MacFadden et al. 1990, Lourens et al. 2004) (Fig. 3). The new megafaunal biostratigraphic zonation for the middle and upper members of the Barstow Formation is illustrated in Figures 2 and 3. Figure 3 shows the stratigraphic ranges of megafaunal taxa from the Barstow Formation.

The stratigraphic ranges illustrated in Figure 3 are from the Barstow Formation only; their lateral extent is considered local. Thus, the term lowest occurrence (LO) and highest occurrence (HO) are used to describe their local stratigraphic ranges. By utilizing geochronologic data acquired from several tuff beds (Woodburne et al. 1990, Berggren et al. 1995, Woodburne 1996, Lourens et al. 2004, Tedford et al. 2004) these ranges have been plotted along a geochronologic time scale on the left of the stratigraphic ranges in Figure 3.

Salvador (1994) defines an "Interval Zone" as, "... a body of fossiliferous strata between two specified biostratigraphic horizons (biohorizons). Such a zone is not itself necessarily the range zone of a taxon or concurrence of taxa; it is defined and identified only on the basis of its bounding biohorizons." The interval zones presented herein are consistently defined at their base on the lowest stratigraphic occurrence (LO) of each defining taxon.

BACKGROUND TO BIOCHRONOLOGY OF THE BARSTOVIAN NALMA

Tedford et al. (1987) expanded on the original Wood Committee definition of the Barstovian NALMA, which until then had only included the fauna from the "fossiliferous tuff member" of the Barstow Formation (essentially equivalent to the Frick First Division fauna in Fig. 2). Through integration of contemporary taxonomic and geochronologic information, Tedford et al. (1987) defined the base of the Barstovian NALMA at the first appearance of the ursid *Plithocyon* (= *Hemicyon*) and the cricetid rodent *Copemys*. This new

definition included faunal assemblages from the unnamed middle member of the Barstow Formation, or the Green Hills Division and Second Division Faunas of Frick (Fig. 2), corresponding to a time frame of approximately 16–12 m.y.

Tedford et al. (2004) made additional revisions to the Barstovian NALMA and incorporated additional geochronologic, magnetostratigraphic, and taxonomic data in their refinements. The base of the Barstovian NALMA was defined on the first appearance of the ursid *Plithocyon* and the mammutid proboscidean *Zygolophodon*. The Barstovian NALMA extends to the first appearance of the gelocid *Pseudoceras*, defines the base of the Clarendonian NALMA, and encompasses a time span of approximately 16–12.5 m.y.

Tedford et al. (2004) divided the Barstovian NALMA into two biochrons, the early Barstovian (Ba1) and late Barstovian (Ba2). The Ba1 was defined as above, by the first appearance of *Plithocyon* and *Zygolophodon*. The Ba1 was also characterized by a number of first and last appearances of taxa. Due to the highly provincial nature of Barstovian faunal assemblages, Tedford and his coauthors made regional characterizations for the Ba1 interval, such as the first appearance of the borophagine canids *Cynarctus* in the midcontinent, and that of *Aelurodon* and *Protepicyon* in the west.

The cricetid rodent genus *Copemys* was used to define the base of the Barstovian NALMA (Tedford et al. 1987, Lindsay 1995) based on a LO at Steepside Quarry (Lindsay 1972). Further collection efforts in the lower portion of the unnamed middle member of the Barstow Formation (the Rak Division of Frick) have yielded specimens of *Copemys* from stratigraphic levels below that of Steepside Quarry (Lindsay 1995), a portion of the Barstow Formation which contains a Hemingfordian faunal assemblage. As a result, Tedford et al. (2004) chose to abandon *Copemys* as a defining taxon for the base of the Barstovian interval.

Tedford et al. (2004) define the base of the Ba2 with the first appearance of gomphotheriid proboscideans, the erinaceids *Lanthanotherium* and *Untermannerix*, the ochotonids *Hesperolagomys* and *Russellagus*, the zapodid *Megasminthus*, the mustelid *Pliogale* and the amphicyonid *Pseudocyon*. Tedford et al. (2004) again comment on the provincial nature of Barstovian assemblages and identify each defining taxon as endemic to the midcontinent or the west. In this work, Tedford et al. (2004) also extensively characterize the Ba2 interval with first and last appearances of numerous taxa, again specifying a geographic province for each.

Due to the diachronous nature of the first appearance of proboscideans in North America, the use of *Zygolophodon* and of Proboscidea in general, the designation of a defining taxon for the base of the Barstovian interval is abandoned. Proboscideans appear as early as 16.5 Ma. in the Great Basin (Prothero et al. 2008a) and as late as 14.5 Ma. in the Great Plains (Prothero et al. 2008b). The earliest appearance of proboscideans in the Massacre Lake local fauna in Nevada predates the Hemingfordian/Barstovian boundary, whereas their appearance in the Great Plains is significantly later

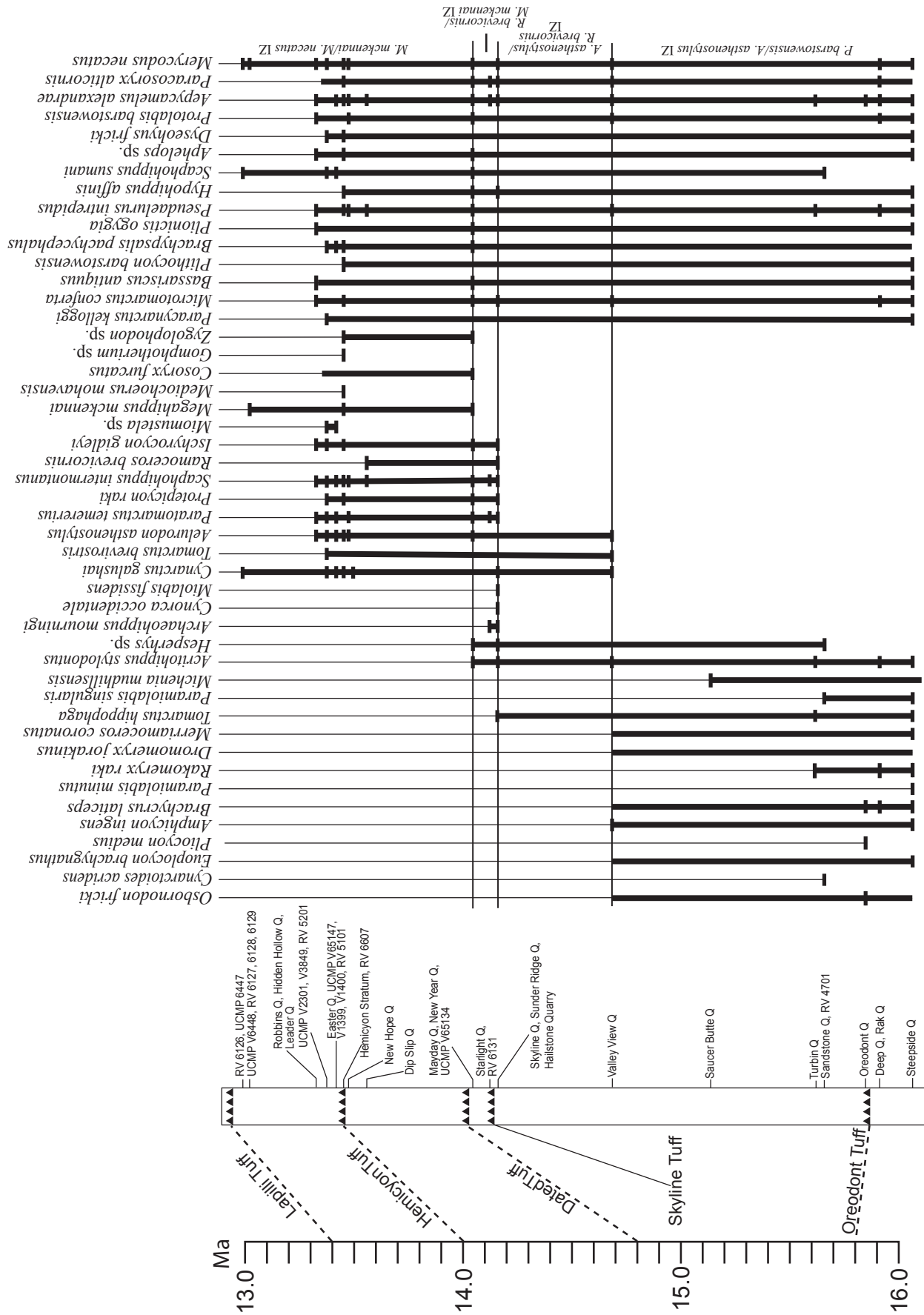


Figure 3. Biostratigraphic ranges of mammalian megafaunal constituents of the Barstow Formation. Solid vertical lines represent known stratigraphic ranges. Horizontal lines represent occurrence at specific localities (indicated to the left of the diagram). Composite lithostratigraphic section (from Figure 1) shows quarry locations. Geochronologic scale at left.

than the base of the Barstovian. As such, Proboscidea has no utility as a defining taxon for the base of the Barstovian NALMA. Tedford et al. (2004) defined the base of the Ba2 biochron based on the first appearance of the proboscidean *Gomphotherium*. The lowest stratigraphic occurrence of *Gomphotherium* in the Barstow Formation is at the level of New Year Quarry (just below the Dated Tuff). As Proboscidea is no longer a valid defining taxon for the base of the Ba2 due to the diachrony of first appearances (Prothero et al. 2008a, b), the use of Gomphotheriidae as a defining taxon is abandoned as well.

REVISED BIOCHRONOLOGY OF THE BARSTOVIAN NALMA

New definition of the Barstovian NALMA

Definition—The beginning of the Barstovian NALMA is defined based on the first appearance of the hemicyonine ursid *Plithocyon* (Tedford et al. 2004). No other taxa can serve as useful first appearance taxa to define the base of the Barstovian NALMA due to the current state of taxonomy and biostratigraphy.

New definition and characterization of Ba1

Definition—As stated above, the base of the Ba1 biochron is defined by the first appearance of *Plithocyon*.

Characterization—Tedford et al. (2004) characterize the Ba1 biochron by the following first appearance taxa: Canidae—*Cynarctus*, *Paratomarctus*, *Aelurodon*, *Carpocyon*; Mustelidae—*Martes*; Procyonidae—*Probassariscus*, *Arctonassua*; Equidae—*Calippus*, *Hipparion*; Tayassuidae—*Dyseohyus*, *Prosthenops*; Camelidae—*Procamelus*, *Rakomylyus*; Antilocapridae—*Ramoceros*, *Cosoryx*; Mylagaulidae—*Umbogaulus*, *Pterogaulus*, *Ceratogaulus*, *Hesperogaulus*; Castoridae—*Monoaulax*; Heteromyidae—*Perognathus*, *Peridiomys*, *Mojavemys*. The “protohippine” equid *Scaphobippus* is added (this study).

Tedford et al. (2004) characterize the Ba1 biochron by the following last appearances of taxa: Canidae—Hesperocyoninae (*Osbornodon*), *Cynarctoides*, *Euoplocyon*; Amphicyonidae—*Pliocyon*, *Amphicyon*; Equidae—*Desmatippus*, *Parahippus*; Tayassuidae—*Cynorca*; Merycoidodontidae—*Brachycrus*, *Merychyus*; Camelidae—Stenomyliinae (*Rakomylyus*), *Paramiolabis*; Moschidae—*Problastomeryx*; Dromomerycidae—*Subdromomeryx*, *Rakomeryx*; Antilocapridae—*Merriamoceros*; Mylagaulidae—*Promylagaulinae* (*Galbreathia*).

In the type area at the Barstow Syncline, the Ba1 biochron is represented by two biozones: the *Plithocyon barstowensis*/*Aelurodon asthenostylus* Interval Zone, and the *Aelurodon asthenostylus*/*Ramoceros brevicornis* Interval Zone.

Plithocyon barstowensis/*Aelurodon asthenostylus* Interval Zone

Definition—Interval from the LO of *Plithocyon barstowensis* Frick 1926 to the LO of *Aelurodon asthenostylus* Henshaw 1942 (Figs. 2–3).

Characterization—The *P. barstowensis*/*A. asthenostylus*

interval zone contains the following lowest local stratigraphic occurrences of taxa: Canidae—*Cynarctoides acridens*, *Paracynarctus kelloggi*, *Microtomarctus conferta*, *Tomarctus hippophaga*; Procyonidae—*Probassariscus antiquus*; Ursidae—*Plithocyon barstowensis*; Amphicyonidae—*Amphicyon ingens*; Mustelidae—*Plionictis ogygia*; Felidae—*Pseudaelurus interpidus*; Equidae—*Hypohippus affinis*, *Acritohippus styodontus*, *Scaphobippus sumani*; Tayassuidae—*Dyseohyus fricki*; Dromomerycidae—*Rakomeryx raki*; Antilocapridae—*Merriamoceros coronatus*.

This IZ contains the following highest local stratigraphic occurrences of these taxa: Canidae—*Osbornodon fricki*, *Cynarctoides acridens*, *Euoplocyon brachygnathus*; Amphicyonidae—*Pliocyon medius*; Merycoidodontidae—*Brachycrus laticeps*; Camelidae—*Paramiolabis singularis*; Dromomerycidae—*Rakomeryx raki*; Antilocapridae—*Merriamoceros coronatus*.

Stratigraphic interval—The *P. barstowensis*/*A. asthenostylus* IZ encompasses the stratigraphic interval of the Barstow Formation from Steepside Quarry (approximately thirty-five meters below the Oreodont Tuff) to Valley View Quarry (about 100 meters below the Skyline Tuff) (Figs. 1, 3).

Geochronologic age—The *P. barstowensis*/*A. asthenostylus* IZ is bracketed by two geochronologic dates. The earliest is from the Oreodont Tuff, with a geochronologic age of 15.88 ± 0.06 Ma. The latest is from the Valley View Tuff, dated to 15.27 ± 0.03 Ma (Woodburne 1996). As such an approximate age for this IZ can be estimated from 16–15.2 m.y.

Correlation to other North American sequences—The *P. barstowensis*/*A. asthenostylus* IZ contains a fossil assemblage equivalent to that of the Mascall Formation of Oregon and the Lower Snake Creek “Fauna” (Olcott Formation) of Nebraska. These biochronologic correlations are based on the shared occurrence of several key taxa, including *Euoplocyon brachygnathus*, *Cynarctoides acridens*, *Tomarctus hippophaga*, *Acritohippus*, *Dromomeryx* and *Scaphobippus sumani* (Downs 1956, Tedford et al. 2004, Curasco et al. 2005, Pagnac 2005a, 2006).

Aelurodon asthenostylus/*Ramoceros brevicornis* Interval Zone

Definition—Interval between the LO of *Aelurodon asthenostylus* Henshaw 1942 to the LO of *Ramoceros brevicornis* Frick 1937 (Fig. 3).

Characterization—The *A. asthenostylus*/*R. brevicornis* Interval Zone contains the following lowest local stratigraphic occurrences of taxa: Canidae—*Cynarctus galushai*, *Tomarctus brevirostris*, *Aelurodon asthenostylus*; Tayassuidae—*Cynorca occidentale*. This IZ also contains the following highest local stratigraphic occurrences of these taxa: Canidae—*Tomarctus hippophaga*; Camelidae—*Michenia mudhillsensis*; Tayassuidae—*Cynorca occidentale*.

Stratigraphic interval—The stratigraphic range of this IZ corresponds to approximately the lower two-thirds of the Frick Second Division unit (Woodburne et al. 1990). It

extends from the stratigraphic level of Valley View Quarry (about 100 meters below the Skyline Tuff) to Skyline Quarry (about 1 meter below the Skyline Tuff) (Figs. 1, 3).

Geochronologic age—The base of this IZ corresponds to the stratigraphic level of Valley View Quarry. The age can be determined based on the close proximity of Valley View Quarry to the Valley View Tuff, with a radioisotopic date of 15.27 ± 0.03 Ma (Woodburne 1996). Thus, the base of the *A. asthenostylus*/*I. gidleyi* IZ corresponds to a radioisotopic date of approximately 15.2 Ma, as it occurs slightly above the Valley View Tuff. The top of this IZ corresponds to the stratigraphic level of Skyline Quarry, near the Skyline Tuff. Accurate geochronologic dates cannot be obtained from the Skyline Tuff, but based on close proximity to the Dated Tuff, with an age of 14.8 ± 0.06 Ma, the top of this zone is estimated at an age of 15.0 m.y.

Correlation to other North American sequences—The *A. asthenostylus*/*R. brevicornis* IZ contains a fossil assemblage with two notable taxa. The first is the tayassuid *Cynorca occidentale*. Occurrences of *C. occidentale* are limited to assemblages such as that of the Temblor Formation of central California (Woodburne 1969) and the Caliente Formation (James 1963) of southern California. The second is the occurrence of the “pliohippine” equid, *Acritohippus styliodontus*. *A. styliodontus* is most commonly found in faunal assemblages such as that of the Bopesta Formation (Quinn 1987, Kelly 1998) and the Punchbowl Formation (Reynolds 1991), both from southern California. Additionally, this biozone contains the notable lack of any taxa defining or characterizing the Ba2 biochron, such as *Megahippus mckennai*, or *Ramoceros brevicornis* (see comments below).

New definition and characterization of the Ba2

Definition—The base of the Ba2 biochron is revised in this study based on the first appearance of the antilocaprid *Ramoceros*. Tedford et al. (2004) additionally define the base of the Ba2 biochron based on the first appearance of the following taxa: Erinaceidae—*Lanthanotherium*, *Untermanerix*; Mustelidae—*Pliogale*; Amphicyonidae—*Pseudocyon*; Ochotonidae—*Hesperolagomys*, *Russellagus*; Zapodidae—*Megasminthus*.

Characterization—Tedford et al. (2004) characterize the Ba2 biochron on the first appearances of these taxa: Canidae—*Cynarctus saxatilis*, *Aelurodon ferox*; Ursidae—*Ursavus pawniensis*; Amphicyonidae—*Ischyrocyon*; Equidae—*Pliohippus mirabilis*, *Pseudhipparion*, *Neohipparion coloradense*, *Cormohipparion*; Merycoidodontidae—*Ustatochoerus medius*; Moschidae—*Longirostromeryx*; Dromomerycidae—*Procranioceras*; Leporidae—Leporinae (*Alilepus*, *Promotolagus*); Mylagaulidae—*Mylagaulus*; Castoridae—*Eucastor*; Geomyidae—*Lignimus*; Eomyidae—*Leptodontomys*; Cricetidae—*Trogomys*. Tedford et al. (2004) utilized two characteristic first appearance taxa for the Ba1 biochron, the borophagine canid *Protepicyon* and the anchitherine equid *Megahippus*, that in this study characterize the Ba2.

In the type area, the Ba2 biochron is represented by two biozones, the *Ramoceros brevicornis*/*Megahippus mckennai* Interval Zone and the *Megahippus mckennai*/*Merycodus necatus* Interval Zone.

Ramoceros brevicornis/*Megahippus mckennai* Interval Zone

Definition—Interval between the LO of *Ramoceros brevicornis* Frick 1937 to the LO of *Megahippus mckennai* Tedford and Alf 1962 (Fig. 3).

Characterization—The *R. brevicornis*/*M. mckennai* IZ contains the following lowest local stratigraphic occurrences of these taxa: Canidae—*Paratomarctus temerarius*, *Protepicyon raki*; Amphicyonidae—*Ischyrocyon gidleyi*; Equidae—*Archaeohippus mourningi*, *Scaphohippus intermontanus*; Camelidae—*Miolabis fissidens*; Antilocapridae—*Ramoceros brevicornis*. This IZ also contains the highest local stratigraphic occurrences of the following taxa: Camelidae—*Miolabis fissidens*; Equidae—*Archaeohippus mourningi*, *Acritohippus styliodontus*; Tayassuidae—*Hesperhys* sp.

Stratigraphic interval—This IZ corresponds to about the upper one-third of the Frick Second Division unit. It extends from the stratigraphic level of Skyline Quarry (about 1 meter below the Skyline Tuff, to the level of New Year Quarry) to about 20 meters above the Skyline Tuff (Figs. 1, 3).

Geochronologic age—The *R. brevicornis*/*M. mckennai* IZ begins at the level of Skyline Quarry, with an estimated age of approximately 15.0 m.y. The top of this IZ is defined at the stratigraphic level of New Year Quarry, stratigraphically just below the Dated Tuff, with a geochronologic age of 14.8 ± 0.06 Ma.

Correlation to other North American sequences—The faunal assemblage from the *R. brevicornis*/*M. mckennai* IZ is difficult to correlate with other North American assemblages. It represents a very narrow stratigraphic interval and corresponds to a very short time period, and also represents a notable gap in preservation of the Barstovian record elsewhere. Based on the occurrence of *Ramoceros*, this IZ correlates to the lowermost portions of the Pojoaque Member of the Tesuque Formation of New Mexico (Frick 1937). Based on the occurrence of the borophagine canid *Protepicyon*, this IZ correlates to portions of the Zia Formation in New Mexico (Wang et al. 1999). The shared occurrence of *Miolabis fissidens* indicates that this IZ likely correlates to the lowermost portions of the Pawnee Creek Formation in Colorado (Carrasco et al. 2005).

Megahippus mckennai/*Merycodus necatus* Interval Zone

Definition—Interval between the LO of *Megahippus mckennai* Tedford and Alf 1962, and the HO *Merycodus necatus* Leidy 1854 (Fig. 3).

Characterization—The *M. mckennai*/*M. necatus* IZ is characterized by the lowest local stratigraphic occurrence of the following taxa: Equidae—*Megahippus mckennai*;

Merycoidodontidae—*Mediochoerus mojavensis*; Antilocapridae—*Cosoryx furcatus*; Proboscidea—*Gomphotherium* sp., *Zygodon* sp. The *M. mckennai*/*M. necatus* IZ extends to the uppermost deposits and localities in the Barstow Formation. Thus, all megafaunal taxa with ranges within this zone have a HO within this zone (Fig. 3).

Stratigraphic Interval—This IZ corresponds to the Frick First Division unit or the Barstow faunal unit of Woodburne et al. (1990). It extends from the level of New Year Quarry (about 20 meters above the Skyline Tuff) to the stratigraphic level of several quarries (RV 6126, UCMP V6447) near the level of the Lapilli Tuff.

Geochronologic age—The *M. mckennai*/*M. necatus* IZ is demarcated at its base by the Dated Tuff with a geochronologic age of 14.8 ± 0.06 Ma. The Lapilli Tuff occurs very near the uppermost exposures of the Barstow Formation, and has been radioisotopically dated to 13.4 ± 0.2 Ma.

Correlation to other North American sequences—Based on the shared occurrence of *Megahippus* and *Cosoryx*, the *M. mckennai*/*M. necatus* IZ correlates to portions of the Pojoaque Member of the Tesuque Formation in New Mexico and the Pawnee Creek Formation in Colorado (Carrasco et al. 2005). Based on the shared occurrence of *Paratomarctus temerarius* and *Ramoceros*, this IZ likely correlates to the Crookston Bridge Member of the Valentine formation in Nebraska (Wang et al. 1999, Carrasco et al. 2005).

Remarks—Further subdivision of the *M. mckennai*/*M. necatus* IZ was attempted. Figure 3 shows a significant loss of taxa near the level of the Hemicyon Tuff, dated to 14.0 ± 0.1 Ma (Woodburne et al. 1990, Woodburne 1996). Ultimately, further subdivision of the upper member of the Barstow Formation was not possible because the loss of so many megafaunal taxa is likely an artifact of collection practices. There are few megafossil localities above the level of the Hemicyon Tuff, and almost none in the uppermost levels of the Barstow Formation. Most localities above this level are UCMP localities collected for microvertebrate fossils by Everett Lindsay. The loss of many megafaunal taxa is likely due to a lack of adequate sampling for large mammals at the uppermost portions of the Barstow Formation.

Aside from the loss of taxa near the Hemicyon Tuff, the *M. mckennai*/*M. necatus* Interval Zone exhibits stasis in taxonomic composition. This is in sharp contrast to the high degree of taxonomic change reported by Lindsay (1972). Lindsay was able to subdivide the upper member of the Barstow Formation into three microfossil zones (Fig. 2). The disparity between taxonomic compositions presents an interesting problem that warrants further investigation. Due to a wealth of new microvertebrate data collected since Lindsay's work in the 1970s, an updated analysis is warranted so that comparisons with the megafossil data are possible.

DISCUSSION

Tedford et al. (2004) define the base of the Barstovian interval by the first appearance of the ursid *Plithocyon* and

the mastodon *Zygodon*. Although the Proboscidea no longer has utility as a defining taxon, *Plithocyon* continues to be a valid taxon for recognizing the base of the Barstovian interval with a LO at Steepside Quarry. Thus, the beginning of the Barstovian NALMA corresponds to the base of the *P. barstowensis*/*A. asthenostylus* Interval Zone.

Four taxa are useful in recognizing the local Ba1 interval: the borophagine canid *Euoplocyon brachygnathus*, the antilocaprid *Merriamoceros coronatus*, the oreodont *Brachycrus laticeps*, and the "pliohippine" equid *Acritohippus stylodontus*. These taxa are all characterized by a LOD in the Ba1 interval.

The borophagine canid *Aelurodon* shows excellent promise as a defining taxon for the Barstovian NALMA, with a continent-wide FOD at this time. However, the LO of *Aelurodon* in the Barstow Formation is at Valley View Quarry, much higher stratigraphically than Steepside Quarry (and at an estimated geochronologic age of approximately 15.2 Ma). Once earlier occurrences of *Aelurodon* can be positively identified in the Barstow Formation, this genus will serve as a very useful defining taxon.

Tedford et al. (2004) define the base of the late Barstovian (Ba2) biochron with the first appearance of gomphotheriid proboscideans. The lowest occurrence of *Gomphotherium* in the Barstow Formation is near the level of New Year Quarry, just below the Dated Tuff (14.8 Ma). As stated above, Proboscidea is no longer a valid taxon for defining the base of the Ba1 or Ba2 interval. Instead, I utilize the antilocaprid *Ramoceros brevicornis* to define the base of the Ba2 interval.

Current definitions of the Barstovian NALMA divide it into an early (Ba1) and late (Ba2) interval (Tedford et al. 2004). This twofold temporal delineation was the highest resolution available based on earlier taxonomy. Outdated megafaunal systematics coupled with the continued usage of Frick lithologic divisions to distinguish "faunas" has limited the division of the type Barstovian assemblage to two biochronologic intervals. At the time, the only biostratigraphic data available were the preliminary ranges published by Tedford (1966) which allowed for only two biochronologic subdivisions. The new biostratigraphy proposed in this study allows for up to four biochronologic subdivisions of the Barstovian NALMA, potentially a doubling of the temporal resolution and correlative utility (each of these four biostratigraphic zones could be converted to a biochronologic subdivision). However, the NALMA system is designed to have utility on a continent-wide scale, and further subdivision of the Barstovian at this time would be premature. The revised biostratigraphy and biochronology of the Barstow Formation and type Barstovian assemblage must now be compared with other correlative units to ascertain if a four-fold subdivision of the Barstovian interval will be applicable to other assemblages of equivalent age. Additionally, systematic and biostratigraphic updates to the microfauna are imperative before further subdivisions of the Barstovian can be applied.

The Barstow Formation in the Mud Hills does not represent the entire time span encompassed by the Barstovian

NALMA. The uppermost megafaunal localities are near the stratigraphic level of the Lapilli Tuff (13.4 ± 0.02 Ma). As such, the base of the Clarendonian NALMA, currently defined with the first appearance of *Pseudoceras* (Tedford et al. 2004) at ca 12.4 Ma, is not recorded. While outlying exposures of the Barstow Formation, such as those in the West Cronese Basin, may record this boundary, stratigraphic correlations with the type area are tentative at best. Extensive collections from this basin are lacking.

The Clarendonian NALMA was originally defined based on the Clarendon local fauna from the Texas Panhandle (Wood et al. 1941). Tedford et al. (2004) defined the base of the CII biochron within the Clarendonian NALMA on the first appearance of the gelocid *Pseudoceras*. The CII biochron is characterized by Tedford et al. (2004) by the first appearance of the beavers *Eucastor planus* and *E. dividerus*; the gomphotheriid proboscideans *Eubelodon* and *Megabelodon*; the borophagine canids *Cynarctus voorhiesi*, *Aelurodon stirtoni*, and *Paratomarctus euthos*; the equids *Pliohippus permix*, *Cormohipparion occidentale*, *Pseudhipparion retrosum*, *Protohippus supremus*, and *Megahippus matthewi*; the oreodont *Ustatochoerus major*; and the dromomerycid *Cranioceras*. Tedford et al. (2004) estimated an age for the base of the CII biochron at 12.4 Ma.

The Dove Spring Formation, at the southern end of the Sierra Nevada range in central California, was one of the Wood Committee's principal correlatives for the original Clarendonian type area. Whistler and Burbank (1992) describe the biostratigraphy and biochronology of the Dove Spring Formation in detail. The lowermost faunal unit of the Dove Spring Formation, the Iron Canyon Fauna, contains elements equivalent to the latest Barstovian Burge Fauna from the Valentine Formation in Nebraska. Contemporary interpretations (Whistler and Burbank 1992, Woodburne 2006) place an age of approximately 12.5 Ma on the lowermost sediments of the Dove Spring Formation. Based on geochronologic and biostratigraphic data, Woodburne (2006) placed the base of the Cerrotejonian stage and the base of the Clarendonian NALMA at the same temporal point, 12.4 Ma, and suggested the first appearance of the antilocaprid *Paracosoryx furlongi* be employed as a defining taxon.

Lindsay (1972) defined an uppermost biozone in the Barstow Formation based on the occurrence of *Copemys russelli*. Whistler and Burbank (1992) note the occurrence of *C. russelli* in the Iron Canyon Fauna, from the lowermost exposures of the Dove Springs Formation. This co-occurrence confirms the close biostratigraphic and faunal affinity of the uppermost Barstow Formation and the lowermost Dove Spring Formation.

Woodburne (2006) outlined in detail the geochronologic age of the Dove Spring Formation, the lowermost portion of which closely corresponds to the 12.4 Ma age for the Barstovian/Clarendonian boundary. Although *Pseudoceras* does not occur in the Dove Spring Formation, the LO of the antilocaprid *Paracosoryx furlongi* and the oreodont *U-*

tatochoerus major (= *Ustatochoerus* cf. *profectus*) corresponds to a geochronologic age of about 12.5 Ma. Woodburne suggested utilizing *P. furlongi* as a defining taxon for the base of the Clarendonian. Tedford et al. (2004) recommended utilizing the oreodont *Ustatochoerus major* as a potential defining taxon for the base of the Clarendonian NALMA.

With regard to the Barstow Formation, comparison with the basal units of the Dove Spring Formation reveals an approximately one-million-year gap between the uppermost exposures of the Barstow Formation and the lowermost exposures of the Dove Spring Formation. At the type area in the Mud Hills, the last one m.y. of the Barstovian NALMA, and hence the Barstovian/Clarendonian boundary, are not recorded. As such, the *Megahippus mckennai*/*Merycodus necatus* Interval Zone may not be the last potential megafaunal zone for the Barstovian. This stratigraphic and temporal gap will need to be filled by examining outlying exposures of the Barstow Formation (and searching for new occurrences of *Paracosoryx furlongi* and/or *Ustatochoerus major*) coupled with biochronologic correlation with assemblages such as that from the Dove Spring Formation.

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APPENDIX I

Plithocyon barstowensis/Aelurodon asthenostylus
Interval Zone**Lowest occurrences**

- Cynarctoides acridens*: F:AM 27539 (Wang et al. 1999), Sandstone Quarry
- Paracynarcus kelloggi*: Six F:AM specimens (Wang et al. 1999), Steepside Quarry
- Microtomarctus conferta*: Five F:AM specimens (Wang et al. 1999), Steepside Quarry
- Tomarctus hippophaga*: Forty-seven F:AM specimens (Wang et al. 1999), Steepside Quarry
- Bassariscus antiquus*: F:AM 27497 (F:AM collections), Steepside Quarry
- Amphicyon ingens*: F:AM 50070 (F:AM collections), Steepside Quarry
- Plithocyon* (= *Hemicyon*) *barstowensis*: F:AM 50062, 50063 (F:AM collections), Steepside Quarry
- Plionictis ogygia*: F:AM 50130 (F:AM collections), Steepside Quarry
- Pseudaelurus interpidus*: Two cranial specimens (Rothwell 2003), Steepside Quarry
- Acritohippus* (= *Atavahippus*) *stylodontus*: F:AM 142489 (F:AM collections), Steepside Quarry
- Scaphobippus sumani*: Abundant dental material (UC Riverside collections), RV 4701
- Dyseobryus fricki*: F:AM 73670 (Woodburne 1969), Steepside Quarry
- Rakomeryx raki*: F:AM 31353 (large collection of cranial material, Frick 1937), Steepside Quarry
- Merriamoceros coronatus*: Thirteen F:AM specimens (Frick 1937), Steepside Quarry

Highest occurrences

- Osbornodon fricki*: F:AM 67066 (Wang 1994), Oreodont Quarry
- Cynarctoides acridens*: F:AM 27539 (Wang et al. 1999), Sandstone Quarry
- Euoplocyon brachygnathus*: Six specimens (Wang et al. 1999), Steepside Quarry
- Pliocyon medius*: F:AM 27503 (F:AM collections), Camp Quarry
- Brachycrus laticeps*: F:AM 42379 (F:AM collections), Deep Quarry
- Paramiolabis singularis*: F:AM 23649 (F:AM collections), Sandstone Quarry
- Rakomeryx raki*: F:AM 31329 (Frick 1937), Oreodont Quarry
- Merriamoceros coronatus*: Thirteen F:AM specimens (Frick 1937), Steepside Quarry

Aelurodon asthenostylus/Ramoceros brevicornis
Interval Zone**Lowest occurrences**

- Cynarctus galushai*: F:AM 27542 (Wang et al. 1999), Valley View Quarry
- Tomarctus brevirostris*: Seven F:AM specimens (Wang et al. 1999), Valley View Quarry
- Aelurodon asthenostylus*: Five F:AM specimens—F:AM 27538, 27544, 31100, 67976, 67986, Valley View Quarry
- Cynorca occidentale*: F:AM 73660 (Woodburne 1969), Valley View Quarry

Highest occurrences

- Tomarctus hippophagus*: F:AM 61213 (Wang et al. 1999), Sunder Ridge Quarry
- Michenia mudhillsensis*: F:AM 62257 (Pagnac 2005b), Saucer Butte Quarry
- Cynorca occidentale*: F:AM 73660 (Woodburne 1969), Valley View Quarry

Ramoceros brevicornis/Megahippus mckennai
Interval Zone**Lowest occurrences**

- Ramoceros brevicornis*: F:AM 31348 (Frick 1937), Skyline Quarry
- Ischyrocyon gidleyi*: F:AM 50089 (Hunt 1998; F:AM collections), Hailstone Quarry
- Protepicyon raki*: F:AM 31103 (Wang et al. 1999), Skyline Quarry
- Archaeohippus mourningi*: UCR 11294 (UCR collections), RV 6121 (stratigraphically equivalent to Starlight Quarry)
- Scaphobippus intermontanus*: AMNH 140702 (Pagnac 2006), Skyline Quarry
- Miolabis fissidens*: F:AM 27305 (F:AM collection), Falkenbach Horse Quarry (immediately below Skyline Tuff)

Highest occurrences

- Miolabis fissidens*: F:AM 27305 (F:AM collection), Falken-

bach Horse Quarry (immediately below Skyline Tuff)

Archaeohippus mourningi: UCMP 19840 (Merriam 1913), UCMP V2058

Acritohippus stylodontus: F:AM 142498 (F:AM collections); New Year Quarry

Megahippus mckennai/*Merycodus necatus*

Interval Zone

Lowest occurrences

Megahippus mckennai: RAM 6500 (Tedford and Alf

1962), UCR V3696

Mediochoerus mojavenis: F:AM 34464 (Schultz and Falkenbach 1941 (= *Ustatochoerus medius mojavenis*)), Hemicyon Quarry

Cosoryx furcatus: Five horncore specimens (Frick 1937), New Year Quarry

Gomphotherium sp.: F:AM 20850 (F:AM collections), Hemicyon Quarry

Zygodon sp.: F:AM 126896 (F:AM collections), approximate stratigraphic level of New Year Quarry