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## A REVIEW OF LATE EOCENE MAMMALIAN FAUNAS FROM NORTH AMERICA

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**ABSTRACT.** The late Eocene-early Oligocene was a time of major changes in the composition and character of mammalian faunas. Broadly, the transition from archaic to modern eutherian families occurred at this time. This is a review of the main North American localities in which late Eocene mammalian faunas have been found and of the general faunal developments during the late Eocene. Major changes included the disappearance of several archaic carnivore and ungulate groups, decline of perissodactyls, the late dominance of protrogomorph rodents, beginning of a major radiation of artiodactyls, and progressive changes in several orders leading toward the appearance of more advanced families either in the late Eocene or early Oligocene. Correlation of the main upper Eocene mammal-bearing localities is discussed.

### INTRODUCTION

Vertebrate paleontologists have long recognized that North American mammalian development during the Cenozoic can be divided into two broad phases. The first occurred during the early Cenozoic—the Paleocene and Eocene—and involved the dominance of a variety of archaic mammals living together with other groups that led into the more advanced and persistent families of the second phase. This second phase began sometime during the late Eocene and resulted in the extinction and replacement of the earlier assemblages by families that have either survived into the Recent or were of a generally more modern aspect than the archaic forms. In the study of group after group of mammals, attention is shifted to the late Eocene-early Oligocene, an interval spanning ten to twelve million years, for evidence on extinction of some groups and origin of others.

The importance of the late Eocene and early Oligocene in the history of mammalian development is shown by the fact that out of 122 living mammalian families, 30 are known first in deposits of this interval. Thus, during this time about 25 percent of the Recent fauna differentiated at the family level from more primitive relatives. When the total number of fossil and Recent mammalian families, 273 recognized at present, is compared to the number of families appearing in the late Eocene and early Oligocene, 71, one finds that about 26 percent of the total number of mammalian families are first recorded from this interval. If those families confined to the Mesozoic and those having either no fossil record or only a Pleistocene occurrence are omitted, 31 percent of the living families appeared during the late Eocene and early Oligocene. Among the newcomers were such families as the Talpidae, Soricidae,

Pongidae, Leporidae, Aplodontidae, Cricetidae, Canidae, Felidae, Viverridae, Suidae and Camelidae. In view of the incomplete state of our knowledge of late Eocene and early Oligocene faunas in Africa and Asia, the first appearance of 31 percent of the Recent families that have a Tertiary fossil record makes this interval a time of considerable significance in mammalian history. The graphic view presented in figure 1 of times of first and last appearance of therian families illustrates clearly the magnitude of the changes during this interval relative to changes at other times from Cretaceous to Recent.

The late Eocene-early Oligocene interval was marked also by a high rate of exchange of mammals between Eurasia and North America, in contrast to lower rates of exchange in the middle Eocene and middle Oligocene (Simpson, 1947). Contact of previously isolated mammalian groups resulting from these exchanges was surely an important factor leading toward some of the faunal changes of the interval. Paleobotanical evidence indicates that the interval was characterized by changes in the floras also. Fossil floras of the early Oligocene show that climatic con-

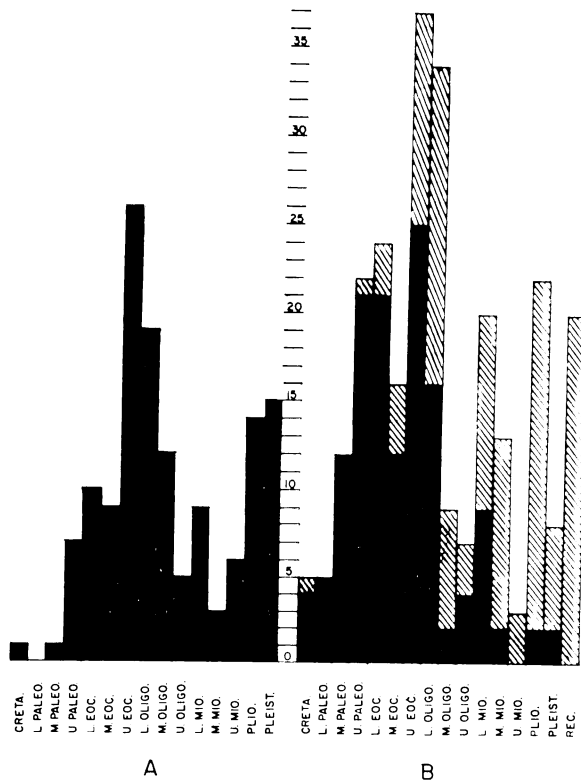


Fig. 1. Families of Cretaceous to Recent therian mammals. A. Times of last appearance by family. B. Times of first appearance by family. Solid lines indicate extinct families; diagonal hatching, extant families.

ditions in temperate regions were becoming cooler and drier, as opposed to the warmer, wetter climates of the Eocene (MacGinitie, 1958, p. 66). The late Eocene-early Oligocene is thus characterized by interrelated changes—paleogeographic, climatic, and biotic.

Our attention was drawn to the late Eocene and early Oligocene by interest in fossil rodents, which reflect, as do many of the larger, more spectacular mammals, glimmers of modernization late in the Eocene. A review of previous studies, examination of collections, and field work in the upper Eocene soon made it apparent that details of the transition from primitive to advanced rodents remain to be established, as do similar details for many other orders, and that a review of North American late Eocene mammalian faunas would be appropriate at this time. Accordingly, this review of North American late Eocene is intended to bring together currently known evidence on the beginnings of a time of transition among mammals and to furnish a basis from which further work may be undertaken. It is not intended here to revise any one fauna or mammalian group nor to establish any new standard for correlation of deposits.

It is encouraging that the attention of several North American, European, and Asian colleagues also is devoted to the late Eocene. Most notable among current North American studies of fossil mammals are those of J. A. Wilson on late Eocene and Oligocene faunas in Texas and W. D. Turnbull on the earliest late Eocene in southern Wyoming. Other work is underway in other parts of the world with activity especially marked in China, Mongolia, France, Switzerland, and Spain (fig. 2).

#### PRESENT DISTRIBUTION OF UPPER EOCENE DEPOSITS IN NORTH AMERICA

Known upper Eocene non-marine, mammal-bearing deposits in North America (fig. 3) contrast with those of the lower and middle Eocene and of the Oligocene in several ways. Lower and middle Eocene deposits occur fairly extensively in basins along the Rocky Mountain chain. Many of these deposits represent stream channel and flood plain deposition, but extensive lakes were present in southwestern Wyoming, northwestern Colorado, and northwestern Utah, where thick sequences of fine grained deposits accumulated. Upper Eocene deposits most comparable to the extensive basin fills of the lower and middle Eocene along the Rocky Mountain chain are those of the Uinta Basin of Utah and the Washakie Basin of Wyoming. In the Wind River Basin of Wyoming upper Eocene deposits were undoubtedly more widespread formerly than at present but now occur only peripherally in the Basin. Local patches of upper Eocene deposits occur farther north, in Montana (Robinson, G. D., 1963) and Saskatchewan (Russell and Wickenden, 1933). To the south, volcanic rocks have protected from removal upper Eocene deposits of the Galisteo Formation, south of Santa Fe in New Mexico (Stearns, 1943, p. 309), the lower part of the Vieja Group of the Big Bend area of Texas (DeFord, 1958), and the lower part of the

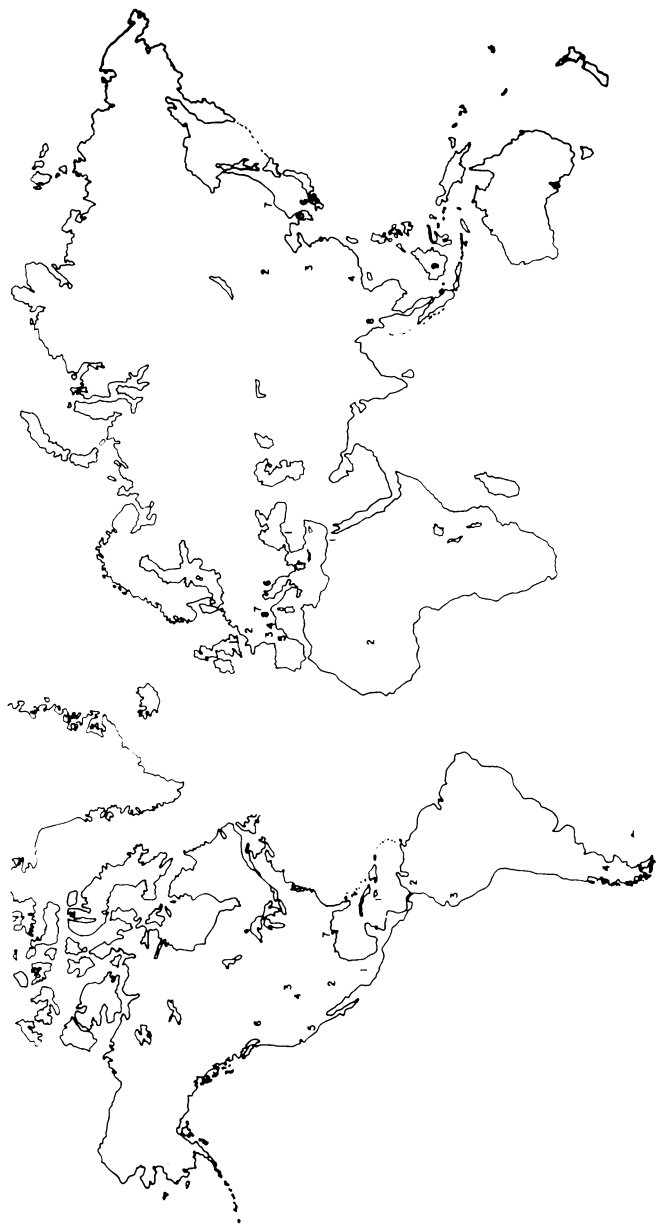


Fig. 2. Areas of major late Eocene mammal-bearing deposits of the world.

- North America: 1. Guanajuato, Mexico; 2. Vieja Group, Texas; 3. Wind River Basin, Wyoming; 4. Uinta Basin, Utah; 5. Sespe formation, California; 6. Kishenchin, British Columbia; 7. Clarke County, Mississippi.
- Europe: 1. England—Isle of Wight, Hampshire Basin; 2. France—Paris Basin and vicinity; 3. France—Aquitanian region; 4. France—Southeastern area; 5. Spain—Sosis; 6. Jugoslavia—Mt. Promina; 7. Germany—Ulm; 8. Switzerland—Mormont (note: these are all Bartonian or early Ludian).
- Africa: 1. Egypt—Fayum; 2. French West Africa—in Tafidet.
- Asia: 1. Turkey—Celtek; 2. Mongolia—Jrdin Manha, Shara Murun, Ulan Shireh; 3. China, north; 4. China, south; 5. Korea—Hosan; 6. Japan—Ube; 7. Eastern USSR—Vladivostok; 8. Burma—Pondaung; 9. Borneo—Melawi.
- South America: 1. Jamaica—Chapelton; 2. Colombia—Tama; 3. Peru—Chiococa; 4. Argentina—Musters.

Chisos Mountain Group of Big Bend National Park, Texas (J. A. Wilson, personal communication, Nov. 1965). But upper Eocene deposits far removed from the region of earlier Eocene intermontane basins are known as well. Non-marine, mammal-bearing deposits occur interbedded with marine deposits in thick sequences of rock in southern California (Savage and Downs, 1954, p. 43-45). River deposits in Mississippi have

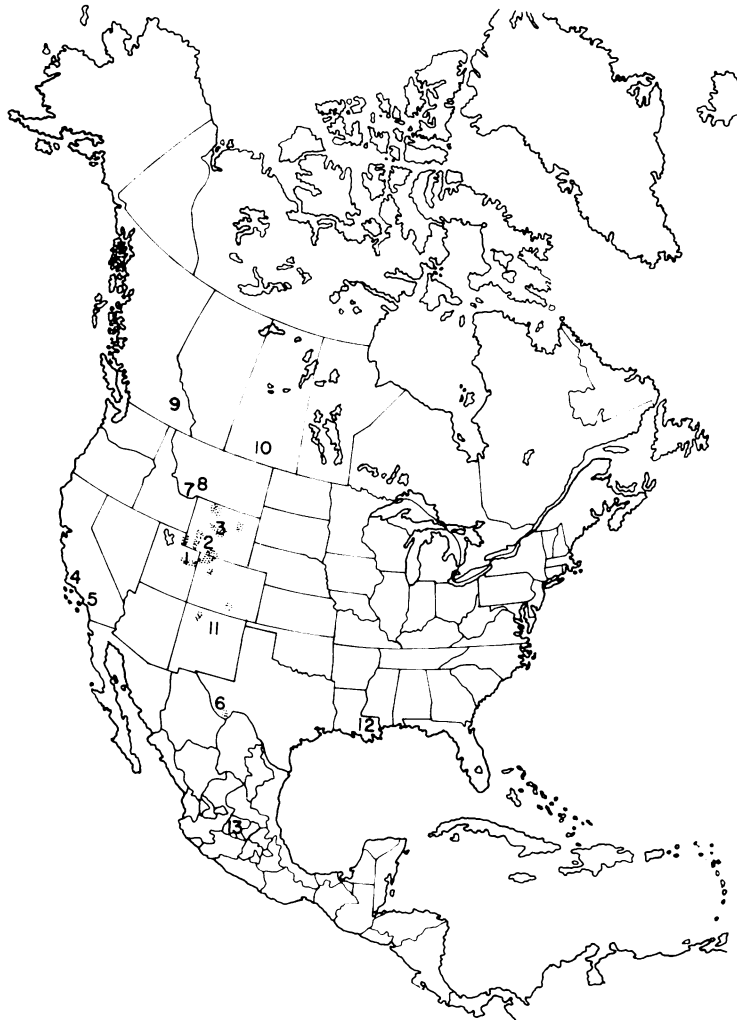


Fig. 3. Eocene mammal-bearing deposits of North America. Stippled areas of main early and middle Eocene deposits. Numbers, main late Eocene localities: 1. Uinta Basin, Utah; 2. Washakie Basin, Wyoming; 3. Wind River Basin, Wyoming; 4. Sespe formation and 5. Poway Conglomerate, California; 6. Vieja Group, Texas; 7. Sage Creek and 8. Climbing Arrow formation, Montana; 9. Kishenehn, British Columbia (? possibly Oligocene); 10. Swift Current Creek, Saskatchewan; 11. Galisteo, New Mexico; 12. Clarke County, Mississippi; 13. Guanajuato, Mexico (or early Oligocene?).

produced a mammal probably of late Eocene age (Gazin and Sullivan, 1942). Deposits of probable late Eocene age are reported from the Guanajuato region of Mexico (Fries, Hibbard, and Dunkle, 1955). Fossiliferous upper Eocene non-marine deposits occur from 22° to 50° north latitude and from 91° to 120° west longitude. Admittedly, the easternmost and southernmost of these deposits have produced only scanty faunas so far but nonetheless, the geographic areas sampled do present a greater spread than do older Eocene deposits and thus may provide more information on ecological diversity and intracontinental dispersal of mammals than can be obtained from earlier Eocene mammalian fossils.

Oligocene deposits present a different picture from those of the Eocene. Laid down largely as broad sheets of flood plain deposits, they are especially well represented by badland areas in eastern Montana, Colorado, and Wyoming, and in western North and South Dakota and Nebraska.

The somewhat scattered nature of upper Eocene deposits as now presented as opposed to the broad basin deposits of the lower and middle Eocene or the extensive badland areas of the Oligocene was probably responsible, in part, for neglect of the upper Eocene by earlier bone hunters. Early exploration led to discovery of the relatively widespread and well-exposed deposits in the Uinta and Washakie Basins, but discovery of the more local deposits did not come until the 20th Century.

#### HISTORY OF DISCOVERIES OF LATE EOCENE FAUNAS

*The Uinta Basin.*—The most adequately represented late Eocene faunas in North America are those derived from the Uinta Formation in the Uinta Basin of northwestern Utah. These deposits and their faunas have been used as the basis for subdivision of the late Eocene into Uintan and Duchesnean ages (Wood, H. E., and others, 1941, p. 10). Exploration of these deposits by vertebrate paleontologists was initiated by O. C. Marsh and personnel of the Yale College Scientific Party of 1870, who made collections of Eocene mammals primarily from badlands along Utah's White River. The faunas were originally regarded by Marsh (1871, p. 196) as being equivalent in age to those from the Bridger Basin of southwestern Wyoming. Princeton University sent an expedition to the Uinta Basin in 1886, and the American Museum of Natural History had fossil collecting parties under O. A. Peterson there in 1893, 1894, and 1895. By 1889 it had been recognized that the Uinta Basin fossils were younger than those of the Bridger Basin, and the deposits were considered to be uppermost Eocene and below the "White River Miocene" (Scott, *in* Scott and Osborn, 1890, p. 466). Later, in Osborn's report (1895, p. 72-74) of the American Museum's expeditions, Peterson suggested a three-fold subdivision of the fossiliferous beds into Uinta "horizons" A, B, and C. Lithologic characters were mentioned, but nature

of the faunas formed the basis upon which these subdivisions were established.

After an interval of about thirteen years, during which major collections were not made in the upper Eocene of the Uinta Basin, Carnegie Museum began expeditions there in 1908 (Douglass, 1910), and the Field Museum of Natural History had a party in the Basin, mostly in Uinta A and B, in 1910 (Riggs, 1912). Carnegie Museum field parties of 1929 and 1930 discovered in the uppermost red beds, which had been referred in part to the Uinta C, fossils of a younger aspect than those of Uinta C, and these were considered by Peterson and Kay (1931) to be post-Eocene, or basal Oligocene, in age. These upper beds, named Duchesne by Scott and emended to Duchesne River by Kay (1934), were divided by Kay into successively higher Randlett, Halfway, and Lapoint "horizons".

In 1934 Uinta A and B were united as the Wagonhound Member, and Uinta C termed the Myton Member (Wood, H. E., 1934, p. 242). Wagonhound and Myton faunal elements form the basis for the Uintan age (Wood, H. E., and others, 1941). Faunal distinctions between the Randlett, Halfway, and Lapoint "horizons" were discussed by Scott (1945). The Randlett has a fauna showing some similarity to that of the Myton Member (Uinta C), the Halfway is sparsely fossiliferous, and the Lapoint yields a more advanced fauna than do lower levels. These faunas form the basis for the North American Duchesnean age, the latest Eocene (Wood, H. E., and others, 1941; Simpson, 1946).

*The Washakie Basin.*—Mammalian fossils were discovered in the Washakie Formation in the Washakie Basin in 1872. One of the finds was quickly brought to the attention of paleontologists when Cope (1872) telegraphed to Philadelphia the news of finding a uintathere in the Basin. Collections were made for both Cope and Marsh for several seasons subsequent to this initial discovery. In 1878 the Princeton Expedition obtained a collection from the relatively unfossiliferous upper beds of the Washakie. Until Osborn's report of 1881 the Washakie Formation was considered equivalent in age to the Bridger Formation in the Bridger Basin, but Osborn (1881, p. 13) noted differences between mammalian fossils from the Bridger and Washakie Formations as well as between those from lower and upper Washakie levels. Scott (*in* Scott and Osborn, 1890, p. 465-466) recognized that the Washakie Formation contains some deposits younger than those of the Bridger Formation, as well as that the two formations are composed of deposits that are contemporaneous in part. He pointed out that fossil mammals from the Washakie, where different from those from the Bridger, resemble those from the Uinta Formation. Work in the Washakie Basin was continued by the American Museum of Natural History, with emphasis on collecting in the upper levels, in 1906. Granger's study (1909) of lithologic characters and faunas of the Washakie Formation led to recognition of the lower Washakie A "horizon", containing a mammalian fauna similar to that from the upper

Bridger of middle Eocene age, and the upper Washakie B "horizon", having a fauna similar to that of the Uinta A and B of early late Eocene age. These "horizons" are currently recognized as faunal zones, not sufficiently distinctive lithologically to be treated as members (Wheeler, 1961, p. 14). In recent years W. D. Turnbull of the Chicago Natural History Museum has worked extensively in the Basin, but results of his studies are not yet available.

*Other intermontane areas.*—Fossil mammals were discovered in 1908 in upper Eocene deposits along Beaver Divide, Wyoming, and in 1909 and 1910 the American Museum of Natural History had parties exploring all Tertiary levels exposed there (Granger, 1910; Sinclair and Granger, 1911). Although the fauna yielded so far by the upper Eocene deposits (upper part of the Wagonbed Springs Formation) is sparse relative to those from the Uinta and Washakie Basins, it is adequate to establish the faunal age as Uintan (Wood, H. E., and others, 1941; Van Houten, 1964, p. 50-53).

Elsewhere in Wyoming a few late Eocene mammals, approximately equivalent in age (Uintan) to the Beaver Divide fauna, are known from the Tepee Trail Formation in northwestern Wyoming (Love, 1939, p. 77-78). A much more adequate fauna is known from deposits considered part of the Tepee Trail Formation along Badwater and Dry Creeks in the northeastern Wind River Basin (Tourtelot, 1957). The first report of a few mammals of Uintan age from these strata was made in 1936 (Wood, H. E., Seton, and Hares, 1936). In 1944 studies on these deposits were begun by the United States Geological Survey (Tourtelot, 1946, 1957), following which the fauna has grown to be one of the important late Eocene assemblages (Gazin, 1956; Robinson, Peter, Black, and Dawson, 1964; Wood, A. E., 1949). The significance of the localities is augmented by a potassium-argon date from a tuff in Tourtelot's (1957) Green and Brown Member of 45.0 million years (Evernden and others, 1964, sample 1024). Current work in the area by Carnegie Museum is emphasizing collection of microfaunal elements from Uintan deposits, especially from the more fossiliferous Hendry Ranch Member.

Late Eocene mammals are known from two areas in southwestern Montana. A small fauna consisting mostly of larger perissodactyls and artiodactyls is known from the Sage Creek area (Douglass, 1903; Wood, H. E., 1934; Hough, 1955). Mixing of collections from the Eocene and Oligocene of the Sage Creek area is indicated, but a late Eocene component is definitely present; opinions on correlation of the late Eocene component range from early Uintan to Duchesnean. A recent study of tapiroids from the Eocene of Sage Creek suggests a late Uintan age for them (Radinsky, 1963, p. 60-62). The second occurrence in southwestern Montana of late Eocene mammals is near Three Forks. Early Oligocene mammals have long been known from the Thompson Creek beds of Douglass (1902, p. 242) in this area, but discovery of a few late Eocene

mammals from the lower part of the Climbing Arrow Formation there was reported more recently (Robinson, G. D., 1963, p. 74-75).

The most northerly of the late Eocene localities occurs in southern Saskatchewan, where conglomeratic sandstones of the Swift Current Creek beds first yielded a vertebrate fauna in 1930. Subsequent work has added to the fauna and shown its age to be Uintan, probably approximately equivalent to Uinta C (Russell and Wickenden, 1933; Russell, 1950).

*New Mexico, Texas, and Mexico.*—Vertebrate fossils were discovered in the upper part of the Galisteo Formation in north-central New Mexico in 1939. The known mammalian fauna, though small, suggests a Duchesnean age (Stearns, 1943), and the deposits hold promise of yielding more evidence on faunal development in this area.

A further geographic spread of late Eocene faunas, this time farther south, was made with the discovery in 1932 of fossil vertebrates in the Rim Rock country of Trans-Pecos, Texas. Additional collections were made starting in 1938 (DeFord, 1958), and expeditions from the University of Texas are continuing to make important discoveries from rocks of the Vieja Group. Faunal comparisons with other areas indicate that late Eocene mammals occur in the Colmena Tuff (J. A. Wilson, personal communication). Potassium-argon dates on the flows interbedded with fossiliferous tuffs of the Vieja Group add to the interest and importance of the localities. Slightly farther southeast in Texas a small fauna, probably Uintan, occurs near Castolon in Big Bend National Park in deposits above rocks dated 42.7 million years (Evernden and others, 1964, p. 193).

Vertebrate fossils were discovered in 1950 in red conglomerates in the Guanajuato district of Mexico. Although the mammalian record is still scanty, evidence from a rodent and a tapiroid suggests that the deposits are late Eocene or early Oligocene in age (Fries, Hibbard, and Dunkle, 1955).

*California.*—The distribution of known North American late Eocene faunas was widened with the discovery of mammalian fossils of this age in the thick Sespe deposits in the Simi Valley region, Ventura County, California, as reported by Stock (1931, 1932). Subsequent work, primarily by expeditions from the California Institute of Technology, led to collections from sites at various levels within the upper Eocene. An approximate correlative of the Uinta C (Myton Member) was found in the Tapo Ranch fauna (C.I.T. localities 180, 202, 207) and of the Duchesne River in the Pearson Ranch fauna (C.I.T. locality 150; see Stock, 1948, and references therein). The non-marine Sespe Formation overlies the marine middle Eocene Llajas Formation.

Somewhat later than the discovery of late Eocene mammals in the Sespe deposits, mammals were reported from the marine and non-marine Poway Conglomerate in San Diego County (Stock, 1937, 1938, 1939; Wilson, 1940a, b). The fauna has been correlated with that from the

Uinta B (Wagonhound Member) of the Uinta Basin. The Poway Conglomerate has been correlated also with the upper Eocene Tejon stage on the basis of marine invertebrates.

The significance of the Californian late Eocene faunas lies not only in their providing representative Uintan and Duchesnean mammals geographically removed from those of more easterly regions but also in their opening the opportunities for correlation of marine and non-marine faunas.

*Eastern North America.*—Probably the earliest report of late Eocene mammals from North America came from the eastern United States, where Eocene whales were discovered early in the 19th Century. These occur, however, in marine deposits of the Gulf and southern Atlantic coastal areas (Kellogg, 1936, p. 3-10). Continental upper Eocene deposits in eastern North America are rare, but remains of a titanotheres have been found in Clarke County, Mississippi. This mammal is in a level of development characteristic of the late Eocene, based on comparisons with titanotheres from western localities, but possible differences due to distance and inadequacy of the eastern fossil record make determination of its age not entirely certain (Gazin and Sullivan, 1942).

#### MAJOR LATE EOCENE LOCALITIES

For the purposes of this review five areas and their faunas are considered to be of primary importance. They are the following: the Uinta Basin, northeastern Utah, on which is based the subdivision of the late Eocene into the North American ages Uintan and Duchesnean and from which has come the bulk of collections of late Eocene mammals; the Washakie Basin of southern Wyoming, containing the best known record of the earliest late Eocene; along Badwater Creek in the northeastern part of the Wind River Basin, central Wyoming, where a varied fauna, including a good representation of smaller mammals, has been found in the Hendry Ranch Member of the Tepee Trail Formation; certain deposits of the Vieja Group in the Big Bend area of Texas; two areas of interbedded marine and non-marine deposits in southern California—one, the Poway Conglomerate north of San Diego, and the other, lower parts of the Sespe Formation in Ventura County. Inclusion of these areas and exclusion of others is based on our present knowledge and is not meant to imply any inherent superiority of these areas nor to suggest that other areas should be neglected in the search for more evidence on the late Eocene. Various faunas that are either transitional between the Duchesnean and Chadronian (early Oligocene) or early Chadronian, such as those from Yoder, Kishenehn, and Titus Canyon, do not concern us here.

In order to understand late Eocene mammals and faunal development, it is important to consider the landscape of the time, especially that of western North America from where most of the fauna comes. The general Eocene landscape in the region of the present Rocky Mountains

would have showed low relief and low general altitude compared to that of the present. Important centers of volcanic activity were present in the region of the Absaroka Mountains and Yellowstone Park in the late Eocene. The region of the Great Basin was probably a lowland in the east, rising to a low highland, in which there was some volcanic activity, in the west (Van Houten, 1956, p. 2819). There were no major mountain barriers farther west cutting off moist air from the Pacific. The region of Oregon and Washington was a broad coastal plain, and there were no coast ranges forming a climatic barrier (King, 1958). Climates of the Eocene covering the parts of North America from which fossil mammals are known are inferred on paleobotanical evidence to range from warm temperate in the north, through subtropical to tropical in the south (Dorf, 1959, map 1). There is some paleobotanical evidence also for a warming trend during the Eocene, culminating in the late Eocene (MacGinitie, 1958, p. 66).

More local events in the areas under consideration may be deciphered from the sediments and general faunal assemblages. In the Uinta Basin the Uinta Formation, composed of sandstones, siltstones, and some claystones, is finer grained in general than the Duchesne River Formation. During Uintan time some lakes were present, and rivers carried sediment from the east. Abundant remains of gars, turtles, and crocodilians add to the lithologic evidence for presence of numerous streams in the Uintan. However, relative to Bridgerian times when extensive lakes were present in the Basin, the Uintan was drier, and probably dryness increased during the Duchesnean. The generally coarser grained Duchesne River Formation, with its coarse sandstones and conglomerates, as well as some shales, was derived from the north and reflects uplift of the Uinta Mountains during the late Uintan and early Duchesnean (Stagner, 1941). Nowhere in the upper Eocene deposits of the Uinta Basin is there any appreciable amount of volcanic material, indicating that mammals of the area were not subjected to the rains of volcanic ash that occurred in some other areas.

The Washakie Basin was probably a shallow basin, sinking with accumulation of sediments from adjacent mountain ranges (Love, 1960, p. 208). This area contrasts with the Uinta Basin in that volcanic debris predominates in the Washakie B (Sinclair, 1909). Deposits of these upper beds are composed of tuffs with pumice, plagioclase feldspars, hornblende, and biotite; quartz is completely absent. Wet conditions are suggested by the presence of a good representation of gars, turtles, and crocodilians.

Late Eocene volcanic activity in the Yellowstone and Absaroka centers is reflected in the mammal-bearing deposits along Badwater Creek, for here again volcanic-rich sediments occur. Most fossils are found in the higher Hendry Ranch Member in greenish-gray volcanic claystones and siltstone, containing plagioclase feldspar, biotite, and some glass shards (Tourtelot, 1957). In these beds scarcity of turtles and

abundance of land snails and lizards suggests an ecology different from those of the Uinta and Washakie Basins, although at some places in the lower, Green and Brown Member, there are beds of limey vitric tuff, and marl and limestone also occur, so the area provided some pond environments. Presence in the fauna from the Hendry Ranch Member of a multi-tuberculate and possibly a dermopteran, unknown since the early Eocene (Robinson, Black, and Dawson, 1964), indicates that the habitat may not be represented among Bridgerian and other Uintan localities. The climate may have been modified by the great volcanic activity about 70 miles northwest (Tourtelot, 1957, p. 22).

Although detailed studies on faunas and localities in the Vieja Group of Texas remain to be published, J. A. Wilson has kindly supplied information on the late Eocene faunas of the area. Volcanic activity was clearly prevalent, each fauna occurring in a tuff overlain by a volcanic flow. Presence of crocodylians suggests a warm, moist habitat.

The thick, interbedded continental and marine deposits of southern California present a different picture and undoubtedly represent a different landscape from those along the Rocky Mountain chain. The Sespe Formation is composed of sandstones, conglomerates, and silts; volcanic material is absent. The Poway Conglomerate, marine and continental in origin, is composed of pebble to boulder conglomerate with interbedded marine sandstone. No fishes or amphibians have been reported from the Californian localities, although this might reflect collecting bias and lack of study of the complete faunas. There seems to be a considerable amount of endemism among the primates and rodents. Absence of leporids and equids further differentiate the faunas from those of the Rocky Mountain basins. Prior to the end of the Eocene, arms of the sea in the San Joaquin and Santa Barbara embayments might have been intermittent barriers to migrations of mammals and thus might have promoted endemism. By the end of the Eocene, seas were withdrawn from the present mainland of California (Reed and Hollister, 1936, p. 1573).

#### COMPARISON OF FAUNAS

The mammalian faunas known from the five major areas considered here offer interesting similarities and differences. Of course, interpretation of any fauna depends on known specimens, and this is directly affected by conditions of preservation and methods employed in collecting. The collections from the Californian localities were largely quarry recoveries; those from the Uinta Basin represent results of quarrying and of surface prospecting; and those from the Vieja Group and Washakie B resulted from surface prospecting. The only area in which washing and screening techniques were used is along Badwater Creek in the Hendry Ranch Member. Results of the use of these different techniques are shown especially well by the abundance of small mammals from the Hendry Ranch Member. Unfortunately, in the present state of our knowledge small mammals cannot be too profitably discussed either

from the viewpoint of phylogeny or of faunal age relationships, and any analysis of faunal development and age relationships must be dependent on more adequately known mammals.

Table 1 presents faunal lists from the main localities of the Rocky Mountain region, California, and Texas. The accuracy of these lists is dependent on the current state of knowledge of each area and of late Eocene taxonomic groups. Lists of mammals from the Uinta Basin faunas are based on collections in the Carnegie Museum and on published records, especially by Peterson (1919), Burke (1934, 1935), and Scott (1945). Studies in progress on the Washakie Basin faunas (W. D. Turnbull) and on those from the Vieja Group (J. A. Wilson) will refine these lists as will our studies on the Hendry Ranch fauna. The California localities were mainly collected and studied by Stock and others of the California Institute of Technology. The faunas come from C. I. T. locality 249 of the Poway Conglomerate (Stock, 1937) and C. I. T. localities 128, 147, 148, 150, 292 (Pearson Ranch fauna), 127, 180, 202, and 207 (Tapo Ranch fauna) in the Sespe Formation (Wilson, 1940a). Recent taxonomic revisions of North American primates (Gazin, 1958), paramyids (Wood, A. E., 1962), tapiroids (Radinsky, 1963), and artiodactyls (Gazin, 1955) render the lists relatively accurate for these groups.

*Development of mammals in North America during the late Eocene.*—Although it will be necessary to await further work before details of the evolution of many groups in the late Eocene can be presented, some broad outlines can be suggested on the basis of known faunas. A study of the faunal lists (table 1) shows a relative lack of most smaller mammals in the orders Marsupialia, Insectivora, and Primates, related to differential preservation that probably does not favor fossilization of delicate skeletal elements and reflects paucity of representation in the record of the habitats in which these mammals abounded. In certain instances this bias reflects collecting technique also, as in the Uintan and Duchesnean faunas from the Uinta Basin, which were not collected by washing and screening techniques. Small mammals are especially poorly represented in Duchesnean faunas. Nevertheless, some generalizations will be attempted on presence and absence in the record for these orders as well as for those more adequately represented. Table 2 presents the range in time of families known from the late Eocene of North America.

The one late Eocene representative of the order Multituberculata, from the Hendry Ranch Member along Badwater Creek, represents a faunal relict. No record of the order is known between the earliest Eocene and this appearance in a Uintan fauna (Robinson, Black, and Dawson, 1964). Mammals as small as this multituberculate are known from the Bridgerian, so the absence in deposits of that age may not be due to collecting bias but may suggest that the habitat required by this surviving branch is not represented among known Bridgerian localities. As far as known this was the latest multituberculate.

TABLE 1  
Mammalian genera in major North American late Eocene faunas

|                       | Wagonhound | Washakie B | Poway | Myton | Hendry Ranch | Tapo Ranch | Colmena | Randlett | Halfway | Lapoint | Pearson Ranch |
|-----------------------|------------|------------|-------|-------|--------------|------------|---------|----------|---------|---------|---------------|
| Multituberculata      |            |            |       |       |              |            |         |          |         |         |               |
| Ptilodontidae         |            |            |       |       |              |            |         |          |         |         |               |
| <i>Ectypodus</i>      |            |            |       |       | X            |            |         |          |         |         |               |
| Marsupialia           |            |            |       |       |              |            |         |          |         |         |               |
| Didelphidae           |            |            |       |       |              |            |         |          |         |         |               |
| <i>Peratherium</i>    |            | X          |       |       | X            | X          |         |          |         |         |               |
| <i>Nanodelphys</i>    |            |            |       |       | X            |            |         |          |         |         |               |
| Insectivora           |            |            |       |       |              |            |         |          |         |         |               |
| Leptictidae           |            |            |       |       |              |            |         |          |         |         |               |
| <i>Sespedectes</i>    |            |            |       |       |              |            |         |          |         |         | X             |
| diacodont             | X          |            |       |       |              |            |         |          |         |         |               |
| leptictid sp.         | X          |            |       |       | X            |            | X       |          |         |         | X             |
| Pantolestidae         |            |            |       |       |              |            |         |          |         |         |               |
| pantolestid sp.       |            |            |       |       | X            |            |         |          |         |         |               |
| Apatemyidae           |            |            |       |       |              |            |         |          |         |         |               |
| <i>Apatemys</i>       |            |            |       |       | X            | X          |         |          |         |         |               |
| <i>Stehlinella</i>    |            |            |       | X     |              |            |         |          |         |         |               |
| Nyctitheriidae        |            |            |       |       |              |            |         |          |         |         |               |
| <i>Nyctitherium</i>   |            |            |       | X     | X            |            |         |          |         |         |               |
| <i>Micropternodus</i> |            |            |       | X     | X            |            |         |          |         |         |               |
| Mixodectidae          |            |            |       |       |              |            |         |          |         |         |               |
| <i>Microsypops</i>    |            |            | X     |       |              |            |         |          |         |         |               |
| <i>Craseops</i>       |            |            |       |       |              | X          |         |          |         |         |               |
| Erinaceidae           |            |            |       |       |              |            |         |          |         |         |               |
| <i>Geolabis</i>       |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Scenopagus?</i>    |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Entomolestes?</i>  |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Ankyledon</i>      |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Proterixoides?</i> |            |            |       |       |              |            |         |          |         |         | X             |
| <i>Protictops</i>     |            |            |       |       |              |            |         |          |         | X       |               |
| Soricidae             |            |            |       |       |              |            |         |          |         |         |               |
| <i>Domnina?</i>       |            |            |       |       | X            |            |         |          |         |         |               |
| Talpidae?             |            |            |       |       |              |            |         |          |         |         |               |
| talpid? sp.           |            |            |       |       | X            |            |         |          |         |         |               |
| Apternodontidae       |            |            |       |       |              |            |         |          |         |         |               |
| <i>Apternodus?</i>    |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Oligoryctes?</i>   |            |            |       |       | X            |            |         |          |         |         |               |
| Dermoptera?           |            |            |       |       |              |            |         |          |         |         |               |
| Plagiomenidae?        |            |            |       |       |              |            |         |          |         |         |               |
| plagiomenid? sp.      |            |            |       |       | X            |            |         |          |         |         |               |
| Primates              |            |            |       |       |              |            |         |          |         |         |               |
| Omonyidae             |            |            |       |       |              |            |         |          |         |         |               |
| <i>Chumashius</i>     |            |            |       |       | X            |            |         |          |         |         | X             |
| <i>Ourayia</i>        | X          |            |       | X     |              |            |         |          |         |         |               |
| <i>Washakius</i>      |            |            | X     |       |              |            |         |          |         |         |               |
| <i>Dyseolemur</i>     |            |            |       |       |              | X          |         |          |         |         |               |
| <i>Stockia</i>        |            |            | X     |       |              |            |         |          |         |         |               |
| <i>Macrotarsius</i>   |            |            |       |       | X            |            |         |          |         |         |               |
| <i>Omomys?</i>        |            |            |       |       |              |            | X       |          |         |         |               |



TABLE 1 (Continued)

|                                | Woganhound | Washakie B     | Poway | Myton | Hendry Ranch   | Tapo Ranch | Colmena | Randlett | Halfway | Lapoint | Pearson Ranch |
|--------------------------------|------------|----------------|-------|-------|----------------|------------|---------|----------|---------|---------|---------------|
| Limnocyoniidae                 |            |                |       |       |                |            |         |          |         |         |               |
| <i>Limnocyon</i>               | X          |                |       |       | X <sup>2</sup> |            |         |          |         |         |               |
| <i>Oxyaenodon</i>              | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Apataelurus</i>             | X          |                |       |       |                |            |         |          |         |         |               |
| Miacidae                       |            |                |       |       |                |            |         |          |         |         |               |
| <i>Uintacyon</i>               |            |                |       | X     |                |            |         |          |         |         |               |
| <i>Miacis</i>                  | X          | X              |       | X     | X              | X          |         |          |         |         |               |
| <i>Prodaphoenus</i>            |            |                |       | X     |                |            |         |          |         |         |               |
| <i>Tapocyon</i>                |            |                |       |       | X              | X          |         |          |         |         |               |
| <i>Plesiomiacis</i>            |            |                |       |       |                | X          |         |          |         |         |               |
| Family Uncertain               |            |                |       |       |                |            |         |          |         |         |               |
| <i>Simidectes</i> <sup>8</sup> |            |                |       | X     |                |            |         |          |         |         | X             |
| Canidae                        |            |                |       |       |                |            |         |          |         |         |               |
| <i>Procyonictis</i>            |            |                |       | X     |                |            |         |          |         |         |               |
| Felidae?                       |            |                |       |       |                |            |         |          |         |         |               |
| <i>Eosictis</i>                |            |                |       |       |                |            |         |          | X       |         |               |
| Condylarthra                   |            |                |       |       |                |            |         |          |         |         |               |
| Hyopsodontidae                 |            |                |       |       |                |            |         |          |         |         |               |
| <i>Hyopsodus</i>               | X          |                |       |       | X              |            |         |          |         |         |               |
| Dinocerata                     |            |                |       |       |                |            |         |          |         |         |               |
| Uintatheriidae                 |            |                |       |       |                |            |         |          |         |         |               |
| <i>Uintatherium</i>            | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Eobasileus</i>              | X          | X              |       |       |                |            |         |          |         |         |               |
| Perissodactyla                 |            |                |       |       |                |            |         |          |         |         |               |
| Equidae                        |            |                |       |       |                |            |         |          |         |         |               |
| <i>Epihippus</i>               | X          |                |       | X     | X              |            | X       |          | X       |         |               |
| Brontotheriidae                |            |                |       |       |                |            |         |          |         |         |               |
| <i>Metarhinus</i>              | X          | X              | X?    |       |                |            |         |          |         |         |               |
| <i>Rhadinorhinus</i>           | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Sphenocoelus</i>            | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Dolichorhinus</i>           | X          | X              |       |       |                |            |         |          |         |         |               |
| <i>Sthenodectes</i>            | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Manteoceras</i>             | X          |                |       | X     |                |            |         |          |         |         |               |
| <i>Protitanotherium</i>        |            |                |       | X     |                |            |         |          | X?      |         |               |
| <i>Teleodus</i>                |            |                |       |       |                |            |         | X        | X       | X       | X             |
| <i>Diplacodon</i>              |            |                |       | X     |                |            |         |          |         |         |               |
| <i>Eotitanotherium</i>         | X          |                |       |       |                |            |         |          |         |         |               |
| <i>Telmatherium</i>            | X          |                |       |       |                |            |         |          |         |         |               |
| brontotheriid sp.              |            |                |       |       | X              | X          | X       |          |         |         |               |
| Eomoropidae                    |            |                |       |       |                |            |         |          |         |         |               |
| <i>Eomoropus</i>               | X          | X              |       |       |                |            |         |          |         |         |               |
| <i>Grangeria?</i>              |            |                |       |       | X              |            |         |          |         |         |               |
| Isectolophidae                 |            |                |       |       |                |            |         |          |         |         |               |
| <i>Isectolophus</i>            | X          |                |       | X     |                |            |         |          |         |         |               |
| Helaletidae                    |            |                |       |       |                |            |         |          |         |         |               |
| <i>Dilophodon</i>              |            | X <sup>4</sup> |       | X     | X              | X          |         | X        |         |         |               |
| <i>Colodon</i>                 |            |                |       |       | X              |            |         |          |         |         |               |
| helaletid sp.                  |            |                |       |       |                |            | X       |          |         |         |               |
| Hyrachyidae                    |            |                |       |       |                |            |         |          |         |         |               |
| <i>Hyrachyus</i>               | X          |                |       | X?    |                |            |         |          |         |         |               |

TABLE 1 (Continued)

|                         | Wagonhound | Washakie B | Poway          | Myton | Hendry Ranch | Tapo Ranch     | Colmena | Randlett | Halfway | Lapoint | Pearson Ranch  |
|-------------------------|------------|------------|----------------|-------|--------------|----------------|---------|----------|---------|---------|----------------|
| Hyracodontidae          |            |            |                |       |              |                |         |          |         |         |                |
| <i>Prothyracodon</i>    | X          |            |                | X     | X            |                |         |          |         |         |                |
| <i>Triplopus</i>        | X          | X?         |                | X     |              |                |         |          |         |         | X              |
| <i>Epitriplopus</i>     |            |            |                | X     | X?           |                | X?      | X        |         |         |                |
| <i>Mesamynodon</i>      |            |            |                |       |              |                |         |          |         | X       |                |
| Amynodontidae           |            |            |                |       |              |                |         |          |         |         |                |
| <i>Amynodon</i>         | X          | X          | X              | X     | X            | X              |         | X        |         |         |                |
| <i>Amynodontopsis</i>   |            |            |                |       |              |                |         |          |         |         | X              |
| <i>Megalamyndon</i>     |            |            |                |       |              |                | X       |          | X       |         |                |
| Rhinocerotidae          |            |            |                |       |              |                |         |          |         |         |                |
| <i>Eotrigonias</i>      | X?         |            |                | X?    |              |                |         |          |         |         |                |
| Artiodactyla            |            |            |                |       |              |                |         |          |         |         |                |
| Dichobunidae            |            |            |                |       |              |                |         |          |         |         |                |
| <i>Pentacemylus</i>     |            | X?         |                | X     | X?           |                |         | X        |         |         |                |
| <i>Mytonomeryx</i>      |            | X?         |                | X     |              |                |         |          |         |         |                |
| <i>Apriculus</i>        |            |            |                |       | X            |                |         |          |         |         |                |
| <i>Hylomeryx</i>        | X          |            |                | X     | X?           |                |         |          |         |         |                |
| <i>Auxontodon</i>       |            |            |                | X     | X?           |                |         |          |         |         |                |
| <i>Bunomeryx</i>        | X          |            |                | X?    |              |                |         |          |         |         |                |
| <i>Mesomeryx</i>        | X?         |            |                | X?    |              |                |         |          |         |         |                |
| <i>Tapochoerus</i>      |            |            |                |       |              | X              |         |          |         |         |                |
| <i>Parahyus</i>         |            | X?         |                |       |              |                |         |          |         |         |                |
| <i>Achaenodon</i>       | X          | X          |                |       |              |                |         |          |         |         |                |
| Entelodontidae?         |            |            |                |       |              |                |         |          |         |         |                |
| <i>Dyscritochoerus</i>  |            |            |                |       |              |                |         |          |         | X       |                |
| Agriochoeridae          |            |            |                |       |              |                |         |          |         |         |                |
| <i>Protoreodon</i>      | X          |            |                | X     | X            |                | X       | X        | X       |         |                |
| <i>Diplobunops</i>      | X          |            |                | X     | X            |                |         | X        |         |         |                |
| agriochoerid sp.        |            |            | X <sup>5</sup> |       |              | X <sup>6</sup> |         |          |         |         | X <sup>6</sup> |
| Leptomerycidae          |            |            |                |       |              |                |         |          |         |         |                |
| <i>Poabromylus</i>      |            |            |                |       |              |                |         |          |         | X       |                |
| <i>Leptotragulus</i>    | X          |            |                | X     | X            |                | X       |          |         |         |                |
| <i>Leptoreodon</i>      | X          |            |                |       | X            | X              |         |          |         |         |                |
| Oromerycidae            |            |            |                |       |              |                |         |          |         |         |                |
| <i>Protylepus</i>       | X          | X          |                | X?    |              |                |         |          |         |         |                |
| <i>Malaquiferous</i>    |            |            |                |       | X            |                |         |          |         |         |                |
| <i>Oromeryx</i>         | X          | X?         |                |       |              |                |         |          |         |         |                |
| oromerycid sp.          |            |            |                |       |              |                | X       |          |         |         |                |
| Hypertragulidae         |            |            |                |       |              |                |         |          |         |         |                |
| <i>Simimeryx</i>        |            |            |                |       |              |                |         |          |         | X       | X              |
| Camelidae               |            |            |                |       |              |                |         |          |         |         |                |
| <i>Poebrodon</i>        |            |            |                | X     |              |                |         |          |         |         |                |
| "oreodont" <sup>3</sup> |            |            |                |       |              |                |         |          |         |         | X              |
| "cameloid" <sup>5</sup> |            |            |                |       |              | X              |         |          |         |         | X              |

<sup>1</sup> Reference to this family uncertain, M. C. McKenna, personal communication, September, 1965.

<sup>2</sup> The symbol X? equals horizon uncertain.

<sup>3</sup> Formerly referred to as *Pleurocyon*, a preoccupied name (G. B. MacIntyre, personal communication, September, 1965).

<sup>4</sup> L. B. Radinsky, personal communication, May, 1965.

<sup>5</sup> J. R. Macdonald, personal communication, May, 1965.

<sup>6</sup> Listed in Stock, 1948, figure 1.



TABLE 2 (Continued)

|                 | earlier | Bridgerian               | early Uintan               | late Uintan                | Duchesnean                 | Chadronian                 | later |
|-----------------|---------|--------------------------|----------------------------|----------------------------|----------------------------|----------------------------|-------|
| Perissodactyla  |         |                          |                            |                            |                            |                            |       |
| Equidae         | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Brontotheriidae | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Eomoropidae     | _____   | _____                    | _____                      | _____                      | ..... ? <sup>1</sup> ..... | ..... ? <sup>1</sup> ..... | _____ |
| Isectolophidae  | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Helaletidae     | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Hyrachyidae     | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Hyrcodontidae   | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Amyndodontidae  | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Rhinocerotidae  | _____   | ..... <sup>3</sup> ..... | ..... ? <sup>1</sup> ..... | ..... ? <sup>1</sup> ..... | .....                      | _____                      | _____ |
| Artiodactyla    |         |                          |                            |                            |                            |                            |       |
| Dichobunidae    | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Agriocheridae   | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Leptomerycidae  | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Oromerycidae    | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Hypertragulidae | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |
| Camelidae       | _____   | _____                    | _____                      | _____                      | _____                      | _____                      | _____ |

<sup>1</sup> Family assignment tentative.

<sup>2</sup> In Asia.

<sup>3</sup> In Europe.

<sup>4</sup> The symbol ? equals stratigraphic position uncertain.

Marsupials were present not only in the continental interior but also in southern California. Their absence from Duchesnean faunas is probably an artifact of collecting and preservation.

Nine insectivore families are known from the late Eocene, but little of the material on which they are based has been critically reviewed. This, coupled with the fragmentary nature of the specimens, makes any statements as to trends within groups or ecological interpretations extremely tenuous. Of modern families, Talpidae, Soricidae, and Erinaceidae are all probably present in the faunas from the Hendry Ranch Member. Absence of these families from most late Eocene faunas is probably due primarily to inadequate sampling and poor preservation. Two other families, the Pantolestidae and Apternodontidae, are also known only from the Badwater Creek localities, again probably for similar reasons. Nyctitheriids, common in the Bridgerian, are known from Badwater Creek and the Myton Member only. Absence of nyctitheriids in the Duchesnean Rocky Mountain fossil record is probably due to inadequate sampling as one genus of the family, *Micropternodus*, occurs in the Uintan Hendry Ranch beds (Robinson, Black, and Dawson, 1964) as well as in early Oligocene deposits of the Rocky Mountain and Great Plains regions. Mixodectids are found only in the California faunas. Their restricted distribution might be due to isolation

where competition with insectivores of more modern aspect was reduced. Mixodectids were most common in the Paleocene and early Eocene; their last record is in the Uintan Tapo Ranch fauna. Within the late Eocene apatemyids are known only from faunas of late Uintan age, but the family occurred in the early and middle Eocene and lasted into the Oligocene, indicating inadequate sampling of the early Uintan and Duchesnean faunas. The most widespread and best documented record of insectivores during the late Eocene is that for the Leptictidae, known through the entire interval and having a distribution from California to the Rocky Mountain area and into Texas. They were seemingly broadly adapted and continued as a very successful group into the Oligocene.

Although the record is still poor, a few specimens from the Hendry Ranch Member seem to represent plagiomenid dermopterans. If this reference is correct this Uintan form is the last known plagiomenid. The fossil record does not document the history of later dermopterans.

Of the two primate families found in the late Eocene, one, the Anaptomorphidae, is known only from the Badwater Creek faunas. The persistence of paromomyines (following McKenna, 1960, p. 70-72), previously thought to have become extinct in the early Eocene, parallels the persistence of multituberculates and dermopterans. The other late Eocene primate family, the Omomyidae, was widely distributed during the late Eocene with six or seven genera known. Out of four omomyids from California, two were distinct from those of the Rocky Mountain basins, with only *Washakius* and *Chumashius* occurring both in the interior and on the west coast. No primates are known from Duchesnean faunas of the Uinta Basin. Although absence of most small mammal fossils from the Duchesne River Formation makes speculation hazardous, it is tempting to speculate that by Duchesnean time forests were no longer extensive and that a more open, drier environment less suited to lower primates had developed in the Uinta Basin region.

The taeniodont *Stylinodon* survived into the earliest late Eocene, represented in the Washakie and Uinta Basins, but the genus, and with it the order Taeniodonta, became extinct before the late Uintan.

There is no record of palaeonodont edentates in the late Eocene, neither of metacheiromyids, which lasted into the middle Eocene, nor of the early to middle Eocene and Oligocene epoicotheriids. Epoicotheriids are rare in the fossil record, and metacheiromyids, though more common, are not abundant (Simpson, 1959, p. 7). Thus, absence of palaeonodonts from the late Eocene record, though interesting, may not be significant.

The lagomorph family Leporidae seems to have originated in the late Eocene, probably in Asia, and its appearance in the late Uintan represents first appearance by immigration. Ecologic conditions in the northern Rocky Mountain basins, perhaps representing settings similar to those in the leporid's Asian source, were favorable for them, whereas

the environments in southern California and the Vieja region seem to have been unsuitable.

Rodentia, although often small in size, seem to be preserved more frequently than are most marsupials, insectivores, and primates. This reflects their greater ecological diversity. The late Eocene record shows persistence in the Uintan of mostly protrogomorph groups—paramyids, cylindrodontids, sciuravids, aplodontids, and protoptychids—but the first myomorphs appeared in the interval, and thus the beginning of a new rodent radiation is documented. Paramyids were especially well represented in the Uintan, when their abundance forms a striking contrast to the early Oligocene picture when all but five paramyid genera had become extinct. The survivors in North America were either large, the manitshines, or specialized in their dentition away from the typical pattern, the prosciurines. Cylindrodontids were common in North America with *Pareumys* ranging widely in time and space in the late Eocene, when it occurred in almost every known fauna. A somewhat more advanced cylindrodontid is known from the Uintan along Badwater Creek. The long ranging sciuravid, *Sciuravus*, is another carry-over from the Bridgerian, but it probably became extinct by the end of the Uintan. Although sciuravids may have been ancestral to some rodent groups, these branches had probably already arisen by the Uintan, and the late Eocene species of *Sciuravus* represent survivors of the ancestral line. The first aplodontids, probable paramyid derivatives, are known from the Uintan of southern California. Origin of this family in a restricted area is an interesting beginning for a family that has always been limited geographically (Shotwell, 1958, p. 475-481). The specialized saltatorial rodent *Protoptychus* seems to have been a protrogomorph experiment that lived in the early Uintan, when its ecological requirements were evidently met only in the Washakie and Uinta Basins. The earliest definite North American eomyids appeared in the Uintan, in the Hendry Ranch beds. By the Duchesnean *Protadajidaumo* had arisen, and the family exploded taxonomically in the early Oligocene (Black, 1965, p. 38-41). Eomyids are known also from the late Eocene of Europe but not of Asia, and the place and time of their origin (from sciuravids?) remains to be determined. Finally, several rodents of uncertain affinities appeared in the Uintan and Duchesnean of southern California. These genera, *Simimys*, *Griphomys*, and *Presbymys*, are not especially closely related to one another and appear to be endemic to southern California. The first seems to have myomorph affinities, the second is enigmatic in relationships, and the last might be a cylindrodontid.

The state of late Eocene Carnivora is one of archaic survivors, perhaps in special niches, together with the beginnings of advanced groups. Mesonychids survived through the late Eocene in North America but did not extend into the Oligocene there. Another group of the late Eocene was the Limnocyonidae, occurring in the Uintan but not thereafter. The family Hyaenodontidae shows another pattern, being absent

in the Uintan but appearing in the late Duchesnean. All late Eocene North American hyaenodontids are members of one subfamily, the Hyaenodontinae, a group of possibly Eurasian origin which did not reach North America until the late Uintan. Fissipeds were well represented by miacids, and the problematic nature of *Procynodictis* and *Eosictis* emphasizes possible miacid transitions to more advanced carnivores.

Most archaic herbivores seem to have become extinct before the late Eocene, although the small condylarth *Hyopsodus* survived into the late Uintan. Uintatheres survived into the interval but were gone by the end of the early Uintan.

A marked faunal change took place in the late Eocene in North America with the beginning of the decline of perissodactyls as the major ungulate element and the ascendance of artiodactyls. The early Uintan is characterized by a large number of brontotheres, eight genera being reported from the Wagonhound. By the Duchesnean only two lineages of brontotheres remained. Most of these large ungulates are known from the Uinta and Washakie Basins, and brontotheres are poorly represented in the Californian faunas. One is present in the Colmena fauna. *Epihippus* was the only late Eocene equid and occurs in all faunas except those in California. Chalicotheres of the family Eomoropidae were present during Uintan time but were rare and known only from the Washakie B, Wagonhound, and Hendry Ranch faunas. Development of chalicotheriids from eomoropids probably took place in Asia, and when chalicotheriids appeared next in North America, in the Miocene, they represent a new immigration (Radinsky, 1964, p. 24). Tapiroids and rhinocerotoids were quite numerous and diverse in the late Eocene, but by the end of that time they, like the brontotheres, are reduced in numbers of kinds. Only one tapiroid and three rhinocerotoid lines carried through into the Oligocene. Most records of these groups in the late Eocene are from intermontane localities. Only two amynodonts are known from the Poway fauna, and one helaletid from the Tapo Ranch fauna in California; no isctolophids or hyracodontids are known from the west coast; and only the hyracodontids were present in Texas. Differences in environmental preference among tapiroids is suggested by the distribution of some isctolophids and helaletids. The isctolophid *Isectolophus* occurs in Uintan Uinta Basin faunas but is absent from Hendry Ranch beds, where the similar sized helaletid *Colodon* occurs (Radinsky, 1963, p. 79). The smaller helaletid *Dilophodon*, however, occurs in the Uinta Basin, the Hendry Ranch beds, and the Sespe (Tapo Ranch) beds. True rhinoceroses occurred in North America in the late Eocene, but they are known poorly and only from the Uinta Basin (Wood, H. E., 1927).

Artiodactyls make up a major component of faunas of the late Eocene, the first time that they assume this position in the fossil record. Known dichobunids were diverse during Uintan time, but only one line persisted into the Duchesnean. Only one species occurred in California,

and no dichobunids have been recovered in the Texas faunas. Their absence in Texas might be due to geographic factors, but their scarcity in California is more probably attributable to ecological factors. Among families making their first appearance during the late Eocene are Agriocheridae, Oromerycidae, Leptomerycidae, Hypertragulidae, and Camelidae. The commonest artiodactyls in most of the faunas were agriocherids. Absence of agriocherids in the Washakie B possibly indicates that the fauna from these beds is slightly older than that of the Uinta B. Hypertragulids were rare in the late Eocene but did appear in the Duchesnean of Utah and California. Oromerycids occurred during Uintan time only in the Washakie and Uinta Basins. The family was present in Texas in the late Eocene, and one line persisted into the early Oligocene of the Great Plains area. Leptomerycids appeared first in the early Uintan in the Uinta Basin. By the late Uintan they were distributed over most of western North America. They persisted into the Oligocene. Another group appearing in the late Eocene, the Camelidae, also ranged into the Oligocene when the family radiated widely. The overall picture of artiodactyl development documents a rather spectacular radiation of modernized North American groups during the late Eocene.

*Relative ages of the main late Eocene faunas.*—Figure 4 shows our view of the relative positions of the major faunas discussed, which is basically that of most North American vertebrate paleontologists (Wood, H. E., and others, 1941). It is not our purpose here to revise correlation of North American continental deposits of the upper Eocene (a task being done by the Committee on Nomenclature and Correlation of North American Continental Tertiary of the Society of Vertebrate Paleontology) but rather to indicate some similarities and differences among the faunas that seem significant and to discuss some problems encountered in attempting to correlate known mammal-bearing deposits of the upper Eocene.

The faunas being compared are spread geographically from the Rocky Mountain area to Texas and to California. A difficulty immediately encountered in making faunal comparisons for purposes of correlation is differentiation of the effects of geographic and ecologic factors on the faunas of these different areas from the effects of time. The standard for correlation must be the established sequence in the Uinta Basin of the Rocky Mountain area.

*Rocky Mountain area.*—The faunas of the Washakie B and the Wagonhound (Uinta A and B) are older than others of the Rocky Mountain late Eocene. The faunas share presence of *Sciuravus*, *Protoptychys*, *Stylinodon*, *Eobasileus*, *Metarhinus*, *Dolichorhinus*, *Amynodon*, and *Achaenodon*. All other late Eocene faunas lack taeniodonts, uintatheres, and *Achaenodon* and are relatively depauperate in brontotheres and limnocyonids. Progress beyond the Bridgerian level is shown especially by the assemblage of rather advanced dichobunid artiodactyls. Slightly younger age of the Uinta B, the upper, more fossiliferous part of

## MAJOR LATE EOCENE OCCURRENCES WESTERN U.S.

| Stage            | UTAH   |  | WYOMING   |   | CALIFORNIA   | TEXAS   |   |  |  |
|------------------|--|--|---|---|--|---|---|--|--|
|                  | Uinta Basin  |  | Wind River Basin<br>NE  | Washakie Basin<br>S                                       |  |   |   |  |  |
| D<br>C<br>B<br>A | D<br>u<br>c<br>h<br>e<br>s<br>s<br>e<br>R<br>i<br>v<br>e<br>r<br>F<br>m. | La Point                                       | P<br>T<br>e<br>p<br>e   | W<br>a<br>g<br>o<br>n                                     | P<br>e<br>a<br>r<br>s<br>o<br>n<br>R<br>a<br>n<br>c<br>h<br>I.<br>f.   | V<br>i<br>e<br>j<br>a<br>F<br>C<br>o<br>l<br>m<br>e<br>n<br>a<br>I.<br>f. |   |  |  |
|                  |  | Halfway  |   |   |  |   | ? |  |  |
|                  |  | Randlett                                       |   |   |  |   |   |  |  |
|                  |  | Myton  | T<br>r<br>a<br>i<br>l<br>F<br>m.                                      | B<br>e<br>d<br>S<br>p<br>r<br>i<br>n<br>g<br>s<br>F<br>m. | F<br>m. T<br>a<br>p<br>o<br>R<br>a<br>n<br>c<br>h<br>P<br>o<br>w<br>a<br>y<br>C<br>o<br>n<br>g<br>l<br>o<br>m<br>e<br>r<br>a | 42.7 <sup>2</sup>   |   |  |  |
|                  |  | W<br>a<br>g<br>o<br>n<br>h<br>o<br>u<br>n<br>d | B<br>a<br>d<br>w<br>a<br>t<br>e<br>r<br>I.<br>f.<br>45.0 <sup>1</sup> | W<br>a<br>s<br>h<br>a<br>k<br>i<br>e                      | P<br>o<br>w<br>a<br>y<br>I.<br>f.  |   |   |  |  |
|                  |  |  |   | F<br>m.   |  |   |   |  |  |

Fig. 4. Correlation of some North American late Eocene faunas of the western United States. <sup>1</sup>KA 1024, <sup>2</sup>KA 1274 (Evernden and others, 1964).

the Wagonhound Member, may be proposed on the basis of appearance of the cylindrodontid *Pareumys* and of agriocherids, but whether or not ecological difference might play a role in these differences from the Washakie B faunas cannot be definitely determined.

The more advanced level of faunas from the Myton Member (Unita C) is shown by the appearance of leporids, *Diplacodon*, leptomerycids, and camelids. All rodents are protrogomorphs. Limnocyonids are absent, and miacids are more varied than in the Wagonhound. As opposed to the radiation of artiodactyls, among perissodactyls, brontotheres are definitely reduced in variety.

The record of mammalian fossils from the Hendry Ranch Member along Badwater Creek is weighted toward presence of smaller mammals, in part because of the suitability of the localities for utilizing a washing technique in collecting. Thus, the fauna shows among the smaller mammals some interesting records of groups thought to have become extinct earlier (multituberculates, plagiomenids) but now known to be

absent in older deposits due to an artifact of collecting. Other groups, relatively advanced, are known as well (talpids, soricids, eomyids), but the use of these rarities in correlation is necessarily limited. The overall level of development within the upper Eocene is shown by presence of a leporid, agriocherids, and oromerycids, abundance of protrogomorph rodents, and presence of several dichobunid artiodactyls; together these suggest a late Uintan age. The Hendry Ranch fauna differs from that of the Myton Member in having *Sciuravus*, *Hyopsodus*, and a chalicothere, all of which are present in early Uintan faunas. The first two are Bridgerian also. Whether they indicate somewhat greater antiquity for the Hendry Ranch fauna than for that from the Myton, or whether ecological differences are involved, cannot be definitely decided. Not much weight can be placed on presence or absence of the usually rare chalicotheres, presence of which in the Wagonhound and Hendry Ranch faunas might be taken as evidence for ecological similarity.

A glance at table 1 suggests the problem immediately encountered in dealing with the Duchesnean faunas of the Uinta Basin. The inadequate mammalian record from the Randlett and Lapoint and still sparser record from the Halfway render their use as a standard very difficult and reduce the significance of absences from the record. The Randlett fauna shares a number of genera with the late Uintan Myton fauna but is advanced in presence of *Protadjidaumo*, which is a non-protrogomorph rodent, and of the brontothere, *Teleodus*. These two genera continue into the Lapoint. Additions to the Lapoint fauna suggestive of progressive change are a relatively advanced leptomerycid, a primitive hypertragulid, and *Hyaenodon*, a possible Old World immigrant. Continued presence of *Leptomomus* and *Epihippus*, and absence of *Mesohippus* and of a diversity of genera in such groups as eomyid rodents, oreodonts, and camelids differentiate this Duchesnean fauna from those of the Chadronian.

*California.*—The fauna from the Poway Conglomerate is clearly the oldest of the Californian Eocene faunas, having a species of *Pareumys* somewhat less advanced than that from Tapo Ranch and distinctly less so than from Pearson Ranch. All rodents from the Poway Conglomerate are protrogomorphs, and in general these present a post-Bridgerian appearance. Probably a level near that of the Wagonhound is represented (Wilson, 1940b, p. 92). The omomyids of the Poway, *Washakius* and *Stockia*, are advanced beyond their Bridgerian relatives (Gazin, 1958, p. 57-60, 94), and the brontothere of the Poway seems to be nearer the Wagonhound level of development than to that presented by Myton forms (Stock, 1937).

The Tapo Ranch faunas document advance beyond the Poway in having more advanced rodents, including some non-protrogomorphs. The omomyid *Dyseolemur* is apparently a descendant of *Washakius* (Gazin, 1958, p. 93). Thus, an age younger than that of the Poway is strongly suggested, but the high degree of endemism exhibited by the

Tapo Ranch faunas makes comparisons with the Rocky Mountain standard very difficult. A late Uintan age is likely.

The stratigraphically higher Pearson Ranch beds (C.I.T. locality 150) contain a fauna having some genera in common with the Tapo Ranch faunas. Although the Pearson Ranch fauna is not well rounded, presence in it of *Hyaenodon* and a hypertragulid, both present in the Lapoint, link the Pearson Ranch with the Rocky Mountain Duchesnean.

*Texas.*—The Colmena fauna of the Big Bend region of Texas is sparse, but indicators of its late Eocene age are *Epihippus*, *Leptotragulus*, and an oromerycid. More detailed comparisons of the fauna are now being made by J. A. Wilson, and these will reveal the closer correlation of the fauna. Both Uintan and Duchesnean genera are represented, and our placement of the fauna in the approximate position of that from the Randlett is to be regarded as tentative.

#### SUMMARY

In several ways the late Eocene was a time of transition in North America. Geologically, the interval is represented by a diversity of continental deposits, some broadly spread in intermontane basins (Uinta, Washakie), others peripheral in basins (Beaver Divide, Badwater), and still others intercalated with marine deposits (southern California, Mississippi). Thus, geologic expression today of this interval contrasts with the predominately broad basin deposits of the earlier Eocene and the widespread flood plain deposits of the Oligocene. Faunally, the interval documents the last appearance of several groups of archaic carnivores and ungulates and the last dominance of the rodent fauna by protrogomorphs. Primates were already diminished from their middle Eocene diversity and at the end of the Eocene only one primate family persisted. Perissodactyls showed the beginning of their decline. An important progressive change was the beginning of the radiation of non-dichobunid artiodactyls, and glimmers of advance were shown among insectivores, rodents, and others. Among the Carnivora, the Miacidae developed toward modernized families. Other faunal changes such as the appearance in North America of leporids and *Hyaenodon* indicate faunal interchange with the Old World, which was taking place at a higher rate during the late Eocene than during the middle Eocene. By the end of the interval the stage was set for radiation of some families that had arisen during the late Eocene (Soricidae, Leporidae, Eomyidae, Leptomerycidae, Camelidae, and others) and the emergence of other progressive groups (Cricetidae, Heteromyidae, Anchitheriinae, Merycoidodontidae)—events of the Oligocene.

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