

An illustration of an oreodont, a large, tusked mammal from the Miocene of North America. The word "Oreodonts" is written in a large, bold, black font, with the 'O' being a large circle that the animal's head and neck pass through.

Oreodonts

Of the White River Badlands of North-America



A taxonomic and geologic study on the history of the extinct oreodonts, based on the fossils of the
University Museum in Utrecht

Master's thesis Biogeology, Universiteit Utrecht.

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Abstract

Fossil skulls of oreodonts, family Merycoidodontidae (Artiodactyla), from the White River Badlands (USA) in the collection of the University Museum in Utrecht were bought late in the twentieth century by Professor Wichmann (UU). The oreodonts, now identified on species level, must have been collected from Oligocene and Eocene layers from the White River Badlands. The fossils range in age from Middle Chadronian (35.7 Ma) to Early Whitneyan (31.4 Ma). An overview of the geological setting of the White river Badlands is given as well as an overview of the Oligocene paleoclimate and paleoenvironment.

Keywords: Oreodont, Merycoidodontidae, White River Badlands, North-America, Oligocene.

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1. Introduction

Ever since 1847, the Oligocene sediments of the White River Badlands (see figure 1) have been an important area of paleontological expeditions and research. This is not surprising, because the fossils found there are very well preserved and are used for reconstructing life around this age and for the interpretation of the paleoenvironment. This type of research shows an ecosystem with both extinct species and species that would evolve into those we know now (O’Harra, 1920).

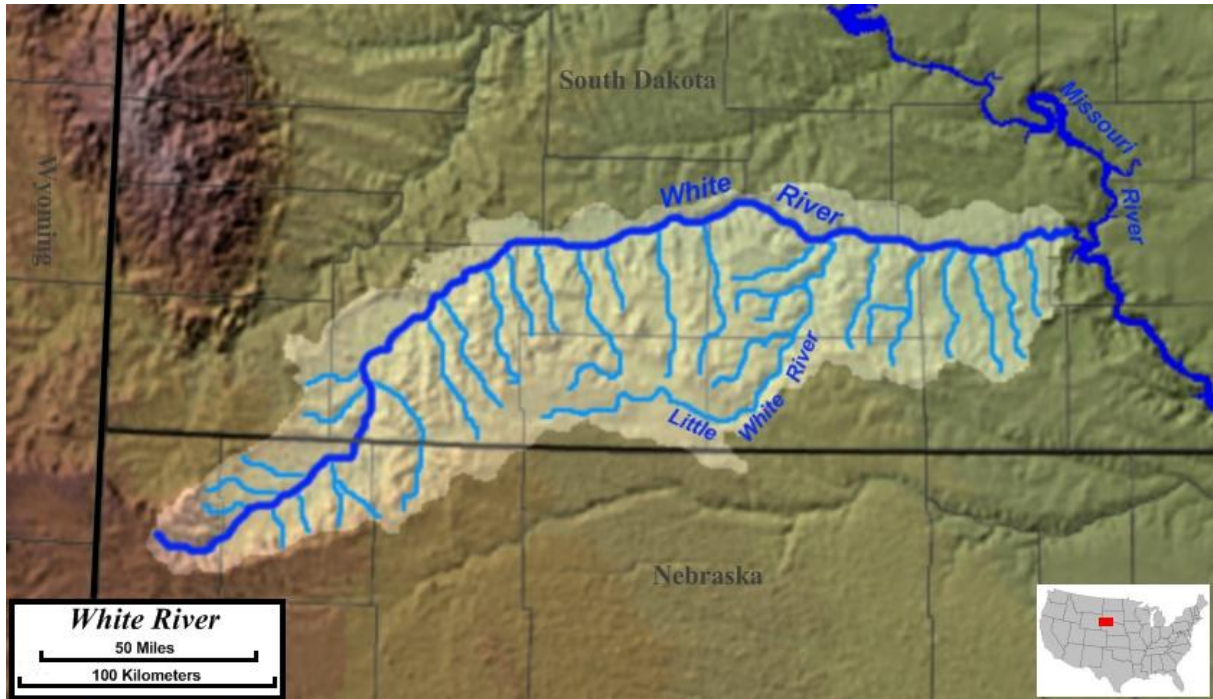


Figure 1. Location of the White River. Insert is a figure of the United States of America, with in red the states visible in the larger picture.

A very important animal in the fauna of the White River Badlands during the Oligocene was the oreodont. Oreodonts were very diverse with at least seventeen taxa, and they are interpreted to have occupied many herbivorous niches. Nowadays 25 percent of all the fossils found in the area is of oreodonts. Such an abundant group must certainly tell us something about the paleoenvironment, since this is where it developed and evolved in.

Not only their abundance, but also their interesting pig-like shape and interpreted way of living make the oreodonts a good subject for studying the environment. Add to that the remarkable preservation of these fossils and you understand why researchers love these species. For this same reason it is not surprising that many museums all over the world have at least one oreodont on display and once you start looking for them you encounter them at many unexpected places (see for example figure 2 for two oreodonts in London).



Figure 2: Example of oreodonts in a museum. Skull and part of skeleton with a skull of *Merycoiododon culbertsoni*. On display in the Natural History Museum, London.

In this paper, the skulls of the University Museum in Utrecht will be described. In the collection are among others bones of ungulates, turtles and fish. One group, the oreodonts, is especially well represented and it is because of this reason that their skulls have been picked out. Measurements of the skulls of this and other museums will be used to be able to put an age on this collection. Before this, a short overview of the geology of the area, as well as some information on the rest of the fauna of the White River Badlands is given, to provide a full picture of exactly how the oreodonts lived. This will be done mainly with the information the first researchers collected, since they were the first ones to describe these subjects and their views have formed the way we think now. Also, when the material was bought in the late nineteenth century, this was all the information that was available to the collectors. By using the same data they had access to, a better understanding of how important researchers such as Wichmann could use the material will be achieved.

The goal of this research is to put a species name and age on the White River material in the collection of the University Musuem. This is done by comparing the material and measurements taken on this material to available literature on the oreodonts. Material from different collections has been used to expand the dataset. Skulls have been used to put a species name, and age, on the material. Their molars have been used to be able to tell something about the diet of the different genera. Because the material of the University Museum is bought in 1899, an overview of the knowledge on the White River Badlands that was available during that time will also be given, together with the most recent views. As an appendix, some data collected from endocasts of two species will be given, since this gives a good picture of what happened during the dwarfing trend of the Miniochoerinae.

1.1 Acknowledgements

I would like to thank Wilma Wessels for introducing me to the subject and for giving advice on how I should construct my research. I am also thankful for Paul Lambers who was so kind to lend me the fossil material, and for Frans van den Hoven for showing me the skull in the University Museum, and letting me see the catalogues. I would also like to thank NCB Naturalis and Teylers Museum for letting me measure their material, and in particular John de Vos, who arranged for both museums that this was possible, gave some good advice on how to write my report and also gave me a very informative tour through Teylers Museum. Marijn van Hoorn from the Library of Teylers Museum took the time to find the early works of Leidy for me. George Lyras helped me with finding literature on oreodont endocasts. Last, I want to thank Jelle Reumer, for being my second supervisor and checking my report.

2. A short overview of research around the beginning of the twentieth century (with some notes on current views).

2.1 Geological setting

The White River Badlands sediment deposits, which are exposed widely in southwestern South Dakota, northwestern Nebraska and north Wyoming (Prothero and Emry, 2004), range from the Cretaceous until the Holocene (see Figure 3).

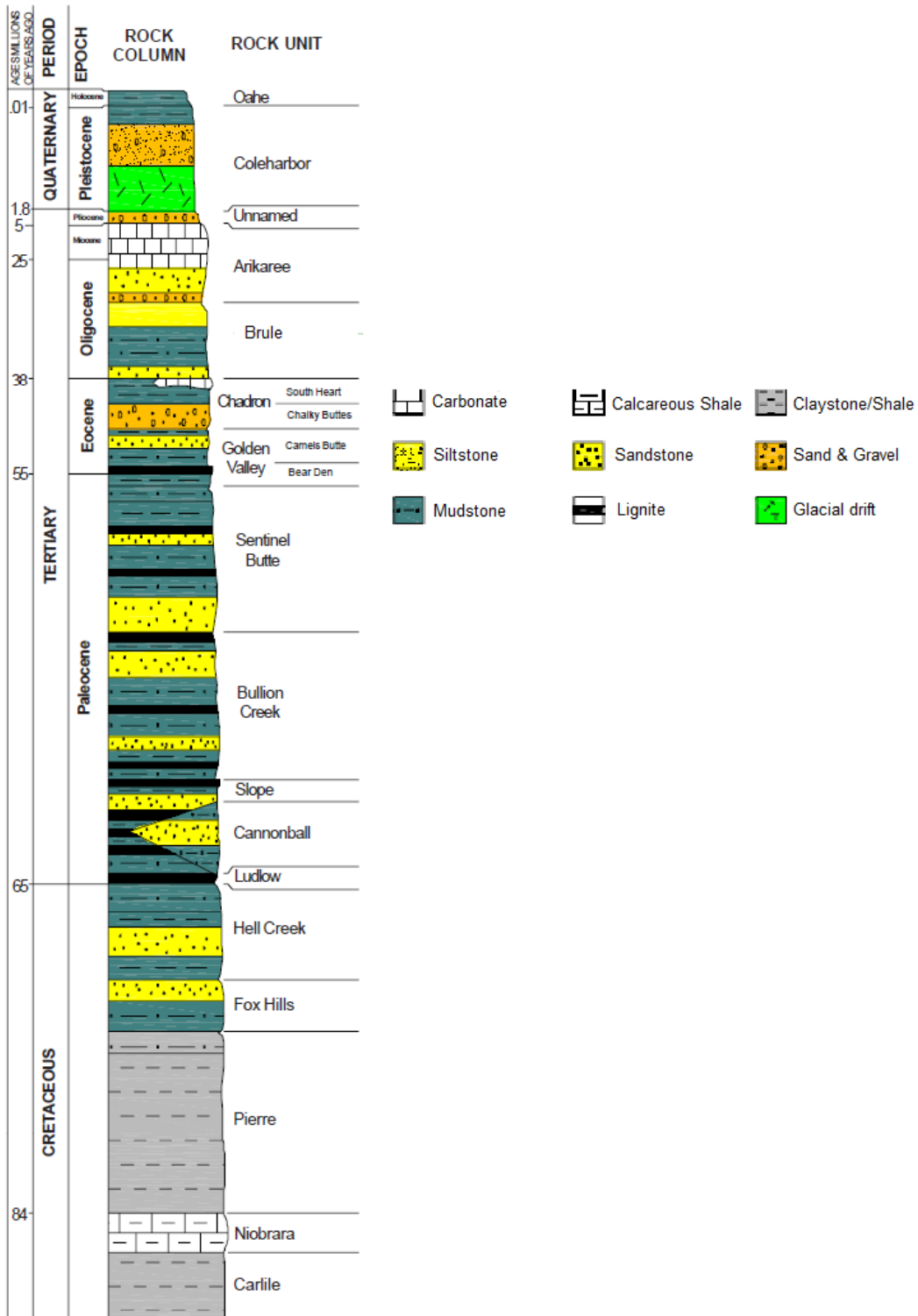


Figure 3. North Dakota stratigraphy. From: <http://www.nd.gov/>.

The area underwent a transition from a vast salt sea in the Cretaceous with muddy bays, to a shallow sea with still brackish conditions present. Tectonics and intrusions of igneous rocks shape the nearby Black Hills and Rocky Mountains and the shallow sea disappears completely and is replaced by freshwater marshlands and deltas. In the Tertiary the White River Badland formations are deposited. New groups of animals are found and in the Late Eocene and Early Oligocene. In Eurasia

and North America there is a similarity in the land mammals that come into existence during this time, for example among the hyaenodontids, several families of fissiped carnivorans, anthracotheriids, tapirids rhinocerotids and several families of rodents. This indicates that Beringia must have been an effective land bridge of land-vertebrate dispersal between North America and Eurasia (Savage and Russell, 1983).

The composition of the sediment differs between different localities and beds. The older deposits are often fine clays interlaid with sand and gravel beds. Limestones are particularly common along the outer margins in the Black Hills region, as well as conglomerates. Volcanic ashes occur at several horizons, and cover great areas in younger formations, mainly in the *Titanotherium* Beds and the Rosebud Beds (Wanless, 1923) (See figure 4 for the different sediments found in the White River member).

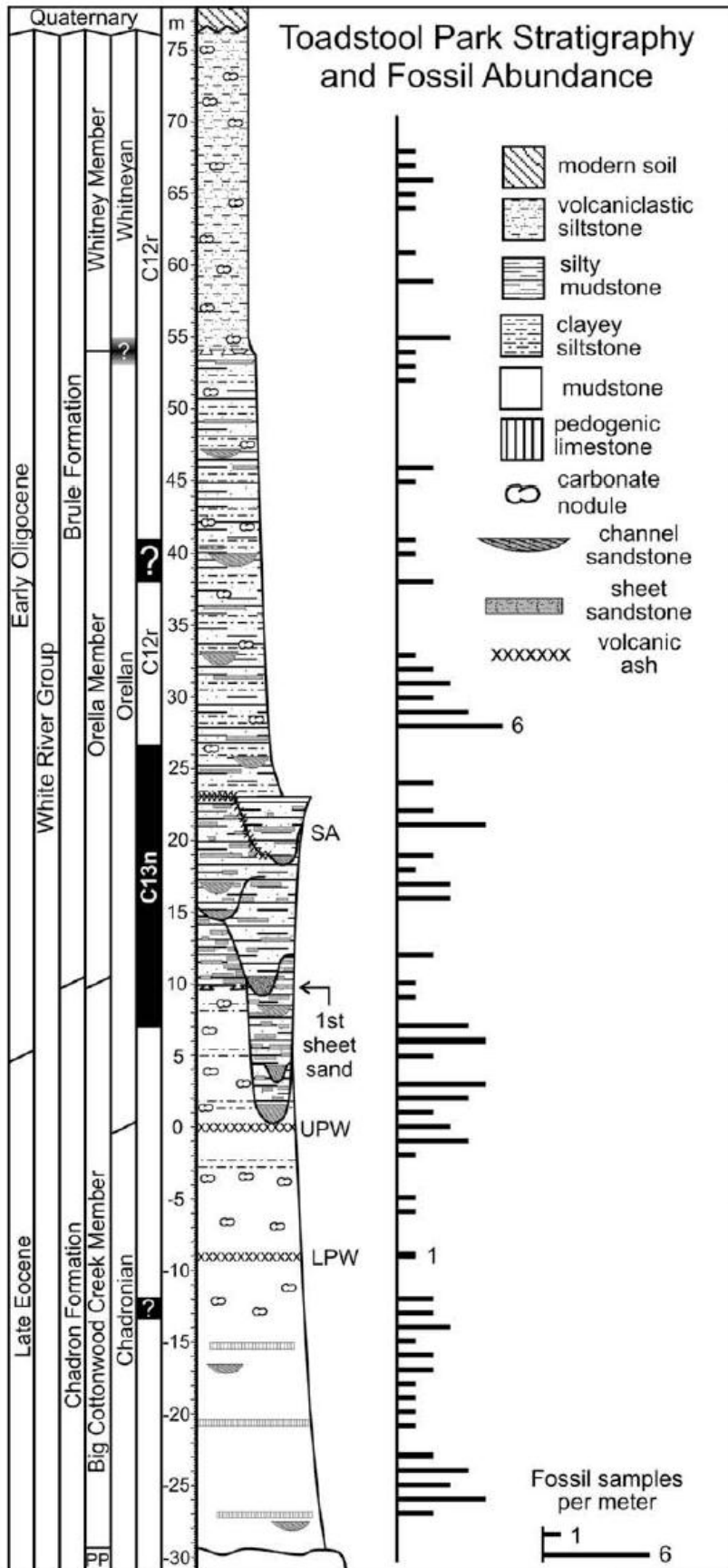


Figure 4. Measured section of the White River Group at Toadstool Geologic Park, NE. Length of bars indicates the number of bones obtained within a 1 m interval (From: Terry, 2009).

Overall, the formations have characteristics that make them easy to distinguish in the field. The Eocene and Oligocene formations are examined here in more detail. This will be done using first the data collected by O’Harra (1920), to fit in the historic overview, and supplementing this with data collected in more recent research.

Eocene and Oligocene Formations

Most fossils of the White River Badlands are found in what were once thought to be the Oligocene layers. Because this epoch consists of two distinct layers of sediments, it is subdivided in the early literature into two formations: the Chadron Formation (also known as the *Titanotherium* beds) and the Brule Formation. The latter can be subdivided into the *Oreodon* Beds and the *Protoceras* Beds. Figure 5 gives an overview of the different formations and the subdivisions within them. As can be seen in this figure, the division of the sediments into the different epochs changed considerably in 45 years. Because of the many changes in these divisions, an overview of the different interpretations through time will be given here.

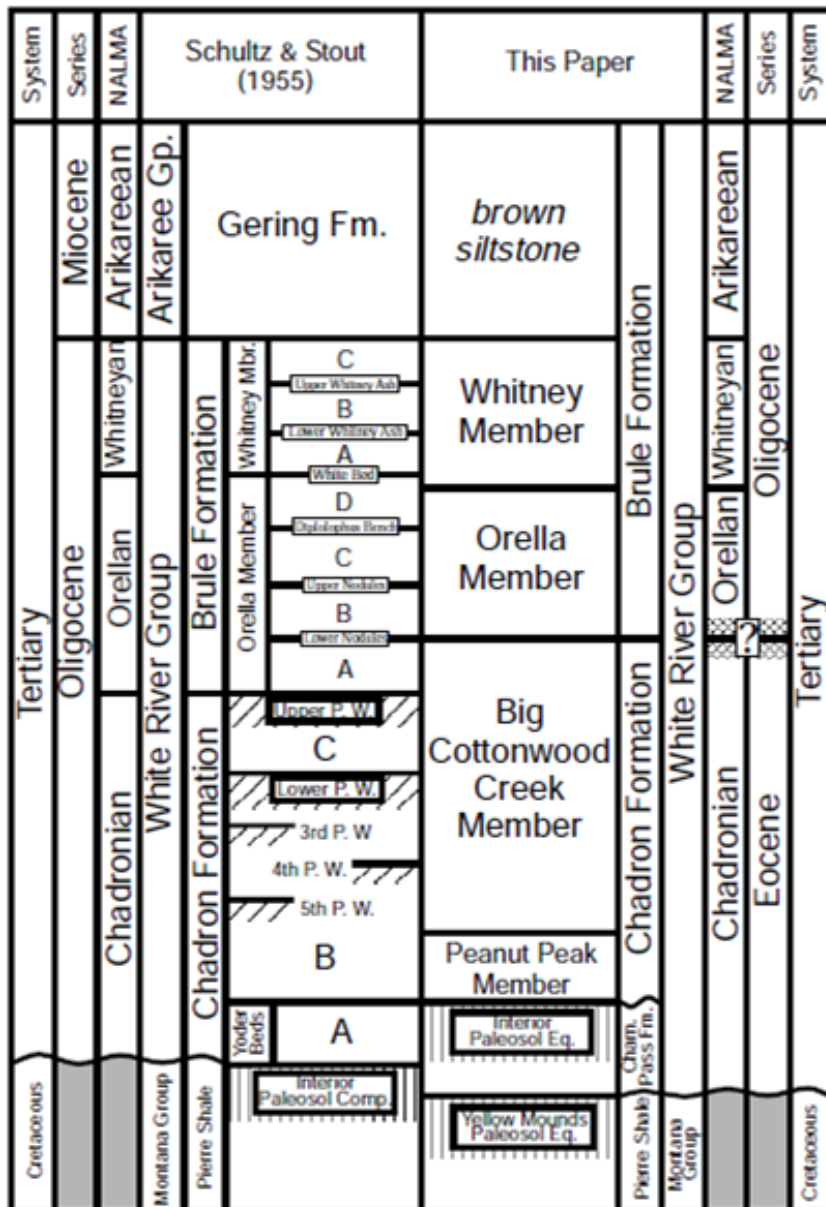


Figure 5. Stratigraphy of the Toadstool Park area. From: Terry (2001).

The Chadron Formation

This formation is best developed in the Big Badlands of South Dakota. The fossils in these sediments do not only include mammals, but also reptiles, marsupials and birds. The formation is made up mainly of sandy clays with a light green colour, which is more of an olive green at fresh exposures. At the bottom there are generally coarser sandy materials, sometimes with gravel or conglomerate deposits of several feet thick. The conglomerate beds are less than a metre thick. They are quite hard, and are held together by carbonate of lime. Immediately above these gravels, the clay beds have a yellow, pink, red or brown colour. At some places the clays are interpreted as plastic and sedimentary, but for the largest part they contain sand. Even though the clays are often compact, there is no cementing material present. Between these clays, thin persistent bands of grey limestone

or lime clay concretions occur. Then they weather, they get a chalky white colour and some of these bands can be followed over large areas (O’Harra, 1920).

The sequence of sandstones, clays and conglomerates varies a lot over the whole area. The maximum thickness of the formation is about 55 meters. Based on the nature of the titanotheres found in the various horizons, it can be subdivided into the Lower (15 m), Middle (30 m) and Upper (9 m) Chadron Formation (O’Harra, 1920).

In 1937, Clark (In: Prothero and Emry, 2004) had proposed a threefold division of the Chadron Formation into Ahearn, Crazy Johnson and Peanut Peak members.

In 1941, Wood *et al.* (In: Prothero and Emry, 2004) defined the Chadronian as the time in which *Mesohippus* and titanotheres coexisted. This included the *Titanotherium* beds. The type locality is near Chadron, Nebraska, the type area northwestern Nebraska and southwestern South Dakota. The problem with this definition is that it combines lithostratigraphy and biochronology. As long no remains of *Mesohippus* or titanotheres were found, it remained workable, but in 1953, titanotheres bones were found by Morris Skinner at 6.5 metres above the “Persistent White Layer”, which had been the marking of the Chadronian-Orellan boundary.

In 1996, Prothero and Emry (In: Prothero and Emry, 2004), decided that the first appearance of *Bathysgenys*, *Merycoiodon dunagani*, *Brachyrhynchocyon dodgei* and *Archaeotherium* are the best indicators of the start of the Chadronian, with *Bathysgenys* as defining taxon. This fauna places the Duchesnean-Chadronian boundary at a mean $^{40}\text{Ar}/^{39}\text{Ar}$ date of 37 Ma.

By 1998, the Chadron formation is placed in the Eocene (see figure 5) and subdivided into three layers (see figure 6). Chadron A consists of basal sands and conglomerates, Chadron B and C consist of mudstones. Chadron B is bluish-green and rich in smectite. Chadron C knows many cliffs, is siltier and knows a wide variety of colours. On top of Chadron C lies volcanic ash in a purplish-white layer (Terry, 1998).

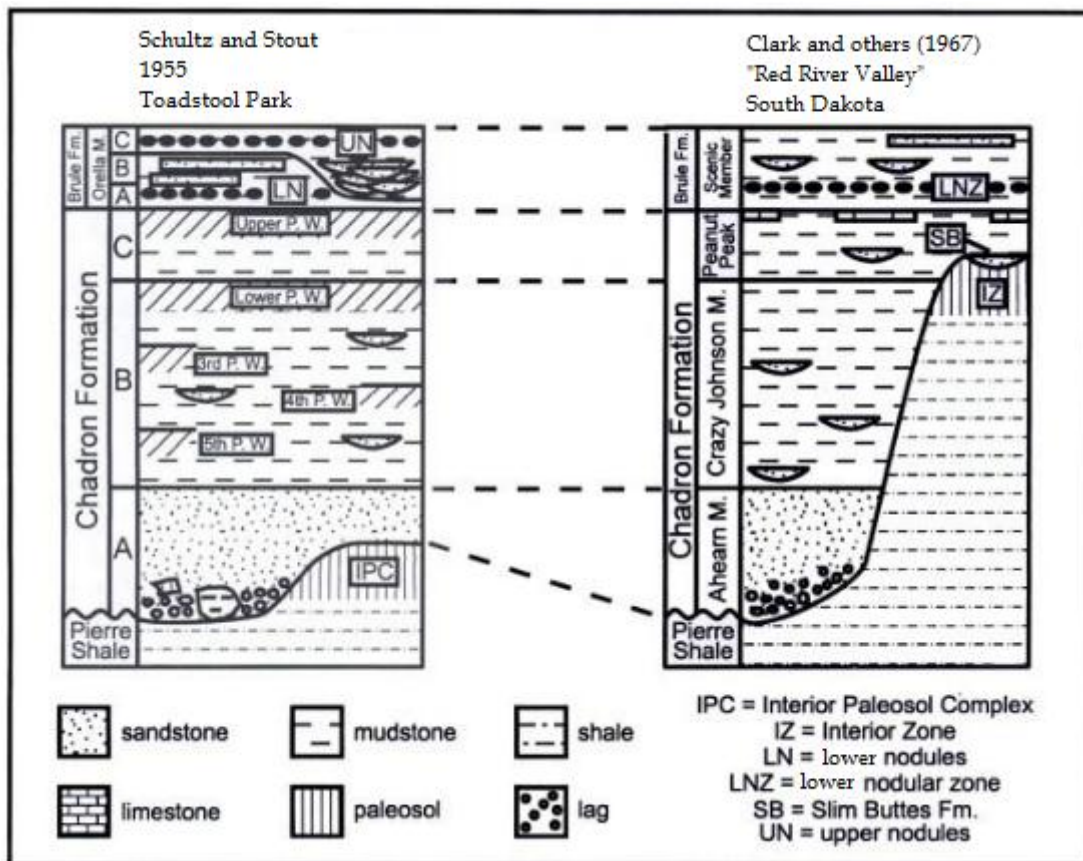


Figure 6. Stratigraphic terminology of the Chadron formation. From: Terry, 1998.

In 1998, there was still the problem of the infrequent and variable occurrence of the latest titanotheres and the definition of Wood *et al* from 1941 was insufficient. Prothero and Whittlesey (in Prothero and Emry, 2004) recommended to place the Chadronian-Orellan boundary at the first appearance of *Hypertragulus calcaratus*, along with other reference taxa.

In 2004, Prothero and Emry designated four biostratigraphically defined intervals, calibrated by magnetostratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ dating. These new intervals were necessary, since the old intervals still used lithostratigraphic units for biochronologic and biostratigraphic concepts and the range of key fossils was poorly documented. These four new intervals are the ones that are used at the moment and will be described in short detail with some faunal information. The information given on these intervals comes from Prothero and Emry (2004).

The first interval is the Earliest Chadronian and ranges from 36.5-37.0 Ma, thus falling into magnetic chron C16r. The base of the section at Flagstaff Rim, Wyoming is the best representative of the interval. Since, among others, *Bathygenys* had its first appearance in this interval, it could be known as the *Bathygenys* Interval Zone. Other taxa that made their first appearance were: *Merycoiodon dunagani*, *Brachyrhynchocyon dodgei* and *Archaeotherium*.

The second interval is called the Late Early Chadronian and ranges from 35.7-36.5 Ma, which correlates with magnetic chron C15n2. For this interval too, the main reference section is at Flagstaff Rim, Wyoming. Taxa which appear in and are limited to this interval include: *Paleolagus primus*, *Merycoidodon presidioensis*, *Pseudoprotoceras semicinctus*, *Litoyoderimys lustrorum*, *Yoderimys stewarti* and *Leptomeryx yoderi*. There were also some taxa that appeared in this interval, but ranged into the next, including: *Daphoenictis tedfordi*, *Hyaenodon montanus*, *Ischyromys veterior*, *Centetodon chadronensis*, *Parvitrugulus priscus*, *Patriomanis americanus*, *Trigenicus profectus* and *Sinclairiella dakotensis*. The interval could also be called the *Leptomeryx yoderi* Interval Zone.

The third interval, the Middle Chadronian is known for its large fossil collections. It correlates with the fauna of the Crazy Johnson member of Clark (1937) and magnetic chrons C15n-C15r. It has also been dated with $^{40}\text{Ar}/^{39}\text{Ar}$, biotite and anorthoclase, resulting in a mean age of 34.7-35.7 Ma. The type section is in the Flagstaff Rim section, from 15 meters below Ash B till 15 meters above Ash G. The interval could also be called the *Leptomeryx mammifer* Interval Zone. Taxa that are limited to this interval include: *Leptomeryx mammifer*, *Zemiodontomys burkei*, *?Miniochoerus forsythae*, *Prosciurus vetustus*, *Hyaenodon microdon*, *Hyaenodon megalodon*, *Chadrolagus emryi* and *Frictops emryi*. Taxa that have their first appearance in this third interval but extend beyond it include: *Palaeolagus temnodon*, *Dinictis felina*, *Meliakrounomys*, *Eutypomys magnus*, *Mesohippus westoni*, *Leptomeryx speciosus*, *Pseudoprotoceras longinaris*, large *Ischyromys*, *Hoplophoneus mentalis*, *Miohippus grandis* and *Megalagus brachyodon*.

The fourth and last interval of the Chadronian is the called the Late Chadronian. The Flagstone Rim section does not carry many fossils from this age, so it is typified by the Seaman Hills section in Niobrara County, Wyoming. The strata correlates with late magnetic chron C13r-C15n. $^{40}\text{Ar}/^{39}\text{Ar}$ dating agrees with this, and the dating for this interval is 34.7-33.7 Ma. At Flagstone Rim, only a few taxa, including *Pseudoprotoceras taylori*, are limited to this interval. In other sections, there are first appearances of *Merycoidodon culbertsoni*, *Poebrotherium franki*, *Miniochoerus chadronensis*, *Ischyromys typus*, *Mesohippus exoletus*, *Mesohippus bairdi* and *Scottimus viduus*. Taxa that last appear in this interval and terminate at the Chadronian-Orellan boundary include: Brontotheriidae, *Xenocranium*, *Hoplophoneus mentalis*, *Miohippus grandis*, *Mesohippus westoni*, *Eotylopus reedi*, *Poebrotherium eximium* and *Archaeotherium coarctatum*. The interval could also be called the *Miniochoerus chadronensis* Interval Zone.

The Chadron formation is followed by the Orellan member of the Brule formation. The $^{40}\text{Ar}/^{39}\text{Ar}$ date of 33.91 ± 0.058 Ma of the Chadronian-Orellan boundary falls very close to the Eocene-Oligocene boundary of 33.7 Ma. As could be seen in the Late Chadronian, many taxa terminated in a short span of stratigraphic section at this boundary (see figure 7). Affected taxa were the titanotheres, the camel-like oromyricids, the mole-like epicotheres, the pantolestids and the

paramyid and cylindrodont rodents. Most of these taxa were not replaced in the early Orellan. There was a diversification of eumyine cricetid rodents and leptauchenine oreodonts appeared. The deer-like *Leptomeryx* and the camel *Poebrotherium* specialized and the oreodont *Miniochoerus* had a reduction of 36 percent in size. Apart from these specialisations and extinctions, the Orellan fauna was similar to that of the late Chadronian. Magnetostratigraphy suggest that the extinction event took no more than 200,000 years. Although this is very rapid, it should not be seen as catastrophic. The groups that went extinct were old, relic, groups of the Eocene and the changes in the species are spread out over the entire timespan. That all the other, here unmentioned, species did not undergo such dramatic changes, leads to the suggestion that there was no indiscriminate extra-terrestrial force at work. Most likely there was ecological and climatic change, since vegetation, soil and reptilians show the same patterns. $\delta^{18}\text{O}$ records of benthic foraminifera, and $\delta^{13}\text{C}$ records of planktonic foraminifera of this age point towards a cooling event. This was caused by a glacio-eustatic fall in sea level which resulted in a global cooling (Prothero, 1985).

In the Middle through Late Chadronian, the Miniochoerinae (except for *Miniochoerus starkensis*) showed a decrease in size. Their proportions stayed the same. In the Orellan, this trend was reversed. This could be because of the environmental stress that the changing climate brought. In the Orellan and Early Arikaree, this stress was relaxed (Stevens and Stevens, 1996).

Most plants known from the Eocene can be found in the Florissant Fossil Beds National Monument, Colorado. In this lake deposit the petrified remains of stumps giant sequoias can be found, together with the seeds, cones, flowers, pollen grains, twigs and leaves of 140 other plant species. The trees and scrubs that lived during this time have their closest descendants now living in south-eastern United States, Mexico and China, suggesting a flora unlike the one now found in the area. Types of plants that lived here were ferns, scrubs, redwoods, pines, cedars and mixed-hardwood. The plants are preserved by showers of ash which buried the dead plants in the lake (Sangress, 2012). Among the plants living in and near the lake were: duckweed (Lemnoideae), grasswort (*Liliopsis*), palms (Areacaceae), sedges (Cyperaceae), Dioscoreacea, grasses in the family Poaceae, pondweed (Potamogetonaceae), greenbrier (Smilacaceae), cattail (Typhaceae), many flowering species of the class Magnoliopsida, cypress (*Chamaecyparis*), pines of the genera (*Pinus*) and (*Picea*), sequoia (*Sequoia*) and yew (*Torreya*) (National Park Service, 2012).

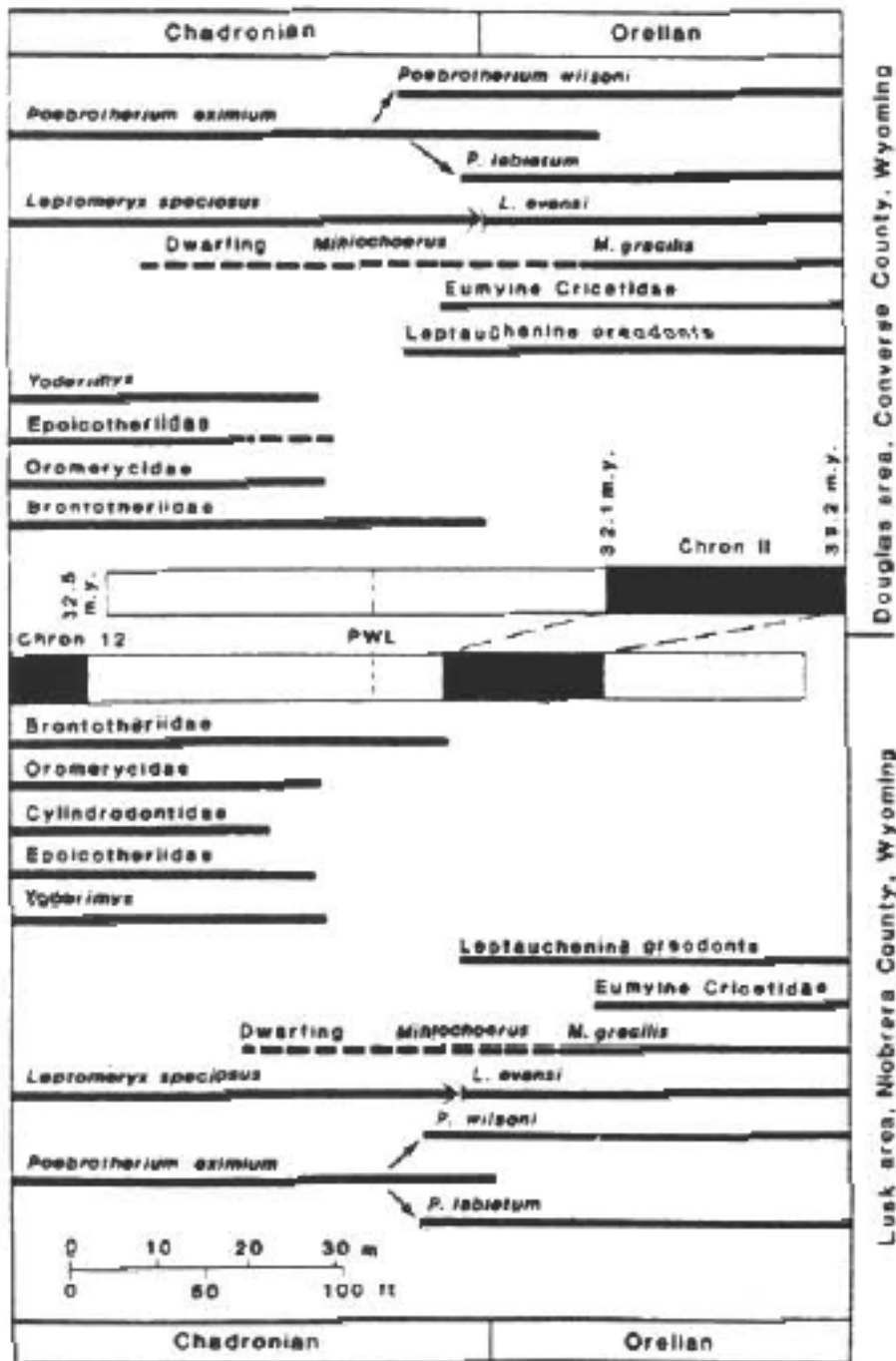


Figure 7. Stratigraphic ranges of mammals that are most strongly affected by the Eocene-Oligocene event in two areas in Wyoming: Douglas, Converse County and Lusk, Niobrara County (From: Prothero, 1985).

The Brule Formation

The Orellan and Whitneyan North American Land Mammal Age (NALMA) fall within the Brule Formation. By the time of O’Harra (1920), this division was not yet made. For that reason, the description by O’Harra of the Brule Formation will be given first, followed by a description of what are now known as the Orellan and Whitneyan.

The Brule Formation can be subdivided into the *Oreodon* beds and the *Protoceras* Beds. There are many layers of different sediments and they can be followed over large lateral distances (see figure 8 for the lithology) (O’Harra, 1920).

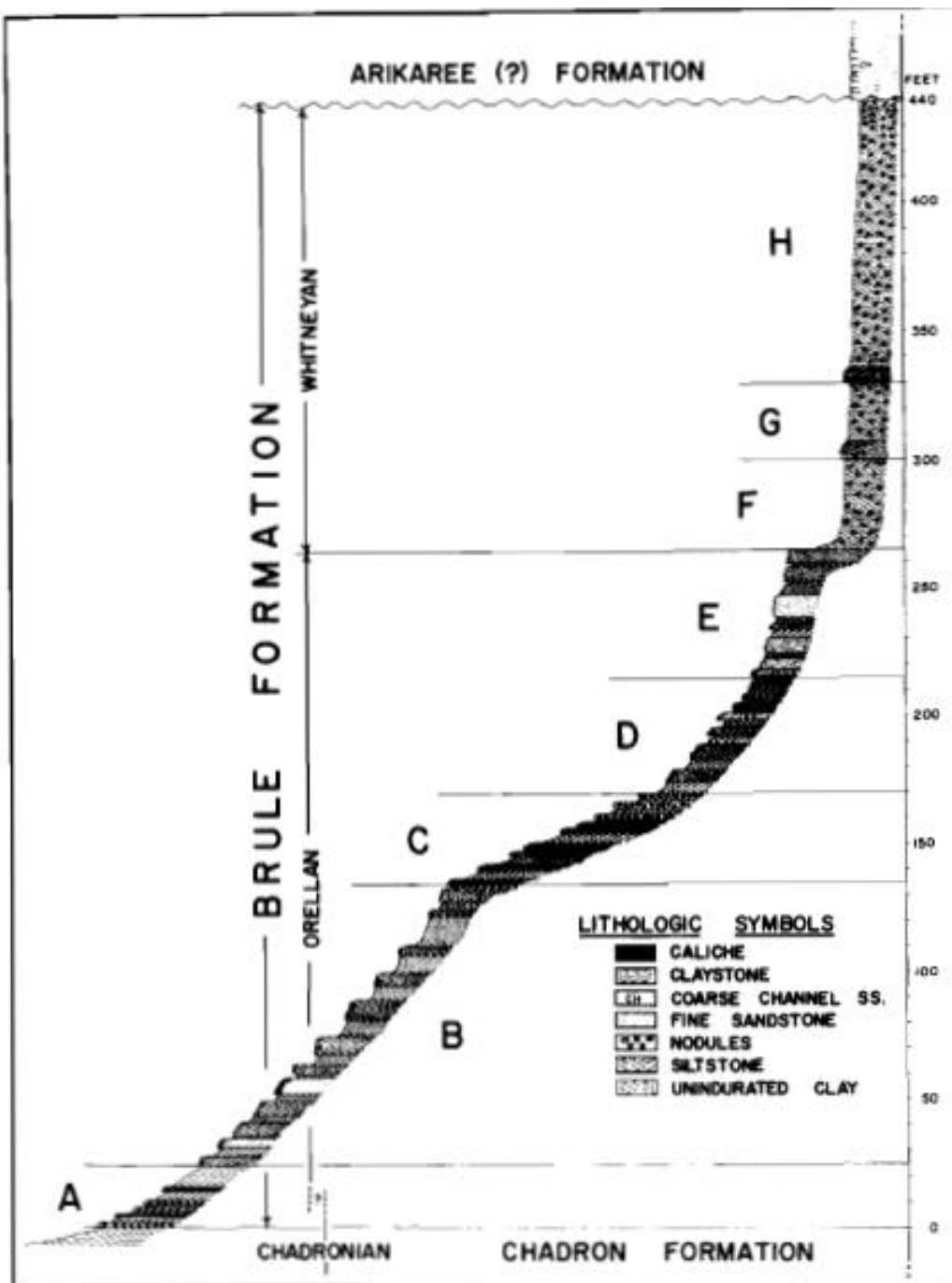


Figure 8. Composite section of the Brule Formation. From: Lillegraven, 1970.

The *Oreodon* beds consist mainly of arenaceous clays, lenticular sandstones and thin layers of nodules. In general, the colour of the beds is grey or faint yellow, but horizontal bands of pink, red or brown occur as well. They are present in varying thicknesses, up to a couple of feet, and can be traced for long distances. These bands sometimes show a repeating of the sequences. The

sandstones do not occur in many places, but when they do, they become quite thick. One large sandstone in the middle of the Big Badlands is abundant in rhinoceros fossils. On top of this sandstone are layers containing nodules. One of these, twelve to fifteen meters above the *Titanotherium* beds, is very important, because it can be traced over a very great distance and the nodules contain fossils of oreodonts and turtles. The fossils are of a reddish cast and have a scale of ferruginous oxide. Twenty till thirty metres above this layer is another one with many fossiliferous nodules. Above this lies a thirty metre thick layer of non-fossiliferous clays. In total, the Oreodon beds are somewhere between 75 and 90 meters thick (O’Harra, 1920).

Above the *Oreodon* beds lie the *Protoceras* beds. First they were considered part of the *Oreodon* beds, but in 1893, J. L. Wortman (in: O’Harra, 1920) differentiated them. The beds are named after the many *Protoceras* fossils that are found here in the sandstones. The beds consist of coarse sandstones, fine-grained clays and nodular layers. The sandstones usually contain fossils, and do not continue far horizontally. On the edges, the sandstones turn into barren clays. Above the sandstones sequence lies a pinkish clay with nodules. Many *Leptauchenia* fossils can be found here, which is the reason these beds are often called *Leptauchenia* zone. In total, the beds (*Protoceras* and *Leptauchenia* zone together) have a thickness of 45 till 55 meters (O’Harra, 1920).

In 1941, the Wood committee (in: Prothero and Emry, 2004), based the Orellan on the Orella member of the Brule Formation. This included the *Oreodon* beds. Orella in northwestern Nebraska, southwestern South Dakota and eastern Wyoming was the type locality. Just as was the problem with the Chadronian, this was a biochronologic concept based on a lithostratigraphic unit. In this same year the committee based the Whitneyan on the Whitney Member of the Brule Formation, with Whitney, northwestern Nebraska as type locality. This too was a biochronologic concept based on a lithostratigraphic unit. Many fossils have been zoned to one of the three subdivisions that can be seen in figure 8.

In 1956, the upper member of the Brule Formation, of Whitneyan age, primarily known as the *Protoceras* beds, was called the Poleslide member. This member could be divided into three units: a unit of barren clays capped with a grey clay band, a unit with *Leptauchenia* nodules and channel sandstones and a unit of vertically weathered silty ash (Bump, 1956).

By 1970, the Brule formation had known many names. Turtle and *Oreodon* beds, the Orella member, *Leptauchenia* beds and *Protoceras* beds all have been used. The lithology of the Brule formation is uniform over large areas, but there is a lot of lateral variation. In the North-South direction, this variation is the largest. The differences also make it difficult to distinguish the different members (Lillegraven, 1970). The Brule formation was still subdivided into two members. The lowest being of Orellan age and consisting of the formerly known *Oreodon* beds, minus the upper *Oreodon* bed and then called the Scenic member. This member can be further divided into two units: the

lower and upper nodular zone. The member is more fossiliferous than the member on top of it (Lillegraven, 1970). It was not sure if the two members follow a continuous sedimentation or not, because the paleontological data is not consistent with the stratigraphic data (Lillegraven, 1970).

In 1998, Terry (in: Prothero and Emry, 2004) transferred Orella A to the Chadron Formation. This meant that the lithostratigraphic Chadron-Orella boundary corresponds more closely to the of the biochronologic and biostratigraphic boundary. Also, the term 'Oreodon beds' applied to many rocks of non-Orellan age. By this new division, all the titanotheres that have been found fall into the Chadronian, so there is no longer a conflict with the Wood committee's criteria for placing the Chadronian-Orellan boundary at the last occurrence of the titanotheres. This is why in the same year, Prothero and Whittlesey (in: Prothero and Emry, 2004) recommended that the Chadronian-Orellan boundary should be redefined as the first appearance of *Hypertralagus calcaratus*, with the first appearances of *Leptomeryx evansi*, *Palaeolagus intermedius* and the small form of *Miniochoerus chadronensis* as characterizing biostratigraphic datums. Another way of defining this boundary is with the last appearances of *Poebrotherium eximium* and *Miohippus grandis*, giving the titanotheres a smaller role.

In South Dakota, there is an unconformity at the Chadron-Brule contact. This can be seen as an abrupt change in sedimentation, since the climate had changed from humid to arid during this time (Terry, 2001).

In 2004, Prothero and Emry described the following division for the Orellan and the Whitneyan based on formal biostratigraphic zones:

The Earliest Orellan is also called the *Hypertralagus calcaratus* Interval Zone. It correlates with the latest part of magnetic chron C13r and the earliest part of chron C13n, giving it an age of 33.7-33.4 Ma. The type section for this interval is the strata 7 to 17 meters above the Douglas area. Apart from *Hypertralagus calcaratus*, *Leptomeryx evansi* and *Palaeolagus intermedius* also have their first appearance. The interval ends at the first appearance of *Miniochoerus affinis*.

The Late Early Orellan, also called *Miniochoerus affinis* Interval Zone is the next interval of the Orellan. It correlates with the later part of magnetic chron C13n and has an age of 33.4-33.1 Ma. The type section is the strata between 17 and 17 meters above the Persistent White Layer of the Chadronian in the Boner Ranch section in the Seaman Hills, near Lusk, Wyoming. Not only *Miniochoerus affinis* makes its first appearance during this interval, also *Eumys elegans*, *Pelycomys brulanus*, *Adjidaumo minutus*, *Cedromus wardi* and *Hoplophoneus occidentalis* appeared during this time. The interval ends with the last appearance of *Ischyromys parvidens* and the first appearance of *Miniochoerus gracilis*.

The Early Late Orellan is also called the *Miniochoerus gracilis* Interval Zone. This dwarfed oreodont had its first appearance in this zone, together with *Mesohippus barbouri*, *Agnotocastor*

reading, *Paradjidaumo validus*, *Eutypomys thomsoni* and *Eumys parvidens*. The end of this zone is characterized in the first appearance of *Merycoiododon bullatus*. The zone correlates with the latest part of chron C13n and the early part of chron C12r, giving it an age of 33.1-32.5 Ma. The type section is the next 25 meters at the Boner Ranch section.

The last part of the Orellan is the Latest Orellan. The type section of this interval is the Upper Nodular Zone on the east side of Sheep Mountain Table in the Big Badlands. The upper part of what were first called Orella C and Orella D are included. The beds correlate with the early part of magnetic chron C12r, giving it an age of 32.0-32.5 Ma. This interval can also be called the *Merycoiododon bullatus* Interval Zone. The Latest Orellan knows many distinctive taxa. Species that had their first appearance here include: *Merycoiododon bullatus*, *Miniochoerus starkensis*, *Palaeolagus burkei*, *Prosciurus magnus*, *Ecclesimus tenuiceps*, *Tenudomys basilaris*, *Pelycomys placidus*, *Heliscomys vetus*, *Heliscomys mcgrewi*, *Wilsonemys planidens* and *Campestrallomys annectens*. Many taxa that were very characteristic for the Orellan have their last appearance in this interval, including *Hyaenodon crucians*, *Ischromys typus*, *Paratylopus labiatus*, *Archaeotherium mortoni*, *Thinohyus lentus*, *Stibarus quadricuspis*, *Leptochoerus emilyae*, *Subhyracodon occidentalis*, "*Hesperocyon*" *coloradensis*, *Prosciurus*, *Pelycomys*, *Protociurus*, *Oligospermophilus*, *Eutopomys*, *Adjidaumo*, *Paradjidaumo*, *Heloscomys*, *Wilsonemys*, *Eoeumys*, *Tenudomys*, *Pipestoneomys*, *Megalagus*, *Palaeolagus intermedius*, *Centetodon marginalis*, *Leptictis haydeni*, *Herpetotherium fugax*, *Copedelphys stevensoni*, *Nanodelphys hunti* and all surviving species of *Mesohippus*. That there are many small mammals among these taxa could be an artifact of poor collecting, but the larger mammals certainly had their last occurrence in the Last Orellan.

In 2001, the first good assemblage of plant material from the Oligocene portion of the White River Formation was found. In the Swan Lake plant locality leaves of willow, cattail and horsetail, stems and twigs of bamboo and pine, roots, seeds, pollen and grasses have been found (Sundell, 2001). The plant material was accompanied by many gastropods, arthropods and bivalves typical for a lake environment. The deposits lie fifteen meters above the Chadronian-Orellan boundary. Because the environment at the White River Group is often alkalizing and oxidizing, not many plant remains can be found. The acidic and reducing nature of the lake made preservation possible. Just as in the Florissant Fossil Beds National Monument, Colorado, the problem is that only plants that lived in or near the lake, or that had means of transportation to the lake are preserved, so these plantfossils do not give a complete overview of the flora of the time.

The Orellan is followed by the Whitneyan. Fossils from this age are scarce and sparsely distributed. The Whitneyan is now divided into two biostratigraphic zones.

The first zone is the Early Whitneyan, which is also called *Leptauchenia major* Interval Zone. Many fossils of *Leptauchenia decora* have been found here. This species is not limited to the Early

Whitneyan, since it also appears in older rocks. Taxa that had their first appearance include: *Leptauchenia major*, *Hydracon leidyani*, *Paratylopus primaevus*, *Paralabis cedrensis*, *Diceratherium tridactylum*, *Protapirus obliquidens*, *Ectopocynus antiquus*, *Oxetocyon cuspidatus*, *Cynodesmus thooides*, *Agnotocastor praetereadens* and *Oropycotis pediasius*. Taxa that had their last occurrence include: *Miniochoerus starkensis*, *Stibarus obtusilobus*, *Hyaenodon horridus*, *Cedromus wilsoni*, *Metadjidaumo hendryi*, *Agnotocastor praetereadens* and *Oropycotis pediasius*. The type section is the Upper *Oreodon* Beds on the south side of Sheep Mountain Table in the Big Badlands of South Dakota. It correlates with the middle of magnetic chron C12r, giving it an age of 32.0-31.4 Ma. $^{40}\text{Ar}/^{39}\text{Ar}$ dating places the zone at 31.8 ± 0.023 Ma.

The second zone is the Late Whitneyan, also called the *Merycoidodon major* Interval Zone. It correlates with late magnetic chron C12r to early chron C11r, or 31.4-30.0 Ma. Two $^{40}\text{Ar}/^{39}\text{Ar}$ datings gave an age of 30.58 ± 0.61 Ma and 30.05 ± 0.19 Ma. The type section for this interval is the strata between thirty and 103 meters above the Scenic-Poleslide contact on the south side of Sheep Mountain Table. Traditionally, this interval consists of the *Protoceras* beds and the *Leptauchenia* beds or Whitney B-C in Nebraska. Based on the faunal change, rather than litology, it is now seen as one interval zone. Taxa that had their first appearance here include: *Merycoidodon major*, *Protoceras celer*, *Pseudolabis dakotensis*, *Miohippus intermedius*, *M. annectens*, *M. equianus* and *M. gidleyi*, *Hoplophoneus dakotensis*, *Eusmilus cerebrialis*, *Nimravus brachyops*, *Hyaenodon brevirostris*, *Eumys brachyodus* and *Scottimus lophatus*. Taxa that had their last occurrence include *Palaeolagus burkei*, *Leptomeryx*, *Merycoidodon*, *Paratylopus*, *Paratylopus*, *Paralabis*, *Perchoerus*, *Heptacodon*, *Leptochoerus*, *Colodon*, *Protapirus*, *Hesperocyon*, *Osbornodon*, *Dinictis*, *Paradjidaumo*, *Eumys* and *Scottimus*.

Miocene

Above the Oligocene deposits, the Miocene sediments can be found. Since the focus of this paper lies on the Oligocene, only a short description of these and later deposits will be given here.

The top of the Brule formation has partly eroded, revealing the Precambrian depositions. On top of this Miocene deposits can be found, although not in the whole area (see figure 9). The lowest Miocene sediments often contain reworked Brule sediments, making it hard to determine the actual boundary between the two epochs (Lillegraven, 1970). A boundary has been placed at about 30 Ma, based on the first appearance datum of several species, including the oreodont *Mesoreodon minor* (Prothero and Whittlesey, 1998).

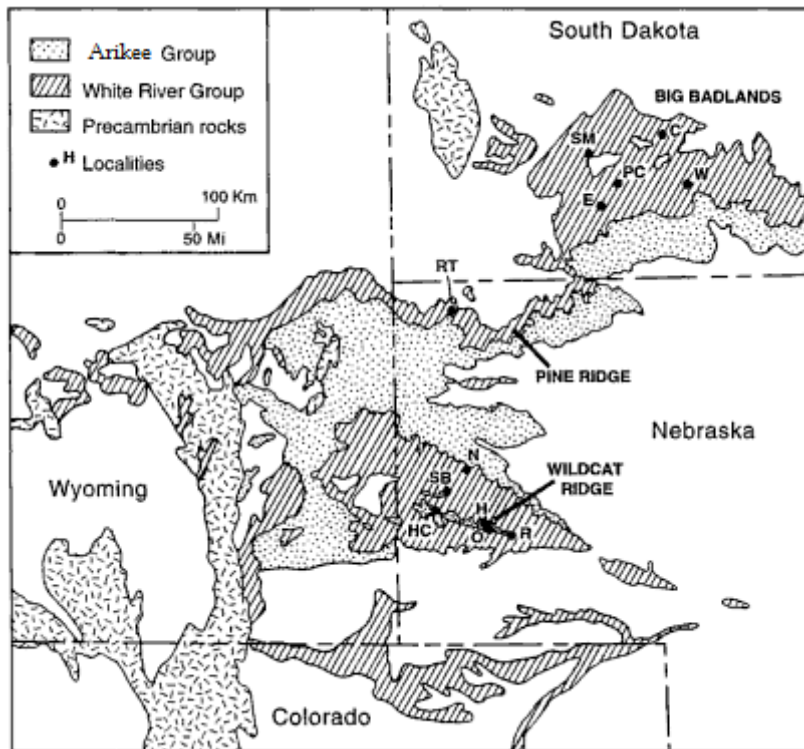


Figure 9. Distribution of Precambrian, White River and Arikaree strata. From: Hoganson *et al.* 1998.

The Miocene is subdivided into the Lower, Middle and Upper Miocene. The Lower Miocene can be further subdivided into the Arikaree formation and the Rosebud beds (O’Harra, 1920).

The Arikaree formation of the Lower Miocene consists mainly of sandstone with a white or grey colour. There are many calcareous concretions. Lithologically and faunally, the Arikaree can be even further subdivided into the Monroe Creek beds, and the Harrison beds above those. The first consist of ninety meters of light coloured, fine-grained massive sandstones and contain little fossils. The Harrison beds are sixty meters of fine-grained incoherent sandstones, with vertical siliceous tubes penetrating them. Also the Daemonelix, corkscrew-like structures in the sediment, which are the fossilized burrows of rodents, for example *Paleocastor*, can be found here (O’Harra, 1920). The present opinion is that the Arikaree falls into the Oligocene (Terry, 2001).

The Rosebud beds above the Arikaree formation are 150 meters thick. At the bottom they are hard clays, followed by softer and sandier layers, topped with quartzitic sandstone. White, flinty calcareous layers occur, and in the middle of the beds, one larger one splits the Rosebud beds in half. In the upper half there are many channels of sandstones and mud-conglomerates. On top of the formation lies a bed of volcanic ash.

The Middle Miocene is about 30 meters thick and consist of soft, fine-grained sandy clays with a yellow-brown colour with calcareous layers. On top lies a layer of volcanic ash with a thickness of sixty centimetres.

The Upper Miocene is represented by the Nebraska beds. They have a thickness of about 45 till sixty metres. The colour of the sandstone is a yellowish brown, and layers of siliceous grits occur (O'Harra, 1920).

Pliocene

Pliocene deposits are very irregularly distributed in the area. They are of a Lower Pliocene age and their fossils are important, because not many fossils of that age are found in North America. But since the animals living in the Pliocene came into existence long after the oreodonts went extinct, these will not be mentioned here, but they include rhinoceroses and horses.

2.2 Paleoenvironment and paleoclimate; a historic overview of interpretations.

In the fifties and sixties of the eighteenth century, the Cenozoic of the White River Badlands of North America was a subject of exploration and many expeditions. Since the first expeditions, there have been many interpretations on the formations of the White River sediments of the Oligocene. The first people to examine the sediments of the area thought them to be a succession of vast fresh-water lakes. The main body of the formation consists of fine-grained calcareous clay, with intercalated beds and lenses of sandstone, pointing indeed to a lacustrine environment (Matthew, 1899). There are, however, a few difficulties with this interpretation, which will be discussed in short below. Some examples of the different hypotheses will be given. By comparing how the different researchers thought about the area, a good overview of the stratigraphy, but also a picture of how the scientific work in the area evolved, can be acquired. This chapter is an historic overview, showing the work of the earliest researchers in the area. Of course, since these first examinations, many other hypothesis regarding depositions and paleoenvironment have been made, so after the theory of Matthes (1899) and the theories following his, as summarized by Wanless (1923), this chapter will end with some of the latest interpretations.

When Culbertson (Culbertson (1851) in: Wanless, 1923) went to the Badlands in 1850, he saw in the landscape that the hills had not been lifted up, but instead that the land between them had sunken. Dutton (in: Wanless, 1923) was one of the first to assume that most of the area was once covered by a large lake. Several years later, in 1867, Hayden inferred that the White River lake must have had a surface area of almost 250,000 km² (Wanless, 1923).

Matthew (1899) was of the opinion that several lines of evidence point to a more aeolian setting in which the bones we now find were buried. This made him the first one to abandon the lacustrine theory (Wanless, 1923).

As Mattheew explained in 1899, part of this evidence is of stratigraphic context. The White River Formation is found in Nebraska, Colorado, Wyoming and South Dakota. If these sediments are

lacustrine, a lake would have covered a huge area, dammed by barriers at the edges. Not only is there no indication of such barriers, there are also no wave-cut terraces, which would be expected with the size the lake was thought to have, and no stratification typical of lakes had been found in the clays (Matthew, 1899).

Other evidence comes from the floral record. The only remains of plants found in this area are from the fluvial layer on top of the clays, which are of a later than Oligocene age (later *Celtis* seeds and leaves were found). It should be noted that the deposits are very well fitted for preserving plant material. Also the found fossil fauna points in an aeolian direction. No fish or aquatic invertebrate fossils have been found, and the reptiles that are present lived on land. There are over fifty genera of mammals found but only three genera of aquatic mammals. These are confined to a single sandstone layer, and the fluvial beds on top (Matthew, 1899).

This evidence makes it unlikely that the area was once a big lake. Plant remains could have meant that the sediment is a delta bed of a lake, where the animals were deposited after being carried by rivers along with the plant material. Since there are no fossil plants found, the only other option is that the deposits of animals were far in the open lake. The lack of stratification makes it clear that there was no strong current and the animals must have just drifted very uniformly over the lake before sinking to the bottom. Especially when comparing this to more recent lake deposits, where fish and aquatic invertebrates are abundant, the lacustrine theory does not hold up very well (Matthew, 1899).

So if the deposits are not lacustrine, how were they formed? At present times, sediments are deposited by rivers and flood plains, and the wind carries prairie loess that has been eroded from arid areas. In the layers of loess, deposited in the Pleistocene, many remains of mammals can be found, some intact, others gnawed on or weathered, as well as traces of lagoons where mingled heaps of bones are situated. The way in which the animals in this layer are scattered and preserved, reminds of the Oligocene layers. It could well be that also the clay sediments from the Pleistocene were mainly deposited by the wind as well. Most of the intersecting sandstones will have a fluvial origin, although some might be Aeolian (Wanless, 1923).

With these new interpretations, a new idea of the climate and conditions during the time these beds were deposited was formed. According to Matthew (1899), the fact that the sediments are formed in the same way as in present times, means that the environment in the area in the past looked much like it does today. Thus the animals living at the time of deposition are expected to have lived in a grassy, open environment. Because the fauna is so abundant, it was expected that the animals lived in a warm and moist environment. However, when compared to present times, the most similar faunal composition can be found in the dry regions of South Africa (Matthew, 1899).

The theory of Matthew was followed in 1900 by the one of Johnson, who was also no supporter of the lacustrine theory, but instead believed that the sediments had an origin in the surrounding mountains and actually were a debris fan. In that same year, professor Fraas had developed yet another theory, in which the White River was a slow stream with a wide delta spread out towards the east, resulting in a swampy land that fell dry in the dry season, and flooded during the wet season. Not only the water, but also the wind brought in materials and. This was followed by a period with a shallow lake where evaporation exceeded the inflow of water and dissolved materials precipitated, which would explain the coloured bands and gypsum layers. On top of this dried out lake was then a deposit of loess (Wanless, 1923).

In 1902 Hatcher (in Wanless, 1923) thought that the sandstones, conglomerates and clays were deposited in river channels, while the limestone lenses, in which remains of molluscs and aquatic plants can be found, originated in shallow ponds and that finer clays were deposited by floodings or wind.

Ward was also in favour of the lacustrine theory, only in a modified form. He thinks that there was a cold or temperate humid climate. The clay deposits extend further than one would expect from a river, even a very wide one, so at least the largest ones must have been formed by lakes. The smaller deposits may have an origin in a flood deposit. The sediments are fine, so there was a lot of weathering, but at the same time these are not oxidised or leached much, so Ward believes that there was uplift in the region, rather than climatic change (Wanless, 1923).

About thirty years after the theory of Matthew, Wanless (1923) wrote a paper in which he summarizes his and other researchers' theories on the climate and depositions of the White River Beds. By the time Wanless wrote his paper, many seeds of *Celtis* (hackberry) had been found in the clays of the *Oreodon* beds of the Brule Formation. Millions of these seeds are found and they seem to be a very important part of the flora. In other outcrops of Oligocene age in the area, leaves of *Celtis* are found which seem to be most related to *Celtis reticula* (netleaf hackberry). Today, this species is common in dry or intermittent water courses and can survive in many extreme conditions. This means that we could say that there was a possible semi-arid climate, but not what the temperature was. In 1970, *Celtis* seeds and leaves still were the only plants found in the Brule Formation and no fish fossils or geological evidence of lacustrine environments had been discovered (Lillegraven, 1970).

Of course, climate was not constant during the time the White River Group was formed. Minor changes recorded in the colour banding and larger changes seen in the gypsum layers and silts. Also, what view you have on the climate and climatic change depends on how you think the sedimentation took place.

Wanless combined the data collected by the researchers before him and gave the following order of climates and methods of deposition (Wanless, 1923):

After the Cretaceous, there was a humid period with much erosion. This is why there is a thick layer of sediments rich in ferric oxide. After this time, there was a drier period, resulting in the disappearance of plants, which made it easier for streams to invade the area, removing the residual soil and carrying pebbles. In this way, a new plain was formed at a higher level. The iron in the soil gave layers from this age (the *Titanotherium* beds) a red colour. When the plain was higher and water was no longer contained between valley walls, downpours could spread over the entire area, depositing a thin silt layer. There was a mild climate with abundant animal and plant life. The water accumulated in lakes and many algae grew in them. This is how the limestone lenses were formed. After a long time, erosion became again a stronger factor in the landscape than sedimentation. It was more humid than before, and the area was completely covered in plants, so that streams had less sediment in them, since the roots of the plants contained the soil.

Once again the climate became more arid, which meant there was much less vegetation, streams could meander over the plain and silts were deposited. The depositions can now be seen as calcareous sediment. This change in climate probably meant the extinction of the Titanotheres, but it gave way to a new varied fauna and aquatic animals, dominated by the rhinoceros *Metamynodon*. After floods, parts of the land fell dry for very long times, and surface silts formed caliche nodules, especially along streams. The oreodon beds are well known to contain these nodules.

Again a more humid period arrived, with more stream channels and ponds. In the field, this period is visible as pink and green layers of sediment. It was, however, drier than the age of the Titanotheres and the sediment contains a larger amount of calcareous sediment. A short time of more arid conditions during which more caliche was formed followed. This time is known as the Upper Nodular layer. Above this layer more shades of green can be found and grains are coarser, so again there was a wide floodplain and a wide main channel. On top of all the previous sediments is a layer formed under arid conditions, with mainly red clays and few channels. The low number of channels resulted in no nodular layers (Wanless, 1923).

In 2001, Terry reinvestigated the paleoclimate of the Chadron Formation. He found a gradual change to more seasonal and arid conditions in the paleosol conditions, fluvial architecture, sedimentology and faunal changes at the Eocene-Oligocene boundary. Over this timespan, the paleosols change from forested to prairie-like settings with trees only found near water. There are progressively less well developed calcic horizons, suggesting a reduction in mean annual precipitation. Plants and gastropods also show a trend to more arid and seasonal conditions. This change in climate seems to have increased during the early middle Chadronian and progressed from west to east.

Retallack (2007) also investigated climate during the Oligocene. He not only used paleosol, but also marine foraminiferal oxygen and carbon isotopic composition. The paleosol data resulted in the same climatic changes found by Terry (2001), but the other two data sets gave different results. The marine oxygen isotope record showed more rapid shifts in temperature and a sloping rather than flat overall trend. This difference in trends could have been caused by a local redirection of ocean currents. The rapid shifts could have been caused by a threshold value at which the Antarctic icesheet grew (at 33 Ma) and melted (at 25 Ma). This effect of the icesheet can be compensated by looking at the Mg/Ca ratios of foraminifera and data from this analysis is indeed more in line with the results from the paleosols. Retallack found that the climate became more warm and wetter near the end of the Oligocene.

2.3 Early research of the fossil mammals.

O'Harra (1920) gives a good overview of the first years of study on the White River Group. The following information will mainly come from him.

The first remark of the White River Badlands dates back to 1847. In this year Dr. H. A. Prout (in: O'Harra, 1920) described the lower jaw of the great *Titanotherium*. Later that year, Dr. J. Leidy described a head of a *Poebrotherium*. These finds led to much interest in the scientific world, and it did not take long before the first expedition to the area took place in 1849. In this year Dr. J. Evans went to the Badlands to study the features and collect additional fossils, so that an age could be assigned to the area. Dr. Evans' journey (through Mr. Owen, in: O'Harra, 1920) to the area was of great scientific value and Dr. Leidy, together with Dr. Evans described the findings of fossils and geology and geography respectively in a report that gave the world a first authentic view of the badland country.

In the following years, also T. A. Culbertson and F. V. Hayden visited the region, collecting even more specimens, which were described by Dr. Leidy. With every publication the importance of the region became more clear, and in 1869 Leidy summarized twenty years of research in his famous work *The Extinct Mammalian Fauna of Dakota and Nebraska*.

Of course this work raised even more interest and even more people and institutions went to the area, among which were several private collectors who, by selling their finds, made the fossils known all over the world. One of the new investigators was Prof. O. C. March. He was not pleased with the crude way in which the fossils were previously collected, so he undertook extensive quarrying himself and developed new methods for fixing broken bones. In this new way more complete and well preserved skeletons were dug up, where before this was not possible. This also meant that a much better view of the nature of the animals was obtained. Expeditions in the late nineteenth century by W. B. Scott resulted in an abundant collection of fossils. These were of great

importance, because they helped with establishing more proper classifications and relationships, and several new species were found (O’Harra, 1920).

The American Museum of Natural History sent parties to the field starting in 1892. They made important discoveries and collected abundant valuable material. A lot of the details of the stratigraphy of the area, subdivisions of the deposits and correlations, as well as habits and characteristics of the animals have been established by or because of this institute. Under the direction of Prof. Scott many complete mounts and beautiful restorations have been made.

In the early twentieth century, expeditions focussed mainly on the Miocene formations, leading to the discovery of even more species (O’Harra, 1920).

Because of the work of these early investigators, the White River Badlands area is now seen as a site with high scientific value, where the influences of erosion and the progress of mammalian life can be studied in great detail.

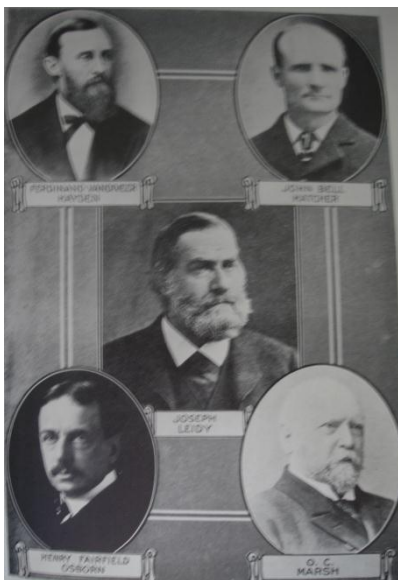


Figure 10. Some of the men who did important first work in the White River area. Starting at the top and clockwise: F. V. Hayden, J. B. Hatcher, O.C. Marsh, H. F. Osborn, J. Leidy. From: O’Harra, 1920.

3. Oreodonts

Oreodonts are extinct Artiodactyla, even-toed animals with five toes on the front legs and four toes on the back. Digits two to five contacted the ground (Stevens and Stevens, 2007). Their bodies were the size of recent sheep (about 50 kg) and they had the shape of pigs and they had long tails (Zanazzi and Kohn, 2008). Oreodonts lived from about 36 Ma till 30 Ma (Prothero and Heaton 1996).

In his book of 1852, Leidy made a first detailed description of the oreodonts. Four years prior to this publication he had described two fragments of an upper and a lower jaw of what he then called *Merycoiodon Culbertsonii*. In 1851 he studied another two specimens, putting them in other species. In his book, Leidy includes all these species into one genus, for which he prefers the name

Oreodon over *Merycoiododon*. This is because their entire body resembles that of ruminants, not just their molar teeth (*Merycoiododon* means ‘ruminating teeth’). Leidy saw Oreodonts as “a remarkable and very peculiar genus” and thought it filled the gap between extant ruminants and the extinct *Anoplotherium* from the Late Eocene and Early Oligocene of Europe and Asia, the latter is now considered a sister taxon of the order of the Merycoiododontidae.

The shape of an oreodonts skull is so peculiar that it is hard to compare it with any living animal, the camel coming closest. In extinct animals, the most resembling taxon is that of the before mentioned *Anoplotherium* Cuvier, 1804, but significant differences exist between these groups of animals, as the oreodonts possess amongst others post-orbital arches, have greater sized orbits and deep lachrymal depressions.

3.1 First descriptions of oreodonts

In 1948, Leidy presented two fossil jaw fragments to the Academy of Natural Sciences in Philadelphia (Leidy, 1948). The fragment of the lower jaw contained the last two molars, the lower jaw the three true molars. The fragments are measured, described and compared to other species, and then put in a new genus: *Merycoiododon* (see figure 11). The species name *Culbertsonii* is now written as *culbertsoni*, because by the rules of nomenclature, species names do not start with a capital letter, even if the species is named after a person. Also the extra ‘i’ at the end of the species name is now omitted.

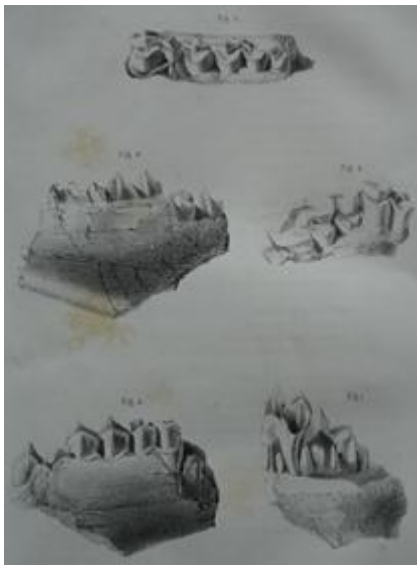


Figure 11. First drawings of *Merycoiododon Culbertsonii*. From from Leidy (1948).

In 1851, Leidy presents several additional remains of fossil ruminant ungulates (Leidy, 1851). One of these is a well conserved piece of a cranium. The three true molars have the same shape as the in 1848 described specimen, but Prof. Baird (Leidy, 1851) brings in a face of a smaller animal with two

true molars present having this same shape, but the fourth premolar has three cusps instead of two, so it is supposed that the animals presented in Leidy (1851) are from a related, but different genus than *Merycoiododon*.

The expression on the face of one of the skulls was very cat-like, because the orbits present more outwards than in other ruminants. Leidy gives this fossil the species name *Oreodon priscum*. There were also a couple of fragments of a smaller animals. The fourth premolar and the true molars had the same form as those of *Oreodon priscum*, but the posterior two inferior molars looked like those of *Merycoiododon*. It was decided that this was another new species, and it was named *Oreodon gracile*.

Another variety in dentition was then presented (Leidy, 1848). This one had probably the same superior true molars as *Oreodon*, but differed from this genus in having three cusps to the fourth premolar, and a very deep hemispherical lachrymal depression. This fragment was given the species name *Cotylops speciosa*.

In 1852, Leidy places all these fossils under *Oreodon culbertsonii*. Because the first described animal was given the genus *Merycoiododon* however, by the modern rules of nomenclature, this first name is the name that has to be used in following nomenclature.

3.2 Dentition

Even though the oreodonts were widely diversified and knew many species, their dentition stayed relatively uniform. They had a nearly complete dentition, with 3143/4343 as dental formula and a closed row of teeth with only behind the upper canines a small diastema. Characteristic for oreodonts is the combination of incisiviform lower canines and caniniform lower first premolars as antagonist of the upper canines. Together, this structure can be seen as true, but vertically implanted fangs. The incisors are small, the premolars have a cutting shape and the upper fourth premolar has two cusps. The upper molars are selenodont and often consist of four or, on rare occasions, five cusps. The lower third molar has a talonid. The onset to hypsodonty is occasionally present, but the total rootless state is never achieved (Kulzer *et al.*, 2005). Presumably the oreodonts were no ruminants. They did have some sort of enlarged fore-stomach, but the derived system of regurgitation and cud chewing were not present (Zanazzi and Kohn, 2008). Zanazzi and Kohn looked at the $\delta^{18}\text{O}$ values in tooth enamel of *Merycoiododon*. The results of this analysis indicated a relatively (compared to other living genera at that time) high water intake. Large amounts of water intake are required for hind-gut fermentation. So the oreodonts were very water dependent fore-gut fermenters, or fore-gut fermentation had not yet (fully) developed in the artiodactyls living at this time.

The occlusal curve of the oreodonts is remarkable, since it curves upward very strongly. Normally this is seen mainly in carnivores, which use this feature to make sure their prey does not escape. Modern browsers, except for the camel, do not show this curving. Zanazzi and Kohn (2008) found that *Merycooidodon* had not, or not fully, developed fore-gut fermentation. If the oreodonts were hind-gut fermenters, they required larger jaw muscles and a greater occlusal surface to process their food. Therefore, the shape of their occlusal curve is the opposite of what one would expect.

3.3 Lifestyle

Oreodonts make up a large part of the fauna of the White River area (25 percent). They were the most common herbivore during the Late Eocene, Oligocene and Miocene, which means they dominated the area for over fifteen million years. The oreodonts were only small animals though, and there were plenty of predators (see table 1). How did they manage to survive for such a long time in such large numbers?

Early investigators thought of the oreodonts more as a sheep- or pig-like ruminant, migrating over the land in large herds which were protected against predators by the size of the herd or by standing in a circle with the weakest animals inside. Their hoofs would have accommodated traveling through mountains, or over large plains (Darwinsgift, 2008). The high placed eyes and nostril could even indicate an aquatic lifestyle, if not for the clawed toes. Recently however (Sundell, 2007), this view has shifted and now it is generally believed that the oreodonts lived in burrows during the time the animals were not eating or looking for mates. The following is a summary of this hypothesis by Sundell (2007).

The first argument towards this new view is that it is not logical for oreodonts to live in herds. Their bodies were stocky, they had small legs and big heads. This gave them no possibility to defend themselves, and even less to outrun predators. Where other ungulates, such as antelopes have evolved long legs suitable for running, the oreodonts became more stout over time. This would minimize the maximum height needed in a burrow. Also they kept the four toes their ancestors had, in favour of reducing their number. With wide toes and a cup-like foot they were well-equipped for fast digging in soft sediments. The many sesamoid bones supporting the joints between the phalanges supported hard usage of the paws. The broad skull could have served as a way to intimidate predators (Sundell, 2007).

While the name oreodont (meaning 'mountain teeth') refers to the molars of these animals, which are well suited for shearing plant material, they had also well-developed canines in the upper jaw, and caniniform first premolars in the lower jaw, that would have proved very useful when protecting themselves and their young from predators such as the sabretooth cats. These teeth were

slightly larger in males, which could be an indication that they helped to protect their family, by entering the burrow last and defending it from the entrance.

Apart from anatomical details, there is also other evidence for the burrowing hypothesis. Pregnant females that are found with up to four unborn foetuses (for an early example see O’Harra, 1930). Juveniles and subadults that are found together in nodules are often of the same age, so we can presume that they are siblings. Multiple young per litter is a trait common in burrowing animals, whereas animals living in open plains often have less young.

Also in nodules with fossils of these animals, it is not uncommon to find multiple specimens together. In such occasions, often animals of varying ages are found, ranging from foetuses and juveniles to subadults and adults. Of these animals the least edible parts remain, mainly skulls and feet. This gives the impression of a family that has died together after the attack of a predator and adds to the burrowing hypothesis, because it is more likely that a predator has entered the burrow and killed the inhabitants, which were unable to flee, than that it was able to kill all the oreodonts in the nodule separately and took the effort to put them all in one place after feeding on them (see Sundell, 2007 for some pictures of nodules with multiple individuals).

Not only the fossils give a clue about the lifestyle of the oreodonts. The sediments in which most of the fossils are found are silty and ash-rich mudstones. The clay in these sediments makes burrows firm, but still soft enough to dig in. These sediments originated when the river flooded. In stream channels, which have coarser conglomerates unsuitable for burrowing, reworked and rare fossils are found. The fossils itself, as stated above are usually found in nodules within these sediments. Since some of these nodules have exactly the shape of a collapsed burrow, sometimes even with a smaller portion looking like an entrance, it is easy to assume that the nodules were formed when groundwater that was rich in calcium entered the burrows where the animals had died (Sundell, 2007).

The oreodonts were very diverse. In the Oligocene there were at least seventeen genera, and any more species with huge intraspecific variation. All available dietary niches were filled by them over time, with specialization only limited by their size (Shoemaker, 1999). There were semi-aquatic oreodonts, as well as trunked browsers and grazers of all sizes and habitats. Sundell (2007) believes that this was caused by their burrowing lifestyle. If the oreodonts had lived together in large herds, their genes would have mixed evenly through the community. By isolation through burrows, genes stayed in certain parts of the area (Sundell, 2007).

This all shows that oreodonts can be better compared to rodents or warthogs, than to sheep or pigs. They most likely lived underground near streams with their young, and only came out of their burrows to feed on scrubs in the neighbourhood, allowing them to retreat quickly into their burrows

at the sight of predators. From the entrance they could block their young and use their canines to fend off predators, which gave them a good way of defence (Sundell, 2007).

That the oreodonts disappeared was probably not because they were overhunted by predators, because they had burrows and fangs for protection. It is more likely that the cooler and dryer climate in the Miocene, and the associated diminishing of clay rich ash as a soft digging stratum, as well as the appearance of savannah with replacement of scrubs by grasses, meant that the way of life of the oreodonts was not possible anymore (Shoemaker, 1999; Sundell, 2007). A study by Prothero (2004) showed that extrinsic environmental factors such as climate change, volcanic eruptions and impacts were not the main reason the oreodonts, and other species of the White River Chronofauna, disappeared, but rather that this was because of intrinsic biological factors, such as community dynamics or evolutionary trends. But it is not clear what exactly has happened.

Not only oreodonts, but also animals such as the titanotheres and *Dinictis* are well known from the Oligocene of the White River Badlands. This gives the impression of a habitat similar to that of the present savannah, with antelopes, elephants and lions. Grasses did not exist in abundance until the late Oligocene however, so the animals probably fed on leaves of scrubs and small trees. The mammals of the White River Group were part of the long-term assemblage the “White River Chronofauna”. Most families and many genera of this fauna appeared in the Late Middle Eocene and in the Late Eocene all groups were in place. In the Early Miocene immigrant groups took over and established the “Clarendonian Chronofauna” (Prothero and Heaton, 1996).

Something remarkable among skulls of the oreodonts, which is seen in many collections, including that of the University Museum, is that most of them are missing a (sometimes quite large) piece of their premaxilla. A theory which explains this is that the predators living at the time took down the oreodonts by grabbing their nose, perhaps suffocating them at the same time.

A study on the collection of a commercial company selling Oligocene fossils from Wyoming (Sundell, 2006) gave a good overview of the composition of the community during the time the oreodonts lived (see table 1). Not all the fossils found by this company are prepared before being sold or donated, but all have at least an identification in a broad group. Specimens used in the study are upper skulls or at least a half skeleton. Because this business not only seeks large skulls, something that often gives a bias in such collections, but also collects skull with a size of less than one inch, and because the fossils are collected on a yearly basis, their finds are representative of the true community.

Fossils, especially articulated skeletons are often found in calcite enriched nodules which are resistant to erosion. The nodules are surrounded by softer mudstone. The calcite caused mineralisation of the bones.

Table 1. Composition of the Oligocene fauna in Wyoming. Source: Sundell (2006).

		%		%	Used burrows
Reptiles	Tortoises	9.90	Total	14.50	yes
	Lizards	3.50			
	Amphisbaenids	0.70			
	Snakes	1.10			
Carnivores	Sabretooth cats	1.20	Total	5.10	
	Large dogs	0.20			
	Small dogs	2.30			
	<i>Hyaenodon</i>	0.80			
	Mustelids	0.20			
	Entelodonts	0.50			no
Insectivores	Leptictids	2.00	Total	3.20	
	Small insectivores	1.20			
Marsupials	Peratherium	2.80	Total	2.80	
Ungulates	Oreodonts	25.25	Total	40.08	yes
	Camels	7.50			
	<i>Hypisodus</i>	2.10			yes
	Leptomeryx	1.90			no
	Horses	1.20			no
	Large rhinoceros	0.60			no
	Small rhinoceros	0.40			no
	Titanothera	0.20			
	Rabbits	Rabbit	23.50	Total	23.50
Rodents	<i>Ischyromys</i>	1.80	Total	9.60	no
	Small rodents	7.80			
Birds	Eggs	0.40	Total	0.40	

Table 1 gives a nice overview of the kind of animals the oreodonts lived together with. Of these animals, more than 81 percent has a burrowing or denning lifestyle, of which tortoises, rabbits and oreodonts are the most common. Above, evidence is given for this lifestyle of the oreodonts. Abandoned burrows may have also served as a place to shelter for other, non-digging, animals. At least 95% of the animals living in the area would have fitted in the burrows made by oreodonts. An animal that dies in a burrow has a good chance of being preserved while being more or less

articulated, since predators that kill them eat them at this spot, and there are no currents which could cause the body drifting apart. The burrow in which the animal has died then collapses, and nodules with bones in them are formed (Sundell, 2007).

An example of the better preservation of skeletons in burrows, is the occurrence many articulated skeletons of *Hypisodus*, but very little of horses and rhinoceroses. These last animals were simply too large to fit in a burrow, so that they had less chance of being preserved. The absence of articulated *Ischyromys* skeletons can be interpreted as a tree dwelling habitat for this large squirrel. That so many animals were burrowers, indicates that the soil and climate must have accommodated this lifestyle. Here, this probably means soft and silty ash rich claystones, low water tables and an arid climate.

3.4 Taxonomy

Oreodonts are now extinct and have not left behind any descendants. Researchers have not yet made a definite agreement on which animals are the closest relatives of the oreodonts. Based on their shape, they are interpreted as relatives of the pigs, hogs, hippos and peccaries. This is why some have placed them in the suborder Suina. Others place the oreodonts in the suborder Tylopoda, together with the camels. As Leidy noted in his book (1852), the skull of the oreodont does resemble that of a camel the most of all living mammals. Another group the oreodonts are placed in is the suborder Ancodonta together with the short-lived cainotheres (see figure 12).

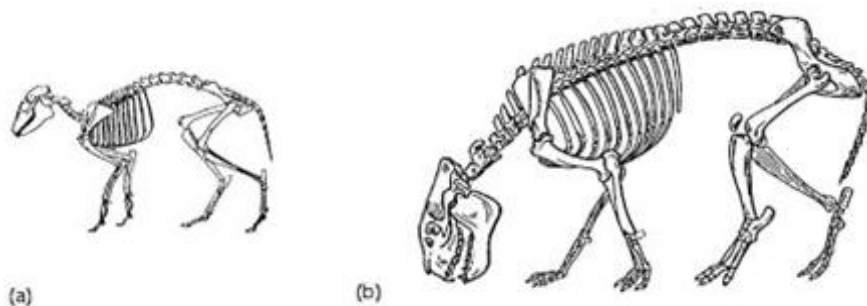


Figure 12. (a) The cainothere *Cainotherium*, from the Oligocene of Europe, approximately 30 cm long. (b) The oreodont *Merycoidodon*, from the Oligocene of North America, approximately 1 m long. (Adapted from <http://forum.zoologist.ru/viewtopic.php?pid=186332>)

Consensus is, that the oreodonts were an early group of artiodactyls. Most evidence puts the oreodonts in the suborder Tylopoda (Wikipedia, 2012). The cranium proper of the oreodonts is similar to that of the llama and camel. Just like these animals, the oreodonts have a large temporal fossa that extends superiorly to the median line of the skull where it rises upon a prominent sagittal crest, which posteriorly, in conjunction with the occiput, forms an eminence projecting above the inion and constituting its summit. Like the camel, the temporal surface is constituted for nearly one

half by the squamous portion of the temporal bone. The zygomatic arch is just as strong as in the camel and they both have their last molar on a line vertical to the post-orbital arch. In dorsal view, the camel and oreodonts have a similar shaped cranium proper and convex forehead. The frontals and backwards directed post-orbital process also look alike. Judging by the many similarities, the oreodonts are family of the camel (Leidy, 1852).

A recent publication with evidence for this theory comes from Spaulding *et al.* (2009). Morphological and molecular data were used to place artiodactyls in a cladogram (see figure 13). This paper focusses on Cetacea and does not tell about what evidence was used for making the cladogram. It does show that the placement of the Camelidamorpha, the clade of the oreodonts, is subject of much debate too, since based on different hypothesis on morphological and molecular data, it can be placed as the first split branch of the artiodactyla, or as one of the last split lineages as a sistergroup of the Ruminantiamorpha (Spaulding *et al.*, 2009).

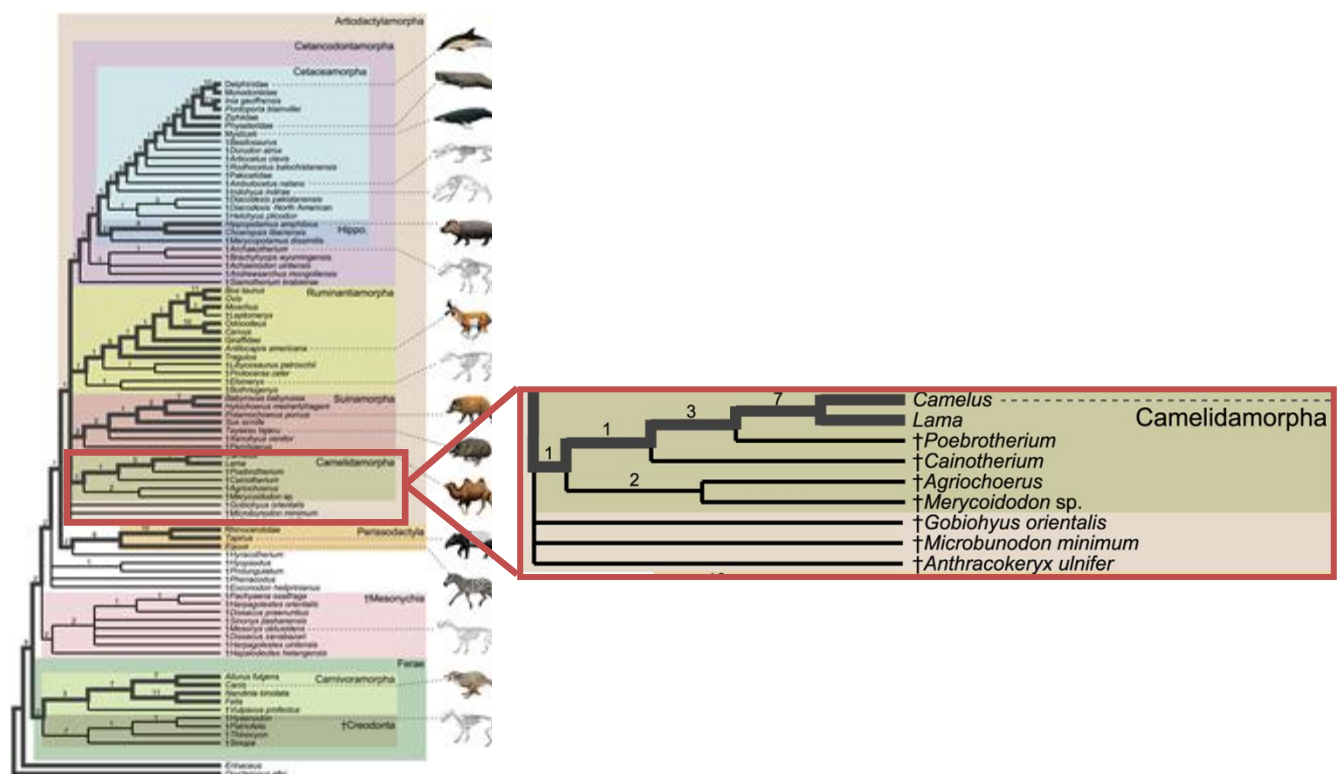


Figure 13. Cladogram of the artiodactyla, with an excerpt of the Camelidamorpha. Strict consensus of 20 minimum length trees for the equally-weighted parsimony analysis of a combined data set (57,269 steps). From: Spaulding *et al.* (2009)

In that same year, Macrini published another cladogram of artiodactyls, this time based on endocasts of extant and extinct species. As can be seen in figure 14, the camels and oreodonts become two sistergroups using this method, not a different clade. What makes the brains of oreodonts different from the other Cetartiodactyla is the presence of large, rounded casts of the tuberculum olfactorum (Macrini, 2009).

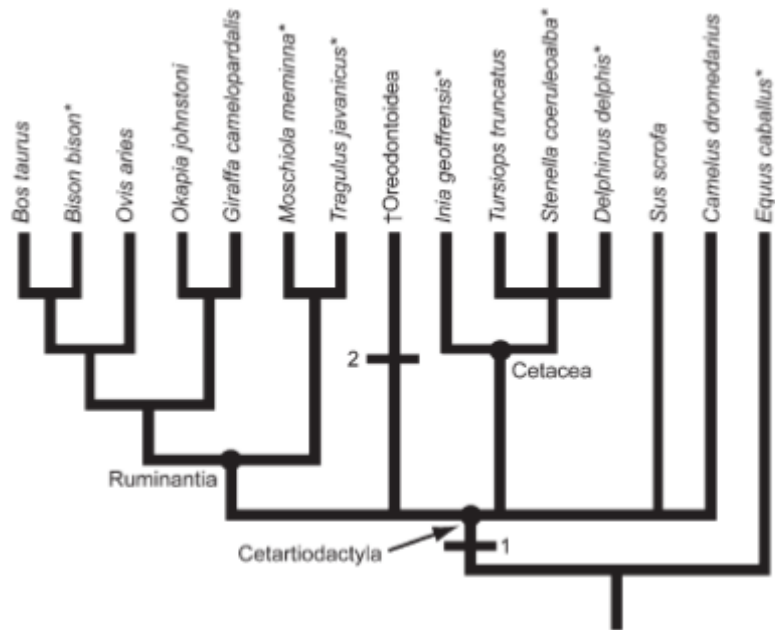


Figure 14. Cladogram showing relationships of extant cetartiodactyls whose brains or endocasts were compared with endocasts of *Bathysenys reevesi* and the RBB sample (From: Macrini, 2009).

These two examples of research show that it is very hard to make a conclusive division, especially since we are limited to the morphological data the fossils give us, and we have no access to DNA, because the fossils are too old and the oreodonts have no living descendants.

Not only within the larger order of the Artiodactyls the placing of the oreodonts proves difficult. Also within the oreodonts there is much debate on how many species existed and in which genus these species belong.

There are two families of oreodonts: the Merycoidodontidae (in older literature called Oreodontidae) and the Agriochoeridae. Together they form the suborder Oreodonta. The last family consists of small, primitive oreodonts. The species in the first family, from which all the material in this paper is originating, are more advanced.

In the forties to sixties of the twentieth century, Schultz and Falkenbach tried to describe all genera of the oreodonts. They covered them in several monographs and described many new species. Once they were finished with their work, however, much critique arose under fellow scientists. Where before the monographs three genera were recognized and less than a dozen species, they were now oversplit in dozens of genera, subfamilies and invalid species. A very striking example is the genus *Miniochoerus*. Schultz and Falkenbach described a specimen of this genus that was dorsoventrally crushed as a whole new genus: *Platychoerus* (flat pig) and a laterally crushed specimen as *Stenopsochoerus* (narrow pig). Another problem with their taxonomy was that it was based more on stratigraphic boundaries, even if that meant that no observable morphologic

differences were present (Prothero and Heaton, 1996). Stevens and Stevens tried to bring some order in the chaos Schultz and Falkenbach had created (1996). The genus *Merycoiododon* has much intraspecific variation. This is one of the reasons it was first subdivided into many different species. Stevens and Stevens have looked again at thousands of samples and have not found any reason to place the animals found at an age of 37.4-32.8 Ma in another species than *Merycoiododon culbertsoni*. Only after this age *M. bullatus* and *M. major* appeared.

As an example of how oversplit the genus *Merycoiododon* was, the following list shows all the former species that are identified as *Merycoiododon culbertsoni* by Stevens and Stevens (1996):

Merycoiododon (Merycoiododon) culbertsoni (Leidy, 1848)

Merycoiododon culbertsonii Leidy, 1848:48

Oreodon culbertsonii periculorum Cope, 1884a:513

Oreodon macrorhinus Douglass, 1903:163

Merycoiododon macrorhinus (Douglass): Douglass, 1907a: 821

Merycoiododon lewisi Clark and Beerbower, in Clark et al., 1967:53

Merycoiododon, Harris, 1967b: 3

Merycoiododon culbertsonii Leidy: Schultz and Falkenbach, 1968:38

Merycoiododon culbertsonii browni Schultz and Falkenbach, 1968:55

Merycoiododon culbertsonii osborni Schultz and Falkenbach, 1968:57

Merycoiododon macrorhinus (Douglass): Schultz and Falkenbach, 1968:72

Prodesmatochoerus meekae Schultz and Falkenbach, 1968:72

Merycoiododon georgei Schultz and Falkenbach, 1968:86

Otionohyus wardi Schultz and Falkenbach, 1968:107

Otionohyus vanderpooli Schultz and Falkenbach, 1968:115

Otionohyus (Otarohyus) bullatus (Leidy): Schultz and Falkenbach, 1968:118, in part

Genetochoerus (Osbornohyus) norbeckensis Schultz and Falkenbach, 1968:143, in part

Genetochoerus periculorum (Cope): Schultz and Falkenbach, 1968:136

Merycoiododontidae, genus and species indeterminate, no. 2, Wilson, 1971:46

Merycoiododontid, gen. et sp. indet., Wilson, 1978:23

Merycoiododon culbertsoni Leidy: Prothero, 1982b:406, in part

Merycoiododon culbertsoni Leidy: Evanoff et al., 1992:123

Stevens and Stevens (1996) remarked that, just as observed in this research, *Miniochoerus affinis* and *M. gracilis* look a lot alike and wondered if they could be combined into one species, just as had other researchers before them. Leidy (1869 in: Stevens and Stevens, 1996) thought *Oreodon affinis* (as it was called then) to be a “doubtfull species”, because he based the species on an

incomplete skull which might just have been a large individual of *Oreodon gracile* (as *Miniochoerus gracilis* was then called). Schultz and Falkenbach (1956) thought that maybe they were one species in two populations. Stevens and Stevens (1996) could not find enough significant reasons for putting *M. affinis* and *M. gracilis* in one species. The coefficient of variation of fifteen measurements made by Stevens and Stevens was large to extremely large, with eight measurements that were more than three standard deviations from the coefficient of variation's mean when they combined these species. *Miniochoerus affinis* has a 4% longer P^1-M^3 length, and a subnasal length that is 67% longer. As can be seen in figure 15, measurements of *M. gracilis* fall mostly out of the range of *M. affinis*. Stevens and Stevens (1996) conclude that the most likely explanation of the similarities of *M. affinis* and *M. gracilis* is that *M. gracilis* has evolved through dwarfing from *Miniochoerus chadronensis*, which is a probable ancestor of *M. affinis*, or that it has evolved directly from early *M. affinis*.

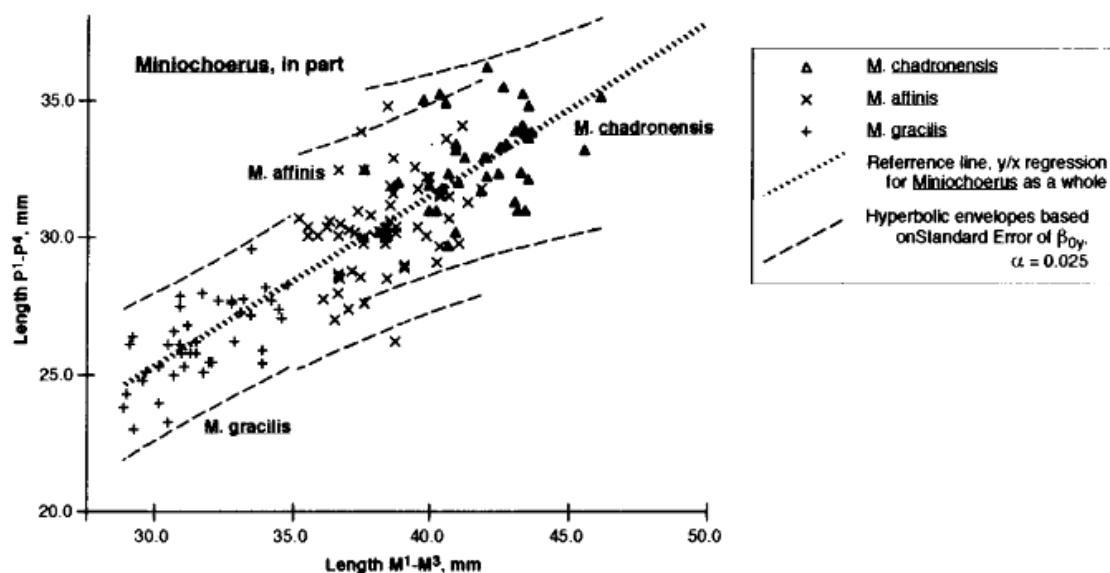


Figure 15. Scatter diagram of P^1-P^4 , M^1-M^3 data, and y/x hyperbolic confidence envelopes for *Miniochoerus chadronensis*, *M. affinis* and *M. gracilis* (Adapted from: Stevens and Stevens, 1996).

The descriptions in this paper have been made based on the drawings in the various Schultz and Falkenbach monographs. In combination with the taxonomy of Stevens and Stevens (1996) the material is named on species level.

At this moment the accepted systematic division is the one given below (Stevens and Stevens, 1996). Only for the genera of which specimens are present in the collection of the University Museum in Utrecht will be given detailed taxonomic information.

Family MERYCOIDODONTIDAE Hay, 1902

Included are: Merycoidodontidae Hay, 1902:665

Merycoidodontidae Hay: Thorpe, 1937a

Merycoidodontidae Hay: Schultz and Falkenbach, 1968

Type species: *Merycoidodon culbertsoni* Leidy, 1848, p. 47.

Subfamily MERYCOIDODONTINAE Hay, 1902:665

Included are: Merycoidodontinae Hay: Schultz and Falkenbach, 1968:24

Promerycochoerinae Schultz and Falkenbach, 1949:140, in part

Desmatochoerinae Schultz and Falkenbach, 1954:163, in part

Type species: *Merycoidodon culbertsoni* Leidy, 1848

Included genera: *Merycoidodon* and *Mesoreodon*.

Merycoidodon Leidy, 1848

Type species: *Merycoidodon culbertsoni* Leidy, 1848.

Included species— *Merycoidodon presidioensis*, Stevens and Stevens, 1996

M. culbertsoni Leidy, 1848

M. bullatus Leidy, 1869

M. major. Leidy, 1853

Merycoidodon (Otarohyus) (Schultz and Falkenbach 1968)

Type species: *Merycoidodon bullatus* (Leidy): Leidy, 1869:109.

Included species: *M. (O.) major* Leidy 1853

Merycoidodon (Otarohyus) bullatus Leidy, 1869

Subfamily MINIOCHOERINAE Schultz and Falkenbach, 1956

Included are: Miniochoerinae Schultz and Falkenbach, 1956:391

Miniochoerinae Schultz and Falkenbach: Schultz and Falkenbach, 1968:382

Type species: *Miniochoerus gracilis* (Leidy), 1851, p. 239.

Included genera: *Miniochoerus* only.

Miniochoerus Leidy, 1851

Type species: *Miniochoerus gracilis* Leidy, 1851, p. 239.

Included species: ?*Miniochoerus forsythae* Schultz and Falkenbach, 1968

M. gracilis Leidy, 1851

M. affinis Leidy, 1869

M. starkensis Schultz and Falkenbach, 1956

M. chadronensis Evanoff *et al.*, 1992

- Miniochoerus gracilis* Leidy, 1851
- Included are: *Oreodon gracile* Leidy, 1851:239.
Miniochoerus {*Paraminiochoerus*} *affinis* (Leidy): Schultz and Falkenbach, 1956:405, in part, tentatively referred.
Miniochoerus (*Paraminiochoerus*) *gracilis* (Leidy): Schultz and Falkenbach, 1956:413.
- Miniochoerus affinis* (Leidy, 1869)
- Included are: *Oreodon affinis* Leidy, 1869:105
Merycoidodon platycephalus Thorpe, 1921b:339
Miniochoerus battlecreekensis Schultz and Falkenbach, 1956:395, in part
Miniochoerus (*Paraminiochoerus*) *affinis* (Leidy): Schultz and Falkenbach, 1956:405, in part
Platychoerus platycephalus (Thorpe): Schultz and Falkenbach, 1956:427, in part
Stenopsochoerus sternbergi Schultz and Falkenbach, 1956:438, in part
- ?*Miniochoerus forsythae* Schultz and Falkenbach, 1968
- Included are: *Prodesmatochoerus natronensis* Schultz and Falkenbach, 1954:228, a *nomen vanum*
Prodesmatochoerus natronensis Schultz and Falkenbach, 1954: Emry, 1992:110
Merycoidodon sp., Clark and Beerbower, in Clark et al., 1967:54, tentatively referred
Merycoidodon forsythae Schultz and Falkenbach, 1968:36
Merycoidodon forsythae Schultz and Falkenbach, 1968: Emry, 1992:110
Otionohyus wardi degrooti Schultz and Falkenbach, 1968:114
- Miniochoerus starkensis* Schultz and Falkenbach, 1956
- Included are: *Miniochoerus starkensis* Schultz and Falkenbach, 1956:398
Miniochoerus nicholsae Schultz and Falkenbach, 1956:400
Miniochoerus cheyennensis Schultz and Falkenbach, 1956:401
Miniochoerus (*Paraminiochoerus*) *helprini* Schultz and Falkenbach, 1956:422
Miniochoerus {*Paraminiochoerus*} *ottensi* Schultz and Falkenbach, 1956:424

Platychoerus heartensis Schultz and Falkenbach, 1956:432

Platychoerus hatereekensis Schultz and Falkenbach, 1956:433

Stenopsochoerus joderensis Schultz and Falkenbach, 1956:441

Stenopsochoerus berardae Schultz and Falkenbach, 1956:441

The subgenus *Merycoidodon* (*Otarohyus*) is still in use after the revision of Stevens and Stevens (1996). Schultz and Falkenbach decided in 1968 that the Merycoidodontinae with small bullae needed to be distinguished from those with large bullae by the use of subgenera. By following the principle of the first reviser, *Otarohyus* is the appropriate name (Stevens and Stevens, 1996).

4. Material and Methods

The University Museum of the University of Utrecht has a collection of material from the White River Series. Some initial determinations have been carried out by the curators of the museum in 1899.

The components of the skulls that have been described are shown in figure 16. Unless stated otherwise, these parts are described frontal to caudal and dorsal to ventral.



Figure 16. Described structures of oreodont skulls and jaws. 1: Zygomatic bone. 2: Orbitosphenoid. 3: Lacrimal. 4: Premaxilla. 5: infraorbital foramen. 6: Coronoid process. 7: Occlusal curve. 8: Ramus. 9: Zygomatic arch. 10: Parietal bone.

11: Mental foramen. 12: Condyle. 13: Base. 14: Angle. The skull has collection number G131/1899 and belongs to species *?Miniochoerus forsythae*.

The measurements have been carried out using a pair of callipers with an accuracy of 1/20 mm, following the advised measurements of Phleger and Putnam (1942). Measurements on the molars have been carried out using ms Paint. In the paper of Phleger and Putnam (1942), 155 *Merycoiodon* skulls are measured in twelve different linear ways. With this research they tried to, among other things, study the direction of evolution within this genus. A problem with their study is that in the work of Schultz and Falkenbach (1956), two of the species used (*Miniochoerus affinis* and *M. gracilis*) are placed in sister genus *Miniochoerus*. This means that the results on evolution within the group cannot be used anymore. However, part of their research also focusses on defining species based on their sizes, and since the authors state that they are quite sure of the identification of the skulls, this part can be used in the present study.

Another, quite important problem with the paper of Phleger and Putnam is that it is not sure how the authors measured the different parts of the skulls. They refer to a guide, which cannot be accessed. As a solution, the measurements of the structures have been taken in the shortest way possible. The molars and premolars have all been measured separate and as a group, resulting in the same measured values.

The used measurements are depicted in figures 17-19. Not depicted are measurements 8: Length of the skull from the anterior edge of the second premolar to the upper edge of the foramen magnum and 9: Length of the skull from the anterior surface of the canine to the bottom of the occipital condyle.

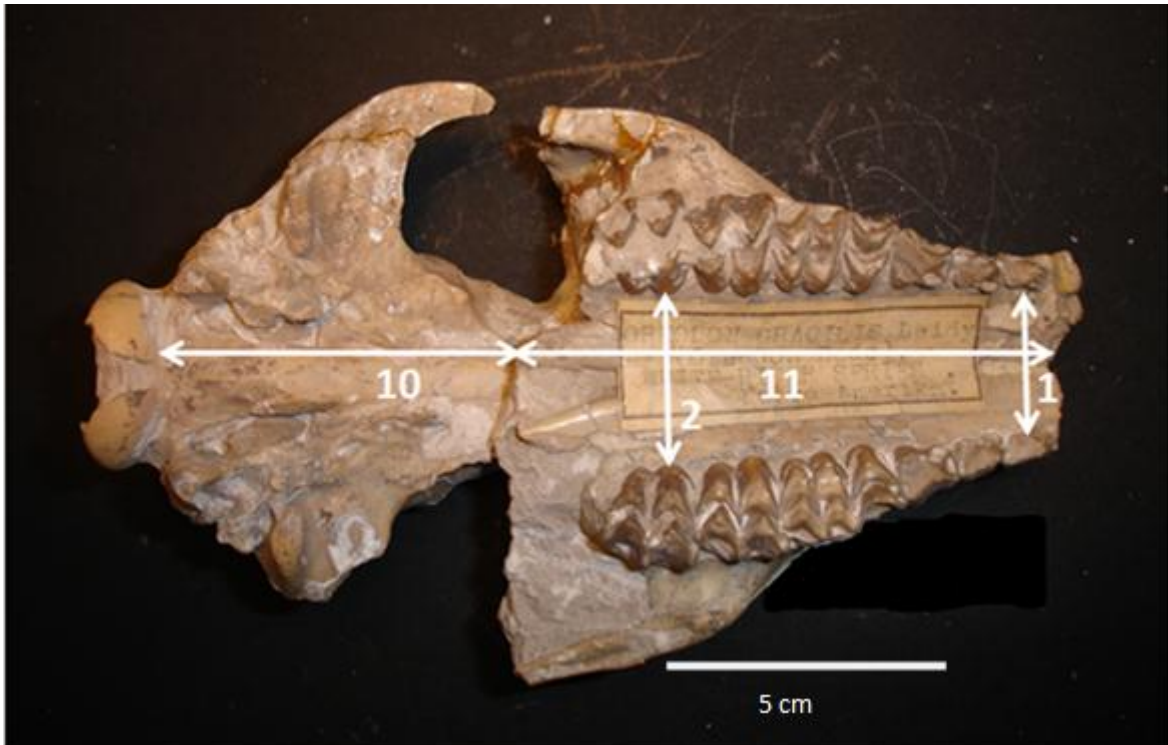


Figure 17. Measurements 1,2, 10 and 11. 1: Width of the palate between the first premolars. 2: Width of the palate between the third molars. 10: Distance from the palatofrontal border to the bottom of the occipital condyle. 11: Distance from the inner edge of the incisors to the palatofrontal border. The skull has collectionnumber G107/1899 and belongs to species *Merycoiodon culbertsoni*.



Figure 18. Measurements 3 and 4. 3: Width of the skull across the posterior edge of the orbits.4: Width of the post-orbital constriction. The skull has collectionnumber G130/1899 and belongs to species *Merycoiodon culbertsoni*.

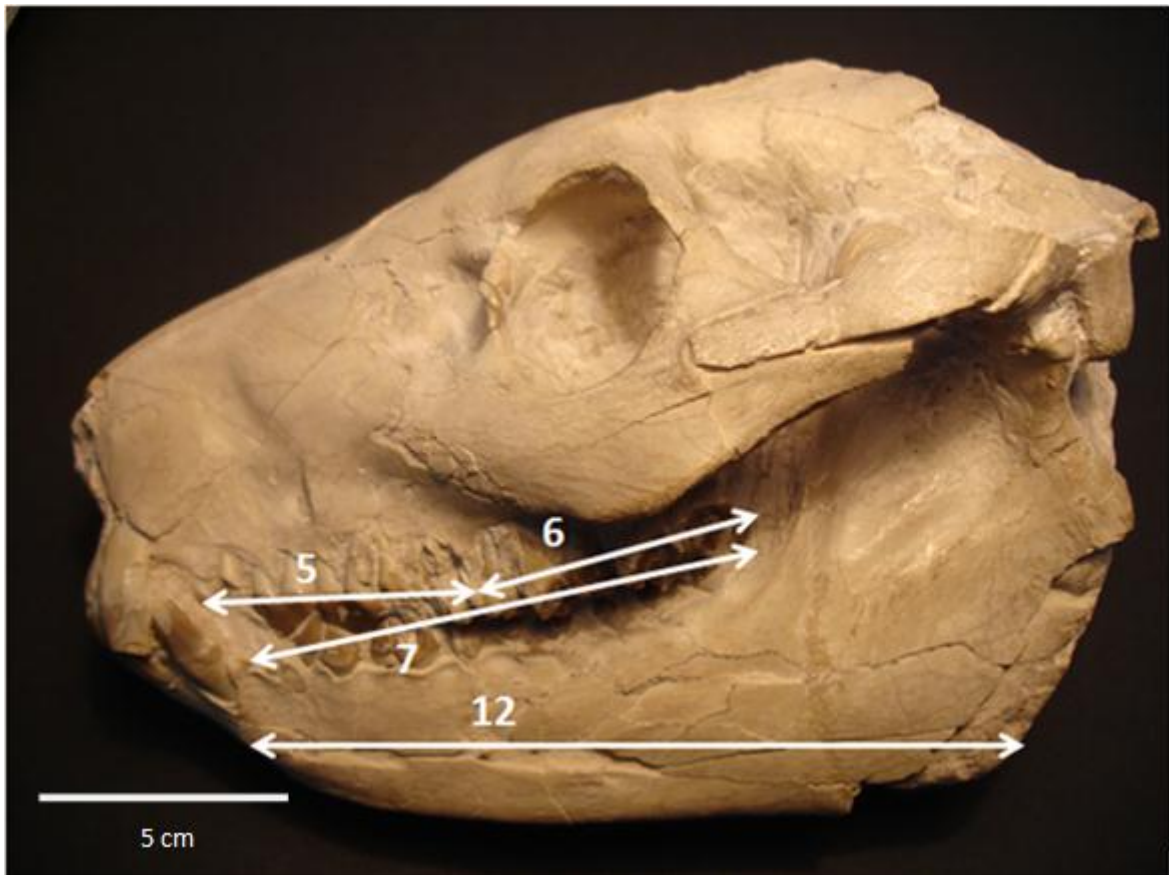


Figure 19. Measurements 5, 6, 7 and 12. 5: Length of the cheek teeth (from the posterior edge of the third molar to the anterior edge of the first premolar). 6: Length of the molar series. 7: Length of the premolar series. 12: Ramus length from symphysis to the most posterior point of the jaw. The skull has collection number G131/1899 and belongs to species *?Miniochoerus forsythae*.

Because the practical goal of this paper was to describe and identify the material of the University Museum in Utrecht, only the skulls and mandibles present in this collection are described in greater detail. Other measured collections are only used for expanding the dataset for better comparison with the literature within species.

A description of the dentition of the specimens in the collection of the University Museum, where the occlusal surface is visible is given. These five descriptions are of skulls and a mandible which have enough characteristics in the bone around the teeth to make a first identification based on those characteristics alone. Since the literature does not have very clear pictures on the dentition, no attempt is made at putting the fragments in a taxon based on dentition alone.

Most of the oreodont skulls and mandibles in this collection are of the genera *Merycooidodon* and *Miniochoerus*. These genera are described by Stevens and Stevens (1996). The smaller skulls are generally of the genus *Miniochoerus*. While Schultz and Falkenbach (1956) did overplit some species dramatically, they do give a good overview on the differences between the two genera. Typical for *Miniochoerinae* are the thinning of the of enamel on the premolar-molar medial crests or selenes

and also trends toward premolar reduction and reduction in preorbital fossae (Schultz and Falkenbach, 1956). They also retain small auditory bullae with deep hyoidal grooves and have relatively short and broad occiputs. They do not have prominent occipital crests. These last two characteristics are probably a result of the fetalization due to the phylogenetic dwarfism relative to their sistergroup the Merycoidontidae. As a result of this, the brain dominates more of the skull than in larger oreodonts (Stevens and Stevens, 1996).

Other fossil material used in this paper consists of lower jaws and endocasts. All the material has been identified using the drawings in Schultz and Falkenbach (1956 and 1968) and species names have been corrected using the paper by Stevens and Stevens (1996), which does not have pictures of the species they describe.

Mesowear analyses have been carried out following the paper of Fortelius and Solounias (2000). The buccal side of the molars is used, since this side is always visible, even in species where the upper and lower jaw are both present and the skull is filled with sediment.

Graphs have been made using Microsoft Office Excel 2010.

4.1 The collections

In this paper, fossil material in the collections of three different institutes in the Netherlands has been used. Below is an overview of these collections, and a short history of how they were established. Readers in the Netherlands who want to see fossils of oreodonts for themselves are advised to go NCB Naturalis for a nice example of age differences within a species, to Teylers Museum for beautiful endocasts of oreodont brains, and to the Museon (skulls not used in this research) in Den Haag for a nice example of an oreodont that is partly still stuck in the matrix. The Natural History Museum in London, England, has two nice skulls on display, one of which is articulated with part of the skeleton (see figure 2).

NCB Naturalis, Leiden

The collection of the National Centre for Biodiversity contains several pieces of fossil oreodonts. The collection is made up of multiple subcollections. It was not possible to find the origins of every piece, but in general the collection can be subdivided into material coming from three cities: Leiden, Amsterdam and Groningen (the collection of Petrus Camper). Over the years, material from these three cities has accumulated at the museum. In the main exhibition of the museum two very complete skulls can be seen of *Merycoidodon culbertsoni*, one is an adult, the other a juvenile. The rest of the material is stored in the tower adjacent to the museum. In this storage, another skull is present, together with six fragments of mandibles. At least one of the mandible fragments is of a perissodactyl.

In this paper, the two skulls from the main exhibition are used for their measurements. This are the specimens with numbers: st18235 and st18236. Also another skull from the depot, RGM 592002 has been used.

Teylers Museum, Haarlem

In Teylers Museum, a skull is present in the main collection. Apart from this, there are also two natural endocasts of the brains of two species of oreodont. The catalogue of the museum does not contain information on where the material is bought. However, on one of the endocasts (named *Oreodon culbertsoni*), the label says Evans' collection. This could be Caleb Evans, an English geologist of the nineteenth century, who had an extensive collection of fossils. The other two fossils do not have such a label. The collection of Teylers Museum is bought with funds from the legacy of Pieter Teyler, a wealthy silk- and clothmanufacturer and banker. The money was meant for the Teylers Foundation for worship, science and art. The material bought by this organization was put together under one roof in 1778, which now still is the museum (John de Vos, 2012 personal communication)

Of the collection of Teylers Museum, two natural endocasts and a skull have been used. These have numbers: 16378, 16380 and 8591 respectively. The determination given by the museum has been kept.

Universiteits Museum, Utrecht

The material in Utrecht is now the property of the University Museum. When Arthur Wichmann became professor of geology in 1878, only the petrological collection of the university was in a good enough state for teaching, the mineral collection was abandoned and a geological collection was missing altogether. This was why in 1881 Wichmann got the disposal of a large amount of money (initially 4000 guilders, later 2000 guilders a year) to buy minerals, rocks, instrument and books used for teaching the students. Most of this material was bought at mineraltraders in Germany, although part of the collection was collected by Wichmann on his expeditions. Starting in 1883 more paleontological material was bought (Pater, 2004). The material in this paper is collected in 1899. One skull (Pa10/1899) has a label from the University of Bonn, the others do not have such a label. In the catalogue of the year 1899, the name of William Berryman Scott is mentioned. (Catalogus, 1899). Scott was an vertebrate paleontologist who has published monographs on the White River Oligocene. It is not clear whether Wichmann bought the fossils directly from Scott, or if his monographs perhaps assisted in the determination of the material.

The material consists of thirteen skulls, two of which are situated in the exhibition of the museum, the others are in the depot, and a mandible.

For measurements on skulls, identification and description of the dentition, the following specimens of the University Museum have been used: G85/1899, G107/1899, G108/1899, G109/1899, G114/1899, G122/1899, G123/1899, G124/1899, G130/1899, G131/1899, G153/1899, G158/1899, G161/1899 and Pa10/1899, all of which contain at least part of the skull, except for G109/1899, which only consists of a lower jaw. Not all of these specimens have been described in total detail (for various reasons G108/1899, G122/1899 and G130/1899 have only been used for their measurements), but each taxon has been covered.

5. Results

5.1 Description of the skulls and dentition

Family MERYCOIDODONTIDAE
Subfamily MERYCOIDODONTINAE Hay, 1902
Genus *MERYCOIDODON* Leidy, 1848
Merycoidodon culbertsoni Leidy, 1948.
(Figures 20 and 21)

G107/1899, identified in the UU collection as *Oreodon gracilis*.

Skull without mandible, around and in eye sockets filled with sediment (figure 20). The premaxilla is not present.

Skull Even though the skull has been identified as *Oreodon gracilis* (now called *Miniochoerus gracilis*), it does not resemble any of the pictures in Schultz and Falkenbach (1956), where the genus of this species is described.

The orbitosphenoid of this skull is shaped like the letter 'D': the connection to the lacrimal fossa is straight, while the more posterior part shows a more curved edge. About 5 mm above the lacrimal fossa and the orbitosphenoid, the skull ends. From a ventral view, the posterior part of the orbitosphenoid is straight, much like *Merycoidodon culbertsonii osborni* in Schultz and Falkenbach (1968). The zygomatic arch, on the other hand, resembles that of *M. culbertsoni*. The infraorbital foramina, which are also filled with sediment, are shaped like a cavity covered from posterior. The occlusal surface is flat at the molars, and makes an angle of about 40 degrees. And in lateral view, the dorsal part of the skull is flattened. The most posterior part misses the top bit, so it is not possible to determine its shape. The occipital condyles are small, as is the foramen magnum. This last structure has a diameter of 1.4 cm. The auditory bullae are very small.

In 1996, Stevens and Stevens put *Merycoiododon culbertsonii osborni* of Schutlz and Falkenbach in *Merycoiododon culbertsoni*. Considering this change and the features of the skull, the species it belongs to is probably *M. culbertsoni*.

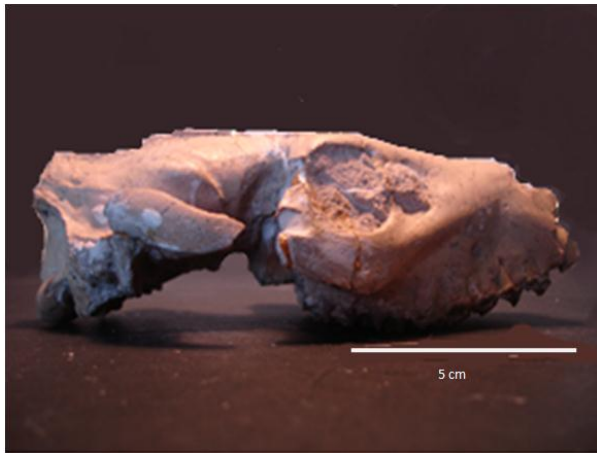


Figure 20. Specimen G107/1899, *Merycoiododon culbertsoni*. Lateral view of the dextral side of the skull.

Dentition All of the molars and premolars are present. Only the upper part of the dextral canine is left. Incisors are missing. The right M^3 is partly covered in sediment and its occlusal surface cannot be studied.

The paraconulus seems to be broken off at the left side, and is covered by sediment on the other, so it is impossible to say what its shape is. There are only very low ridges on the buccal surface of the paracone and metacone. The apex of these structures is just a small zone. In the M^3 this is also found in the protocone and hypocone, but in the other molars the structure becomes larger. The molars are not large compared to others in the collection, and square in shape. The P^4 has two cusps and the P^3 is very broad. The premolars are large in comparison to the molars.

Table 2: Measurements of the molars of mandible G107/1899, *Merycoiododon culbertsoni*, with approximate maximum measurements (in cm). In this table, width stands for the buccal-lingual distance, and length for mesial-distal distance.

Sizes:	Dextral width	length	Sinistral width	length
P^1	0.6	0.8	0.6	0.8
P^2	0.7	0.8	0.7	0.8
P^3	0.9	1.0	0.9	0.9
P^4	1.3	0.9	1.2	0.8
M^1	1.4	1.1	1.3	1.2
M^2	1.6	1.3	1.5	1.3
M^3	1.6	1.3	1.6	1.4

Pa10/1899, identified in the UU collection as *Oreodon culbertsoni*.

Very brown, large skull (figure 21). The premaxilla and the parietal are missing. There is also no mandible present.

Skull On the dextral side of the skull, the zygomatic bone is too fragmented, and on the sinistral side of the skull, the ventral side of the zygomatic bone, and the zygomatic arch are missing, so it is not really possible to say something about the shape of this structure. The curve towards the infraorbital foramen is broad, but not extending much. The orbitosphenoid lies close to the top of the skull and is large and shaped like a D. There is no opening in the upper rostral corner. The lacrimal fossa too is very large, at least two thirds of the orbitosphenoid, and has a small ridge extending in from the anterior edge. The infraorbital foramen is totally filled up with sediment, but seems to be round and big, and possibly deep too. It is situated above the P³. Many molars and parts of them are missing, so it is not possible to say something about the occlusal curve. Posterior of the nasal, the skull curves upward a bit in lateral view, but since the rest is missing shortly after this, it is not known how the skull was formed in this region.

The first determination of *M. culbertsoni* seems to be right. The D-shaped eye socket and the placement and shape of the lacrimal fossa point towards *Merycoiododon culbertsoni osborni*, a subspecies of Schultz and Falkenbach (1968). Since the revision of this genus by Stevens and Stevens (1996), this skull belongs to the species *Merycoiododon culbertsoni*.

This skull is placed together with skull G161/1899, *Miniochoerus starkensis*, in a different part of the collection than the other skulls. Skull G161/1899 is maybe a bit darker brown than the other skulls, but certainly not as much as Pa10/1899, and there is no documentation on why these skulls are separated from the others. The label on G161/1899 is the same as on the other material, but the label on Pa10/1899 is different. It is from the collection of B. Stürtz in Bonn.

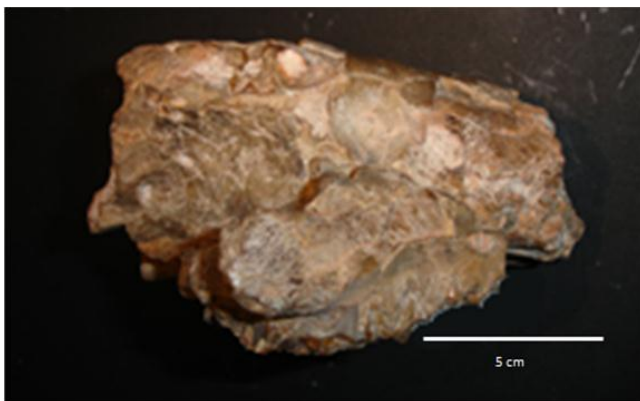


Figure 21. Specimen Pa10/1899, *Merycoiododon culbertsoni*. Lateral view of the dextral side of the skull.

Dentition Skull with most of the molars and premolars present, however most of them are broken off at the point where they come out of the bone of the skull. M³sin is the only totally complete

molar. This molar is square. The protocone has a large lingual edge, leaving only enough space for a thin paraconulus. The tip of the mesostyle has broken off. The hypocone structure is small in comparison to the protocone. The metacone curves deeply inward. Both the metacone and the paracone have a well-developed ridge. The other molars seem to be shaped more or less the same. The premolars do not have any visible characteristic structures left.

Table 3: Measurements of the molars of mandible Pa10/1899, *Merycoiododon culbertsoni*, with approximate maximum measurements (in cm). In this table, width stands for the buccal-lingual distance, and length for mesial-distal distance.

Sizes:	Dextral width	length	Sinistral width	length
M ³	NA	NA	1.8	1.7

Genus *MERYCOIODODON (OTAROHYUS)* (Schultz and Falkenbach 1968)

Merycoiododon (Otarohyus) sp.

(Figure 22)

G158/1899, identified in the UU collection as *Oreodon* sp.

Small skull with every part anterior of the orbitosphenoid missing and no mandible (figure 22). The skull does have very large auditory bullae. The skull does not seem smaller than the other skulls because of the large number of missing parts, but the distance from the orbitosphenoid to the edge of the parietal is actually smaller. Remarkable in this skull is the large size of the molars.

Skull The zygomatic bone and arch lie some distance from the molars, which can also be seen in dorsal view, as it really sticks out from the rest of the skull, and the bottom of this structure is very straight. The curve in the bone can be followed beyond the infraorbital foramen, but it is not possible to say how much further, since the rest of the skull misses after this point. The orbitosphenoid is a bit shaped like a clockwise diagonally tilted oval. There is no opening in the upper anterior corner. Instead, the bone here is pointing a bit outward. In the corner opposite, the bone points inward. What is left of the lacrimal fossa seems to be a shallow and small triangular shape. The infraorbital foramen lies above P³ and is deep and large. The last part of the occlusal curve has a very strong curve. In lateral view, the top of the skull is very straight. The parietal has a V-shaped ridge on each side.

The determination of this skull is complicated by the missing parts. A good point of comparison seems to be the area around the orbitosphenoid and the zygomatic arch, as seen in dorsal view. None of the skulls in the *Miniochoerus* genus (pictures in Schultz and Falkenbach, 1956) show the same width and shape ratios as the skull. Also the skulls in the other genera in this article do not look like the one described here. In Schultz and Falkenbach (1968), there are some species

which look more like the skull. The genus *Merycoiododon* (*Otarohyus*) is much alike in having a straight top in lateral view, and a straight zygomatic structure. Also the size of their teeth is comparable, plus they have large bullae. The species most comparable are probably *M. (O.) h. helenae* and *M. (O.) alexi*, with the latter being a better fit when also looking at the premaxillae, but the first when looking at spatial distributions of the different structures. The only problem with this determination is that the species in this genus are larger than skull G158/1899. The genus *Genetochoerus* has straight lines too (pictures in Schultz and Falkenbach, 1968), but also a lot of bone above the orbitosphenoid, something the skull here does not have. A further problem is the shape of the molars, which is unlike any other in this collection, being much wider. The molars are also remarkably large compared to the small skull. They look a bit like those of *Leptauchenia*, but the rest of the skull does not.

Based on this, the skull could belong to the genus *Merycoiododon* (*Otarohyus*), but it is not possible to say with full certainty to which species.

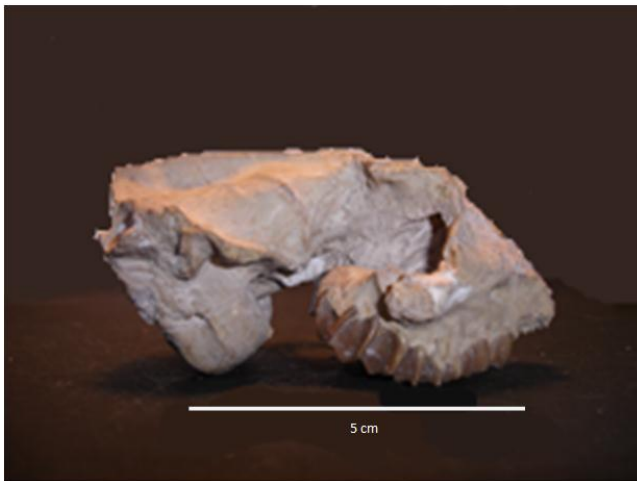


Figure 22. Specimen G158/1899, *Merycoiododon* (*Otarohyus*). Lateral view of the dextral side of the skull.

Dentition On the left side of this skull, P⁴-M³ are present, the right side has P³-M³ left. The molars are shaped diagonally, with buccal structures, especially the parastyle, extending more mesial than their lingual counterparts. The paraconulus is not present. The apex of the paracone of the M³ is placed almost directly at the buccal edge of the molar, with no triangular edge leading towards it. In the other molars the edge is a bit wider. The metacone is the same. In the M¹, these structures are halfway in the molar. There is still no steep edge leading to it, but instead a shallow slope. The mesostyle is a single apex. The first two molars are somewhat square, but the width of the last molar narrows a lot at the distal side.

Table 4: Measurements of the molars of skull G158/1899, *Otarohyus*, with approximate maximum measurements (in cm). In this table, width stands for the buccal-lingual distance, and length for mesial-distal distance.

Sizes:	Dextral width	length	Sinistral width	length
P ³	0.6	0.5	NA	NA
P ⁴	0.8	0.7	0.7	0.7
M ¹	1.1	0.9	0.8	0.9
M ²	1.2	1.2	1.2	1.3
M ³	1.1	1	1	1.4

Subfamily MINIOCHOERINAE

Genus MINIOCHOERUS Schultz and Falkenbach, 1956

Miniochoerus gracilis Leidy, 1851

(Figures 23-25)

G109/1899, identified in the UU collection as *Oreodon* sp.

Part of a small mandible (figure 23). The mandible is partly fragmented, but the pieces are large. The molars that are present are: M₁₋₃ dex (the last one only partly), M₁₋₂ sin (the first only half and the second damaged), P₁₋₄ dex and P₂₋₄ sin. The incisors and canines are all absent.

The molars are selenodont. The posterior part of the mandible is broken off at both sides, so it is not possible to describe anything of the structures here. The base of the mandible seems to have some curvature, but this too is hard to say with certainty, because of fractures in this area. The mental foramen is situated below the P₂ and is very small. Where the two halves of the jaw meet, there is a ridge extending to the ventral side.

The many missing parts and fractures make it not easy to identify this mandible. Because of the size, it could be compared to the genus *Miniochoerus*. Pictures and a description of this genus can be found in Schultz and Falkenbach (1956) and Stevens and Stevens (1996). The shape and positioning of the molars is similar to that of *Miniochoerus gracilis*, and also the mental foramen is placed at the right position. However, other characteristics apart from the molars and the mental foramen cannot be compared in this mandible because they are missing, and even the molars are not complete. Therefore it is not really possible to say which species the mandible belongs to.

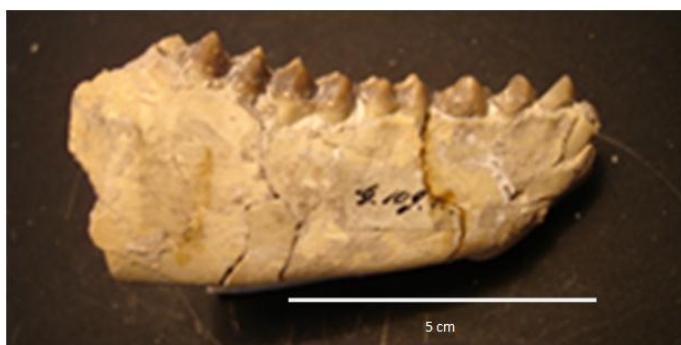


Figure 23. Specimen G109/1899, *Miniochoerus gracilis*. Lateral view of the dextral side of the mandible.

Dentition

Mandible with very sharp molars and premolars. P₁-M₃ dex (although the first premolar has only its base left and the last molar misses the most distal third) and P₂₋₄ and M₁₋₂ sin (the second premolar is broken off above the base, and the first molar misses the distal half) are present.

The fourth premolar has two cusps. In the molars, the distance between the protoconid and the metaconid, as well as the distance between the hypoconid and the entoconid is quite large. The protoconid and hypoconid triangles have sharp angles.

Table 5: Measurements of the molars of mandible G109/1899, *Miniochoerus gracilis*, with approximate maximum measurements (in cm). In this table, width stands for the buccal-lingual distance, and length for mesial-distal distance.

Sizes:	Dextral width	length	Sinistral width	length
P ₁	0.5	0.6	NA	NA
P ₂	0.4	0.7	NA	NA
P ₃	0.5	0.8	0.6	0.7
P ₄	0.6	0.9	0.6	0.8
M ₁	0.7	1.0	NA	NA
M ₂	0.9	1.1	0.8	1.2
M ₃	0.9	NA	NA	NA

G123/1899, identified in the UU collection as *Oreodon* sp.

Small skull with mandible, but the premaxilla is missing, molars and premolars are prepared free of sediment (figure 24).

Skull The left side of the skull misses part of the zygomatic arch and the bone around the orbitosphenoid. On the right side is visible that the orbitosphenoid is small and more or less round, with in the upper anterior edge an opening. The lacrimal fossa is not connected to the orbitosphenoid, and is deep. Although the inner parts of the infraorbital foramen are filled with sediment, it is visible that this structure is deep too. The coronoid process almost reaches the top of the orbitosphenoid. The occlusal curve starts straight, but has reached a strong upward curve at the molars. The parietal is mostly intact, and curves upward a bit. At the condyle, which is small and pointy, the ramus of the mandible is deep. The zygomatic arch extends above the zygomatic bone and makes a clear angle of about 90 degrees at the posterior end. The angle of the zygomatic bone is more obtuse, and the ridge is not extending far towards the premaxilla. Like the infraorbital foramen,

the mental foramen is small but not too shallow. It has a somewhat squared shape. The base of the mandible is mainly straight, and curves downward only a bit at the angle.

When comparing this skull with the literature, there is a resemblance to *Miniochoerus gracilis* (Schultz and Falkenbach, 1956). The placement of the lacrimal fossa in their figure 3, and the opening in the orbitosphenoid are much alike. However, the strong curve in the zygomatic arch is not visible in this picture of Schultz and Falkenbach. In the mandible, the ramus and the downward curve of the angle are the same in the skull and the picture. O’Harra (1920) also has an image of *M. gracilis*, which looks a lot like skull G123. And also size-wise the skull matches this species. So although there are some differences with the literature, the determination for this skull is *M. gracilis*.



Figure 24. Specimen G123/1899, *Miniochoerus gracilis*. Lateral view of the dextral side of the skull.

G124/1899, identified in the UU collection as *Oreodon* sp.

Small skull with large mandible (figure 25). A large area around the premaxilla is missing, and part of the sinistral side of the skull is covered with sediment.

Skull The zygomatic bone on the dextral side of the skull is partly broken off, on the other side it is missing completely. The curved shape does not visibly extend very far laterally. The orbitosphenoid has the same problem, with only a small, round, part left, though enough of it is left to see an opening in the top anterior corner. It is hard to say something about the lacrimal fossa, since the left side of the head has a covered up orbitosphenoid and a very deep lacrimal fossa with broken structures around it, and the right side of the head shows a somewhat more shallow lacrimal fossa. The infraorbital foramen is round, quite large and seems to be deep, although this cannot be said with certainty since it is filled up with sediment. The zygomatic arch is missing on both sides. In dorsal view, the skull is very small. In lateral view it is hard to say something about the dorsal side of the skull, because the bone has broken into several pieces in this area. The occlusal curve is present throughout, but very strong at the molars.

Mandible The mandible has a broad coronoid but short process. The condyle is small, but sticks out laterally, making the ramus deep at its side, although it is shallow in other areas. The base is a mainly straight line with some bumps and the angle is only gently curved, but very wide. The mental foramen is oval.

This skull has some characteristics of *Miniochoerus gracilis* (pictures in Schultz and Falkenbach, 1956). It is quite small, but the mandible is very wide at the angle. The zygomatic bone is a small structure above a strongly curved occlusal surface. So probably this individual belongs to this species.



Figure 25. Specimen G124/1899, *Miniochoerus gracilis*. Lateral view of the dextral side of the skull.

Miniochoerus affinis Leidy, 1869

(Figure 26)

G85/1899, identified in the UU collection as *Oreodon* sp.

Middle-sized skull with mandible (figure 26). Exterior part of skull mostly free of sediment, interiorly filled. The premaxilla is intact except for the most anterior portion. The rest of the skull and the mandible have lost some protruding parts.

Skull The zygomatic bone of the animal is broken off posteriorly at both sides, together with the zygomatic arch. The remaining part shows that the curvature of this structure extends well towards and above the infraorbital foramen. The orbitosphenoid also misses the posterior part at both sides. The part that is preserved is round, with an opening in the upper anterior corner. The lacrimal fossa is shallow and not connected to the orbitosphenoid. The infraorbital foramen is not very large and filled with sediment. The occlusal curve is a bit S-shaped, curving upwards at the premolars and more anterior, and curving downwards at the molars. The upper part of the parietal bone is missing, so its shape is unknown.

Mandible In the mandible, the coronoid process too is missing at both the sinistral and the dextral side. The condyle is small, but the ramus is very deep, with multiple structures in it. Below the

molars, the base is slightly curved, but further it is straight, with no significant curve towards the angle, which itself is also not curved that much. The mental foramen is situated at the most anterior part of the base. It is small and oval.

The flat shape and the intermediate size of the skull looks like individual F :A.M. 44977 in Schultz and Falkenbach (1956). The area around the infraorbital foramen and the lacrimal fossa as well as the lack of curving in the base of the mandible are also similar. Most characteristics point towards *Miniochoerus affinis*, parts of the skull are missing, which makes the identification uncertain, resulting in the determination *Miniochoerus affinis cf.*



Figure 26. Specimen G85/1899, *Miniochoerus affinis cf.* Lateral view of the sinistral side of the skull.

?*Miniochoerus forsythae* Schultz and Falkenbach, 1968

(Figure 27)

G131/1899, identified in the UU collection as *Oreodon culbertsoni*.

Large, almost complete skull with mandible, identified as *Oreodon culbertsoni* (figure 27). The premaxilla is very much complete for its largest part. The nasal is only missing the most anterior part. Also some teeth, part of the parietal and angle as well as the right zygomatic arch and part of the orbitosphenoid on that side are missing.

Skull The zygomatic bone makes a not so strong curve, and is followable for only a small distance. The structure ends about a centimetre before the infraorbital foramen. None of the zygomatic arches is complete, but it is visible that the whole zygomatic structure does not extend far laterally from the rest of the skull. The orbitosphenoid is not round, but pointy at the posterior end. In the upper anterior corner, there is an opening. The lacrimal fossa is very elongate, and consists of three compartments separated by little lumps of bone. The outer edge of the infraorbital foramen is very straight. The hole is medium sized, but filled with sediment, so the depth is unknown. It is situated between P² and P³ The occlusal curving is very slight, but present through the whole surface. In dorsal view, there is an opening above the orbitosphenoid, with a dent leading towards it.

Mandible The mandible does not have a high coronoid process. It is close to the height of the condyle, which is sticking out a bit. The ramus is small and a bit deep at the anterior side, and there is a ridge on the bottom, which is extending upwards. The bone around both mental foramina has been fragmented, so it is not possible to say something about their shape. The base of the mandible is very straight. The angle is missing on both sides.

The individual has been identified as *Oreodon culbertsoni*. This species has been described as *Merycoiodon culbertsoni* by Schultz and Falkenbach (1968). When comparing the drawing in this article with the skull, there are some similarities, but also some differences. The lacrimal fossa is elongated in both cases, and the deep opening above the orbitosphenoid is also situated at about the same place. However, the zygomatic bone has a much sharper curve in the skull, above the last molar, while in the picture the curve is hardly visible and a molar earlier. The shape and placement of the coronoid process and the condyle in the mandible, look like these structures in *Merycoiodon forsythae* in the paper of Schultz and Falkenbach (1968), which is now placed in the genus *Miniochoerus*. When looking at the skull of this species, the zygomatic structure, as well as the shape of the lacrimal fossa and the orbitosphenoid look much alike the skull described here. Also the general, bulky shape of the skull resembles that in the picture. Considering these points, is it probable that the skull does belong to the species *Merycoiodon forsythae*. In 1996, Stevens and Stevens (1996) put this species in the genus *Miniochoerus*.



Figure 27. Specimen G131/1899, ?*Miniochoerus forsythae*. Lateral view of the sinistral side of the skull.

Miniochoerus starkensis Schultz and Falkenbach, 1956

(Figure 28)

G161/1899, no prior identification

Skull covered for a large part in sediment (figure 28). The mandible is missing. The premaxilla is not present, the molars and premolars are partly covered in stone, just like most of the left side of the skull.

Skull The skull has a flat shape and is quite long. The zygomatic bone is very thick, with a round angle and very straight after that. Based on the zygomatic arch, the skull could be of *Miniochoerus helprini* (Schultz and Falkenbach, 1956). In dorsal view, the skull also matches this species in figure 3 of Schultz and Falkenbach, 1956. The infraorbital foramen, although filled with stone, seems to resemble this picture too.

Only the buccal side of the molars is visible, showing a selenodont dentition. The enamel is about 1 dm wide, and maybe somewhat thicker anterior than posterior.

Considering these characteristics, the skull probably belongs to *M. helprini*. In 1996, however, Stevens and Stevens considered all fossils from this species as *Miniochoerus starkensis*.



Figure 28. Specimen G161/1899, *Miniochoerus starkensis*. Lateral view of the dextral side of the skull.

Family MERYCOIDODONTIDAE

Genus INDET.

species INDET.

(Figures 29 and 30)

G114/1899, identified in the UU collection as *Oreodon bullatus*.

Small fragment of the top of a skull (figure 29).

Skull The posterior end of the zygomatic arch in the picture in Schultz and Falkenbach (1968) is a bit similar to that of the skull. The skull has on the dorsal side of the parietal eight small openings on each half. The drawing shows only three of them, but they are drawn at the same place. Unfortunately, the occipital condyles at the ventral-posterior end of the skull are missing in the drawing, and other points of comparison are lacking.

It could be that the initial determination of this skull is correct, but the bone is so fragmented, and there are so little characteristics which can be compared to the literature, that it is not possible to say to which species the skull belonged.



Figure 29. Specimen G114/1899, Genus INDET species INDET. Lateral view of the dextral side of the skull.

G153/1899, identified in the UU collection as *Oreodon* sp.

Large part of a skull with M¹⁻³ on both sides (figure 30). On the dorsal side, some bone is visible, but most of the rest of the skull is either covered in sediment or missing.

Skull The occlusal curve at the molars is a light upward curve. The skull has been identified as a lower jaw. It is easy to see how this mistake has been made, since large parts dorsal of the molars are missing, and the top of the skull is lying flat on it, making it easier to see the structure upside down. However, when you look closely, parts of the structure of the palate can be seen, in comparison to the empty structure that is present between the two halves of a mandible.

The molars can be described as square. In comparison to the *Miniochoerus* molars, they are large. There are not enough characteristics present to identify the skull.



Figure 30. Specimen G153/1899, Genus INDET species INDET. Lateral view of the dextral side of the skull.

Dentition Only the M¹⁻³ on both sides are preserved, the rest of the dentition is missing.

The most buccal part of mesostyle is not one point, but instead consists of two apices with a valley inbetween. The paraconulus is a very apparent structure in the M³, in the M² it is very small and seems to consist of two apices, but in the first upper molar, this structure is so big, it takes the place of the protocone, which appears to be pushed out towards the mesial side. In the second and third

upper molars, the structure between the protocone and the hypocone forms an extra little apex. All the apices in the molars are sharp and triangular. The M² and M³ are square, the M¹ is elongate. The shape of the M¹ is not similar to any picture in the available literature, meaning it is either a different genus than the other ones present, or a mutated animal.

In table 6 an overview of the sizes of the molars is given. In this table, the difference between the square and elongate molars is evident.

Table 6: Measurements of the molars of skull G153/1899, Genus INDET species INDET, with approximate maximum measurements (in cm). In this table, width stands for the buccal-lingual distance, and length for mesial-distal distance.

Sizes:	Dextral width	length	Sinistral width	length
M ¹	1.4	1.8	1.5	1.8
M ²	1.8	1.7	1.7	1.7
M ³	2.1	2	2.2	2

5.2 Measurements of the skulls and dentition

The measurements that have been carried out are given in the table 7

Table 7. Measurements carried out on the skulls and mandibles. Measurements are in mm. Descriptions of the measurements can be found in the Material and Methods section of this research. Collection numbers starting with a G are from the collection of the University Museum in Utrecht, numbers starting with st or RGM are from NCB Naturalis, and numbers with TM are from Teylers Museum.

Species	Collection number	Width Measurements			Tooth Length Measurements				Skull Length Measurements				
		1	2	3	4	5	6	7	8	9	10	11	12
<i>Merycoiododon (Otarohyus) sp.</i>	G158/1899		23			21.2		27.55		88.1			
<i>Merycoiododon culbertsoni</i>	Pa10/1899		32					41.2					90
<i>Merycoiododon culbertsoni</i>	G107/1899	21.5	25	66.1	29.5	74.75	38.85	37.7	148.2	150			
<i>Merycoiododon culbertsoni</i>	st 18236			78.7	29.75	83.1	42.85	42.65	152.15				136.45
<i>Merycoiododon culbertsoni</i>	st 18235				24.4			26.15	94.85	98			88
<i>Merycoiododon culbertsoni</i>	TM 8591				34.25	82.15	47.5	38					
<i>Merycoiododon culbertsoni</i>	G130/1899			91.9	29.3	88.35	47.1	44	198	205			176
<i>Merycoiododon major</i>	RGM 592002					79.15	48.85	41.6					
<i>Miniochoerus affinis cf.</i>	G85/1899				27	68.4	35.5	34	123.4	131.1			114.8
? <i>Miniochoerus forsythae</i>	G131/1899				29	80.25	43	38					
<i>Miniochoerus gracilis</i>	G109/1899												
<i>Miniochoerus gracilis</i>	G124/1899					62.4	34.65	29.4					105.65
<i>Miniochoerus gracilis</i>	G108/1899	12.35	21.55	62.75	26	60.55	34.71	27.45	114.05	120.6	52.2	69.35	
<i>Miniochoerus gracilis</i>	G122/1899			58.2	23.7	54.25	30.7	21.95					101.65
<i>Miniochoerus gracilis</i>	G123/1899				25	55.5	30.25	25.6					
<i>Miniochoerus starkensis</i>	G161/1899		32			96.65	47.6	45					
Merycoiodontidae gen et sp. indet.	G114/1899												
Merycoiodontidae gen et sp. indet.	G153/1899		23					55					

These measurements have been compared to similar ones from Phleger and Putnam (1942). For this purpose, used are the data of two of their figures. First is the one which compares the length of the molar series to the length of the premolar series. Their results, combined with the ones found in this research can be seen in figure 31.

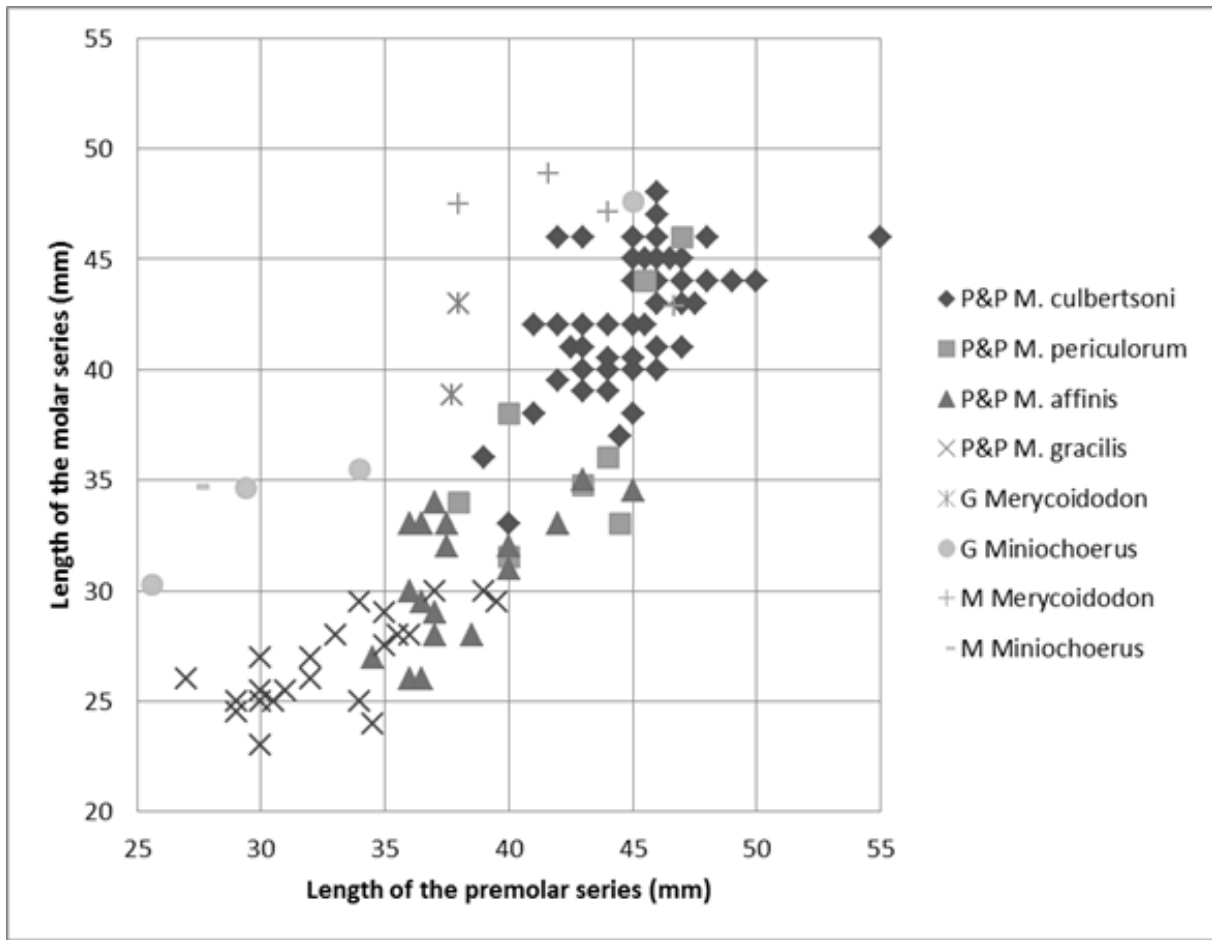


Figure 31. Plot of the length of the molar series against the length of the premolar series. P&P in the legend stands for measurements taken by Phleger and Putnam (1942). They had specimens from two genera and four species: *Merycoiododon culbertsoni* and *M. periculorum* and *Miniochoerus affinis* and *M. gracilis*. G stands for measurements taken by the author, on species identified by the author, M stands for measurements taken by the author with taxa based on identifications by the various institutions. Based on: Phleger and Putnam (1942).

The original measurements of Phleger and Putnam are evenly spread across the scale. Even though the later added measurements of the author of this research fall somewhat out of the range of the original data, they are spread vertically in a similar way and both groups can be divided into two using a molar series length of around 35 mm. For clarity, the later added measurements are grouped by genus instead of species.

Interesting is the *Miniochoerus* specimen at the point with coordinates (45;47.6) in figure 31, since this one falls so far above the other *Miniochoerus* samples. The other three points are *M. affinis* and *M. gracilis*, while the upper dot is *M. starkensis*. In the original data *M. affinis* and *M. gracilis* also are close together, with in both cases *M. affinis* as the larger species.

The second comparison to the Phleger and Putnam article (1942) is on different lengths of the skull. These results can be seen in figure 32.

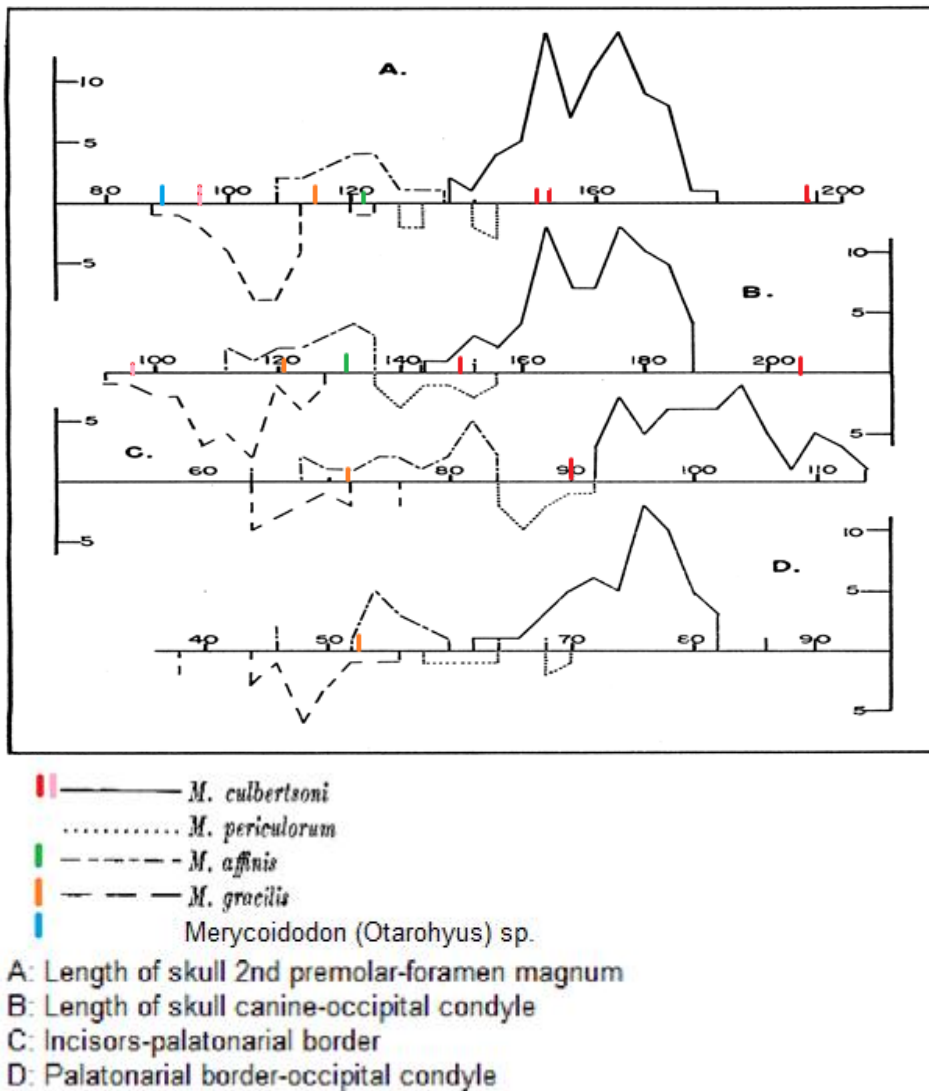


Figure 32. Different skull lengths (horizontal axes in mm, vertical axes are the frequency). The pink bar stands for a young specimen. While the vertical axis in the original picture stands for the number of specimens, the coloured bars represent only one individual. The horizontal axis are the sizes in mm. A is the length of the skull from the anterior of the second premolar to the top of the foramen magnum, B is the length of the skull from the anterior surface of the canine to the bottom of the occipital condyle, C is the distance from the inner edge of the incisors to the palatinal border and D is from the palatinal border to the bottom of the occipital condyle. Based on: Phleger and Putnam (1942).

Visible in figure 32, is that the values of *Miniochoerus affinis* and *gracilis* are close together, and fall in or near the range given by Phleger and Putnam. *Merycoiodon culbertsoni* specimens are clearly larger than the other species. The young individual falls in the range of *M. affinis*, and is taken up in this comparison to make visible the differences in size between young animals and adults.

In general, the width measurements are less reliable than the length measurements, since the skulls are more likely to be crushed, than to undergo longitudinal distortion. There is also a problem with protruding structures such as zygomatic arches (Phleger and Putnam, 1942). Therefore, it is advisable to limit comparisons to length measurements.

5.3 Mesowear

Mesowear (or macrowear) analyses can tell something about what type of food the animal ate during its life, in contrast to microwear analyses, which focus on small abrasions in the enamel, thus depicting mainly what the animal ate the day (or season) it died. For determining the lifestyle of an animal, both methods are useful.

The great advantage of the mesowear analysis is that it is in comparison very easy to carry out, less time-consuming and cheaper (it is best to do it with the naked eye or hand lens). This method is used here to describe the dentition in further detail and interpret the way of living of the oreodonts. With this method, the contribution of tooth-on-food (abrasion) and tooth-on-tooth (attrition) wear can be determined. Since oreodonts have selenodont teeth, they cut their fibrous diet by pushing their cutting edges right through the food. This means they have a precise occlusion and there is a lot of tooth-on-tooth wear (Fortelius and Solounias, 2000).

Not only worn teeth can give clues on the diet of the animal. Also the unworn (or preformed) morphology is very important. It provides information on the long-term adaptations of the species to the environment it lives in and evolves in and what food the animal could have processed. A clear example of this in the oreodonts is their hypsodonty (Fortelius and Solounias, 2000).

Hypsodonty is a derived condition of the molars and to a lesser extent premolars, often found in grazing mammals. When an animal has hypsodont molars, the molars are high crowned. This means that the teeth are higher than the primitive mammalian condition of brachydonty and sometimes roots disappear. As the crown wears down, more of the tooth erupts, since part of it is retained in the jaw. Since the tooth is higher, the animal can use it for a longer period of time, thus allowing it to eat more abrasive food than low crowned species which will wear their tooth down. Hypsodonty has evolved several times independently in mammals of very different sizes, from rodents like voles to horses, cows and deer. Abrasiveness can be caused by for example phytoliths in grass, and grit on the food. Other reasons for developing hypsodonty can be high occlusal stress, or mastication of large amounts of food (Fortelius and Solounias, 2000).

Soil, dust, sand and wind-blown grit are important inorganic factors determining the wear rate of the molars. Food lying or growing on the ground is often covered in part by soil, especially when an animal pulls the plants out and eats the roots too. In open, arid habitats, wind can resuspend the soil and deposit it on leaves. In this type of area, the splash raindrops make when falling on the ground can also mean large amounts of soil ending up on the higher vegetation. In more humid areas, however, rain will clean the dirt of the plants, but at the same time the ground will be more muddy and disturbance by animals will make more soil adhere to the lower parts of the

plants growing there. When grazing is intense and the food becomes more scarce, there will also be more grit taken in, because the animals will be less selective for food (Damuth and Janis, 2011).

The mesowear analysis of Fortelius and Solounias (2000) focusses on two points of the teeth: sharpness of the cusps and occlusal relief. Occlusal relief is the relative distance in height between the valleys and apices of the cusps (figure 29). This is in relation to the actual length of the cusp and does not have to be measured but rather it is more important how the relief appears in lateral view. As one would expect, a combination of high attrition and abrasion results in a low occlusal relief. When the teeth undergo lower occlusal stress, a higher occlusal relief develops. This is seen in grazers of fresh grass, but the theory behind this is not yet clear.

In the analysis of the cusp shapes, the paracone or metacone of a tooth is described as sharp, rounded or blunt (see figure 33). The paracone and metacone are usually identical in mesowear in one animal, so both can be used, but it is best to take the sharpest apex, since sharpness cannot be caused by wear, but bluntness can.

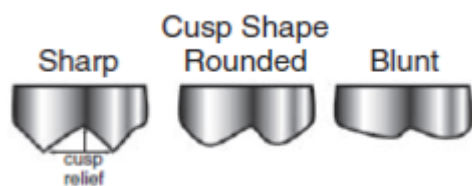


Figure 33. Cusp shape and occlusal relief explained in molars with different shapes and relief. From: White *et al* (2009).

The theory behind the shape of the cusps is that it is dependent on whether abrasion or attrition is more dominant. If the cusps are still sharp, even after years of usage, it means that attrition contributes relatively more to the wear. In blunt cusps, the opposite is the case.

To distinguish between the two possibilities of relief, the vertical distance between two apices surrounding a valley is divided by the length of the whole tooth (from apex till end of enamel) (see figure 34).

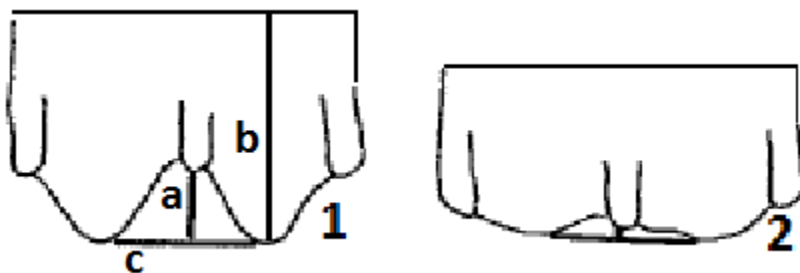


Figure 34. High vs. low occlusal relief. 1 is a molar with high occlusal relief, 2 a molar with low occlusal relief. Both show the buccal side of the molar. A is the vertical distance from apex to valley, b is the height of the whole tooth and c is the distance between two apices. Adapted from Fortelius and Solounias (2000).

Fortelius and Solounias place the boundary between high and low at 0.1, with low occlusal relief <0.1. In table 8 the values measured in the collection of the University Museum can be found (for an example from this collection, see figure 35), along with the cusp shape. It is tried is to, where possible, always take the second molar for these measurements, since without measurements the three molars seem to have the same relief, and being in the middle, the second molar would give an average value.

Table 8. Occlusal relief and cusp shape of the oreodonts of the University Museum.

Collection number	Apice length (pixels)	Whole tooth length (pixels)	Relief value	Cusp shape	Species
G85/1899	33	135	0.24444444	Sharp	<i>Miniochoerus affinis</i>
G. 107/1899	not enough data				<i>Merycoiododon culbertsoni</i>
G.109/1899	71	155	0.45806452	A bit rounded	<i>Miniochoerus gracilis</i>
G. 114/1899	no teeth present				sp. indet.
G. 123/1899	60	82	0.73170732	Very rounded	<i>Miniochoerus gracilis</i>
G. 124/1899	76	248	0.30645161	Sharp	<i>Miniochoerus gracilis</i>
G. 131/1899	38	89	0.42696629	Sharp	<i>Miniochoerus forsythae</i>
G. 153/1899	Top of molars broken off				sp. indet.
G. 158/1899	67	290	0.23103448	Left blunt, right sharp	<i>Merycoiododon (Otarohyus) sp.</i>
G. 161/1899	38	62	0.61290323	Rounded/blunt	<i>Miniochoerus</i>
Pa 10/1899	48	155	0.30967742	Sharp/rounded	<i>Merycoiododon culbertsoni</i>

Most of the skulls and the mandible in the collection of the University Museum have sharp teeth, but there are also some animals with rounded or even blunt teeth. All the teeth however have a high occlusal relief.

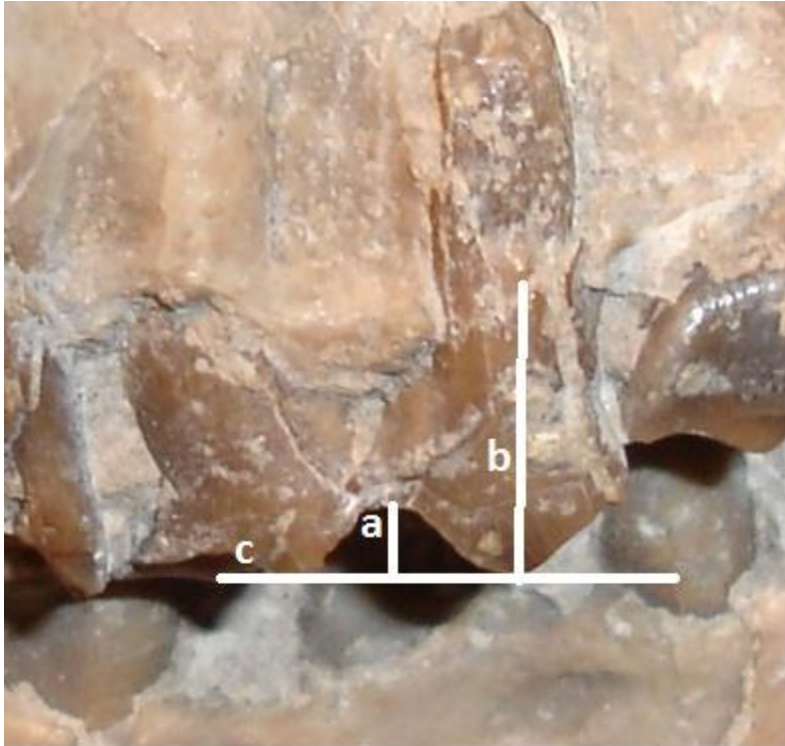


Figure 35. Specimen G85/1899, showing lines where the molar has been measured. The tooth is measured on the computer using pixels as unit). In this picture, a is the vertical distance from apex to valley, b is the height of the whole tooth (until where the tooth enters the bone of the skull) and c is the distance between two apices.

Figure 36 gives an overview of the shapes, within the two genera *Merycoiododon* and *Miniochoerus*. *Miniochoerus starkensis* has blunt molars. A division has been made in University Museum specimens (UM), specimens from other musea, which also have not been used in table 7 (other) and these two groups together (total). This figure shows that both genera start off sharp since both genera have specimens with sharp teeth, and sharpness cannot be caused by wear. Not clearly visible in this figure, but in the specimens, is that *Miniochoerus* specimens have often either sharp or rounded cusps, and the one blunt one in the collection was doubtful. *Merycoiododon* is often very sharp and real blunt cusps could be found in this genus.

Not every specimen could be used, because some had tooth that were damaged in a way that indicated that the damage was done during the excavation. It is possible that some of the animals noted here as blunt have come in this category because of such an event, but care has been taken not to include them. Rounded teeth were clearly round and did not show signs of post-mortem reworking.

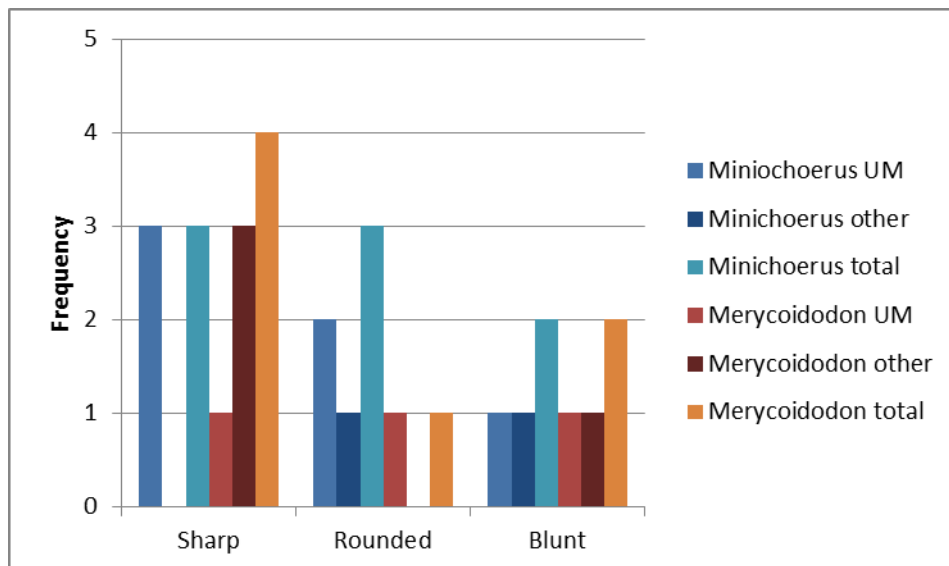


Figure 36. Frequency chart of cusp shapes per genus. UM stands for specimens from the University Museum, other are specimens from other museums and total is the previous two groups taken together.

6. Discussion

Based on the description and identification of the skulls of the University Museum in Utrecht, the following taxa are present:

- *Merycoiododon culbertsoni*, specimens: G107/1899, G130/1899 and Pa10/1899.
- *Merycoiododon (Otarohyus) sp.*, specimen: G158/1899
- *Miniochoerus affinis*, specimen: G85/1899
- *Miniochoerus gracilis*, specimens: G108/1899, G109/1899, G122/1899, G123/1899 and G124/1899
- *Miniochoerus forsythae*, specimen: G131/1899
- Merycoiodontidae gen. et sp. Indet, specimens: G114/1899 and G153/1899

Merycoiododon culbertsoni is a species which has a large intraspecific variation. So much, that Schultz and Falkenbach (1968) extremely oversplit this species. When using only their article to identify the skulls from the UU museum, all the skulls now identified as *Merycoiododon culbertsoni* ended up in their (no longer existant) subspecies *M. c. osborni*. The species has known a lot of variation, but all the skulls here look more or less the same. This could indicate that they are of a similar geologic age. The catalogue of the museum is not very clear on how and from where the skulls were obtained, so this could indicate that the skulls come from one location. Another possibility is that the skulls do come from different layers or places and convergent evolution has taken place, meaning they do not necessarily belong in the same geologic age.

As can be seen in figure 37, *Merycoiododon* and *Miniochoerus* species have an overlap in time in which they lived around 33.5-33 Ma.

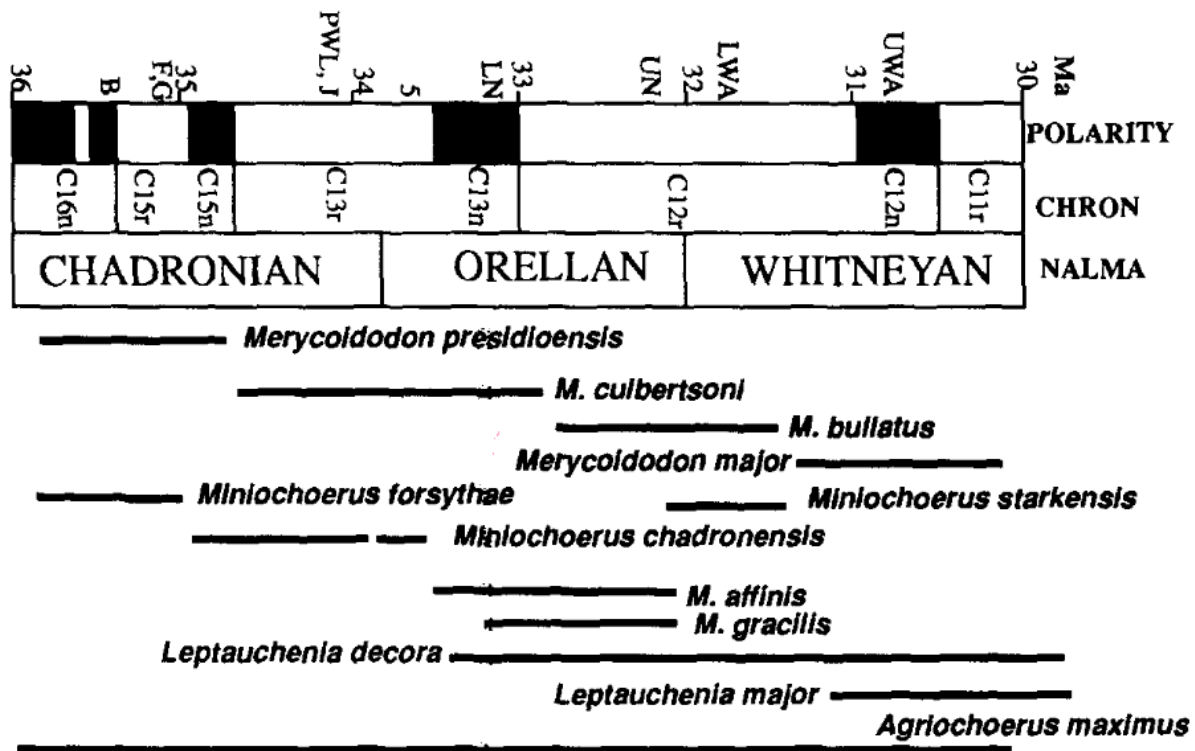


Figure 37. Ages during which the different species of oreodonts lived. The Eocene-Oligocene boundary is situated between the Chadronian and Orellan (33.7 Ma). Adapted from: Prothero and Heaton (1996).

As mentioned in the descriptions of the fossils, one fossil differs in colour from the others. Skull Pa10/1899, identified as *Merycoidodon culbertsoni*, is of a dark brown colour. It is from the collection of B. Stürtz in Bonn. So even though all the material has been brought into the collection in the same year, 1899, it seems that Pa10/1899 has been collected from a different source, which would explain the different colour. The different colour is probably the result of a different medium in which the animal fossilized, so Pa10/1899 does not come from the same location and probably also not the same age as the other animals.

Measurements

The values measured in the skulls from the various collections fall nicely into those of Phleger and Putnam (1942) (see figure 32). The species in their research show a normal distribution for the measured values and the values of the skulls measured in this research fall mostly within these curves, often near the optimum. This indicates that the species names that were given to the specimens in this research could be correct, because based on size they fall in the same range as the skulls identified by Phleger and Putnam (1942).

The measurements of the molars and premolars (see figure 31) follow the same pattern as the genera used by Phleger and Putnam and the molar series have the same lengths, only the premolar

series have different values. This is probably because in this paper another way of measuring the premolars has been used. Because the values found in this research do not fall in the groups found by Phleger and Putnam (1942), it is not possible to say that the specimens in this research belong to the same species, but when accounting for measuring errors, the same species do have more or less the same molar series length.

Mesowear

How can the results of the mesowear analysis be interpreted for the different genera? Both have a high occlusal relief, so they had a similar diet in terms of low occlusal stress as have present day grazers of fresh grass, with a side note that grasses were not as widely spread as in present times during the age of the oreodonts.

The sharp shape of the *Merycoidodon* molars means that attrition (tooth-on-tooth wear) was the most important for the wear of their tooth than abrasion. In *Miniochoerus* molars, abrasion also was an important factor in the wear, but abrasion (tooth-on-food wear) also played a role.

Species in the genus *Merycoidodon* larger than in the genus *Miniochoerus* (estimated bodyweight 62.3 vs 18.3 kg (Mendoza *et al.*, 2006)). It could reach branches that were higher up and perhaps less covered in abrasive dirt. This difference was enhanced because *Miniochoerus* underwent a dwarfing trend, with a size reduction of 30% over one million years. This trend meant that *Miniochoerus* could only reach even lower vegetation (Prothero, 1996). Another possibility is that *Merycoidodon* liked to browse in wetter areas where the leaves were rained clean.

Merycoidodon's first appearance was 37.2 Ma, in the Chadronian, while the genus *Miniochoerus* did not start to radiate before 35 Ma at the end of the Chadronian (see also figure 38).

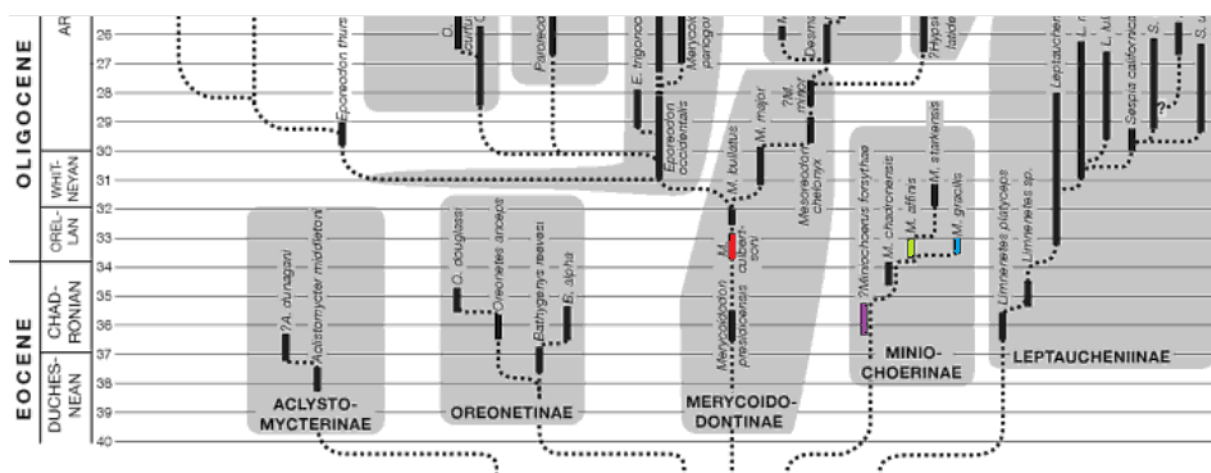


Figure 38. Part of a phylogenetic history of the Family Merycoidodontidae on the species level (Adapted from: Stevens and

Stevens, 2007). Numbers on the vertical indicate age in Ma. Species found in this research are coloured. Red: *Merycoiododon culbertsoni*, purple: *?Miniochoerus forsythae*, green: *Miniochoerus affinis*, *Miniochoerus gracilis*.

The habitat in which these genera developed and lived was not the same. In the Early Eocene, there was a humid, sub-tropical climate and they were forested. In the middle Eocene this type of vegetation and climate was maintained, but throughout the Chadronian it was becoming drier, cooler and more like a savannah. With the disappearance of wooded habitats, the availability of fruit plants became less, so a shift in diet was necessary (MihlBachler and Solounias, 2006). The Oligocene had again a temperate, semiarid-to-arid savannah ecosystem and forests could only be found near rivers and ponds (Ostrander, 1984). This shift in climate corresponds to the shift in dental wear that is found here.

7. Conclusions

Based on pictures, descriptions and measurements in literature species names have been given to several specimens of the collection of the University Museum in Utrecht. The measurements fit into those given in the literature, giving some confirmation on the determinations. The patterns seen in the mesowear analysis mimic those expected by known climate changes during the time the oreodonts evolved.

That the genera *Merycoiododon* and *Miniochoerus* both are found in the collection of the University Museum, together with the fact that the *Merycoiododon* specimens have little variation, the colour of the skulls and mandibles, which are with only one exception of a yellowish white and the equality of the sediment still attached to the fossils could mean that the fossils are found in the same layer at the same time by the same collector. Unless more data on the purchase of these fossils will be found however, there will most likely never be formed a conclusive answer to the question of where exactly the fossils come from. The found species all lived across the whole area of the White River Badlands, so putting a location on the fossils is almost impossible, but we can say something about the age of the fossils.

?Miniochoerus forsythae is limited to the Middle Chadronian (34.7-35.7 Ma). *Merycoiododon culbertsoni* had its first appearance in the Late Chadronian (34.7-33.7 Ma). *Miniochoerus affinis* had its first appearance in the Late Early Orellan (33.4-33.1 Ma). *Miniochoerus gracilis* had its first appearance in the Early Late Orellan (33.1-32.5). *Miniochoerus starkensis* had its first appearance in the Latest Orellan (32.5-32.0) and its last appearance in the Early Whitneyan (32.0-31.4). These ages do not really overlap. As can be seen in figures 37 and 38, *Merycoiododon culbertsoni*, *Miniochoerus affinis* and *Miniochoerus gracilis* have a short period of time during which they all occurred, but *?Miniochoerus forsythae* and *Miniochoerus starkensis* do not fall in this range in time.

Based on the different species found and the geographic ages during which they lived, it is unlikely that they come from the same geographic layer of sediments. Since the White River Badlands consists of sediments from the Cretaceous to the Pleistocene, they could have been found at the same locality, except for specimen Pa10/1899, which differs too much in colour.

The fossils range in age from Middle Chadronian (35.7 Ma) to Early Whitneyan (31.4 Ma).

8. References

- Bump, J. D. (1956) Geographic names for members of the Brule Formation of the Big Badlands of South Dakota. *American Journal of Science* 254, 429-432.
- Catalogus Universiteits Museum Utrecht (1899).
- Clark, J. (1937) The stratigraphy and paleontology of the Chadron Formation in the Big Badlands of South Dakota. *Annals of the Carnegie Museum of Natural History* 25, 261-350.
- Culbertson, T. A. (1851) Journal of an Expedition to the Mauvaises Terres and the Upper Missouri in 1850. *Smithsonian Institution, Fifth Annual Report 1851*, 84-145.
- Darwinsgift, 2008. *Oreodont*. [video online] Available at:
<<http://www.youtube.com/watch?v=o6NwTcgqE8w>> (accessed 24 April 2012).
- Damuth, J., C. M. Janis (2011) On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biological Reviews* 86, 733-758.
- Fortelius, M., N. Solounias (2000) Functional Characterization of Ungulate Molars Using the Abrasion-Attrition Wear Gradient: A New Method for Reconstructing Paleodiets. *American Museum of Natural History* 3301, 1-36.
- Grandstaff, D. E., D. O. Terry Jr. (2009) Rare earth element composition of Paleogene vertebrate fossils from Toadstool Geologic Park, Nebraska, USA. *Applied Geochemistry* 24, 733-745.
- Hoganson, J. W., E. C. Murphy, N. F. Forsman (1998) Lithostratigraphy, paleontology, and biochronology of the Chadron, Brule, and Arikaree Formations in North Dakota. *Geographic Society of America Special paper* 325, 185-196.
- Kulzer, E., M. S. Fischer, J. Niethammer, H. Schliemann (2005) *Handbuch der Zoologie. Band VIII Mammalia*. Walter de Gruyter & Co, Berlin, 198 pp.
- Leidy, J. M. D. (1848) *Proceedings of the Academy of Natural Sciences of Philadelphia Vol IV*, 47-51.
- Leidy, J. M. D. (1851) *Proceedings of the Academy of Natural Sciences of Philadelphia Vol V*, 237-239.
- Leidy, J. M. D. (1852) *The ancient fauna of Nebraska: or, A description of remains of extinct Mammalia and Chelonia, from the Mauvaises Terres of Nebraska*. Smithsonian Contributions to Knowledge 6 (7), 126 pp.

- Leidy, J. M. D. (1869) The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences, Philadelphia, series 2, 7*, 1-472.
- Lillegraven, J. A. (1970) Stratigraphy, Structure and Vertebrate Fossils of the Oligocene Brule Formation, Slim Buttes, Northwestern South Dakota. *Geological Society of America Bulletin 81*, 831-850.
- Lyras, G. A. (2009) The evolution of the brain in Canidae (Mammalia: Carnivora). *Scripta Geologica 139*, 1-93.
- Macrini, T. E. (2009) Description of a digital cranial endocast of *Bathygenys reevesi* (Merycoidodontidae; Oreodontoidea) and implications for apomorphy-based diagnosis of isolated, natural endocasts. *Journal of Vertebrate Paleontology 29(4)*, 1199–1211.
- Matthew, W.D. (1899) Is the White River Tertiary an æolian Formation? *The American Naturalist 33*, 403-408.
- Mendoza, M., C. M. Janis, P. Palmqvist (2006) Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology 270(1)*, 90-101.
- Mihlbachler, M. C. and Solounias, N. (2006). Coevolution of Tooth Crown Height and Diet in Oreodonts (Merycoidodontidae, Artiodactyla) Examined with Phylogenetically Independent Contrasts. *Journal of Mammalian Evolution 13*, 11-36.
- National Park Service (2012). Explore The World of Florissant Paleontology. Available at: <http://planning.nps.gov/flfo/default.cfm> (Accessed on 6 August 2012).
- O'Harra, C. C. (1920) *The White River Badlands*. Rapid City, South Dakota, 181 pp.
- O'Harra, C.C. (1930) A Fossil Mammal with Unborn Twins. *Science, New Series 71*, 341-342.
- Ostrander, G. E. (1984). The Early Oligocene (Chadronian) Raben Ranch Local Fauna, Northwest Nebraska: Multituberculata; with Comments on the Extinction of the Allotheria. *Transactions of the Nebraska Academy of Sciences and Affiliated Societies 239*, 71-80.
- Owen, D. D. (1852) Incidental Observations on the Missouri River, and on the Mauvais Terres (Badlands). *Report of the Geological Survey of Wisconsin, Iowa and Minnesota and Incidentally a Portion of Nebraska Territory, by David Dale Owen, United States Geologist, Philadelphia*, 194-206.
- Pater, B., C. (2004) *Minnaars der aarde, ver van huis en haard: over 125 jaar geowetenschappen aan de Universiteit Utrecht*. Faculteit geowetenschappen, Universiteit Utrecht, 232 pp.
- Phleger, F. B., W. S. Putnam (1942) Analysis of Merycoidodon skulls, *American Journal of Science 240*, 547-566.

- Prothero, D.R. (1985) Mid-Oligocene extinction event in North American land mammals. *Science*, 229, 550-551.
- Prothero, D. R., T. H. Heaton (1996) Faunal Stability during the Early Oligocene climatic crash. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127, 257-283.
- Prothero, D. R., K. E. Whitlessey (1998) Magnetic stratigraphy and biostratigraphy of the Orrellan and Whitneyan land-mammal “ages” in the White River Group. *Geological Society of America Special paper* 325, 41–61.
- Prothero, D. R. (2004) Did impacts, volcanic eruptions, or climate change affect mammalian evolution? *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 283– 294.
- Prothero, D.R., R. J. Emry (2004) The Chadronian, Orellan, and Whitneyan North American land mammal ages. in: Woodburne, M.O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York, 156-168.
- Prothero, D.R., R. J. Emry (2006) Summary. in: Prothero, D.R., R. J. Emry, *The terrestrial Eocene-Oligocene transition in North America*. Cambridge University Press, 646-664.
- Prout, H. A. (1847) A description of a Fossil Maxillary Bone of Paleotherium from near White River. *American Journal of Science, second series*, 3, 248-250.
- Retallack, G. J. (2007) Cenozoic Paleoclimate on Land in North America. *The Journal of Geology* 115, 271-294.
- Sangress (2012). Florissant Fossil Beds National Monument. Available at: <http://www.sangres.com/colorado/national-parks/florissant.htm> (accessed on 6 August 2012).
- Savage, D. E., D. E. Russell (1983) *Mammalian paleofaunas of the world*. Addison-Wesley, London.
- Schultz, C. B., C. H. Falkenbach (1956) Miniochoerinae and Oreonetinae, two new subfamilies of oreodonts. *Bulletin of the American Museum of Natural History* 109, 377-482.
- Schultz, C. B., C. H. Falkenbach (1968) The phylogeny of the Oreodonts. *Bulletin of the American Museum of Natural History* 139, 498 pp.
- Shoemaker, A. (1999) *Oreodonts. Merycoidodon, Eporeodon, Leptauchenia, Miniochoerus*. [online] Available at: whiteriver.weebly.com (accessed 24 April 2012).
- Spaulding, M., M. A. O’Leary, J. Gatesy (2009) Relationships of Cetacea (Artiodactyla) Among Mammals: Increased Taxon Sampling Alters Interpretations of Key Fossils and Character Evolution. *PLoS One* 4, e7062.
- Stevens, M. S., J. B. Stevens (1996) Merycoidodontinae and Miniochoerinae. In: Prothero, D. R., R. J. Emry, *The Terrestrial Eocene-Oligocene Transition in North America*, 498-573.

- Stevens, M. S., J. B. Stevens (2007) Family Merycoidontidae. In: Prothero, D.R., S. Foss, *The Evolution of Artiodactyls*. Johns Hopkins Univ. Press, Baltimore, MD, 157-168. .
- Sundell, K. A. (2001) Preliminary Paleocology of the Swan Lake Quarries: An Orellan plant, invertebrate, and vertebrate bearing lake deposit from the White River Formation, Converse County. *Wyoming Journal of Vertebrate Paleontology*, V. 21, 3, 106A.
- Sundell, K.A. (2006) Burrowers of the Oligocene: Taphonomic Studies and Interpretation of the White River Underground. In: Tate 2006 Guidebook -*Trackways and Trace Fossils, 12th annual symposium*, 73-77.
- Sundell, K. A. (2007) Oreodonts: Extinct large burrowing mammals of the Oligocene. Tate Museum Publication 2, *1997 field conference guidebook*, 31-43.
- Terry Jr., D. O. (1998) Lithostratigraphic revision and correlation of the lower part of the White River Group: south Dakota to Nebraska. *Geological Society of America Special paper 325*, 15–37.
- Terry Jr., D. O. (2001) Paleopedology of the Chadron Formation of Northwestern Nebraska: implications for paleoclimatic change in the North American midcontinent across the Eocene-Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168, 1-38.
- Wanless, H.R. (1923) The Stratigraphy of the White River Beds of South Dakota. *Proceedings of the American Philosophical Society* 62, 190-269.
- White, D. T., S. H. Ambrose, G. Suwa, D. F. Su, D. DeGusta, R. L. Bernor, J. Boisserie, M. Brunet, E. Delson, S. Frost, N.Garcia, I. X. Giaourtsakis, Y. Haile-Selassie, F. C. Howell, T. Lehmann, A. Likius, C. Pehlevan, H. Saegusa, G. Semprebon, M. Teaforde, E. Vrba (2009) Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus*. *Science* 326, 67-93.
- Wikipedia (2012) Oreodont. Available at: <http://en.wikipedia.org/wiki/Oreodont> (accessed on 9 June 2012).
- Wood, H. E. II., R. W. Chaney Jr., J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, C. Stock (1941) Nomenclature and correlation of the North American continental Tertiary. *Geological Society of America Bulletin* 52, 1-48.
- Wortman, J. L. (1893) On the Divisions of the White River or Lower Miocene of North Dakota. *Bulletin of the American Museum of Natural History* 5, 95-105.
- Zanazzi, A., M. J. Kohn (2008) Ecology and physiology of White River mammals based on stable isotope ratios of teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257, 22-37.

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Appendix: Measurements of Endocasts

Palaeoneurology, the study of the nervous system of fossil animals, has always been an important part of paleontology. As early as 1804, Cuvier used the cast of the brain cavity of fossil vertebrates to gain information about the external anatomy of the brain. Placental mammals prove very useful for this study, since, with a few exceptions, their brain fills most of the neurocranium and casts of the brain cavity (called endocasts) show many features of the outside of the brain anatomy. There are two types of endocranial casts. First, there are stone casts, in which the neurocranium has been filled with sediments which have later been fossilized. The other way of obtaining an endocast is using the neurocranium as a mould for a latex cast, after removing the sediment from the cavity (Lyras, 2009). In figure A1 and A2 the endocasts of Teylers Museum can be seen. According to the description in the museum, they are of the following species: *Merycoiododon culbertsoni* (specimen 16378) and *Miniochoerus gracilis* (specimen 16380). These endocasts are natural endocasts.

The lines in the pictures indicate where measurements have been taken. The results of these measurements can be seen in table A1. No conclusions have been formed based on these brains, since this is beyond the scope of the paper and because of limited knowledge by the author on fossil brains. The names of the structures have been taken from Macrini (2009).

The goal of presenting the reader with these fossils is to show that much more research is possible with oreodonts and in how many ways information about these animals can be collected, plus the retaining of size of the brains during the dwarfing trend is visible in the measurements made here. Also, the endocasts are so nicely preserved, that it would be a shame not to include them here.

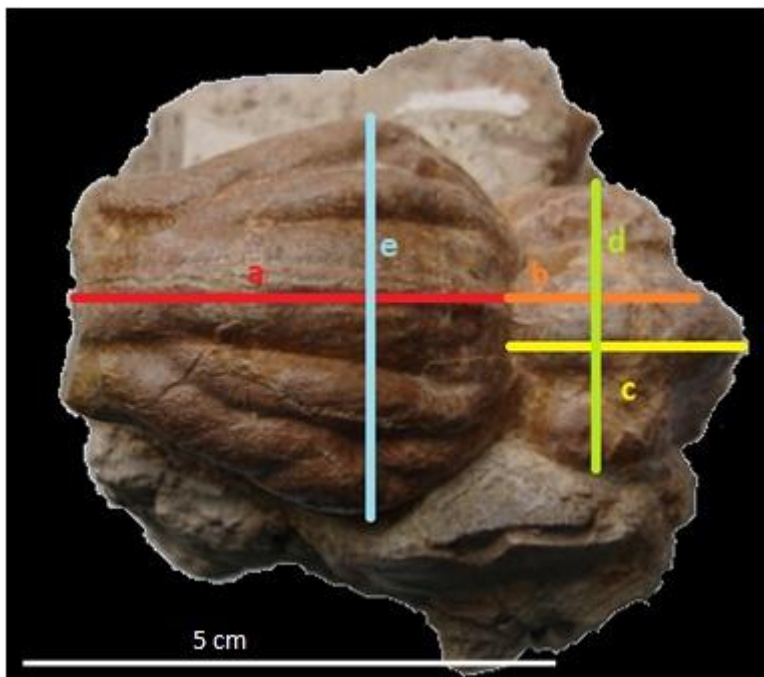


Figure A1. Measurements taken on specimen 16378, *Merycoiododon culbertsoni*, of Teylers Museum. The letters correspond to those in table A1.

The first endocast is of *Merycoiodon culbertsoni*. Only the dorsal part is visible, since the rest is still stuck in the sediment. The cerebellar cast had a long small appendix, the total length of this structure is indicated by length c. Results of the measurements that have been taken can be found in table 8.

Table A1. Measurements of an endocast of *Merycoiodon culbertsoni*.

Name in picture	Structure	Size (mm)
A	maximum length of cerebral cast exclusive of olfactory bulbs	43.1
B	maximum length of cerebellar cast	24
C		35.85
D	maximum width of cerebellar cast	29.85
E	maximum width of cerebral cast	39.85

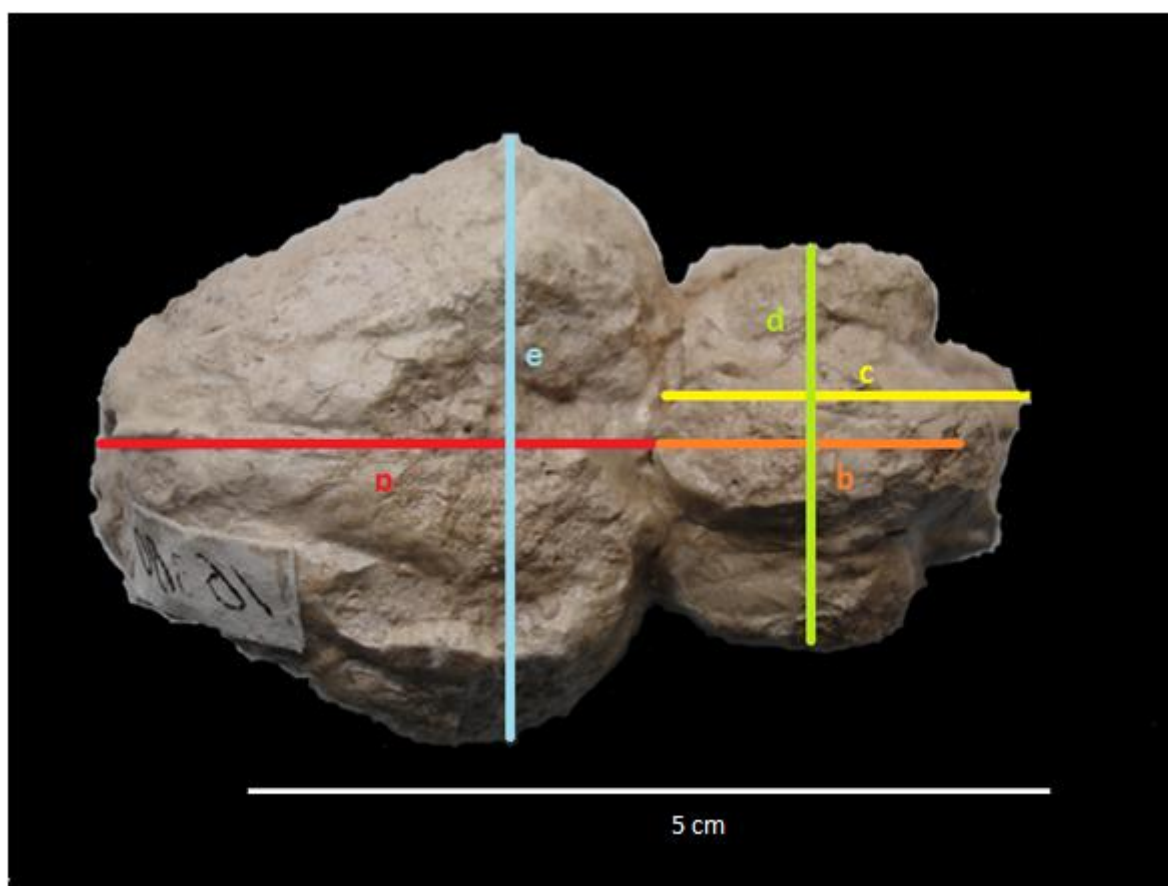


Figure A2. Measurements taken on specimen 16380, *Miniochoerus gracilis*, of Teylers Museum. The letters correspond to those in table A2.

The second endocast is of *Miniochoerus gracilis*. As can be seen in table A1 and A2, the measurements of the two species lie very close together. The skull of *M. gracilis*, however, is smaller

than that of *M. culbertsoni*. As Stevens and Stevens (1996) note, the phylogenetic dwarfing of the genus *Miniochoerus* caused a relatively large brain in a small skull. This could be the reason the two brains are similar in size. Another possibility is that on or both of the endocasts have been identified incorrectly and that they are of the same species, or two even different species, one of which is represented by a juvenile which has brains that still have to grow.

Table A2. Measurements of an endocast of *Miniochoerus gracilis*.

Name in picture	Structure	Size (mm)
A	maximum length of cerebral cast exclusive of olfactory bulbs	43
B	maximum length of cerebellar cast	25
C		33
D	maximum width of cerebellar cast	28
E	maximum width of cerebral cast	43.8

This second endocast is completely free of the sediment and has a remarkable conservation of its shape and that of its arteries (see figure A3).



Figure A3. Lateral and ventral view of specimen 16380, showing very good preservation of the shape of the arteries.