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A species level revision of Bridgerian and Uintan brontotheres (Mammalia, Perissodactyla) exclusive of *Palaeosyops*

BRYN J. MADER

Department of Biological Sciences and Geology, Queensborough Community College, 222-05 56th Avenue, Bayside, NY, 11364-1497
Long Island Natural History Museum, P.O. Box 262, Levittown, NY, 11756. E-mail: bmader@qcc.cuny.edu

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Abstract

A systematic revision based on a morphological and statistical analysis recognizes the following Bridgerian and Uintan brontothere species as valid: *Mesatirhinus megarhinus*, *Metarhinus fluviatilis*, *Metarhinus diploconus*, *Sphenocoelus uintensis*, *Sphenocoelus intermedius*, *Sphenocoelus hyognathus*, *Telmatherium validus*, *Protitanotherium emarginatum*, *Pseudodiplacodon progressum*, *Eotitanotherium osborni*, *Sthenodectes incisivum*, and *Metatelmatherium ultimum*. The valid Bridgerian genus *Palaeosyops* is not discussed in the present paper. *Mesatirhinus*, *Metarhinus*, and *Sphenocoelus* are grouped within the subfamily Dolichorhininae; *Telmatherium*, *Protitanotherium*, *Pseudodiplacodon*, and *Eotitanotherium* are grouped within the subfamily Brontotheriinae; and *Sthenodectes* and *Metatelmatherium* are listed as Brontotheriidae incertae sedis. It is possible that *Metatelmatherium* may be a member of the subfamily Brontotheriinae or that it may be closely related to *Sthenodectes*, justifying the recognition of another North American brontothere subfamily, the Metatelmatheriinae.

Key words: titanothere, Brontotheriidae, Eocene, *Mesatirhinus*, *Metarhinus*, *Sphenocoelus*, *Dolichorhinus*, *Telmatherium*, *Protitanotherium*, *Pseudodiplacodon*, *Diplacodon*, *Eotitanotherium*, *Metatelmatherium*, *Sthenodectes*

Introduction

Mader (1989; 1998) published two major revisions of North American brontothere genera, the first significant revisions since Osborn's monographic treatment in 1929, which had greatly oversplit the taxa (Prothero & Schoch 1989). The 1998 paper included lists of valid species among the genera recognized, but did not specify the reasons for their acceptance or for the rejection of others. The present paper provides the formal justification for most of those systematic conclusions. Specifically, it will address the Bridgerian and Uintan genera *Telmatherium*, *Mesatirhinus*, *Metarhinus*, *Sphenocoelus* (= *Dolichorhinus*), *Protitanotherium*, *Pseudodiplacodon*, *Eotitanotherium*, *Metatelmatherium*, and *Sthenodectes*. This paper will not address the plesiomorphic brontotheres *Eotitanops* or *Palaeosyops*, or the highly derived eubrontotheres (see Mader 1989 and 1998 for definition) of the Duchesnean and Chadronian. *Eotitanops* and *Palaeosyops* were recently revised by Gunnell and Yarborough (2000), whose conclusions are very similar to my own (Mader 1998).

Abbreviations

Institutional. AMNH, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia; **CM**, Carnegie Museum of Natural History, Pittsburgh; **DMNH**, Denver Museum of Natural History, Denver; **FMNH**, **FMNH P**, and **FMNH PM**, Field Museum of Natural History, Chicago; **GSI**, Geological Survey of India collection, Geological Museum, Calcutta; **LACM** Natural History Museum of Los Angeles County, Los Angeles; **LACM (CIT)**, California Institute of Technology collection, Natural History Museum of Los Angeles County, Los Angeles; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **TMM,** Texas Memorial Museum, University of Texas, Austin; **UCM**, University of Colorado Museum, Boulder; **UCMP**, Museum of Paleontology, University of California, Berkeley; **UFH**, Utah Field House of Natural History, Vernal; **USNM,** United States National Museum, Smithsonian Institution, Washington, D. C.; **UW,** Geological Museum, University of Wyoming, Laramie; **YPM,** Peabody Museum of Natural History, Yale University, New Haven; **YPM-PU**, Princeton University Collection, Peabody Museum of Natural History, Yale University, New Haven.

Statistical. DF, degrees of freedom; **n**, number of cases in sample; **s**, standard deviation of sample; **V**, coefficient of variation.

Methods

Brontothere skulls, lower jaws, and postcranial elements are rarely found in association. Accordingly, the generic and species-level identifications assigned to lower jaws and postcranials in many museum collections and in the work of some notable authors (Earle 1892; Osborn 1929) are often conjectural. For this reason, and because most of the type materials consist of cranial and upper dental remains, the present study focuses almost exclusively on cranial and upper dental morphology and measurements.

The systematic conclusions presented in this paper are primarily the result of morphologic analysis in which the presence of shared derived characters is the major criterion for the recognition of taxa (for information regarding character polarities see Mader 1989; 1991; 1998). In general, characters were identified as plesiomorphic if found in *Eotitanops*, the earliest known brontothere, or in primitive outgroup perissodactyls such as *Hyracotherium*, *Hyrachyus*, or *Homogalax*.

Specimens were sorted into several morphologically homogeneous groups that could not be subdivided further on the basis of their anatomy. Most of these groups were recognized as genera by Mader (1989) and most were suspected of being monospecific. Acknowledging, however, that some taxa are very similar morphologically and are more easily separated by size, several quantitative methods were employed in the making of the final systematic decisions. If numeric analysis suggested that more than one group was present in what was originally taken to be a homogeneous assemblage, the specimens involved were re-examined to determine whether important morphological differences had been overlooked. A final decision was then made taking all factors into consideration. Taxa distinguished by these means were recognized as species within the genera already identified. In general, a conservative approach was taken, and taxa were not recognized unless there was compelling evidence to support their validity.

Measurements were taken in millimeters following the method of Osborn (1929, Fig. 255). In collecting the metric data it was necessary to take into account the effects of ontogenetic growth, dental wear, and taphonomic deformation, all of which could confuse the systematic interpretation. To prevent the maturity of the specimens from having an influence on the results, only specimens with adult dentitions (M3 fully erupted) were used. Tooth wear was not an important factor because tooth measurements were taken very low on the tooth crown; below the area normally affected by even extensive wear. Only on severely worn upper first molars was the wear so great as to affect the size of the tooth. In those cases in which wear was a factor affecting tooth size, the measurement was usually not taken unless it was deemed that the effect of wear on tooth size was extremely minor (see below).

Taphonomic deformation, however, often distorted the skeletal dimensions and also affected the length of various parts of the cheek tooth series by spreading or compacting the teeth. To minimize the effects of deformation on skull size and the size of the cheek tooth series, an average value for both the left and right sides of the same specimen was calculated whenever possible. Often, however, only the left side or right side of a specimen was preserved and in such cases the measurement that was available was used unless deformation was deemed to be so extreme as to make measurement impractical.

In general, estimated values were scrupulously avoided to prevent their exerting an undue influence on the precision of the calculated results. In some cases, however, where the defect in a structure to be measured was minor (such as a small chip of enamel missing from the surface of a tooth) an estimated measurement was taken, but only if the uncertainty involved in making the estimate was exceedingly small. Tooth measurements were not taken if the defect was larger than 1mm, and tooth row or skull length measurements were rejected if the defect was more than a few millimeters. The size of the defect was itself evaluated by comparison to surrounding intact structures.

Three statistical procedures were routinely employed in the making of systematic decisions: analysis of the coefficient of variation, cluster analysis, and *t*-tests. According to Simpson *et al.* (1960) the coefficient of variation for a set of identical linear measurements in most extant mammalian species ranges from 4 to 10 and has an average value of about 5 or 6. If the coefficient of variation is much less than 4, then the sample size is probably too small to show the variability actually present. If the coefficient is much greater than 10, then the sample is probably not homogeneous and may consist of more than one taxon. My own statistical survey of several extant eutherian mammal species confirms that the range of V in a single species is typically 4 to 10, as reported by Simpson *et al*. The average value for the coefficient, however, may be as high as 7.

For the systematic conclusions in the present paper, the coefficient of variation was typically analyzed for thirty four linear measurements and evaluated according to Simpson *et al*.'s (1960) criteria. An average value of V was also calculated and compared to the ideal range of 5 to 7. It is important to stress that although analysis of the coefficient of variation can provide a useful index for evaluating the homogeneity of a sample, no single value of V should be accorded great significance. The evaluation of several values of V can provide a clearer profile of the sample homogeneity, as can the average value of V for several variables, but here again it must be remembered that the results only provide a qualitative indication of the sample characteristics.

Cluster analysis is a multivariate nonparametric exploratory technique that compares any number of variables simultaneously and determines whether the data are essentially homogeneous or tend to "cluster" into distinct categories. The results are plotted on a dendrogram, which gives a visual representation of the group characteristics. In the cluster analyses performed for the present study the distance metric employed was Euclidean distance and the method of linkage was nearest neighbor (single linkage). Euclidean distance and single linkage were preferred over other analytical options because they make direct comparisons between specimens and do not resort to standardizing the data or to comparing the data against some measure of central tendency (such as the mean). While cluster analysis may suggest relationships that exist between groups of specimens, it is not possible to determine with this technique whether the groups generated by the analysis represent different taxa, different size groups within a single species (such as males and females or juveniles and adults), or coincidental groupings. It is necessary, therefore, that this technique be used in conjunction with other methods (both statistical and morphological) of evaluating the sample.

If cluster analysis suggested that more than one group was present, *t*-tests were performed to determine whether the group means were significantly different or whether the samples could have been drawn at random from a single large population. Because a standard *t*-test with pooled variances is only appropriate when the variances of both groups are equal, an F-test was performed first to confirm that the group variances were homogeneous. If the size of one of the groups consisted of fewer than ten cases (the usual situation in the brontothere samples) then Box's approximation of F for small samples was employed. If an F-test indicated that the group variances were not homogeneous, Welch's *t*' (*t*-test with separate variances) was used instead of a standard *t*-test. A nonparametric test would have been advantageous if the groups had been very large and of about equal size, but under the present circumstances, with small groups of often unequal size, the separate *t*-test has greater statistical power.

It must be assumed that at least some *t*-test results will falsely reject the null hypothesis and will, instead, suggest that a significant difference exists where there is none (Type I error, see Abdi 2007). The formula $1-(1-\alpha)^k$ can be used to calculate the likelihood of such an event occurring at least once in a group of tests, where α is the probability used per individual test (.05 for these analyses) and k is the number of *t*-tests performed (usually 34 in this study). Thus, in each *t*-test analysis reported in the present paper, there is usually an 83% chance that at least one significant result will be invalid (i.e., a false rejection of the null hypothesis), a fact that should be taken into account when interpreting the results.

A Bonferroni Correction is not appropriate for the *t*-tests appearing in this study since it is not required that each individual *t*-test prove a significant difference between the groups. Bonferroni adjustments concern the Universal Null Hypothesis, namely that two groups are identical, rather than different, for each variable that is being considered (see Perneger 1998). If we allow for the possibility that males and females of a single species, or that two closely related species, might have some measurable attributes that are essentially the same, then the correction does not apply and will result in an over-abundance of Type II errors.

Revision of Bridgerian and Uintan Brontotheres

Order PERISSODACTYLA Owen 1848

Family BRONTOTHERIIDAE Marsh 1873

Subfamily DOLICHORHININAE Riggs 1912

(Includes Rhadinorhininae Osborn 1929)

Diagnosis. Brontotheres distinguished from all others by the presence of a suborbital protuberance (= infraorbital process). There is a tendency among all members of the subfamily to have relatively elongated molars.

Discussion. The subfamily name Dolichorhinae (emended to Dolichorhininae by Osborn 1929) was proposed by Riggs in 1912. Although *Dolichorhinus*, the type genus of this family-group name, is recognized as a junior synonym of *Sphenocoelus* in the present paper, the name Dolichorhininae remains a valid taxonomic term (Article 40, International Code of Zoological Nomenclature, Ride *et al.* 1999).

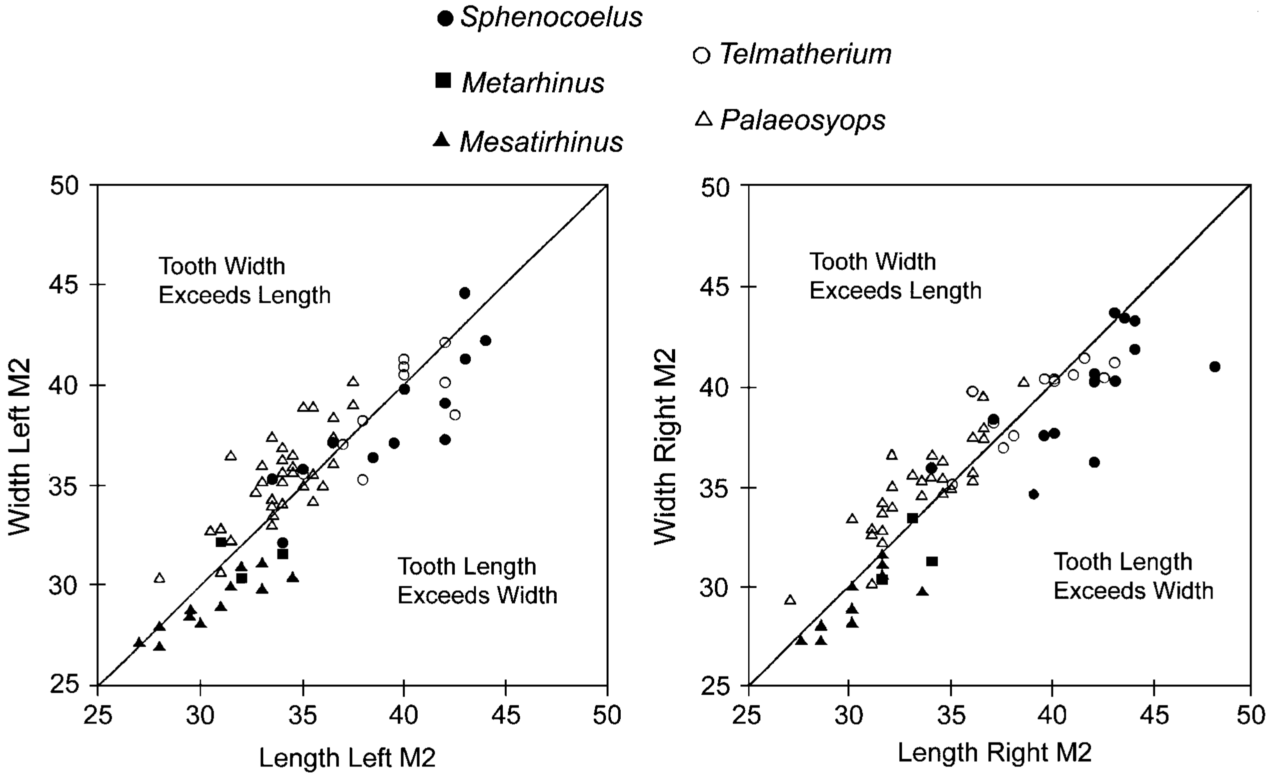

FIGURE 1. Scatter plots showing length of M2 plotted against width of M2 for five brontothere genera. The solid diagonal line that crosses both graphs represents the points at which the length and width of the tooth are equal. Specimens that plot out above the line have teeth that are wider than long, while specimens that plot out below the line have teeth that are longer than wide. Specimens that plot out directly on the line have teeth in which the length is equal to the width and are thus square in shape. Black symbols, subfamily Dolichorhininae; white symbols, other brontothere genera (*Palaeosyops* and *Telmatherium*).

Mader (1989) diagnosed the subfamily Dolichorhininae by the presence of a suborbital protuberance and a reduced canine. I am now (Mader 1998; present paper) less certain of the validity of this last character, however, because skulls of *Sphenocoelus* (= *Dolichorhinus*) that I identify as males have relatively large canines. On skulls of *Sphenocoelus* that I identify as females, however, the canines are quite small and delicate.

Another character that distinguishes the dolichorhinine brontotheres from others is the tendency to have relatively elongated molars. This characteristic is found in all genera here assigned to the subfamily, but is not exhibited by all individuals. Thus, these dental proportions are not uniformly diagnostic of the subfamily, since some individual dolichorhinine brontotheres have relatively square teeth.

It will be noted from Figure 1 that, as a rule, members of the subfamily Dolichorhininae (black symbols) have teeth that are relatively elongated (plot below the line) while other brontotheres (white symbols) tend to have wider teeth (plot on or above the line). Some individual dolichorhinines, however, have teeth that are either square or are wider than they are long, while some non-dolichorhinine brontotheres have relatively elongated teeth.

Mihlbachler (2005) performed a phylogenetic analysis of brontotheres in which the Dolichorhininae as recognized by Mader (1989; 1998; present paper) was determined to be paraphyletic. Although there was much merit to this detailed analysis, I believe that there are several important problems with the characters that must be addressed. This is beyond the scope of the present paper, however. The validity of the Dolichorhininae was strongly supported in a phylogenetic analysis done by Mader (1991), in which twenty-one evolutionary steps were required to account for twenty-one character states (Consistency Index of 100%).

Genus *MESATIRHINUS* Osborn 1908

Age. Bridgerian.

Subage. Twinbuttean.

Type species. *M. megarhinus* (Earle 1891).

Included species. Genus is monospecific.

Diagnosis. Medium-sized (length P2 to M3 approximately 128–145 mm) dolichorhinine brontothere with no hypocone on M3, well developed suborbital protuberance, and nasals that are moderately flared distally (see Fig. 2). Within the Dolichorhininae, *Mesatirhinus* lacks distinctive generic autapomorphies and is distinguished from other dolichorhinine brontotheres by its plesiomorphic morphology.

Discussion. In 1891, Charles Earle described the skull of a small brontothere from the Washakie Basin, which he named *Palaeosyops megarhinus*. In 1908, Osborn recognized that this skull was generically distinct from *Palaeosyops* and gave it the new generic name *Mesatirhinus*. In the same paper, Osborn also named a second species of *Mesatirhinus*, *M. petersoni*, which he distinguished from the type species by its longer skull (especially in the preorbital region) and its longer cheek tooth series. Somewhat cryptically, Osborn added that *Mesatirhinus petersoni* was further distinguished from *M. megarhinus* by "an average advance in all the rectigradations (i.e., new morphologic characters)". According to Osborn these evolutionary advances proved that the differences in size and form that he cited between the species were "not merely due to fluctuations of size or differences of sex". In 1929, Osborn (p. 389) restated this observation almost verbatim, but changed it to read "an average advance in the premolar rectigradations" rather than "in all the rectigradations". In this section of the paper Osborn did not elaborate on what these evolutionary advances in premolar morphology were, but elsewhere (p. 393) he stated that *M. petersoni* was distinguished from *M. megarhinus* by the former's longer diastema, more pronounced posterior cusp or tritocone (= metacone) on P1, more cingulate P2, and by having a slight rudiment of a protoconule on P2 and P3. According to Osborn, one specimen of *M. petersoni* (formerly AMNH 1556, specimen now in the British Museum) had a slight elevation of the tetartocone (= hypocone) on P4, a supposed evolutionary advance.

In 1929, Osborn referred the fragmentary holotype of *Palaeosyops junius* Leidy, 1872 (ANSP 10349), to the genus *Mesatirhinus*. Leidy had based the species on several small fragments from the right side of the jaw and a sketch of a larger fragment from the left side containing the last premolar and all of the molars. Of this type material, Osborn was only able to locate the right P4 and posterior half of right M3 in 1906 (Osborn 1929). The type was reportedly collected near Fort Bridger and Osborn speculated that it had been collected from level B (now part of the Blacks Fork Member) of the Bridger Formation. Because of its small size and presumed early geologic occurrence, Osborn regarded the material as representing a distinct species of *Mesatirhinus*, *M. junius*.

Mesatirhinus (Fig. 2) is known from essentially contemporaneous deposits in both the Washakie and Green River Basins. Most specimens used in this study were from the Green River Basin, but because the sample size was relatively small (no more than ten individuals for any given variable) the sample was supplemented by specimens from the Washakie Basin.

The coefficient of variation (Table 1) for most variables in the combined *Mesatirhinus* sample falls within the range of 4 to 10 and the average value for all variables (excluding diastema length) is 5.7. Thus, the variation observed in the sample is consistent with the possibility that only a single species is represented. There is nothing about the range or average value of V to suggest that there is any heterogeneity in the sample.

Similarly, cluster analysis of all variables (Fig. 3) shows that all the specimens are closely grouped together and there is no indication that more than a single group is present. If, however, a cluster analysis is run using only the length of the skull, length of the cheek tooth series, and length of the molar series, then two distinct size groups emerge (Fig. 4). Significantly, it was these same variables that Osborn (1908; 1929) used to distinguish *Mesatirhinus megarhinus* from *M. petersoni*, and specimens assigned by Osborn to *M. megarhinus* consistently fall into one size group (the smaller) while specimens that Osborn assigned to *M. petersoni* tend to fall into the other. A single specimen (AMNH 1651a) that Osborn provisionally referred to *M. petersoni*, however, groups out separately. This specimen is a large individual and can probably be included in the large-size group but, because of its uncertain association in the cluster dendrogram, it has been excluded from further analysis. *T*-tests (Tables 2 and 3) confirm that for many variables the means of both size groups (excluding AMNH 1651a) are significantly different (18 out of 30 variables have probabilities less than .05). Based on the formula given in the Methods section of this paper, there is a 78% chance that at least one of these significant results is in error, but it seems highly unlikely that more than half the results could be attributed to error.

Thus the two size groups recognized by Osborn do exist although they are only evident when certain linear measurements are considered. It must be determined, therefore, whether these size groups represent two species (as Osborn thought) or are members of a single dimorphic species.

Tables 4 and 5 present the summary statistics for each of the two size groups of *Mesatirhinus* suggested by the cluster analysis in Figure 3 (AMNH 1651a not included). It will be noted from Table 4 that, although the average value of V for the smaller-size group is typical of extant species (= 4.5), the individual values of V are generally rather low (half are less than 4). The sample size for most variables, however, is probably sufficiently large to show most of the variation that is present. It should be noted that the average value of V is raised somewhat by the high variability of the length of the second upper premolars (values of V over 10), but even if the length of P2 is excluded from the calculation, the average value of V remains more-or-less typical of extant mammalian species (average V = 3.9)

In the larger-size group (Table 5) the average value of V is rather low (= 3.4) as are the individual values of V (two thirds are less than 4). Some of this low variability, however, may be due to the small sample sizes in the larger-size group. Once again the length of P2 is found to be highly variable with values of V in excess of 10 and, if the length of P2 is excluded from the calculation of the average (as well as diastema length), then the average value drops to 2.8.

Most of the characters used by Osborn (1908; 1929) to separate *Mesatirhinus megarhinus* from *M. petersoni* can be attributed to intraspecific variation. This is especially true of skull length and length of the molars. Although differences in molar dimension could indicate a difference in function (and thus a potential taxonomic difference), the overall dimensions of the molars in both groups are actually closely similar. A comparison of Tables 4 and 5 shows that individual molar dimensions in both groups often overlap and, in those cases where there is a size interval between the groups, the difference is no more than 1.5 mm. Similarly, there is a size interval between the length of the molar series in both groups, but the difference is only 3.3 mm.

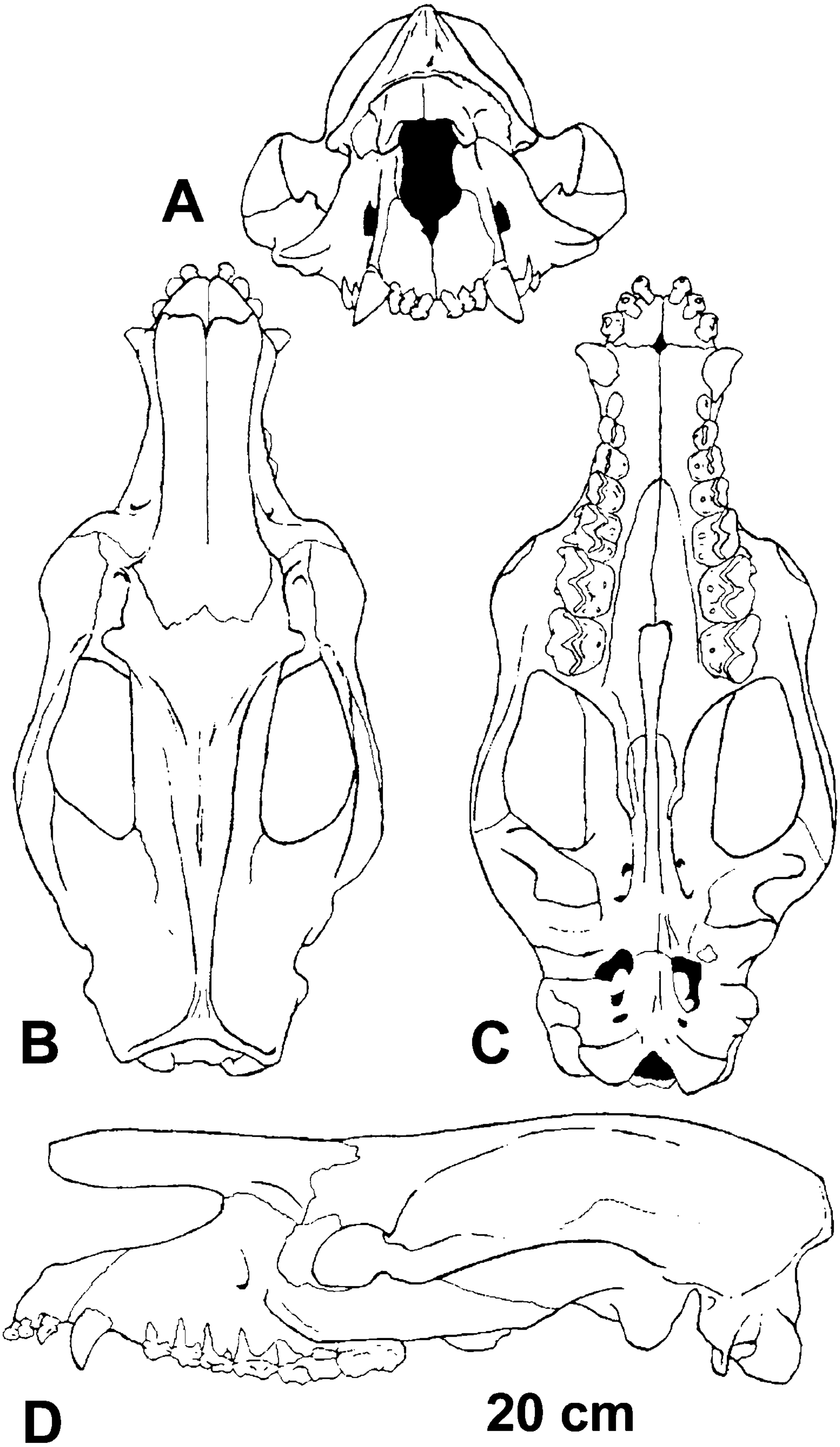

FIGURE 2. Skull of *Mesatirhinus megarhinus* in **A**, anterior; **B**, dorsal; **C**, ventral; and **D**, lateral view. After Osborn. 1929.

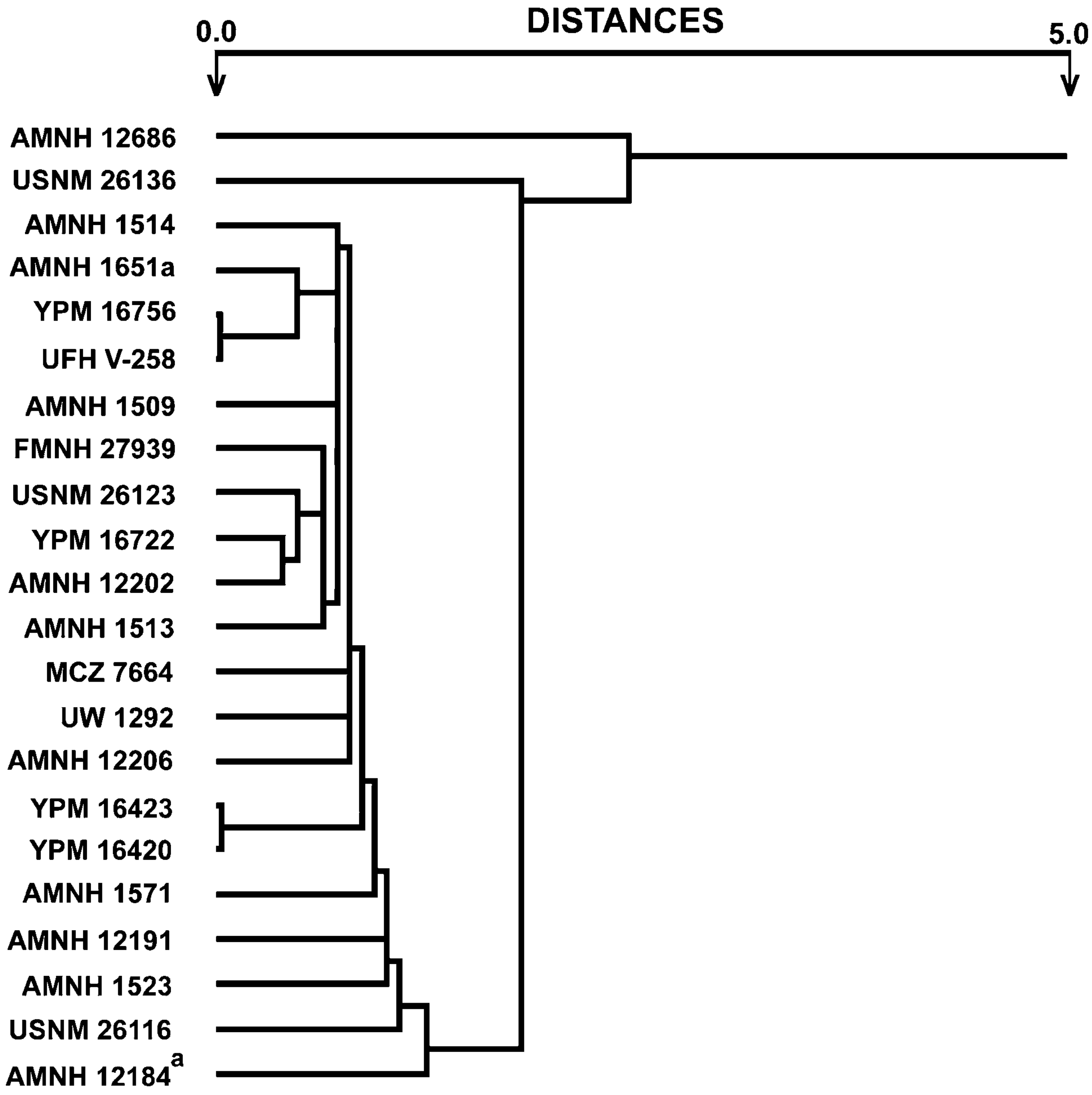

FIGURE 3. Cluster dendrogram for specimens of *Mesatirhinus* from the Green River and Washakie Basins resulting from a cluster analysis of all variables listed in Table 1. **a**, holotype of *Mesatirhinus petersoni*.

Osborn's suggestion that skulls of *Mesatirhinus petersoni* have a longer face than specimens of *M. megarhinus* is a more convincing argument that the two are separate species, but I have not been able to confirm this observation. Most skulls of *Mesatirhinus* are very imperfectly preserved, making it impossible to compare facial length to overall skull length. My own impression has been that the preorbital region in both groups is of the same proportional size although, in absolute terms, the face in the larger-size group is naturally longer. It is of interest to note that despite Osborn's claims, the faciocephalic index (see Osborn 1929, p. 255 for definition) that he reported (1929) for the two species was identical (= 48). Thus, by Osborn's own figures, there is no proportional difference in the length of the preorbital region in either group. Even if the differences in facial length suggested by Osborn had been correct, however, the proportional difference could be attributed to allometric changes in a single species rather than to phylogenetic differences.

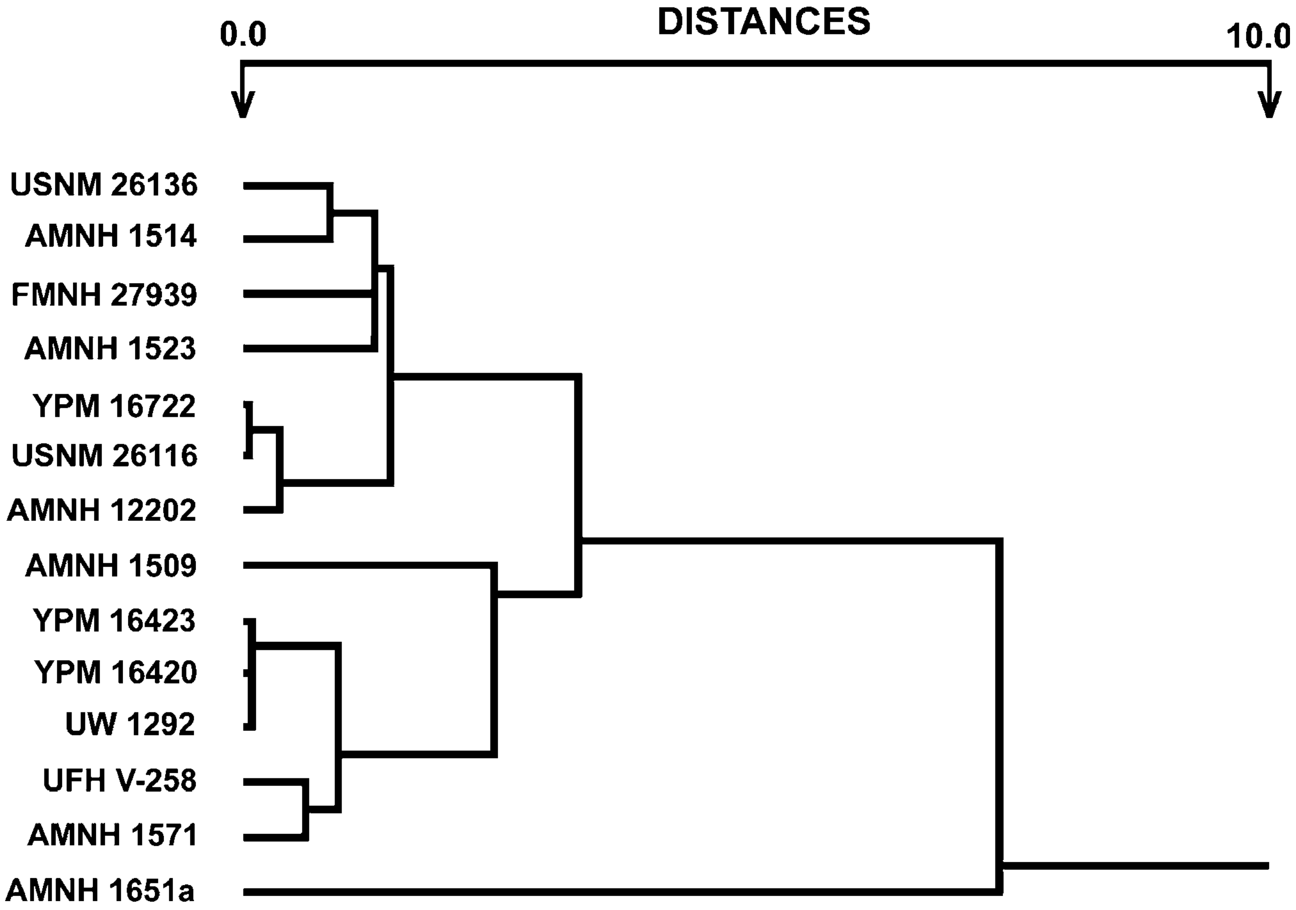

FIGURE 4. Cluster dendrogram for specimens of *Mesatirhinus* from the Green River and Washakie Basins resulting from a cluster analysis of basilar skull length, length of cheek tooth series, and length of molar series.

Contrary to Osborn's statement, specimens that are included in the larger-size group (his *Mesatirhinus petersoni*) do not have a longer diastema than specimens belonging to the smaller-size group (*M. megarhinus*). The actual range of diastema lengths recorded for the larger size group is 3.9–6.0 mm (based on three individuals), while in the smaller size group the range is 5.8–8.8 mm (also based on three individuals). A specimen (AMNH 12206) referred to *M. megarhinus* by Osborn (1929), but not included in the cluster analysis that produced the two size groups (Fig. 3) because of insufficient data, has a diastema length of 12.0 mm. Thus, specimens that Osborn referred to *M. megarhinus* actually have a diastema that is longer than in any specimen that he referred to *M. petersoni*.

This observation should not be interpreted to mean, however, that the smaller-size group can be defined as having a longer diastema than in the larger-size group. In all brontotheres the length of the diastema is highly variable (note the values for V in various genera reported in this paper) making it a poor character to use in a systematic assessment. In actuality there is a considerable overlap of diastema length in both size groups, and a cluster analysis (Fig. 5) of diastema length alone shows that specimens belonging to both groups do not cluster separately. A *t*-test comparison (Table 3) verifies that the difference between the means of diastema length in both size groups is not statistically significant.

TABLE 1. Summary statistics for the genus *Mesatirhinus*. (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	5	377.0–408.0	391.2	±15.3	3.9
Length Cheek Tooth Series[a]	9	140.0–158.5	150.0	±6.9	4.6
Length P2 to M3[a]	12	128.0–145.0	137.6	±4.9	3.6
Length Premolar Series[a]	11	60.5–69.5	65.0	±3.2	4.9
Length Molar Series[a]	14	80.5–99.5	87.1	±5.0	5.7
Length Diastema[a]	8	4.2–11.2	6.9	±2.2	31.9
Length Left M3	13	29.0–40.0	31.6	±2.9	9.2
Length Right M3	13	26.5–33.5	30.2	±1.6	5.3
Width Left M3	12	28.7–32.7	30.0	±1.2	4.0
Width Right M3	13	27.2–32.2	30.0	±1.4	4.7
Length Left M2	14	27.0–34.5	30.5	±2.1	6.9
Length Right M2	12	27.5–33.5	30.3	±1.6	5.3
Width Left M2	13	27.0–31.2	29.1	±1.3	4.5
Width Right M2	10	27.2–31.5	29.2	±1.6	5.5
Length Left M1	14	21.0–27.0	24.6	±1.5	6.1
Length Right M1	11	21.0–27.0	24.5	±1.9	7.8
Width Left M1	11	23.1–24.5	24.2	±0.9	3.7
Width Right M1	7	21.2–25.7	24.4	±1.5	6.2
Length Left P4	12	15.0–19.0	17.4	±1.2	6.9
Length Right P4	14	14.5–19.5	17.5	±1.2	6.9
Width Left P4	12	21.4–24.0	22.6	±0.8	3.5
Width Right P4	13	19.9–23.8	22.2	±1.0	4.5
Length Left P3	13	14.5–18.0	16.8	±0.9	5.4
Length Right P3	13	15.0–18.0	16.7	±1.0	6.0
Width Left P3	12	17.8–20.7	19.1	±0.9	4.7
Width Right P3	12	17.3–20.5	19.1	±0.9	4.7
Length Left P2	12	14.0–18.5	16.1	±1.6	9.9
Length Right P2	11	13.0–18.0	15.8	±1.8	11.4
Width Left P2	13	13.5–15.9	14.9	±0.7	4.7
Width Right P2	10	14.3–15.7	15.0	±0.6	4.0
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	1	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	1	—[b]	—[b]	—[b]	—[b]
AVERAGE V					5.7[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length.

TABLE 2. F-Test comparisons for the small-size group (Group 1) and large-size group (Group 2) of *Mesatirhinus*.

	n Group 1	n Group 2	F	Probability	*T*-Test
Basilar Length Skull[a]	3	2	0.053	0.820	Pooled
Length Cheek Tooth Series[a]	5	4	2.179	0.142	Pooled
Length P2 to M3[a]	5	5	0.790	0.375	Pooled
Length Premolar Series[a]	5	4	0.354	0.553	Pooled
Length Molar Series[a]	7	6	0.584	0.445	Pooled
Length Diastema[a]	3	3	0.390	0.535	Pooled
Length Left M3	7	4	0.002	0.961	Pooled
Length Right M3	5	5	0.162	0.688	Pooled
Width Left M3	7	4	1.469	0.227	Pooled
Width Right M3	5	5	0.034	0.854	Pooled
Length Left M2	6	4	0.588	0.444	Pooled
Length Right M2	5	5	0.068	0.795	Pooled
Width Left M2	7	4	0.024	0.878	Pooled
Width Right M2	5	5	0.070	0.791	Pooled
Length Left M1	7	4	1.251	0.265	Pooled
Length Right M1	6	3	0.381	0.574	Pooled
Width Left M1	5	3	2.646	0.108	Pooled
Width Right M1	2	3	0.011	0.918	Pooled
Length Left P4	5	3	0.625	0.432	Pooled
Length Right P4	6	4	0.202	0.654	Pooled
Width Left P4	5	3	0.007	0.934	Pooled
Width Right P4	6	5	0.775	0.379	Pooled
Length Left P3	4	5	1.602	0.208	Pooled
Length Right P3	5	4	0.335	0.564	Pooled
Width Left P3	5	3	1.331	0.252	Pooled
Width Right P3	4	4	2.278	0.134	Pooled
Length Left P2	3	5	0.020	0.889	Pooled
Length Right P2	3	4	0.345	0.559	Pooled
Width Left P2	4	5	3.360	0.069	Pooled
Width Right P2	3	3	0.001	0.981	Pooled
Buccal-Lingual Width Left Canine	0	0	—	—	—[b]
Buccal-Lingual Width Right Canine	1	0	—	—	—[b]
Mesial-Distal Width Left Canine	0	0	—	—	—[b]
Mesial-Distal Width Right Canine	1	0	—	—	—[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] There is no variance in either of the two groups being compared.

TABLE 3. *T*-Test comparisons for the two size groups of *Mesatirhinus*.

	T	DF	Probability
Basilar Length Skull[a]	0.623	3.0	0.578
Length Cheek Tooth Series[a]	5.430	7.0	0.001
Length P2 to M3[a]	3.294	8.0	0.011
Length Premolar Series[a]	5.276	7.0	0.001
Length Molar Series[a]	6.999	11.0	0.000
Length Diastema[a]	1.812	4.0	0.144
Length Left M3	1.001	9.0	0.343
Length Right M3	0.168	8.0	0.871
Width Left M3	2.912	9.0	0.017
Width Right M3	3.219	8.0	0.012
Length Left M2	5.567	8.0	0.001
Length Right M2	3.657	8.0	0.006
Width Left M2	5.269	9.0	0.001
Width Right M2	5.723	8.0	0.000
Length Left M1	3.963	9.0	0.003
Length Right M1	3.188	7.0	0.015
Width Left M1	2.191	6.0	0.071
Width Right M1	6.152	3.0	0.009
Length Left P4	2.635	6.0	0.039
Length Right P4	1.632	8.0	0.141
Width Left P4	2.981	6.0	0.025
Width Right P4	3.435	9.0	0.007
Length Left P3	1.758	7.0	0.122
Length Right P3	1.151	7.0	0.287
Width Left P3	3.540	6.0	0.012
Width Right P3	2.691	6.0	0.036
Length Left P2	0.133	6.0	0.899
Length Right P2	0.543	5.0	0.610
Width Left P2	2.110	7.0	0.073
Width Right P2	1.165	4.0	0.309
Buccal-Lingual Width Left Canine	—[b]	—	—
Buccal-Lingual Width Right Canine	—[b]	—	—
Mesial-Distal Width Left Canine	—[b]	—	—
Mesial-Distal Width Right Canine	—[b]	—	—

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data for *t*-test.

TABLE 4. Summary statistics for the genus *Mesatirhinus.* Group 1 (small-size group). (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	3	377.0–408.0	387.4	±17.8	4.6
Length Cheek Tooth Series[a]	5	140.0–149.5	144.8	±4.1	2.8
Length P2 to M3[a]	5	128.0–138.0	133.5	±3.9	2.9
Length Premolar Series[a]	5	60.5–65.3	62.4	±1.9	3.1
Length Molar Series[a]	7	80.5–85.0	83.1	±1.9	2.3
Length Diastema[a]	3	5.8–8.8	7.0	±1.5	21.4
Length Left M3	7	29.0–33.0	30.3	±1.4	4.6
Length Right M3	5	29.0–31.0	30.3	±0.8	2.6
Width Left M3	7	28.7–30.0	29.3	±0.5	1.7
Width Right M3	5	28.0–30.0	29.2	±0.8	2.7
Length Left M2	6	27.0–30.0	28.7	±1.2	4.2
Length Right M2	5	27.5–30.0	28.9	±1.1	3.8
Width Left M2	7	27.0–29.0	28.1	±0.8	2.9
Width Right M2	5	27.2–28.8	27.8	±0.7	2.5
Length Left M1	7	21.0–24.5	23.6	±1.2	5.1
Length Right M1	6	22.0–25.0	23.8	±1.1	4.6
Width Left M1	5	23.1–24.0	23.6	±0.4	1.7
Width Right M1	2	24.0–24.3	24.2	±0.2	0.8
Length Left P4	5	15.0–17.5	16.6	±1.0	6.0
Length Right P4	6	14.5–18.0	16.8	±1.3	7.7
Width Left P4	5	21.4–22.4	22.0	±0.4	1.8
Width Right P4	6	19.9–22.4	21.5	±0.9	4.2
Length Left P3	4	14.5–17.0	16.3	±1.2	7.4
Length Right P3	5	15.0–18.0	16.3	±1.2	7.4
Width Left P3	5	17.8–19.4	18.4	±0.6	3.3
Width Right P3	4	17.3–19.1	18.5	±0.8	4.3
Length Left P2	3	14.0–17.0	15.8	±1.6	10.1
Length Right P2	3	13.0–17.5	15.8	±2.5	15.8
Width Left P2	4	13.5–15.5	14.4	±1.0	6.9
Width Right P2	3	14.3–15.3	14.8	±0.5	3.4
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	1	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	1	—[b]	—[b]	—[b]	—[b]
AVERAGE V					4.5[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length.

TABLE 5. Summary statistics for the genus *Mesatirhinus*. Group 2 (large-size group). (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	2	387.0–406.8	396.9	±14.0	3.5
Length Cheek Tooth Series[a]	4	154.8–158.5	156.6	±1.6	1.0
Length P2 to M3[a]	5	138.0–143.5	140.3	±2.4	1.7
Length Premolar Series[a]	4	66.5–69.5	68.3	±1.3	1.9
Length Molar Series[a]	6	88.3–92.0	89.5	±1.3	1.5
Length Diastema[a]	3	4.2–6.0	5.1	±0.9	17.7
Length Left M3	4	30.0–33.0	31.1	±1.3	4.2
Length Right M3	5	29.0–31.5	30.2	±1.0	3.3
Width Left M3	4	29.8–31.7	30.5	±0.9	3.0
Width Right M3	5	29.8–32.2	30.9	±0.9	2.9
Length Left M2	4	31.5–33.0	32.4	±0.8	2.5
Length Right M2	5	30.0–33.5	31.6	±1.3	4.1
Width Left M2	4	29.9–31.2	30.5	±0.7	2.3
Width Right M2	5	29.6–31.5	30.5	±0.8	2.6
Length Left M1	4	25.5–27.0	26.3	±0.7	2.7
Length Right M1	3	25.5–27.0	26.2	±0.8	3.1
Width Left M1	3	23.5–25.5	24.7	±1.0	4.1
Width Right M1	3	25.3–25.7	25.4	±0.2	0.8
Length Left P4	3	18.0–19.0	18.3	±0.6	3.3
Length Right P4	4	17.0–19.5	18.1	±1.0	5.5
Width Left P4	3	22.5–23.4	23.0	±0.5	2.2
Width Right P4	5	22.3–23.8	23.2	±0.6	2.6
Length Left P3	5	16.5–18.0	17.3	±0.6	3.5
Length Right P3	4	16.0–18.0	17.1	±0.9	5.3
Width Left P3	3	19.5–20.0	19.8	±0.3	1.5
Width Right P3	4	19.2–19.9	19.6	±0.3	1.5
Length Left P2	5	14.0–18.5	16.0	±1.8	11.3
Length Right P2	4	13.0–17.0	15.0	±1.6	10.7
Width Left P2	5	15.1–15.9	15.4	±0.3	2.0
Width Right P2	3	14.7–15.7	15.3	±0.5	3.3
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
AVERAGE V					3.4[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length.

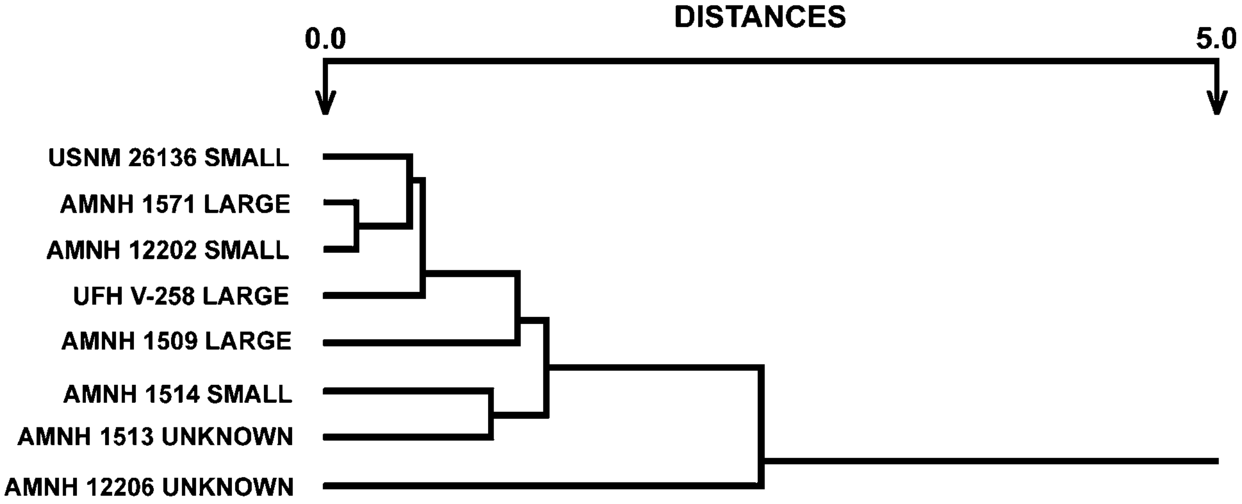

FIGURE 5. Cluster dendrogram for specimens of *Mesatirhinus* from the Green River and Washakie Basins resulting from a cluster analysis of diastema length. **SMALL**, individual belonging to small-size group; **LARGE**, individual belonging to large-size group; **UNKNOWN**, size-group to which individual belongs was not determined.

Perhaps Osborn's most convincing argument that the two groups represent two different species, are the supposed differences in premolar morphology. I have concluded from my own study, however, that there is no consistent morphological difference between the size groups. Differences in premolar morphology can be attributed to intraspecific variation and to differences in wear and preservation.

The weight of the evidence suggests that there is only a single species of *Mesatirhinus* present in the sample and that the two size groups probably represent males and females. That a single species is represented is indicated by the fact that: 1, members of both groups appear to be morphologically identical; 2, the values of V for each of the size groups tend to be rather low while the values of V for all specimens of *Mesatirhinus* taken together are more typical of extant mammalian species; and 3, although there is a size difference between both groups, in most cases this difference is not appreciable. It would have been desirable to compare canine widths within the two size groups to establish whether there was bimodality (as might be expected if the groups were two distinct species) but, unfortunately, the canines in most of the specimens of *Mesatirhinus* examined were very poorly preserved. If bimodality of canine size within the groups could be established, I would be willing to regard them as separate species but, without this information, I do not believe that there is enough evidence to justify the recognition of more than a single taxon.

If the alternate approach were to be taken and the two size groups interpreted as representing different species, then there would be a problem in determining which trivial name should be applied to each. Although the type of *Mesatirhinus petersoni* clearly belongs to the larger-size group, the holotype of the type species of *Mesatirhinus, M. megarhinus,* is almost too fragmentary to measure. I was only able to obtain estimated measurements for the length of the left M3 (30 mm) and the length of the right M2 (also 30 mm). It will be noted from Tables 4 and 5 that these measurements could apply to either size group. Therefore, contrary to Osborn's conclusion, it is not certain that the type of *M. megarhinus* belongs to the smaller-size group.

A further potential complication is presented by the holotype of *Palaeosyops junius* Leidy, which Osborn (1929) referred to the genus *Mesatirhinus*. Because the holotype consists of only two isolated lower cheek teeth, it is difficult to be certain which genus it actually represents. Of the three recognized genera of Bridgerian aged brontotheres (*Palaeosyops*, *Mesatirhinus*, and *Telmatherium*), the small size of the type is most consistent with *Mesatirhinus* although the teeth of *Mesatirhinus* are typically a little larger.

Based on the locality information available, Osborn (1929) suggested that the type of *Mesatirhinus junius* was from Bridger B (Blacks Fork Member) but, the only brontothere clearly documented from this level is

Palaeosyops. The type of *M. junius* is much smaller than any specimen of *Palaeosyops*, however, and the occlussal surfaces of the teeth lack the circular wear facets typical of that genus.

The small size of the holotype of *Mesatirhinus junius* is not, by itself, a sufficient argument for accepting *M. junius* as a distinct species. Osborn (1929) provisionally referred one other specimen (AMNH 12686, a right M1 and M3) to the species *M. junius* based on its small size, but I have included this same specimen in the small-size group of *M. megarhinus*. Although AMNH 12686 is a diminutive individual, it will be noted from Table 1 that, for the most part, the values of V for the length and width of right M1 and M3 were not unusually high (although the value of V for length of RM1 is 7.8). Thus, the teeth of AMNH 12686 and those of the other specimens of *Mesatirhinus* analyzed, all generally fall within the range of size variation typically encountered in a single extant mammalian species. In my opinion, AMNH 12686 probably represents a small *Mesatirhinus megarhinus*, not a separate taxon.

If it could be demonstrated that the holotype of *Mesatirhinus junius* is actually from the Blacks Fork Member of the Bridger Formation, then the possibility exists that it might represent a smaller species from that level. Before this conclusion could be reached, however, it would be necessary to obtain a sample of *Mesatirhinus* from the Blacks Fork Member so that it could be statistically compared against the sample already documented from the Twin Buttes Member. In the absence of such a sample it is important to note that no other specimen of *Mesatirhinus* has ever been collected from the Blacks Fork Member and that the stratigraphic placement of the holotype of *Mesatirhinus junius* in the Blacks Fork Member is doubtful at best. The only locality information that is available for the specimen is that it was collected "near Fort Bridger". The expression "near" is obviously a subjective term that could refer to several feet or several miles. Although it is true that only outcrops of the Blacks Fork Member occur in the immediate vicinity of Fort Bridger, outcrops of the Twin Buttes Member begin to occur approximately twelve miles (19 km) to the east. In my opinion the holotype of *Mesatirhinus junius* is probably from the Twin Buttes Member.

If the holotype of *Mesatirhinus junius* is a specimen of *Mesatirhinus*, it almost certainly belongs to the small-size group of *Mesatirhinus* discussed above. If the two size groups of *Mesatirhinus* were to be interpreted as representing two species, then *M. junius* would have nomenclatural priority among members of the small-size group. Thus, if Osborn were correct in referring *M. megarhinus* (the type species) to this size group, then *M. megarhinus* is invalid because it is a junior synonym of *M. junius*. Alternatively, the holotype of *M. megarhinus* could belong to the larger size group, in which case *M. megarhinus* would remain valid and be a senior synonym of *M. petersoni* while *M. junius* would continue to be the valid name for the small size group.

My present conclusion, however, is that there is only a single species of *Mesatirhinus* represented by all of the *Mesatirhinus* specimens collected from the Green River and Washakie Basins, a conclusion supported by the recent work of Mihlbachler (2005). If the generic assignment of Leidy's *Palaeosyops junius* to the genus *Mesatirhinus* is correct, therefore, the type species of *Mesatirhinus* (*M. megarhinus*) is invalid because it is a junior synonym of *M. junius*. Mihlbachler (2005) accepted this synonymy, but, for the present, I prefer to treat *M. junius* as a nomen dubium because of the meagerness of the type material and its questionable generic identity. Gunnell and Yarborough (2000) regarded *Palaeosyops junius* as a junior synonym of *Palaeosyops paludosus*, the type species of *Palaeosyops*, which is a genus that is clearly distinct from *Mesatirhinus*.

Species *MESATIRHINUS megarhinus* (Earle 1891)

= *M. junius*? (Leidy 1872, treated here as a nomen dubium)
= *M. petersoni* Osborn 1908

Holotype of *M. megarhinus*. YPM-PU 10008, a partial skull.

Holotype of *M. junius* (potential senior synonym of *M. megarhinus*). ANSP 10349, right P4 and posterior half of right M3.

Referred specimens. AMNH 1509, AMNH 1513, AMNH 1514, AMNH 1523, AMNH 1571, AMNH 1651a, AMNH 12184 (holotype of *M. petersoni*), AMNH 12191, AMNH 12202, AMNH 12206, AMNH 12686, FMNH 27939, MCZ 7664 (in part), UFH V-258, USNM 26116, USNM 26123, USNM 26136, UW 1292, YPM 16420, YPM 16423, YPM 16722, YPM 16756.

Diagnosis. Same as the generic diagnosis.

Genus *METARHINUS* Osborn 1908

= *Rhadinorhinus* Riggs 1912
= *Heterotitanops* Peterson 1914b

Age. Uintan.

Subage. Early Uintan.

Type species. *M. fluviatilis* Osborn 1908.

Included species. *M. diploconus* (Osborn 1895).

Diagnosis. Medium sized (length P2 to M3 approximately 137–157 mm) dolichorhinine brontothere with prominent orbits and a very deep lateral nasal incision. Often there is no upper diastema and the suborbital protuberance may be small.

Discussion. In 1908 Osborn named a new genus, *Metarhinus*, for which he recognized three species: *M. fluviatilis*, *M. earlei*, and *M. diploconus*. The type species, *M. fluviatilis*, was based on a badly crushed and fragmentary skull (AMNH 1500, see Fig. 6) from the Uinta Basin, *M. earlei* was based on a skull (AMNH 13166) from the Washakie Basin (Washakie B of Granger 1909) lacking the nasals and most of the frontal region, and *M. diploconus* was based on a skull (AMNH 1863) from the Uinta Basin that Osborn had originally described as a new species of "*Telmatotherium*" (=*Telmatherium*) and had named (Osborn 1895) *T. diploconum* (note the emendation of the trivial name). It should be noted, however, that although Osborn referred to a taxon "*M. diploconus*" in the 1908 paper, it is not perfectly clear from the context whether the genus is meant to be *Metarhinus* or *Mesatirhinus*. In his monograph of 1929, however, Osborn stated that it was his intention to refer *T. diploconum* to *Metarhinus*.

In 1912 Riggs described a large collection of Uintan brontotheres collected two years earlier from the Uinta Basin of Utah by an expedition from the Field Museum. Among these specimens were skulls with deep lateral nasal incisions and prominent orbits, most of which Riggs referred to *Metarhinus*. Many of the skulls that Riggs referred to this genus were characterized by peculiar, broad, spoon-shaped nasals (see Fig. 7), although some of the skulls were incomplete and lacked the nasals entirely. One skull, however, while sharing with the other specimens a deep nasal incision and prominent orbits, had short, distally tapered nasals (Fig. 8A) and Riggs assigned this skull to a new genus *Rhadinorhinus* (type species *R. abbotti*). Riggs also assigned Osborn's taxon, *Metarhinus diploconus* to this new genus and this new generic assignment was accepted by Osborn in 1929.

Mader (1989) provisionally accepted Riggs' (1912) and Osborn's (1929) conclusion that the type species of *Metarhinus*, *M. fluviatilis*, represents the brontothere with spoon-shaped nasals and that this form is generically distinct from the brontothere with distally tapered nasals, *Rhadinorhinus*. Mader questioned whether these two forms should be recognized as distinct genera, however, and suggested that it might be more appropriate to recognize them as separate species of the same genus or even as males and females of a single species. After further consideration I now believe that specimens with both nasal morphologies are similar enough to justify placing them in a single genus, *Metarhinus*, but for reasons that will be discussed below, I do not believe that they are sexual variants of a single species.

In addition to naming the new genus *Rhadinorhinus*, Riggs (1912) also named two new species of *Metarhinus* from supposedly higher levels of the Uinta Formation and representing more "advanced" stages of evolution. The first of these species, *M. riparius*, was based on a laterally crushed skull (FMNH 12186). Riggs listed the following as diagnostic characters of the species: skull long and narrow, anterior cranial region expanded, sagittal crest short, interorbital region relatively narrow and rounded, rudimentary horn cores above orbits, canines large, molar series short, hypocone usually present on M3, mandible straight in the ramus, and lower canine long and recurved. It should be noted that the type specimen of *M. riparius* lacks the lower jaws and that the last two characters were based on referred materials.

The second species, *Metarhinus cristatus*, was based on a skull (FMNH 12194) lacking the nasals and most of the upper jaw (maxilla and premaxilla). Riggs listed the following as diagnostic characters of this species: skull length approximately 380 mm, molar series 94 mm, frontal region broad, sagittal crest long and high, molars short-crowned, no hypocone on M3, arches relatively heavy. Because the type skull lacks most of the upper jaw and Riggs did not refer any other specimens to this taxon, it is difficult to understand why he listed an estimate of skull length in the diagnosis of the species, given the extreme degree of error this estimate must necessarily have.

In addition to the two new species of *Metarhinus* named in the paper, Riggs also referred additional material to *Metarhinus earlei* Osborn and gave the following revised diagnosis of that species based on both the type and the new referred materials: skull short and broad in frontal region; length 388–405 mm; breadth 245–255 mm; molar series broad and low-crowned; no hypocone on M3; linea aspera uniting by regular curves above posterior margins of zygomata to form a short, thickened sagittal crest; canines slender; diastema short; P2 oblique; P3 and P4 subrectangular in outline; molars broad and low-crowned; mandible with ramus slightly curved.

Osborn (1929) recognized both *Metarhinus riparius* and *M. cristatus* as valid species, although he suggested that *M. cristatus* might be a junior synonym of *M. fluviatilis*. The diagnoses of these taxa given by Osborn are taken directly from Riggs (1912). Osborn provided his own diagnosis, however, for *M. earlei* (1929, p. 426), based in part on his original diagnosis (Osborn 1908) and that of Riggs (1912). According to this diagnosis *M. earlei* is defined by, "Skull (AMNH 13166, type) length 393 millimeters, breadth 240, or 388:245, or 405:255; cephalic index 60–63. Occipital condyles narrow (78 mm), premaxillary symphysis elongate, nasals elongate, spreading distally, prominent infraorbital shelf. Type p1–m3, 167 millimeters. Molar series broad and low crowned, no hypocone on m3; canines slender, diastema short."

Although Riggs (1912) and Osborn (1929) cited numerous differences between the cranial morphologies of the various taxa that they recognized, all of the morphological differences that are of any consequence are directly attributable to taphonomic deformation and, to a lesser degree, sexual dimorphism. For example, Osborn (1929) cited a high and prominent sagittal crest as a diagnostic character of *Metarhinus fluviatilis*, but this character is due entirely to the effects of crushing on the type skull. The same crushing may also account for some of the prominence of the circumorbital ridges also cited by Osborn as a character of the species. Similarly, both Osborn (1929) and Riggs (1912) stated that a long and narrow skull as well as a narrow and rounded interorbital region are diagnostic characters of *M. riparius*. The type skull of *M. riparius*, however, has been crushed laterally, exaggerating the cranial proportions. This crushing accounts for both of the characters cited by Osborn and Riggs. The size of the infraorbital shelf (=suborbital protuberance) and canine are probably sexually dimorphic characters in *Metarhinus* and should not be used in the diagnosis of a species (see Mader 1989 and below).

The dental differences cited by Riggs and Osborn are rather trivial and, in my opinion, do not justify the recognition of distinct taxa. As in other brontothere genera, the presence or absence of a hypocone on M3 and minor differences in the shape of various cheek teeth are poor diagnostic characters, and may generally be attributed to intraspecific variation.

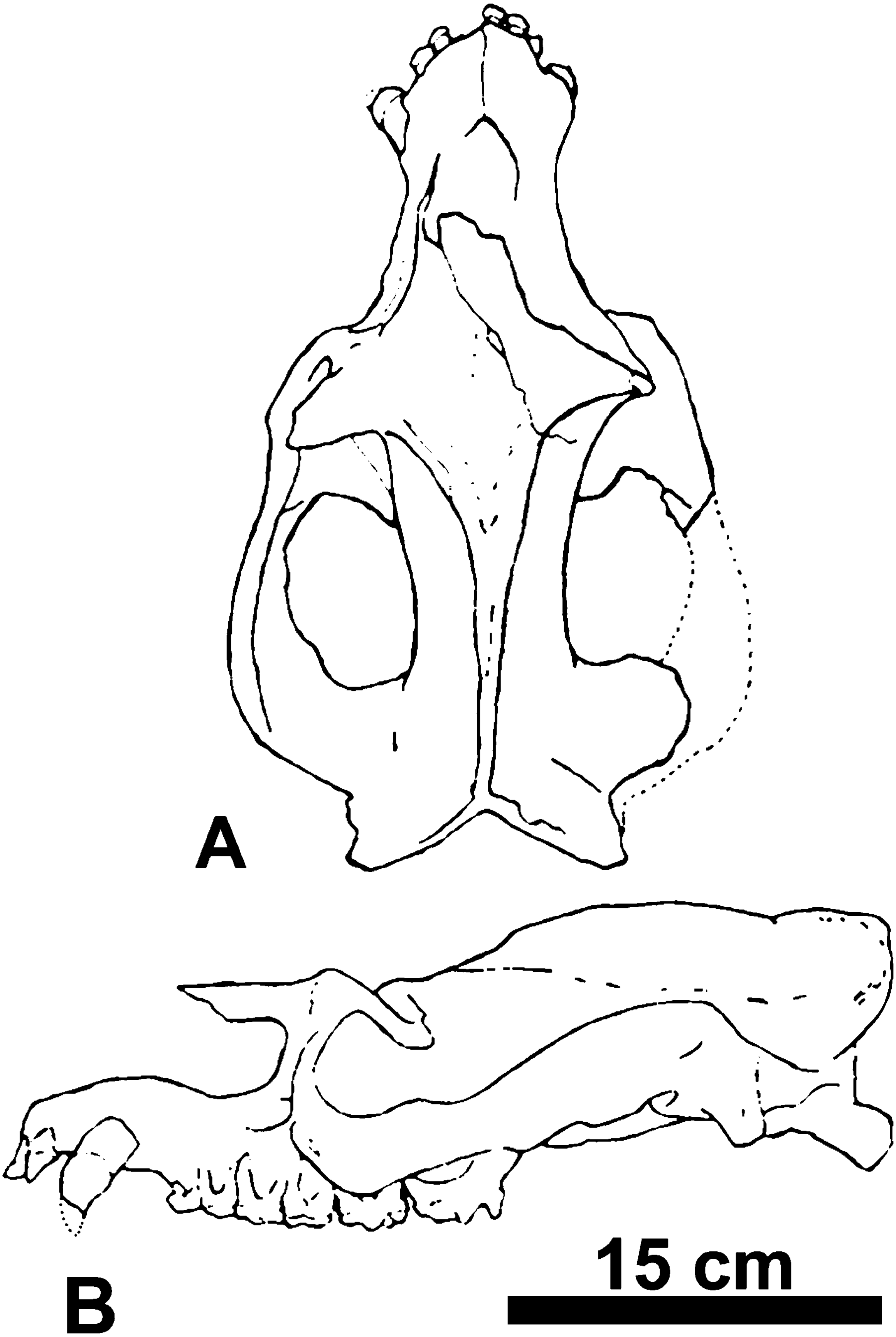

FIGURE 6. Holotype skull of *Metarhinus fluviatilis* (AMNH 1500) in **A**, dorsal; and **B**, lateral views. After Osborn, 1929.

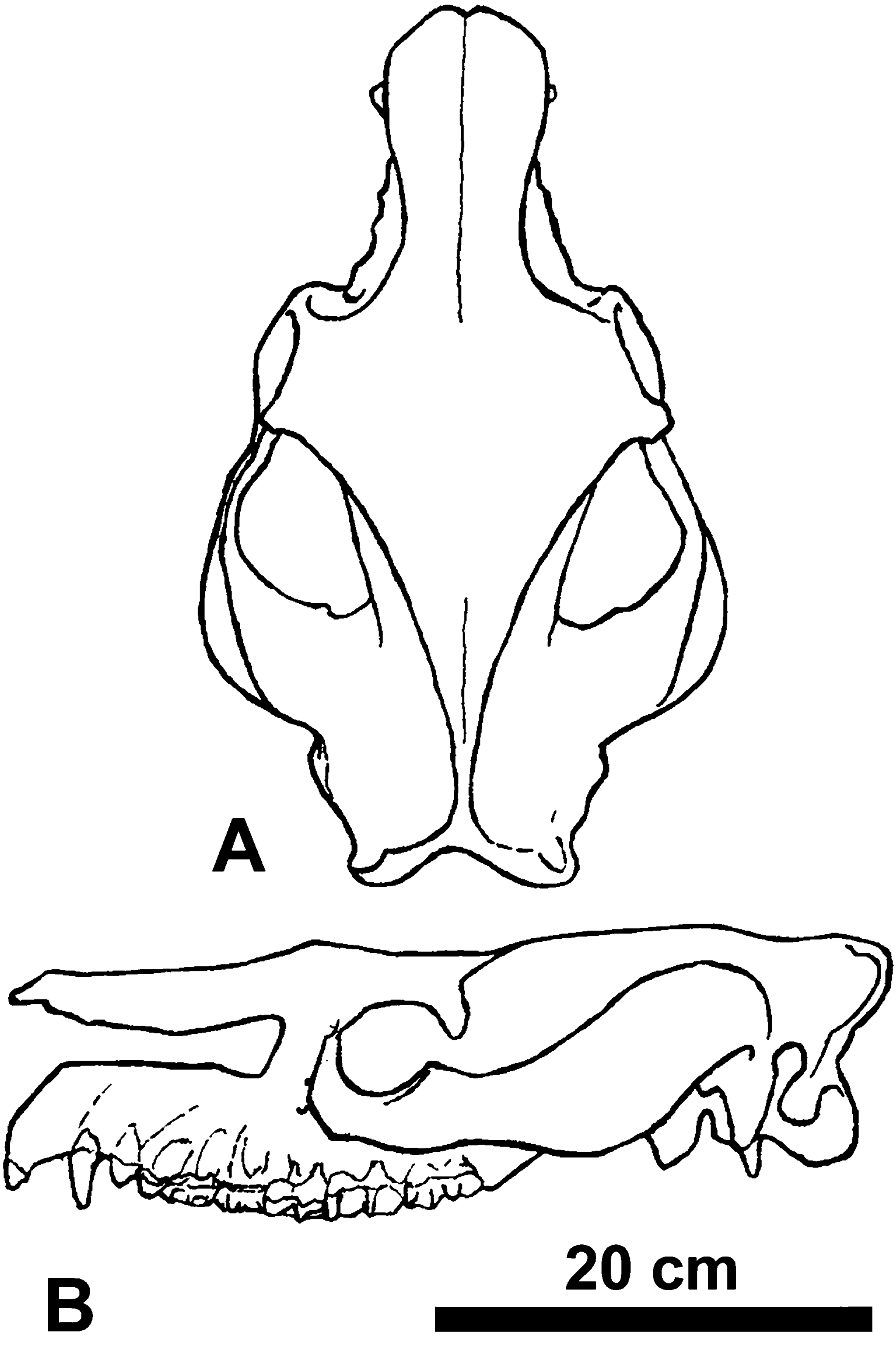

FIGURE 7. Skull of *Metarhinus fluviatilis* in **A**, dorsal; and **B**, lateral views.

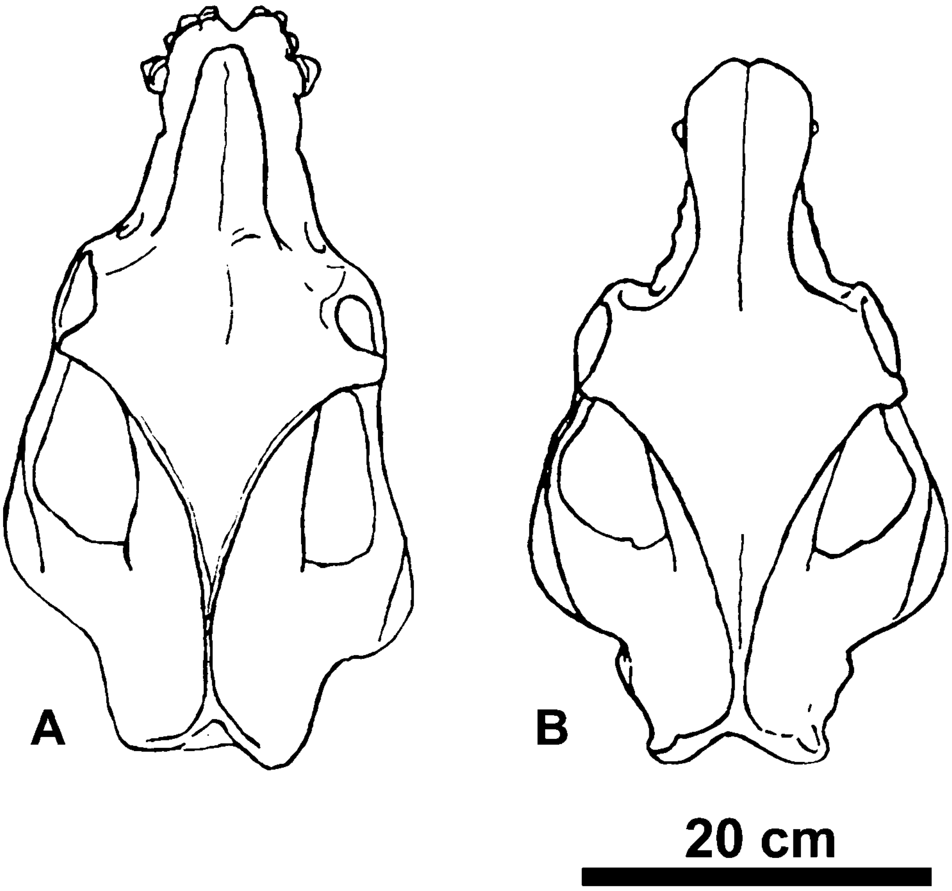

FIGURE 8. Skulls of **A**, *Metarhinus diploconus*; and **B**, *Metarhinus fluviatilis* in dorsal view.

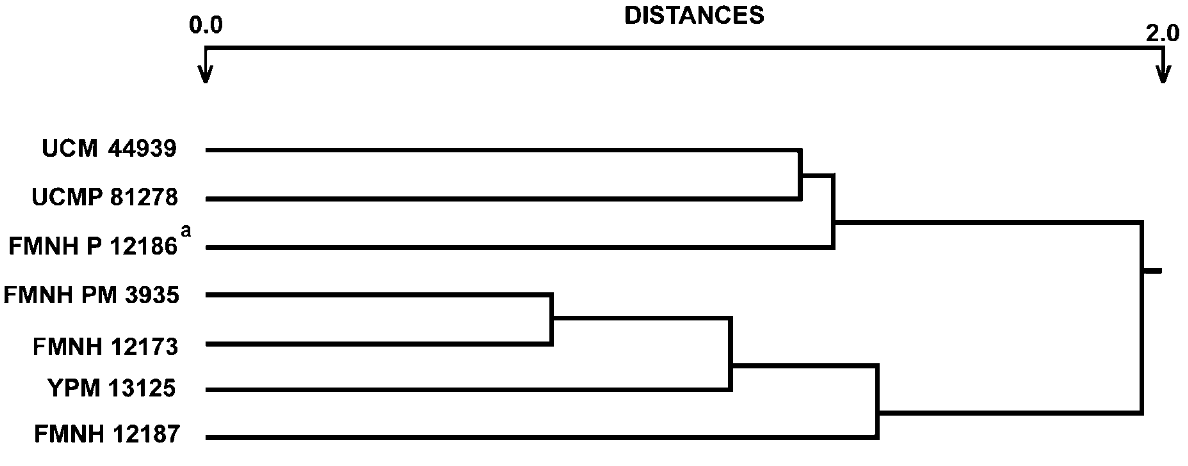

FIGURE 9. Cluster dendrogram for specimens of *Metarhinus* with spoon-shaped nasals (*Metarhinus fluviatilis*) resulting from a cluster analysis of all variables listed in Table 6. **a**, type of *Metarhinus riparius*.

As indicated above, the skulls with tapered and spoon-shaped nasals probably represent different species of a single genus, *Metarhinus*. That they are not males and females of a single species is suggested by the size variation of the suborbital protuberance in at least the form with tapered nasals (which is probably sexually dimorphic), and by the relatively high value of V for canine size in the form with spoon-shaped nasals (see below), which also suggests sexual dimorphism. The possible identification of males and females in the two groups represented by the two nasal morphologies, suggests that these groups are taxonomically distinct. It is possible, however, that there could be more than one species with spoon-shaped or distally tapered nasals.

The sample of *Metarhinus* with tapered nasals is very small (n = 4) and those specimens that are available are, for the most part, too poorly preserved to measure in detail. Despite Riggs' (1912) and Osborn's (1929) recognition of two species of *Metarhinus* with distally tapered nasals (which they referred to the genus *Rhadinorhinus*), I find no important morphological differences between any of the specimens with this nasal morphology. Given that all specimens with distally tapered nasals are morphologically alike and that the sample is insufficient to perform a statistical analysis, there is no basis for the recognition of more than one taxon. I, therefore, regard all specimens of *Metarhinus* with distally tapered nasals as representing a single species, *Metarhinus diploconus* (see below). If a larger sample of specimens with this nasal morphology should become available, however, further analysis testing this conclusion would be justified.

Riggs (1912) and Osborn (1929) also recognized more than one species of *Metarhinus* with spoon-shaped nasals, but once again, I have been unable to identify any important morphological differences between specimens of *Metarhinus* with this nasal morphology. The sample of *Metarhinus* with spoon-shaped nasals is also rather small, but is large enough to perform at least a preliminary statistical analysis.

All specimens of the variety of *Metarhinus* with spoon-shaped nasals are from the Wagonhound Member of the Uinta Formation (Uinta Basin) or from chronologically equivalent strata in the Adobe Town Member of the Washakie Formation (Washakie Basin). Because the sample of specimens from both locations is small, they were combined for the purpose of analysis.

Table 6 presents the summary statistics for the sample of *Metarhinus* with spoon-shaped nasals. Although the average value of V for this sample is within the range of typical extant mammalian species (= 4.9), only slightly more than half of the individual values of V are within the expected range of 4 to 10. Ten individual values of V are below 4 (rounded to the nearest whole number), but seven of these were calculated from samples consisting of four or fewer cases. I believe that these samples are probably too small to show all of the variation that is actually present. If all variables with fewer than four cases are eliminated from consideration, over three quarters of those remaining have values of V between 4 and 10 and the average value for the sample remains relatively unchanged (= 5.0).

The high values of V for the right canine suggests that canine size may be sexually dimorphic in the variety of *Metarhinus* with spoon-shaped nasals. The sample for the left canine, however, is too small to reflect this. The high values of V for canine size affect the average value of V for the sample only slightly. If canine size is excluded from the calculation of the average value of V, the resulting value is, in general, typical of extant mammalian species (average V = 4.5). If variables with fewer than four cases are eliminated from consideration as well as canine size, the average value of V for the sample becomes 4.8.

Cluster analysis (Fig. 9) of all of the variables listed in Table 6 indicates that there are two size groups present in the form with spoon-shaped nasals. These groups are not greatly different in size, however, and both join at a distance of only 1.9 mm. It is possible that these groups could represent two different species, two groups within a single species (such as males and females), or could possibly be an aberration due to the small sample size.

Based on the present results, I do not believe that there is justification for the recognition of more than a single species of *Metarhinus* with spoon-shaped nasals. The individual and average values of V for the entire sample are generally within the parameters recognized for a single species and, although cluster analysis suggests two size groups, these groups are separated by only a very small size interval. Normally I would have performed *t*-test analyses to compare both size groups suggested by the cluster analysis, and values of V would be calculated for each. The small sample size of both size groups, however, makes this impractical. If a larger sample should become available, statistical analyses should be performed again to determine whether the conclusions reached here remain valid. Specifically, it should be confirmed whether the individual and average values of V for the combined sample are within the normal parameters of a single species and whether two size groups are actually present. If two size groups are, in fact, present then tests should be performed to determine whether the group means are significantly different and whether the individual and average values of V for each group are within the range of a single species.

TABLE 6. Summary statistics for specimens of *Metarhinus* with spoon-shaped nasals. (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	3	397.8–406.8	403.5	±5.0	1.2
Length Cheek Tooth Series[a]	3	152.5–157.8	155.7	±2.8	1.8
Length P2 to M3[a]	7	137.0–144.5	140.8	±2.8	2.0
Length Premolar Series[a]	2	65.5–66.0	65.8	±0.4	0.6
Length Molar Series[a]	4	90.3–94.5	92.5	±1.9	2.1
Length Diastema[a]	3	6.0–8.0	7.3	±1.1	15.1
Length Left M3	4	30.0–34.0	31.9	±1.8	5.6
Length Right M3	6	30.5–34.5	32.3	±1.6	5.0
Width Left M3	5	30.5–35.2	32.4	±1.8	5.6
Width Right M3	5	30.3–35.0	32.6	±1.8	5.5
Length Left M2	5	30.0–34.0	32.1	±1.7	5.3
Length Right M2	5	31.5–34.0	32.6	±1.1	3.4
Width Left M2	4	30.4–34.3	32.1	±1.7	5.3
Width Right M2	4	30.2–34.4	32.2	±2.0	6.2
Length Left M1	2	27.0–28.0	27.5	±0.7	2.6
Length Right M1	4	25.0–28.0	26.6	±1.3	4.9
Width Left M1	2	26.7–29.5	28.1	±2.0	7.1
Width Right M1	3	25.8–27.3	26.5	±0.8	3.0
Length Left P4	5	18.0–20.0	18.8	±0.8	4.3
Length Right P4	5	18.0–19.5	18.4	±0.7	3.8
Width Left P4	5	22.8–24.8	23.9	±0.8	3.4
Width Right P4	6	23.4–25.9	24.3	±1.0	4.1
Length Left P3	5	16.0–18.0	16.7	±1.0	6.0
Length Right P3	5	14.5–18.0	16.6	±1.4	8.4
Width Left P3	5	19.2–22.0	20.6	±1.1	5.3
Width Right P3	4	20.1–21.0	20.6	±0.4	1.9
Length Left P2	3	13.0–15.0	14.0	±1.0	7.1
Length Right P2	4	13.5–15.5	14.5	±0.9	6.2
Width Left P2	4	15.2–17.9	16.7	±1.2	7.2
Width Right P2	4	16.4–17.8	16.8	±0.7	4.2
Buccal-Lingual Width Left Canine	1	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	4	15.0–18.3	16.6	±1.7	10.2
Mesial-Distal Width Left Canine	2	16.9–18.2	17.5	±0.9	5.1
Mesial-Distal Width Right Canine	3	16.1–19.7	17.3	±2.1	12.1
AVERAGE V					4.9[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length.

Generally, the forms with spoon-shaped and distally tapered nasals are easily distinguished from one another, but if the nasals are lacking, it is difficult to distinguish between them because, exclusive of the nasals, the size and morphology of both are rather similar. The form with spoon-shaped nasals tends to have a relatively small suborbital protuberance compared to the form with tapered nasals, but some specimens with tapered nasals (interpreted as probable females by Mader 1989 and above) also have suborbital protuberances that are weakly developed. Similarly, some specimens with spoon-shaped nasals have a distinctive, sharply downturned zygomatic arch that is similar to that of *Palaeosyops* but not as robust (see Fig. 7). I have found no specimens of *Metarhinus* with distally tapered nasals that have this zygomatic arch morphology, but the zygomatic arch is often poorly preserved in specimens of *Metarhinus*. It is not certain, therefore, that all specimens of *Metarhinus* with spoon-shaped nasals share this zygomatic arch morphology and that at least some specimens of *Metarhinus* with tapered nasals do not.

As a group, specimens with tapered nasals appear to be slightly larger in size than specimens with spoon-shaped nasals (compare the sizes in Fig. 8). This size difference is most evident when the basilar length of the skull, length of the cheek tooth series, or length of the cheek tooth series exclusive of the first premolar is considered, although my data indicate that the size difference between the largest individual with spoon-shaped nasals and the smallest individual with distally tapered nasals is no more than 0.5 to 2 millimeters for these linear measurements. Length of the premolar series, length of the molar series, and individual tooth dimensions overlap in the few specimens that are available for comparison and it would not be surprising with a larger sample to find that the skull length and length of the cheek tooth series (with or without P1) overlap as well.

Because of the extremely small size of the holotype, the type species of *Metarhinus*, *M. fluviatilis*, probably belongs to the variety of *Metarhinus* with spoon-shaped nasals, as Riggs (1912) and Osborn (1929) concluded. Similarly, the type of Osborn's "*Telmatotherium*" *diploconum* is rather large, and probably represents the variety of *Metarhinus* with tapered nasals, again as Riggs and Osborn had concluded. Unfortunately, the type of *M. earlei* is intermediate in size and it is not certain to which morphological group it belongs. It is also impossible to determine which group the type of *M. cristatus* belongs to based on size because the specimen is insufficiently preserved. Based solely on the size of the type specimens, I provisionally accept *M. fluviatilis* as representing the form with the spoon-shaped nasals and *M. diploconus* as representing the form with distally tapered nasals. *Metarhinus earlei* and *M. cristatus* are treated as a nomina dubia, because they could be junior synonyms of either *M. fluviatilis* or *M. diploconus*.

Peterson (1914b) described the partial skeleton (CM 2909) of a very young brontothere from the Uinta Basin, which he identified as a new genus, *Heterotitanops* (type species *H. parvum*). W.K. Gregory, however, concluded that this specimen probably represents a very young individual belonging to an undetermined species of *Metarhinus* or *Rhadinorhinus* (Osborn 1929, p. 196) and Osborn (1929, p. 425) suggested that it might represent an extremely young (perhaps fetal) *Metarhinus fluviatilis*. An examination of the skull of CM 2909 shows the extreme depth of the narial incision, the lateral border of which lies in close proximity to the orbit. This morphology is clearly diagnostic of *Metarhinus* but, unfortunately, the lack of nasals and permanent teeth makes it difficult to determine which species is represented. I provisionally regard *Metarhinus parvum* as a nomen dubium.

Stock (1937) described the fragmentary right facial region, LACM (CIT) 2037, of a small brontothere from San Diego County, California. According to Stock, this specimen is from the Poway Conglomerate, but the formation from which the specimen was taken is now known as the Friars Formation (Golz 1976; Golz & Lillegraven 1977). Stock identified the specimen as a new species, which he provisionally referred to *Metarhinus*, and named *Metarhinus* (?) *pater*. Stock gave the following diagnosis for the new taxon:

> "Muzzle elongate; naso-maxillary recess deep and reaching back of antorbital [= infraorbital] foramen; antorbital foramen large and situated above anterior border of M2. P1 and P2 small; P4 relatively long in comparison to its width. Size larger than *Metarhinus fluviatilis* and *M. riparius*, similar to that of *M. earlei* and smaller than *Mesatirhinus superior* [= *Sphenocoelus intermedius*]."

In comparing the type of *Metarhinus* (?) *pater* to specimens that Riggs (1912) and Osborn (1929) had referred to *Metarhinus* and *Rhadinorhinus*, Stock noted that in all these materials the infraorbital foramen is in close proximity to the orbit. Stock further noted that the type of *Metarhinus* (?) *pater* and specimens referred to *Metarhinus* have a postnarial notch that is positioned slightly anterior to the back of M2, and a P1 that is small in size.

According to Stock, *Metarhinus* (?) *pater* differs from specimens referred to *Metarhinus* in having a deeper naso-maxillary recess, a longer snout, longer postcanine diastema, longer P4, and more posteriorly positioned infraorbital foramen (located over the front of M2). Stock distinguished *Metarhinus* (?) *pater* from *Rhadinorhinus* (= *Metarhinus diploconus* in the present paper), by the former's possession of a P2 that is not subquadrate, longer postcanine diastema, more posteriorly positioned postnarial notch, better developed infraorbital shelf (= suborbital protuberance), and more posteriorly positioned antorbital (= infraorbital) foramen (position relative to M1). Stock also noted that *Metarhinus pater* lacked the upwardly curved cheek tooth series that Osborn (1929) had cited as a character of "*Rhadinorhinus*".

The relatively elongated upper molars in the type of *Metarhinus* (?) *pater* suggest that the identification of the specimen as a dolichorhinine brontothere is probably correct. In a scatter plot that I performed (not shown here) comparing length against width for M2, the type of *Metarhinus* (?) *pater* plotted among specimens that belong to the subfamily Dolichorhininae and below the diagonal line (see Fig. 1) indicating equality of length and width (i.e., among specimens in which the tooth length exceeds the width). Because of the close proximity of the infraorbital foramen to the orbital rim, and because it appears that the lateral nasal incision was probably very deep, I accept Stock's assignment of the specimen to *Metarhinus*.

Of the two species of *Metarhinus* recognized as valid in the present paper, the type of *Metarhinus pater* is most similar in size to the larger species, *M. diploconus*, which was formerly referred to the genus *Rhadinorhinus*. The type of *M. pater* is slightly smaller (based on the length of the cheek tooth series exclusive of P1 and length of the molar series) than the type of *M. diploconus*, but is larger than any of the specimens I refer to that species, below.

In my opinion, the characters used by Stock to distinguish *Metarhinus pater* from *M. diploconus* (i.e., *Rhadinorhinus*) are probably not sufficient to justify the recognition of a distinct species. Two of the characters, diastema length and squareness of the P2, are highly variable in brontotheres and are generally not useful for diagnostic purposes. Two other characters, the position of the postnarial notch and position of the infraorbital foramen, are potentially better for diagnostic purposes, but I am not convinced that the difference is significant. Stock's assertion that the suborbital protuberance of *M. pater* is larger than that of *M. diploconus* was entirely conjectural because, as he noted (1937, p. 50), the jugal has been completely broken away along the plane of the jugal-maxillary border and the region of the suborbital protuberance is thus not preserved. Finally, as indicated above, Osborn was incorrect when he cited the curvature of the cheek tooth series as a diagnostic character of "*Rhadinorhinus*" because this observation was based on one or more taphonomically distorted specimens. This is not a valid distinction, therefore, between *M. pater* and *M. diploconus*. For the purposes of the present paper I accept *M. pater* as a possible junior synonym of *M. diploconus*.

William Turnbull and David Martill (Martill & Turnbull, abstract 1986; Turnbull & Martill 1988) have reported the existence of a monospecific brontothere assemblage from the Adobe Town Member of the Washakie Formation (Washakie Basin). The specimens range from juvenile to very old individuals and are believed to have been killed in a single mass mortality event. The specimens were provisionally referred to the genus *Mesatirhinus* but, after a preliminary examination I believe that they probably represent the genus *Metarhinus*, a conclusion also reached by McCarroll *et al.* (1996) and accepted by Mihlbachler (2005). This identification is further suggested by the stratigraphic level (TWKA2), which represents early Uintan age. An analysis of this quarry sample may help to solve some of the taxonomic uncertainties discussed above by more clearly establishing the size and morphological variation present in a single species of *Metarhinus*.

Species *METARHINUS fluviatilis* Osborn 1908

= *M. riparius* Riggs 1912

Holotype. AMNH 1500, a partial skull lacking the nasals.

Referred specimens. FMNH 12173, FMNH 12187, FMNH P 12186 (type of *M. riparius*), FMNH PM 3935, UCM 44939, UCMP 81278, YPM 13125.

Diagnosis. Small species of *Metarhinus* with nasals that are broadly flared distally and constricted at the base giving them a distinctive spoon-shape.

Discussion. As indicated in the discussion above, the holotype skull of *Metarhinus fluviatilis* lacks the nasals and is, therefore, only provisionally accepted as representing the variety of *Metarhinus* with spoon-shaped nasals. This conclusion is based solely on the diminutive size of the type specimen, which is smaller than any of the specimens of *Metarhinus* with spoon-shaped nasals for which I have data. The size of the skull is probably inconsistent with the possibility that it represents the variety of *Metarhinus* with tapered nasals because individuals with this nasal morphology appear to be larger than those with spoon-shaped nasals. If later work should demonstrate that the *Metarhinus* with spoon-shaped nasals does not represent the type species (*M. fluviatilis*) then the next available name for this taxon is probably *M. riparius*, which was based on a skull (FMNH P 12186) clearly possessing the spoon-shaped nasal morphology.

Mihlbachler (2005) suggested that, because the holotype of *Metarhinus fluviatilis* lacks nasals, it would be advisable to designate a neotype for the species in which the nasals are preserved. Mihlbachler proposed FMNH PM 12187, but this specimen can have no validity as a name-holder according to Article 75 of the International Code of Zoological Nomenclature (Ride *et al*. 1999), since the original type specimen (AMNH 1500) is still preserved.

Species *METARHINUS diploconus* (Osborn 1895)

= *M. abbotti* (Riggs 1912)
= *M. pater*? Stock 1937

Holotype. AMNH 1863, a skull lacking the nasals.

Referred specimens. CM 2866, CM 3098, CM 3510, FMNH P 12179 (type of *M. abbotti*, type species of *Rhadinorhinus*), LACM (CIT) 2037 (type of *M. pater*).

Diagnosis. Large species of *Metarhinus* with nasals that are strongly tapered distally.

Discussion. The holotype of *Metarhinus diploconus* lacks the nasals and the conclusion that it represents the form with distally tapered nasals is based solely upon the large size of the type. If this conclusion should prove to be in error (either because *Metarhinus diploconus* represents the *Metarhinus* with spoon-shaped nasals or is a nomen dubium) then the next available name for the taxon with tapered nasals is *Metarhinus abbotti* (Riggs), which was based on a skull (FMNH P 12179) that clearly exhibits this nasal morphology.

In his recently completed doctoral dissertation, Mihlbachler (2005) recognized the holotype of *Metarhinus diploconus* as representing an entirely new genus. Among the distinguishing characters were less prominent orbits, more strongly upturned rostrum, more deeply concave dorsal midcranial surface, and small premolar hypocone. In my opinion, however, all of these characters can be attributed to taphonomic deformation and individual variation. More compellingly, Mihlbachler noted a pair of large fossae in the floor of the rostrum and inside the nasal chamber that had not been observed by previous authors and seemed to distinguish the specimen from *Metarhinus*. The genus *Metarhinus* is characterized by a highly unusual nasal morphology, however, which has never been described, but is evident in a skull (UCM 44939) with distally flared nasals here referred to the species *M. fluviatilis* (see list of referred specimens for that species). Based on

Mihlbachler's description, it seems doubtful that the morphology of the holotype of *M. diploconus* shall be found to be significantly different from that of UCM 44939.

As indicated in the Discussion section for the genus *Metarhinus*, the type of *Metarhinus pater* Stock is provisionally referred to the species *M. diploconus* based on its size.

Genus *SPHENOCOELUS* Osborn 1895

= *Dolichorhinus* Hatcher 1895
= *Tanyorhinus* Cook 1926
= *Dolichorhinoides* Granger and Gregory 1943

Type species. *S. uintensis* Osborn 1895

Included species. *S. intermedius* (Osborn 1908), *S. hyognathus* (Osborn 1890), *S. angustidens* (Granger & Gregory 1943, an Asian taxon not discussed in detail in the present paper).

Age. early Uintan

Diagnosis. Medium to large sized (length P1 to M3 approximately 173–287 mm, length M1 to M3 approximately 101–173 mm) dolichorhinine brontothere with extremely long (hyperdolichocephalic) skull. The genus is also distinguished from other dolichorhinine brontotheres by a small, angular horn at the frontonasal boundary over the orbit and by a double suborbital protuberance in which there is a small anterior flange and a large posterior flange. The horn is weak or absent in at least some specimens of *Sphenocoelus uintensis*, however, and the anterior flange of the suborbital protuberance is weak or absent in certain specimens of *S. uintensis* and *S. intermedius*. The condition of the suborbital protuberance is not known with certainty in *S. angustidens*.

Discussion. The single unifying synapomorphy that consistently unites all specimens of *Sphenocoelus* within the family Dolichorhininae is the highly unusual hyperdolichocephalic skull (Mader 1998). Many specimens of *Sphenocoelus* (spanning all recognized species) also have a small horn over the orbit, but this may be weakly developed or absent in some specimens of the most plesiomorphic species, S. *uintensis*. Although the presence of a horn is clearly a synapomorphy, its absence in certain specimens limits the use of this character for diagnostic purposes. Furthermore, there are some specimens of the plesiomorphic dolichorhinine brontothere *Mesatirhinus* that may exhibit an incipient horn (Osborn 1929; McCarroll *et al*. 1996).

Similarly, in many specimens of *Sphenocoelus* the suborbital protuberance is divided into a small anterior flange and a large posterior flange, a character that is clearly lacking in the other two North American dolichorhinine brontothere genera: *Mesatirhinus* and *Metarhinus*. The anterior flange is weak or absent, however, in some specimens of *S. uintensis* and *S. intermedius*, (and the condition is unknown in *S. angustidens*) limiting the usefulness of the character in making identifications.

Finally, in most specimens of *Sphenocoelus,* the orbit is vertically elongated and angled backwards, which is also a derived condition (compare to other brontotheres and outgroup perissodactyls). However, some specimens of *Mesatirhinus* have a similar orbital morphology (e.g., UFH V-258), which prevents use of this character as a distinctive synapomorphy for *Sphenocoelus*.

In my previously published diagnoses of brontothere genera (Mader 1989; 1998) I have used several descriptive terms to indicate brontothere sizes. These descriptive terms were loosely related to measurements appearing in Mader (1989) of the length of the upper cheek tooth series or the length of the upper cheek tooth series exclusive of the first premolar. The second measurement (length P2 to M3) was the preferred measurement since the first premolar is often missing in brontothere skulls.

Sphenocoelus (= *Dolichorhinus*) was described in both of my papers (Mader 1989; 1998) as being "moderately large-sized" a description that I used for brontotheres in which the length of P2 to M3 was approximately 164–193 mm. It will be noted that, in the present paper, the size is described as "medium to large size," which reflects a slightly different size range. Based on my previous usage, the length of P2 to M3 in "medium" sized brontotheres would be approximately 128–165 mm, and in "large" sized brontotheres the length of P2 to M3 would be approximately 195–255 mm. The change in description is necessitated by the relatively diminutive size of *S. intermedius* (P2 to M3 approximately 154–175 mm) and the substantial size of *S. angustidens,* which were not taken into account in my previous papers.

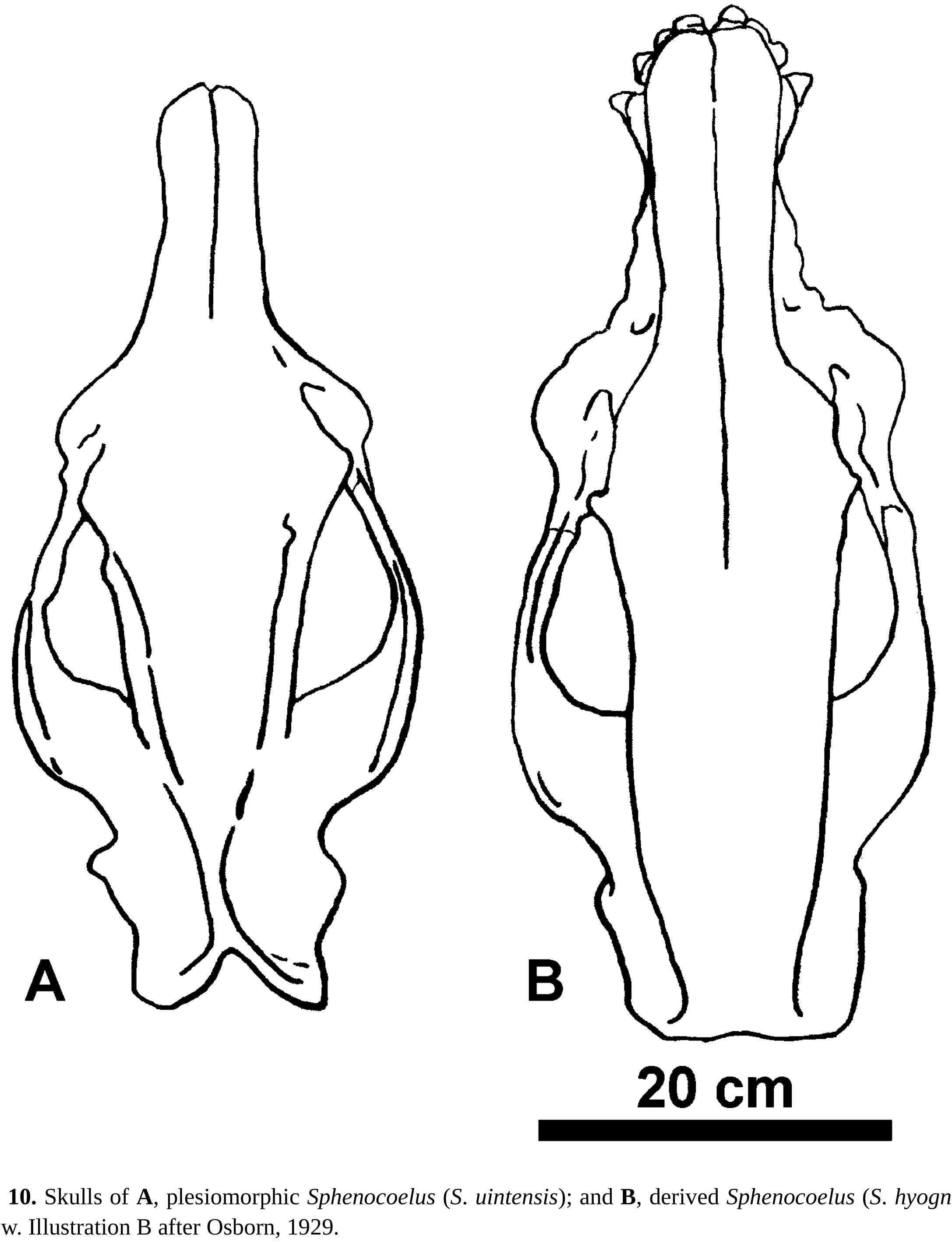

FIGURE 10. Skulls of **A**, plesiomorphic *Sphenocoelus* (*S. uintensis*); and **B**, derived *Sphenocoelus* (*S. hyognathus*) in dorsal view. Illustration B after Osborn, 1929.

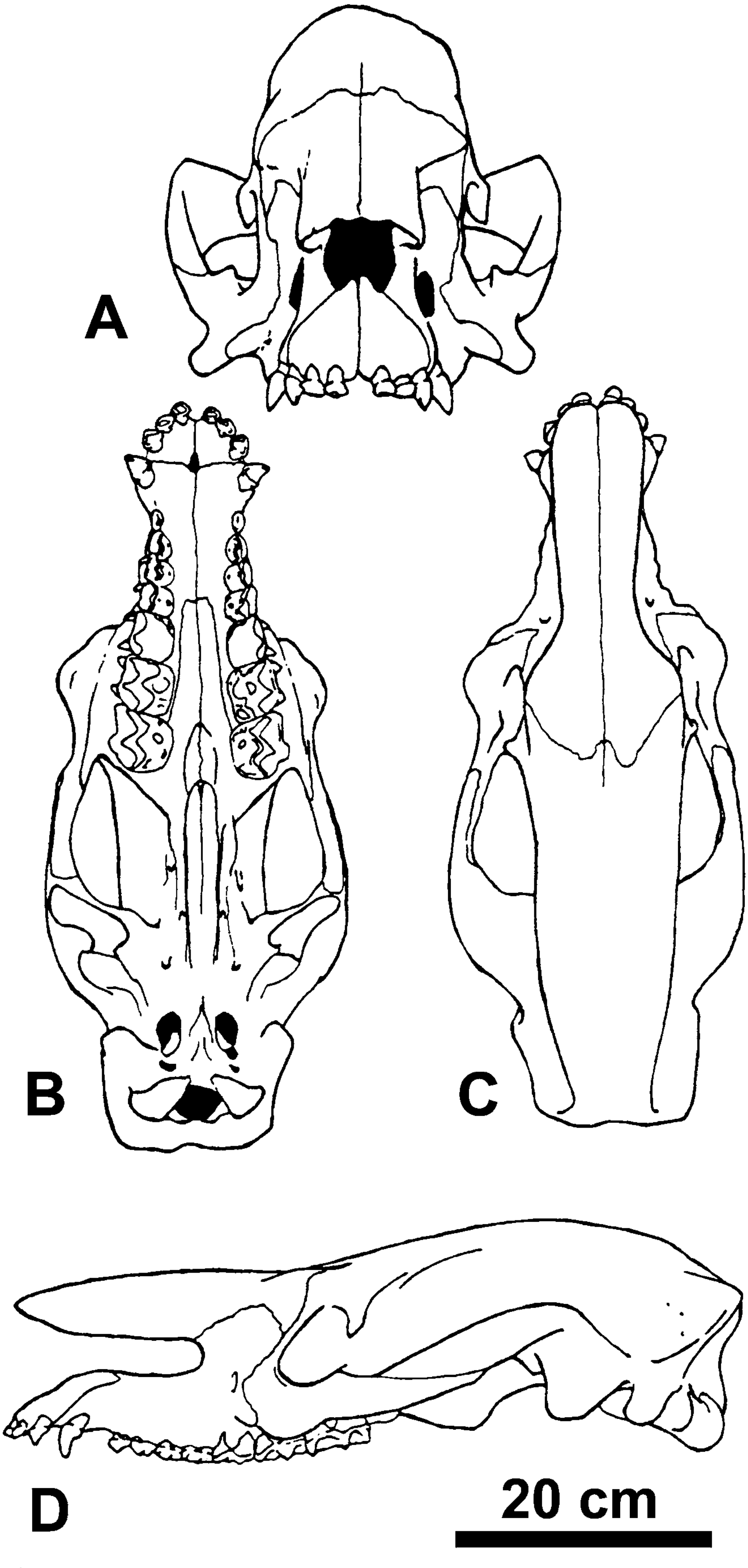

FIGURE 11. Skull of *Sphenocoelus hyognathus* in **A**, anterior; **B**, ventral; **C**, dorsal; and **D**, lateral views. After Osborn, 1929.

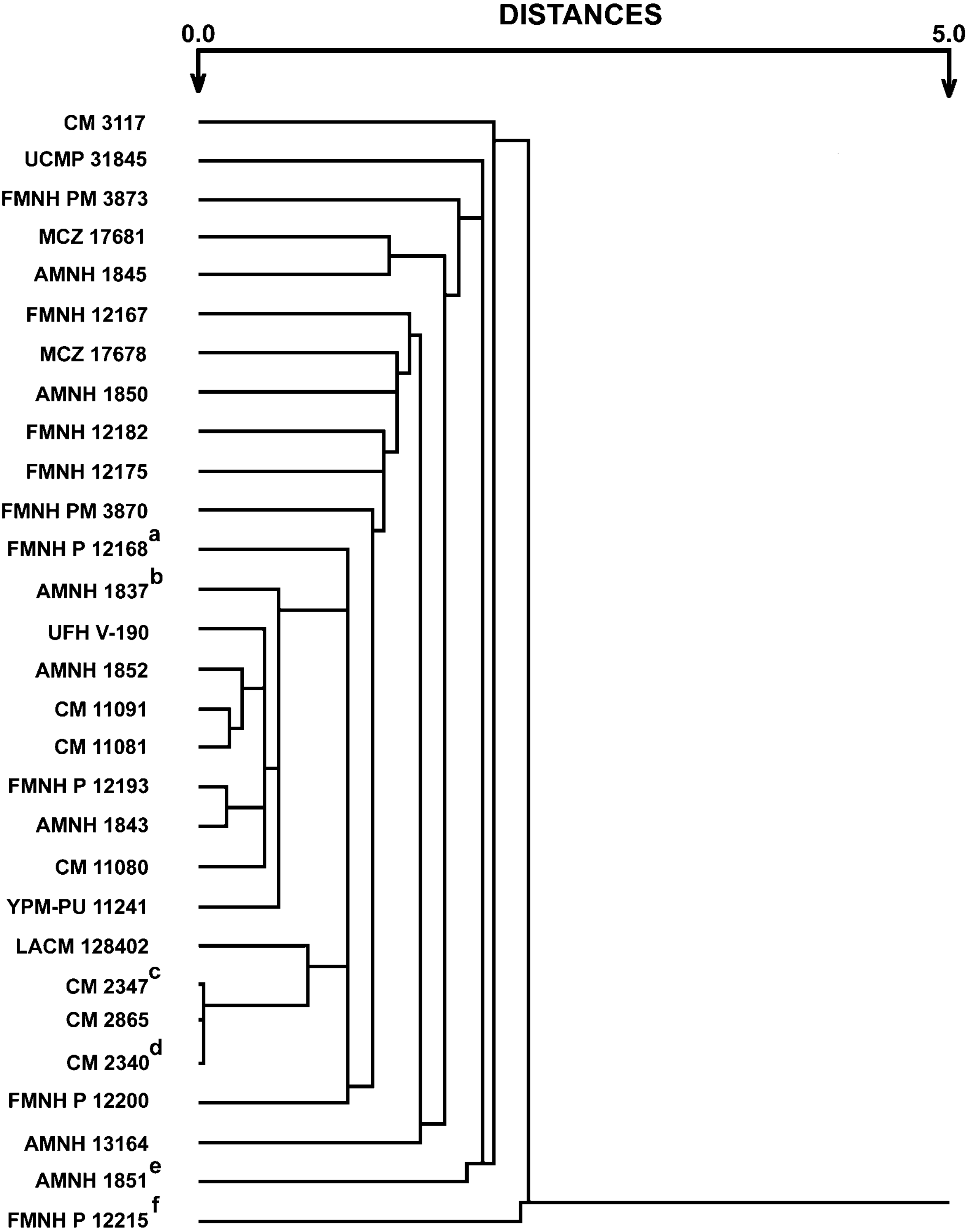

FIGURE 12. Cluster dendrogram for specimens of derived *Sphenocoelus* from the Uinta and Washakie Basins resulting from a cluster analysis of all variables listed in Table 7. **a**, type of *Sphenocoelus superior*; **b**, type of *S. intermedius*; **c**, type of *S. longiceps*; **d**, type of *S. heterodon*; **e**, type of *S. cornutum*; **f**, type of *S. fluminalis*.

It should be noted that I have not personally taken measurements from the type and only known specimen of *S. angustidens*, although Granger and Gregory (1943) reported that the length of the cheek tooth series (P1 to M3) is approximately 287 mm. Although this is not my preferred measurement, comparison of Granger and Gregory's measurement against measurements of the cheek tooth series from my own data places the type of *S. angustidens* in the "large" to "very large" category. Since I had intended the term "very large" for the largest brontotheres (e.g., *Brontops* and *Megacerops*, minimal length of P1 to M3 approximately 300 mm), and the type of *S. angustidens* is slightly smaller than these, the descriptive term "large" seems to be the most appropriate one to apply to *S. angustidens*.

Among North American specimens of *Sphenocoelus* there are two general skull morphologies (Fig. 10): a plesiomorphic form with a prominent sagittal crest (similar to that of *Eotitanops*, the earliest and most primitive known brontothere, and outgroup perissodactyls) and a more derived form in which the cranial vertex has been widened and the sagittal crest lost. In the past, these more derived specimens have been referred to the genus *Dolichorhinus* (e.g., Riggs 1912; Peterson 1924; Osborn 1929; Granger & Gregory 1943; Simpson 1945; Mader 1989; McCarroll *et al*. 1996). More recently, however, Mader (1998) recognized *Dolichorhinus* as a junior synonym of *Sphenocoelus* (Osborn 1895), as did McKenna and Bell (1997), apparently based upon Mader's conclusions (which were unpublished, but available to them at that time).

Mihlbachler (2005), however, has continued to regard *Sphenocoelus* as generically distinct from *Dolichorhinus*, although characters that he regarded as distinctive at the generic level are regarded here as distinctive only at the species level. Of greater consequence, however, is that in Mihlbachler's phylogenetic analysis (2005), *Sphenocoelus* did not group with *Dolichorhinus* as would be necessary if they are both members of a single monophyletic taxon. In my opinion there are several important problems with the characters used in the Mihlbachler study that will need to be addressed. For the present I continue to regard *Sphenocoelus* and *Dolichorhinus* as synonyms.

Several specimens exhibiting the plesiomorphic morphology were referred to a new genus, *Tanyorhinus*, by Cook (1926). West and Dawson (1975), however, noted a similarity between Cook's specimens of *Tanyorhinus* and specimens of *Dolichorhinus*, and stated that the two names could be regarded as synonyms. Mader (1998) accepted this synonymy and further synonymized *Tanyorhinus* and *Dolichorhinus* with *Sphenocoelus* (see above).

Specimens exhibiting the plesiomorphic morphology are all very similar to each other and any minor dissimilarities can be attributed to intraspecific variation and to differences in ontogeny, dental wear, and preservation. Because there is insufficient material to perform a statistical analysis, it cannot be determined whether or not there is more than one size group among these specimens, which might be accorded species status. I conclude, therefore, that all of this material should be referred to a single species, *Sphenocoelus uintensis*.

Specimens exhibiting the derived morphology, previously referred to *Dolichorhinus* (Fig. 11), are known in sufficient numbers to analyze quantitatively. Mihlbachler has placed all of these under a single species, *Dolichorhinus hyognathus*, but the analysis that follows, suggests that two species are actually present.

Most of these derived specimens were collected from the Uinta Formation (Wagonhound Member) of the Uinta Basin of Utah (indeed, most *Sphenocoelus* specimens in museum collections, including most of the type specimens, are from this formation and locality). Because the sample size was relatively small (fewer than twenty individuals for any given variable studied) the sample was supplemented by three specimens from the Washakie Basin of Wyoming (Washakie Formation, Adobe Town Member).

Table 7 presents summary statistics for all specimens of derived *Sphenocoelus* examined for this study, including specimens from both the Uinta and Washakie Basins. For most variables, the coefficient of variation falls within the range of 4 to 10 although, in many cases, the values of V are at the higher end of this range. The average value of V for the sample (excluding diastema length, which I have found to be extremely variable in all brontotheres) is also rather high (8.7), but this is due in part to the high values of V for canine size. Canine size is often sexually dimorphic in perissodactyls and sexually dimorphic characters frequently have high values of V associated with them. Even if canine dimensions are excluded from the calculation of the average, however, the average value of V for the sample remains high (7.9). The high average value of V suggests that there may be some heterogeneity in the overall derived *Sphenocoelus* sample.

A cluster analysis of all of the variables used to generate the statistics appearing in Table 7 (34 variables in all) does not indicate that more than a single group is present (Fig. 12). Interestingly, however, a cluster analysis using only the length of the skull, length of the cheek tooth series (exclusive of P1), and length of the molar series, results in two major size groups (Fig. 13). These were the same variables that delineated two size groups among specimens of *Mesatirhinus* (see above).

Tables 8 and 9 present the *t*-test results for the two *Sphenocoelus* size groups, which demonstrates that, for most variables, the means of the two size groups are significantly different. Out of thirty-four variables, well over three quarters (82%) have probabilities of .05 or less and over half (65%) have probabilities of .01 or less. Of all the cheek tooth and cheek tooth series measurements, only one (width of left P4) has a probability greater than .05 and this is so close (.061) that it can probably be discounted. Even though there is an 83% chance (see Methods section, above) that at least one significant result in this analysis will be invalid (i.e., a false rejection of the null hypothesis), it seems highly unlikely that well over three quarters of the results would be attributable to Type I errors.

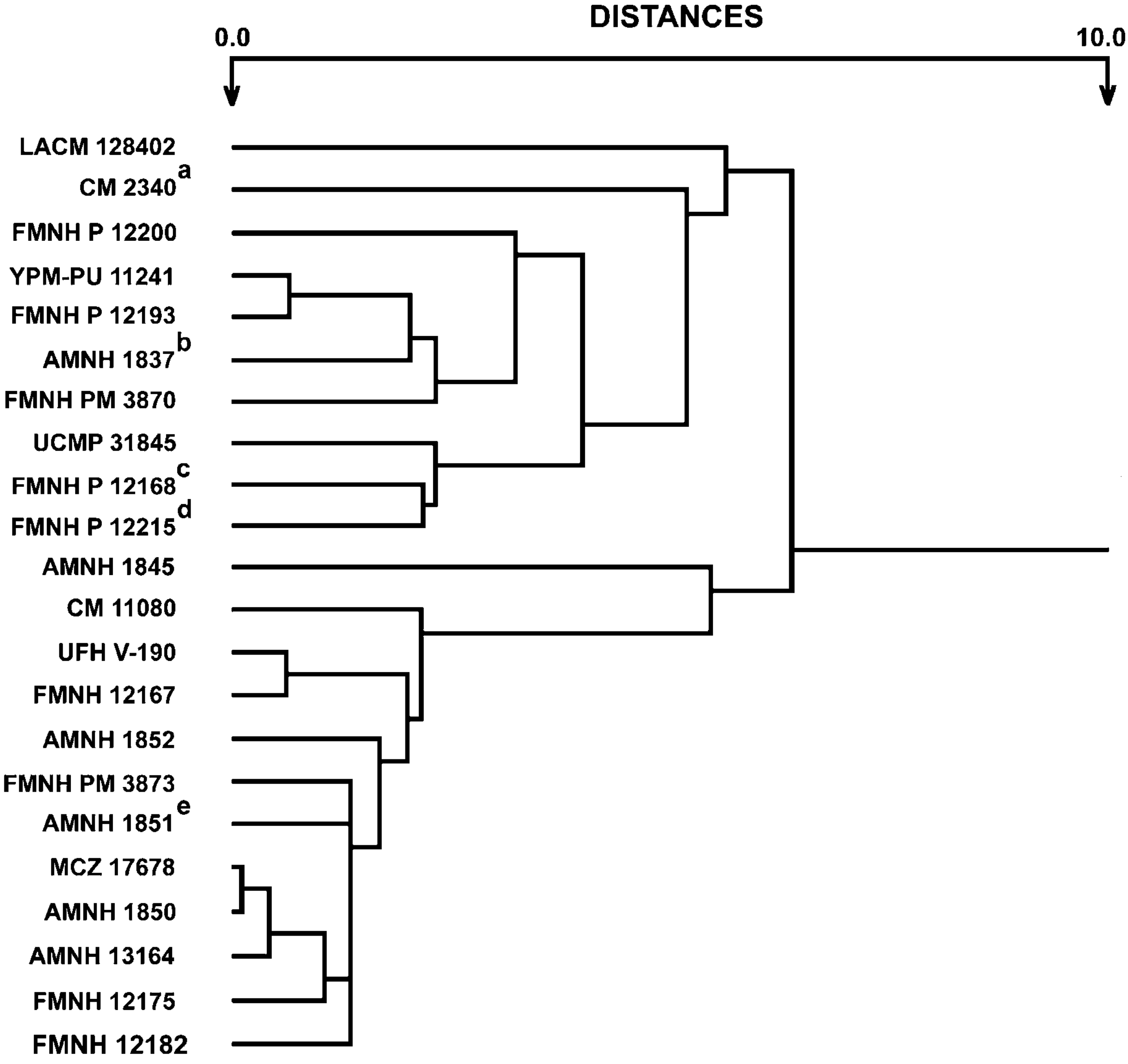

FIGURE 13. Cluster dendrogram for specimens of derived *Sphenocoelus* from the Uinta and Washakie Basins resulting from a cluster analysis of basilar skull length, length of cheek tooth series, and length of molar series. **a**, type of *Sphenocoelus heterodon*; **b**, type of *S. intermedius*; **c**, type of *S. superior*; **d**, type of *S. fluminalis*; **e**, type of *S. cornutum*.

TABLE 7. Summary statistics for the genus *Sphenocoelus*. (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	9	466.0–582.0	534.4	±42.6	8.0
Length Cheek Tooth Series[a]	14	172.5–216.0	196.3	±15.7	8.0
Length P2 to M3[a]	17	154.0–192.0	177.0	±13.6	7.7
Length Premolar Series[a]	14	69.5–87.0	79.7	±5.6	7.0
Length Molar Series[a]	18	100.5–131.0	116.6	±9.4	8.1
Length Diastema[a]	11	9.5–23.0	16.8	±4.1	24.4
Length Left M3	17	35.0–48.0	40.7	±3.3	8.1
Length Right M3	19	36.5–47.5	42.5	±3.0	7.1
Width Left M3	18	31.5–44.0	38.9	±3.7	9.5
Width Right M3	19	32.6–43.8	38.3	±3.2	8.4
Length Left M2	17	33.5–48.0	40.4	±3.8	9.4
Length Right M2	16	34.0–48.0	41.4	±3.2	7.7
Width Left M2	17	32.2–44.7	38.7	±3.4	8.8
Width Right M2	16	34.5–43.5	39.3	±2.8	7.1
Length Left M1	16	28.0–39.0	33.9	±3.1	9.2
Length Right M1	18	27.0–38.5	34.3	±3.1	9.0
Width Left M1	13	28.2–36.6	32.1	±2.4	7.5
Width Right M1	15	29.5–36.0	32.4	±1.7	5.3
Length Left P4	14	20.5–25.0	22.9	±1.4	6.1
Length Right P4	15	20.0–24.5	22.3	±1.5	6.7
Width Left P4	15	25.1–29.9	27.3	±1.5	5.5
Width Right P4	17	21.7–30.0	27.2	±2.2	8.1
Length Left P3	17	16.0–25.0	20.9	±2.1	10.1
Length Right P3	17	17.0–24.0	20.5	±1.7	8.3
Width Left P3	16	19.5–25.0	22.5	±1.6	7.1
Width Right P3	15	19.3–24.4	22.2	±1.6	7.2
Length Left P2	17	15.5–22.0	18.2	±1.9	10.4
Length Right P2	16	15.0–21.0	18.4	±1.6	8.7
Width Left P2	16	14.7–19.1	17.5	±1.4	8.0
Width Right P2	12	16.0–20.0	18.1	±1.2	6.6
Buccal-Lingual Width Left Canine	9	15.0–22.9	17.5	±2.8	16.0
Buccal-Lingual Width Right Canine	9	15.0–23.0	17.8	±2.9	16.3
Mesial-Distal Width Left Canine	8	17.0–23.5	19.5	±2.0	10.3
Mesial-Distal Width Right Canine	11	16.0–25.9	20.5	±2.9	14.2
AVERAGE V					8.7[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Excluding Diastema Length.

The only variables that are not significantly different in the two size groups are canine size and diastema length. As indicated above, both canine size and diastema length are highly variable in brontotheres. Furthermore, because canine size is probably sexually dimorphic, it may have a bi-modal distribution. It would not be surprising, therefore, if *t*-test results for these measurements could not establish significant differences between the groups, since *t*-tests are sensitive to outlying data points and non-normal distributions.

Thus, two size categories appear to exist in the data and it must be determined whether they represent two distinct taxa or are two groups within a single species (such as males and females). Tables 10 and 11 present the summary statistics for each of the two size groups suggested by the cluster analysis in Figure 13, and it will be noted from these tables that the average value of V for each group is more typical of extant mammalian species than the average value when the two groups were combined (Table 7). Once again, the individual values of V for the canine measurements are rather high and this has some influence on the average value of V for both groups. If canine dimensions are eliminated from the calculation of the average, however, the average value of V in both groups remains quite acceptable. In the smaller-size group (Table 10) the average value of V would become 5.8 and in the larger-size group (Table 11) it would become 4.8.

Although the average value of V for both groups is within the acceptable range of extant mammalian species, a relatively large fraction (one fifth to one seventh) of the individual values of V (rounded to the nearest whole number) fall below 4. These low values are of consequence because the sample sizes are probably large enough to show most of the variation that is actually present. Thus, while the range and average value of V in the combined sample suggests that more than a single taxon may be present, analysis of V in the two groups within that sample is not conclusive. The average value of V for each group suggests that each might represent a distinct species, but some of the individual values of V tend to support the possibility that the groups represent size categories within a single species.

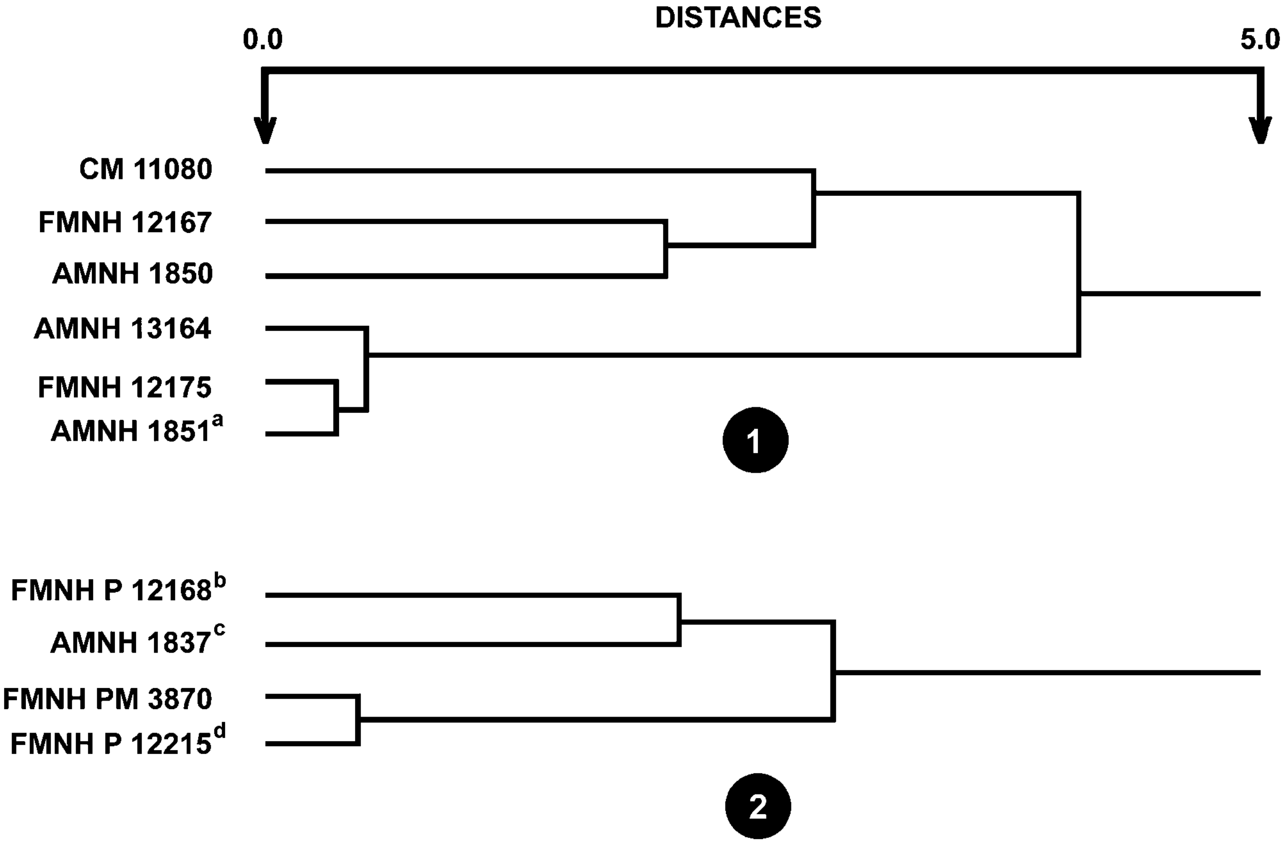

FIGURE 14. Cluster dendrograms for specimens belonging to the **1**, large-size group; and **2**, small-size group of derived *Sphenocoelus* resulting from a cluster analysis of canine size. **a**, type of *Sphenocoelus cornutum*; **b**, type of *S. superior*; **c**, type of *S. intermedius*; **d**, type of *S. fluminalis*.

TABLE 8 F-Test comparisons for the large-size group (Group 1) and small-size group (Group 2) of derived *Sphenocoelus*

	n Group 1	n Group 2	F	Probability	*T*-Test
Basilar Length Skull[a]	6	3	0.332	0.566	Pooled
Length Cheek Tooth Series[a]	8	6	2.039	0.154	Pooled
Length P2 to M3[a]	9	8	6.545	0.011	Separate
Length Premolar Series[a]	7	6	0.969	0.326	Pooled
Length Molar Series[a]	11	7	0.953	0.329	Pooled
Length Diastema[a]	5	5	0.720	0.397	Pooled
Length Left M3	8	7	0.308	0.579	Pooled
Length Right M3	12	4	0.554	0.458	Pooled
Width Left M3	9	7	0.645	0.422	Pooled
Width Right M3	10	6	6.066	0.014	Separate
Length Left M2	8	8	0.751	0.387	Pooled
Length Right M2	10	4	0.756	0.386	Pooled
Width Left M2	9	8	0.128	0.721	Pooled
Width Right M2	10	5	3.226	0.073	Pooled
Length Left M1	9	6	0.412	0.521	Pooled
Length Right M1	11	5	1.220	0.270	Pooled
Width Left M1	8	5	0.850	0.357	Pooled
Width Right M1	10	5	1.081	0.299	Pooled
Length Left P4	7	4	0.002	0.962	Pooled
Length Right P4	7	7	0.401	0.527	Pooled
Width Left P4	9	5	0.006	0.939	Pooled
Width Right P4	10	6	0.700	0.403	Pooled
Length Left P3	10	6	0.546	0.461	Pooled
Length Right P3	8	7	0.024	0.876	Pooled
Width Left P3	8	7	0.009	0.923	Pooled
Width Right P3	7	6	0.916	0.339	Pooled
Length Left P2	8	8	1.474	0.225	Pooled
Length Right P2	7	6	0.001	0.971	Pooled
Width Left P2	8	8	9.175	0.003	Separate
Width Right P2	7	3	0.198	0.657	Pooled
Buccal-Lingual Width Left Canine	5	3	0.500	0.482	Pooled
Buccal-Lingual Width Right Canine	5	3	2.007	0.160	Pooled
Mesial-Distal Width Left Canine	4	3	0.057	0.812	Pooled
Mesial-Distal Width Right Canine	6	4	0.392	0.532	Pooled

[a] Based, whenever possible, on an average of left and right measurements.

TABLE 9. *T*-Test comparisons between the large-size group and small-size group of derived *Sphenocoelus.*

	T	DF	Probability
Basilar Length Skull[a]	5.092	7.0	0.001
Length Cheek Tooth Series[a]	9.723	12.0	0.000
Length P2 to M3[a]	10.028b	8.6	0.000
Length Premolar Series[a]	3.639	11.0	0.004
Length Molar Series[a]	9.554	16.0	0.000
Length Diastema[a]	0.017	8.0	0.987
Length Left M3	3.641	13.0	0.003
Length Right M3	4.022	14.0	0.001
Width Left M3	3.454	14.0	0.004
Width Right M3	2.674b	11.5	0.022
Length Left M2	4.584	14.0	0.000
Length Right M2	4.617	12.0	0.001
Width Left M2	4.154	15.0	0.001
Width Right M2	3.440	13.0	0.004
Length Left M1	6.097	13.0	0.000
Length Right M1	6.612	14.0	0.000
Width Left M1	2.533	11.0	0.028
Width Right M1	2.499	13.0	0.027
Length Left P4	6.543	9.0	0.000
Length Right P4	6.595	12.0	0.000
Width Left P4	2.063	12.0	0.061
Width Right P4	2.791	14.0	0.014
Length Left P3	3.056	14.0	0.009
Length Right P3	2.779	13.0	0.016
Width Left P3	3.434	13.0	0.004
Width Right P3	2.226	11.0	0.048
Length Left P2	4.919	14.0	0.000
Length Right P2	3.816	11.0	0.003
Width Left P2	5.587b	14.0	0.000
Width Right P2	4.649	8.0	0.002
Buccal-Lingual Width Left Canine	0.132	6.0	0.899
Buccal-Lingual Width Right Canine	0.329	6.0	0.753
Mesial-Distal Width Left Canine	0.467	5.0	0.660
Mesial-Distal Width Right Canine	1.565	8.0	0.156

[a] Based, whenever possible, on an average of left and right measurements.
[b] Separate *t*-test.

The high values of V for the canine dimensions in both size groups are particularly informative because they suggest that canine size may be dimorphic in each. Although there are relatively few individuals within each group that had measurable canines (a problem with many brontothere specimens), cluster analyses (Fig. 14) support the hypothesis that canine size is bimodal in each of the groups. In both groups the canines form two distinct clusters strongly suggestive of males and females.

In my opinion, the weight of the evidence suggests that there are two species present. This conclusion is suggested by the high values of V for the combined derived *Sphenocoelus* sample and the more typical average value of V that results when the two groups within that sample are analyzed separately. Although some of the individual values of V in the two size groups are rather low, most are within the acceptable range and cluster analysis of canine size demonstrates that there are probably males and females within each group.

The large-size group of derived *Sphenocoelus* includes the holotype of the type species of *Dolichorhinus*, *D. cornutum*. According to Osborn (1929) *Dolichorhinus cornutum* is a junior synonym of *Palaeosyops hyognathus* Osborn. Previously I had not decided whether Osborn's conclusion was correct (Mader 1989) but now agree that both species are synonymous. For a discussion of the reasons for my acceptance of this synonymy, see the Discussion section below for the species *S. hyognathus*.

The types of several species fall into the smaller-size group and, of these, *Sphenocoelus intermedius* (Osborn) has nomenclatural priority. *Sphenocoelus intermedius* and its junior synonyms are discussed in detail in the Discussion section for that species below.

In 1929, Osborn provisionally referred the lectotype lower jaw (AMNH 5098) of *Palaeosyops vallidens* Cope (1872) to the genus "*Dolichorhinus*" and, if he was correct, then the species name *Sphenocoelus vallidens* might have nomenclatural priority over one of the two species of derived *Sphenocoelus* recognized here. In 1989 Mader provisionally referred the same specimen to *Telmatherium*, however, while noting that the stratigraphic occurrence suggests that it might belong to "*Dolichorhinus*" (= *Sphenocoelus* in the present paper).

According to Osborn (1929) the type of *Palaeosyops vallidens* is from "Washakie B" (Uintan-aged deposits in the Washakie Basin), which would suggest that it is a specimen of *Sphenocoelus*. The locality recorded by Cope, however, may allow for a Bridgerian age, which is inconsistent with assignment to *Sphenocoelus*, but is consistent with *Telmatherium* as suggested by Mader. The specimen is described by Cope as being from Mammoth Buttes (= Haystack Mountain, according to Osborn 1929, p. 85) near the headwaters of Bitter Creek. This seems to place the locality on the north side of Haystack Mountain where both Uintan and Bridgerian ("Washakie A") deposits are found (see Osborn 1929, Figs. 60 and 61). Interestingly, a partial skull referred to the Bridgerian genus *Palaeosyops* (AMNH 5105) was also described by Cope (1873) as being from Bitter Creek, but was provisionally identified as being from Washakie B (Uintan) by Osborn (1929, p. 163). It seems plausible, therefore, that the type of *Palaeosyops vallidens* is also from Bridgerian deposits. I continue to regard the specimen as being referable to *Telmatherium*, although, perhaps, the name *Palaeosyops vallidens* should be regarded as a nomen dubium.

Despite the fact that two derived species of *Sphenocoelus* are recognized in the present paper, there does not appear to be any consistent morphological difference between them (at least with regard to cranial anatomy). The suborbital protuberance may lack an anterior flange in some specimens of the small species, *S. intermedius* (e.g., UCMP 31845) but other specimens of this same species have a slight indication of this flange (UCMP 31846). It is quite possible that a study of the lower jaw or postcranial skeleton will reveal some consistent anatomical differences, but until then, size remains the only ready means of identification (see Fig. 15). Skull length, length of the upper cheek tooth series (with or without first upper premolar), and length of the upper molar series are the most effective parameters to use in identification because there is a relatively large size interval between the two species. Length of the premolar series and individual cheek tooth measurements are less useful for diagnostic purposes because there is at least some size overlap between the taxa (indeed, this statistical "noise" may explain why the cluster dendrogram appearing in Figure 12 did not clearly delineate more than one size group). If these less effective measurements must be used, identification will only be possible if the specimen is a small member of the smaller species (*S. intermedius*) or a large member of the larger species (*S. hyognathus*). Canine size and diastema length probably should be avoided in making a diagnosis because these dimensions are highly variable and overlap considerably.

TABLE 10. Summary statistics for the small-size group of derived *Sphenocoelus*. (*Sphenocoelus intermedius*, all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	3	466.0–514.3	484.0	±26.4	5.5
Length Cheek Tooth Series[a]	6	172.5–191.0	179.8	±7.2	4.0
Length P2 to M3[a]	8	154.0–174.5	163.9	±6.6	4.0
Length Premolar Series[a]	6	69.5–82.8	75.3	±4.9	6.5
Length Molar Series[a]	7	100.5–112.3	106.0	±4.6	4.3
Length Diastema[a]	5	9.5–23.0	16.4	±5.1	31.1
Length Left M3	7	35.0–41.5	38.1	±2.3	6.0
Length Right M3	4	36.5–42.0	38.9	±2.5	6.4
Width Left M3	7	31.5–38.5	36.2	±2.3	6.4
Width Right M3	6	35.8–38.5	36.8	±1.1	3.0
Length Left M2	8	33.5–41.5	37.3	±3.0	8.0
Length Right M2	4	34.0–40.0	37.6	±2.8	7.5
Width Left M2	8	32.2–39.9	36.1	±2.2	6.1
Width Right M2	5	35.8–38.2	37.2	±0.9	2.4
Length Left M1	6	28.0–33.0	30.7	±1.9	6.2
Length Right M1	5	27.0–32.5	30.4	±2.2	7.2
Width Left M1	5	28.2–32.0	30.3	±1.4	4.6
Width Right M1	5	29.5–32.0	31.1	±1.0	3.2
Length Left P4	4	20.5–22.0	21.4	±0.6	2.8
Length Right P4	7	20.0–22.0	21.0	±0.7	3.3
Width Left P4	5	25.1–28.1	26.4	±1.4	5.3
Width Right P4	6	21.7–28.8	25.5	±2.3	9.0
Length Left P3	6	16.0–21.5	19.2	±2.1	10.9
Length Right P3	7	17.0–21.5	19.5	±1.5	7.7
Width Left P3	7	19.5–23.0	21.3	±1.1	5.2
Width Right P3	6	19.3–24.0	21.2	±1.8	8.5
Length Left P2	8	15.5–18.0	16.8	±0.9	5.4
Length Right P2	6	15.0–18.0	17.1	±1.1	6.4
Width Left P2	8	14.7–18.1	16.4	±1.1	6.7
Width Right P2	3	16.0–17.6	16.6	±0.9	5.4
Buccal-Lingual Width Left Canine	3	15.0–18.8	17.5	±2.1	12.0
Buccal-Lingual Width Right Canine	3	15.7–18.0	17.0	±1.2	7.1
Mesial-Distal Width Left Canine	3	17.0–20.7	19.2	±2.0	10.4
Mesial-Distal Width Right Canine	4	16.0–20.5	18.6	±2.1	11.3
AVERAGE V					6.3[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Excluding Diastema Length.

TABLE 11. Summary statistics for the large-size group of derived *Sphenocoelus*. (*Sphenocoelus hyognathus*, all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	6	541.3–582.0	559.7	±18.5	3.3
Length Cheek Tooth Series[a]	8	203.0–216.0	208.7	±3.9	1.9
Length P2 to M3[a]	9	184.0–192.0	188.7	±2.4	1.3
Length Premolar Series[a]	7	77.8–87.0	83.6	±3.2	3.8
Length Molar Series[a]	11	118.8–131.0	123.3	±3.2	2.6
Length Diastema[a]	5	13.3–21.7	16.4	±3.2	19.5
Length Left M3	8	39.5–48.0	43.0	±2.8	6.5
Length Right M3	12	40.5–46.5	43.5	±1.8	4.1
Width Left M3	9	34.4–44.0	41.2	±3.2	7.8
Width Right M3	10	32.6–43.8	40.0	±3.5	8.8
Length Left M2	8	41.0–48.0	43.3	±2.1	4.9
Length Right M2	10	42.0–48.0	43.4	±1.8	4.2
Width Left M2	9	37.4–44.7	40.9	±2.5	6.1
Width Right M2	10	36.1–43.5	40.8	±2.2	5.4
Length Left M1	9	34.0–39.0	36.1	±1.5	4.2
Length Right M1	11	34.0–38.5	36.2	±1.4	3.9
Width Left M1	8	29.6–36.6	33.2	±2.2	6.6
Width Right M1	10	30.1–36.0	33.1	±1.6	4.8
Length Left P4	7	23.0–25.0	24.0	±0.7	2.9
Length Right P4	7	22.0–24.5	23.6	±0.9	3.8
Width Left P4	9	25.3–29.9	28.0	±1.4	5.0
Width Right P4	10	24.8–30.0	28.3	±1.6	5.7
Length Left P3	10	19.5–25.0	22.0	±1.6	7.3
Length Right P3	8	19.5–24.0	21.6	±1.4	6.5
Width Left P3	8	21.6–24.5	23.3	±1.1	4.7
Width Right P3	7	21.4–24.4	23.1	±1.2	5.2
Length Left P2	8	17.5–22.0	19.7	±1.4	7.1
Length Right P2	7	18.0–21.0	19.4	±1.1	5.7
Width Left P2	8	18.2–19.1	18.7	±0.3	1.6
Width Right P2	7	17.8–20.0	18.9	±0.7	3.7
Buccal-Lingual Width Left Canine	5	15.0–22.9	17.8	±3.6	20.2
Buccal-Lingual Width Right Canine	5	15.0–23.0	17.8	±3.7	20.8
Mesial-Distal Width Left Canine	4	18.3–23.5	20.0	±2.4	12.0
Mesial-Distal Width Right Canine	6	18.7–25.9	21.3	±3.0	14.1
AVERAGE V					6.3[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Excluding Diastema Length.

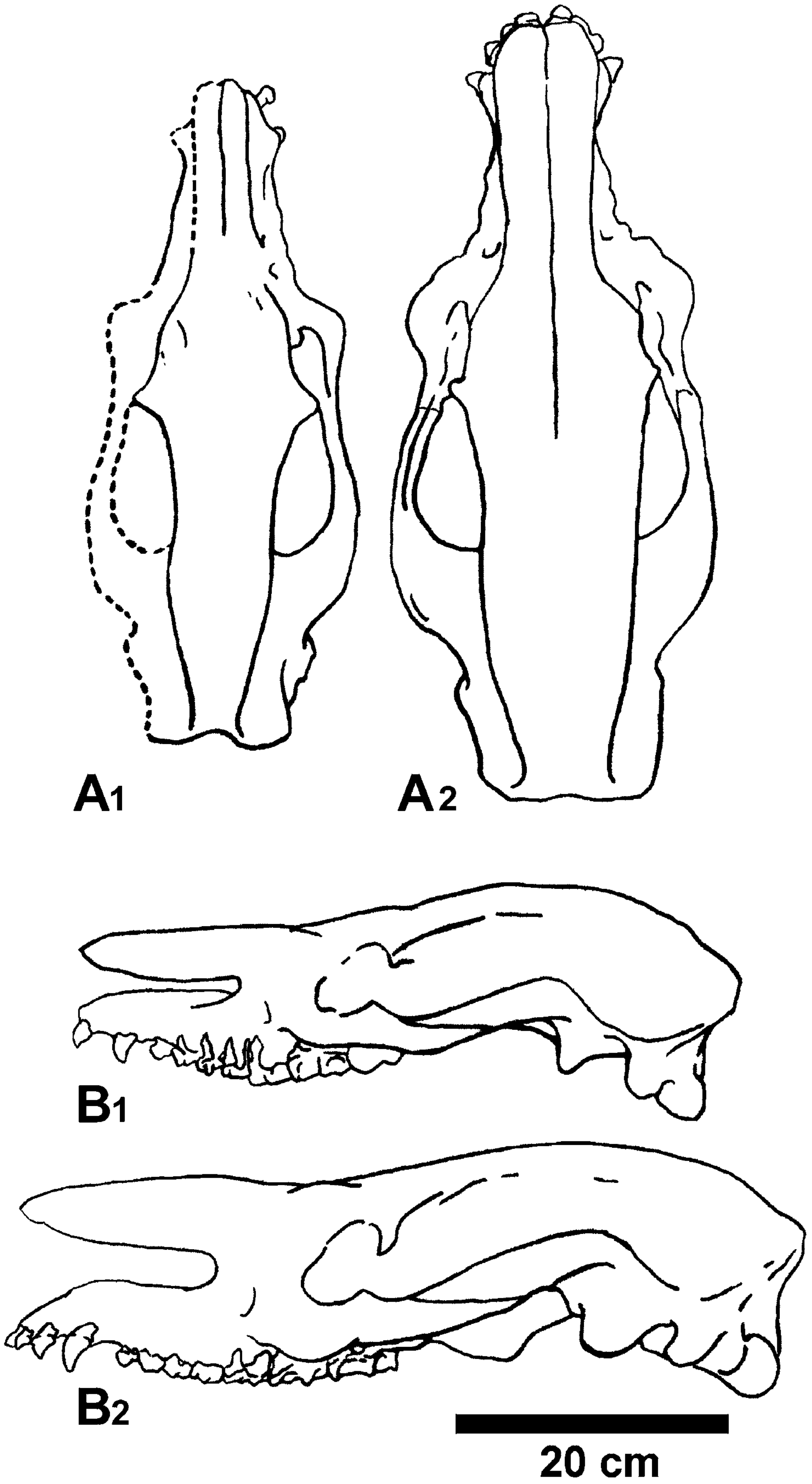

FIGURE 15. Skulls of *Sphenocoelus intermedius* and *Sphenocoelus hyognathus* in **A**, dorsal; and **B**, lateral views. **A1**, **B1**, *Sphenocoelus intermedius*; **A2**, **B2**, *Sphenocoelus hyognathus*. All illustrations after Osborn, 1929.

Although the stratigraphic data is limited for the specimens examined in this study, it appears that *Sphenocoelus intermedius* and *Sphenocoelus hyognathus* were contemporaneous. Both occur in the parts of the Wagonhound Member of the Uinta Formation designated as Uinta B1 and Uinta B2 by Osborn (1929). It is possible that further investigation may reveal that the two species occupy slightly different geologic or faunal settings within the Uinta and Washakie Formations, but this will probably require the discovery of new specimens with highly detailed field data.

Since both *Sphenocoelus intermedius* and *S. hyognathus* share the derived (widened) morphology of the cranial vertex (while *S. uintensis* does not), *S. intermedius* and *S. hyognathus* can be regarded as immediate sister species. Since *S. intermedius* and *S. hyognathus* were the species originally incorporated under the name "*Dolichorhinus*," it is possible to regard *Dolichorhinus* as a valid subgenus of *Sphenocoelus*.

Species *SPHENOCOELUS uintensis* Osborn 1895

= *S. blairi* (Cook 1926)
= *S. bridgeri* (Cook 1926)
= *S. harundivorax* (Cook 1926)

Holotype. AMNH 1501, the posterior part of a skull.

Referred specimens. DMNH 479, DMNH 484, DMNH 541, DMNH 507, DMNH 8000, and UCMP 81301.

Diagnosis. Plesiomorphic species of *Sphenocoelus* of moderately large to large size (length P1 to M3 approximately 190–214 mm, length P2 to M3 approximately 172–199 mm, length M1 to M3 approximately 114–128 mm, based on DMNH 507 and DMNH 541) with a prominent sagittal crest (plesiomorphic character state) and very large occipital condyles (presumably a derived condition). The horn and the anterior flange of the suborbital protuberance may be absent or weakly developed in specimens of this species.

Discussion. The massive size of the occipital condyles appears to be a synapomorphy diagnostic of this species, although the occipital condyles of the more derived species, *S. angustidens*, are unknown. The occipital condyles of *S. intermedius* and *S. hyognathus* are proportionately smaller and appear to be similar to those of other brontotheres and outgroup perissodactyls such as *Hyrachyus*.

Skulls referred by Cook to *Tanyorhinus* are more plesiomorphic than those that have been assigned to *Dolichorhinus* or *Dolichorhinoides* in that there is a narrow sagittal crest similar to that of other early brontotheres (e.g., *Palaeosyops*, *Mesatirhinus*, and *Metarhinus*) and outgroup perissodactyls. In specimens referred to both *Dolichorhinus* and *Dolichorhinoides* the cranial vertex is widened, a derived condition paralleling the widened cranial vertex seen in the brontotheriine brontotheres (see Mader 1998). Skulls of *Tanyorhinus* compare very closely, however, with the partial type skull of *Sphenocoelus uintensis*, which is hyperdolichocephalic and has a narrow sagittal crest, and a skull (UCMP 81301) insightfully identified as *S. uintensis* by Bruce Hanson in the UCMP catalog.

Among these plesiomorphic specimens of *Sphenocoelus*, four species have been recognized: *S. uintensis* (the type species), *S. blairi*, *S. bridgeri*, and *S. harundivorax*. The last three were the three species originally assigned to the genus *Tanyorhinus* by Cook (1926).

Cook did not specify which of the three species that he recognized was the type species for *Tanyorhinus* and the type species was never formally fixed by any subsequent systematic reviser. The catalog of the Denver Museum of Natural History (the institution where Cook's specimens are housed) identifies the type of *T. blairi* (the first species mentioned in Cook's publication) as the holotype of the type species, but this cannot be recognized as an official determination. In their published catalog of type specimens in the Denver Museum, however, Woods and Stucky (1992) cite *T. blairi* as the type species of *Tanyorhinus* Cook and, by doing so, have effectively fixed it as such under Article 69 of the International Code of Zoological Nomenclature (Ride *et al*. 1999).

West and Dawson (1975) argued that the three species of *Tanyorhinus* that Cook had recognized are biologically unnecessary because the differences that Cook cited between them could be attributed to sexual dimorphism and ontogenetic age. I concur with West and Dawson that only one species is probably represented, but note that the type of *T. harundivorax* (DMNH 552) is a partial lower jaw and is, thus, not directly comparable with at least one of the other *Tanyorhinus* types. *Tanyorhinus bridgeri* was based on a skull only (DMNH 479), while *Tanyorhinus blairi* was based on a skull (DMNH 541) and jaw (DMNH 542). The skull and jaw were not found in articulation, however, but rather a few feet apart and were only assumed to represent the same individual (Cook 1926).

Species *SPHENOCOELUS intermedius* (Osborn 1908)

= *S. heterodon* (Douglass 1909)
= *S. fluminalis* (Riggs 1912)
= *S. superior* (Riggs 1912)

Holotype. AMNH 1837, a skull and associated postcranials.

Referred specimens. CM 2340 (holotype of *S. heterodon*), FMNH P 12168 (holotype of *S. superior*), FMNH P 12193, FMNH P 12200, FMNH P 12205 (holotype of *S. fluminalis*), FMNH PM 3870, LACM 128402, UCMP 31845, UCMP 31846, YPM-PU 11241.

Diagnosis. Derived species of *Sphenocoelus*, similar to *S. hyognathus*, but 10% to 15% smaller in size (length P1 to M3 approximately 173–191 mm, length P2 to M3 approximately 154–175 mm, length M1 to M3 approximately 101–112 mm). The anterior flange on the suborbital protuberance is usually small or absent in this species.

Discussion. In 1908 Osborn briefly described the type skull (AMNH 1837) of a small *Sphenocoelus* from the Uinta Basin of Utah, which he identified as a new species of *Dolichorhinus*, *D. intermedius*. Osborn distinguished "*Dolichorhinus*" *intermedius* from "*Dolichorhinus*" *hyognathus*, by its smaller size, less progressive premolars with subconic deuterocones (= protocones), less robust cingula, more pointed and less distally expanded nasals, and narrower infraorbital shelf. In 1929, Osborn speculated that "*Dolichorhinus*" *intermedius* was a dwarfed side branch of "*Dolichorhinus*" not directly related to "*Dolichorhinus*" *hyognathus*.

In 1909 Earl Douglass named two new species of "*Dolichorhinus*," "*D.*" *heterodon* (= *Sphenocoelus intermedius* in the present paper) and "*D.*" *longiceps* (= *S. hyognathus*, see discussion for *S. hyognathus*, below). Douglass described the holotype skull of "*Dolichorhinus*" *heterodon* (CM 2340) in some detail, but he did not compare it to either "*Dolichorhinus*" *hyognathus* or "*Dolichorhinus*" *intermedius*. Osborn (1929, p. 416), however, who accepted "*Dolichorhinus*" *heterodon* as a valid species, distinguished it from "*D.*" *hyognathus* by its smaller size and from "*D.*" *intermedius* by its heavier cingula, well developed mesostyle on P4, and prominent parastyle on P3 and P4. Osborn stated that "*D.*" *heterodon* might be a more progressive successor of "*D.*" *intermedius*, but elsewhere (1929, p. 188) expressed doubt that it could be separated taxonomically from "*D.*" *intermedius*.

My own impression is that the upper dentition of the holotype of "*Dolichorhinus*" *heterodon* falls within the morphological continuum of dentitions here referred to *Sphenocoelus intermedius*. Although the presence of a mesostyle on P4 is somewhat uncommon, this and other unusual premolar morphologies are occasionally found in brontothere genera. The holotype of "*Dolichorhinus*" *fluminalis* (FMNH P 12205, discussed below) also appears to have a mesostyle on P4 (observation based on a cast of the type) as does CM 11081, a specimen of *Sphenocoelus hyognathus*. The presence of a mesostyle on P4 is probably not a good diagnostic character for any brontothere species and appears to be an anomaly restricted to certain exceptional individuals.

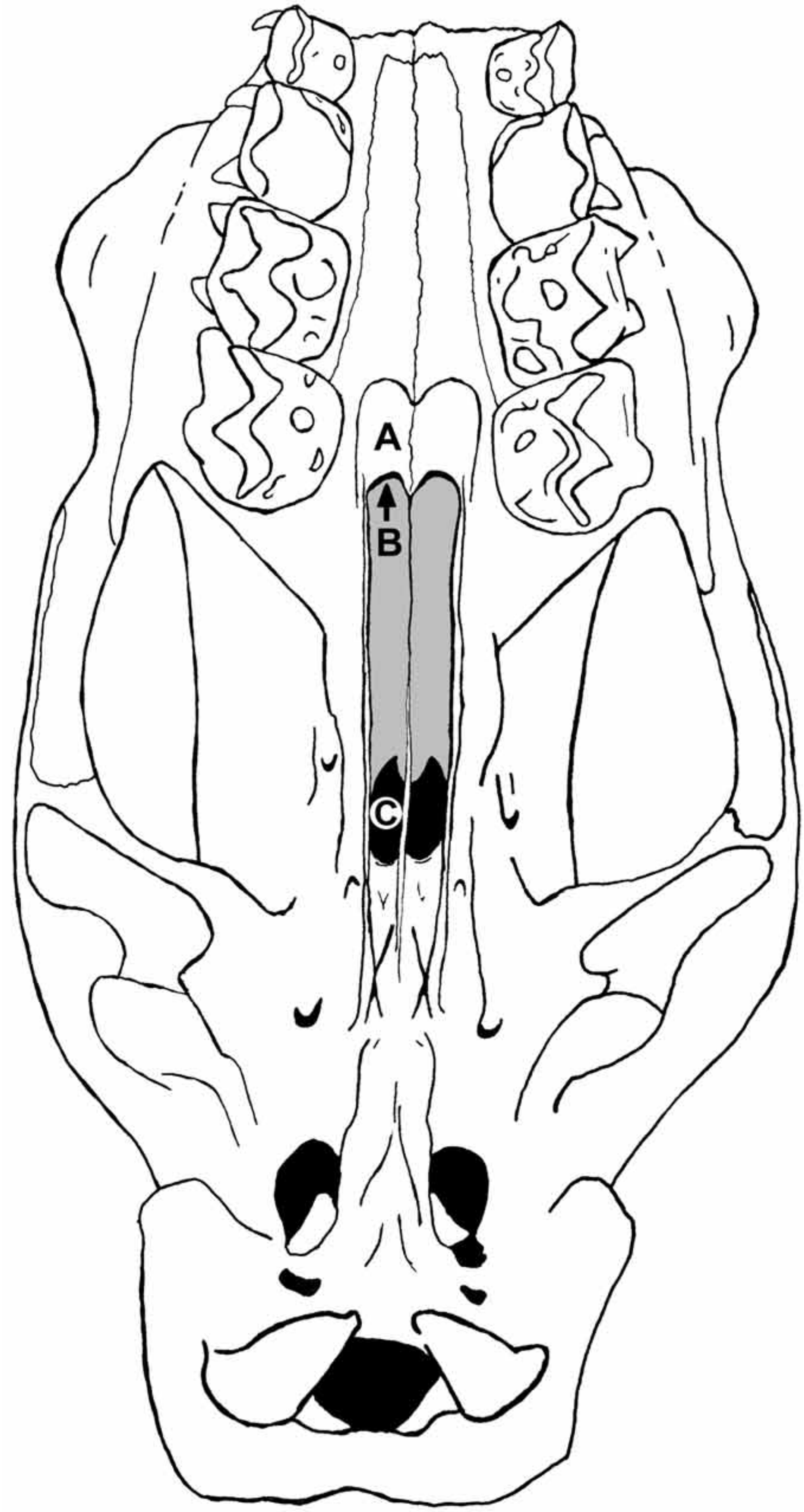

FIGURE 16. Skull of *Sphenocoelus hyognathus* in ventral view illustrating the anatomy of the palatine and pterygoid regions. **A**, depression in palate marking probable original location of internal nares; **B**, actual location of internal nares (which are apparently closed off); **C**, apertures in pterygoid region at the termination of the nasal passage (functional internal nares). Choanal pouches shaded gray. Illustration based on AMNH 1851 (after Osborn, 1929) and AMNH 13164.

In 1912 Elmer Riggs described several new brontothere taxa based on specimens collected from the Uinta Basin by the Field Museum expedition of 1910. Among the materials that Riggs described was the type of a new species of "*Dolichorhinus*," "*D.*" *fluminalis*. According to Riggs the primary diagnostic character of "*D.*" *fluminalis* was that the internal nares were located further posteriorly (between the hamular processes) than in any other species. Otherwise Riggs regarded "*D.*" *fluminalis* as being rather closely related to "*D.*" *intermedius*, except that the skull of "*D.*" *fluminalis* was longer and the molars much smaller. Riggs also noted that the skull of "*D.*" *fluminalis* was more gracile than that of "*D.*" *cornutum* and that the postorbital process of the jugal (incorrectly described as the "jugal process of the maxillaries" on page 34) was located posterior to the last molar rather than adjacent to it as in *D. longiceps*.

Peterson (1924) provisionally accepted "*Dolichorhinus*" *fluminalis* as valid, but argued that the internal nares are located very far back in all specimens of "*Dolichorhinus*." As Peterson noted, the true position of the internal nares was seldom observed by his contemporaries because of the inherent frailty of this region of the skull. The anatomy of the palatine and pterygoid regions of *Sphenocoelus* is rather unusual and a description of it is warranted here to help clarify Peterson's observations on the narial morphology.

Figure 16 illustrates the palatine and pterygoid region in a well-preserved specimen of *Sphenocoelus* (in this case *S. hyognathus*, discussed below, based mostly on AMNH 13164). It will be noted from this illustration that adjacent to M3 there is a depression in the palate (marked "A") that may represent the plesiomorphic position of the internal nares (Peterson 1924). Osborn, (1929, p. 411 and fig. 347) described this depression as a secondary palatal plate formed by a backward and upward extension of the dorsal surface of the palatine. Behind the depression is an orifice (marked "B") that represents the actual position of the internal nares, although these were evidently sealed off and non-functional. Extending posteriorly from this orifice to the basicranial region is an extension of the nasal septum that forms a thin flange of bone that projects ventrally between the pterygoids. This posterior narial flange (vomerine plate of Peterson 1924) is a common feature of brontothere skulls and has been identified in the majority of genera (Mader 1998).

In well-preserved skulls of *Sphenocoelus*, thin-walled, bony pouches (shaded gray on the diagram) surround the vomerine plate on either side. Peterson described these pouch-like structures but, in the text of his paper, did not identify the bones from which they are formed. In his figure captions for plate XLV, fig. 3 (illustrating CM 11080) and plate XLVI, fig. 2 (illustrating CM 11081), however, he identified these pouches as the choanae, an identification that seems plausible. Posterior to the choanal pouches and near the termination of the vomerine plate at the basicranium are two large apertures (marked "C" on the diagram) that appear to have been the functional internal nares.

The palatine and pterygoid region of the holotype of "*Dolichorhinus*" *fluminalis* thus do not appear to be anatomically different from that of other specimens of *Sphenocoelus* (such as AMNH 1845 and AMNH 13164, both specimens of the large derived *Sphenocoelus* species, *S. hyognathus*). Peterson was correct, therefore, in not accepting the position of the internal nares in *S. fluminalis* as a diagnostic character of the species.

The location of the postorbital process of the jugal posterior to the third molar is also not an appropriate diagnostic character for *Sphenocoelus fluminalis* because the position of the process in the holotype skull has been altered by taphonomic deformation. In the holotype the dorsal surface of the skull is shifted posteriorly while the ventral surface is shifted anteriorly. Thus, the lambdoidal crest is sharply angled backward and the nasals are retracted from their normal position over the premaxillary region. As a result of this deformation the postorbital process has been shifted backward so that it lies behind the third molar rather than adjacent to it.

It should be noted that the basilar length of the skull in the type of *Sphenocoelus fluminalis* is rather large (about 515 mm), and is only about 5% shorter than the smallest skull belonging to the larger derived *Sphenocoelus* size group (FMNH P 12175, approximately 541 mm). It is possible, therefore, that *S. fluminalis* might be a junior synonym of *S. hyognathus* rather than *S. intermedius*. Dental measurements for the type of *S. fluminalis*, however, all fall clearly within the size range of *S. intermedius*.

In addition to the holotype of "*Dolichorhinus*" *fluminalis*, Riggs (1912) also described a skull (FMNH P 12168) that he identified as a new species of *Mesatirhinus*, *M. superior.* Peterson (1924) and Osborn (1929), however, correctly recognized that this skull is actually a specimen of the hyperdolichocephalic brontothere here called *Sphenocoelus*. Peterson (1924) discussed the taxon in his review of species of "*Dolichorhinus*," but did not state whether he accepted its validity. Osborn (1929) regarded "*Dolichorhinus*" *superior* as being transitional between *Mesatirhinus* and "*Dolichorhinus*," but provisionally accepted it as a valid species of "*Dolichorhinus*." Osborn (1929, p. 405) listed a number of diagnostic characters for "*Dolichorhinus*" *superior* (quoted verbatim from Riggs 1912) that presumably distinguish it from all other species of "*Dolichorhinus*," but only one of the characters (that the internal nares open opposite the anterior margin of the third upper molar) is unique. Each of the other characters cited by Osborn could be applied to almost any small specimen of derived *Sphenocoelus*.

Although the position of the internal nares would at first seem to be a valid diagnostic character, Peterson (1924) noted that the type skull is poorly preserved in this region. I agree with Peterson that, in the skull's original state, the morphology of the palate and internal nares was probably quite similar to that of other specimens of *Sphenocoelus*. In the holotype of *Sphenocoelus superior*, the typical "secondary palatal plate" formed by the backward and upward extension of the palatines has been destroyed, causing the internal nares to appear to be further forward than they actually were.

Species *SPHENOCOELUS hyoganthus* (Osborn 1890)

= *S. cornutum* (Osborn 1895, the type species of *Dolichorhinus*)
= *S. longiceps* (Douglass 1909)

Holotype. YPM-PU 10273, partial lower jaw.

Referred specimens. AMNH 1845, AMNH 1850, AMNH 1851 (holotype of *S. cornutum*), AMNH 1852, AMNH 13164, CM 2347 (holotype of *S. longiceps*), CM 11080, FMNH P 12167, FMNH P 12175, FMNH P 12182, FMNH PM 3873, MCZ 17678, UFH V-190.

Diagnosis. Derived species of *Sphenocoelus* similar to *S. intermedius* but 10% to 15% larger in size (length P1 to M3 approximately 203–216 mm, length P2 to M3 approximately 184–192 mm, length M1 to M3 approximately 119–131 mm).

Discussion. In 1890, Osborn described an extremely elongated lower jaw (YPM-PU 10273), which he provisionally referred to the genus *Palaeosyops* and named *P. hyognathus*. In 1929, Osborn recognized that this was actually the lower jaw of "*Dolichorhinus*" (i.e., *Sphenocoelus*) and argued that it represented the same species as "*Dolichorhinus*" *cornutum*, the type species of *Dolichorhinus*. Thus, according to Osborn, the type species of *Dolichorhinus*, *D. cornutum*, would be invalid because it is a junior synonym of *D. hyognathus*.

Although I was previously unsure whether Osborn was correct (Mader 1989), I now agree that both species are synonymous. The holotype jaw of *Sphenocoelus hyognathus* is imperfectly preserved but the dimensions that can be ascertained indicate that it belongs to the large-size group of derived *Sphenocoelus*, which includes the type skull of *S. cornutum*. In *Sphenocoelus* the length of p2 to m3 on the lower jaw should slightly exceed the length of the upper check tooth series. The length of p2 to m3 in the type jaw of *S. hyognathus* is approximately 213 mm, which is much longer than the cheek tooth series in all specimens of *S. intermedius* but is within the size range of specimens belonging to the large-size group. Furthermore, the length of the type jaw of *S. hyognathus* from the mental symphysis to the back of the angle of the jaw is approximately 490 mm, which is longer than the entire basilar length of the skull in some specimens of *S. intermedius*. Even the longest skull of *S. intermedius* for which I have data is only 24 mm longer than the type jaw of *S. hyognathus*, which is much too short for the skull and jaw to articulate. Skulls belonging to the large-size group of *Sphenocoelus*, however, are generally of a sufficient length to have articulated with the jaws.

Thus, the dimensions of the type lower jaw of *S. hyognathus* would seem to preclude the possibility that it represents the small species, *S. intermedius*. Although there is a slight possibility that the jaw could represent *S. uintensis* (based on size), the rarity of this species in the Uinta Formation and the chronologically equivalent strata in the Washakie Formation, makes this seem highly improbable.

As explained in the Discussion section for *Sphenocoelus intermedius*, Earl Douglass described the holotype skull of *"Dolichorhinus*" *longiceps* in 1909 along with the holotype skull of "*Dolichorhinus*" *heterodon* (= *S. intermedius*). According to Douglass, the skull and teeth of "*Dolichorhinus*" *longiceps* are larger than those of "*Dolichorhinus*" *heterodon*, but morphologically the teeth of the two species are indistinguishable. Douglass (1909) distinguished "*Dolichorhinus*" *longiceps* from "*Dolichorhinus*" *hyognathus* by its broader skull, morphologically different suborbital process (= suborbital protuberance), more gracile postglenoid process, broader palate, and more narrowed cranium anterior to the crest of the occiput. Douglass did not compare "*Dolichorhinus*" *longiceps* to "*Dolichorhinus*" *intermedius*, the only other species of "*Dolichorhinus*" named up to that time.

Peterson (1924), however, expressed reservations about each of the characters that Douglass had used to establish "*Dolichorhinus*" *longiceps*. According to Peterson the wideness of both the skull and palate in the holotype of "*Dolichorhinus*" *longiceps* is probably the result of crushing and is not indicative of the original cranial proportions. Peterson also noted that the postglenoid process of the type is imperfectly preserved so that its shape cannot be accurately compared to that of "*Dolichorhinus*" *cornutum*. Peterson believed that the other characters listed by Douglass could be attributed to individual variation (including sexual dimorphism) within a single species ("*Dolichorhinus*" *cornutum*) and need not imply a distinct taxon. In a footnote on page 408 of his 1924 paper Peterson stated that "*Dolichorhinus*" *longiceps* Douglass might be a female of "*Dolichorhinus*" *cornutum* Osborn. Nevertheless, Peterson provisionally recognized "*Dolichorhinus*" *longiceps* as valid, noting the low stratigraphic horizon (the lower part of Uinta horizon B) and the fact that no other "*Dolichorhinus*" skull with "large osseous knobs on the nasals" had been previously recorded from these lower beds.

In 1929, Osborn also recognized "*Dolichorhinus*" *longiceps* as valid and suggested that it was directly ancestral to "*Dolichorhinus*" *hyognathus* (p. 405). Osborn did, however, express some doubt concerning the species' validity. Although Osborn clearly stated (p. 406) that Douglass' (1909) recognition of "*Dolichorhinus*" *longiceps* as a distinct species was "fully confirmed" by additional specimens collected by Riggs, elsewhere (p. 189) he remarked that the status of "*Dolichorhinus*" *longiceps* as a distinct species is "somewhat doubtful." Osborn's ambivalence concerning this taxon is further suggested by his mention (1929, pp. 406–407) of a specimen (AMNH 1852) that "appears to bridge over" the size differences between "*Dolichorhinus*" *longiceps* and "*Dolichorhinus*" *cornutum* (which Osborn synonymized with "*Dolichorhinus*" *hyognathus*).

The holotype skull of "*Dolichorhinus*" *longiceps* is rather poorly preserved, but clearly belongs to the larger-sized derived *Sphenocoelus* group (i.e., *S. hyognathus*) based on its dorsal dimensions. The basilar length of the skull, as well as most of the dentition, was too poorly preserved to measure. I was only able to obtain precise measurements for the length of the left premolar series, length of left M1, length of left P4, and the length and width of left P3. The relatively few measurements that are available for comparison between specimens probably explains why the type of *"D." longiceps* tends to group with specimens of *S. intermedius* in some cluster analyses (e.g., in Fig. 1, the type of "*D.*" *longiceps* groups very near to the type of *"D." heterodon*), since individual tooth measurements can overlap between *S. intermedius* and *S. hyognathus*.

Subfamily BRONTOTHERIINAE Marsh 1873

(Includes Telmatheriinae Osborn 1914; Manteoceratinae Osborn 1914; Diplacodontinae Osborn 1914; Brontopinae Osborn 1914; and Megaceropinae Osborn 1914)
(= Telmatheriinae, sensu Mader 1989)

Diagnosis. Brontotheres distinguished from all others by the presence of a widened cranial vertex, long, triangular projection of the frontal overlapping the nasal, and a bony prominence or horn over the facial concavity.

Discussion. Mader (1989) selected Telmatheriinae (Osborn 1914) as the most logical name for this subfamily because *Telmatherium* is this group's most primitive member. In 1995, however, Mader and Alexander pointed out that the valid subfamily name is Brontotheriinae Marsh (1873) based on the Principle of Coordination (Article 36, International Code of Zoological Nomenclature, Ride *et al*. 1999).

As noted in the diagnosis, above, brontotheriine brontotheres are distinguished from all others by the presence of a widened cranial vertex. Figure 17 illustrates the cranial vertex of the brontothere genera *Palaeosyops*, *Mesatirhinus*, and *Telmatherium*. *Palaeosyops* and *Mesatirhinus* exhibit the plesiomorphic cranial vertex morphology in which there is a well developed sagittal crest. In *Telmatherium*, however, the cranial vertex adjacent to the temporal fossa is widened and the sagittal crest is lost in this region. Further posteriorly, however, the sagittal crest is still present but is relatively wide compared to that of non-brontotheriine brontotheres. The sagittal crest of most brontothere genera has a distinct median cleft but, in *Telmatherium*, instead of a median cleft there is a deep pit-like fossa. *Telmatherium* is the most plesiomorphic brontotheriine genus and in all other brontotheriine genera the cranial vertex is greatly widened and the sagittal crest is completely lost.

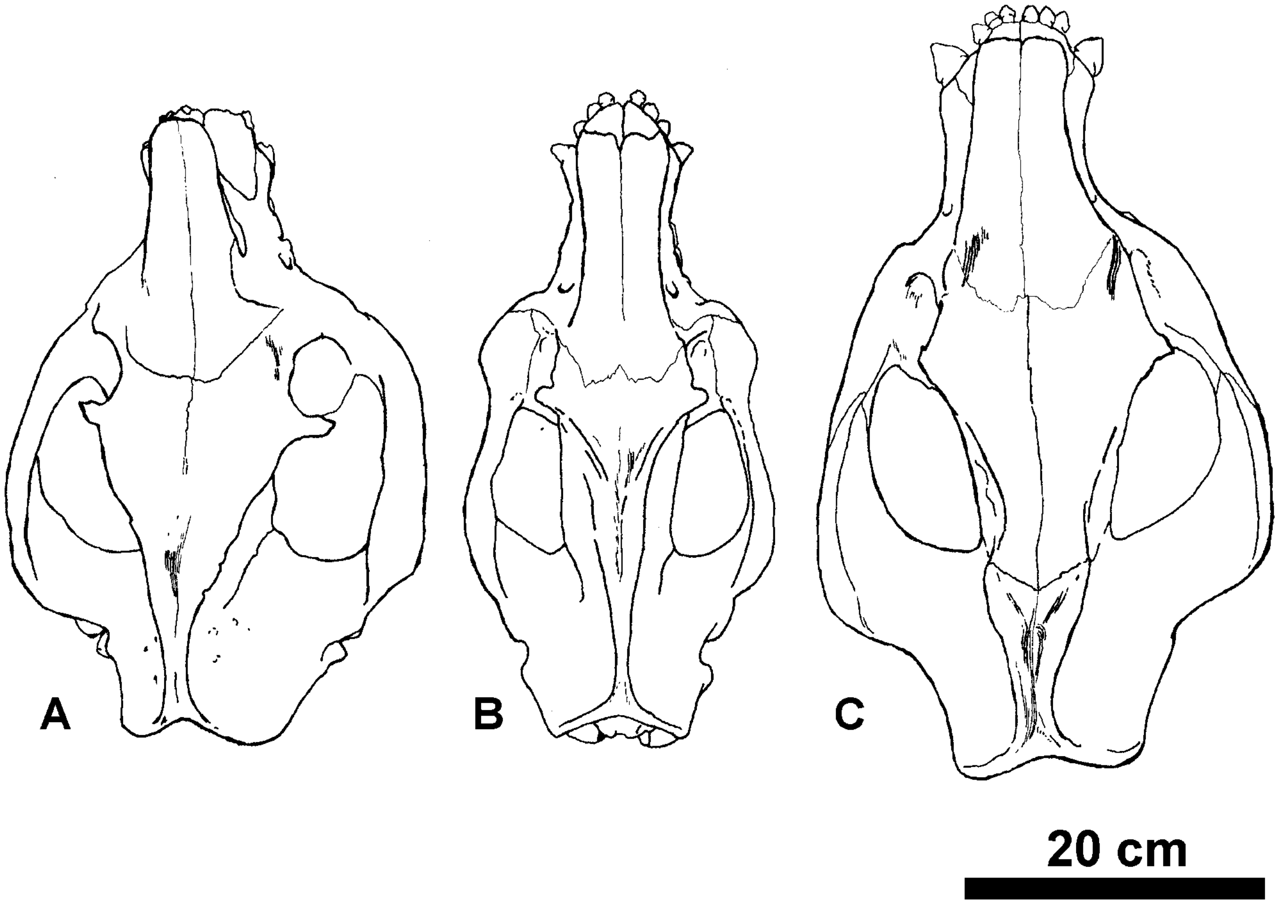

FIGURE 17. Skulls of three brontotheres in dorsal view showing the width of the cranial vertex. **A**, *Palaeosyops*; **B**, *Mesatirhinus*; **C**, *Telmatherium*.

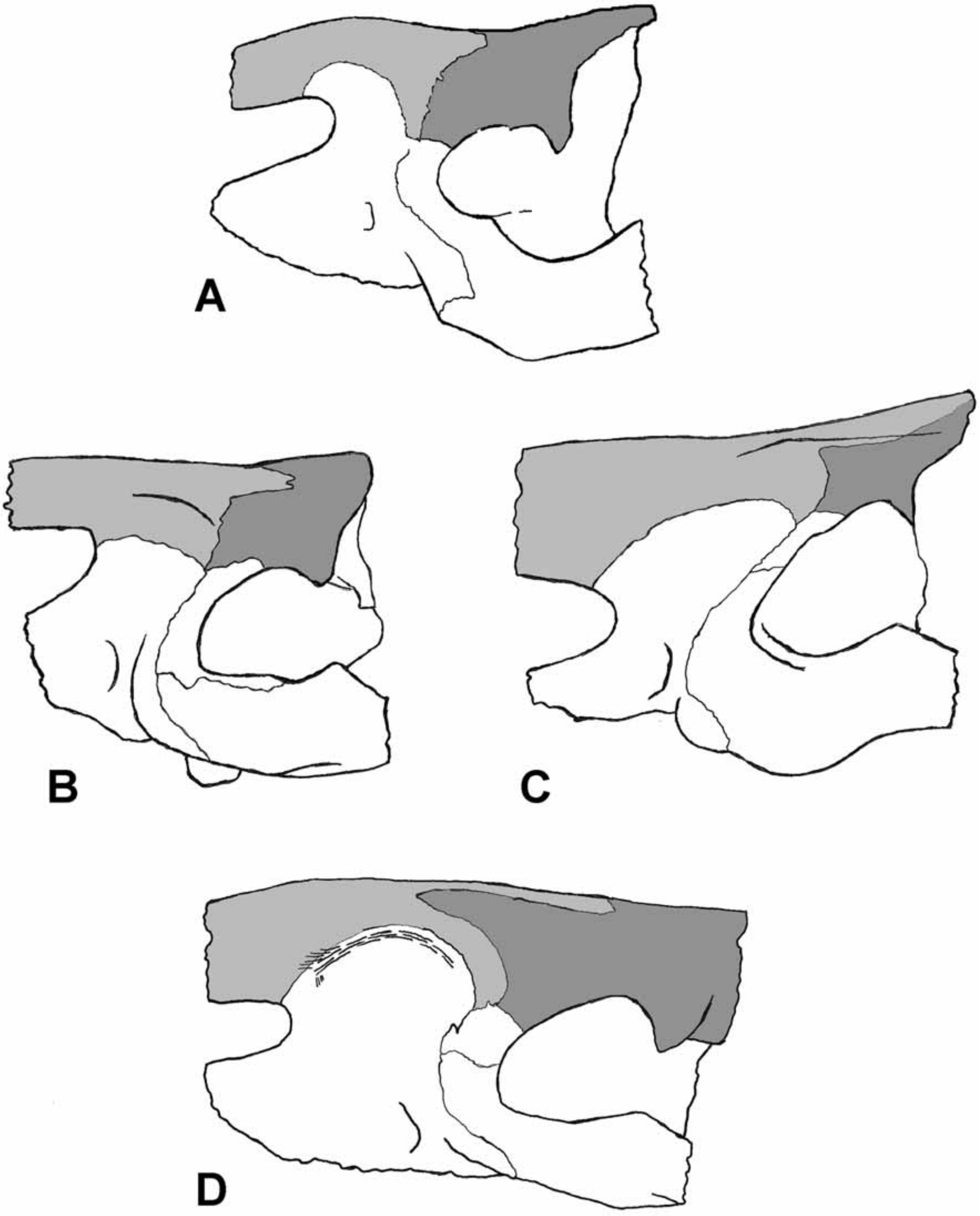

FIGURE 18. Suture pattern between the frontal (dark gray) and nasal (light gray) in **A**, *Palaeosyops*; **B**, *Mesatirhinus*; **C**, *Sphenocoelus*; and **D**, *Telmatherium*. Figures modified from Osborn, 1929, and not to scale.

Brontotheriine brontotheres are further distinguished by having a long, triangular projection of the frontal that overlaps the nasal (Fig. 18D), while in other brontotheres the frontal-nasal contact is usually rather straight (Fig. 18A, B, and C). In one specimen of the dolichorhinine brontothere *Metarhinus* (UCM 44939), however, there is a very slight triangular projection of the frontal overlapping the nasal. The frontal-nasal suture in the Brontotheriinae is located over the facial concavity and is incorporated into the horn.

Within the Brontotheriinae there are two monophyletic subsets: the diplacodonts (= diplacodonts sensu lato of Mader 1989; 1998) and eubrontotheres. These names are informal taxonomic terms but useful in discussions of brontothere phylogeny.

The diplacodonts are synonymous with the "horned brontotheres" mentioned by Mader (1989; 2000; present paper). The group is defined by the presence of "true" horns (that is, the presence of a distinct bony projection over the facial concavity rather than a slightly thickened bony prominence), vertically enlarged external nares, concave lateral cranial profile, facial region of the skull 40 % or less of the entire skull length, and complete loss of the sagittal crest due to widening of the cranial vertex. Most diplacodonts also have partially molarized premolars in which there are two lingual cusps on the third and fourth upper premolars. The most plesiomorphic diplacodont taxon, however, has only a single lingual cusp present on the third and fourth upper premolar in some individuals. This taxon is a *Protitanotherium*-like brontothere and includes the type specimen of "*Sthenodectes*" *australis* Wilson (see Discussion section for *Protitanotherium*).

The term "eubrontothere" was first used by Schoch and Lucas (1985) for *Duchesneodus* and typical Chadronian brontotheres such as *Brontops*. Eubrontotheres (not revised in the present paper) are defined by the presence of a greatly widened cranial vertex, well developed hypocone that is consistently present on M3, and the loss of the diastema.

Genus *TELMATHERIUM* Marsh 1872

= *Leurocephalus* Osborn *et al*. 1878
= "*Telmatotherium*" Marsh 1880
= *Manteoceras* Hatcher 1895

Age. Bridgerian.

Subage. Twinbuttean.

Type species. *T. validus* Marsh 1872.

Included species. Genus is monospecific.

Diagnosis. Medium to moderately large-sized (length P2 to M3 approximately 160–190 mm) brontotheriine brontothere with a small but distinctive horn-like prominence developed on the frontonasal boundary over facial concavity and a deep pit-like fossa in the middle of the sagittal crest near the back of the skull.

Discussion. In 1872 O.C. Marsh named a new brontothere taxon, *Telmatherium validus*, based upon "the greater portion of a skull with teeth, and portions of several other skeletons." Marsh did not identify these materials by catalog number but Osborn (1929, p. 160) identified the skull as YPM 11120. Osborn (1929) cited this skull as the holotype of *T. validus* as did Mader (1989), who believed the type cited by Osborn to be accurate. Marsh, however, had based the species upon a type series, even though he treated the skull as his principal specimen and gave locality information for it alone. Thus, YPM 11120 would more properly be regarded as a lectotype for the species, although neither Osborn nor Mader (1989) formally designated it as such. In 1998, however, Mader, cognizant that a type series existed, listed YPM 11120 as the “lectotype” of *T. validus*, effectively establishing it as such, although he did not explicitly state that it was his intention to fix the type. If subsequent researchers should conclude that the type of *T. validus* was not properly fixed by Mader (1998), then, as the first reviser to directly address this problem, I now formally select YPM 11120 as the lectotype for the species *T. validus* Marsh. The taxonomic purpose for this designation (as per the requirements of the International Code of Zoological Nomenclature, Article 74.7.3, Ride *et al*. 1999) is to avoid confusion and nomenclatural instability should it be determined that the specimens of the original type series belong to different genera. This is a distinct possibility given that three contemporaneous brontothere genera existed at the time (Twinbuttean) and that early authors, such as Marsh, often had an imprecise conception of the taxa they described.

Five years after Marsh's description of *Telmatherium validus* Henry Fairfield Osborn and William Berryman Scott made an amateur collecting trip to the Bridger (Green River) Basin to celebrate their graduation from Princeton (Howard 1975, pp. 258–259). This first "Princeton Expedition" (Osborn 1929; p. 338) resulted in the collection of a second specimen of *Telmatherium* (YPM-PU 10027, the right side of a skull and lower jaw). Osborn *et al*. (1878) identified this specimen as a new genus, *Leurocephalus* (type species *L. cultridens*), but subsequent authors (e.g., Earle 1892; Osborn 1929; Mader 1989) have recognized that it is a specimen of *Telmatherium*.

The first complete skulls of *Telmatherium* were discovered in 1893 by an American Museum expedition to the Washakie Basin led by J. L. Wortman. In a letter from the field dated June 1, 1893, Wortman wrote Osborn that he believed that the skulls represented a new genus for which he suggested three possible names *Manteoceras*, *Manteotherium*, or *Manteocephalus*, (= "prophecy" + "horn", "animal", or "head").

Osborn (1895) disagreed with Wortman's assessment of these skulls, however, and instead identified them as specimens of *Palaeosyops vallidens* Cope (a taxon based on a lower jaw, AMNH 5098), which Osborn referred to the genus "*Telmatotherium*". Osborn's interpretation of "*Telmatotherium*" was very broad, and he included under this generic name *Telmatherium* and all of the valid dolichorhinine genera. Hatcher (1895) recognized that "*Telmatotherium*" as defined by Osborn consisted of several distinct taxa and proposed that the type jaw of Cope's *Palaeosyops vallidens* be given the new generic name *Manteoceras* ("prophet horn"), following the original suggestion of Wortman.

In a surprising turn of events Osborn (1929) concluded that the lectotype lower jaw of *Palaeosyops vallidens* Cope did not represent the same taxon as Wortman's skulls after all but rather represented the same genus as the holotype skull of "*Telmatotherium*" *cornutum*, the type species of *Dolichorhinus*. Both *Manteoceras* and *Dolichorhinus* were named in the same paper (Hatcher 1895) and, if Osborn was correct, *Dolichorhinus* could be recognized as a junior synonym of *Manteoceras*.

Osborn (1929) attempted to avoid this situation by contending that Hatcher had "*Telmatotherium*" *vallidens*, sensu Osborn (1895), in mind when he named *Manteoceras* and not *Palaeosyops vallidens* Cope. Osborn supported this argument by pointing out that Hatcher's figures of "*Telmatotherium*" *vallidens* were based on Osborn's figures of Wortman's skulls and that Hatcher's diagnosis of *Manteoceras* (which was based entirely upon cranial characters) was inapplicable to the lectotype lower jaw of *Palaeosyops vallidens*.

Osborn accepted *Manteoceras* as the valid generic name for Wortman's skulls (because this is what Hatcher had intended), but could not recognize *Manteoceras vallidens* as the type species. Osborn was forced, therefore, to look in the subsequent literature for an appropriate type species. In 1899 Matthew had published a faunal list in which the name *Palaeosyops manteoceras* appeared. This was a new trivial name meant to apply to Wortman's skulls, which Matthew took from an unpublished Osborn manuscript. Matthew, however, did not designate a type or provide a diagnosis. As Osborn (1929) pointed out, *Palaeosyops manteoceras* Matthew was, therefore, a nomen nudum.

In his Bibliography and Catalogue of the Fossil Vertebrata of North America, Hay (1902) listed as the type of the genus *Manteoceras* Hatcher, *Palaeosyops manteoceras* Osborn and gave as figure references Osborn's and Hatcher's illustrations of Wortman's skulls. Hay did not provide a diagnosis for the species. According to Osborn (1929) the giving of the figure references was essentially the same as designating a type because they specifically identified the specimens to which the name was to be applied. The figures in question illustrated two skulls, AMNH 1569 and AMNH 1570, of which Osborn (1929) selected AMNH 1569 as a lectotype.

Thus, by highly circuitous reasoning, Osborn (1929) concluded that the type species of *Manteoceras* was *M. manteoceras* Hay, because *M. manteoceras* was a synonym of "*Telmatotherium*" *vallidens*, sensu Osborn. As I have previously pointed out (Mader 1989), if Osborn was correct in establishing that the lectotype jaw of *Palaeosyops vallidens* represents the same genus as Hatcher's *Dolichorhinus*, then the conclusion that *Manteoceras* and *Dolichorhinus* are synonyms is inescapable. Hatcher clearly stated that the type of *Palaeosyops vallidens* was to be given the new generic name *Manteoceras* and, regardless of what Hatcher's concept of that genus might have been, the name stays with the type originally specified. The type species of *Manteoceras*, therefore, is *Palaeosyops vallidens* Cope not "*Telmatotherium*" *vallidens*, sensu Osborn.

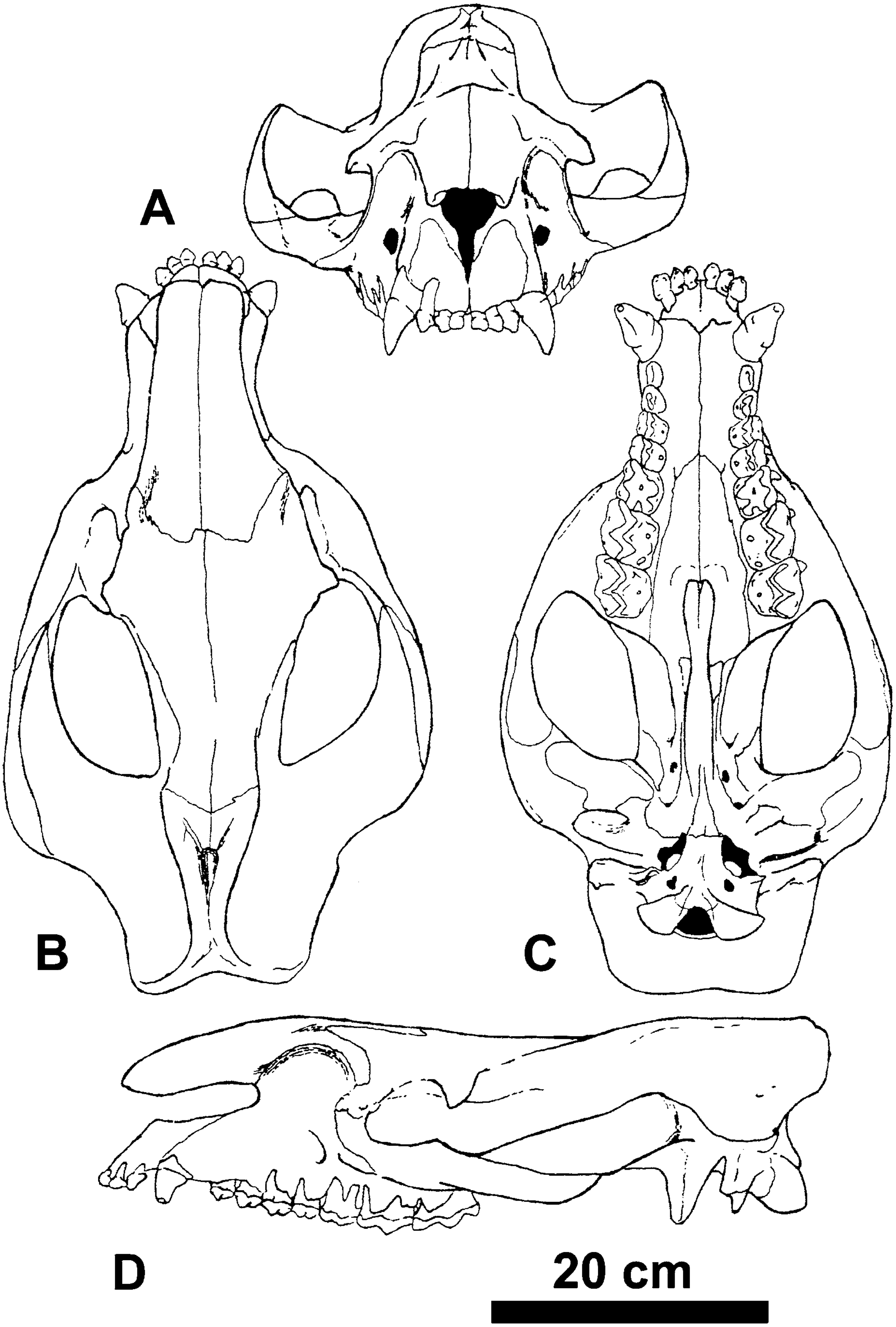

FIGURE 19. Skull of *Telmatherium validus* in **A**, anterior; **B**, dorsal; **C**, ventral; and **D**, lateral views. After Osborn, 1929.

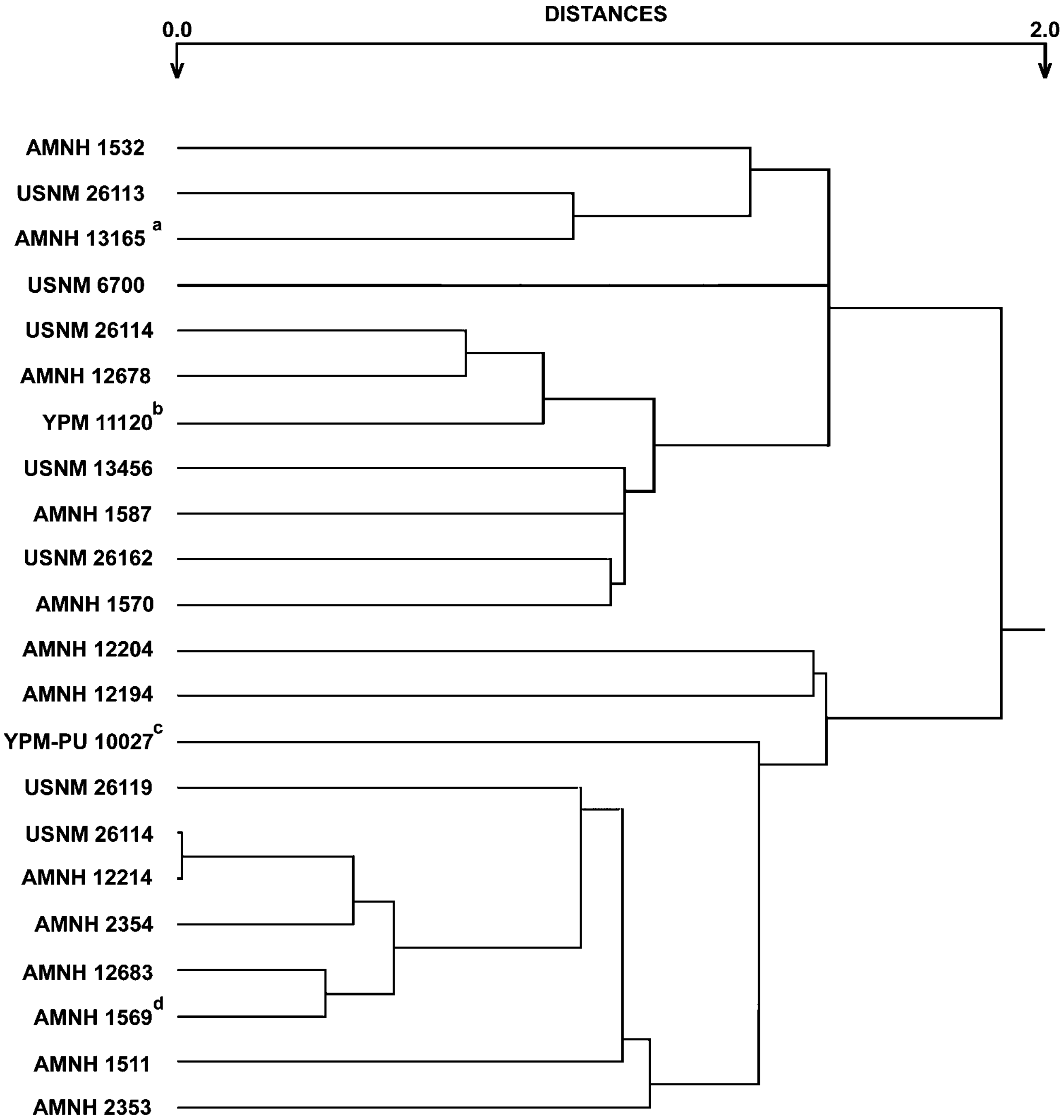

FIGURE 20. Cluster dendrogram for specimens of *Telmatherium* from the Green River and Washakie Basins resulting from a cluster analysis of all variables listed in Table 12. **a**, type of *Telmatherium washakiensis*; **b**, type of *T. validus*; **c**, type of *T. cultridens*; **d**, Osborn's lectotype of *T. manteoceras*.

Because the recognition of *Manteoceras* and *Dolichorhinus* as synonyms could create confusion, Mader (1989) recommended that any author attempting to synonymize the genera formally choose *Dolichorhinus* as the name having priority (see recommendation 24A in the International Code of Zoological Nomenclature, Ride *et al*. 1999). *Manteoceras* would thus be a junior synonym of *Dolichorhinus* rather than a junior synonym of *Telmatherium* (as it is treated here). I continue to recommend this assignment of nomenclatural priority, but note that it is now less critical because, even if *Manteoceras* and *Dolichorhinus* are synonymous, both terms would be junior synonyms of *Sphenocoelus* (see Discussion section for the genus *Sphenocoelus*).

Osborn (1929) recognized both *Telmatherium* and *Manteoceras* as valid genera. In practice he referred fragmentary specimens of *Telmatherium* to the genus *Telmatherium* and more complete specimens to the genus *Manteoceras*. Although Osborn cited a number of differences between *Telmatherium* and *Manteoceras*, these differences are either trivial or based upon comparisons with the unrelated brontothere genus *Metatelmatherium* (see below).

Telmatherium disappeared from the fossil record at the end of the Bridgerian, but Osborn (1908; 1929) regarded Uintan aged specimens now referred to the genus *Metatelmatherium* as a later form of *Telmatherium*. Interestingly, for both of the genera that Osborn split *Telmatherium* into (*Telmatherium* and *Manteoceras*), he recognized Uintan descendents that are all specimens of *Metatelmatherium ultimum*. Thus Osborn recognized *Telmatherium ultimum* (now *Metatelmatherium ultimum*) as the supposed Uintan successor of *T. validus* and *T. cultridens*, and *Manteoceras uintensis* (= *Metatelmatherium ultimum*) as the presumed successor of *M. manteoceras* and *M. washakiensis* (see section on *Metatelmatherium*).

In 1908, Osborn described a new species of *Manteoceras* from the highest level of Washakie A, which he named *M. washakiensis* (type AMNH 13165, a skull). Osborn (1908; 1929) distinguished *M. washakiensis* from *M. manteoceras* by its larger skull size, larger cheek teeth, more complete cingula on the cheek teeth, morphology of the canine (obtuse, recurved, and with a heavy posterior cingulum), better developed "deuterocone" (= protocone) on P2 (Osborn 1929, p. 371, stated that the internal lobes of P2 and P3 are broadening, with a shelf for the development of the deuterocone), shorter face, moderate zygomata, and relatively inconspicuous horns. Under the heading "Progressive Characters" Osborn (1929, p. 371) also stated that the molar series of *M. washakiensis* is relatively longer than that of *M. manteoceras*, in which the premolar length is 76% that of the molar length (averaged for six individuals), while in *M. washakiensis* the premolars are only 71% of the molar length. Osborn regarded this as a progressive character because there is an increase in the relative length of the molar series over the course of brontothere evolution.

In my opinion, all of the characters (both cranial and dental) used by Osborn to distinguish *Manteoceras washakiensis* from *M. manteoceras* are quite minor and are insufficient to establish a new taxon. I also find no basis for Osborn's statement that the type skull of *M. washakiensis* is larger than skulls that he referred to *M. manteoceras*. The type of *M. washakiensis* lacks the premaxillary region and thus Osborn (1929) was only able to provide an estimated skull length (= 490 mm) for it. The amount of bone missing from the type skull and the degree to which it is crushed make this a very rough estimate, and as a result, any taxonomic conclusions based upon skull length are necessarily suspect. In addition, in a table (1929, p. 364) Osborn listed skull lengths and estimates of skull lengths for specimens that he referred to *M. manteoceras* that equal or exceed Osborn's estimated value for the skull length in the type of *M. washakiensis*. Thus AMNH 12204, identified as a female *M. manteoceras* by Osborn, has an estimated skull length of 490 mm (equal to that of *M. washakiensis*) and AMNH 1545, identified as a male *M. manteoceras,* has a skull length of 523 mm (which exceeds that of *M. washakiensis*).

I also find no evidence that the molar series is longer in the type of *Manteoceras washakiensis* than in skulls that Osborn referred to *M. manteoceras*. As previously noted, Osborn stated that the length of the premolar series in the type skull of *M. washakiensis* is 71% that of the molar length. This is very similar to the value obtained from my own data which results in the premolar length being 70% of the molar length. Osborn's statement that in *M. manteoceras* the premolar length was 76% that of the molar length, however, was based on an average value for six individuals. If these six individuals are among the specimens that Osborn listed in the table noted above (1929, p. 364), then these specimens would be AMNH 12683, AMNH 1511, AMNH 2353, AMNH 1569, AMNH 1570, and AMNH 1545; the only specimens for which the length of both the premolar series and molar series are reported. Although Osborn was correct in reporting that the average value for premolar length relative to molar length is 76% for these specimens, in one specimen (AMNH 1545) the premolar length is 70% of the molar length, which is virtually the same as in the type of *M. washakiensis*.

TABLE 12. Summary statistics for the genus *Telmatherium.* (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	1	495.0–495.0	495.0	±0.0	0.0
Length Cheek Tooth Series[a]	10	172.0–203.0	188.1	±10.7	5.7
Length P2 to M3[a]	11	160.5–189.0	172.1	±10.1	5.4
Length Premolar Series[a]	9	74.8–87.8	82.2	±4.3	5.2
Length Molar Series[a]	17	99.5–126.0	109.2	±7.2	6.6
Length Diastema[a]	8	8.4–23.1	12.3	±4.7	38.2
Length Left M3	16	34.5–42.5	39.5	±2.3	5.8
Length Right M3	16	34.5–42.5	39.1	±2.3	5.9
Width Left M3	15	37.1–43.8	40.1	±2.1	5.2
Width Right M3	15	37.0–43.7	40.2	±2.5	6.2
Length Left M2	17	35.0–42.5	39.3	±2.4	6.1
Length Right M2	15	35.0–43.5	39.4	±2.6	6.6
Width Left M2	14	35.4–42.2	39.2	±2.2	5.6
Width Right M2	15	35.0–41.3	39.0	±1.8	4.6
Length Left M1	14	25.5–34.5	30.8	±2.9	9.4
Length Right M1	14	28.0–35.0	30.9	±2.2	7.1
Width Left M1	12	28.5–37.9	32.2	±2.6	8.1
Width Right M1	10	28.9–35.1	31.6	±1.9	6.0
Length Left P4	14	18.5–24.5	21.7	±1.3	6.0
Length Right P4	13	20.0–25.0	22.3	±1.5	6.7
Width Left P4	12	25.2–32.4	28.5	±1.9	6.7
Width Right P4	10	25.5–31.7	28.6	±1.8	6.3
Length Left P3	12	17.0–22.0	19.5	±1.5	7.7
Length Right P3	11	17.5–22.0	19.9	±1.3	6.5
Width Left P3	10	20.8–26.1	23.9	±1.8	7.5
Width Right P3	9	21.6–26.4	24.2	±1.5	6.2
Length Left P2	8	18.0–21.0	19.8	±0.9	4.6
Length Right P2	10	18.0–22.5	20.0	±1.4	7.0
Width Left P2	9	14.9–20.2	17.4	±1.6	9.2
Width Right P2	8	15.0–19.4	17.9	±1.4	7.8
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
AVERAGE V					6.5[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length and Basilar Length of Skull.

TABLE 13. F-Test comparisons for the small-size group (Group 1) and large-size group (Group 2) of *Telmatherium.*

	n Group 1	n Group 2	F	Probability	*T*-Test
Basilar Length Skull[a]	0	1	—	—	—[b]
Length Cheek Tooth Series[a]	5	5	0.016	0.901	Pooled
Length P2 to M3[a]	4	7	3.907	0.050	Separate
Length Premolar Series[a]	4	5	0.113	0.738	Pooled
Length Molar Series[a]	9	8	5.484	0.019	Separate
Length Diastema[a]	4	4	1.822	0.180	Pooled
Length Left M3	8	8	1.835	0.176	Pooled
Length Right M3	9	7	0.220	0.639	Pooled
Width Left M3	7	8	1.140	0.286	Pooled
Width Right M3	8	7	0.235	0.628	Pooled
Length Left M2	8	9	0.026	0.872	Pooled
Length Right M2	6	9	0.595	0.441	Pooled
Width Left M2	6	8	0.148	0.701	Pooled
Width Right M2	8	7	5.877	0.016	Separate
Length Left M1	7	7	0.231	0.631	Pooled
Length Right M1	8	6	0.219	0.640	Pooled
Width Left M1	5	7	1.300	0.255	Pooled
Width Right M1	5	5	0.232	0.631	Pooled
Length Left P4	7	7	0.000	1.000	Pooled
Length Right P4	5	8	0.141	0.707	Pooled
Width Left P4	6	6	0.000	0.988	Pooled
Width Right P4	4	6	0.015	0.904	Pooled
Length Left P3	6	6	0.001	0.980	Pooled
Length Right P3	4	7	0.022	0.883	Pooled
Width Left P3	5	5	2.891	0.091	Pooled
Width Right P3	3	6	0.060	0.807	Pooled
Length Left P2	3	5	0.263	0.610	Pooled
Length Right P2	5	5	1.548	0.215	Pooled
Width Left P2	5	4	0.179	0.673	Pooled
Width Right P2	4	4	1.445	0.232	Pooled
Buccal-Lingual Width Left Canine	0	0	—	—	—[b]
Buccal-Lingual Width Right Canine	2	0	—	—	—[b]
Mesial-Distal Width Left Canine	0	0	—	—	—[b]
Mesial-Distal Width Right Canine	2	0	—	—	—[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] There is no variance in one of the groups being compared.

TABLE 14. *T*-Test comparisons for the two size groups of *Telmatherium.*

	T	DF	Probability
Basilar Length Skull[a]	—[b]	—	—
Length Cheek Tooth Series[a]	6.142	8.0	0.000
Length P2 to M3[a]	4.763[c]	7.5	0.002
Length Premolar Series[a]	3.044	7.0	0.019
Length Molar Series[a]	5.614[c]	9.0	0.001
Length Diastema[a]	0.994	6.0	0.358
Length Left M3	5.276	14.0	0.000
Length Right M3	3.772	14.0	0.002
Width Left M3	4.147	13.0	0.001
Width Right M3	8.732	13.0	0.000
Length Left M2	7.051	15.0	0.000
Length Right M2	3.983	13.0	0.002
Width Left M2	5.236	12.0	0.000
Width Right M2	5.416[c]	8.7	0.001
Length Left M1	5.945	12.0	0.000
Length Right M1	6.110	12.0	0.000
Width Left M1	4.512	10.0	0.001
Width Right M1	3.070	8.0	0.015
Length Left P4	2.475	12.0	0.029
Length Right P4	5.451	11.0	0.000
Width Left P4	3.663	10.0	0.004
Width Right P4	3.534	8.0	0.008
Length Left P3	3.796	10.0	0.004
Length Right P3	1.813	9.0	0.103
Width Left P3	3.098	8.0	0.015
Width Right P3	5.091	7.0	0.001
Length Left P2	0.046	6.0	0.965
Length Right P2	0.970	8.0	0.361
Width Left P2	1.136	7.0	0.293
Width Right P2	1.851	6.0	0.114
Buccal-Lingual Width Left Canine	—[b]	—	—
Buccal-Lingual Width Right Canine	—[b]	—	—
Mesial-Distal Width Left Canine	—[b]	—	—
Mesial-Distal Width Right Canine	—[b]	—	—

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data for *t*-test.

[c] Separate *t*-test.

TABLE 15. Summary statistics for the small-size group of *Telmatherium.* (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	0	—[b]	—[b]	—[b]	—[b]
Length Cheek Tooth Series[a]	5	172.0–185.5	178.9	±4.9	2.7
Length P2 to M3[a]	4	160.5–165.5	162.3	±2.3	1.4
Length Premolar Series[a]	4	74.8–82.0	78.8	±3.3	4.2
Length Molar Series[a]	9	99.5–107.0	103.7	±2.2	2.1
Length Diastema[a]	4	10.0–23.1	14.0	±6.1	43.6
Length Left M3	8	34.5–39.5	37.7	±1.7	4.5
Length Right M3	9	34.5–40.5	37.7	±1.8	4.8
Width Left M3	7	37.1–40.0	38.5	±1.1	2.9
Width Right M3	8	37.0–40.1	38.2	±1.1	2.9
Length Left M2	8	35.0–39.0	37.1	±1.2	3.2
Length Right M2	6	35.0–39.0	37.1	±1.4	3.8
Width Left M2	6	35.4–39.0	37.1	±1.4	3.8
Width Right M2	8	35.0–39.6	37.7	±1.4	3.7
Length Left M1	7	25.5–30.5	28.4	±1.7	6.0
Length Right M1	8	28.0–31.0	29.3	±1.0	3.4
Width Left M1	5	28.5–30.8	29.8	±1.0	3.4
Width Right M1	5	28.9–32.0	30.3	±1.2	4.0
Length Left P4	7	18.5–22.0	20.9	±1.1	5.3
Length Right P4	5	20.0–21.8	20.7	±0.7	3.4
Width Left P4	6	25.2–28.2	27.1	±1.3	4.8
Width Right P4	4	25.5–28.3	27.0	±1.2	4.4
Length Left P3	6	17.0–19.5	18.4	±1.0	5.4
Length Right P3	4	17.5–20.5	19.1	±1.3	6.8
Width Left P3	5	20.8–24.7	22.6	±1.7	7.5
Width Right P3	3	21.6–23.3	22.4	±0.8	3.6
Length Left P2	3	19.0–20.5	19.8	±0.8	4.0
Length Right P2	5	18.0–22.5	19.5	±1.8	9.2
Width Left P2	5	14.9–18.6	16.8	±1.4	8.3
Width Right P2	4	14.6–18.4	17.1	±1.5	8.8
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
AVERAGE V					4.6[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length.

TABLE 16. Summary statistics for the large-size group of *Telmatherium.* (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	1	495.0–495.0	495.0	±0.0	0.0
Length Cheek Tooth Series[a]	5	190.5–203.0	197.3	± 4.6	2.3
Length P2 to M3[a]	7	168.0–189.0	177.7	± 8.1	4.6
Length Premolar Series[a]	5	80.5–87.8	85.0	±2.7	3.2
Length Molar Series[a]	8	110.3–126.0	115.3	±5.5	4.8
Length Diastema[a]	4	8.4–13.5	10.7	±2.5	23.4
Length Left M3	8	40.0–42.5	41.3	±1.0	2.4
Length Right M3	7	38.0–42.5	40.9	±1.5	3.7
Width Left M3	8	38.3–43.8	41.6	±1.7	4.1
Width Right M3	7	41.1–43.7	42.5	±0.9	2.1
Length Left M2	9	40.0–42.5	41.2	±1.2	2.9
Length Right M2	9	37.0–43.5	40.9	±2.0	4.9
Width Left M2	8	38.6–42.2	40.7	±1.2	3.0
Width Right M2	7	40.1–41.3	40.5	±0.5	1.2
Length Left M1	7	31.0–34.5	33.1	±1.4	4.2
Length Right M1	6	31.5–35.0	33.0	±1.3	3.9
Width Left M1	7	32.6–37.9	33.9	1.8	5.3
Width Right M1	5	31.0–35.1	32.9	±1.5	4.6
Length Left P4	7	21.0–24.5	22.4	±1.1	4.9
Length Right P4	8	22.0–25.0	23.3	±0.9	3.9
Width Left P4	6	28.9–32.4	29.9	±1.3	4.4
Width Right P4	6	28.5–31.7	29.6	±1.1	3.7
Length Left P3	6	19.0–22.0	20.7	±1.0	4.8
Length Right P3	7	18.5–22.0	20.4	±1.2	5.9
Width Left P3	5	24.5–26.1	25.1	±0.6	2.4
Width Right P3	6	24.5–26.4	25.1	±0.7	2.8
Length Left P2	5	18.0–21.0	19.8	±1.1	5.6
Length Right P2	5	19.0–21.0	20.4	±0.9	4.4
Width Left P2	4	15.8–20.2	18.0	±1.8	10.0
Width Right P2	4	17.7–19.4	18.7	±0.7	3.7
Buccal-Lingual Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Buccal-Lingual Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Left Canine	0	—[b]	—[b]	—[b]	—[b]
Mesial-Distal Width Right Canine	0	—[b]	—[b]	—[b]	—[b]
AVERAGE V					4.1[c]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Insufficient data.

[c] Excluding Diastema Length and Basilar Length Skull.

The main reason for Osborn's recognition of *Manteoceras washakiensis* as a species distinct from *M. manteoceras* appears to be the former's higher stratigraphic occurrence. Osborn stated that the "decidedly progressive characters (of *M. washakiensis*) beyond those of *M. manteoceras* ... perfectly accord with its somewhat higher geologic level." In my opinion, the "decidedly progressive characters" noted by Osborn are illusory and the supposed higher stratigraphic level is not by itself, sufficient grounds for the recognition of a taxon.

The genus *Telmatherium* (Fig. 19) is known from contemporaneous deposits in the Green River and Washakie Basins. Most specimens are from the Green River Basin, but since the sample size from that location is relatively low (no more than thirteen individuals for any given variable) the sample was supplemented with five individuals from the Washakie Basin for the purpose of statistical analysis.

The coefficient of variation (Table 12) for most variables in the combined Green River and Washakie sample of *Telmatherium* lie within the range of 4 to 10, and the average value for all variables (excluding diastema and skull length) is 6.5. Diastema length and skull length are eliminated from consideration because of the high variability in diastema length in Pre-Chadronian brontotheres in general (see Summary Statistics tables in the present paper and in Mader 1991) and because the sample for skull length consisted of only a single individual. Thus, the variation present in all of the specimens of *Telmatherium* from the Green River and Washakie Basins is no more than is ordinarily encountered in a single extant mammalian species.

Cluster analysis of all variables, however, shows remarkably clear delineation into two size groups (Fig. 20). *T*-tests (Tables 13 and 14) confirm that, for most variables, the means of these size groups are significantly different. Approximately three quarters of the variables for which a value of *T* could be calculated had a probability of less than .05 and over one half had a probability of less than .01. Although the *t*-test for the length of the right third upper premolar fails to show a significant difference, the *t*-test for the length of the left P3 and *t*-tests for the widths of both P3's do show a significant difference. Thus, the *t*-test result for the length of the right P3 is probably a chance occurrence. The only variables that truly appear to have no significant difference between the two size groups are the length of the diastema and the lengths and widths of both second upper premolars. It should be noted that there is a 77% chance that at least one significant result in this study is due to error (see Methods). Given the great quantity of significant results, however, it seems that the statistical reality of the two size groups is firmly established.

The summary statistics for each of the two size groups of *Telmatherium* are presented in Tables 15 and 16. Almost one-third of the variables in both size groups (excluding the basilar length of the skull in the large-size group) have values of V that are below 4 (values rounded to the nearest whole number). In addition, although the average value of V for the smaller size group is within the expected range for a single species, the average value for the larger size group is rather low (4.1). These results suggest that in both size groups there is less variation than is typically encountered in extant mammalian species (although most of the samples are probably large enough to show most of the variation present).

Thus, although two size groups are clearly present, the variation within each is probably too low for them to be regarded as separate species. Despite the fact that cluster analysis strongly differentiates between these size groups, an inspection of the size ranges reported in Tables 15 and 16 will show that in absolute terms, the size difference between the groups is quite minimal. I conclude, therefore, that the two clusters in the dendrogram in Figure 20 probably represent two size groups within a single species (perhaps males and females).

It would have been desirable to analyze canine size and horn size in *Telmatherium* to determine whether these variables were bimodal within each of the size groups (as might be expected if they were two different species). Unfortunately, the canines were very poorly preserved in most of the specimens of *Telmatherium* measured and horn size is difficult to measure precisely because there is no definite horn base (my impression, however, is that horn size does not vary appreciably in any specimens of *Telmatherium*).

If bimodality could have been established for either canine or horn size I would be willing to regard the two size groups as distinct species because there would then be evidence that males and females were present in each size group. If the two size groups of *Telmatherium* were to be interpreted as being two species, then the type species (*T. validus*) would be represented by the larger size group while the name *T. cultridens* would be applied to the smaller-size group. *Manteoceras washakiensis* would remain a junior synonym of *T. validus* but *M. manteoceras* would become a junior synonym of *T. cultridens*.

Species *TELMATHERIUM validus* Marsh 1872

= *T. cultridens* (Osborn *et al*. 1878)
= *T. manteoceras* (Hay 1902)
=*T. washakiensis* (Osborn 1908)

Lectotype. YPM 11120, a partial palate with most of the upper dentition and fragments of the zygomatic arches, nasals, and occipital region preserved.

Referred specimens. AMNH 1511, AMNH 1532, AMNH 1569 (lectotype of *T. manteoceras*), AMNH 1570, AMNH 1587, AMNH 2353, AMNH 2354, AMNH 12194, AMNH 12204, AMNH 12214, AMNH 12678, AMNH 12683, AMNH 13165 (type of *T. washakiensis*), USNM 6700, USNM 13456, USNM 26113, USNM 26114, USNM 26119, USNM 26140, USNM 26162, YPM-PU 10027 (type of *T. cultridens*, type species of *Leurocephalus*).

Diagnosis. Same as the generic diagnosis.

Genus *PROTITANOTHERIUM* Hatcher 1895

Age. Uintan.

Subage. Late Uintan.

Type species. *P. emarginatum* (Hatcher 1895).

Included species. Genus is monospecific.

Diagnosis (based on holotype of type species only)–Large-sized (cheek tooth series measurements unknown) plesiomorphic diplacodont brontothere with laterally directed horns that are elliptical in cross-section, short, broad nasals, and a robust canine.

Discussion. In 1895 Hatcher described an unusual brontothere skull with small horns (YPM-PU 11242, see Fig. 21) that he provisionally referred to the genus *Diplacodon* Marsh (type species *D. elatus*). Although Marsh (1875) had asserted that *Diplacodon* lacked horns, Hatcher pointed out that Marsh's claim was probably conjectural, because the type of *Diplacodon elatus* (YPM 11180) lacked the entire horn and nasal region. Hatcher argued that in all other respects his specimen appeared to be identical to *Diplacodon elatus* but larger in size. He therefore recognized the specimen as a new species of *Diplacodon*, which he named *Diplacodon emarginatum*. Hatcher proposed that the generic name *Protitanotherium* be applied to the specimen, however, if there should prove to be hornless forms with the same dental characters.

According to Hatcher (1895), the cranial vertex in the type of *Protitanotherium emarginatum* is "slightly concave antero-posteriorly? and is further characterized by the absence of a sagittal crest." Because only the anterior part of the type skull is preserved this statement may be conjectural, but it is possible that Hatcher observed the cranial vertex in the field. Hatcher (1895) stated that when the type of *P. emarginatum* was collected, the posterior part of the skull had already weathered out and was badly damaged but many of the pieces were fitted together. According to Hatcher, these fragments show some of the more important characters of the posterior region of the skull. If any portion of the posterior part of the skull was collected by Hatcher, however, none of it is preserved in the Princeton collection at Yale University.

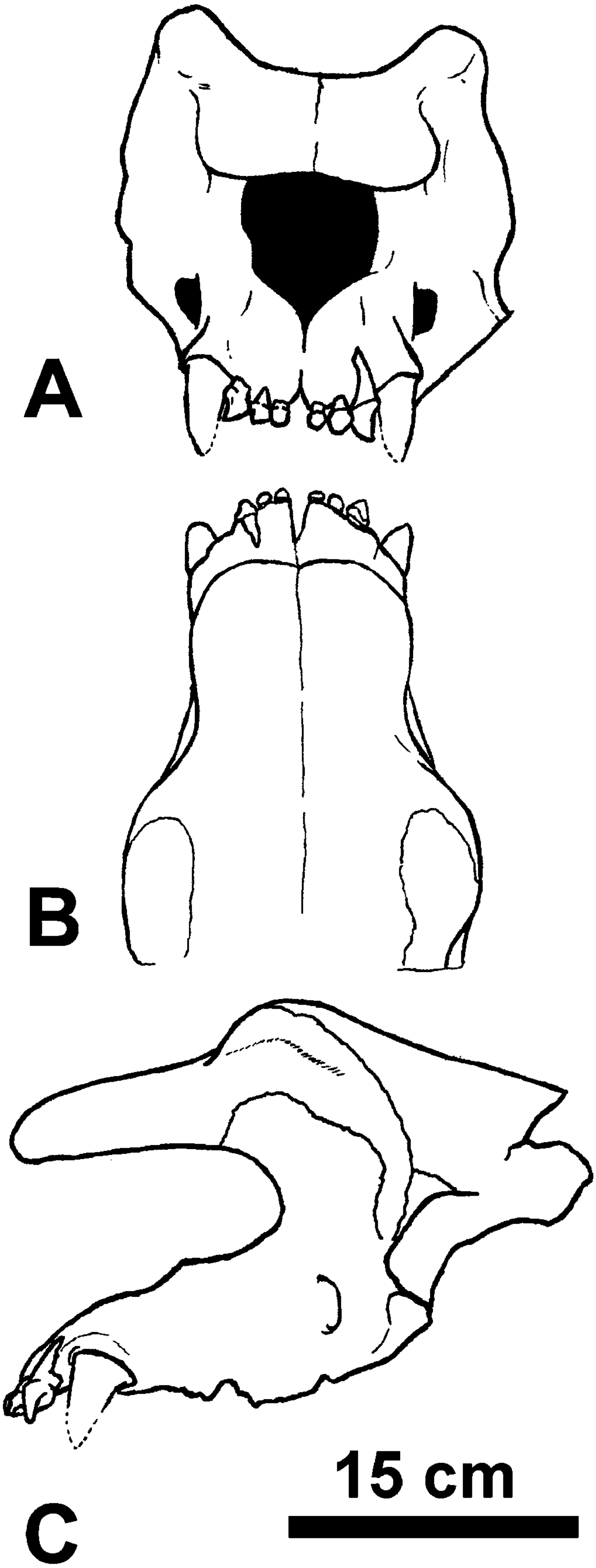

FIGURE 21. Holotype skull (YPM-PU 11242) of *Protitanotherium emarginatum* in **A**, anterior; **B**, dorsal; and **C**, lateral views. A and C after Osborn, 1929; B after Hatcher, 1895.

Osborn (1929) recognized the genus *Protitanotherium* as valid and argued that it was distinct from *Diplacodon* regardless of whether *Diplacodon* had horns or not. Most subsequent authors have also recognized *Protitanotherium* as valid (Simpson 1945; Mader 1989; 1998; McKenna & Bell 1997), although Lucas (1983) and Schoch and Lucas (1985) synonymized *Protitanotherium* with *Diplacodon*. Mader (1989; 2000) argued that *Protitanotherium* is valid and that *Diplacodon* is a possible senior synonym of *Eotitanotherium* (see also Osborn 1929, p. 196).

In 1908 Osborn described the lower jaw (AMNH 2501) of a very large brontothere from the Uinta Basin, which he referred to the genus *Protitanotherium*. Osborn noted several differences between this specimen and the jaw included in the type material of *Protitanotherium emarginatum* and concluded that it represented a new species of *Protitanotherium*, which he named *P. superbum*. Osborn (1908; 1929) never fully explained why he referred the specimen to *Protitanotherium* and admitted some doubt as to whether the generic assignment was correct (1929, p. 185).

The type of *Protitanotherium emarginatum* has large, robust, canine tusks; short, broadly rounded horns that are elliptical in cross-section at the base; and distinctive nasals that are short and distally squared. No other specimens with this exact combination of morphological characters has been recovered from the Uinta Formation or chronologically equivalent deposits. There are, however, two distinct Uintan aged forms that possess horns very similar to those of the type of *P. emarginatum*.

The first of these forms is represented by a single, nearly complete skull (CM 10200) with a widened, saddle-shaped cranial vertex and both horns and nasals that are very similar morphologically to those of the type of *Protitanotherium emarginatum*. Unlike the type of *P. emarginatum*, however, CM 10200 has a canine that is rather small in size.

The second form is represented by a series of skulls (AMNH 117163; TMM 41723-3, the holotype of "*Sthenodectes*" *australis* Wilson; TMM 41747-106; and UFH V 81.3.1) from localities in Utah (Uinta Formation), Wyoming (Wiggins Formation), and Texas (Devil's Graveyard Formation). These specimens represent a single taxon that is similar to the type of *Protitanotherium emarginatum* in the shape of the horns and presence of a large canine tusk, but differing in the shape of the nasals, which are relatively longer and distally rounded. The nasals of this form are virtually identical to those of *Pseudodiplacodon progressum* and *Eotitanotherium osborni*.

Regardless of the generic identity of the second form, it is the most plesiomorphic horned brontothere known. The cranial vertex, although sufficiently widened to eliminate the sagittal crest, is very narrow and does not nearly approach the wide, saddle-shaped morphology characteristic of all other horned brontotheres (diplacodonts). Furthermore, the premolars are rather plesiomorphic, in that some specimens (TMM 41723-3) do not possess more than a single lingual cusp on P3 and P4 (as in *Eotitanops* and the outgroup perissodactyls *Hyracotherium* and *Homogalax*) while other specimens (AMNH 117163) have two lingual cusps on these teeth as do all other horned brontotheres.

Given the incompleteness of the type specimen of *Protitanotherium emarginatum*, it is possible that either CM 10200 or the plesiomorphic series of skulls discussed above could be referable to the genus *Protitanotherium*. Both forms are similar to the type of *P. emarginatum* in some respects but exhibit important differences as well. I do not believe that both forms could be referable to *Protitanotherium* because the primitiveness of one form (the series of skulls) and the more highly derived state of the other (CM 10200) seem to preclude the possibility that they represent the same genus.

Thus, at least two brontotheres with short, broadly rounded horns existed during the Uintan Land Mammal Age. One of these is *Protitanotherium* and the other may be represented by either CM 10200 or the series of skulls listed above. Alternatively, the type of *Protitanotherium emarginatum*, CM 10200, and the series of skulls could all represent different genera, in which case there are three Uintan brontothere genera with similar horn morphology.

Because of the uncertainties involved, I am reluctant to assign generic names to either of the two forms discussed above and choose to restrict the name *Protitanotherium* to the type of *P. emarginatum* only. Mihlbachler (2005), however, has concluded that the name *Protitanotherium* should be applied to the plesiomorphic form that includes the holotype of "*Sthenodectes*" *australis* (TMM 41723-3).

Species *PROTITANOTHERIUM emarginatum* (Hatcher 1895)

Holotype. YPM-PU 11242, the anterior part of a skull with lower jaws.

Referred specimens. Type specimen only.

Diagnosis. Same as the generic diagnosis.

Genus *PSEUDODIPLACODON* Mader 2000

Age. Uintan.

Subage. Early? and Late Uintan.

Type species. *P. progressum* (Peterson 1934).

Included species. Genus is monospecific.

Diagnosis. Large-sized (length P2 to M3 approximately 207–234 mm) plesiomorphic diplacodont brontothere with bulbous horns that are roughly circular in cross-section; robust nasals that are rounded distally, curved ventrally, and shorter than in *Eotitanotherium*; small canines, and two poorly separated lingual cusps on P4. In general, the length of the cheek tooth series is usually shorter than in specimens of *Eotitanotherium*, but the skull is larger in size.

Discussion. The first primitive horned brontothere (diplacodont) material to be discovered was described by Marsh in 1875 and given the name *Diplacodon elatus*. In 1934 Petersen described a new species, which he referred to this genus, and named *D. progressum*. Mader (1989; 1991; 1998), however, found that “*Diplacodon*” *progressum* is not referable to *Diplacodon* Marsh, which he regarded as a nomen dubium or as a possible senior synonym of *Eotitanotherium*. Accordingly, Mader (2000) assigned the new generic name *Pseudodiplacodon* (literally “false *Diplacodon*”) to this species.

Mihlbachler (2005), however, disagreed with Mader and synonymized *Diplacodon*, *Pseudodiplacodon*, and *Eotitanotherium*. Furthermore, Mihlbachler referred all specimens belonging to these taxa to a single species, *Diplacodon elatus*. According to Mader (1989; 1998; 2000) *Pseudodiplacodon* and *Eotitanotherium* are distinguished from each other by their horn morphology and the morphology of the cusps on the posterior premolars. Mihlbachler, however, asserted that there is a continuum of horn sizes between the specimens assigned to both genera and that the premolar morphology is variable. Mihlbachler further suggested that the difference in horn size between *Pseudodiplacodon* and *Eotitanotherium* is generally consistent with the pattern of cranial variation found in other brontotheres, including *Megacerops* as well as a monospecific quarry sample of *Duchesneodus*. Based on my own observations, however, the variation in horn size and morphology in the *Duchesneodus* quarry sample is minor compared to the difference between the horns in *Pseudodiplacodon* and *Eotitanotherium* and, in my opinion, Mihlbachler (see Mihlbachler *et al*. 2004) has incorporated several distinct genera under the name *Megacerops*.

With regard to horn morphology, it should be noted that it is not only the size of the horn that distinguishes *Pseudodiplacodon* from *Eotitanotherium*, but also the shape. In *Pseudodiplacodon* the horn is round in cross-section and tends to be rather bulbous, although the length of the horn may vary. In *Eotitanotherium*, however, the horn has a distinct elliptical cross-section and, in this sense, it is much more similar to the horn of *Protitanotherium*, but is not as robust.

Regarding the premolars, it should be noted that in 1989 and 1998 Mader stated that *Pseudodiplacodon* is characterized by poorly separated lingual cusps on P3 and P4 (whereas they are well separated in *Eotitanotherium*), but in 2000 he restricted this observation to P4. The term "poorly separated" was meant to indicate that the cusps are more-or-less connected to each other as opposed to meaning that the cusps are located close together. Although Mihlbachler has stated that specimens assigned to *Pseudodiplacodon* by Mader distinctly vary in the degree to which the lingual cusps are "separated," his own description of several specimens indicates that the protocone and hypocone on the posterior premolars are connected by a crest (i.e., they are poorly separated from each other in the sense of Mader). Although Mihlbachler stated that in the holotype of *Pseudodiplacodon progressum* there is no such crest on the left P4 (but there is one on the right), my own notes concerning the specimen reflect that a thin connecting ridge is present on both sides.

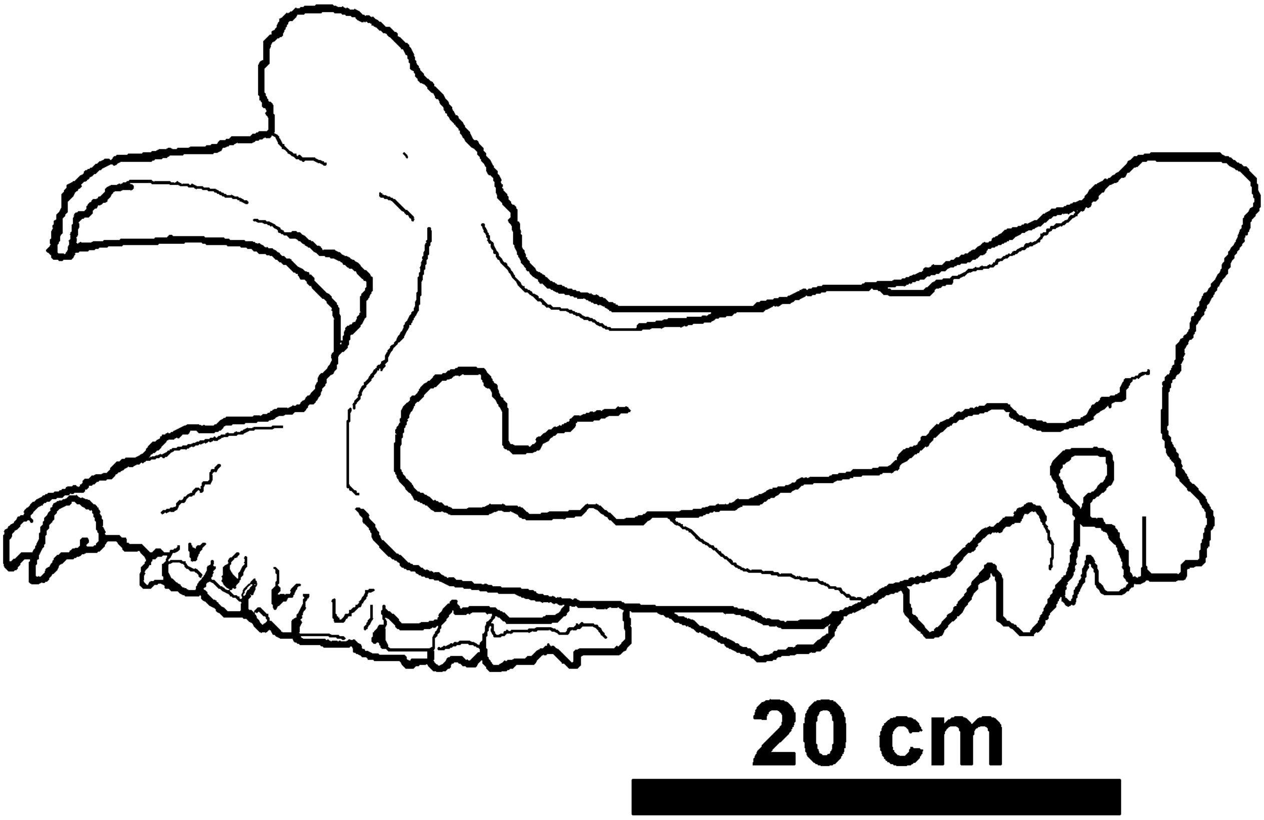

FIGURE 22. Holotype skull of *Pseudodiplacodon progressum* (CM 11879A) in lateral view.

As a final consideration, I would like to point out that several of the diagnostic characters used by Mihlbachler to distinguish *Diplacodon* (including both *Pseudodiplacodon* and *Eotitanotherium*) from *Protitanotherium* (as defined by Mihlbachler) are not valid. According to Mihlbachler, in *Diplacodon* the nasal process has upturned sides, elevated and widely separated horns, and a dorsoventrally deep nasal incision where the posterior notch of the incision rises much higher than the orbit. There is a specimen (AMNH 117163) referable to *Protitanotherium* (sensu Mihlbachler), however, which has each of these characters, demonstrating that they are not unique.

I continue to regard *Pseudodiplacodon* and *Eotitanotherium* as distinct forms. In addition to the reasons cited above, this distinction is further suggested by skull size and proportional differences in the dentition. I estimate that the holotype skull of *Pseudodiplacodon progressum* is 15 to 20% larger than the holotype of *Eotitanotherium osborni* (determined by digitally scaling images of the skulls). Despite the fact that *Pseudodiplacodon* is larger than *Eotitanotherium,* however, the tooth row tends to be shorter (although the dental size ranges actually overlap). This suggests to me a possible adaptive difference between the forms, implying that they are different taxa.

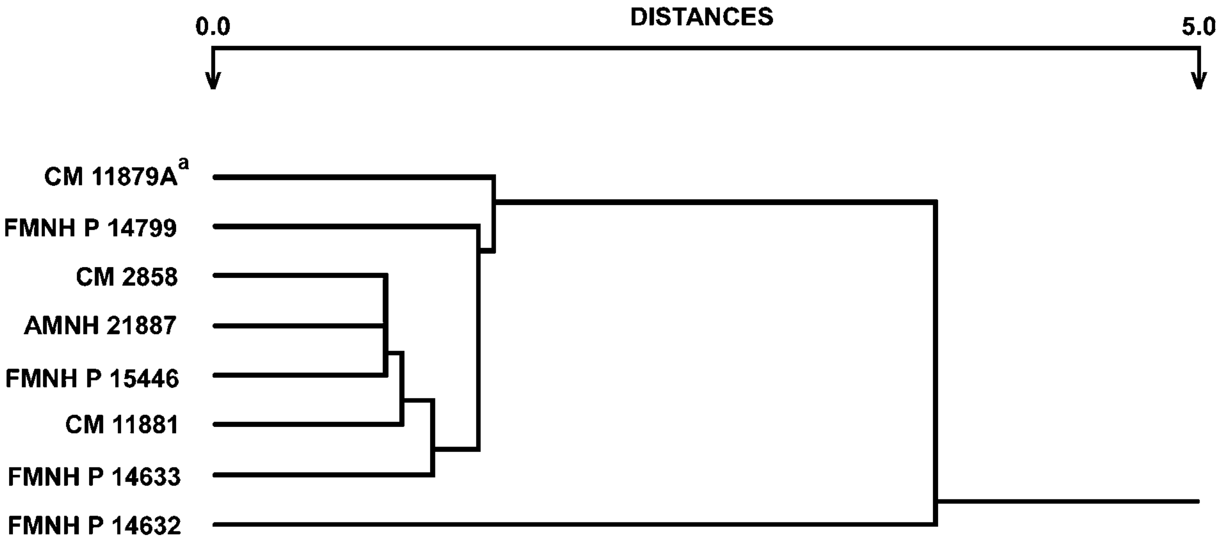

FIGURE 23. Cluster dendrogram for specimens of *Pseudodiplacodon* resulting from a cluster analysis of all variables listed in Table 17. **a**, type of *Pseudodiplacodon progressum*.

All of the known specimens of *Pseudodiplacodon* (Fig. 22) are from the Uinta Basin of Utah and all but one are recorded from the Myton Member of the Uinta Formation. CM 2858 was originally reported (Peterson 1914a) from the upper part of Uinta B (Wagonhound Member), but in 1934 Peterson stated that this level might be at the base of Uinta C (Myton Member). Regardless of the correct stratigraphic level, there does not appear to be any morphological difference between CM 2858 and the specimens of *Pseudodiplacodon* clearly documented from the Myton Member. Furthermore, although CM 2858 is rather poorly preserved and cannot be thoroughly measured, it appears to fall within the size range of the Myton specimens as well. Thus, there is no reason at present to separate CM 2858 from the other specimens for the purpose of statistical analysis. Table 17 shows that the individual and average values of V for the sample of *Pseudodiplacodon* are generally within the parameters of a single extant mammalian species. Almost three quarters of the individual values of V are within the range of 4 to 10 and, of those that are not, five out of nine are less than 4, suggesting that the samples from which they are derived are too small to show all of the variation originally present. Two of the values of V that are greater than 10 are based on canine size, which might suggest sexual dimorphism. Diastema length is another variable for which the value of V is greater than 10, but the value of V for diastema length is very high in all brontothere genera analyzed for this study. Only a single value of V greater than 10 (width of left P3) cannot be attributed to high intraspecific variation or to sexual dimorphism. The values of V (rounded to the nearest whole number) for the width of the right P3 and the length of both P3's is within the range of 4 to 10, however, so this single high value can probably be discounted. Thus, an analysis of the coefficient of variation for the sample suggests that the sample is homogeneous and gives no indication that more than a single taxon is represented.

Cluster analysis (Fig. 23) also generally suggests homogeneity in the sample, although there is a single specimen (FMNH P 14632) that groups out separately. This is a very large individual that is well outside of the size range for most *Pseudodiplacodon* specimens and is within the size range of *Eotitanotherium*. Although the large size of this individual could suggest that it represents a distinct and as yet unnamed species, I am not inclined to recognize a new taxon at this time. I do not believe that the finding of a single discontinuously large individual is sufficient grounds for the recognition of a new species, especially considering that the coefficient of variation for the majority of variables in the total *Pseudodiplacodon* sample is well within the limits established for a single species. In my opinion, in order to demonstrate that a second taxon is present, a sample of larger individuals would have to be obtained that can be compared statistically against the specimens of more typical size already analyzed.

TABLE 17. Summary statistics for the genus *Pseudodiplacodon.* (all measurements in millimeters)

	n	Range	M	s	V
Basilar Length Skull[a]	4	530.8–587.8	563.9	±24.1	4.3
Length Cheek Tooth Series[a]	6	223.5–248.5	231.8	±9.0	3.9
Length P2 to M3[a]	6	207.3–232.3	217.0	±8.9	4.1
Length Premolar Series[a]	6	84.5–94.5	88.5	±3.4	3.8
Length Molar Series[a]	6	138.0–156.8	145.9	±6.3	4.3
Length Diastema[a]	3	20.5–32.5	25.5	±6.3	24.7
Length Left M3	5	54.0–59.0	55.8	±2.0	3.6
Length Right M3	6	52.5–63.0	55.9	±4.0	7.2
Width Left M3	5	49.8–56.3	52.4	±2.6	5.0
Width Right M3	4	49.5–52.6	51.2	±1.4	2.7
Length Left M2	2	50.0–53.0	51.5	±2.1	4.1
Length Right M2	5	51.0–54.5	52.3	±1.4	2.7
Width Left M2	5	46.8–54.4	49.2	±3.1	6.3
Width Right M2	4	46.3–52.4	49.6	±2.6	5.2
Length Left M1	2	39.0–41.5	40.3	±1.8	4.5
Length Right M1	5	36.5–41.0	39.2	±2.1	5.4
Width Left M1	3	39.2–42.0	40.7	±1.4	3.4
Width Right M1	3	37.5–41.5	39.8	±2.1	5.3
Length Left P4	5	25.0–29.0	27.5	±1.6	5.8
Length Right P4	5	26.0–28.0	27.2	±0.9	3.3
Width Left P4	5	32.3–37.8	35.2	±2.6	7.4
Width Right P4	6	32.0–38.8	34.3	±2.5	7.3
Length Left P3	4	23.5–27.0	24.9	±1.5	6.0
Length Right P3	5	24.0–26.5	25.3	±1.0	4.0
Width Left P3	5	24.7–33.7	28.6	±3.5	12.2
Width Right P3	6	24.9–33.6	28.5	±2.9	10.2
Length Left P2	6	20.0–23.0	21.9	±1.1	5.0
Length Right P2	5	21.0–22.5	21.8	±0.6	2.8
Width Left P2	7	22.2–25.8	23.2	±1.2	5.2
Width Right P2	4	22.0–27.1	23.8	±2.2	9.2
Buccal-Lingual Width Left Canine	3	20.1–24.7	22.0	±2.4	10.9
Buccal-Lingual Width Right Canine	3	19.2–24.9	21.4	±3.1	14.5
Mesial-Distal Width Left Canine	2	21.4–23.2	22.3	±1.2	5.4
Mesial-Distal Width Right Canine	4	20.6–24.2	21.9	±1.6	7.3
AVERAGE V					5.8[b]

[a] Based, whenever possible, on an average of left and right measurements.

[b] Excluding Diastema Length.

As indicated above, two of the coefficients of variation for canine size (buccal-lingual width of the left and right canines) are greater than 10 and may indicate that canine size is sexually dimorphic. Unfortunately, the samples upon which these figures are based are too small to clearly establish whether canine size is bimodally distributed. It should be noted, however, that the high coefficient of variation for these two variables is due entirely to the single large individual (FMNH P 14632) discussed above. If this individual is dropped from the analysis and the coefficient of variation recalculated with the remaining two individuals in the sample, the values for V become 3.8 and 3.1 for the left and right canine respectively. Thus, if the large individual represents a distinct taxon, there is no evidence at present for sexual dimorphism in canine size for the smaller members of the sample. Alternatively, the single large individual could represent a male while the other seven individuals represent females.

As pointed out by Mader (2000), the low sample size in this statistical study limits its reliability. It should be repeated, therefore, if additional specimens of *Pseudodiplacodon* become available.

Species *PSEUDODIPLACODON progressum* (Peterson 1934)

Holotype. CM 11879A, a skull (Fig. 22) and lower jaw.

Referred specimens. AMNH 21887, CM 2858, CM 11881, FMNH P 14632, FMNH P 14633, FMNH P 14799, FMNH P 15446.

Diagnosis. Same as the generic diagnosis.

Genus *EOTITANOTHERIUM* Peterson 1914c

= *Diploceras* sensu Peterson 1914a

Age. Uintan.

Subage. Late Uintan.

Type species. *E. osborni* (Peterson 1914a).

Included species. Genus is monospecific.

Diagnosis. Large-sized (length P2 to M3 approximately 221–236 mm) diplacodont brontothere with short, angular horns that are elliptical in cross-section; gracile nasals that are distally rounded and downturned; and two well separated lingual cusps on P4. In general, the length of the cheek tooth series is longer than in most specimens of *Pseudodiplacodon*, but the skull is smaller in size.

Discussion. In 1914 O.A. Peterson described a new brontothere taxon, *Diploceras osborni*, based on the anterior part of a skull (Fig. 24) and jaws with a large part of the postcranial skeleton (CM 2859; Peterson 1914a). Shortly later, Peterson (1914c) changed the generic name to *Eotitanotherium* when it came to his attention that the name *Diploceras* was occupied by a mollusk. In addition to the type specimen, Peterson (1914a) had also designated several paratypes for "*Diploceras*" *osborni*, which included a skull (CM 2858) that is referable to *Pseudodiplacodon progressum* (see Mader 2000).

Osborn (1929, p. 196) stated that *Eotitanotherium* is doubtfully separated from *Diplacodon* Marsh, but he provisionally (p. 435) recognized both as valid genera. Mader (1989; 2000) also noted the close similarity between *Eotitanotherium* and *Diplacodon* but refrained from synonymizing the genera because of the poor condition of Marsh's type of *Diplacodon elatus* (the type species of *Diplacodon*), the relatively few specimens of *Eotitanotherium* that are known, and our poor understanding of Uintan horned brontotheres in general.

Eotitanotherium has two distinct lingual cusps on the third and fourth upper premolars. This morphology contrasts with specimens of *Pseudodiplacodon*, in which the lingual cusps on P3 and P4 are poorly separated. The premolars of *Eotitanotherium* are very similar, however, to the premolars of the type of *Diplacodon elatus*, in which the lingual cusps on P3 and P4 are quite distinct and well separated.

Mader (1989) reported that the type of *Diplacodon elatus* is 6 to 7% larger (based on tooth measurements) than the largest specimen of *Pseudodiplacodon*, while it is very similar in size to specimens of *Eotitanothe-*

rium. Later, however, Mader (2000) noted that this observation is no longer entirely valid since there is one specimen of *Pseudodiplacodon* (FMNH P 14632) that falls within the size range of *Eotitanotherium* and the type of *Diplacodon elatus*.

It is very likely that *Eotitanotherium* is a junior synonym of *Diplacodon*, but the type of *Diplacodon elatus* is so poorly preserved that it is difficult to be certain of this. Furthermore, the specimens of *Eotitanotherium* that are available are so few and so fragmentary that it cannot be honestly said that the taxon has been well characterized. As a group, Uintan aged horned brontotheres are still rather poorly known, and I believe that there is at least one valid genus in addition to the three recognized here (see Discussion section for *Protitanotherium*). I continue, therefore, to refrain from formally synonymizing *Eotitanotherium* and *Diplacodon*. For the purposes of the present paper I regard *Eotitanotherium* as a valid taxon but treat *Diplacodon* as a nomen dubium. When Uintan horned brontotheres are better understood, it may be possible to determine with certainty whether the type of *Diplacodon elatus* represents the same taxon as the type of *Eotitanotherium osborni*.

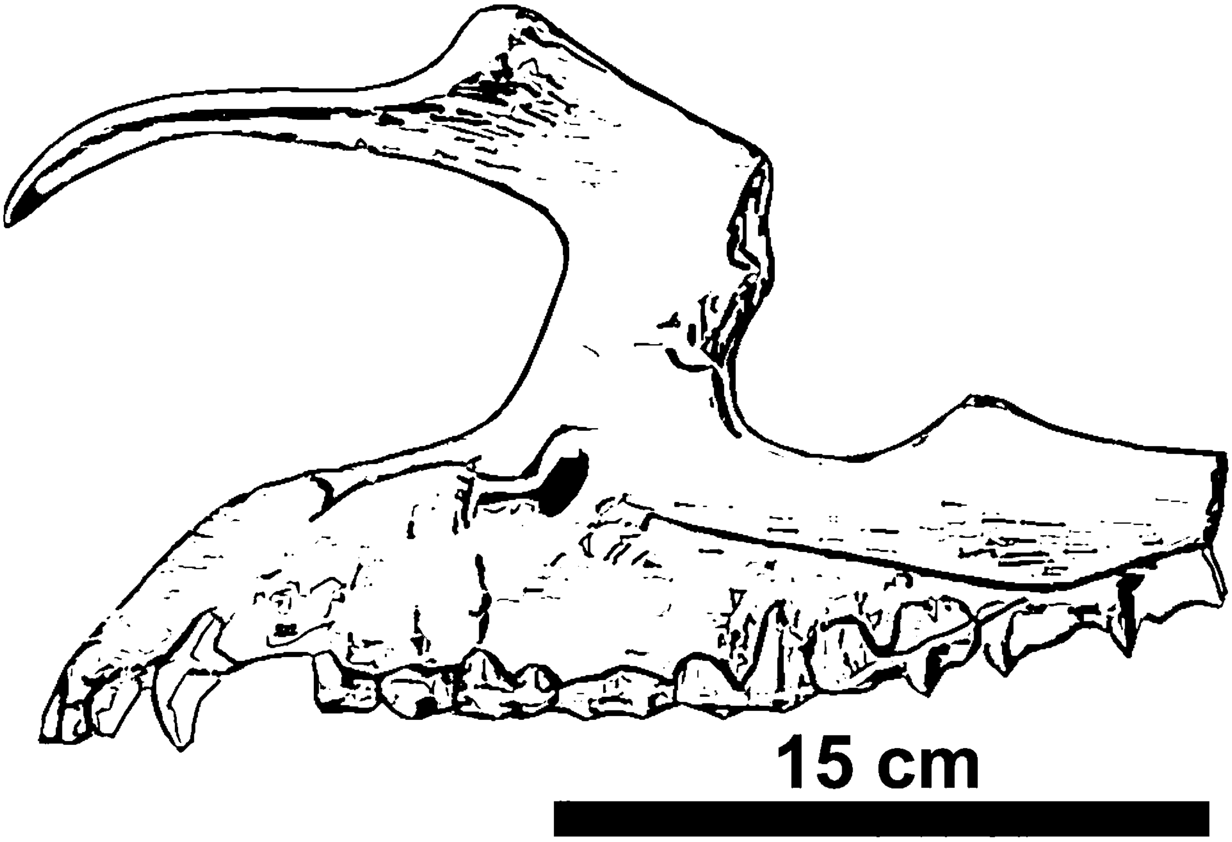

FIGURE 24. Holotype skull of *Eotitanotherium osborni* (CM 2859) in lateral view. After Peterson, 1914a.

As noted with regard to the genus *Pseudodiplacodon*, above, Mihlbachler (2005) synonymized that taxon with *Eotitanotherium* and incorporated both into a single species, *Diplacodon elatus*. Although Mihlbachler asserted that there is a morphological continuum between specimens assigned by Mader (1989; 2000) to *Pseudodiplacodon* and *Eotitanotherium,* I believe that there are several important faults with his analysis. The morphology of the horn (as opposed to horn size) is distinctly different between the two forms and, despite the claim to the contrary, the differences in premolar morphology cited by Mader (2000; present paper) remain valid. Furthermore, the fact that *Eotitanotherium* is smaller in size, but has a longer tooth row than *Pseudodiplacodon,* suggests an adaptive difference and implies that they should be considered discreet taxa. For a more detailed consideration of these various arguments, see the Discussion section of the present paper for the genus *Pseudodiplacodon*.

Pilgrim (1925) described several brontothere remains from the Pondaung Formation of Burma, which he provisionally referred to the genus *Eotitanotherium* and named *Eotitanotherium* (?) *lahrii*. Colbert (1938) selected from among Pilgrim's cotypes a right maxilla fragment with two teeth intact (GSI C342) as a lectotype for the species. Colbert, however, tentatively recognized this taxon as a valid species of *Metatelmatherium* rather than of *Eotitanotherium*. As Colbert (1938) noted, the lectotype of this taxon is so imperfectly preserved that it is practically impossible to make conclusions about its taxonomic position and, in light of this difficulty, I believe that *Eotitanotherium* (?) *lahrii* should probably be regarded as a nomen dubium.

No other North American species of *Eotitanotherium* have been proposed since Peterson named the type species in 1914. Only three skulls are known (see referred specimens for *E. osborni* below) and none of these are complete. Thus the sample is insufficient for a detailed morphologic or statistical analysis and there is no basis for the recognition of more than a single species.

Species *EOTITANOTHERIUM osborni* (Peterson 1914a)

Holotype. CM 2859, the anterior part of a skull with jaws, atlas, axis, scapula, pelvis, and various foot bones.

Referred specimens. CM 11828, CM 11895.

Diagnosis. Same as the generic diagnosis.

BRONTOTHERIIDAE incertae sedis

Genus *STHENODECTES* Gregory 1912

Age. Uintan.

Subage. Early Uintan.

Type species. *S. incisivum* (Douglass 1909).

Included species. Genus is monospecific.

Diagnosis. Large-sized (average length P2 to M3 in CM 2398 is 195 mm) brontothere with six very large, spatulate upper incisors and a very long, pointed canine.

Discussion. The type skull of *Sthenodectes incisivum* (Fig. 25) was described in 1909 by Douglass who provisionally identified it as a new species of *Telmatherium*, *T. incisivum*. Despite this identification, Douglass believed that the skull probably represented a genus distinct from *Telmatherium* but preferred not to create a new generic name at that time. In 1912, W.K. Gregory also concluded that the specimen was generically distinct from *Telmatherium* and proposed for it the new generic name *Sthenodectes*.

Wilson (1977) named a new species of *Sthenodectes*, *S. australis*, based on a skull (TMM 41723-3) from the Pruett Formation (now the Devil's Graveyard Formation) of Texas. Mader (1989), however, concluded that *Sthenodectes australis* is not referable to this genus at all, but rather is a diplacodont similar to *Protitanotherium*. Mader also stated that the exact generic assignment of "*Sthenodectes*" *australis* is unclear and that it could represent an entirely new genus (see the Discussion section of the present paper for *Protitanotherium*).

Sthenodectes is known from only two or three skulls and, given the extremely small sample size, statistical analysis is not practical at this time. All of these skulls are very imperfectly preserved, but they appear to be very similar in morphology. At present, therefore, there is no basis for the recognition of more than one species.

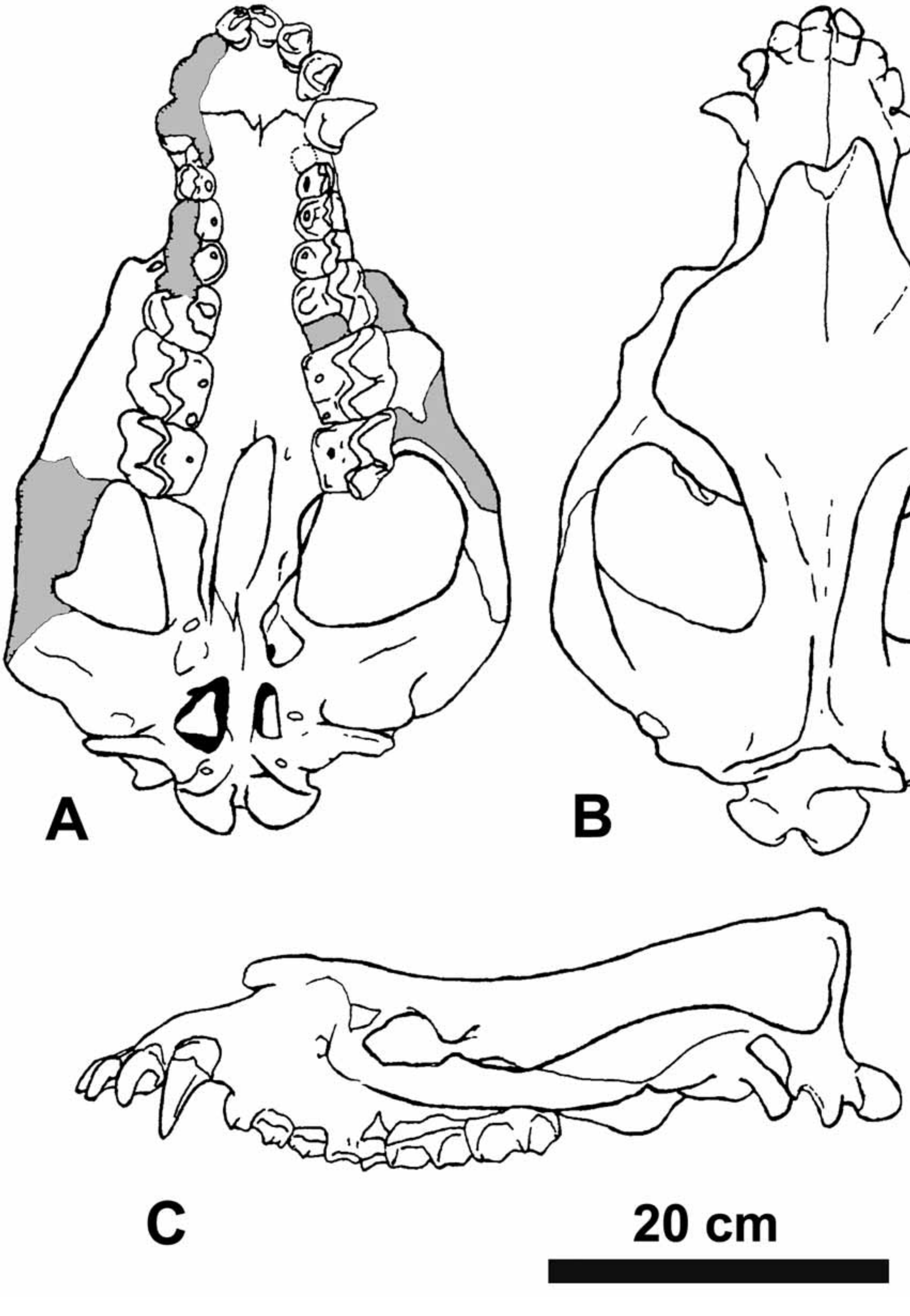

FIGURE 25. Holotype skull of *Sthenodectes incisivum* (CM 2398) in **A**, ventral; **B**, dorsal; and **C**, lateral views. Areas shaded gray are reconstructed. After Osborn, 1929.

Species *STHENODECTES incisivum* (Douglass 1909)

Holotype. CM 2398, a skull crushed dorsoventrally.

Referred specimens. CM 11437, FMNH 12165.

Diagnosis. Same as the generic diagnosis.

Genus *METATELMATHERIUM* Granger and Gregory 1938

Age. Uintan.

Subage. Late Uintan (one specimen assigned to this genus, CM 11380, is from earliest Uintan deposits in the Sand Wash Basin).

Type species. *M. cristatum* Granger and Gregory 1938.

Included species. *M. ultimum* (Osborn 1908).

Diagnosis. Large-sized (length P2 to M3 is approximately 200–211 mm) brontothere in which the zygomatic arch typically exhibits a prominent flange on the ventral surface of the jugal near to where it borders on the squamosal; and in which the lateral nasal incision is shifted forward so as to lie over the upper diastema or P1.

Discussion. *Metatelmatherium* is one of the few brontotheres known to have existed in both North America and central Asia. Specimens of the North American species (Fig. 26) were the first to be discovered and were originally described (Osborn 1908) as a new species of *Telmatherium*, *T. ultimum*. Granger and Gregory (1938), however, correctly concluded that this taxon was not referable to the genus *Telmatherium*, but instead was congeneric with a skull and jaw (AMNH 26411) that they were studying from the Irdin Manha Formation of central Asia to which they assigned the new generic name *Metatelmatherium*.

The type species of *Metatelmatherium*, *M. cristatum*, is from Asia and, according to Granger and Gregory (1938; 1943; see also Mader 1989), is distinguished from the North American species, *M. ultimum*, by its slightly larger size. It should be noted, however, that although the type of *M. cristatum* is larger than any North American specimen of *Metatelmatherium* that I have measured, for most variables the size difference between *M. cristatum* and some North American specimens is minimal. The sample of North American *Metatelmatherium* is small (n = 6) and it is quite possible that North American specimens will eventually be recovered that more closely approach or even exceed the size of the type of *M. cristatum*. There is at least reason to question whether the population from which the type of *M. cristatum* was drawn was significantly larger (in a statistical sense) than the population from which the North American specimens were drawn. I do not believe, therefore, that there is sufficient evidence to separate the North American and central Asiatic forms at the species level on the basis of size.

In addition to the presumed greater size of *Metatelmatherium cristatum* over *M. ultimum*, Granger and Gregory (1943) listed the following as "specific and individual" characters of *M. cristatum*: P1 very large and roundly compressed; P2 large and asymmetric; P3 and P4 moderately wide with but a slight cingulum; anterior border of orbit to front of canine 190 mm (160 mm in *M. ultimum*); occiput relatively broad; lower jaw differing from *M. ultimum* in its short, low, broad coronoid process, relatively deeper ramus, and longer more sloping symphysis; and P3 relatively wider than in *Epimanteoceras* (an Asian taxon not discussed in the present paper) but relatively less wide than in *Desmatotitan* (another Asian taxon). Because Granger and Gregory list these as specific and "individual" characteristics, they evidently did not regard all of these characters as diagnostic of the species but considered some to be merely descriptive of the type specimen. If this is the case, Granger and Gregory did not specify which of these characters they regarded as diagnostic.

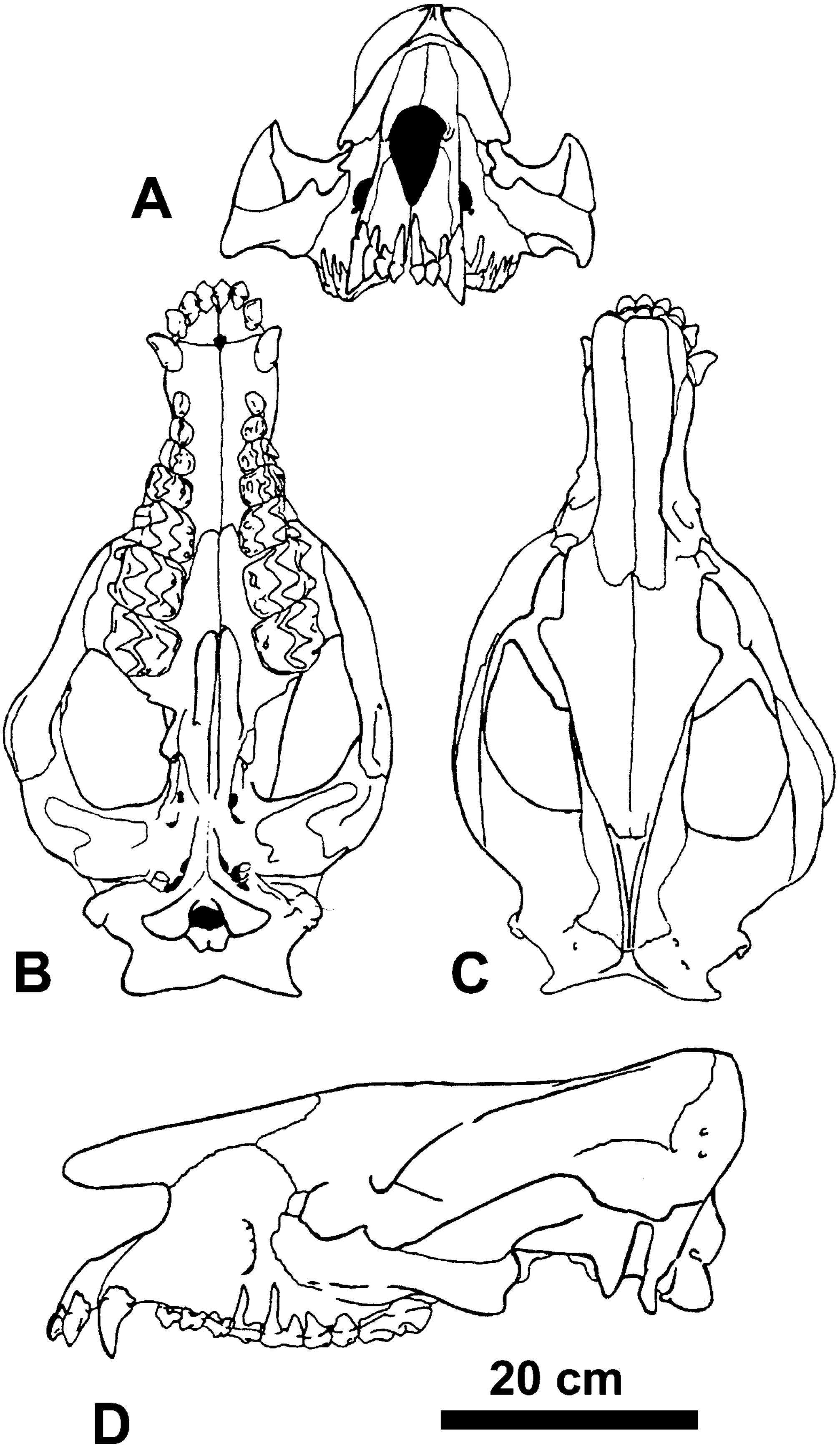

FIGURE 26. Holotype skull of *Metatelmatherium ultimum* (AMNH 2060) in **A**, anterior; **B**, ventral; **C**, dorsal; and **D**, lateral views. A, B, and C after Osborn, 1929; D after Osborn, 1908 and 1929.

After my own examination of the type of *Metatelmatherium cristatum* I find that the following characters (cited in part by Granger and Gregory) are potentially diagnostic of the species: compared to specimens of *M. ultimum* the posterior cusp on P1 is higher and wider, the P2 is proportionately larger, the cingula on P3 and P4 are thinner, the occiput is broader, the coronoid process is broader, and the mental symphysis is longer and more sloping. Because these morphological difference are based on a comparison of only a few specimens (AMNH 26411, the type of *M. cristatum*; AMNH 2060, the type of *M. ultimum*; and AMNH 2004, a referred specimen of *M. ultimum*), however, I am skeptical that they will all prove to be of diagnostic value once the intraspecific variation of each species is better understood. Of all the characters listed above, the relatively long and more sloping mandibular symphysis of *M. cristatum* seems most likely to continue to be a valid diagnostic character when more specimens become available. Most recently, Mihlbachler (2005) has synonymized *M. cristatum* with *M. ultimum*, but for the present, given their wide geographic separation, I prefer to continue regarding them as distinct. If Mihlbachler is correct, however, then *M. cristatum* Granger and Gregory, 1938, (the type species of *Metatelmatherium*) will become invalid and a junior synonym of *M. ultimum* (Osborn 1908).

In addition to *Metatelmatherium cristatum*, two other Asian species of *Metatelmatherium* have been named: *M. browni* from the Pondaung Formation of Burma (Colbert 1938), and *M. parvum* from the Irdin Manha Formation of central Asia (Granger & Gregory 1943). A third Asian taxon, *Eotitanotherium* (?) *lahrii* from the Pondaung Formation of Burma, was referred to *Metatelmatherium* by Colbert (1938). In my opinion, *M. browni*, *M. parvum*, and *M. lahrii* are all probably nomina dubia (and are treated here as such), but, since these are Asian taxa, a detailed discussion of the reasons for not accepting their validity is beyond the scope of the present paper.

In North America only a few skulls of *Metatelmatherium* are known, most of Late Uintan age. There are four Late Uintan specimens that are clearly referable to *Metatelmatherium* (AMNH 2060, the type of *M. ultimum*; AMNH 2004; CM 2339; and CM 2388, the type of "*Manteoceras*" *uintensis*), all from the Myton Member of the Uinta Formation. Of these four specimens, only three are measurable (CM 2339 lacks dentition), making the sample too small to analyze statistically. A badly crushed skull (AMNH 2029) from the Myton Member of the Uinta Formation is also probably referable to *Metatelmatherium*, but does not significantly increase the sample size. All of the Late Uintan specimens are highly similar in morphology and there is no basis for the recognition of more than a single Late Uintan species of *Metatelmatherium*. A skull (CM 11380) from the Sand Wash Basin of Colorado, however, may represent a distinct Early Uintan species and Mihlbachler (2005) has gone even further and assigned this specimen to a new genus.

The Sand Wash specimen is of earliest Uintan age and lacks the characteristic flange on the zygomatic arch. In all other respects, however, it closely resembles specimens of *Metatelmatherium ultimum* from the Uinta Basin. Given the earlier temporal occurrence and difference in zygomatic arch morphology, the Sand Wash skull might represent a species different from *M. ultimum*. Although I have previously stated (Mader 1989) that I am inclined to regard the difference in zygomatic arch morphology as intraspecific variation and probably sexual dimorphism, I am now less certain of this conclusion. I am not willing, however, to recognize a new taxon until more Late Uintan specimens of *Metatelmatherium ultimum* are available so that the variation of *M. ultimum* can be better documented. Even if the specimen should be regarded as a new species, however, I find no justification for Mihlbachler's (2005) suggestion that it be placed in a new genus.

Osborn (1908; 1929) illustrated (see Figs. 26D and 27A) a lateral view of the type skull of *Metatelmatherium ultimum* showing an arrangement of the cranial sutures in which the nasal is excluded from contact with the lacrimal by the frontal and maxilla, which are in broad contact. The same morphology occurs in metamynodontine rhinoceroses, and Wall (1989) has used this suture pattern as one of the synapomorphies defining that tribe. If Osborn was correct in his interpretation of the cranial sutures, this pattern would be an excellent derived character for *M. ultimum* and perhaps for the genus *Metatelmatherium* in general. Gregory (1920) demonstrated that the nasal-lacrimal contact is plesiomorphic for perissodactyls, and it appears that this is the typical arrangement in brontotheres. I have confirmed that the nasal is in contact with the lacrimal in *Palaeosyops*, *Mesatirhinus*, *Metarhinus*, *Sphenocoelus* (= *Dolichorhinus*), and *Telmatherium*.

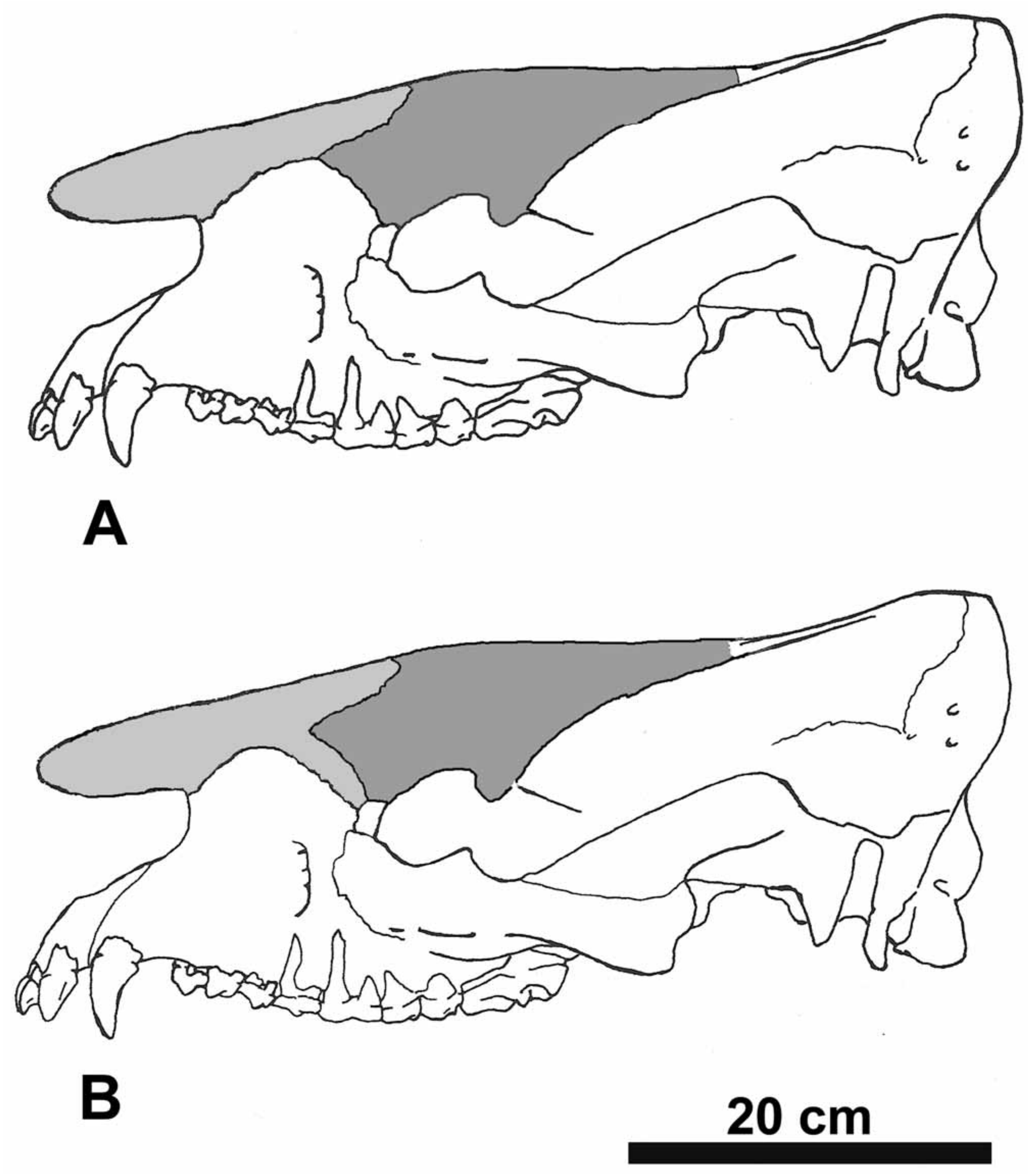

FIGURE 27. Reconstruction of the anterior cranial suture pattern in the holotype of *Metatelmatherium ultimum* (AMNH 2060). **A**, pattern according to Osborn, 1908 and 1929; **B**, pattern suggested in the present paper based on the morphology of other brontothere genera. Light gray shading, nasals; dark gray shading, frontals. Both illustrations after Osborn, 1908 and 1929.

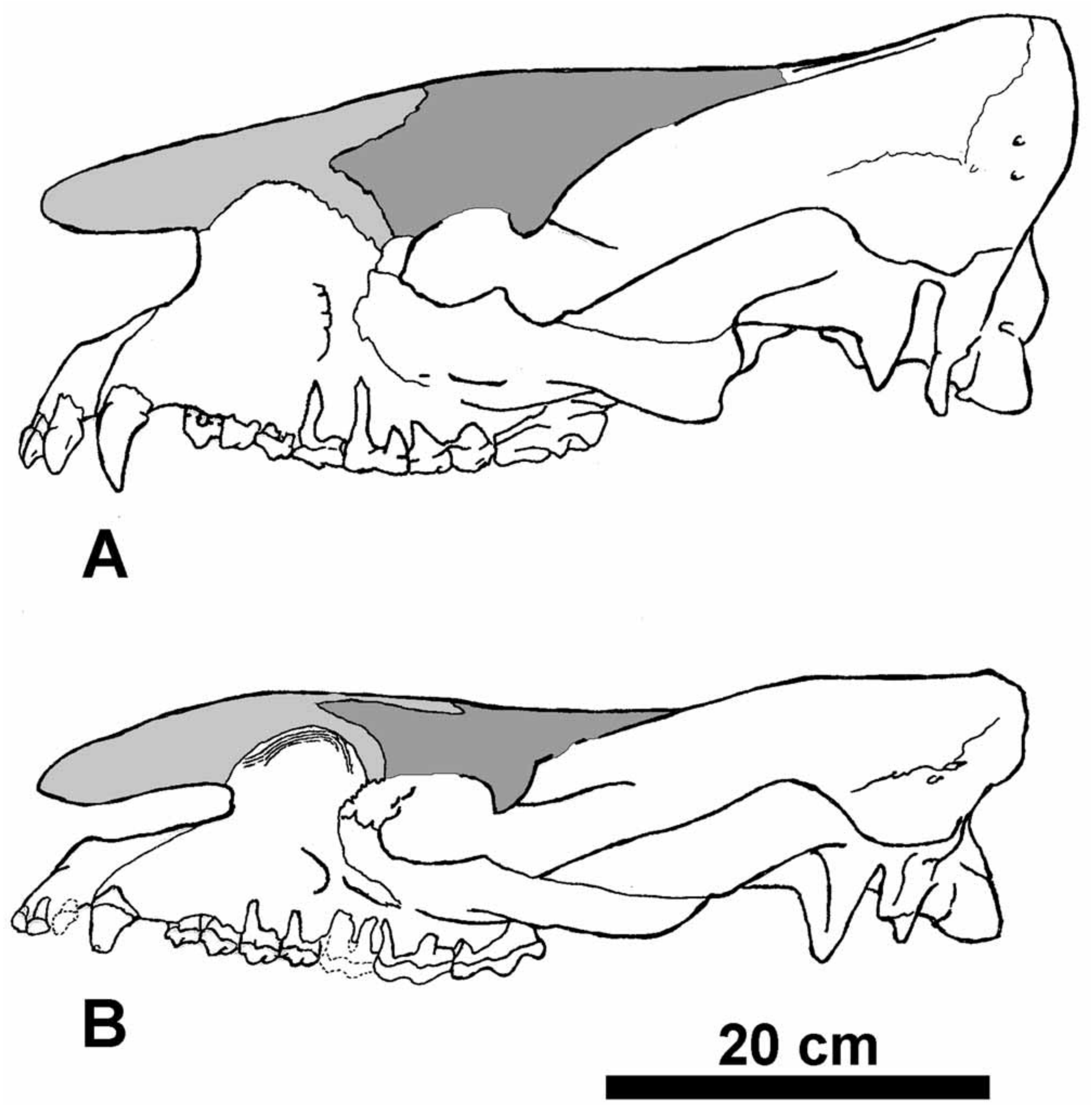

FIGURE 28. Comparison between the anterior cranial suture pattern of *Metatelmatherium* and the brontotheriine brontothere *Telmatherium*. **A**, partly hypothetical (see text) reconstruction of the cranial suture pattern in *Metatelmatherium ultimum* (AMNH 2060, type); **B**, anterior cranial suture pattern of *Telmatherium validus* (AMNH 12678). Light gray shading, nasals; dark gray shading, frontals. A after Osborn, 1908 and 1929; B after Osborn, 1929.

It is very difficult to discern the pattern of cranial sutures in the type skull of *Metatelmatherium ultimum*, however, and I have not been able to confirm Osborn's observation on this or any other specimen of *M. ultimum* that I have examined. I suspect that the arrangement of the nasal and lacrimal may be the same in *M. ultimum* as it is in other brontotheres (see Fig. 27B and 28). At least the exclusion of the contact between the nasal and lacrimal should not be used as a diagnostic character of *M. ultimum* or the genus *Metatelmatherium* until this arrangement can be more clearly demonstrated.

Although I have not been able to confirm that the nasals are excluded from contact with the lacrimal, I have been able to confirm that a triangular projection of the frontal overlaps the nasal as illustrated by Osborn.

This morphology is rather similar to that of the Brontotheriinae and may indicate that *Metatelmatherium* is either a member of this subfamily or is closely allied to it (see Fig. 28).

Interestingly, it is possible to artificially approximate the skull of *Metatelmatherium* by electronically warping an image of a *Telmatherium* skull. Figure 29 shows a skull of *Telmatherium* that has been modified using the transform (warp and distort) function of Adobe Photoshop CS3 Extended. By warping the entire image and selected parts of it separately, it is possible to produce an illustration that is very similar in appearance to *Metatelmatherium*. Based on this photographic manipulation it seems entirely plausible that *Metatelmatherium* may have been directly derived from *Telmatherium* or something very much like it (although this is certainly not proven).

I have previously expressed the opinion, however, that *Metatelmatherium* may be closely allied to *Sthenodectes* and have suggested that the two might be placed in a separate brontothere subfamily the *Metatelmatheriinae* (Mader 1989). This relationship is suggested by the relatively large size of the incisors in both genera and by the possibility that the lateral nasal incision may be shifted forward in *Sthenodectes* as it is in *Metatelmatherium*. Given the present uncertainties, I have chosen not to assign *Metatelmatherium* and *Sthenodectes* to a particular subfamily and have instead treated them as Brontotheriidae incertae sedis.

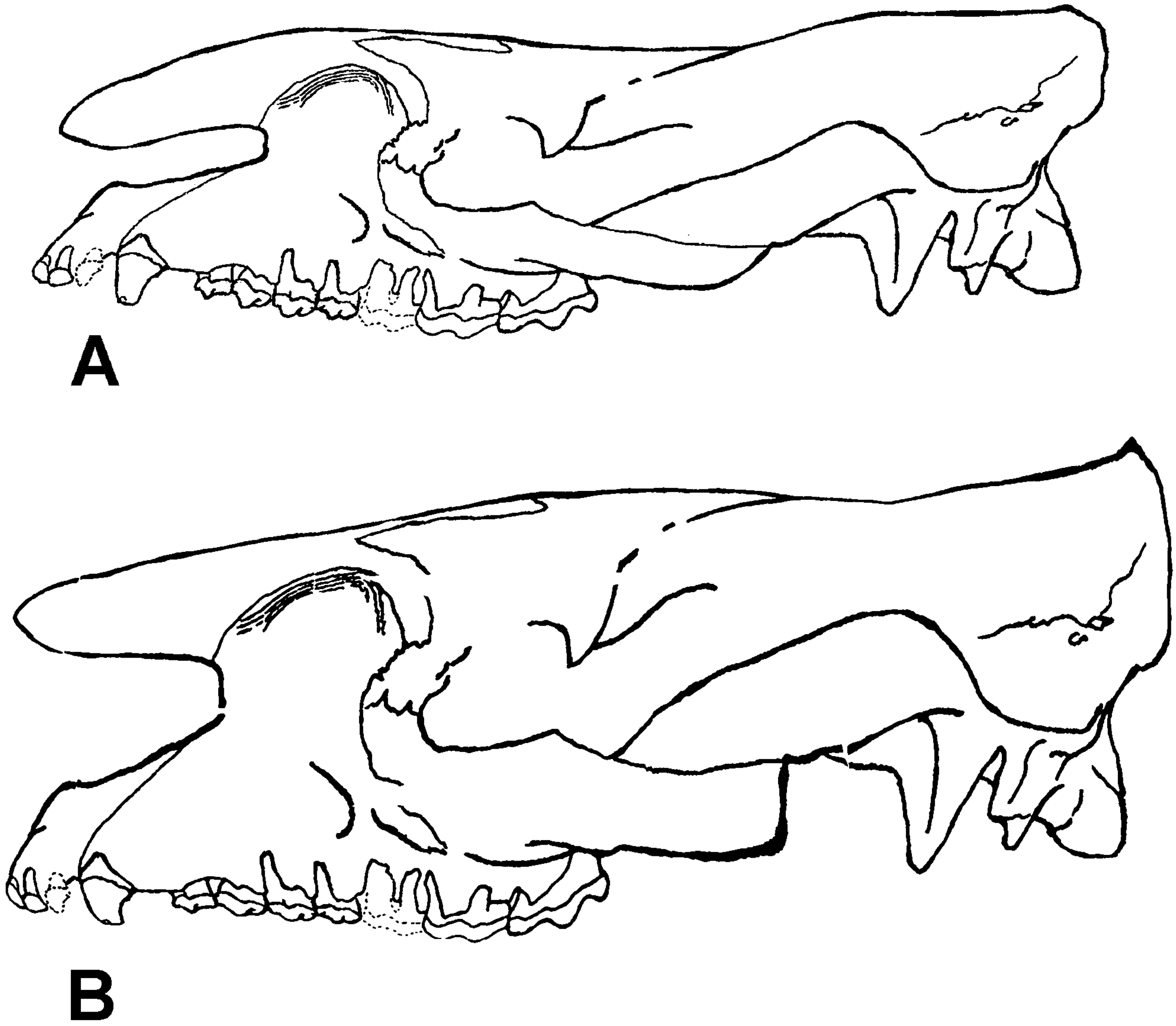

FIGURE 29. Electronically altered image of *Telmatherium* skull approximating the morphology of *Metatelmatherium*. **A**, skull of *Telmatherium* (AMNH 12678); **B**, the same image modified using the transform (warp and distort) function of Adobe Photoshop. A after Osborn, 1929.

Species *METATELMATHERIUM cristatum* Granger and Gregory 1938

Holotype. AMNH 26411, a skull and lower jaw.

Referred specimens. Type specimen only.

Diagnosis. Species of *Metatelmatherium*, probably distinguished by an elongated and broadly sloping mandibular symphysis. The taxon may also be distinguished by a relatively high and wide posterior cusp on P1, relatively large P2, relatively thin cingula on P3 and P4, relatively broad occiput, and a relatively broad coronoid process.

Discussion. Because the type species of *Metatelmatherium* is an Asian taxon it is not properly within the scope of the present paper. Nevertheless, because it is the type species of a taxon found in North America, it must be briefly discussed here. As noted above, Mihlbachler (2005) has regarded this species as a junior synonym of *M. ultimum* from North America, but for the present, I prefer to continue to regard *M. cristatum* as valid.

The type specimen of *Metatelmatherium cristatum* was collected by the American Museum of Natural History's Central Asiatic Expedition of 1930 from the Camp Margetts Area (Huhebolhe Cliff), 25 miles (approximately 40 km) south-southwest of Erhlien (Iren Dabasu) in the Inner Mongolian Autonomous Region (Li & Ting 1983, p. 25). Since that time no other specimen of *M. cristatum* has been reported although, several authors (Chow 1957; Tang & Chow 1964; Tang *et al*. 1974; Ding *et al*. 1977) have referred material from the Guangxi Province of southern China to *M. browni* (here regarded as a nomen dubium) or *Metatelmatherium* sp. I am not certain whether this material represents the genus *Metatelmatherium* but, if it does, it may be referable to *M. cristatum*.

Species *METATELMATHERIUM ultimum* (Osborn 1908)

= *M. uintensis* (Douglass 1909)

Holotype. AMNH 2060, a skull and lower jaw.

Referred specimens. AMNH 2004, CM 2339, CM 2388 (holotype of "*Manteoceras*" *uintensis*), CM 11380. AMNH 2029, a badly crushed skull also appears to be referable to this species.

Diagnosis. Species of *Metatelmatherium* distinguished from the type species by the shorter mandibular symphysis and possibly by a relatively short and less wide posterior cusp on P1, relatively small P2, relatively thick cingulum on P3 and P4, relatively narrow occiput, and relatively narrow coronoid process.

Discussion. As noted in the preceding discussion for the genus *Metatelmatherium*, Osborn described the holotype skull (Fig. 26) and lower jaw of *M. ultimum* (AMNH 2060) in 1908 and recognized it as a new species of *Telmatherium*. After examining this specimen, however, Granger and Gregory (1938) correctly concluded that *Telmatherium ultimum* Osborn was congeneric with the Asian brontothere *Metatelmatherium cristatum*.

In 1909 Douglass described the front part of a skull (CM 2388) from the Uinta Basin of Utah, which he identified as a new species of *Manteoceras, M. uintensis* (Fig. 30A1 and A2). In 1929 Osborn upheld this identification, but Mader (1989) concluded that this skull is not referable to *Telmatherium* (= *Manteoceras*) but is instead a specimen of *Metatelmatherium*. This conclusion was based on the skull's large canine, long diastema, and forwardly placed lateral incision of the external nares, all of which are diagnostic of *Metatelmatherium* (see Fig. 30). The zygomatic arches are imperfectly preserved in the type skull of "*Manteoceras*" *uintensis*, but may have had the flange on the underside of the jugal that is also diagnostic of *Metatelmatherium*.

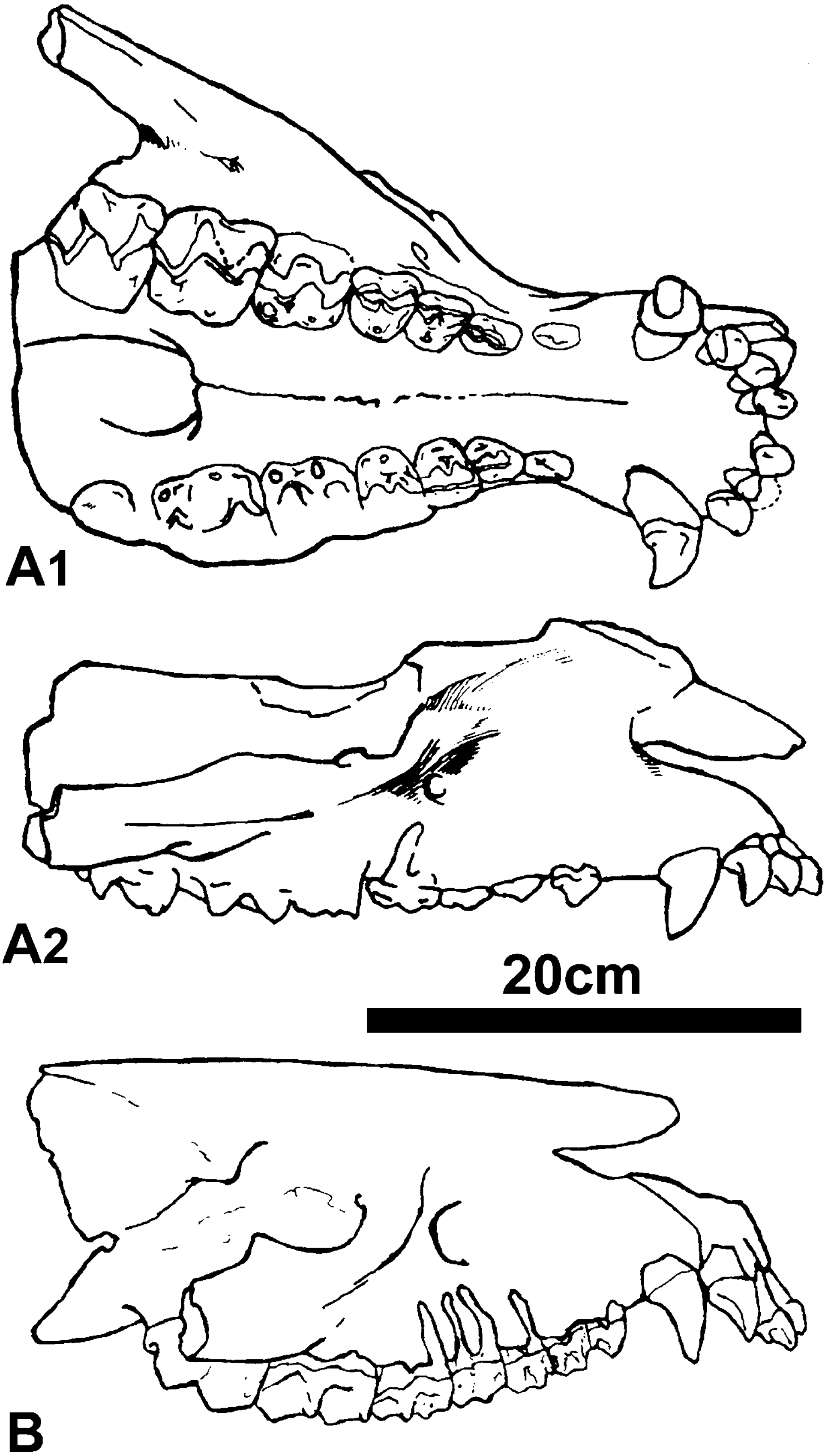

FIGURE 30. Comparison between the holotype skull of *Manteoceras uintensis* (CM 2388) and a skull of *Metatelmatherium ultimum*. A1, holotype skull of *Manteoceras uintensis* in ventral view; A2, the same in lateral view; B, skull of *Metatelmatherium ultimum* (AMNH 2004, reversed). All figures after Osborn, 1929.

Osborn (1929) listed the following characters, which he believed allied Douglass's specimen to *Manteoceras*: the presence of round-topped incisors; robust, recurved canines; twin convexities on the premolar ectolophs; a broad, subhypsodont M3 with large parastyle and mesostyle; and widely arched zygomata. Each one of these characters is also typical of *Metatelmatherium*, however, and I restate my opinion that the similarities to *Metatelmatherium* heavily outweigh any similarities to *Telmatherium*.

Most specimens of *Metatelmatherium ultimum* have the distinct flange on the base of the jugal that is apomorphic for the genus. As noted above, however, a skull (CM 11380) referable to *Metatelmatherium* from the Sand Wash Basin of Colorado lacks the characteristic flange but resembles specimens of *Metatelmatherium ultimum* in all other respects. Because of this morphologic difference and the earlier age of the Sand Wash specimen, it is possible that the specimen represents an entirely new species. Until the intraspecific variation of *M. ultimum* can be better documented, however, I choose to regard the Sand Wash specimen as representing *M. ultimum* and have included it in the list of referred specimens above. Even if the specimen should prove to be a distinct species, however, I find no basis for referring it to a new genus as suggested by Mihlbachler (2005).

Conclusion

I have employed a conservative approach in reaching taxonomic conclusions for the present paper and have not accepted species as valid unless the weight of evidence (morphological and statistical) justified their recognition. Of the nine genera discussed only three are recognized as including more than a single species—*Metarhinus*, *Sphenocoelus*, and *Metatelmatherium*.

Two other genera, *Mesatirhinus* and *Telmatherium*, may include additional species (as suggested by previous authors and supported by cluster analysis), but the evidence for this is not compelling. Morphological analysis and analysis of the coefficient of variation suggest that only a single species should be recognized for each.

It should be noted that, in order to increase the sample size available for statistical analysis, specimens from nearby sedimentary basins were pooled for this study. Thus specimens of *Telmatherium* and *Mesatirhinus* from the Green River Basin were pooled with specimens belonging to the same genera from the Washakie Basin. Similarly, specimens of *Metarhinus* and derived *Sphenocoelus* (formerly *Dolichorhinus*) from the Uinta Basin were pooled with specimens from the Washakie Basin. In the future, should more specimens from these individual basins be collected, it might be useful to repeat these studies to determine whether there are any a significant size differences between the samples from the different locations. My preliminary analysis, however, suggests that the samples taken from nearby basins are essentially the same, both morphologically and statistically (see Mader 1991 for statistical comparisons).

As this paper was being prepared for publication, it came to my attention that a revision of North American and Asian brontotheres by Matthew Mihlbachler was in press. Since the paper has not been published, however, but is based on his doctoral dissertation (2005), I have made several references to that dissertation in the present paper. I assume that the published version, when it becomes available, will not differ significantly from the conclusions appearing in the thesis, but readers would do well to consult the published work once it is in print.

Among the more serious differences between Mihlbachler and the present paper is Mihlbachler’s failure to recognize the validity of the subfamily Dolichorhininae and the erection of two new North American genera that are not considered valid here (being synonyms of *Metarhinus* and *Metatelmatherium*). Mihlbachler gave names to these new taxa, but since they are not yet formally published, it would be improper to cite them here. Similarly, Mihlbachler synonymized *Pseudodiplacodon* and *Eotitanotherium*, which is a conclusion that is not supported in the present study, and regarded *Sphenocoelus* and *Dolichorhinus* (here synonymized) as distinct and not particularly closely related. A neotype suggested by Mihlbachler for *Metarhinus fluviatilis* cannot be regarded as valid according to the international rules of nomenclature, since the original type specimen is still available. There are also several other relatively minor differences between Mader and Mihlbachler, which are addressed in various Discussion sections in the present paper.

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References

Abdi, H. (2007) Bonferroni and Sidak corrections for multiple comparisons. *In*: Salkind, N. J. (Ed), *Encyclopedia of Measurement and Statistics.* Sage Publications, Thousand Oaks, pp. 103–107.

Chow, M.M. (1957) On some Eocene and Oligocene mammals from Kwangsi and Yunnan. *Vertebrata Palasiatica*, 1(3), 201–214.

Colbert, E.H. (1938) Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, 74 (6), 435–436.

Cook, H.J. (1926) New Eocene titanotheres from Moffat County, Colorado. *Proceedings of the Colorado Museum of Natural History*, 6 (3), 12–18.

Cope, E.D. (1872) Second notice of extinct vertebrates from Bitter Creek, Wyoming. *Paleontological Bulletin*, 7, 1–2.

Cope, E.D. (1873) On the new perissodactyls from the Bridger Eocene. *Paleontological Bulletin*, 11, 1–2.

Ding, S., Zheng, J., Zhang, Y. & Tong, Y. (1977) The age and characteristics of the Liuniu and the Dongjun faunas, Bose Basin of Guangxi. *Vertebrata Palasiatica*, 15 (1), 35–45.

Douglass, E. (1909) Preliminary descriptions of some new titanotheres from the Uinta deposits. *Annals of the Carnegie Museum*, 6(2), 304–313.

Earle, C. (1891) On a new species of *Palaeosyops*, *Palaeosyops megarhinus* sp.nov. *American Naturalist*, 25 (289), 45–47.

Earle, C. (1892) A memoir upon the genus *Palaeosyops* Leidy and its allies. *Journal of the Academy of Natural Sciences of Philadelphia*, 2nd series, 9(6), 267–388.

Golz, D.J. (1976) Eocene Artiodactyla of southern California. *Natural History Museum of Los Angeles County Bulletin*, 26, 1–85.

Golz, D.J. & Lillegraven, J.A. (1977) Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. *Contributions to Geology, University of Wyoming*, 15(1), 43–65.

Granger, W. (1909) Faunal horizons of the Washakie Formation of southern Wyoming. *Bulletin of the American Museum of Natural History*, 26 (3), 13–24.

Granger, W. & Gregory, W.K. (1938) Addendum. A new titanothere genus from the upper Eocene of Mongolia and North America. *In*: Colbert, E. H., Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, 74 (6), 435–436.

Granger, W. & Gregory, W.K. (1943) A revision of the Mongolian titanotheres. *Bulletin of the American Museum of Nat-*

ural History, 80 (10), 349–389.

Gregory, W.K. (1912) Note on the upper Eocene titanotheroid *Telmatherium*? *incisivum* Douglass, from the Uinta Basin. *Science*, new ser., 35 (901), 545.

Gregory, W.K. (1920) Studies in comparative myology and osteology, no. IV. A review of the evolution of the lachrymal bone of vertebrates with special reference to that of mammals. *Bulletin of the American Museum of Natural History,* 42, 95–263.

Gunnell, G.F. & Yarborough, V.L. (2000) Brontotheriidae (Perissodactyla) from the late Early and middle Eocene (Bridgerian), Wasatch and Bridger Formations, southern Green River Basin, south western Wyoming. *Journal of Vertebrate Paleontology,* 20 (2), 349–368.

Hatcher, J.B. (1895) On a new species of *Diplacodon*, with a discussion of the relations of that genus to *Telmatotherium*. *American Naturalist*, 29, 1084–1090.

Hay, O.P. (1902) Bibliography and catalogue of the fossil Vertebrata of North America. *Bulletin of the United States Geological Survey*, 179, 1–868.

Howard, R.W. (1975) *The dawnseekers: the first history of American paleontology.* Harcourt, Brace, Jovanovich, Inc., New York, 314 pp.

Leidy, J. (1872) On fossils from Wyoming. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 24, 277.

Li, C. & Ting, S. (1983) The Paleogene mammals of China. *Bulletin of the Carnegie Museum of Natural History*, 21, 1–93.

Lucas, S.G. (1983) *Protitanotherium* (Mammalia, Perissodactyla) from the Eocene Baca Formation, west-central New Mexico. *New Mexico Journal of Sciences*, 23 (2), 39–47.

Mader, B.J. (1989) The Brontotheriidae: a systematic revision and preliminary phylogeny of North American genera. *In*: Prothero, D. R. & Schoch, R. M. (Eds), *The Evolution of Perissodactyls*. Oxford University Press, Oxford Monographs on Geology and Geophysics (15), New York, pp. 458–484.

Mader, B.J. (1991) *The systematics and phylogeny of North American Eocene brontotheres (Mammalia, Perissodactyla).* University of Massachusetts, Amherst, 388 pp.

Mader, B.J. (1998) Brontotheriidae. *In*: Janis, C. M., Scott, K. M. & Jacobs, L. L. (Eds), *Evolution of Tertiary Mammals of North America*. *Volume I: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. Cambridge University Press, New York, pp. 525–536.

Mader, B.J. (2000) *Pseudodiplacodon*, a new generic name for *Diplacodon progressum* Peterson (Mammalia, Perissodactyla, Brontotheriidae). *Journal of Vertebrate Paleontology,* 20(1), 164–166.

Mader, B.J. & Alexander, J.P. (1995) *Megacerops kuwagatarhinus* n. sp., and unusual brontothere (Mammalia, Perissodactyla) with distally forked horns. *Journal of Paleontology*, 69(3), 581–587.

Marsh, O.C. (1872) Preliminary description of new Tertiary mammals, Part I. *American Journal of Science*, 3d series, 4, 122–130.

Marsh, O.C. (1873) Notice of new Tertiary mammals. *American Journal of Science*, 3d series, 5, 407–411, 485–488.

Marsh, O.C. (1875) Notice of new Tertiary mammals, IV. *American Journal of Science*, 3d series, 9, 239–250.

Marsh, O.C. (1880) *List of genera established by Professor O.C. Marsh, 1862–1879*. New Haven, 12 pp.

Martill, D.M. & Turnbull, W.D. (1986) Taphonomy and preservation of a monospecific titanothere assemblage from the Washakie Formation (late Eocene), southern Wyoming. *Fourth North American Paleontological Convention, abstracts*, A53.

Matthew, W.D. (1899) A provisional classification of the fresh-water Tertiary of the west. *Bulletin of the American Museum of Natural History*, 12 (3), 19–75.

McCarroll, S.M., Flynn J.J. & Turnbull, W.D. (1996) The mammalian faunas of the Washakie Formation, Eocene age of southern Wyoming. Part III. The perissodactyls. *Fieldiana*, new series, 33, 1–38.

McKenna, M.C. & Bell, S.K. (1997) *Classification of mammals above the species level*. Columbia University Press, New York, 631 pp.

Mihlbachler, M.C. (2005) *Phylogenetic systematics of the Brontotheriidae (Mammalia, Perissodactyla)*. Columbia University, New York, 763 pp.

Mihlbachler, M.C., Lucas, S.G. & Emry, R.J. (2004) The holotype specimen of *Menodus giganteus*, and the “insoluble” problem of Chadronian brontothere taxonomy. *In*: Lucas, S. G., Zeigler, K. E. & Kondrashov, P. E. (Eds). *Paleogene mammals*. New Mexico Museum of Natural History and Science Bulletin 26, pp. 129–135.

Osborn, H.F. (1890) The Mammalia of the Uinta formation, Part 3, the Perissodactyla. *Transactions of the American Philosophical Society*, new series, 16 (9), 461–572.

Osborn, H.F. (1895) Fossil mammals of the Uinta Basin, Expedition of 1894. *Bulletin of the American Museum of Natural History*, 7 (2), 71–105.

Osborn, H.F. (1908) New or little known titanotheres from the Eocene and Oligocene. *Bulletin of the American Museum of Natural History*, 24 (32), 599–617.

Osborn, H.F. (1914) Recent results in the phylogeny of the titanotheres. *Bulletin of the Geological Society of America*, 25, 403–405.

Osborn, H.F. (1929) *The titanotheres of ancient Wyoming, Dakota, and Nebraska*. U.S. Geological Survey, Monograph 55 (2 volumes), 953pp.

Osborn, H.F., Scott, W.B. & Speir, F. (1878) Paleontological report of the Princeton scientific expedition of 1877. *Contributions from the Museum of Geology and Archaeology of Princeton College*, 1, 1–106.

Owen, R. (1848) Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W.

coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, 4, 103–141.

Perneger, T.V. (1998) What is wrong with Bonferroni adjustments. *British Medical Journal*, 316, 1236–1238.

Peterson, O.A. (1914a) A new titanothere from the Uinta Eocene. *Annals of the Carnegie Museum*, 9 (1–2), 29–52.

Peterson, O.A. (1914b) A small titanothere from the lower Uinta beds. *Annals of the Carnegie Museum*, 9 (1–2), 53–57.

Peterson, O.A. (1914c) Correction of generic name. *Annals of the Carnegie Museum*, 9, 220.

Peterson, O.A. (1924) Osteology of *Dolichorhinus longiceps* Douglass, with a review of the species of *Dolichorhinus* in the order of their publication. *Memoirs of the Carnegie Museum*, 9 (4), 405–473.

Peterson, O.A. (1934) New titanotheres from the Uinta Eocene in Utah. *Annals of the Carnegie Museum*, 22 (3–4), 351–361.

Pilgrim, G.E. (1925) The Perissodactyla of the Eocene of Burma. *Memoirs of the Geological Survey of India* (new series), 8 (3), 1–28.

Prothero, D.R. & Schoch, R.M. (1989) Origin and evolution of the Perissodactyla: summary and synthesis. *In*: Prothero, D. R. & Schoch, R. M. (Eds), *The Evolution of Perissodactyls*. Oxford University Press, Oxford Monographs on Geology and Geophysics (15), New York, 504–529.

Ride, W.D.L., Cogger, H. G., Dupuis, C., Kraus, O., Minelli, A., Thompson, F. C. & Tubbs, P. K. (1999) International Code of Zoological Nomenclature (4th edition), International Trust for Zoological Nomenclature, London. Available from http://www.iczn.org/iczn/ (accessed 22 April 2008).

Riggs, E.S. (1912) New or little known titanotheres from the lower Uinta Formations. *Field Museum of Natural History Publication 159, Geological Series*, 4 (2), 17–41.

Schoch, R.M. & Lucas, S.G. (1985) The Brontotheriidae a group of Eocene and Oligocene perissodactyls from North America, Asia, and Eastern Europe. *In*: Fuller, W.A., Nietfeld, M.T. & Harris, M.A. (Eds), *Abstracts of papers and posters, Fourth International Theriological Congress, Edmonton, Alberta, Canada*, Abstract 0558.

Simpson, G.G. (1945) The principles of classification and a classification of mammals *Bulletin of the American Museum of Natural History*, 85, 1–350.

Simpson, G.G., Roe, A. & Lewontin, R.C. (1960) *Quantitative Zoology*. Harcourt, Brace and World, Inc., New York, 440 pp.

Stock, C. (1937) An Eocene titanothere from San Diego County, California, with remarks on the age of the Poway Conglomerate. *Proceedings of the National Academy of Sciences, Contribution 219*, 23 (2), 48–53.

Tang, X. & Chow, M. (1964) A review of vertebrate-bearing Lower Tertiary of south China. *Vertebrata Palasiatica*, 8(2), 119–133.

Tang, Y., You, Y., Xu, Q., Qiu, Z. & Hu, Y. (1974) The lower Tertiary of the Bose and Yongle Basins of the Guangxi Zhuang Autonomous Region. *Vertebrata Palasiatica*, 12(4), 279–292.

Turbull, W.D. & Martill, D.M. (1988) Taphonomy and preservation of a monospecific titanothere assemblage from the Washakie Formation (late Eocene), southern Wyoming. An ecological accident in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 63, 91–108.

Wall, W.P. (1989) The phylogenetic history and adaptive radiation of the Amynodontidae. *In*: Prothero. D. R. & Schoch, R. M. (Eds), *The Evolution of Perissodactyls*. Oxford University Press, Oxford Monographs on Geology and Geophysics (15), New York, pp. 341–354.

West, R.M. & Dawson, M.R. (1975) Eocene fossil Mammalia from the Sand Wash Basin, northwestern Moffat County, Colorado. *Annals of the Carnegie Museum*, 45 (11), 231–253.

Wilson, J.A. (1977) Early Tertiary vertebrate faunas Big Bend area Trans-Pecos Texas: Brontotheriidae. *The Pearce - Sellard Series*, 25, 1–17.

Woods, S.C. & Stucky, R.K. (1992) Catalogue of the type specimens of fossil vertebrates Denver Museum of Natural History. *Proceedings of the Denver Museum of Natural History*, 3 (2), 1–12.