

2. Methods

SPECIMENS, MEASUREMENT, AND TERMINOLOGY

This study is based on research begun by Earl Manning in the American Museum of Natural History during the early 1970s (when he originally curated the Frick rhino collection), and then continued by myself in the late 1970s and early 1980s until the present. The AMNH and FAM rhino collection served as the nucleus for this study, since in most cases, dozens of skulls, jaws, and even skeletons are known for taxa that were once known only from a single jaw or skull. During the late 1970s and 1980s, I also visited the important rhino collections in most of the important museums around North America, including the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; the Yale Peabody Museum of Natural History, New Haven, Connecticut; the Princeton University collection (now at Yale); the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the Academy of Natural Sciences, Philadelphia, Pennsylvania; the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; the Florida Museum of Natural History, Gainesville, Florida; the Field Museum of Natural History, Chicago, Illinois; the Saskatchewan Museum of Natural History, Regina, Saskatchewan; the University of Nebraska State Museum, Lincoln, Nebraska; the South Dakota School of Mines and Technology, Rapid City, South Dakota; the University of Kansas Museum of Natural History, Lawrence, Kansas; the Texas Memorial Museum, University of Texas, Austin, Texas; the Colorado Museum of Natural History, Denver, Colorado (now the Denver Museum of Nature and Science); the University of California Museum of Paleontology, Berkeley, California; the Natural History Museum of Los Angeles County, Los Angeles, California; and the collections at John Day Fossil Beds, Oregon.

In each of these collections, a standard series of measurements (see the tables in Chapters 4 and 5) were taken with dial

calipers for most of the available specimens. A meter stick and tape-measure were used for longer measurements. Most important specimens were photographed on 35-mm black-and-white film using Nikon cameras, and the descriptions of new specimens were often written in longhand on the spot. In the early 1980s, before personal computers (let alone laptops) and digital calipers, this resulted in an enormous pile of manuscript written on yellow legal pads, and thousands of measurements and sketches on 3" x 5" index cards. Many of these data cards were lost when People Express Airlines (deservedly now out of business) lost my luggage, so I had to return to several museums to remeasure hundreds of specimens. Most of the statistics for these measurements were calculated using Excel spreadsheets.

The landmarks for the measurements of skulls, jaws, and teeth are shown in Figure 2.1. In most cases (such as dental measurements), the landmarks are relatively straightforward, so one can assume that past workers have measured specimens in comparable ways. Whenever possible, I have checked my measurements against those by previous authors such as Wood (1927, 1964) and Tanner (1969, 1975, 1977; Tanner and Martin, 1972), and in most cases, my measurements match theirs within a millimeter or two. In the case of premolar and molar measurements, the landmarks are easy to recognize, since the teeth are nearly rectangular (especially after wear), and the maximum length and width is easy to measure on most specimens. Some variability is introduced on highly worn specimens, because the width of the cheek teeth tends to increase when the tooth is worn down nearly to the base. To a lesser extent, there can be variability of the anteroposterior length of teeth when interstitial or interdental wear takes place. In most cases, if the specimen was extremely worn so that the tooth measurements might be unreliable, or the teeth were damaged or visibly distorted, the measurements were not taken, or notations were made about their reliability.

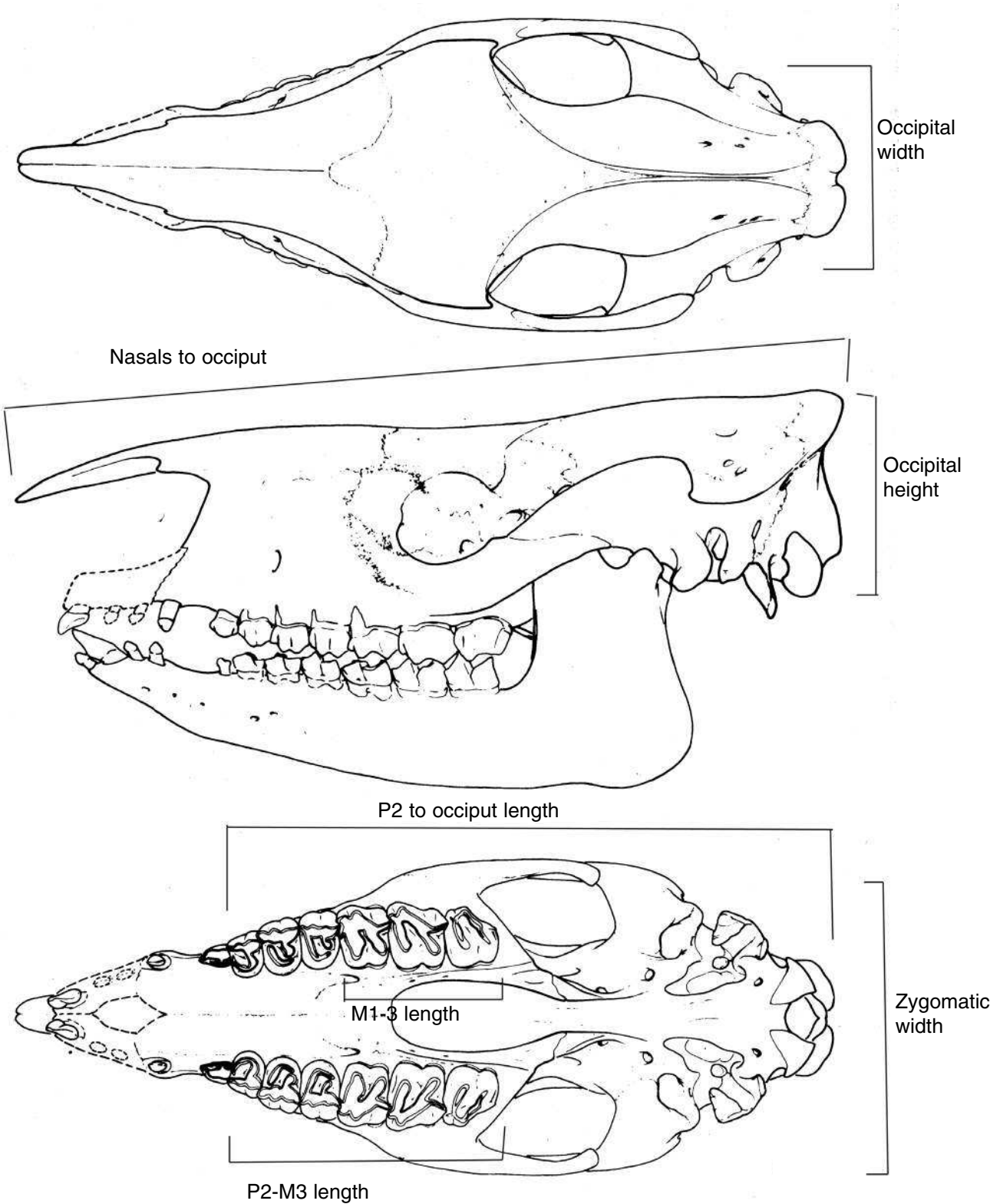


Figure 2.1. Standard measurements of rhinoceros skulls and teeth used in this study. Illustration of *Teletaceras radinskyi* after Hanson (1989). Measurements on the crowns of each tooth are taken at the maximum antero-posterior diameter along the middle of the tooth, and the maximum transverse width measured from the lingual base to the labial base of the tooth. Similar measurements were taken for the lower teeth as well.

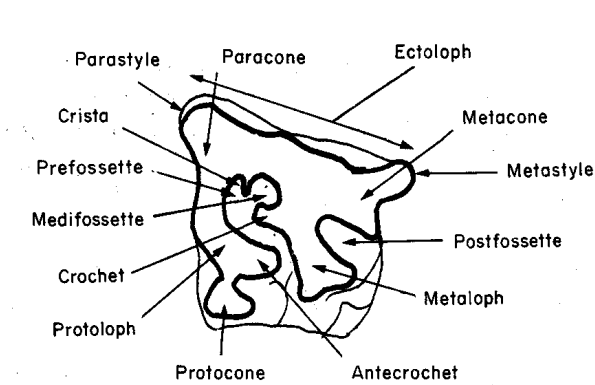


Figure 2.2. Terminology of a typical rhinoceros upper molar (after Prothero *et al.*, 1986).

Anatomical terminology of the skull and skeleton follow Sisson and Grossman (1975) and Scott (1941), and is discussed further in Chapter 5. Dental terminology follows Osborn (1898c, 1904) and is shown in Figure 2.2. Instead of the cumbersome system of superscripts and subscripts for upper and lower teeth, I follow the computer-friendly system of Jepsen (1966) where upper-case letters indicate upper teeth (I1–3 C P1–4 M1–3 for upper incisors, canines, premolars, and molars) and lower-case letters indicate lower teeth (i1–3 c p1–4 m1–3). Biostratigraphic correlations follow the chapters in the Woodburne (2004) volume, as well as other papers cited in the appropriate places. The time scale for the Cenozoic follows Berggren *et al.* (1995) as applied to the North American land mammal “ages” by the chapters in the Janis *et al.* (1998) volume. Other abbreviations are as follows:

dP or dp	deciduous premolars
ht.	height (in tables)
l.f.	local fauna, a stratigraphically and geographic restricted vertebrate assemblage
Ma	millions of years before present
Mc	metacarpal
Mt	metatarsal
m.y.	millions of years as a duration of time
N	sample size
SD	standard deviation

INSTITUTIONAL ABBREVIATIONS

AMNH	Department of Paleontology, American Museum of Natural History, New York
BVM	Buena Vista Museum, Bakersfield, California
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

DMNH	Denver Museum of Natural History (now Colorado Museum of Nature and Science), Dener, Colorado
F:AM	Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York
FLMNH	Florida Museum of Natural History, Gainesville, Florida
FMNH	Field Museum of Natural History, Chicago, Illinois
JODA	John Day Fossil Beds National Monument, Oregon
KU	Museum of Natural History, University of Kansas, Lawrence, Kansas
LACM	Natural History Museum of Los Angeles County, Los Angeles, California
LACM (CIT)	California Institute of Technology collection (now housed at the LACM)
LSUMG	Louisiana State University Museum of Geology, Baton Rouge, Louisiana
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MGS	Mississippi Geological Survey, Jackson, Mississippi
MSU	Midwestern State University, Wichita Falls, Texas
OMNH	Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma
ROM	Royal Ontario Museum, Toronto, Ontario
SDSM	Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota
SMNH	Saskatchewan Museum of Natural History, Regina, Saskatchewan
TMM	Texas Memorial Museum, University of Texas, Austin, Texas
UCMP	University of California Museum of Paleontology, Berkeley, California
UCR	University of California, Riverside, collection (now housed at UCMP)
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida
UNSM	University of Nebraska State Museum, Lincoln, Nebraska
UO	University of Oregon Condon Museum of Geology, Eugene, Oregon
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UW	University of Washington Burke Museum, Seattle, Washington
YPM	Yale Peabody Museum, New Haven, Connecticut
YPM-PU	Princeton University collection (now housed in the collections of YPM)

THE EVOLUTION OF NORTH AMERICAN RHINOCEROSES

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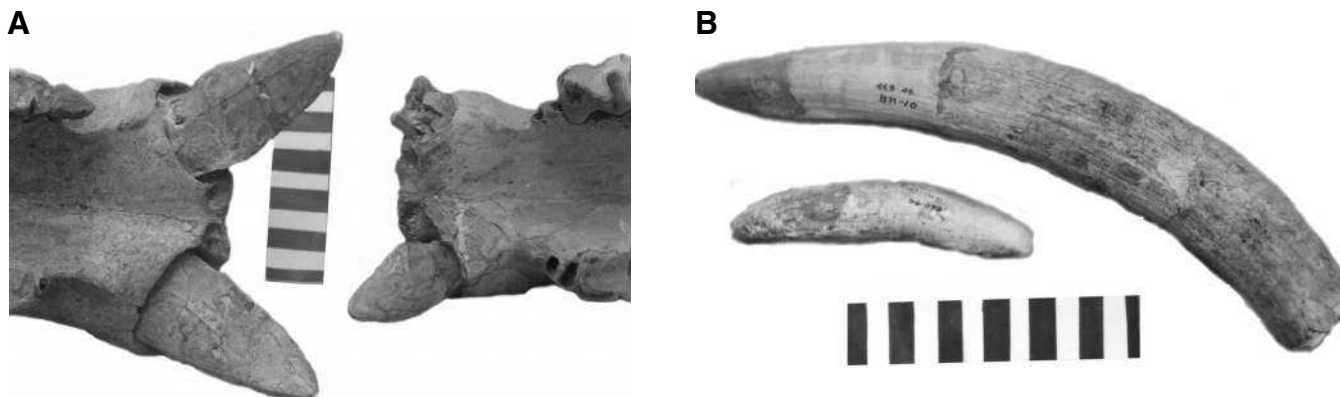


Figure 2.3. Comparison of mandibles with male and female i2 tusks. A. Male (left) and female (right) *Teleoceras fossiger* (AMNH 8391 on left, AMNH 2606 on right). B. Contrast between male and female i2 tusks of *Peraceras superciliosum* from Hottell Ranch, Nebraska (unnumbered UNSM specimens). In general, male i2 tusks are longer, larger, and have no separation between the root and the crown, and are worn much of the length of the crown. Female tusks are shorter, blunter, with a distinct base on the crown separating it from the the root. Scale bar in cm.

A NOTE ON SPELLINGS

According to the *International Code of Zoological Nomenclature* (fourth edition, 1999), adjectival species names must agree with the gender of the genus. Unfortunately, paleontologists are not always well trained in Latin, and have a long tradition of making mistakes in gender of Latinized names, and applying the wrong endings. Generic suffixes such as *-ceros* (“horn” in Greek), *-odus* and *-odon* (“tooth” in Greek), and *-opus* (“foot” in Greek) are masculine, and require a masculine adjectival ending. Generic suffixes such as *-ceras* (another Greek word for “horn”) and *-therium* (“beast” in Greek) are neuter, and require neuter adjectival endings in the species name. Thus, the common misspellings such as *Peraceras “superciliosus”* and *“profectus”* should be *superciliosum* and *profectum*; *Teleoceras “medicornutus”* should be *medicornutum*; *Diceratherium “niobrarensis”* should be *niobrarense*; *Brachypotherium “americanus”* should be *americanum*, and so on. When species names are transferred to genera of different genders, the adjectival endings must also change, so *“Aceratherium mite”* (neuter) becomes *Subhyracodon mitis* (masculine), and *“Aceratherium platycephalum”* (neuter) become *Amphicaenopus platycephalus* (masculine). Likewise, paleontologists persist in misspellings like “rhinoceratids” and “rhinoceratoids,” even in recent publications. However, the stem is the name *Rhinoceros*, so when the suffix is changed, the root is *rhinocero-* (not *rhinocera-*), and the proper spelling is “rhinocerotids” and “rhinocerotoids.”

VARIATION DUE TO SEXUAL DIMORPHISM

A persistent question when assessing large sample sizes of rhinos is how much that size variation could be due to sexual

dimorphism, and how much is too great to be explained as a population sample from a single species, and indicates differences in species. Fortunately, the sex of many rhino fossils is easy to assess, and there are large samples of both living and extinct rhinoceroses that allow us to assess this problem.

Tusk dimorphism

Osborn (1898c, 1904) first pointed out that the i2 tusks of rhinoceroses are highly dimorphic. In most rhinos, male tusks (Fig. 2.3) are typically long and curved, with a continuous taper of the tooth crown. Female tusks have a distinct base around the crown, and the point of the tusk tends to be shorter and blunter. This pattern is well established for the three living rhinoceros species have lower i2 tusks (*Rhinoceros unicornis*, *R. sondaicus*, *Dicerorhinus sumatrensis*), and was confirmed by Voorhies and Stover (1978) when they found probable fetal bones in the pelvic regions of presumed female skeletons of *Teleoceras major* from Ashfall Fossil Bed State Park, Nebraska. Mead (2000) and Muhlbachler (2004) have further documented the size and growth patterns of rhino tusks. For large samples that include lower jaws, this tusk morphology allows for the assessment of sexual dimorphism. Tusks are very important for survival in some living rhinos. For example, Dinerstein (2003) reports that the Indian rhinoceros, *Rhinoceros unicornis*, uses its lower tusks, rather than its horn, as its primary weapon in both intraspecific and inter-specific combat.

Horn dimorphism

The second potentially sexually dimorphic character is the horn. Living rhinoceroses show variations in horn dimorphism. *Diceros bicornis* shows no dimorphism (Berger, 1994), while those of *Ceratotherium simum* and *Rhinoceros unicornis* show slight dimorphism (Rachlow and Berger, 1997; Dinerstein, 1991). Data for the rare cryptic forest

species *R. sondaicus* and *Dicerorhinus sumatrensis* are sparse, but appear to show slight dimorphism (Pocock, 1945; Groves, 1982). Although the keratinous horn is not preserved in most fossil rhinos (except *Coelodonta antiquitata*, the woolly rhino), it seems clear (based on the size of the bony boss that supported the horn) that there was sexual dimorphism in some horned species of extinct rhinoceroses, as first documented by Osborn (1904) and Peterson (1920). Horn dimorphism is most apparent in the paired-horn rhinos *Diceratherium* and *Menoceras* (Fig. 2.4). In both cases, the presumed males (as established by the i2 tusks) have larger, more developed nasal ridges or bosses, and those of presumed females are faint or absent. As pointed out in Chapter 4, the failure to recognize this dimorphism led to the creation of a number of invalid species that were simply based on hornless females of *Diceratherium* or *Menoceras*. Some dimorphism of the horns may also occur in *Peraceras superciliosum*, where presumed males (based on their i2 tusks) have broad, blunt robust nasals with a highly rugose tip (Fig. 4.32B–D), while those of females are smooth and slender. No dimorphism has been observed in the small horn bosses of *Teleoceras*, however.

Size dimorphism

In this case, the data are less clear-cut. In living rhinos, there is relatively little size dimorphism for most species, including the black rhino (Freeman and King, 1969), the Indian rhino (Dinerstein, 2003), or the Sumatran rhino (Dinerstein, 2003); the Javan rhino is too poorly known to establish its tendencies. Only the white rhino shows some dimorphism, with males about 20% larger than females (Owen-Smith, 1988). Bales (1995) conducted an extensive multivariate study on the skulls and jaws of all five living species, and most of the extinct species, and found that they showed no statistically significant sexual dimorphism in either size or shape of the skull and jaws. Based on all the literature available to them, Prothero and Sereno (1982, p. 16) and Prothero and Manning (1987) argued that most rhinos do not show significant size dimorphism, and so ruled out sexual size differences to account for the dwarf species of rhino from the Texas Gulf Coastal Plain.

Mead (2000) analyzed the large sample of complete articulated skeletons of *Teleoceras major* from Ashfall Fossil Bed State Park, and argued that they do show significant sexual dimorphism. According to Mead (2000), males tend to be significantly larger not only in cranial dimensions, but also in

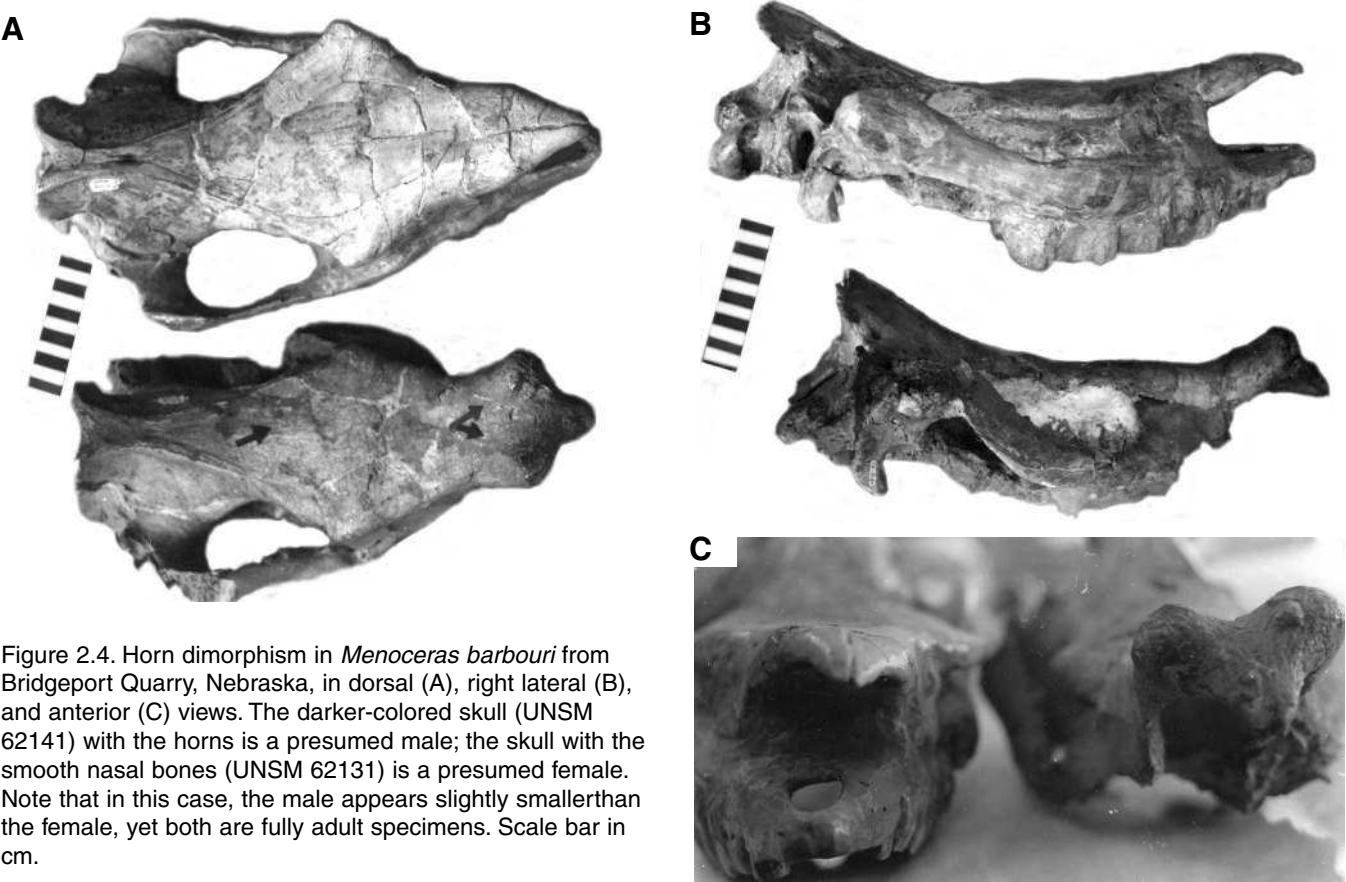


Table 2.1. Statistics of samples of presumed male and female skulls and jaws (based on horns and lower incisor tusks) of *Menoceras arikarens* from Agate Springs Quarry. In the upper teeth, the males average slightly larger than females, but in the lower teeth, they are smaller, although none of these differences is statistically significant (P value at 95% confidence level for significance of difference, using a t-test).

	p2-4	m1-3	P2-4	M1-3
Males				
Mean	66.5	96.4	65.0	91.3
Standard Deviation	1.3	2.4	4.5	4.2
Females				
Mean	63.5	93.5	67.2	93.2
Standard Deviation	0.7	5.6	4.3	4.4
P	0.006	0.369	0.725	0.557

limb bone dimensions by 20-29%. He also contended that there are differences in the skulls as well, with males having deeper jaws and more massive mandibular-angular regions. However, this shape difference was not substantiated in the multivariate analysis conducted by Bales (1995) for some of the same taxa. In addition, Muhlbachler (2004) found no consistent evidence of size dimorphism in many different quarry samples of both *Teleoceras* and *Aphelops*, and concluded that the Ashfall sample was exceptional among rhinos for its apparent size dimorphism.

To reassess this problem, I measured the same standard variables in large quarry samples of male and females of a number of species, and plotted the data as bivariate plots. Large quarry samples exist for *Diceratherium armatum* and *D. annectens* from the Frick 77 Hill Quarry, Niobrara County, Wyoming. Because males and females of both species are found in the same quarry, we can rule out the possibility that the smaller *D. annectens* is a female of *D. armatum*; there are large female skulls of *D. armatum*, and small male skulls of *D. annectens*, in this and several other quarry samples. Males and females are also abundant in the samples of *Menoceras arikarens* from Agate Springs Quarry, Sioux County, Nebraska, and in several large quarry samples of *M. barbouri*.

Representative data are shown in Table 2.1. In general, there is no consistent trend that can be statistically supported. Measurements of male and female lower jaws (as established by i2 tusks) of *M. arikarens* show that the males tend to be larger than females (but by only 10% at the greatest, and there is overlap), but the male and female skulls (as established by horn bosses) and upper teeth from the same quarry sample show the *opposite* trend—males tend to be smaller than females! Most other plots of quarry samples of *Diceratherium* and *Menoceras* showed no consistent trend. Males and females tended to overlap greatly in body size, or if females were smaller, they were no more than 10% smaller. Muhlbachler (in press) has measured a much larger sample of *Menoceras arikarens* from Agate Springs, and came to the

same conclusion: there was no significant dimorphism in size as measured by teeth, and the females actually did have slightly larger upper cheek teeth. The same could be said for other species that have been sexed. Prothero and Manning (1987, fig. 15, here shown in Fig. 2.5) found no consistent sexual size separation of *Teleoceras medicornutum* from the Barstovian Frick Horse and Mastodon Quarry, Pawnee Creek Formation, Colorado. More germane to the point of this plot, the specimens identified as *T. meridianum* are significantly smaller than even the smallest known females of *T. medicornutum*, so they are distinct dwarfed species, and not sexual dimorphs.

In summary, although as much as 20% size difference in some species due to sexual dimorphism can be documented in a few cases, in most living and fossil rhinoceros species there is either no statistically significant dimorphism, or the females tend to be less than 10% smaller than males. Thus, when assessing the range of size variation of a population to determine whether one or more species are present, these are the guidelines that I will follow.

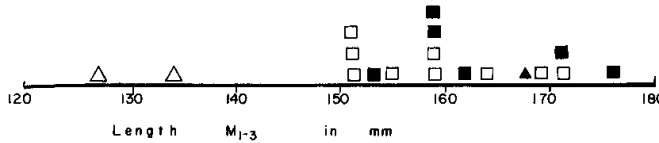


Figure 2.5. Comparison of m1-3 lengths of late Barstovian *Teleoceras*. Solid squares = male *T. medicornutum*, Frick Horse and Mastodon Quarry; open squares = females from same quarry. Solid triangle = type specimen of *T. medicornutum*. Open triangles = *T. meridianum* (after Prothero and Manning, 1987: fig. 15).

VARIATION IN TOOTH CROWN PATTERNS

Molarization of upper premolars

In addition to intrapopulation variation due to sexual dimorphism, another significant source of variation occurs in the cusp and crest patterns of rhinoceros teeth. Traditionally, paleontologists have treated the crown patterns of most mammalian teeth as infallible guides to species-level distinctions, and rarely considered the possibility of variation of tooth crown patterns within a single population. As reviewed in Chapter 3, the paleontologists of the late nineteenth and early twentieth centuries were typological “splitters,” who recognized new taxa based on every slight variation in teeth. Consequently, the taxonomy of North American fossil rhinos was grossly oversplit based on the slight difference of the crown pattern of each new specimen.

By the mid-twentieth century, however, paleontologists such as Matthew and Simpson began to think of fossils as parts of living populations, rather than objects that get new names each time they appeared slightly different. Such “population” thinking (and the statistical approach to fossil samples, also introduced to vertebrate paleontology by Simpson and his wife Anne Roe) has now become customary in paleontology, yet because of the slow pace of revision of many groups, the literature is full of invalid taxa created by splitters from over a century ago.

This problem was highlighted in North American rhinos with the discovery and publication of the *Trigonias* Quarry sample from the Chadronian Horsetail Creek Formation in Weld County, Colorado (Gregory and Cook, 1928). In this sample were over a dozen skulls with highly variable crests and cusps on the upper premolars, yet the entire sample was very homogeneous in size and all other features (Fig. 2.6). Gregory and Cook (1928, p. 4) recognized that this suggested that all the specimens were members of a single population, but “for the sake of convenience in describing and cataloguing the material we nevertheless designate the various groups or individuals as variants or ‘species’ realizing full well that these terms in this instance, and perhaps in many others, merely signify a definable set of characters in certain individuals.” Consequently, they recognized six species of *Trigonias* (four of them new) and labeled yet another specimen *Caenopus premitis* because its upper premolars were more advanced than the other *Trigonias*.

Matthew (1931, 1932), on the other hand, applied essentially modern population concepts to these samples and

argued effectively that they could not represent more than one species. His extended discussion (Matthew, 1931, pp. 5–6) of the criteria for species distinctions reads as if it were written very recently. Wood (1931), however, was caught in the middle. He had created many different species within the primitive rhinocerotoids in his 1927 paper, so he was unwilling to discount the importance of minor cusp variations in recognizing species. Still, he reduced Gregory and Cook’s (1928) seven species to only three, but then erected another species of *Trigonias*, *T. cooki*, based on minor variations of upper premolars. As detailed in Chapter 3, the same problem occurred with the large, highly variable quarry sample of *Menoceras arikarens* from Agate Springs Quarry when Troxell and Cook split off a number of invalid species, or the large quarry sample of *Teleoceras hicksi* from Wray, Colorado, when Cook and Lane erected multiple species for a single homogeneous population sample (see discussion of each of these species in Chapter 4). The problem tends to be most severe in the more primitive taxa whose upper premolars are not completely molarized (e.g., *Hyracodon*, *Subhyracodon*, *Trigonias*), but it also occurs to a lesser degree in taxa (such as *Diceratherium*, *Menoceras* or *Teleoceras*) with completely molarized upper premolars.

So how do we assess whether variations in cusp morphology are worthy of species recognition? Ideally, a large sample from a single population is required, which is known in only a few instances (e.g., the Ashfall Fossil Bed State Park *Teleoceras major*, which is an instantaneous death assemblage). The next best substitute for a single population is a large quarry sample, which presumably represents individuals from a limited geographic range and span in time (years or at most decades) and approaches a population sample. Such large quarry samples are available for many rhino species, as detailed in Chapter 4. For many oversplit species, we have quarry samples that clearly demonstrate the upper premolar variability in *Trigonias osborni* (the Colorado sample discussed above) and *Subhyracodon occidentalis* (the Harvard Fossil Reserve sample from Goshen County, Wyoming). Lacking a single quarry sample, the best approach is to examine all the specimens from a single restricted stratigraphic level and geographic area (e.g., Prothero, 1996, with *Hyracodon* from the lower Scenic Member of the western Big Badlands). Although there is undoubtedly some time averaging involved, such samples are the best proxy we have for a contemporary population in many instances.

For the variation in molarizing upper premolars, Prothero

Figure 2.6 (opposite page). Variability of upper premolar crests of the *Trigonias* Quarry sample. A. DMNH 884, *T. osborni* “var. *secundus*.” B. DMNH 897, *T. osborni* “var. *figginsi*.” C. DMNH 1025, “*Caenopus premitis*.” D. DMNH 881, *T. osborni* “var. *figginsi*.” E. DMNH 1029, *T. “taylori*.” F. DMNH 886, *T. “hypostylus*.” G. DMNH 414, *T. “precopei*.” H. DMNH 878, *T. “preoccidentalis*.” (After Gregory and Cook, 1928, Plates III–VI). All of these specimens are about the same size and morphology, and differ only in the details of premolar crests, suggesting that they are a single species, *T. osborni*, and none of these species are valid.