New remains of *Rhynchotherium falconeri* (Mammalia, Proboscidea) from the earliest Pleistocene 111 Ranch, Arizona, U.S.A. with a discussion on sexual dimorphism and paleoenvironment of rhynchotheres

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Abstract

A new specimen of *Rhynchotherium* from the 111 Ranch Beds, southeastern Arizona is described here. I compare the mandible and molars to other specimens and with the more recent taxonomic revisions, assigning the specimen to *R. falconeri*. I follow this with a discussion on the current evidence tentatively suggesting that sexual size dimorphism is displayed in *Rhynchotherium* that would parallel other proboscideans. I conclude with a discussion on the distribution and paleoenvironment of *Rhynchotherium*. Rhynchotheres are found only in southern latitudes of North America with a preferred environment that included savannas and nearby water sources.

K e y w o r d s : *Rhynchotherium*, Proboscidea, symphysis, Arizona.

Zusammenfassung

Ein neues Exemplar von *Rhynchotheruium falconeri* aus den 111 Ranch Beds in Arizona wird beschrieben. Ich vergleiche Unterkiefer und Molaren mit anderen Exemplaren von *Rhynchotherium* und mit neueren taxonomischen Revisionen, nach denen das Exemplar *R. falconeri* zugeordnet wird. Ich folge dieser Zuordnung und diskutiere die Befunde, die dafür sprechen, dass es bei *Rhynchotherium* einen sexuellen Größendimorphismus, ähnlich wie bei anderen Proboscidiern, gibt. Abschließend folgt eine Diskussion über Verbreitung und Paläoenvironment von *Rhynchotherium*. Rhynchotherien gab es nur in den südlichen Breiten von Nordamerika. Ihr bevorzugtes Habitat waren Savannen und die Nähe zu Wasser.

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1. Introduction

Geologic and stratigraphic setting.-The earliest Pleistocene 111 Ranch is a fossiliferous locality area located southeast of Safford in southeastern Arizona, USA (Fig. 1). Originally, the 111 Ranch fauna was named for a number of fossil localities occurring in the Whitlock Mountain area, named after the 111 Ranch which occurs nearby. However, a number of fossil localities throughout the San Simon Valley, and the geologic unit they are in, are believed to be correlative with the 111 Ranch fauna so the informal name "111 Ranch Beds" has been used (RICHTER et al. 1981, DREWES et al. 1985, HOUSER 1990, THRASHER 2007). The 111 Ranch Beds are part of the Gila Group that extends into New Mexico. There are 11 stratigraphic units at 111 Ranch composed of sands, gravels, silts, marls, limestones, diatomite, and chert (SEFF 1960, 1962), which HOUSER (1990) considered to represent lacustrine and fluvial conditions. The mandible described here was discovered in the common silty sandstones (SkAFF 2001). The elevation at 111 Ranch ranges between 1049 and 1155m asl (Skaff 2001; PASENKO 2007). Originally two superimposed faunas at 111 Ranch: the Flat Tire Fauna (Blancan Land Mammal Age, or latest Pliocene) and the Tusker Fauna (Irvingtonian LMA, or earliest Pleistocene) were described in Wood (1962), but LINDSAY & TESSMAN (1974) united both faunas within the Blancan LMA. Radiometric and fission-track dates for the 111 Ranch fauna are between 2.3 and 2.47 Ma (DICKSON & IZETT 1981; GALUSHA et al. 1984; HOUSER et al. 2004). Recently, the International Commission on Stratigraphy redefined the Pliocene-Pleistocene boundary at 2.6 Ma (HEAD et al. 2008; OGG & PILLANS



Fig. 1. Location of 111 Ranch in southeastern Arizona (modified from TOMIDA 1987).

2008). In this regard the 111 Ranch Beds are now considered to be within the Pleistocene.

Taxonomic setting. - Gomphotheriidae is a diverse family of extinct proboscideans sharing the characteristic of bunolophodont teeth. Gomphotheriids are represented in North America by four sub-families and eight genera: Amebelodontinae, (Platybelodon, BORISSIAK 1928, Amebelodon, BARBOUR 1927), Gomphotheriinae (Gomphotherium, BURMEISTER 1837), Cuvieroniinae (Cuvieronius, CABRERA 1929, Stegomastodon, POHLIG 1912), Rhynchotheriinae (Rhynchotherium, FALCONER 1868) and by two additional genera (Gnathabelodon, BARBOUR & STERNBERG 1935 and Eubelodon, BARBOUR 1914) presently not assigned to subfamilies (SHOSHANI & TASSY 2005). However, Cuvieronius and Rhvnchotherium are considered to be closely related on the basis of several shared traits (LUCAS & MORGAN 2008). Rhynchotherium, Stegomastodon, and Cuvieronius have all been reported from the 111 Ranch Beds, but there are no published descriptions of the Cuvieronius material. It is possible that some material assigned to Cuvieronius may in fact be Rhynchotherium given the similarities of the molars and tusks between these taxa.

(PASENKO & LUCAS 2011). A Stegomastodon molar was described from 111 Ranch in WOOD'S (1962) dissertation, but the whereabouts of this molar is currently unknown. More recently, an un-described skull, mandible, and partial skeleton of a Stegomastodon have been found at 111 Ranch (AZMNH collections). The 111 Ranch Beds also include immigrant taxa such as Glyptotherium, Glossotherium, and Neochoerus from South America (LINDSAY 1978; WEBB 1985). The Great American Biotic Interchange between North and South America began around 2.5 Ma (WEBB 1991), or just prior to the dates reported at 111 Ranch.

A i m. – The genus *Rhynchotherium* has a problematic history due mainly to abundance of splitting by early paleontologists, a questionable type specimen, rarity of complete specimens, and the small number of distinguishing characteristics. The purpose of this paper is to describe a mandible that shows the distinguishing characteristics separating the genus *Rhynchotherium* from the earlier *Gomphotherium* and later *Cuvieronius*. As noted here and in previous literature, a mandible with a preserved symphysis is the most conclusive way to separate *Rhynchotherium* from *Cuvieronius*. In addition, I also discuss the possibility that sexual dimorphism was displayed in *Rhynchotherium*.

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2. Material and methods

M a t e r i a 1: AZMNH p3708, partial right corpus with m2 and m3, and basal portion of right ascending rami.

Methods: Mandibular measurements follow those illustrated by TASSY (1996) and MILLER (1980). These include the ventral length, height of ramus, deflection of symphysis, angle between horizontal and ascending rami, and length and width of molars. All measurements are in mm. The measurements and morphology of the mandible and molars are here compared to other specimens of *Rhynchotherium*. I use the system of dp2, dp3, dp4, m1, m2, and m3 for the nomenclature of the lower cheek tooth, and follow the terminology of bunodont gomphotheriids in TOBIEN (1973). The statistical methods used for a discussion of sexual dimorphism in *Rhynchotherium* were the mean method with the coefficient variation calculated using HALDANE'S (1955) correction for small samples.

Institutional Abbreviations

AMNH F:AM	Frick Collection, American Museum of Natural							
	History, New York							
AMNH FM	American Museum of Natural History, New							
	York							
AZMNH	Arizona Museum of Natural History, Mesa							
UALP	University of Arizona Laboratory of Paleonto-							
	logy, Tucson							
UCR	University of California, Riverside							
	-							

3. Systematic paleontology

Order Proboscidea ILLIGER, 1811 Family Gomphotheriidae HAY, 1922

Genus Rhynchotherium FALCONER, 1868

Rhynchotherium falconeri OSBORN, 1923

Rhynchotherium simpsoni OLSEN, 1957 Rhynchotherium edense FRICK, 1933 Rhynchotherium browni OSBORN, 1936

D i a g n o s i s. – Gomphothere with spiraled enamel bands on the upper tusks, lophodont cheek teeth with 4-4.5 lophs/lophids on M3/m3, cheek teeth with single to double trefoils, straight enamel bands on the lower tusks that may be absent, from wear, in mature adults, low and blunt coronoid process, stout corpus, a symphysis deflected ventrally at an angle of 45°, or greater, and an angle approximating 90° between the corpus and ascending ramus (PASENKO 2007, LUCAS & MORGAN 2008).

Description. - The lateral side of the partially preserved right dentary (Fig. 2A), and the lateral and occlusal surfaces of the m2 and m3 are exposed (Fig. 2B). The medial side remains partially encased, for support, in a plaster jacket. No lower tusk is preserved, but the alveolus for the tusk is present. This specimen was preliminarily described in Skaff (2001) and is amended here. The rostralmost portion of the symphysis is missing, reflecting a preserved ventral length of 540 + mm for the mandible. The preserved portion of the symphysis is stout and deflected ventrally through an angle approximating 60°. The anterior edge of the ascending ramus is missing. Therefore, the angle between the corpus and ascending ramus, based on several measurements, is estimated between 90° and 100°. The height of the corpus mesial to the m2, at the symphysis border is 215 mm, and the height at the root of the ascending ramus is 145 mm. This indicates an increase rostrally in the height of the dentary. Two foramina are visible anterior to the m2.

A small piece of the mesial portion of the m2 is missing. The m2 consists of three lophids, which are joined together by wear exposing large portions of the dentine. The m3 is not completely erupted. There are four complete lophids visible on the m3, and a 5th lophid is partially exposed, being still covered by part of the plaster jacket, and not fully erupted. The width of the m3 across the 1st and 2nd lophids is 88 mm and 77 mm respectively. The protoconid and metaconid show extensive wear resulting in large areas of enamel exposed in a contiguous pattern between the two conids. The protoconid still displays a posterior conule. The hypoconid and entoconid have moderate wear with the hypoconid displaying anterior and posterior conules, and the entoconid displaying a small anterior conule. The pretrite 3rd half-lophid of the talonid has very little wear, and displays anterior and posterior conules. There is a small anterior conule on the posttrite 3rd half-lophid of the talonid. Because the m3 is not fully erupted the conule development for the remaining portion of the talonid is not distinguishable. The conule development for the m3 reflects an incipient double trefoil pattern. A trefoil pattern develops from the wearing down, through attrition, of the main cones and attached conules. Anterior and posterior conules on the pretrite side only result in a single trefoil pattern. When anterior and posterior conules are present on the posttrite side this results in a double trefoil pattern. The posttrite half-lophids (lingual) are slightly more mesial than the corresponding pretrite half-lophids (buccal). There is a well-developed cingulum on the buccal side.

The wear patterns on the molars and the eruption sequence displayed allows for and inference to be made on the age of the individual. The tooth eruption sequence and wear pattern for the molars of AZMNH p3708 compares to that of a mature, but not old-aged mastodont or gomphothere as described in SAVAGE (1955), SIMPSON & PAULO COUTO (1957) and SAUNDERS (1977). Based on LAWS (1966) this would approximate an age of 34 African Elephant Years.

The assignment of AZMNH p3708 to Rhynchotherium is based on the above diagnosis. Although no lower tusk is preserved, the alveolus for the lower tusk is present. The only two other gomphotheriids in North America, during the earliest Pleistocene, were Stegomastodon and Cuvieronius, both of which have more abbreviated symphyses (brevirostrines) that are less deflected ventrally, and no i2 s. AZMNH p3708 compares closely to another mandible from 111 Ranch (UALP 23404) identified as Rhynchotherium falconeri (PASENKO 2007), and is similar in size and morphology to the holotype for R. falconeri (AMNH FM 8532) from Texas (see COPE 1893, OSBORN 1923, 1936). All three have a strongly downward-deflected symphysis, and an angle between a stout corpus and the vertical ramus that approaches 90°, and evidence of i2 s. The m3 s for AZMNH p3708 and UALP 23404 are similar in size and both have incipient posttrite trefoils. Measurements for AZMNH p3708 and other specimens of R. falconeri are provided in Table 1.

Discussion. – It is generally believed that *Rhynchotherium* derived from a basal *Gomphotherium* stock in North America sometime during the Miocene, but the exact



Fig. 2. Rhynchotherium falconeri, AZMNH p3708. – A. Right dentary with m2-m3 (lateral view). B. Right m3 (occlusal view). – Scales: 10 cm.

relationships between *Gomphotherium*, *Rhynchotherium* and Late Pliocene/Pleistocene gomphotheriids of North and South America such as *Cuvieronius*, *Haplomastodon* and *Stegomastodon* remain unclear. A possible relationship, based on some similarities in the mandibles, between the earlier *Rhynchotherium* and later *Haplomastodon* and *Stegomastodon* has previously been discussed (SAVAGE 1955; SIMPSON & PAULA COUTO 1957; TOBIEN 1973). There is a similarity between the deflected, but more abbreviated, tusk-less symphyses of specimens referred to *Hap*- *lomastodon* and those of *Rhynchotherium*. More recently, FERRETTI (2008a) has shown synapomorphies of the skull for *Rhynchotherium* and *Haplomastodon*. The upper tusks of *Rhynchotherium* are similar to *Cuvieronius* in having varying degrees of spiraled, enamel-banded upper tusks (PASENKO 2007). LUCAS & MORGAN (2008) suggest *Cuvieronius* evolved from *Rhynchotherium* based on this trait and the brevirostrine lower jaws of the former. It is also known that some specimens of *Cuvieronius* possess vestigial lower incisors (FERRETTI 2008b), which would be a

Locality	111 Ranch, Arizona	Blanco, Texas	111 Ranch, Arizona	Bone Valley, Florida	Greenlee County, Arizona	
Catno	AZMNH p3708	AM 8532*	UALP 23404	FLMNH 5450	LVMNH 871	
Measurement						
Ventral Length	540+	630+	638+	562	703	
Height of corpus at symphysis border	215	215 175 1		170	190	
Height of corpus at ascending ramus	145	135	148	148	129	
Angle between corpus and ascending ramus (degrees)	91	88	95	90	90	
Deflections of symphysis (degrees)	60	60	61	65	65	
m3 length	190+	174	197	194	173	
m3 width	88	75	91	83	83	

Tab. 1. *Rhynchotherium falconeri*, dentaries from several localities in southern USA. Specimens UALP 23404, LVMNH 871, FLMNH 5450, and AM 8532 are taken from PASENKO (2007). The measurements are in millimeters. (* = holotype).

homologous trait shared with *Rhynchotherium*. The similarities and difficulties in distinguishing between isolated molars and tusks of *Rhynchotherium* and *Cuvieronius* has been previously discussed (SIMPSON & PAULA COUTO 1957; PASENKO 2007; LUCAS & MORGAN 2008).

The genus Rhynchotherium was first established by FALCONER (1868) based on a mandible (now only represented by a cast: AMNH FM 27003) from Sonora, Mexico. This mandible does not have an assigned age, but is believed to be Pliocene in age. OSBORN (1918) validated the genus by naming a species, R. tlascalae, for the type and referred several other specimens and species to the genus. As many as 11 species have been referred to Rhynchotherium (OSBORN 1936), but recent revisions have reduced this number to one or two species. TOBIEN (1973) believed that R. blicki and the type R. tlascalae were members of Gomphotherium and that all other specimens then known for Rhynchotherium represent one species. MILLER (1980, 1990) discussed the number of valid species, concluding that two to three species were valid depending on the validity of the type AMNH FM 27003 and those specimens referred to R. blicki. PASENKO (2007) also discussed the validity of the type, AMNH FM 27003 and R. blicki, and considered two to three species were valid based on the presence or absence of enamel bands on the lower tusks, presence or absence of posttrite conules, deflection of symphysis, and angle between the horizontal and vertical rami. LUCAS & MORGAN (2008) recognize one to two species as being valid depending on whether specimens of R. blicki are considered a primitive form of Rhynchotherium or a derived form of Gomphotherium. In all revisions three main concepts have emerged. First, the type specimen AMNH FM 27003 is inadequate as a type; second, R. blicki from Central America may in fact be a form of Gomphotherium; and third, species *R. falconeri*, *R. browni*, *R. simpsoni*, and *R. edense* are conspecific. The factors, concerning the type specimen, led to a proposal that *Rhynchotherium falconeri* (AMNH FM 8532) be designated as the type species (LUCAS 2010), and now *R. blicki* has been considered a derived form of *Gomphotherium* (LUCAS & ALVARADO 2010).

4. Sexual dimorphism

Sexual dimorphism in extant and extinct proboscideans such as Mammut americanum (HAYNES 1989; FISHER 1990; GREEN 2006), Gomphotherium angustidens (TASSY 1996), Mammuthus (Lister 1996; Lister & Agenbroad 1994), Loxodonta africanus and Elephas maximus (HAYNES 1991; TODD 2010) has been discussed, but no study has been performed on the genus Rhvnchotherium. This is due mostly to the rarity of complete specimens. There are only three described specimens that include cranial, mandibular, and skeletal elements. These are AMNH F:AM 18225 from the Mt. Eden fauna, California, UCR 13449 from the Warren local fauna, California, and UALP from the 111 Ranch, Arizona. Specimen AMNH F:AM 18225 was supposed to be a female because of the smaller size of the molars, more slender tusks, and shorter longbones (see Table 2) (FRICK 1933). A comparison of the skeletal material of AMNH F:AM 18225 and UALP 23404 indicated the latter was larger and may be a male while the former was smaller and may represent a female (PASENKO 2007). It was suggested also that the partial cranium, mandible, and skeleton of UCR 13449 was a female because of its smaller size (PASENKO 2011) (see Table 2). A large number of molars, referred to Rhynchotherium, is available, but many of these

Specimen	Humerus length	Femur length	Tibia length	m3 length	m3 width	
UALP 23404	902	905+	657	197	83	
UCR 13449	700	738+	493	175	75	
F:AM 18225	660	860	490	176	80	

Tab. 2. Selected measurements of postcranial elements and m3 s for *Rhynchotherium falconeri*. Measurements are provided in mm (data derived from PASENKO 2007, 2011).

Tab. 3. Statistical data for the m3 s of specimens of *Rhynchotherium* (data derived from specimen described here, WEBB & TESSMAN 1968, MAY 1981, PASENKO 2007, LUCAS & MORGAN 2008).

	Smaller m3s (females?)				Larger m3s (males?)						
	n	min-max	mean	SD	CV	n	min-max	mean	SD	CV	
Length	7	153–176	170.7	8.03	4.9	8	185-200	194.0	4.60	2.4	
Width	7	66–87	78.4	7.02	9.3	8	70–97	82.9	8.49	10.6	
Combined											
	Length Mean = 183.1, SD = 13.5						Width Mean = 80.4, SD = 7.18				
Length CV = 7.5					Width $CV = 9.1$						
	Mean Method SD Ratio for Length = 1.14					Mean Method SD Ratio for Width = 1.06					

are isolated occurrences and may not be easily assigned to *Rhynchotherium* or *Cuvieronius*.

Since there is so little skeletal material, I have taken a small sample of m3 s to test whether sexual dimorphism is evident. Since the sex of the rhynchotheres is unknown, I have grouped the m3 s into smaller and larger groups by using the mean method, based on the length of the tooth. This kept the number of teeth the same for the statistical methods. The lengths for the molars of modern African elephants show a higher dimorphic rate than the widths (ROTH 1992). These data are presented in Table 3 and Figure 3. The widths of the m3 s show a higher variation than length for the smaller and larger groups as well as when combined. The lengths of the m3 s displayed the least variation. The smaller and larger groups showed less variation than when combined, as can be expected. The combined coefficient variation (CV) for length of the m3 s was higher than the separate larger and smaller samples. However, the combined CV for the widths was lower. This means that the lengths of the m3 s would be more favorable to use than the widths for examining sexual dimorphism. The data provided in ROTH (1992) for modern African elephants showed a dimorphic tendency in which the male's teeth were on average, longer and wider than females. However, for the African elephants CV values did not increase significantly when male and female samples were pooled. By looking at the mean method standard deviation (SD) for the combined m3 s, the lengths also show a slightly more significance (1.14) for sexual dimorphism than the widths (1.06), but would not be considered largely dimorphic. The



Fig. 3. A bivariate plot of the length and width of m3 s for specimens of *Rhynchotherium* (in mm). Data was derived from the presently described specimen, and data in WEBB & TESSMAN 1968, MAY 1981, PASENKO 2007, and LUCAS & MORGAN 2008.

mean method SD for two samples of m3 s for *Mammut* americanum had similar ratios of 1.14 and 1.12 which the author did not consider significant (GREEN 2006). It should be noted that geographical variation, the unusual horizontal succession of proboscidean teeth, and differences in measuring techniques should be considered as part of the variation shown (see ROTH 1992). These data show that sexual dimorphism may have been present in *Rhynchotherium*, but a larger sample is needed.

5. Distribution and paleoenvironment

Specimens of Rhynchotherium are rare, but including AZMNH p3708, possibly five individuals have been found in southern Arizona. Two specimens have been found at 111 Ranch (UALP 23404, AZMNH p3708). An undescribed manus, found in the 111 Ranch beds, may also represent Rhvnchotherium (PASENKO, unpublished data). MILLER (1990) described a skull and mandible of R. falconeri from Greenlee County, east of 111 Ranch, and KNECHTEL (1936) mentioned another possible maxilla of Rhynchotherium from Bear Springs just west of 111 Ranch. An un-described mandible catalogued as Rhynchotherium sp. (AMNH FM 103270) was discovered further west at the Redington Quarry in Pima County. A partial skull from the late Pliocene St. David Formation near Benson, Arizona could either be *Rhynchotherium* or *Cuvieronius*, based on the similarities between these genera (PASENKO & LUCAS 2011).

Rhynchotherium is known only from the southern latitudes of North America, and its temporal distribution is latest Hemphillian to earliest Pleistocene. Records occur in Arizona, Florida, Texas, New Mexico, California, and Mexico. The latitudinal restriction for rhynchotheres was probably due to environmental limitations. Previous studies on rhynchothere localities have revealed that a savanna-type environment with nearby water sources was preferred (Miller & CARRANZA-CASTAÑEDA 1984; MILLER 1990; McCullough et al. 2002). This distribution coincides with WEBB's (1977) description of a persistent Pliocene savanna that encompassed areas around the Gulf of Mexico down into Mexico and Central America. Apparently the climatic change during the Pliocene resulting in more aridity was delayed in the Gulf region due to the higher moisture there maintaining savannas longer than in areas further north (WEBB 1977; MILLER & CARRANZA-CASTAÑEDA 1984). It is plausible that there was more moisture on the Pacific coast that extended the range of Rhvnchotherium west to include California and Baja, Mexico. Even though there are immigrant taxa from South America present in the 111 Ranch Beds, no remains of Rhynchotherium have currently been found in South America. DUDLEY (1996) believed that an expansion of the "tropical rain forest biome" may have occurred at the Plio-Pleistocene boundary that shrank the previous savanna environment and thus prevented some proboscideans from crossing into South America. And although gomphotheriids were traditionally considered to be browsers, eating leaves, bark, forbs, and stems, isotope studies performed on rhynchotheres indicates a diet predominantly of C4 grasses (Macfadden & Cerling 1996; Skaff 2001). This may be associated with the progressiveness (posttrite conules) displayed in some molars of rhynchotheres. The co-occurrence of Rhynchotherium and *Stegomastodon* in the 111 Ranch Beds indicates these genera preferred similar environments or occasionally overlapped in their home ranges.

6. Summary and conclusions

The rhynchothere mandible described here is referred to Rhynchotherium falconeri on the basis of the deflected symphysis, presence of an alveolus for the i2, and the size and morphology of the m3. The mandible is similar to another one previously described from the earliest Pleistocene 111 Ranch Beds and compares to the holotype for R. falconeri. Several more specimens of Rhvnchotherium are known from Pliocene-Pleistocene deposits in southern Arizona, which is consistent with the known distribution of rhynchotheres and what has been described as their preferred environments. Rhynchotheres are found only in the southern latitudes of North America associated with faunas suggesting a savanna type environment was present. Complete specimens of Rhvnchotherium are rare hindering a complete study to determine if sexual dimorphism was displayed in rhynchotheres. A preliminary analysis on molar size suggests sexual dimorphism may have been exhibited by rhynchotheres.

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