Searching for the Pliocene: Southern Exposures

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Review of proboscideans from the Middle Miocene Barstow Formation of California

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Introduction

Tracks and skeletal remains of proboscideans are rare in Miocene aged strata in North America. The earliest immigrants were the Mammutidae (represented by Zygolophodon) which arrived in the late Hemingfordian (Webb 1992; Tedford et al. 2004; Prothero et al. 2008), while the Gomphotheriidae (represented by Gomphotherium) migrated in the early Barstovian (Tedford et al. 1987; Tedford et al. 2004). Zygolophodon and Gomphotherium are both present in the unnamed upper member of the Barstow Formation (Tedford et al. 1987; Woodburne et al. 1990; Tedford et al. 2004; Pagnac 2005, 2009; Lofgren et al. 2011; Lofgren and Anand 2011), located in the Mud Hills north of Barstow California (Figure 1).

The first proboscidean remains reported from the Barstow Formation were tooth fragments (Merriam 1919). Later, large scale quarrying by Frick Laboratory crews from the 1920’s to the 1950’s (specimens now housed at the American Museum of Natural History) yielded about a dozen proboscidean specimens including two isolated teeth designated as co-types of "Trilophodon bartonis" (Frick 1933).

Barstow Formation field work by the Raymond M. Alf Museum of Paleontology (RAM) was initiated in 1936 by Raymond Alf. It wasn’t until the late 1950’s that Alf located proboscidean remains. Early finds by the Alf Museum included a dentary with tusk/m3 of Zygolophodon, a partial skull of Zygolophodon, and a track way consisting of four tracks (Loigren and Anand 2010; Lofgren and Anand 2011). Concerted prospecting efforts in the Barstow Formation by RAM crews (which includes students and faculty of The Webb Schools on whose campus the RAM is located) since the early 1990’s, has resulted in the recovery of additional proboscidean specimens. The size of the RAM proboscidean collection from the Barstow Formation now exceeds that of any other institution.

In spite of their rarity, few proboscidean specimens from the Barstow Formation have been described. Here we review the proboscidean collections housed at the RAM, as well as those at the American Museum of Natural History, the Natural History Museum of Los Angeles County, and the San Bernardino County Museum.

Abbreviations

Institutional abbreviations—AMNH, American Museum of Natural History, New York, New York; F:AM, Frick American Museum, New York, New York; LACM, Los Angeles County Museum, Los Angeles, California; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California; SBCM, San Bernardino County Museum, San Bernardino, California

Other abbreviations— Ba1, Barstovian Biochron 1; Ba2, Barstovian Biochron 2; BAR, field collection crate number for F:AM specimens; NALMA, North American Land Mammal Age; RAM vertebrate locality records employ a V followed by numbers (e.g., V94276).

Survey of Barstow proboscidean specimens

Molars of Zygolophodon and Gomphotherium, the only proboscidean genera known from the Barstow Formation, are morphologically distinct. The valleys between the lophs of molars in Zygolophodon lack accessory cusps and Gomphotherium molars have accessory cusps in the
valleys between lophs. Thus, isolated molars from the Barstow Formation can easily be identified to genus.

Identification of the premolars and deciduous teeth is more difficult because comparative material for this part of the dentition of *Zygolophodon* is very rare. To identify non-molar cheek teeth, we used absence or presence of accessory cusps in the valleys between lophs. Those with accessory cups in valleys between lophs were referred to *Gomphotherium*, and those that lacked these accessory cusps were assigned to *Zygolophodon*. The accessory cusp distinction for molars of *Zygolophodon* and *Gomphotherium* also appears to apply to premolars and deciduous teeth because SBCM A489-200 (likely a dp4) has cusps in the valleys between its three lophs, and therefore represents *Gomphotherium*.

Compounding the difficulty of generic identification is the uncertainty of the tooth site of isolated premolars and deciduous teeth from the Barstow Formation. Identifications were provided by Frick (1926, 1933) for Paleogene and Neogene North American proboscideans, but good examples for Middle Miocene proboscideans are few. Tooth site identifications that are questionable are noted for those specimens. Much work needs to be done to confirm the tooth site and generic assignment of isolated deciduous teeth and premolars of these early records of North American proboscideans.

RAM specimens were collected from 1959 to 2011 and we provide a collection date for all specimens where it was recorded. Two RAM specimens (RAM 187 and RAM 908) are from sites about 1.5 km east of Owl Canyon. All other proboscidean fossils in the RAM collections are from sites within sections 9, 14, 15, and 16 (Township 11 north, Range 2 west), an area informally known in old Alf Museum locality records as "West Barstow." This general area is over 5 km west of Owl Canyon.

AMNH specimens from the Barstow Formation were collected over a long span of time, from at least 1927 to 1950, by crews employed by Childs Frick. These fossils were packed into crates and each was assigned a unique number preceded by BAR. We refer to these uncataloged AMNH specimens by their BAR numbers. All locality data recorded on AMNH specimen labels is repeated here. The majority of AMNH proboscidean fossils were collected from areas described as "near Chert Ridge Quarry" or "north end of formation," which would be the same general area as "West Barstow."

As presently known, all proboscidean specimens from the Barstow Formation are from the unnamed upper member whose base is equal to the stratigraphic position of the Skyline Tuff (Figure 2). The one exception is impressions from a site in the Calico Mountains to the east of the Mud Hills identified as proboscidean tracks from strata interpreted to be equivalent to the Middle Member (Reynolds and Woodburne 2001).

Digital calipers were used to measure all specimens except RAM 187 which required a standard a measuring tape.

**Proboscipeda sp.**

**Specimen and locality:** RAM 187 is a track way consisting of four well-preserved tracks that average 42.6 cm in diameter and record a stride length of 267.0 cm, from RAM locality V94176. This site is located about 40 meters above the Skyline Tuff, which would place it at the approximate stratigraphic position of the Dated Tuff (Figure 2) of Woodburne et al. (1990); the Dated Tuff is not present in the local stratigraphic section that yielded RAM 187.

**Description—discussion:** In the late 1960’s, a set of four well preserved tracks were discovered on steeply
inclined strata of the unnamed upper member (Figure 3). Because proboscidean tracks are very rare, the track way (RAM 187) was collected in 1969 to preserve it from vandals and erosion. By 1971, this track way was on exhibit and it is still displayed at the RAM more than 40 years later (Figure 4).

RAM 187 was described by Reynolds (1999) who did not assign the tracks to a known ichnogenus. We refer them to Proboscipeda sp. based on comparison to tracks of similar size and shape from Copper Canyon in Death Valley National Park described by Scrivner and Bottjer (1986). RAM 187 has four sets of oval prints with their large size indicating they were made by an adult proboscidean (Figure 4). With proboscidean tracks, an overstepping pattern can be assumed, as a modern elephant always places its left or right hind foot in the track of its respective front foot as it walks. Thus, each preserved track of RAM 187 is representative of the pes, as manus impressions have been overprinted.

Miocene proboscidean track ways are rare. Some other described examples include specimens from Romania (Panin and Avram 1962), the United Arab Emirates (Higgs et al. 2005), and other sites in California (Scrivner and Bottjer 1986; Reynolds 1999; Reynolds and Woodburne 2001). RAM 187 remains the best preserved track way of a proboscidean from Miocene strata in North America.

**Zygolophodon cf. Z. proavus**

**Specimen and locality:** RAM 908, a crushed partial skull of Zygolophodon cf. Z. proavus preserving the ventral portion of the palate, zygomatic arches, and basicranium, with complete RM3 and LM3 and partial RM2 and LM2 (Figure 5), from RAM locality V201006.

**Description:** RAM 908 is a partial skull preserving most of the ventral surface of the cranium posterior to the M2’s. The thin zygomatic arches, broad glenoid fossa, robust occipital condyles, and well preserved M3’s are the most distinct features of RAM 908. The maximum cranial width of RAM 908 at the zygomatic arches is 54.3 cm, length of the skull from the occipital condyles to the anterior edge of the M2’s is 56.0 cm, and the length and maximum width of the M3’s are about 127.5 mm and 75.0 mm respectively. Additional measurements and a complete description of RAM 908 are provided by Lofgren and Anand (2011).
Discussion: In 1965, Webb faculty member Ken Monroe found RAM 908 from a site described in the RAM locality database as “about one mile east of Owl Canyon.” Thus, although its precise stratigraphic level is unknown, RAM 908 is thought to be from a thick section of the upper member exposed about one mile east of Owl Canyon. RAM 908 is of particular interest due to its rarity and size as it represents the only known skull of Zygolophodon from North America (Lofgren and Anand 2011). The M3’s of RAM 908 are smaller than those of Z. proavus, which indicates that the skull probably represents a smaller individual of Z. proavus whose size may be a reflection of sexual dimorphism in the species (Lofgren and Anand 2011).

Specimen and locality: RAM 907, a damaged right dentary with tusk and m3 of Zygolophodon cf. Z. proavus (Figure 6), from RAM locality V201205.

Description: RAM 907 has a worn m3 with four lophs and a tusk with a flat lingual face. The length of the m3 is 144.43 mm, and the widths of the lophs are 62.94 mm (first), 59.36 mm (second), 57.50 mm (third), and 52.14 mm (fourth). The maximum diameter of the tusk is 40 mm. The lack of cuspules between lophs indicates that RAM 907 is a zygodont mammutid. The size of the m3 of RAM 907 is larger but still relatively similar to M3’s of RAM 908, the partial skull of Zygolophodon cf. Z. proavus also from the Barstow Formation. Thus, RAM 907 is referred to that taxon as well.

Discussion: In 1959, while prospecting outcrops in the Fullers Earth Canyon area, Webb student Al Korber found RAM 907, which remains the only proboscidian jaw ever recovered from the Barstow Formation (Lofgren and Anand 2010). The locality of RAM 907 was not carefully recorded so V201205 represents outcrops in the general area of Fullers Earth Canyon.

Zygolophodon?
Specimen and locality: RAM 6505, a slightly damaged right dp4? (Figure 7), probably of Zygolophodon, collected in February 1992 from RAM locality V94042.

Description: RAM 6505 has two lophs both of which exhibit heavy to moderate wear. The first loph is narrower than the second loph and the enamel is broken and absent on the postero-lingual and posterior margin of the second loph. RAM 6505 probably represents Zygolophodon as there is no evidence of accessory cuspules in the valley between lophs. The length of RAM 6505 is 45.2 mm and the width is 31.1 mm.

Specimen and locality: RAM 6504, a left dP4? (Figure 8) probably of Zygolophodon, collected in April 1994 from RAM locality V94184.
Description: RAM 6504 has two lophs which are moderately worn, with the anterior loph narrower than the posterior loph. A well-developed valley is present between lophs and accessory cuspules are absent. RAM 6504 is referred to *Zygolophodon* based on this morphology. This specimen resembles F:AM 20850B (see below) in shape and morphology. The length of RAM 6504 is 32.5 mm and the width is 29.7 mm.

**Specimen and locality:** RAM 7626, a damaged left dp4? (Figure 9) probably of *Zygolophodon*, collected in May 2006 from RAM locality V200047.

**Description:** RAM 7626 has two lophs. The first loph is slightly worn and has two distinct cuspules. The second loph is heavily worn and is missing a significant portion of its posterior and postero-labial margins. The second loph is wider than the first loph. RAM 7626 is referred to *Zygolophodon* because it lacks accessory cuspules between lophs. The length of RAM 7626 is 48.6 mm and the width is 37.8 mm.

**Specimen and locality:** F:AM 20850B, maxilla fragment with dp3 identified and described by Frick (1933; figure 33) as one of two holotypes of “*Trilophodon bartonis*” (F:AM 20850A is the other). F:AM 20850B is probably a dp4 and was collected in 1927 from an unrecorded locality (was in Box 80 of the Frick collections from Barstow).

**Description—discussion:** F:AM 20850B is very slightly worn and has a length of 44.9 mm and a width of 33.6 mm. Two lophs are present, the anterior of which is the narrower one. F:AM 20850B has a well-developed cingulum on its entire margin except for its labial side, with accessory cuspules developed on its anterior and posterior cingulum. Valleys between lophs lack accessory cuspules indicating that F:AM 20850B probably represents *Zygolophodon*. Specimens referred to “*Trilophodon bartonis*” by Frick (1933) should now be referred to *Zygolophodon*, the only zygodont proboscidean recognized from the Barstow Formation (Loofgren and Anand 2011) and from Middle Miocene strata in North America (Lambert and Shoshani 1998). The holotypes of “*Trilophodon bartonis*” are inadequate to define a taxon distinct from *Zygolophodon*.

**Gomphotherium**

**Specimen and locality:** RAM 10362, a damaged right M2 of *Gomphotherium* (Figure 10), collected in November 2007 from RAM locality V98004, a site about 30 meters below the tuff that underlies the *Hemicyon* Quarry (Loofgren et al. 2011).

**Description:** RAM 10362 has three slightly worn lophs, all of which are missing parts of their enamel. The first loph is more worn than the others and is it also missing its anterior margin due to breakage. RAM 10362 has accessory cuspules that invade the valleys between lophs, so it is
clearly aligned with *Gomphotherium*. RAM 10362 is 95.9 mm in length and 65.7 mm in width.

**Discussion:** Previously, the oldest known occurrence of *Gomphotherium* in the Barstow Formation was a tooth (F:AM 20850A) from the *Hemicyon* Quarry, collected by Frick Laboratory crews in 1933. RAM 10362 was collected from strata about 30 meters below the *Hemicyon* Quarry and now represents the oldest well-documented occurrence of *Gomphotherium* from the Barstow Formation (Figure 2).

**Specimen and locality:** SBCM A489-200, a damaged dp4? (Figure 11) of *Gomphotherium*, from the SW ¼, NW ¼, NE ¼ of Section 15, Township 11 north, Range 2 west (pers. comm.. R. Reynolds 2012), donated to the SBCM in 1967 by a private collector.

**Description—discussion:** SBCM A489-200 has at least three lophs and an incipient fourth loph consisting of two small low cusps (Figure 11) on the tooth’s posterior. The front part of the tooth and half of the first loph are missing due to breakage. The second and third lophs each have two main cusps. Accessory cusps invade the valleys between lophs indicating that SBCM A489-200 is *Gomphotherium*. This is the second well-documented occurrence of *Gomphotherium* in the Barstow Formation (RAM 10362 is the other). SBCM A489-200 has a width of 34.0 mm and the minimum length of this incomplete tooth is 55.1 mm. This specimen was donated to the SBCM in 1967 and was labeled as found in Pierre Canyon. There is no Pierre Canyon in the Mud Hills, but Pirie’s Canyon is the informal name of a drainage (Lindsay 1972;figure 1) now labeled Fossil Canyon on the Mud Hills quadrangle topographic map. However, R. Reynolds describes the specimen locality as the canyon north of Fuller’s Earth Canyon that contains Rodent Hill. Thus, SBCM A489-200 probably is from section 15 where there is also extensive outcrop of the upper member.

**Proboscidea Sp.**

**Specimen and locality:** RAM 6905, a damaged left P4 (Figure 12), collected in March 2000 from RAM locality V200009.

**Description:** RAM 6905 has two heavily worn lophs. The postero-labial corner and most of the posterior margin of RAM 6905 is missing due to breakage. In occlusal view (Figure 12), RAM 6905 is distinctly ovate in outline. The lack of a well-developed valley between the lophs of RAM 6905 precludes its identification to genus. The length of RAM 6905 is 41.1 mm and the width is 39.3 mm.

**Specimen and locality:** RAM 9347, a slightly damaged P3? (Figure 13), collected before 1990 from RAM locality V94281.

**Description:** RAM 9347 lacks easily discernible dental landmarks and this makes identification problematic. RAM 9347 appears to have two weakly developed lophs that are slightly worn. The length of RAM 9347 is 29.6 mm.

**Figure 10:** Occlusal view of RAM 10362, right M2 of *Gomphotherium*. Scale in cm.

**Figure 11:** Occlusal view of SBCM A489-200, a dp4? of *Gomphotherium*. Scale in cm.

**Figure 12:** Occlusal view of RAM 6905, left P4. Scale in cm.
mm and the width is 24.5 mm (if we orientated the tooth properly).

**Specimen and locality:** RAM 7625, a slightly damaged P3? (Figure 14), collected in October 2005 from RAM locality V200149.

**Description:** RAM 7625 exhibits heavy wear and some damage due to breakage and lack of enamel. RAM 7625 has a roughly ovate shape but less so than RAM 6905 and RAM 6906 which are P4's. This specimen is too worn to identify to genus and its tooth site is uncertain. The length of RAM 7625 is 29.8 mm and the width is 24.3 mm.

**Specimen and locality:** RAM 6906, a left P4 (Figure 15), collected in May 2000 from RAM locality V95052.

**Description:** RAM 6906 has two lophs which have merged into a single wear facet on the labial half of the tooth because of heavy wear. RAM 6906 has a distinct ovate outline in occlusal view (Figure 15) like RAM 6905 (Figure 12). Lack of a well-developed valley between lophs of RAM 6906 precludes its identification to genus. The length of RAM 6906 is 45.2 mm and the width is 32.1 mm.

**Specimen and locality:** F:AM 20850A, an isolated tooth identified as a left p4 and described by Frick (1933; figure 36) as the second holotype of “Trilophodon bartonis” (F:AM 20850B is the other). F:AM 20850A probably is a dp4 and was collected in 1933 from Hemicyon Quarry (in box 74 of Frick Barstow field collections).

**Description—discussion:** F:AM 20850A is 39.3 mm in length and 33.1 mm in width and has two lophs. The anterior loph is slightly worn while the higher posterior loph has moderate wear. The shape and morphology of F:AM 20850A is similar to RAM 6505 and 7626, but F:AM 20850A is smaller. As noted above, the name “Trilophodon bartonis” should be abandoned. F:AM 20850A could be Zygolophodon or Gomphotherium.

**Specimen and locality:** LACM 27181, a left P4 (Figure 16), from LACM locality 7133 (Rainbow Basin), collected May 1971.

**Description:** LACM 27181 is 40.3 mm in length and 35.6 mm in width. The tooth is very heavily worn which has erased most of its occlusal morphology. LACM 27181 is very similar to RAM 6905 and RAM 6906, but is slightly smaller.

**Specimen and locality:** Uncataloged AMNH left p3?, from crate BAR 99-32, collected in 1928 from north end of formation, layer #3.

**Description:** This uncataloged tooth is slightly worn and has four cusps arranged in a box pattern. Its length is 29.5 mm and its width is 23.4 mm.

**Specimen and locality:** Uncataloged AMNH tusk fragment, from crate BAR 439H, collected in 1950 about 300
feet above Chert Ridge Quarry. Specimen is too fragmentary for additional identification.

**Specimen and locality:** Uncataloged AMNH upper tusk fragments (two), from crate BAR 326-1773, collected in 1935 from miscellaneous localities above Leader Quarry horizon. Specimens are too fragmentary for additional identification.

**Specimen and locality:** Uncataloged AMNH molar root, from crate BAR 99-32, collected in 1928 from north end of formation, layer #3. Specimen is too fragmentary for additional identification.

**Specimens and localities:** Proboscidean tooth fragments collected by RAM crews between 1993 and 2011, cataloged as RAM 8413, RAM 7169, RAM 8550, RAM 14272, RAM 11637, RAM 11624, RAM 14271, RAM 14274, RAM 7642, RAM 14601, and RAM 7644, from RAM localities V94028, V94039, V95092, V200154, V200155, V200025, V200206, and V200511. Although not identifiable to taxon, tooth fragments are useful for documenting the stratigraphic occurrence of proboscideans within the formation.

**Specimen and Locality:** RAM 6862, an unciform, collected in April 1995 from RAM locality V95092.

**Specimen and locality:** RAM 14273, an unciform, collected before 1990 from RAM locality V94033.

**Specimen and locality:** RAM 9352, an unciform, collected in November 2004 from RAM locality V200405.

**Specimen and locality:** RAM 6861, a distal humerus fragment, collected in October 1992 from RAM locality V94049.

**Specimen and locality:** Uncataloged AMNH sesmoid, from box 162, collected in 1930 from north end of formation, lower strata.

**Specimen and locality:** Uncataloged AMNH metapodial, from crate BAR 439-J, collected in 1950 from north end of Chert Ridge Quarry horizon, about 150 yards east of quarry, first division.

**Specimen and locality:** Uncataloged AMNH rib capitulum, from crate BAR 439-L, collected in 1950 from Chert Ridge Quarry, north end.

**Specimen and locality:** Uncataloged AMNH limb fragments (two), from crate BAR 439-K, collected in 1950 from north end of Chert Ridge Quarry, about 150 yards east of quarry.

**Specimen and locality:** Uncataloged AMNH patella, from crate BAR 439-I, collected in 1930 from north end of Chert Ridge Quarry, about 150 yards east of Chert Ridge horizon, first division.

**Discussion—summary**

Cataloged and uncataloged proboscidean fossils from the Barstow Formation housed at the RAM, AMNH, LACM, and SBCM total nearly 50 specimens. The RAM collection is largest (26 specimens) and includes a trackway, a dentary with tusk and m3, a partial skull, eight isolated teeth, eleven tooth fragments, three carpals, and a humerus fragment. The AMNH has 16 proboscidean specimens, of which three are isolated teeth, three are tooth fragments, and the others are postcranial elements. The LACM and SBCM each house one isolated tooth.

The most complete specimens are a partial skull referred to *Zygolophodon cf. Z. proavus* (Lofgren and Anand 2011) and a dentary we refer to the same taxon. *Zygolophodon* is the only zygodont mammutid genus known from the Barstow Formation and other Middle Miocene strata in North America (Lambert and Shoshani 1998). It is likely *Zygolophodon cf. Z. proavus* is also represented by four isolated teeth, but we take a cautious approach and refer them to *Zygolophodon*?
The only other known proboscidean from the Barstow Formation is Gomphotherium, whose molars have accessory cusps in the valleys between lophs, unlike Zygolophodon. We only identified two specimens as Gomphotherium, suggesting that Gomphotherium is less common in the Barstow Formation than Zygolophodon. An m2 (RAM 10362) referred to Gomphotherium is from RAM locality V98004, a site 30 meters below the tuff that underlies the Hemicyon Quarry. An isolated proboscidean tooth (F:AM 20850A) collected from the Hemicyon Quarry in 1933, was described as a holotype of “Trilophodon bartonis” (Frick 1933). Later, F:AM 20850A was informally identified as Gomphotherium (Woodburne et al. 1990; Pagnac 2005, 2009) which, at that time, indicated that F:AM 20850A represented the oldest record of Gomphotherium from the Barstow Formation. We question whether this specimen can be identified to genus. In any case, RAM 10362 is now the oldest occurrence of Gomphotherium in the Barstow Formation.

RAM V98004 is an important site because it yields whole elements of large and small mammals as well as birds. The holotype of Megahippus mckennai (RAM 910), a partial skull, was collected at V98004 in 1957 and described in 1962 (Tedford and Alf 1962). Recent collections from V98004 include a carapace-plastron with post-cranial material of Xerobates mohavensis, and numerous specimens of Aepycamelus, Protolabis, and Scaphohippus. The elements of small birds and mammals at V98004 are concentrated within a 5cm thick lens of siltstone that is about 2 meters wide. Excavation of this fossil rich siltstone lens has yet to be completed.

Locality data is poor for many proboscidean specimens collected from the Barstow Formation prior to the 1970’s. With the exception of some impressions identified as proboscidean tracks in the Calico Mountains (Reynolds and Woodburne 2001), all proboscidean remains with precise locality data were recovered from the unnamed upper member of the Barstow Formation. The oldest Zygolophodon specimen (F:AM 126896; now lost) is a tooth from Rainbow Quarry Prospect, at the approximate stratigraphic level of the Dated Tuff (Figure 2) or New Years Quarry, low in the upper member (Pagnac 2005, 2009). RAM 10362, the oldest known specimen of Gomphotherium, is from strata higher in the upper member. Thus, the proboscidean track way (RAM 187) from strata low in the upper member was probably made by Zygolophodon.

The unnamed upper member of the Barstow Formation is late Barstovian (Ba2 biochron) in age (Woodburne et al. 1990; Tedford et al. 2004; Pagnac 2009). Thus, all proboscidean body fossils from the Barstow Formation are late Barstovian (Ba2). Early Barstovian (Ba1) records of Zygolophodon and Gomphotherium are reported from central California, Oregon, and Mexico (Tedford et al. 1987, 2004). These areas are in relatively close proximity to the Barstow depositional basin. Why proboscidean body fossils are not known from early Barstovian strata of the Barstow Formation after 100 years of prospecting is unclear, but it is likely not a factor of inadequate sampling.

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References cited


