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Paleoecology and taphonomy of megaherbivores (Mammalia: Proboscidea and Rhinocerotidae) from Stratum 3 of the late Hemphillian Montbrook Local Fauna, Florida

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Abstract

Nine years of excavations at Montbrook (ca. 5.9 Ma, Levy Co., Florida) have recovered ca. 250,000 vertebrate fossils from an area of 525 m². Over 90% are fish, alligator, turtle, and other aquatic taxa; this in addition to sedimentological evidence supports a fluvial depositional environment. Three fossil-bearing units are recognized, Strata 2, 2A, and 3. The lowest unit Stratum 3 consists of alternating beds of unconsolidated to semiconsolidated quartz sand 2–50 cm thick and dark, compacted clay 0.3–1.5 cm thick. Unlike the other Montbrook strata, it preserves multiple associated and/or partially articulated skeletons of three mammalian megaherbivores, the gomphothere *Rhynchotherium* sp., the mastodon *Mammut* sp., and the rhinocerotid *Teleoceras* sp. Isolated fossils of these three taxa are present in Strata 2 and 2A, but are relatively uncommon, in contrast to those of smaller ungulates such as equids and cervids. No associated skeletons of smaller ungulates have been found at the site. The bones making up each associated megaherbivore skeleton have no evidence of weathering or water wear, but damage by postmortem compaction is often extensive. Right and left dentaries remain attached at the symphysis, except in very young juveniles. Articulations are most often found between foot bones or vertebrae/ribs. At least 35 skeletons of *Rhynchotherium* sp. were recovered ranging in age from young juveniles to full adults. Almost 60% of the dentaries belong to subadults (dp4-m1 in wear, m2 unerupted or erupting). Only four skeletons of *Mammut* sp. have been found, all juveniles or subadults. Eight skeletons of *Teleoceras* sp. are known; of these, three are juveniles, one a subadult, and the remainder adults. In addition to the difference in age structure, the rhino skeletons are more scattered, less complete, and more rarely articulated than those of the two proboscideans. We hypothesize that the primary large scavengers in this aquatic ecosystem were alligators, which were capable of completely dismembering and consuming the entire carcasses of relatively small ungulates, but for the most part could only remove the soft tissues of very large carcasses, such as adult *Teleoceras* sp. and both subadult and adult proboscideans. Spatial and stratigraphic relationships of the Stratum 3 skeletons suggest that they were not the result of a single mass mortality event, but rather record deaths over an interval that lasted decades to centuries.

Montbrook Recap

Montbrook (UF/VP locality no. LV070 and PBDB 200705) is a multitaxic bone bed located in northcentral Florida (Fig. 1). This region of the state has produced dozens of major vertebrate fossil localities ranging from early Miocene to latest Pleistocene and hundreds of smaller sites, but Montbrook is now the area's richest in terms of numbers of specimens. Montbrook was discovered in November 2015 after the Hodges, the property owners, dug a pit to recover sediment to build dirt roads, serendipitously exposing highly fossiliferous strata lying ca. 4 m below current ground level. Since then, crews of FLMNH staff, curators, and volunteers, UF grad and undergrad students, and college-level classes from other schools both inside and outside Florida have worked ca. 34,000 person-hours excavating an area over 525 m². These efforts have recovered ca. 250,000 identifiable vertebrate fossils, of which 126K have been identified and assigned to 77.5K individual UF/VP catalog numbers (Fig. 2). Currently uncatalogged specimens are either in hundreds of unprepared plaster jackets (mostly turtle shells or proboscidean bones) or uncurated microverts from screenwashing XXXX kg of sediment from the site (mostly fish).

Fossils of bony fish and reptiles are the most common vertebrates at Montbrook (Fig. 2). The latter mostly belong to freshwater or amphibious taxa, predominantly *Trachemys*, *Macrochelys*, *Apalone*, and *Alligator*. The former group is also dominated by freshwater or euryhaline forms, especially *Ictalurus*, *Lepisosteus*, *Atractosteus*, *Centropomus*, *Aplodonotus*, *Lepomis*, and *Micropterus*. At Montbrook, mammals are the only taxonomic group comprised mostly by fully terrestrial species.

Geologic Age of Montbrook

Biochronology strongly supports a latest Hemphillian (Hh4) NALMA (ca. 6.02–4.75 Ma; Tedford et al., 2004; Drury et al., 2017) for the Montbrook local fauna (Table 1).

The earlier portion of the Hh4 interval, ca. 6.02–5.33 Ma, correlates with the latest Miocene (late Messinian) and is here designated as Hh4a; the later portion of the Hh4, Hh4b, ca. 5.33–4.75 Ma, correlates with the earliest Pliocene (early Zanclean). The late Messinian is known to be cooler than the succeeding early Zanclean, with lower levels of atmospheric CO_2, moderate sea-level oscillations, and some continental glaciation at high latitudes (Hodell et al., 2001; Holbourn et al., 2018; Tanner et al., 2020). Several lines of evidence favors a Hh4a age for Montbrook, including 1) a few lineages with "more primitive" features than found in the Hh4b Palmetto Fauna of southcentral Florida (Webb et al., 2008; Killingsworth, 2023); 2) deposition during a time of much lower sea level than the Hh4b Palmetto Fauna; 3) good correlation with the Hh4a Mt. Eden local fauna of California (Albright, 1999); and 4) a mean $^{87}Sr/^{86}Sr$ ratio date from shark tooth enamel of 5.86 Ma (n=18; 2s.e.: 5.6–6.02 Ma; Killingsworth, 2023 and pers. comm.).

Figure 1. Right, outline of Florida with a star indicating the Montbrook Fossil Site. Left, field image of Montbrook showing strata 2, 2A, and 3.

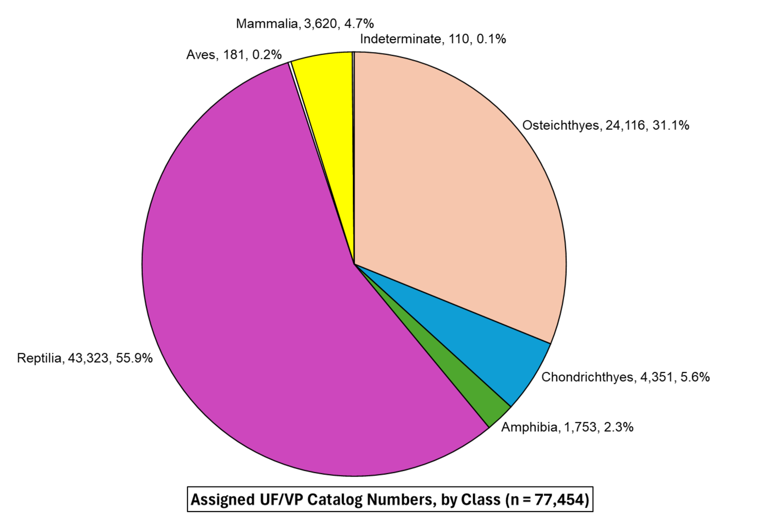


Figure 2. Relative abundances of vertebrate classes at Montbrook, based on catalog numbers.

Table 1. Biochronology of Montbrook. Hh, subages of the Hemphillian NALMA; Bl, Blancan NALMA (Tedford et al., 2004).

Montbrook taxa	Hh1	Hh2	Hh3	Hh4	Bl1-2	Bl3-4	Bl5
Borophagus hilli				X	X		
Lontra sp.				X	X	X	X
Enhydritherium terraenovae		X	X	X			
"Felis" rexroadensis				X	X	X	
Rhizosmilodon fiteae				X			
Nannippus aztecus		X	X	X			
Pseudhipparion simpsoni				X			
Tapirus polkensis		X		X			
Teleoceras sp.		X	X	X	?		
Protherohyus brachydontus				X	X		
Hemiauchenia edensis				X			
Pleiolama vera	X	X	X	X			
Hexameryx simpsoni				X			
Cervidae				X	X	X	X
Rhynchotherium sp.			X	X	X	X	
Bensonomys sp.			X	X	X	X	X
Baiomys sp.				X	X	X	X
Geomys sp.				X	X	X	X

Table 3. Stratigraphic distribution and relative abundances of large mammalian herbivores at Montbrook.

Taxon	size[2]	Stratum 2 NISP[3]	Stratum 2A NISP	Stratum 3 NISP	TOTAL[1] NISP
Nannippus aztecus	1	3	40	41	89
Pseudhipparion simpsoni	1	2	14	19	44
Medium-sized hipparion(s)[4]	2	0	5	9	20
small Equidae indet.	1	5	43	58	147
Tapirus polkensis	2	0	0	8	9
Teleoceras sp.	3	13	9	285	365
Protherohyus brachydontus	2	0	22	51	79
Pleiolama vera	2	2	2	13	21
Hemiauchenia edensis	2	2	11	18	48
Subantilocapra garciae	1	0	3	8	15
Hexameryx simpsoni	2	0	4	6	11
Cervidae indet.	2	1	1	2	11
Rumenantia indet.[5]	2	0	8	9	20
Artiodactyla indet.	1–2	2	12	18	43
Mammut sp.	3	0	0	50	51
Rhynchotherium sp.	3	0	6	271	306
Proboscidea indet.	3	93	99	1762	2324
Total all taxa		123	278	2627	3612
Total all non-MH taxa[6]	1–2	17	165	260	557
Total all MH taxa	3	106	114	2368	3046
% non-MH taxa		13.8%	59.1%	9.9%	15.5%
% MH taxa		86.2%	40.9%	90.1%	84.5%

[1]values in this column combine all specimens from Montbrook, including those with missing or ambiguous stratigraphic provenience, so they are greater than the sum from Strata 2, 2A, and 3.
[2]size categories for adult body mass: 1, >5kg & <100kg; 2, >100 kg & <250kg; and 3, > 1000kg.
[3]NISP, number of identifiable specimens.
[4]could be either *Cormohipparion emsliei* or *Neohipparion eurystyle*.
[5]includes postcranial bones that could be either Cervidae or Antilocapridae.
[6]MH, megaherbivores.

Geology

We recognize four siliciclastic strata at the Montbrook Site (Table 2). Almost all the vertebrate fossils from the site derive from Stratum 2A or Stratum 3. The descriptions and interpretations in Table 2 are based on the authors' observations across the entire site, but these are augmented by the results of a detailed sedimentological analysis of a single vertical section of Stratum 3 near the NW margin of the site (Ziegler, 2019). Ziegler (2019) noted significantly different sedimentary structures and features between the upper and lower portions of Stratum 3, that he interpreted as representing a major change in flow regime that occurred during a transgression. These correspond well to differences we observe in fossil preservation, thickness of sand layers, and changes in compactness and clay-content of the sand layers. The overall thickness of upper Stratum 3 varies from about 75 to 150 cm; the boundary between its upper and lower portions is typically gradual.

A well core drilled by the Florida Geological Survey near the Montbrook site produced about 8 m of siliciclastic sediments overlying the local Eocene limestone bedrock. Because of the highly irregular unconformity on the top of the region's limestone, that thickness will vary greatly across lateral transects. If that value is a true average, then we should be able to excavate deeper in the site by about two additional meters before encountering limestone bedrock.

The unconformity marking the contact between Strata 1 and 2 represents about 5.5 my of missing geologic history, essentially the entire Pliocene and Pleistocene epochs. An early Holocene age for Stratum 1 is based on the presence of early Archaic stone tools. The uncemented beds of Strata 2, 2A, and 3 are well compacted and many of their fossil bones show a high degree of post-burial crushing. This indicates that they were once covered by a thick sequence of now-missing sediments or rocks. During the Pliocene, high sea levels would have inundated the entire area in the vicinity of Montbrook, likely producing plentiful coastal and nearshore marine deposits. During the Pleistocene, the area would have been above sea level and subject to net erosion during glacial and weak interglacial intervals, but periodically submerged during major interglacials.

Montbrook Herbivores

As shown in Figure 2, mammals make up a small percentage of the total Montbrook vertebrate fauna. Over 4,000 specimens have been collected, if those in unprepared plaster jackets are added to those already cataloged. The current total of recognized mammals ranges between 29 and 31 species, with the uncertainty due to whether there are one or two species of conical-toothed felids present and one or two medium-sized species of hipparion equids. Eight of the mammalian species are of small size (adult BM < 5 kg) and include both herbivorous (rodent, leporid) and faunivorous (eulipotyphlans) taxa. A few of the eight (or nine) carnivorans were likely omnivorous, including a vulpine canid, a tremarctine bear, and a procyonid, but all of these are very rare. The remaining mammals, larger herbivores, consist of five or six perissodactyls, six traditional artiodactyls, and two proboscideans (Table 3). One of the artiodactyls is a tayassuid, whose extant species are omnivorous, but we include it in this study. Only the rhino *Teleoceras* and the proboscideans *Mammut* and *Rhynchotherium* fall within the traditional definition of a megaherbivore (adult BM > 1000 kg; Owen-Smith, 1988). The remaining Montbrook herbivores are small- to medium-sized taxa (adult BM < 200 kg), with a large gap in body size between them and the megaherbivores. We prefer not to assign the Montbrook megaherbivores to particular species until taxonomic studies and comparisons are published but are confident in our generic identifications. Although the ecological significance of megaherbivores was first realized over 30 years ago, new studies on their roles in modern ecosystems appear regularly (e.g., Hyvarinen et al., 2021; Pringle et al., 2023; Berzaghi et al., 2023), providing new insights for paleontologists studying fossil megaherbivores.

All of the larger mammalian herbivores present at Montbrook have been found in Stratum 3 (Table 3). All but two are also present in Stratum 2A, so there is little evidence for faunal turnover. Fossils of terrestrial mammals in Stratum 2A are generally less complete than those of Stratum 3, with greater degree of waterwear and breakage. Similar fossils are also recovered in Stratum 3, but so are those that are complete and better preserved.

Fossils of the small, non-megaherbivores make up a much larger percentage of the Stratum 2A total NISP, about 60%, compared to just 10% in Stratum 3. The volume of excavated Stratum 3 sediment is at least 20X that of Stratum 2A. The relative rarity of megaherivore specimens from Stratum 2A cannot be completely explained by the smaller widths of the Stratum 2A channels, as many of their isolated bones and teeth could easily be accommodated within these channels. Snapping turtle carapaces over 1 m in length and complete skulls of large alligators were found in Stratum 2A. Clearly Stratum 2A and Stratum 3 are taphonomically quite distinct.

Acknowledgments

We thank the Hodge family, especially Eddie and Chase Hodge, for allowing the FLMNH to collect the Montbrook fossils on their land and use their mining equipment to remove overburden, build dams, and transport large plaster jackets. As we enter our tenth year of digging at Montbrook in 2025, we remain awed, delighted, and inspired by the support we receive from our volunteer diggers. Most of the fossils described in this study were found by volunteers. Volunteers are also an essential component in our efforts to prepare plaster jackets, screen-wash and pick matrix, and curate the Montbrook fossils.

Montbrook excavations were funded by NSF award 1645530 and the Felburn Foundation. NSF grant 1756306 provided funding for specimen curation and preparation. Another grant from the Felburn Foundation provided much of the funds to purchase and renovate a storage warehouse in NW Gainesville to house fossils from Montbrook and other localities.

Table 2. Description and interpretation of the Montbrook strata.

	Lithology	grain size/ sorting	sedimentary features	contacts	depositional environment	vertebrate fossils
Stratum 1	almost pure quartz, unconsolidated	fine-grained; well sorted	some cross-bedding	upper: none lower: erosional unconformity	aeolian; reworking of coastal dunes to west	none
Stratum 2A	ca. 70% quartz, 30% phosphatic grains and internal molds of mollusks and barnacles; partially consolidated due to compaction	coarse sand- to granule-sized grains; vert poorly sorted	fining upward sequences; clay balls; no internal bedding	upper: conformable lower: erosional unconformity	flood or storm event cut-and-fill channels	extremely abundant and well mineralized; both macro- and microfossils common; frequent assoc. &/or artic. skeletons of freshwater taxa
Stratum 2	well compacted mix of reddish orange sediments that when dry hardens into an adobe-like consistency	poorly sorted mix of clay-, silt-, and sand-sized grains	massively bedded; burrow traces	upper: erosional unconformity lower: conformable, some-times with interbedding, sometimes sharp	oxbow swamp or salt marsh	poorly preserved, relatively uncommon, and found only close to contact with Stratum 3
Upper Stratum 3	alternating layers of: 1) pale tan, clayey quartz and phosphatic grains; and 2) dark gray to black pure clay. Sand layers consolidated.	sand layers are moderately well sorted; fine to medium sand-size grains; occasional lenses of coarser material (like Stratum 2A)	soft sediment deformation features; abundant shrimp burrows, clay balls	upper and lower: conformable	channel deposit near mouth of a very low gradient, tidally dominated river	well mineralized, typically dark in color; abundance varies laterally from rare to extremely common; skeletons of fresh-water taxa and terrestrial mega-herbivores
Lower Stratum 3	as in Upper Stratum 3, but quartz sand layers much thicker, lighter in color, lack clay, and are much more unconsolidated	sand layers well sorted; fine-grained; highly porous	minor cross-bedding; soft sediment deformation features; clay balls	upper: conformable lower: not observed	channel deposit of a low gradient, current-dominated river	poorly mineralized, typically light in color; abundance varies laterally from rare to common; skeletons of freshwater taxa and terrestrial megaherbivores

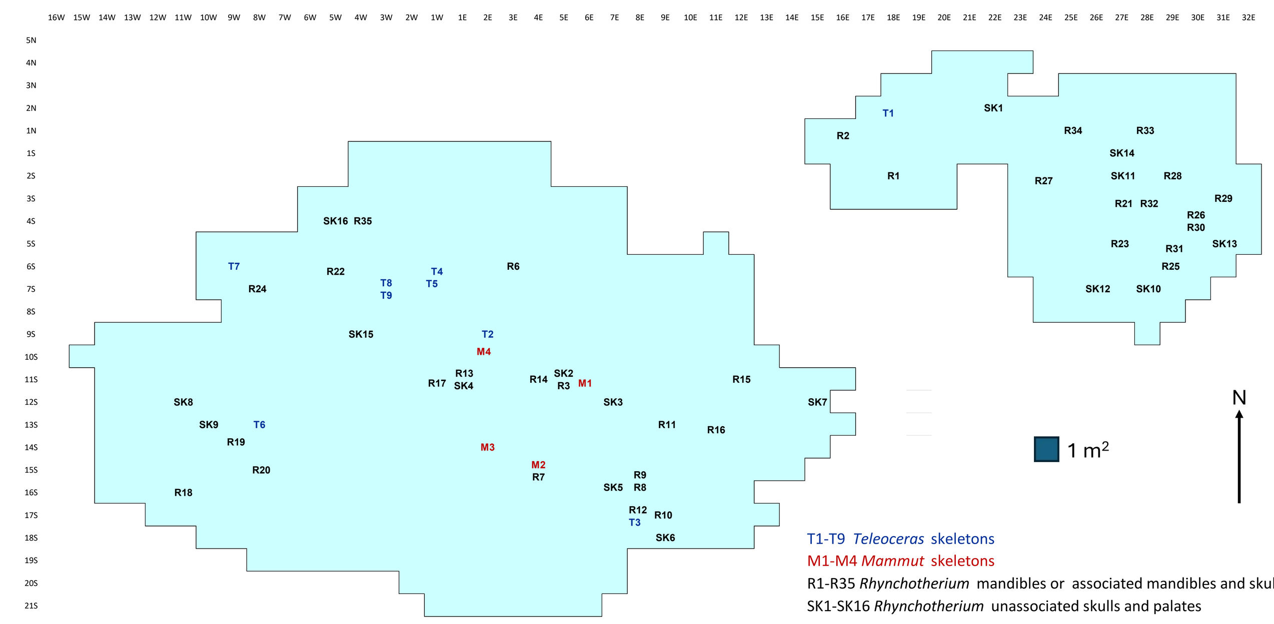


Figure 3. Map of Montbrook showing locations of megaherbivore skeletons. Areas excavated shaded in light blue. Indicated locations show position of skull and/or mandible; lateral extent of entire carcass much greater. Carcasses shown adjacent to each other in some cases overlie each other in different layers of Stratum 3. Numbers above and along left side are the coordinates of our grid system.

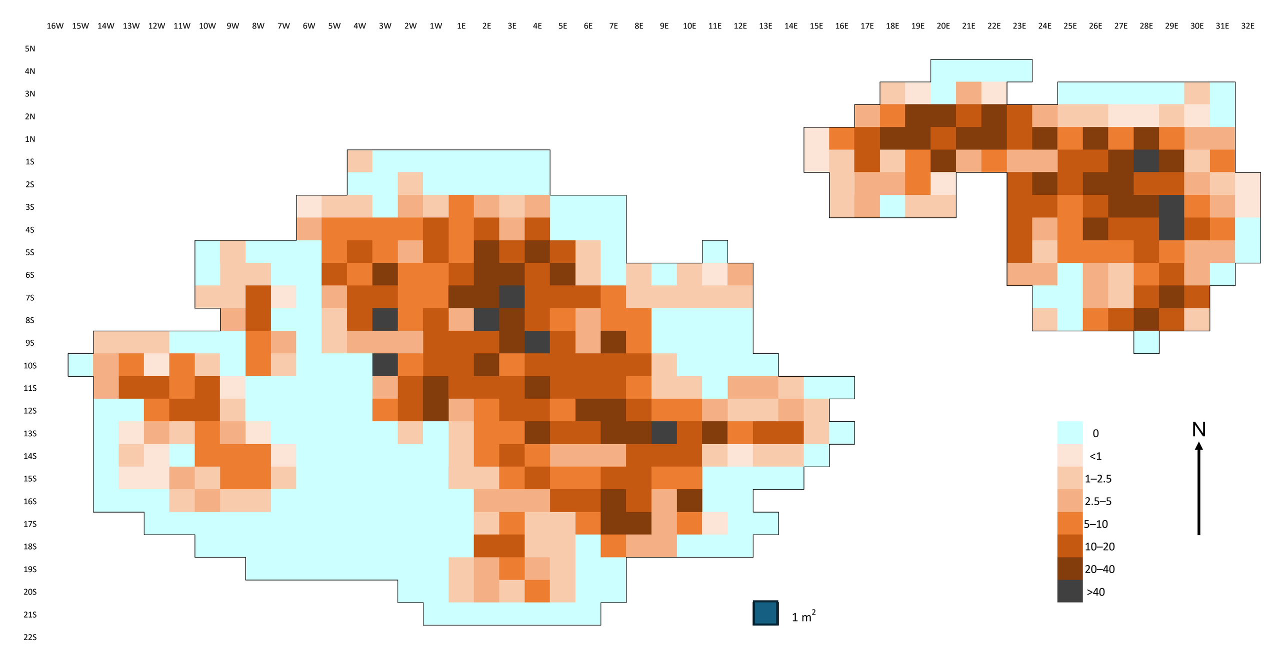


Figure 4. Map of Montbrook Site showing number of recovered proboscidean fossils in each square meter. Note similarity in overall bone concentrations and locations of skulls and/or mandibles in Figure 3.

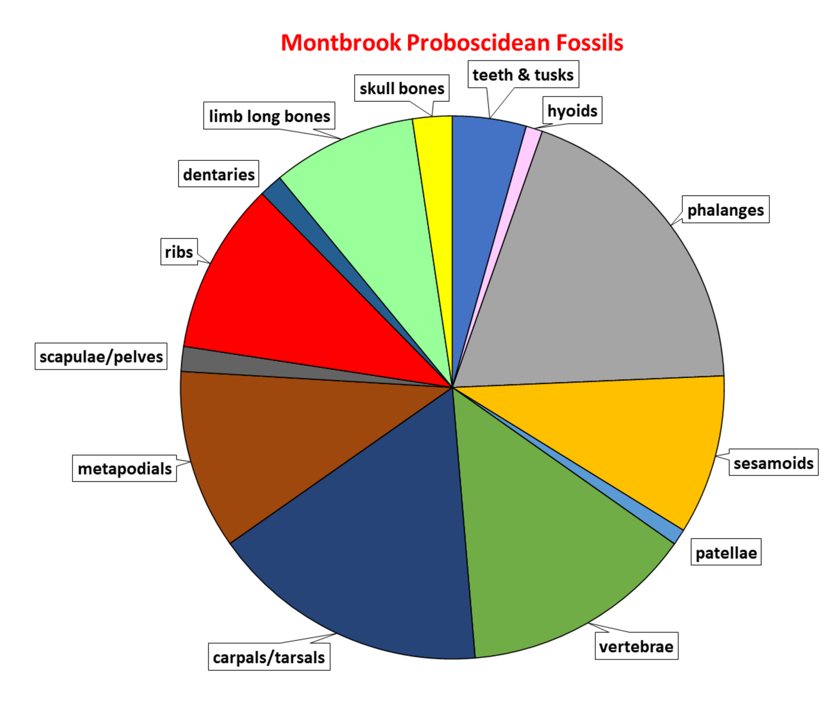


Figure 5. Relative abundance of proboscidean skeletal elements at Montbrook. N = 3442.

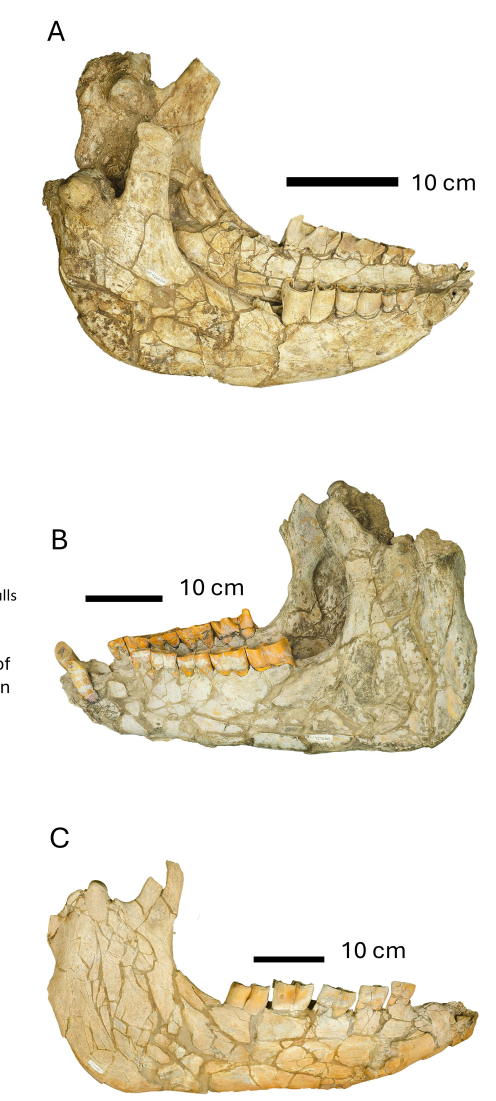


Figure 6. *Teleoceras* sp. from Montbrook. A, UF/VP 426000, young juvenile mandible. B, UF/VP 427000, adult female mandible. C, UF/VP 5558000, young adult male mandible. All in lateral view, scale = 10 cm.

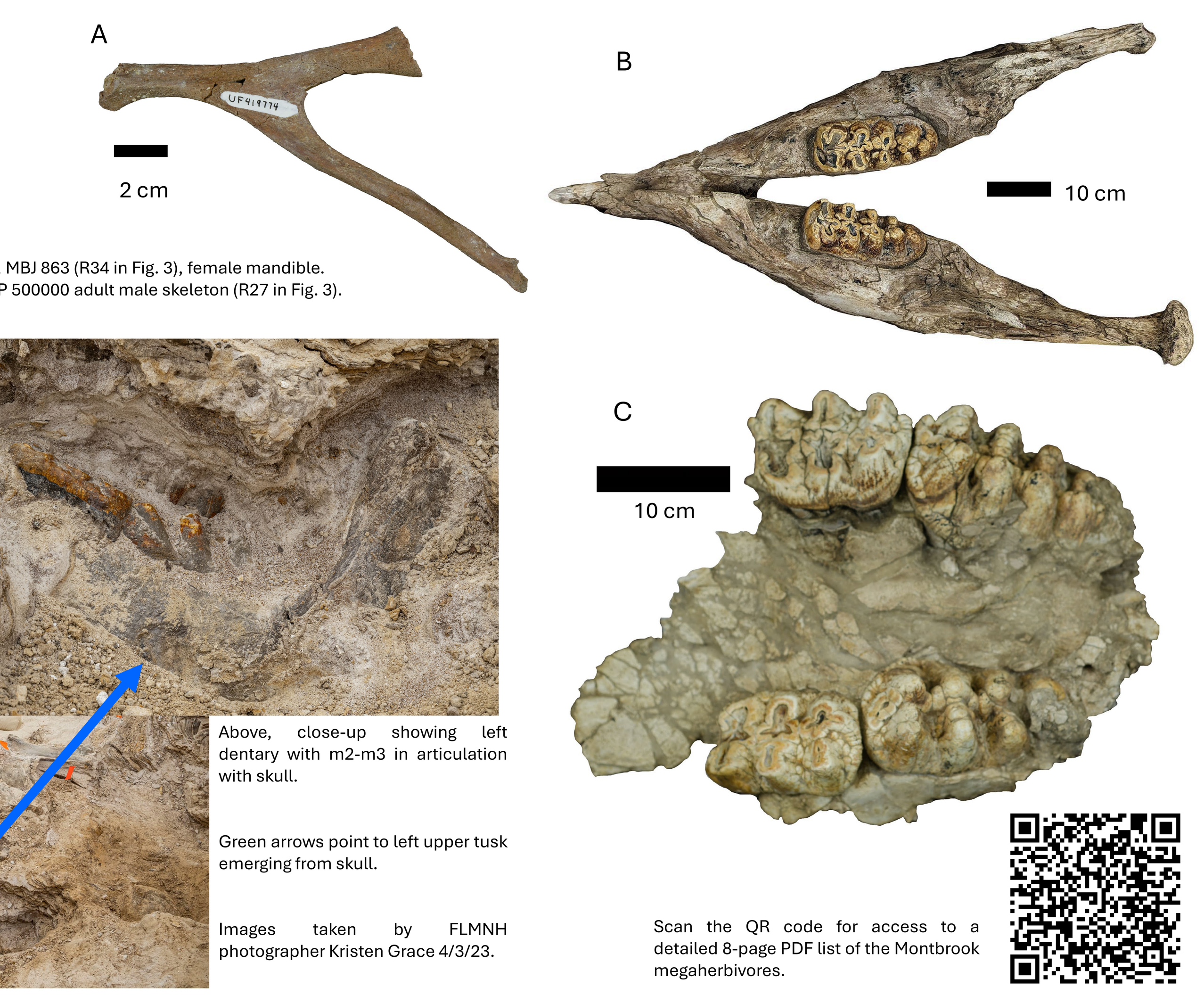
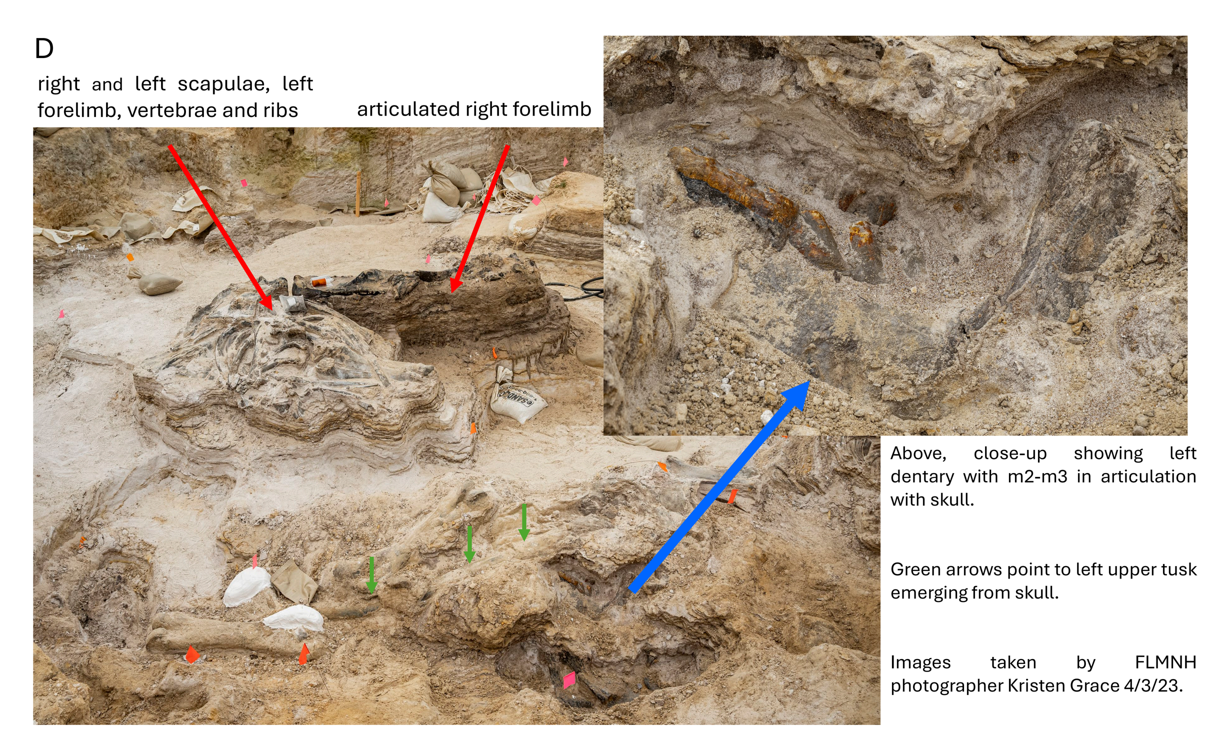


Figure 7. *Rhynchotherium* from Montbrook. A, UF/VP 419774, stylohyoid. B, MBJ 863 (R34 in Fig. 3), female mandible. C, UF/VP 440000 (SK6 in Fig. 3), palate with M2–M3. D, Field images of UF/VP 500000 adult male skeleton (R27 in Fig. 3).



Above, close-up showing left dentary with m2-m3 in articulation with skull.

Green arrows point to left upper tusk emerging from skull.

Images taken by FLMNH photographer Kristen Grace 4/3/23.

Megaherbivore Carcasses

To date we have collected a minimum of 48 megaherbivore individuals at Montbrook (Table 4; Fig. 3). A detailed description of these specimens can be loaded using the QR code in the lower right corner of this poster. Most of the limb bones of the proboscideans remain unprepared in plaster jackets, so it is difficult to associate them with a particular mandible or skull. We are also currently unable to distinguish between the postcranial bones of *Mammut* and *Rhynchotherium*.

Fossils of *Teleoceras* are widely distributed across the site but are notably concen-trated in the northwestern portion (Figs. 3 and 6). All four *Mammut* individuals were found within a relatively limited area of the site. The far NE corner of the site has the densest concentration of *Rhynchotherium*, followed by a SE-NW trending area across the central portion of the site (which overlaps the areas of concentration for both the *Teleoceras* and *Mammut*), and a lesser concentration in the westernmost part of the site. Other areas of the site lack or have very few megaherbivore skeletons, although they do contain fossils of other taxa. The greatest densities of proboscidean fossils occur in the same regions of the site with the most skulls and mandibles (compare Figs. 3 and 4).

Ample field and taphonomic evidence support the hypothesis that almost all the fossils of megaherbivores in Stratum 3 derive from complete or almost complete carcasses of dead individuals that became fully submerged in the deeper portions of the river channel. Turtles such as *Trachemys* and *Apalone*, *Alligator*, fish, crus-taceans, other invertebrates, and bacteria would have been the major agents removing the soft tissues (Orihuela-Torres et al., 2024). After defleshing of the carcass, currents would disarticulate and scatter the bones of the skeleton. The degree to which this occurred would depend on the length of time it took for sediments to cover the bones, accounting for the widely varying observed degree of articulation ranging from none to almost 100% (Fig. 7D). The following are some of the lines of evidence supporting this scenario.

- Carcasses of large mammals in fully terrestrial settings or even those lying partially submerged in shallow water are scavenged by carnivores which consume some smaller bones entirely and softer portions of others. Punctures and other distinctive marks caused by teeth are found on the surfaces of bones (Haynes and Hutson, 2020). None of these affected the Montbrook megaherb-ivore carcasses.
- No signs of weathering, waterwear, or other types of pre-burial bone modifica-tion on the fossils comprising the megaherbivore carcasses (Shipman, 1981).
- Relative abundances of skeletal elements of all sizes are very close to abundances in original entire skeletons (Fig. 5).
- Complete mandibles (both right and left dentaries joined at the symphysis) of megaherbivores are much more common than partial jaws or isolated teeth (Fig. 6).
- In cases where articulation is absent, association of fossils supported by matching right and left elements, similarity in size and ontogeny, and ability to rearticulate.

Finally, after many years of excavation, why have no skeletons of any of the smaller herbivores ever been found, such as equids or camelids? Their fossils are in Stratum 3, including some well-preserved but isolated specimens. An extinct species of *Alligator*, similar in size to the extant *A. mississippiensis*, is very common at Montbrook. A complete carcass of a small ungulate can be completely torn apart and consumed by several large alligators. In contrast, assuming they can penetrate the hide of a dead megaherbivore, a group of alligators would quickly satiate themselves on just a small portion of its carcass, leaving the rest for other animals to scavenge.

Table 4. Distribution of age classes and gender among the Montbrook megaherbivores. Many of the *Rhynchotherium* specimens remain unprepared; once prepared, their age and gender will be known.

	juveniles	subadults	adults	undeterm.	total
Teleoceras sp. sex indet.	3	1	0	0	4
Teleoceras sp. males	0	0	3	0	3
Teleoceras sp. females	0	0	1	0	1
Mammut sp. sex indet.	2	2	0	0	4
Rhynchotherium sp. sex indeterminate	10	7	2	8	27
Rhynchotherium sp. males	0	0	2	0	2
Rhynchotherium sp. females	0	3	3	0	6

Scan the QR code for access to a detailed 8-page PDF list of the Montbrook megaherbivores.

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