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ORIGINAL PAPER

Ontogeny and Sexual Dimorphism of *Glyptotherium texanum* (Xenarthra, Cingulata) from the Pliocene and Pleistocene (Blancan and Irvingtonian NALMA) of Arizona, New Mexico, and Mexico

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Abstract North American glyptodonts originated from South American ancestors during the Great American Biotic Interchange no later than early Blancan North American Land Mammal Age (NALMA). A substantial expansion in population samples from the late Blancan 111 Ranch fauna of southeastern Arizona, several late Blancan faunas in New Mexico, and the early Blancan–Irvingtonian faunas of Guanajuato, Mexico, permit, analysis of sexual dimorphism and ontogeny of *Glyptotherium texanum* Osborn, 1903. Growth of carapacial osteoderms was allometric, including changes of the external sculpturing. Overall anatomy of the carapace changed with growth, with development of distinctive pre-iliac and post-iliac regions in lateral profile of adults. Skulls of adults possess a unique boss on the anterior surface of the descending process of the zygomatic arch that is not present in juveniles. Sexual dimorphism involves differences in anatomy of lateral and posterior osteoderms. *Glyptotherium arizonae* Gidley, 1926, is a junior synonym of *G. texanum*. The temporal distribution of *G. texanum* extends from early Blancan NALMA to Irvingtonian NALMA, with geographical distribution from Central America and Mexico to southern United States.

Keywords *Glyptotherium* · Glyptodonts · Cingulata · Xenarthra · Blancan · Irvingtonian

Introduction

Glyptodonts, pampatheres, and armadillos (Xenarthra, Cingulata) originated in South America in the early Paleogene (Fernicola et al. 2008; Vizcaíno and Loughry 2008). The Cingulata were already diverse and widespread (Gaudin and McDonald 2008; Fernicola et al. 2008) when the juxtaposition of North America and South America in the Neogene facilitated dispersal of South American terrestrial taxa into Central America (Webb 1991; McDonald 2005; Morgan 2008) as part of the Great American Biotic Interchange (GABI) (Woodburne 2010 and references therein).

Only one clade of glyptodonts (Fig. 1) established successful populations in Central America. The founder population expanded through Central America and Mexico, and eventually reached latitudes in southern United States that include Arizona, New Mexico, Texas, Oklahoma, the Gulf Coastal Plain, and the Atlantic Coastal Plain as far north as South Carolina (Gillette and Ray 1981). The history of the geographic expansions and contractions of glyptodonts in North America has been elusive. The North American genus *Glyptotherium* Osborn, 1903, appears to be more closely related to *Boreostemma* Carlini et al., 2008, from northern South

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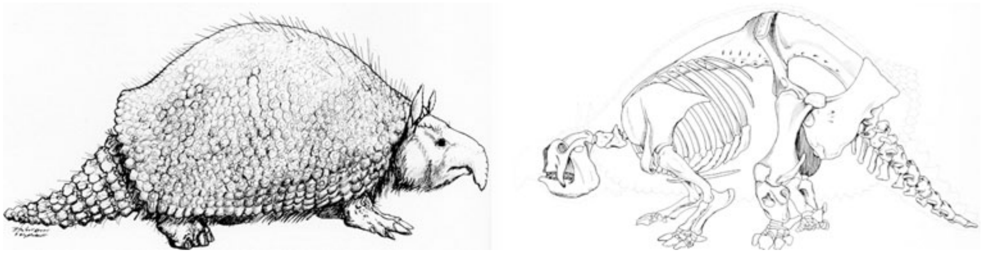

Fig. 1 Reconstruction of *Glyptotherium texanum* in life (left) and non-carapacial skeleton (right), from Gillette and Ray (1981); drawing on left by Bonnie Dalzell, drawing on right by Larry Isham, both originally identified as *G. arizonae*, now considered a synonym of *G. texanum*

America, known from middle Miocene to Pliocene (Zurita et al. 2011a, 2013), than any other genus.

Gillette and Ray (1981) recognized *Glyptotherium* as the only genus in North America, with five species: *G. texanum*, *G. arizonae*, *G. floridanum*, *G. mexicanum*, and *G. cylindricum*. They broadly described a history of anagenesis (McDonald and Naples 2007) that began with *G. texanum* in the late Blancan North American Land Mammal Age (NALMA), continued into the Irvingtonian NALMA as *G. arizonae*, and culminated with *G. floridanum* in the Rancholabrean NALMA. This hypothesis did not postulate the evolutionary positions of two species known only from incomplete holotype specimens, *G. mexicanum* and *G. cylindricum*, both from Mexico. By that interpretation, three species of glyptodonts were diagnostic for a succession of three land mammal ages, except for a problematical overlap of apparent *G. texanum* and *G. arizonae* in Florida in the Blancan NALMA.

Newly discovered specimens from the Blancan and Irvingtonian NALMAs in Mexico, Arizona, and New Mexico (Thrasher 2000; Morgan and Lucas 2000, 2003; Morgan 2008; Morgan et al. 2008, 2011; Carranza-Castañeda and Gillette 2011; Gillette et al. 2012) (Fig. 2) now permit a reevaluation of ontogeny, sexual dimorphism, temporal range, and taxonomy. Records of *Glyptotherium* from Guanajuato, central Mexico, are the oldest known glyptodonts in North America, with radiometric dates that indicate an origin of the genus no later than 3.9 mya (Carranza-Castañeda and Miller 2004; Carranza-Castañeda 2006; Carranza-Castañeda and Gillette 2011, 2013; Gillette et al. 2012).

The taxonomic framework below follows Gillette and Ray (1981). The synonymy of two Blancan-Irvingtonian species of *Glyptotherium* presented here is a first step in comprehensive review of the taxonomy and paleobiology of this genus, in line with the recommendations of Gaudin and McDonald (2008). The recognition of this synonymy was facilitated by an expansion in the number of specimens from the 111 Ranch fauna in southeastern Arizona (Thrasher 2004; White and Morgan 2005; Morgan and White 2005) and review of the specimens from Guanajuato, Mexico (Carranza-Castañeda and Miller 1997; Miller and Carranza-Castañeda 1999; Carranza-Castañeda et al. 2002; Carranza-Castañeda 2006, 2007), both of which include specimens critical to understanding ontogeny and sexual dimorphism.

Prior to this review of two species of *Glyptotherium*, the only recent evaluation of species in this genus in North America was presented by Gillette and Whisler (1986), who confirmed the conspecific status of the Rancholabrean glyptodonts that occupied the Gulf Coast in Florida and Texas (*G. floridanum*).

Abbreviations **AMNH** American Museum of Natural History; **ChM** Charleston Museum; **F:AM** Frick Collection, American Museum of Natural History; **GABI** Great American Biotic Interchange; **GTO** Guanajuato, Mexico, also locality prefix for sites in Guanajuato, Mexico; **IGM** Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria; **MPGJ** Museo de Paleontología, Centro de Geociencias Juriquilla; **MSM** Arizona Museum of Natural History (formerly Mesa Southwest Museum); **ma**, megannum, one million years in the radioisotopic time scale; **mya**, million years ago; **N^1–N^8** upper dentition, all molariform; **N_1–N_8** lower dentition, all molariform; **NALMA** North American Land Mammal Age; **NMMNH&S** New Mexico Museum of Natural History and Science; **UNAM** Universidad Nacional Autónoma de México.

Definitions Anatomical terminology for glyptodonts is generally well known and consistently applied. However, osteological and orientational terminology that applies to the armor has been varied and inconsistent. Gillette and Ray (1981) used the term ‘scute’ for the individual plates of bone that coalesce to form the armor in *Glyptotherium*. The term ‘osteoderm’ has gained wide usage as a replacement for “scute,” and is adopted here. The armor consists of conjoined osteoderms arranged as a plate on the dorsal surface of the skull (“casque osteoderms”), the conjoined osteoderms that cover the dorsal and lateral surfaces of the body as a “carapace” (also “dorsal carapace”), the bands of armor formed by 1–3 rows of osteoderms that surround successive caudal

Fig. 2 Principal Blancan and Irvingtonian NALMA sites with *Glyptotherium* in United States and Mexico plotted on paleogeographic map reconstruction for 5 mya, courtesy Ron Blakey, Colorado Plateau Geosystems (Blakey nd). **1**,Guanajuato, Mexico; **2**, 111 Ranch, near Safford, AZ; **3**, Curtis Ranch, AZ (type locality of *G. arizonae*); **4**, southwestern New Mexico; **5**, southern New Mexico; **6**, Rio Grande drainage, New Mexico; **7**, western Texas; **8**, Crosby County, Texas (type locality of *G. texanum*); **9**, Holloman, Oklahoma; **10**, Carmen, Oklahoma; **11**, Florida sites; map reconstruction approximates shorelines and topography immediately before and during initial population expansion into North America from South America in the early GABI

vertebrae ("caudal rings"), and isolated ossifications in the dermis ("dermal ossicles").

Hill (2006) adopted useful orientational and osteological terminology that we have applied in the present contribution. Especially confusing are terms that express the outer and inner surfaces of the dermal osteoderms; we follow Hill (2006) in the use of "superficial" and "deep" (= "external" and "internal", or "external" and "deep" of other authors). Figure 3 illustrates the most frequently used terminology.

Systematic Paleontology

Order CINGULATA Illiger, 1811
Family GLYPTODONTIDAE Gray, 1869
Subfamily GLYPTODONTINAE Gray, 1869

Genus *GLYPTOTHERIUM* Osborn, 1903

Type Species *Glyptotherium texanum* Osborn, 1903

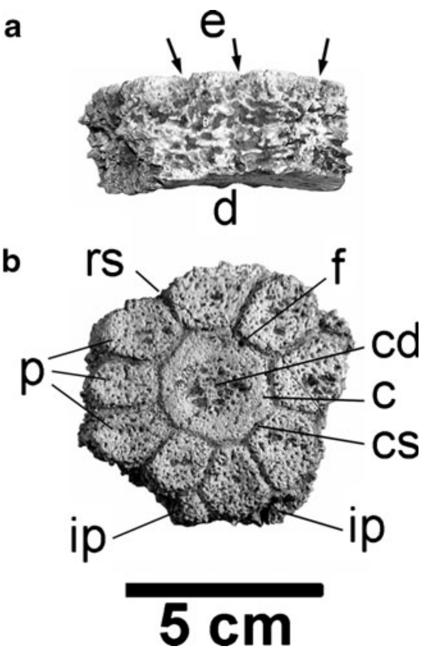

Fig. 3 Osteoderm terminology. This slightly irregular, hexagonal osteoderm from an adult *Glyptotherium texanum* has nine peripheral figures, three intercalated peripheral figures, an octagonal central figure, and slightly convex central figure with weak central depression. **a**, edge view; **b**, superficial (external) surface. **Abbreviations: c**, central figure; **cd**, central depression; **cs**, central sulcus; **d**, deep (internal) surface; **f**, hair follicle; **ip**, one of three intercalated (incomplete) peripheral figures; **p**, peripheral figures; **rs**, radial sulcus; **s**, superficial (external) surface; arrows indicate positions of several radial sulci

Included Species *Glyptotherium mexicanum* (Cuatáparo and Ramírez, 1875); *G. texanum* Osborn, 1903; *G. cylindricum* (Brown, 1912); *G. arizonae* Gidley, 1926; *G. floridanum* (Simpson, 1929).

Occurrence Southern United States, Mexico, Central America, northern South America, and Brazil. *Glyptotherium* occupied central Mexico as early as early Blancan NALMA, and subsequently expanded to southern United States in the late Blancan NALMA and early Irvingtonian NALMA (*G. texanum*).

Remarks There are no records of *Glyptotherium* in the United States in medial and late Irvingtonian NALMA sites, the “glyptodont gap,” after which the genus reappears in southern United States (*G. floridanum*). Geographic distribution of the genus in Mexico and Central Mexico was probably continuous from early Blancan NALMA through the Rancholabrean NALMA, with expansions and contractions of populations with changes in environmental conditions. Newly recovered specimens from central Mexico and southwestern United States, described below, indicate synonymy of *G. texanum* and *G. arizonae*.

Emended Diagnosis This emendation is restricted to certain aspects of carapacial armor; see Gillette and Ray (1981) for complete diagnosis. Carapace short, moderately to highly arched; carapacial osteoderms firmly ankylosed in adults, immovable except in anterolateral region; superficial surfaces of midbody osteoderms of carapace marked by shallow sulcus ornamentation that delimits a polygonal central figure, and a single row of six to ten peripheral figures; central figures tend toward octagonal shape; peripheral figures occasionally overlap to an adjoining osteoderm, and rarely form intercalated figures that add an additional complete or partial row to an osteoderm; central figures slightly larger than, equal to, or slightly smaller than peripherals; central figures slightly raised over the level of peripheral figures, and strongly to weakly convex, flat, or weakly concave, some with central depressions; carapacial osteoderms polygonal, tending toward symmetrical, hexagonal shape at midline; breadth of midbody osteoderms of adults greater than three times the thickness; adult carapace recurved, with convex preiliac and concave postiliac profile; osteoderms of anterolateral region quadrilateral; osteoderms of lateral margin increasingly conical toward rear in males, flat in females; peripheral osteoderms surrounding caudal aperture of adults strongly conical in males, weakly conical to nearly flat in females. See also diagnosis and discussion for *Glyptotherium* Osborn, 1903, in Gillette and Ray (1981). Carapacial anatomy of *Glyptotherium* differs from other late Neogene genera in relatively small size, relatively thin osteoderms, shallow depth of sulci on the external surface of osteoderms, and simple caudal armor.

Glyptotherium texanum Osborn, 1903

Glyptotherium texanum Osborn 1903:492, pl. 42 (original description).

Glyptotherium texanum: Gillette and Ray 1981:11, Figs. 5, 6–9, 18–19, 28–31, 33–41, 45–47, 50, 52, 53, 56–72, 74, 76, 79–82, 92.

Glyptotherium arizonae Gidley 1926:96, Fig. 4, pl. 40–44 (original description).

Glyptotherium arizonae: Gillette and Ray 1981:12, figs. 10, 13–14, 18–20, 24, 27, 32, 42–43, 48, 51, 54, 75, 77, 83–86, 93.

Glyptotherium arizonae: Czaplewski 2004:8, Figs. 5–8.

Emended Specific Diagnosis Central figures of internal (hexagonal, symmetrical) osteoderms of the middle region of the carapace of adults markedly convex to flat, larger than or equal to peripheral figures.

Hypodigm All specimens listed in Gillette and Ray (1981) for *G. texanum* and *G. arizonae*; and all new specimens of *G. texanum* described below.

Holotype AMNH 10704, carapace, caudal vertebrae, caudal armor, pelvis, seven chevrons.

Type Locality Llano Estacado, Texas; exact locality uncertain; probably “Blanco Locality,” Crosby County, Texas, of Johnson and Savage (1955).

Age Early Blancan NALMA–early Irvingtonian NALMA. Confirmed early Blancan NALMA records of this species are restricted to central Mexico. In the United States, the oldest

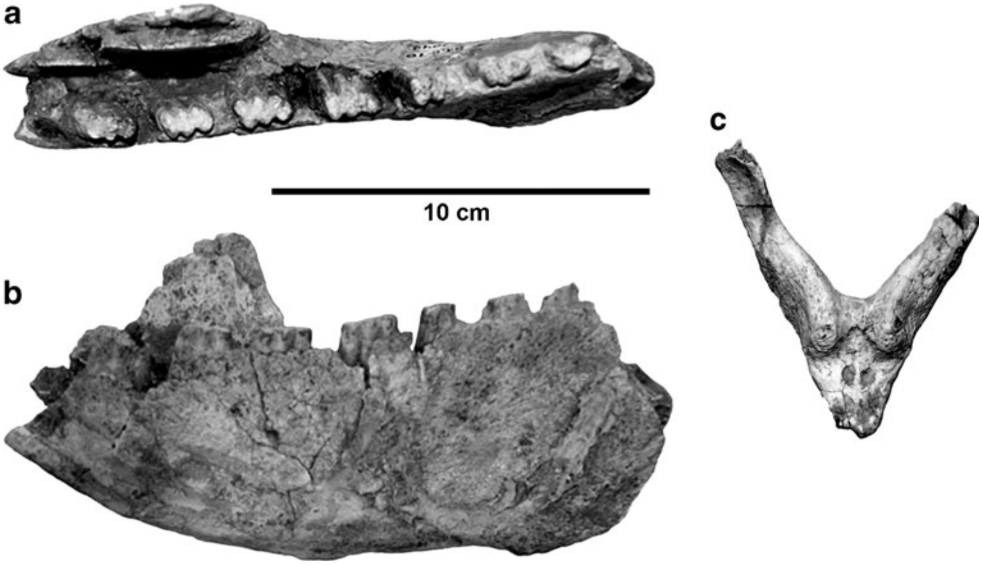

Fig. 4 Left lower jaw of a baby *Glyptotherium texanum* (MPGJ 2043) and a hyoid from an adult *G. texanum* (MPGJ 2042) from Guanajuato, Mexico. **a**, occlusal aspect of lower jaw; **b**, medial aspect of lower jaw, anterior to right; **c**, hyoid

records of this species are late Blancan NALMA. The species is known from early Irvingtonian NALMA sites in Mexico and southern United States. There are no confirmed records of this species younger than early Irvingtonian NALMA.

Remarks Gillette and Ray (1981) concluded that the lateral profile of the carapace of *G. texanum* was convex with little or no pre-iliac and post-iliac distinction. This conclusion is invalidated by ontogenetic changes in carapace anatomy reported below. Most of the hypodigm of *G. texanum* available to Gillette and Ray (1981) was juvenile, and the hypodigm of *G. arizonae* was adult, according to the conclusions presented below. In addition, *G. texanum* appeared to be much smaller than *G. arizonae*, a difference now attributable to ontogeny instead.

Previous Work

Gillette and Ray (1981) reviewed all known glyptodonts from North America, based largely on the exceptional specimens from the 111 Ranch fauna in southeastern Arizona. They described the osteology of a skull (F:AM 59583), a nearly complete individual including a skull (F:AM 95737), and isolated elements of *G. texanum* collected many years earlier by Theodore Galusha for the American Museum of Natural History. These specimens permitted an expanded description of the osteology of *G. texanum*, previously known mainly from the holotype (AMNH 10704) from the Blanco

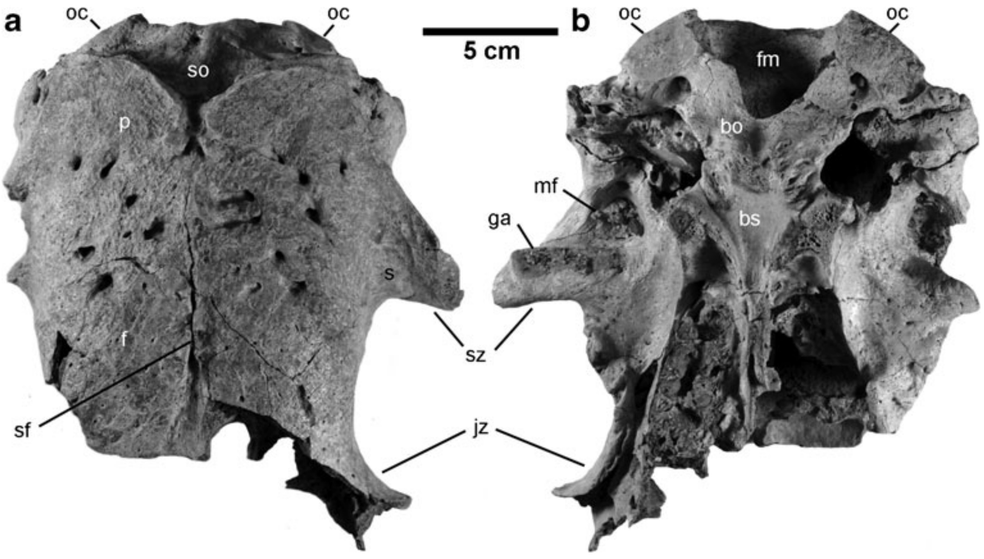

Fig. 5 Skull of an adult *Glyptotherium texanum* (MSM P8538) from the 111 Ranch fauna, Arizona. **a**, cranium fragment, dorsal aspect; **b**, cranium fragment, ventral aspect. **Abbreviations: bo**, basioccipital; **bs**, basisphenoid; **f**, frontal; **fm**, foramen magnum; **ga**, glenoid articular facet (note pebbles adhering to otherwise smooth surface); **jz**, horizontal (zygomatic) process of jugal; **mf**, mandibular fossa (note pebbles); **oc**, occipital condyle; **p**, parietal; **s**, squamosal; **sf**, sagittal furrow; **so**, supraoccipital; **sz**, zygomatic process of squamosal

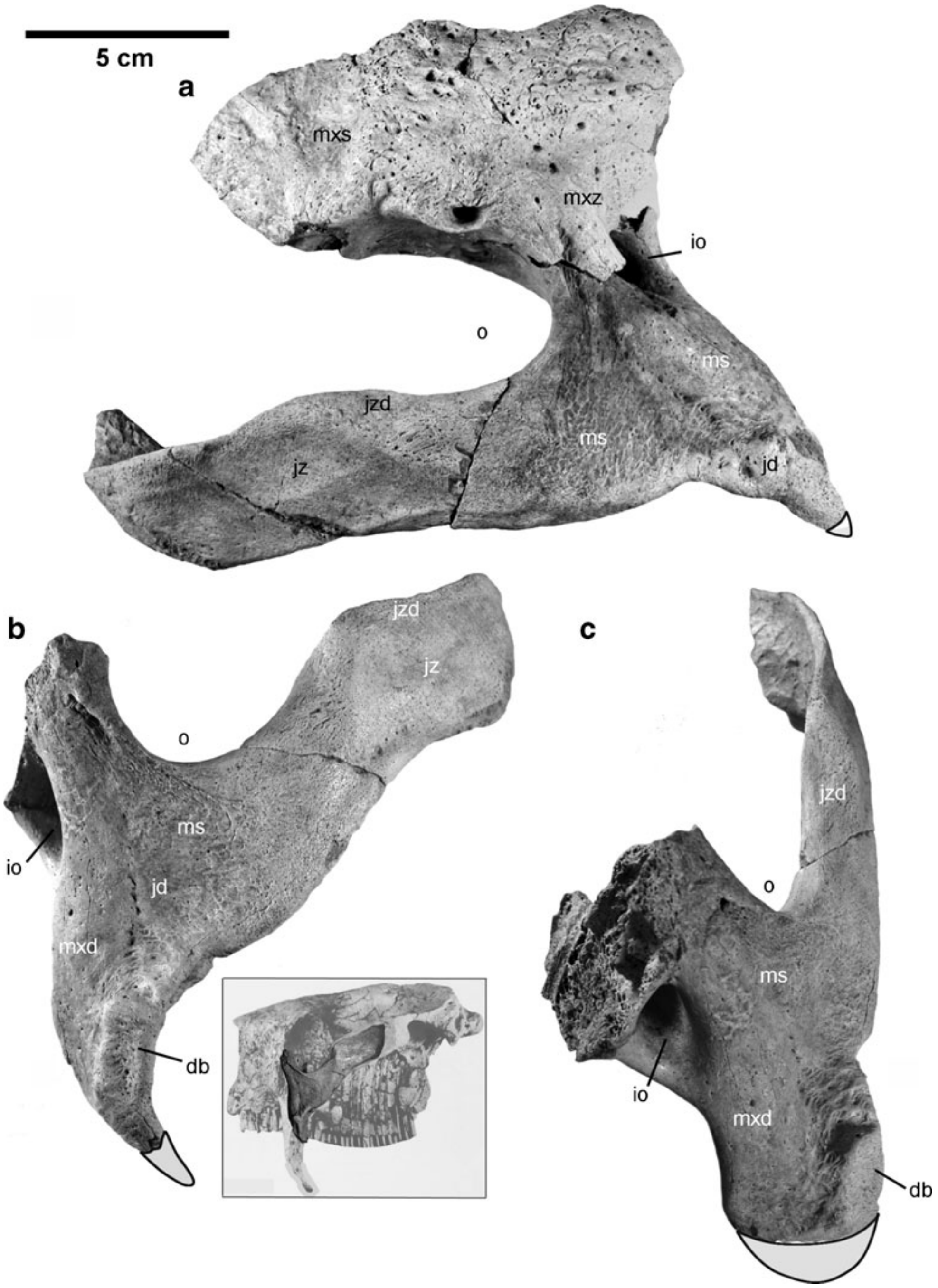

Fig. 6 Left and right zygomatic regions of the cranium of an adult *Glyptotherium texanum* (MSM P8538) from the 111 Ranch fauna, Arizona. **a**, nearly complete right zygomatic arch, lateral aspect; **b**, anterior fragment of left zygomatic arch, oblique anterolateral aspect; **c**, anterior fragment of left zygomatic arch, dorsal aspect; tip of descending process in **b** and **c** indicated by solid line; insert, anterior fragment of left zygomatic arch (**b**) in lateral view superimposed on adult skull UMMP 34826 (reversed to left from right) for orientation. **Abbreviations: db**, raised boss on anterior surface of descending process of maxilla-jugal; **io**, infraorbital canal; **jd**, descending process of jugal; **jz**, horizontal (zygomatic) process of jugal; **jzd**, dorsal surface of zygomatic process of jugal; **ms**, muscle scars on anterior and lateral faces of jugal; **mxd**, descending process of maxilla; **mxs**, superior process of maxilla; **mxz**, zygomatic process of maxilla; **o**, orbit

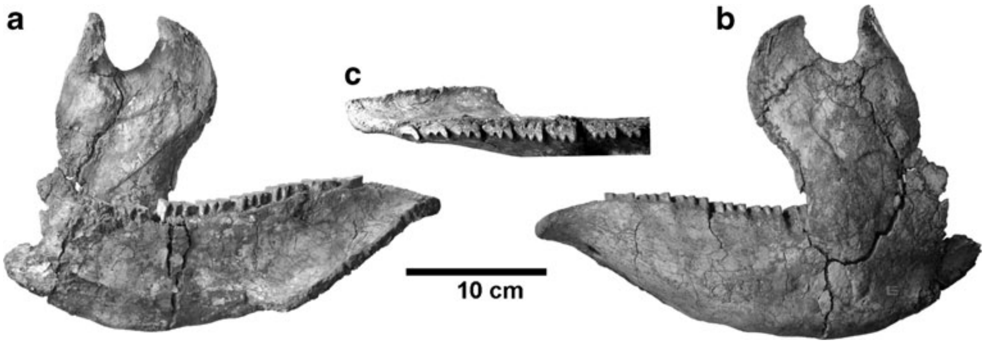

Fig. 7 Left lower jaw of *Glyptotherium texanum* (MSM P4818). **a**, medial aspect; **b**, lateral aspect; **c,** tooth row, occlusal aspect, anterior to left, N_8 is incomplete, and angle is broken and incomplete

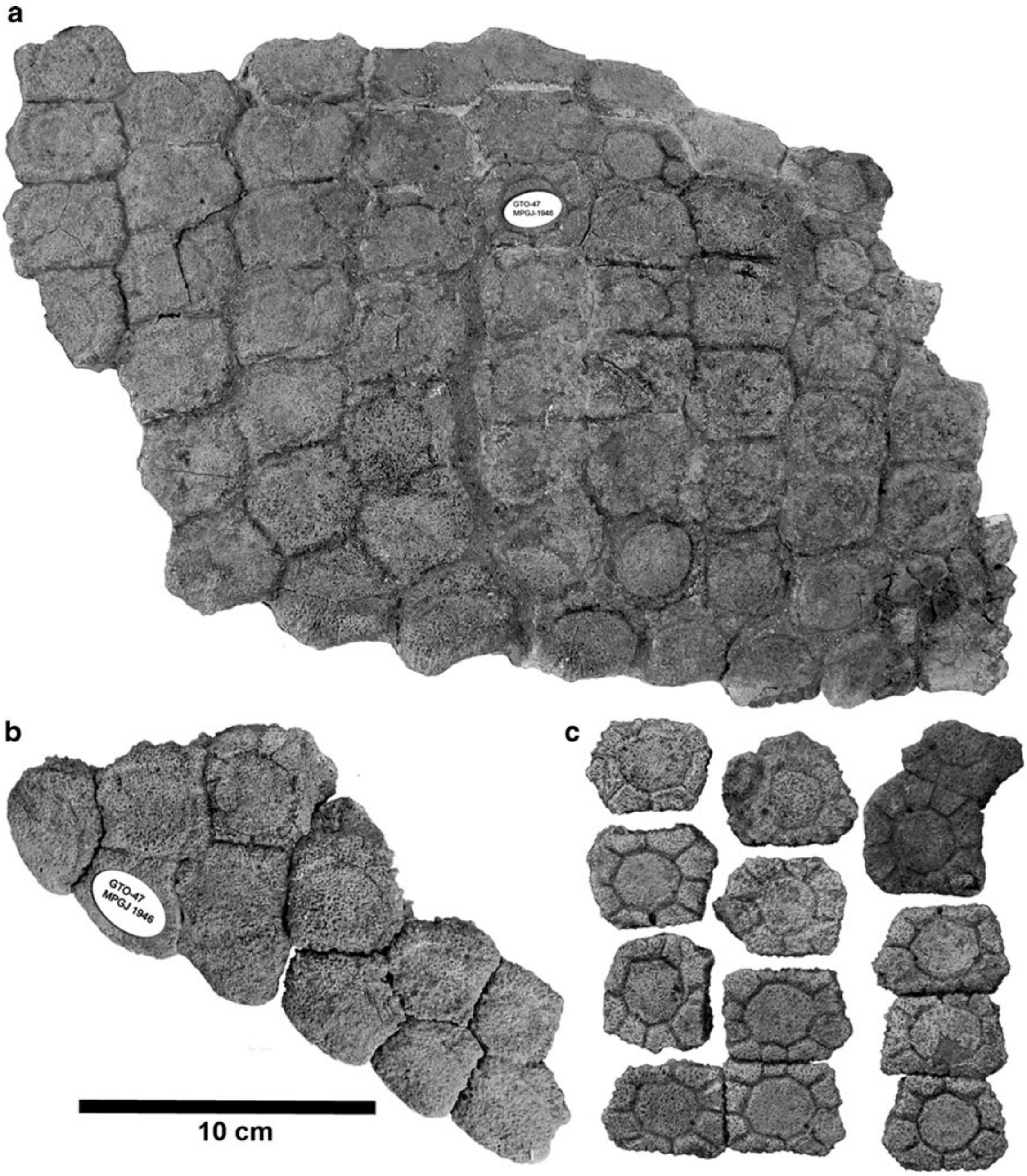

Fig. 8 Partial carapace and osteoderms of a juvenile *Glyptotherium texanum* (MPGJ 1946) from Arroyo Belén, Guanajuato. **a**, section of carapace from the cephalic region; **b**, carapace fragment from the anterolateral region; **c**, isolated osteoderms

Beds of western Texas. Gillette and Ray (1981) considered *G. texanum* to be older and characteristic of late Blancan NALMA faunas, and *G. arizonae* somewhat younger and characteristic of Irvingtonian NALMA faunas. In addition, they concluded that *G. texanum* was smaller, with a convex carapace, and that *G. arizonae* was larger, with a more complicated lateral profile of the carapace and clearly delineated preiliac and postiliac segments. These two species are the subject of this revision.

Blancan NALMA glyptodonts in Mexico and Central America

Newly recovered specimens of glyptodonts from the Pliocene of Los Galvanes and Coecillos areas, San Miguel de Allende Basin in Guanajuato, central Mexico extend the known temporal range of *Glyptotherium* (Carranza-Castañeda and Miller 2004; Flynn et al. 2005; Carranza-Castañeda 2006) to early Blancan NALMA. Confirmation of the identity of the *Glyptotherium* records in this and overlying beds in central Mexico was critical to elucidation of the taxonomic revision of the genus proposed below.

Blancan-Irvingtonian records of *Glyptotherium* in Costa Rica include Lucas et al. (1997), Valerio et al. (2005), Mora et al. (2005), and Valerio and Laurito (2011a, 2011b). Lucas et al. (1997) identified two small osteoderms from a site in northwestern Costa Rica as *Glyptodon* sp. If this assignment is correct, it represents one of three occurrences of *Glyptodon* in Central America. However, these hexagonal osteoderms have a large central figure and rosette pattern that are consistent with juvenile morphology of *Glyptotherium* sp., to which we tentatively assign these osteoderms. Gomez (1986) and Alvarado (1986) recorded four additional sites with *Glyptodon* in Costa Rica for which the specimens are lost according to Lucas et al. (1997).

Late Blancan − Irvingtonian NALMA glyptodonts in the United States

Morgan (2005, 2008) summarized the GABI in Florida and North America, respectively. He recognized an early pulse of the GABI that began in Florida in the early Hemphillian NALMA (late Miocene, 8–9 ma), and a second pulse in the late Blancan NALMA (Pliocene-Pleistocene, 2.7–1.5 ma) by ten genera of birds and mammals that included the first appearance of *Glyptotherium* from tropical America.

Gillette and Ray (1981) summarized records of Blancan and Irvingtonian glyptodonts in the American Southwest, including faunas from sites in Oklahoma, Texas, and Arizona. Glyptodonts from those faunas and subsequent discoveries (Appendix 1–2) in New Mexico (Vanderhill 1986; Lucas et al. 1993; Morgan and Lucas 2000, 2003; Morgan 2008; Morgan et al. 2008) and Oklahoma (Czaplewski 2004) are now assigned by synonymy to *G. texanum*.

Description of New Material

Skull and Jaws

Cranial elements of *Glyptotherium* are not common. Gillette and Ray (1981) described one nearly complete skull and one partial skull, both with upper dentition, of juveniles from the 111 Ranch fauna as *G. texanum*; and the nearly complete skull of an adult from the Seymour Formation, Gilliland local fauna of northern Texas, as *G. arizonae*.

The lower jaw of a baby (Irvingtonian NALMA) and teeth from an adult (early Blancan NALMA) from the San Miguel de Allende basin in Guanajuato; and lower jaw, a partial cranium, and partial lower jaw and teeth from a baby glyptodont from separate sites in the 111 Ranch fauna (late Blancan NALMA) substantially improve understanding of variation, growth, and development of the skull.

The partial left lower jaw of the baby (MPGJ 2043) is preserved from the symphysis to N_7, with an incomplete ascending ramus (Fig. 4a–b). It contains N_1–N_7 and shows no trace of N_8, which is either not preserved or not erupted. N_1–N_6 are complete, N_7 is damaged and incomplete. As a landmark for development, the anterior margin of the ascending ramus is in line with the middle of N_5, so that N_5 is only partially visible in lateral aspect. With growth, the position of N_5 would advance forward as the horizontal ramus increased in length and the anterior margin of the ascending ramus eventually lined up with the middle lobe of N_6. Teeth are tapered, but all show occlusal attrition. Lobes are less angular than in adults. Individual spacing between the teeth is very wide at occlusal surfaces, but much closer deep within the alveoli. N_1 is semilunar, with three weakly expressed lobes on the buccal surface and only a smoothly convex surface lingually. N_2 is weakly trilobate, N_3–N_4 are increasingly trilobate, and N_5–N_7 are markedly trilobate. Orthodentine rims and osteodentine rami are not recognizable except on N_6 and appear not to have developed at this stage of growth, perhaps an indication the baby had not begun to feed independently. The wide space between teeth probably indicates that at this age the baby was still suckling and not dependent on an herbivorous diet. The apparent later eruption of N_2 and N_3 might indicate at least a portion of the eruption sequence during development. The rim on N_6 is only faintly expressed. Growth lines are not discernable in gross aspect, although indistinct growth lines can be recognized in at least one tooth (N_6) under magnification. Cementum is present on all the teeth, especially in reentrant angles between the orthodentine rim and the bony wall of the alveoli. The association of a large number of osteoderms with this jaw confirms identification as a baby.

Eight partial teeth (three upper posterior teeth and five lowers) and one complete tooth (N_3) of an adult (MPGJ 2042) resemble corresponding teeth from the 111 Ranch fauna previously described (Gillette and Ray 1981) and the newly recovered specimens from 111 Ranch described below. These teeth all have distinct growth lines on the external surface of the orthodentine rims. One complete tooth (N_3) has a line count of approximately 15 per mm through its 80 mm length, for a total of approximately 120 lines from occlusal surface to the growth plate. Poor preservation of the occlusal surface obscures fine detail of the osteodentine rami in all but one tooth in which secondary and tertiary ramifications are evident but not very distinct. Associated osteoderms and partial carapace confirm the identification as *G. texanum*.

The new skull from 111 Ranch (MSM P8538, Figs. 5–6) is the only mature adult cranium known from this fauna and it materially expands the range of variation in cranial characters and dimensions known for *G. texanum*. Gillette and Ray

(1981) described the skulls of a young adult (F:AM 59583) and a juvenile (F:AM 95737) as *G. texanum*, both smaller than MSM P8538; the skulls of two adults from the Seymour Formation of northern Texas (UMMP 34826 and UMMP 38761) as *G. arizonae*, which are approximately the same size as MSM P8538; and fragmentary cranial elements they assigned to *G. floridanum* from southeastern United States. This skull includes most of the cranium except for the palate, dentition, and anterior snout. Fragments of left N^7 and N^8 remain in their alveoli but their occlusal surfaces are broken and missing. Small pebbles and sand in some pockets within the skull indicate burial in a beach or fluvial setting. Dimensions (Table 1) are approximately 10 % greater than corresponding dimensions of the two juveniles from the 111 Ranch fauna, and approximately the same as UMMP 34826 from the Seymour fauna (see Gillette and Ray 1981: Table 1). Sutures are ankylosed and surficial anatomy clearly delineates the boundaries of muscle attachments, unlike the anatomy on the juvenile skulls in which muscle scars are not clearly discernable.

The most striking differences on the adult skull are on the zygomatic arches (Fig. 6). The horizontal processes on both sides of the skull are nearly complete, and the descending processes are complete except for their inferior tips. The descending processes arise from the maxillae and unite with the zygomatic processes of the jugals. The dorsal and lateral surfaces of the zygomatic arch are flattened. The descending processes of the maxilla and jugal are expanded inferiorly as an enlarged maxillary-jugal boss that grades posteriorly into a marked, rearward extending ridge along the inferior border of the jugal. This ridge converges with a smaller ridge on the inferior surface of the horizontal ramus, together producing a large concave surface at the anterior extremity of the inferior border of the horizontal ramus. The bosses are rugose and clearly indicate muscle attachment surfaces for snout and facial muscles. Additional muscle scars on the anterior surface of the zygomatic processes of the maxillae and jugals are prominent. The bosses, associated ridges, and muscle scars are not evident on the juvenile skulls from the 111 Ranch fauna, even though those individuals were nearly full grown. Development of these surfaces is ontogenetic, appearing at maturity rather than in juvenile stages of growth.

The deep cleft in the basioccipital differs from the smooth, non-clefted anatomy of the juveniles, and resembles the cleft anatomy in the late Pleistocene skull fragment of a fully grown adult *G. floridanum* from South Carolina (ChM 2415) illustrated in Gillette and Ray (1981): Fig. 12). The basioccipital cleft thus appears to be ontogenetic, and therefore not a species distinction as proposed by Gillette and Ray (1981). Gillette and Ray (1981) recognized the sagittal furrow separating the frontals and parietals in the juvenile skulls from the 111 Ranch fauna; this furrow is equally prominent in the adult skull (MSM P8538). In other respects this skull resembles those of the two juveniles from 111 Ranch fauna, the adult skull from the Seymour fauna, and the late Pleistocene skull fragments from southeastern United States (Gillette and Ray 1981).

Two lower jaws (MSM P4818, Fig. 7, Table 2, and MSM P4462) are the only mandibular material known from the 111 Ranch fauna. Left mandible MSM P4818 is nearly as large as the lower jaws (USNM 10536, 38761) of two adult individuals in the Seymour fauna and is approximately the size expected for the adult skull (MSM P8538) described above. The ventral profile of the horizontal ramus is deepest immediately beneath the anterior margin of the ascending ramus. The lateral profile of the symphysis is slightly downturned, whereas in the Seymour mandibles the ramus is deepest more anteriorly (beneath N_5) and the symphysis profile is horizontal. The symphysis terminates posteriorly in approximately the position of the junction between N_4–N_5. The dentition is complete except for the posterior lobe of N_8. The occlusal surface of N_1 is semilunar, with a weakly expressed separation of three lobes on the labial margin. N_2–N_4 are increasingly trilobate, and N_5–N_8 are fully trilobate. The interior ridge of osteodentine possesses secondary rami that branch into the lobes and these in turn have tertiary rami. In other respects, this mandible and dentition are similar to the corresponding elements in the Seymour fauna, supporting the assertion that the differences are ontogenetic or sexual rather than taxonomic. The other mandible (MSM P4462) is not as well preserved,

Table 1 Dimensions (mm) of the cranium, *Glyptotherium texanum*; * approximate, ^{a} dimensions from Gillette and Ray (1981)

Dimension	MSM P8538 (adult)	F:AM 59583^a (juvenile)	F:AM 95737^a (juvenile	UMMP 34826^a (adult)
1. Transverse outside diameter, occipital condyles	104	87	88	108
2. Transverse diameter, occipital condyle left facet	29	30 *	34	25
3. Transverse diameter, occipital condyle right facet	32	25	–	33
4. Inferosuperior diameter, occipital condyle left facet	25	23	22	31
5. Inferosuperior diameter, occipital condyle right facet	23	21	21	29
6. Anteroposterior diameter, mandibular facet to infraorbital canal, lower anterior margin, left/right	154/-	-/-	127/125	150/ 150

Table 2 Dimensions (mm) of the mandibles of adult *Glyptotherium*; * approximate, [a] dimensions from Gillette and Ray (1981)

Dimension	MSM P4818	USNM 10536[a]	UMMP 38761[a]
1. Height of ascending ramus, from condyle through posterior lobe of N_7 to lower margin of horizontal ramus	220	230	245
2. Maximum transverse diameter, articular condyle	49	49*	39
3. Anterior-posterior diameter, articular condyle	33	49	39
4. Vertical depth, horizontal ramus at N_7, including tooth	92	107	100*
5. Vertical depth, horizontal ramus at N_5, including tooth	88	106	104
6. Vertical depth, horizontal ramus at N_3, including tooth	76	96	–
7. Length of horizontal ramus along tooth row	300	–	–
8. Length of tooth row	195*	–	–

but its size and anatomy are consistent with the one described above.

Postcranial Skeleton

MPGJ 2042 from Guanajuato, Mexico, includes fragments of the pelvis and the hyoid. The hyoid (Fig. 4c) is V-shaped, with simple cornua that lack their extremities, and relatively simple body. One surface of the body has a pair of raised bosses, each adjacent to a depression.

A variety of postcranial elements in the Arizona Museum of Natural History collection (Appendix 1) have been collected by recent field parties, most of them isolated bones. The partial skeleton (MSM P4818) of an adult male includes a large portion of the postcranial skeleton: atlas, thoracic tube (ankylosed vertebrae), caudal vertebrae, forelimb, manus, innominate, and hind limb in addition to the lower jaw described above and partial carapace described below. The postcranial elements are large compared to previously published elements (juveniles) from the 111 Ranch fauna (Gillette and Ray 1981), approximating the size of corresponding elements from the Gilliland and Curtis Ranch local faunas. Dimensions of the individual elements of the forelimb (Table 3) are roughly the same or even slightly larger than in the largest individuals in the genus (Gillette and Ray 1981). Muscle attachment surfaces are more pronounced than in juveniles, in keeping with the adult age of this individual. The manus is tightly flexed and in full articulation. In all respects other than its large size, it resembles the manus of the juvenile *G. texanum* described by Gillette and Ray (1981).

A left rear foot (MSM P7911) including calcaneum, astragalus, metatarsals, and digits recovered with a nearly complete carapace is similarly preserved in a flexed condition. This foot is complete, with proximal paired sesamoids for digits 2–4, and single sesamoids at the distal joints of the same digits. This foot and carapace have not been fully prepared. The elements of the foot appear to be rather small, indicating the individual is a juvenile. An isolated, complete caudal vertebra (MSM P4818) from approximately position no. 7 is likewise similar to caudal vertebra 7 of the juvenile *G. texanum* described by Gillette and Ray (1981).

Other postcranial bones in the fauna are generally fragmentary. No new osteological distinctions can be discerned from the postcranial elements in the 111 Ranch fauna, supporting the conclusion that *G. texanum* and *G. arizonae* cannot be distinguished by size or morphology. Similarly, carapacial and skeletal elements recovered from central and southern New Mexico (Appendix 1) are all consistent with the range of variation established for the 111 Ranch fauna.

Carapace and dermal armor

The addition of numerous carapacial elements from Mexico, Arizona, and New Mexico greatly expands our understanding of *G. texanum* with respect to growth and development. Carapace MPGJ 1946 from the San Miguel de Allende fauna of Guanajuato includes a large part of the lateral portion of the cephalic region (Fig. 8a). It is organized into eight parallel rows each with eight osteoderms as preserved. The first marginal row has eight triangular osteoderms that unite dorsally with the adjacent second row. In each osteoderm of the marginal row, the distal portion has an elongated marginal border; the central figure in each osteoderm occupies nearly ninety percent of the surface, the peripheral figures are indeterminate and reduced in number; each osteoderm has several follicles in the dorsal region.

Osteoderms of the second row are quadrilateral, with small and poorly defined peripheral figures; the central figures are round and flat, occupying an average of approximately eighty percent of the total surface. Osteoderms of the third row range from almost square to hexagonal; the central figures are round and occupy approximately seventy per cent of the total surface, and the peripheral figures are more clearly defined.

Osteoderms of the fifth and sixth rows are hexagonal, with elongation in the anteroposterior axis. The central figures are rounded and occupy approximately fifty percent of the surface; peripheral figures are irregular in shape and size, usually eight and occasionally seven per osteoderm. The sulci that

Table 3 Selected dimensions (mm) of the forelimb skeleton of *Glyptotherium texanum*; * approximate, [a] dimensions from Gillette and Ray (1981)

Dimension	MSM 4818 (adult)	F:AM 95,737 [a] (juvenile)	F:AM 59,585 [a] (juvenile)	UMMP 38,761 [a] (adult) (l/r)	TMM 40664-245 [a] (adult)	USNM 10536 [a] (adult)
1. Humerus, maximum length from proximal articulating surface of head to distal extremity of trochlear facet	390	258	–	–	–	365
2. Humerus, maximum transverse diameter across epicondyles	109	85	–	–	119	114
3. Radius, maximum transverse diameter, proximal articular facets	58	43	56	56/59	–	59
4. Radius, minimum transverse diameter of shaft	26	15	22	–	–	25
5. Radius, maximum anteroposterior diameter of proximal articular facet	34	23	33	–	–	32*
6. Ulna, maximum proximodistal length	276	194	–	–	–	270
7. Ulna, minimum anteroposterior diameter of shaft distal to semilunar notch	41	42	–	–	–	59
8. Ulna, minimum anteroposterior diameter through semilunar notch	52	39	–	–	–	56
9. Ulna, length of olecranon above semilunar notch (anconeal process to proximal extremity)	94	59	–	–	–	98

surround the central figures are wide and contain a few foramina. As preserved, the osteoderms are arranged into nine transverse rows from the margin to the dorsal part of the carapace. The typical pattern of sculpturing marked by the sulci is two rows of peripheral figures separating each central figure but sulci of some peripheral figures are continuous with the sulci of adjoining osteoderms. In this case, the resulting pattern is one row of peripheral figures separating the central figures, rather than two. Similar patterns of distribution of peripheral figures are known from 111 Ranch glyptodonts.

Another fragment of MPGJ 1946 (Fig. 8b) consists of twelve fused osteoderms from the marginal part of the caudal area. These are the thickest osteoderms of this carapace. All of the osteoderms in the first row (marginals) are triangular, with elongated marginal border posteriorly. In the second row of five irregular osteoderms, the central figure occupies more than ninety per cent of the surface, with four or five peripheral figures, irregular in shape and size. Isolated osteoderms (Fig. 8c) of this individual belong to different parts of the lateral and dorsal region of the carapace; two fragments, each with three united osteoderms probably belong to the middle region on the anterior carapace. One of these fragments has three trapezoidal osteoderms, each with a flat, slightly concave and rounded central figure, and eight peripheral figures of different size and shape. The peripheral figures are characterized by contiguous sulci of the peripheral figures between adjoining osteoderms. Another fragment differs in having rectangular osteoderms, each with nine peripheral figures; the sulci are contiguous between adjoining osteoderms. One and a half osteoderms from the dorsal area are pentagonal, with a convex central figure with central concavity and nine peripheral figures that overlap the junction of the adjoining osteoderms.

Two additional specimens were collected at the same stratigraphic level. One is a hexagonal osteoderm of the dorsal region with weakly convex central figure and ten peripheral figures (Fig. 9a). The central figure is slightly concave and occupies approximately half of the total surface of the osteoderm. Its sulcus houses six foramina. The other osteoderm is an irregular hexagon, with round, concave central figure that occupies approximately half of the total surface osteoderm and twelve pentagonal peripheral figures; the sulcus surrounding the central figure has nine follicles (Fig. 9b).

The partial carapace of a baby (MPGJ 2043) includes a large fragment from the dorsal region, from the caudal row of osteoderms forward to the medial part of the cephalic region, including the pre-iliac and post-iliac regions (Fig. 10). The caudal aperture has nine preserved marginal osteoderms, and positions for three missing, indicating a total of 12 osteoderms along the caudal border. As preserved, it has approximately 23 transverse rows anterior to the caudal aperture. The iliac crest occupies a position roughly between precaudal rows 10–19 (that is, counting from the rear row forward). The

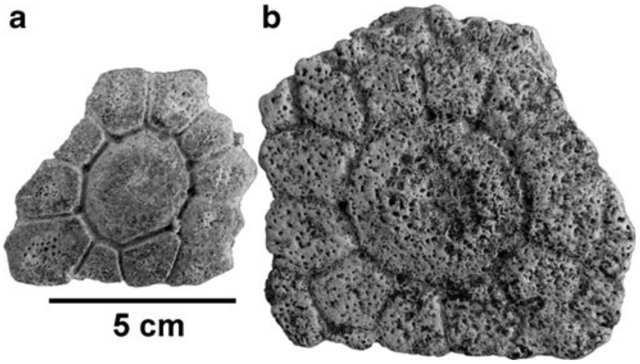

Fig. 9 Isolated carapacial osteoderms of adult *Glyptotherium texanum* from Arroyo Belén, Guanajuato. **a**, MPGJ 398; **b**, MPGJ 2745

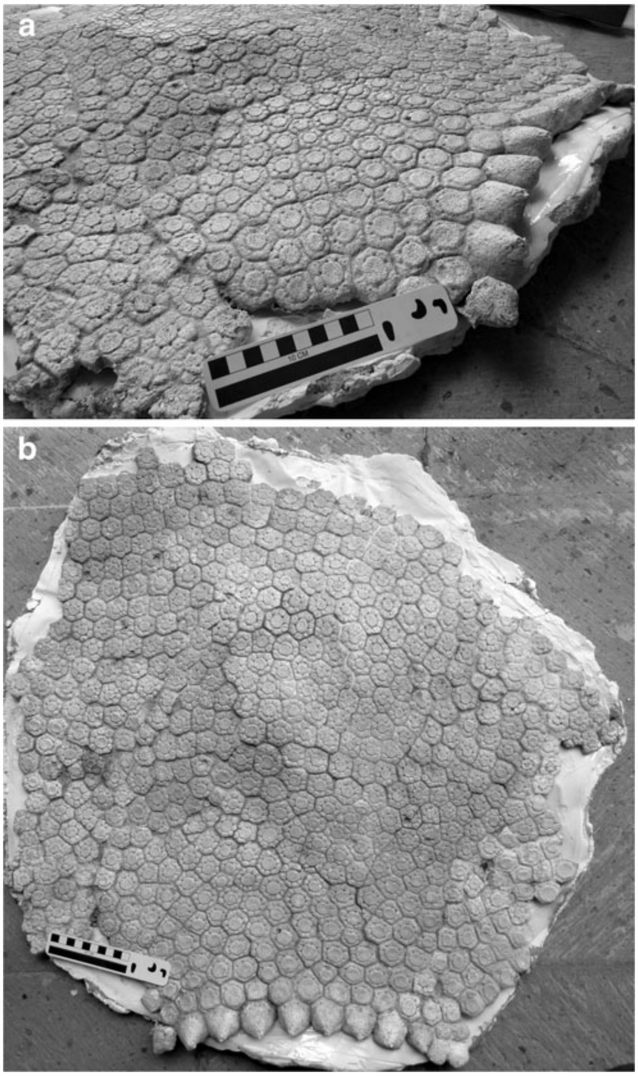

Fig. 10 Partial carapace of a baby *Glyptotherium texanum* (MPGJ 2043) from the Irvingtonian NALMA of Guanajuato, Mexico. **a**, oblique aspect of left posterolateral region, caudal aperture to right; **b**, dorsal view of entire specimen, caudal aperture at bottom, anterior to top. Photo scales 10 cm

post-iliac portion includes precaudal rows 1–9; the pre-iliac region is anterior to precaudal row 19. Dorsal osteoderms are hexagonal to nearly round. Pre-iliac osteoderms are arranged in parallel rows, an organization also observed in another large fragment of the dorsal area, together indicating at least fourteen parallel, pre-iliac rows. In an additional large lateral fragment of the middle region, osteoderms are hexagonal with transverse elongation, and they are intercalated with square or rectangular osteoderms that lack external sculpturing. In the caudal region, the osteoderms of the caudal border have uneven development. The central osteoderm is the largest, with pentagonal base and conical boss. Three osteoderms of nearly the same size and design occupy each side of the marginal border; the remaining osteoderms are smaller but retain the conical boss. The second row of osteoderms is the only one that is parallel to the caudal margin. Others are arranged in oblique bands from the edge toward the dorsal area but the rows are interrupted before reaching the dorsal region of the carapace. In an additional fragment of the anterolateral region of the carapace, osteoderms vary in shape from quadrilateral, pentagonal, or elongated hexagons, all arranged in parallel rows (Fig. 11a). All the osteoderms have a round, slightly concave central figure that occupies roughly half of the entire surface. In some osteoderms near the caudal margin, the central figure occupies more than seventy-five percent of the surface. In the anterolateral part of the carapace, with quadrangular and pentagonal osteoderms, the central figures occupy approximately fifty percent of the total surface. The peripheral figures are smaller and slightly concave, with rather consistent number, shape, and size. In hexagonal osteoderms (Fig. 11b), the typical number of peripheral figures is eight; only a few have nine and ten. The sulcus that separates the central and the peripheral figures is relatively wide; in the anterior and middle region of the carapace the sulci generally have five hair follicles, but fewer follicles in osteoderms from the lateral, caudal, and rear positions of the carapace.

MPGJ 2042, an adult, includes two sections of the carapace (Fig. 12a–b). The preservation is poor, with osteoderms from the anterior part of the shield partially destroyed by erosion. The osteoderms are arranged in parallel transverse rows. The marginal osteoderms are triangular, with central figures that occupy nearly ninety percent of osteoderm surface. The marginal edge of each is rounded or terminates with a pointed tip, and the peripheral figures are very small and indistinct. Osteoderms of the second row are quadrilateral, with the central figures that are slightly convex and cover approximately seventy percent of the total surface in the osteoderm; peripheral figures are small and poorly defined. Osteoderms of the fourth row are polyhedral, with slightly convex central figures and eight well defined peripheral figures. From the fifth row to the middle region of the carapace, the osteoderms vary from hexagonal to pentagonal, central figures are round and flat. Central figures of these osteoderms occupy slightly more than half the total surface area, and each osteoderm has eight peripheral figures that are frequently shared with adjoining osteoderms (Fig. 12c).

Several incomplete carapaces, numerous smaller sections of carapacial armor, and isolated osteoderms in the 111 Ranch fauna permit a broader understanding of growth and development. MSM P4818 (Fig. 13) includes a partial, undistorted carapace of a large adult and much of the noncarapacial skeleton. Dimensions and anatomy indicate an adult male that is slightly larger than the type specimen of *G. arizonae*, hitherto regarded as the species with the largest adults in this genus (Gillette and Ray 1981). The carapace fragment is the left side, with left margin intact but the anterior and posterior apertures are not preserved, precluding assignment of sex (but see caudal armor, below). Osteoderms extend from the margin to near

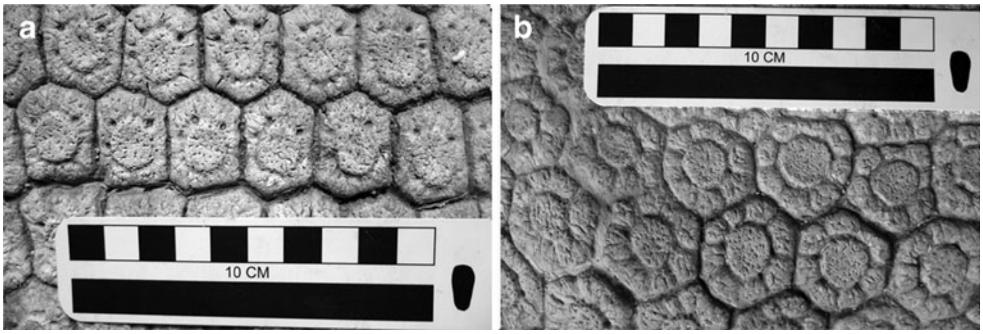

Fig. 11 Close-up photographs of interior osteoderms of the baby *Glyptotherium texanum* (MPGJ 2043) from the Irvingtonian NALMA of Guanajuato, Mexico. **a**, transitional osteoderms between lateral and dorsal carapace; **b**, symmetrical hexagonal osteoderms from the dorsal carapace. Photo scales 10 cm

the sagittal plane. It includes approximately 239 osteoderms arranged in 25 diagonal rows that reach the lateral margin and terminate with a single, enlarged conical osteoderm. Lateral osteoderms increase in size rearward. Osteoderms tend toward quadrilateral and pentagonal near the margins, and hexagonal toward the midline. Osteoderms in the first four rows of the anterolateral carapace are smaller than osteoderms in the interior, and their shape is approximately rectangular but with raised surface. The rosette pattern on the superficial surface of these osteoderms is inconspicuous, owing to the very large central figures that occupy at least three-fourths of the surface. Rosette patterns of interior osteoderms include weakly convex to flat central figures that are always greater than half the side-to-side diameter, single rows of peripheral figures, and relatively shallow sulci that house typically no, one, or two follicles. Most of the central figures have a concave central depression. Hexagonal osteoderms from the interior region of the carapace typically have eight or nine peripheral figures that may be shared with adjoining osteoderms. Dimensions of a sample osteoderm with symmetrical hexagonal shape are: side-to-side diameter, 44 mm; diameter of central figure, 28 mm; sulcus depth no greater than 2 mm; depth of central depression, no greater than 3 mm. This carapace does not include the iliac region, and therefore lacks information concerning the preiliac and postiliac profile.

The carapace of MSM P4465 (Fig. 14a–b) is on display at the Arizona Museum of Natural History. The cephalic aperture and lateral margins are incomplete, but the caudal aperture is complete and the entire section is preserved in a three dimensional condition. In lateral aspect (Fig. 14b), the preiliac region is convex and the post-iliac region is concave. Osteoderms of the caudal aperture (Fig. 14c) are flat rather than markedly conical, by definition indicating this individual is a female. Anterior-posterior diameter along the sagittal line as preserved is 138 cm along curve, 126 cm in straight line dimensions. Transverse diameter along curvature (marginal osteoderms are lacking on both sides) is 105 cm, 94 cm in straight line, which is a fair approximation of the side-to-side diameter of the carapace in life. Interior osteoderms are hexagonal, with central figures larger than peripherals (Fig. 14d). Central figures are slightly raised (convex) above the level of the peripherals, and some possess central depressions. Osteoderms are arranged in approximately 31 transverse rows, with progressively less perfect organization posteriorly.

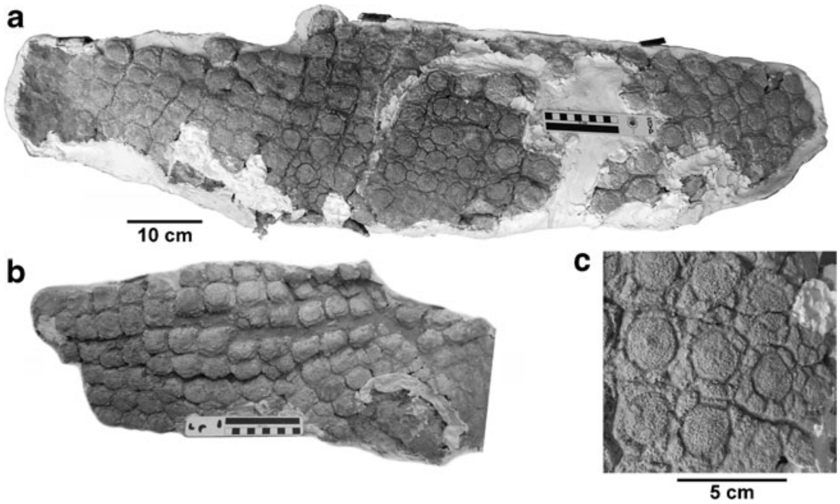

Fig. 12 Partial carapace of an adult *Glyptotherium texanum* (MPGJ 2042) from Arroyo El Ingadazo, Guanajuato. **a**, dorsolateral section of carapace; **b**, anterolateral section of carapace; **c**, close-up of osteoderms showing shared peripheral figures

Fig. 13 Partial carapace, left side, of adult *Glyptotherium texanum* from the 111 Ranch fauna, Arizona (MSM P4818), oblique view from left rear looking forward. Scale equals 10 cm

Shapes change toward the margins to asymmetrical hexagons and irregular pentagons. Anterolateral osteoderms are not present on the mounted carapace, but isolated osteoderms in the collections are consistent with pentagonal and quadrilateral shapes found in other carapaces in the 111 Ranch collection.

In the extensive 111 Ranch glyptodont fauna (Appendices 1–2), which includes many additional osteoderms and partial carapaces, most osteoderms have weakly convex central figures, but in some individuals they are strongly convex and in others they are mostly flat. These are traits that can now be attributed with greater confidence to variation within the population rather than taxonomic distinction. To date, we have not recognized any consistent correlation with stage of growth or sex of the individuals for this variation on central figure morphology.

The caudal armor of MSM P4818 includes four caudal rings from the terminal extremity of the tail, presumably caudal rings 8–11. Rings 8 and 9 are biseriate, and the terminal ring, consisting of conjoined rings 10 and 11, is tetraseriate and forms a short caudal tube that encased caudal vertebrae 10 and 11, and possibly caudal vertebra 12 (fidé Gillette and Ray 1981). Osteoderms of the external row of each ring are only weakly raised, not strongly tuberculate, indicating this individual was a female. Nothing in the anatomy of these rings differs from that previously described for *G. texanum* in Gillette and Ray (1981).

MSM P3875 (Fig. 15) is a partial carapace of a young juvenile consisting of approximately 37 small osteoderms in articulation among which about half have contacts with adjoining osteoderms that are intergrown and tightly united but apparently not ankylosed, the other half not intergrown, with open contacts. The osteoderms are arranged in eight rows, and all have slightly raised, convex central figures, most with a weakly developed central depression. These osteoderms are all pentagonal to hexagonal, typically 22–25 mm wide, 10–12 mm thick. Central figures are relatively large, all greater than half the side-to-side diameter. Peripheral figures are indistinct, most with three to five follicles in the sulci, always on one side of the central figure.

All specimens from New Mexico listed in Appendix 1 include carapacial armor that is consistent with the armor described above. Several can be tentatively assigned to sex and age. MSM P4818 and NMMNH&S P58275 also have a large number of isolated dermal ossicles, presumably from the skin in areas of the body not covered by the carapace.

Discussion

Growth and Ontogeny

Population samples of glyptodonts are generally too small to permit evaluation of growth and ontogeny. Ideally, ontogeny is studied from complete specimens at several stages of growth. Gillette and Ray (1981) recognized juvenile individuals of *G. texanum*, but could not determine their position in growth progression. Only one relatively complete skeleton of *Glyptotherium*, a juvenile, had been recovered prior to the collection of the new specimens described here. The addition of new specimens from the 111 Ranch fauna for the present study substantially expands the sample from this fauna, permitting a more detailed examination of ontogeny and sexual dimorphism. Zurita et al. (2011b) evaluated ontogeny in several South American genera in the context of taxonomy, with similar results.

The discovery of an unborn baby and its mother of a closely related species in South America (*Glyptodon* sp., cf. *G. elongatus*) provided a rare glimpse into growth and ontogeny of the skull and jaws (Zurita et al. 2009) that has direct application to *Glyptotherium*. The anterior profile of the ascending ramus of the lower jaw of the baby *Glyptodon* is nearly 90° with respect to the tooth row, whereas the profile of this element in the mother is steeply inclined forward at an angle of 60°–70°. This change in profile indicates that growth in the lower jaw is allometric, rather than isometric, as expected but hitherto not fully documented. The angle of the ascending ramus with the tooth row in *Glyptotherium* also changed with growth, indicating that this is not a reliable trait for species definition.

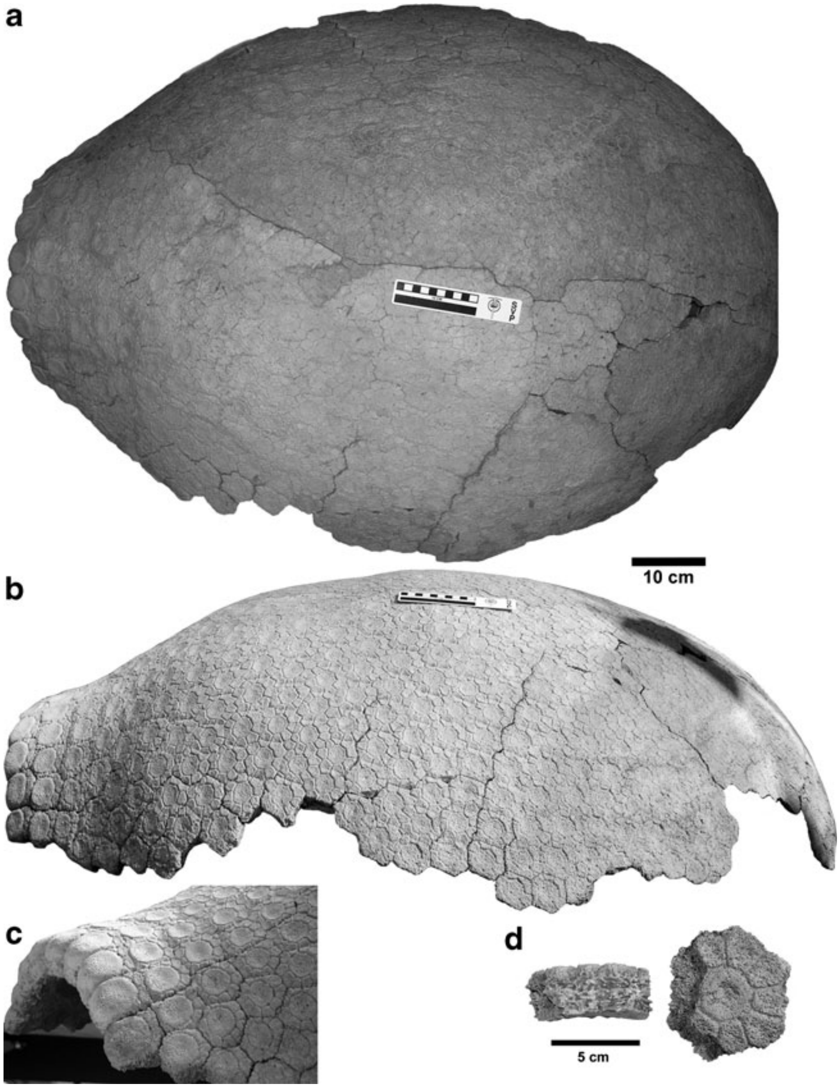

Fig. 14 Partial carapace (MSM P4465) and an osteoderm of *Glyptotherium texanum* female from 111 Ranch fauna. **a**, dorsal aspect, anterior to right, cephalic aperture truncated; **b**, lateral aspect, right side; **c**, oblique, close up aspect of caudal aperture, left side, reversed for comparison, slightly enlarged; **d**, isolated hexagonal osteoderm, side view and **e**, superficial aspect. Line scales **a**–**c**, 10 cm; **d** and **e**, 5 cm; photo scales on carapace 10 cm

The lower jaw of that baby includes four unerupted molariform teeth. They are markedly tapered, with increasing anterior-posterior length deep within the alveolus. Simpson (1929), Holmes and Simpson (1931), and Gillette and Ray (1981) reported tapering teeth in babies of *Glyptotherium*. Differences in tooth morphology of adult *Glyptotherium* that previously seemed to distinguish between species can be attributed instead to ontogeny. Because the teeth were ever-growing (hypselodont), it is reasonable to expect changes in morphology over time. One consistent trait with respect to the teeth of *Glyptotherium* is the serial branching of the osteodentine rami at all stages of growth.

Newly recovered immature individuals of *G. texanum* in the 111 Ranch and Coecillos faunas demonstrate fully articulated osteoderm-to-osteoderm contact (Figs. 10–11) even at very young age. Growth of osteoderms continued through juvenile and at least young adult ontogeny, and ceased only when they became ankylosed to adjoining osteoderms. Osteoderms that are not ankylosed instead represent immature individuals, as originally described by Simpson (1929). Small osteoderms that are anklylosed, on the other hand, are probably female, and large osteoderms that are ankylosed are probably male.

Two morphs are evident among adult individuals in the 111 Ranch population of *G. texanum*. The caudal aperture of the carapace of *G. texanum* is a highly arched rim of fully ankylosed, enlarged conical osteoderms that protected the base of the tail. The marginal osteoderms of males (by arbitrary definition) are markedly conical, whereas the marginal osteoderms of females are only weakly conical or nearly flat. This difference may not be clearly recognizable in juveniles. However, in the carapace of the baby (MPGJ 2043) from the Arroyo Emilio-Gliptodont site, Guanajuato, the markedly conical anatomy of the osteoderms of the caudal notch is clearly expressed (Fig. 10) even at very young age, indicating it is a male. Zurita et al. (2011a) commented on the apparent

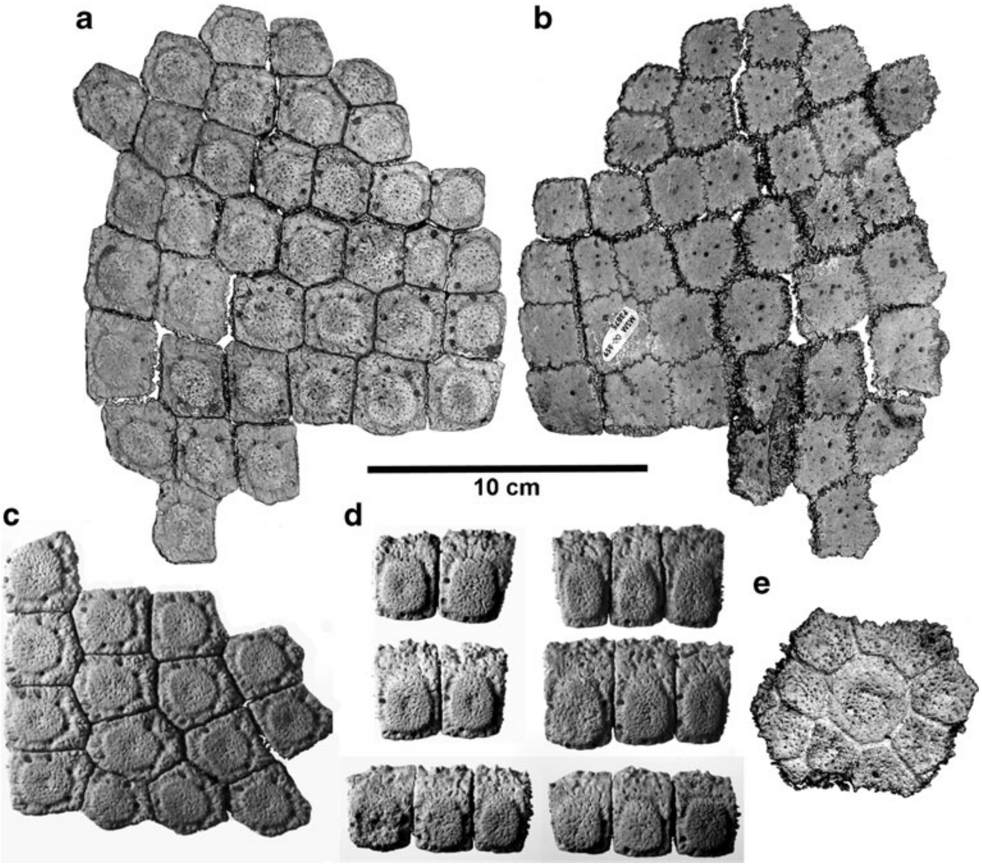

Fig. 15 Partial carapace from near the lateral margin of a baby *Glyptotherium texanum* (MSM P3875) from the 111 Ranch fauna (**a–d**), and an adult osteoderm (MSM P4818) for comparison (**e**). **a**, superficial surface; **b**, deep surface; **c**, another section of carapace, superficial surface; **d**, six sets of articulated osteoderms from caudal rings, positions indeterminate; **e**, hexagonal osteoderm of an adult individual at same scale. Note the very large central figures in the baby compared to that of the adult

lack of conical osteoderms along the caudal aperture in *G. texanum*, which we now recognize is the condition in females of this species, with adult males having prominent, conical osteoderms identical to those previously identified as members of *G. arizonae*.

In addition, the lateral profile of the carapace of juveniles (e.g., the holotype AMNH 10704 from the Blanco Beds of western Texas and F:AM 95737 from the 111 Ranch fauna) is gently convex, but the profile of adults in the 111 Ranch fauna is more highly arched and markedly recurved, with distinctive pre-iliac (convex) and post-iliac (concave) outline. Recognition of this ontogenetic change with growth in turn eliminates one important character difference established by Gillette and Ray (1981), who stated that the carapace of *G. texanum* is not recurved or is only slightly recurved, and that of *G. arizonae* is markedly recurved. The new specimens indicate that the pre-iliac and post-iliac divisions of the carapace were as pronounced in adults of *G. texanum* as in the type specimens of *G. arizonae*. Also, the adults of the 111 Ranch fauna were as large as adults previously identified as *G. arizonae*, eliminating another character difference (size) that is instead attributable to ontogeny.

A third aspect of growth of the armor concerns ontogenetic changes in the relative size of the 'figures' formed by the sulci on the superficial surface of individual osteoderms (Fig. 16). Typically in *Glyptotherium*, interior osteoderms (osteoderms located at least six or seven rows interior to the quadrangular marginals) are polygonal, usually hexagonal (but ranging from quadrilateral to octagonal), and have a single central figure with seven, eight, or nine peripheral figures. A few peripheral figures and sulci may overlap adjoining osteoderms, or include a partial set of intercalated peripheral figures that do not share a sulcus with the central figure (Fig. 16b–c). Interior osteoderms along the midline of the carapace tend to be symmetrical hexagons, with decreasing symmetry toward the margins of the carapace.

Gillette and Ray (1981) used general proportions of the central and peripheral figures to distinguish between *G. floridanum* (diameter of central figure less than half the overall diameter of the osteoderm) and *G. arizonae* and *G. texanum* (diameter of central figure greater than half the overall diameter). This distinction arises from ontogenetic changes, and may not be attributable to taxonomy. The periphery of each osteoderm grew relatively faster than the center. As a consequence, the central-figure-to-peripheral-figure proportions changed with growth. The central figures are largest relative to peripheral figures in babies and juveniles (Fig. 16a), and become relatively smaller in juveniles (Fig. 16b) and adults (Fig. 16c). Central figures of interior

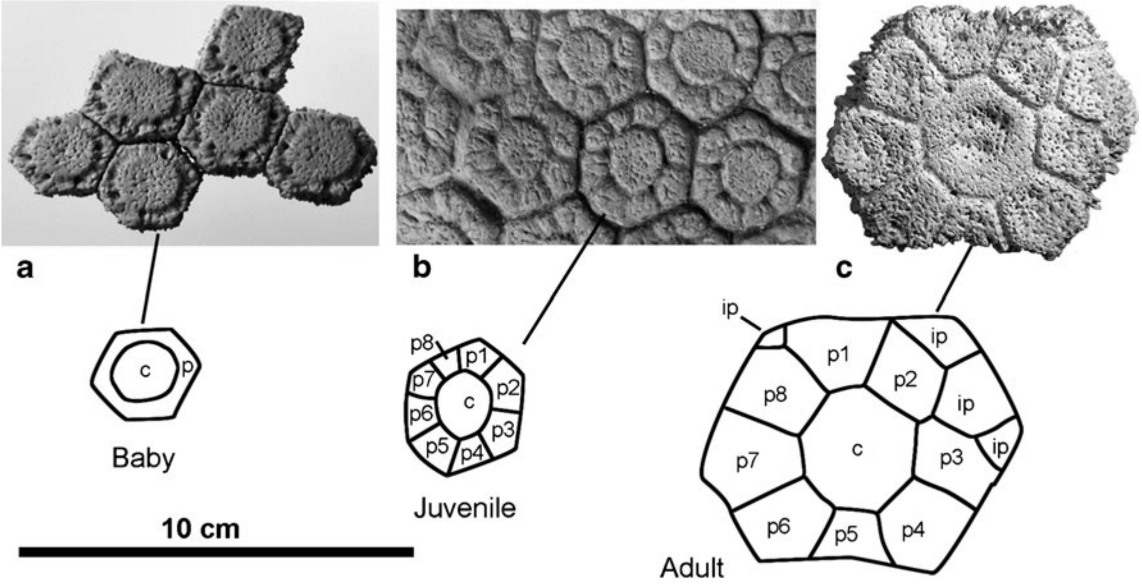

Fig. 16 Ontogeny of carapacial osteoderms in *Glyptotherium texanum*. **a**, symmetrical hexagonal osteoderm from the dorsolateral region of a young baby (MSM P3875); **b**, symmetrical hexagonal osteoderms from the dorsolateral region of an older baby (MPGJ 2043); **c**, single hexagonal symmetrical osteoderm from the dorsolateral region of an adult (MSM P4818). Line drawing interpretations of individual osteoderms show change of proportions of central figure and increasing definition of peripheral figures with growth. **Abbreviations: c**, central figure; **ip**, intercalated peripheral figures; **p**, undifferentiated peripheral figures; **p1–p8**, peripheral figures

(symmetrical hexagonal) osteoderms in juveniles of *G. texanum* are very large (much more than half the diameter of the osteoderm), whereas central figures in adults are only slightly larger than peripheral figures in adults.

In *G. texanum*, osteoderm growth generally ceased before the central figure became less than half the side-to-side diameter of the osteoderm. In *G. floridanum*, on the other hand, osteoderm growth was either faster, or continued longer through ontogeny, or both, with the central figure generally smaller than half the overall diameter in adults. This proportional difference in the anatomy of interior osteoderms does not apply to peripheral osteoderms near the sides or either end of the carapace, where central figures remain very large through the entire growth progression. This appears to be the only consistent distinction between *G. texanum* and *G. floridanum* with respect to the carapace anatomy.

Another aspect of osteoderm ontogeny of *Glyptotherium* is the relative thickness, or ratio of thickness to breadth (Fig. 17). With growth, the rate of increase in side-to-side diameter (breadth) of individual osteoderms exceeded the rate of increase in thickness (Table 4). Osteoderms from the central region of the carapace of *Glyptotherium* adults (that is, osteoderms that approximate a regular symmetrical hexagon) have breadth to thickness ratio of approximately 3.3:1 (range roughly 3.2:1–3.4:1). This ratio is much lower in babies and juveniles, indicating that osteoderms of young individuals are relatively thicker than those of adults. This allometric growth of osteoderms complicates efforts to identify species based on isolated carapacial elements without knowing relative age of the individual. Zurita et al. (2011a) compared this thickness ratio of *Glyptotherium* to that of related South American genera (2.3:1–5.4:1 in three species of *Boreostemma*; 2.1:1–2.3:1 in *Glyptodon*). Such quantification might prove to be valuable in future analyses of the taxonomy of glyptodonts from both continents. These ratios of individual osteoderms may be useful in turn for determination of growth stage of an individual. Relatively thick mid-carapace osteoderms from a population of a given species belong to babies and juveniles, whereas relatively thin osteoderms belong to adults.

The Great American Biotic Interchange (GABI)

A considerable body of literature has addressed the Great American Biotic Interchange (Webb 1974, 1976, 1985, 1991; McDonald 2005; Morgan 2005, 2008; Carranza-Castañeda 2006; Woodburne et al. 2006; McDonald and Naples 2007; Carlini et al. 2008a, 2008b; Rincón et al. 2008; Zurita et al. 2008, 2011a, 2013; Woodburne 2010; Gillette et al. 2012; Fariña et al. 2013) and with it the history of expansion of xenarthran taxa into North America and later re-expansion into South America as far south as Brazil (Oliveira 2010).

McDonald (2005) proposed that the dispersing members of each group of xenarthrans that expanded into Central and North America were generalists and tended to be small, and subsequent members were more specialized and larger. These conclusions were consistent with the taxonomic framework of Gillette and Ray (1981) for *Glyptotherium*, but they are not supported within the systematic revision presented herein.

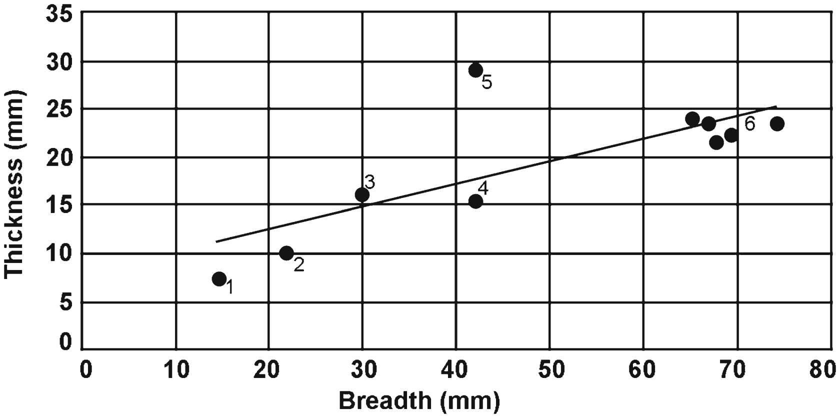

Fig. 17 Bivariate plot of data presented in Table 4; numbers correspond to numbered specimens from the table

Zurita et al. (2011a) suggested that the early taxon (*G. texanum* from the Blancan NALMA) in this lineage might differ from the late taxon (Rancholabrean NALMA) at the generic level. Our analysis of the osteology of *Glyptotherium* now indicates that what then appeared to be generic differences are, at most, no more than species-level distinctions. There is no support for the existence of more than one genus in North America.

Synonymy

The recognition of synonymy of *G. texanum* and *G. arizonae* calls into question the identity of the remaining three species. *Glyptotherium mexicanum* is known only from a carapace (the holotype), and *G. cylindricum* is known only from a carapace, partial dentition, hyoid fragment, rib fragment, chevron, and caudal ring fragment, all presumably from a single individual (holotype). *Glyptotherium floridanum* is known from multiple sites along the Gulf Coast and southeastern Coastal Plain of the United States, but from generally isolated and incomplete material. The species has also been identified in Mexico, including localities not directly tied to a coastal setting. Likewise, *G. cylindricum* has been identified from a variety of late Pleistocene sites in Mexico, Central America, and northern South America (Carlini et al. 2008a, 2008b; Oliveira 2010). The relationships between *G. cylindricum* and the other species remain to be evaluated. The hypothesis that all four species are synonymous requires further testing.

Evolutionary History

The synonymy of the two species proposed here leads to a larger question concerning the evolutionary history of *Glyptotherium*. We postulate a narrowed range of morphological change spanning the four million year history of this genus, which may be viewed as either anagenesis or evolutionary stasis.

Differences in the dermal armor that Gillette and Ray (1981) used to distinguish *G. texanum* from *G. arizonae* are now attributed to growth and ontogeny. Gillette and Ray (1981) stated that *G. texanum* adults were smaller than adults of the other species. Other authors (McDonald 2005; McDonald and Naples 2007) in turn interpreted that difference to indicate an overall trend through time, in which adults of the

Table 4 Sample osteoderm breadth to thickness proportions arranged in ontogenetic order; osteoderms selected are symmetrical hexagons, from dorsal region of carapace; numbers in parentheses correspond to plotted values in Fig. 17

Specimen No.	Age	Breadth (mm)	Thickness (mm)	Ratio
1. NMMNH&S unnumbered, Locality 2971 (1)	baby	14.6	7.5	1.9
2. MSM P3875 (2)	Young juvenile	22.0	10.0	2.2
3. MPGJ 2043 (3)	juvenile	30.0	16.0	1.9
4. NMMNH&S 39734 (4)	young adult	42.0	29.0	1.4
5. MSM 4465 (5)	young adult	41.9	15.5	2.7
6. MSM P4818 (6)	adult	65.3	24.0	2.72
	adult	67.0	23.5	2.9
	adult	69.5	22.1	3.1
	adult	70.0	22.0	3.2
	adult	74.2	23.5	3.2

earliest glyptodonts in North America were smaller than adults of the later species. With the recognition of *Glyptotherium* in central Mexico, the temporal range of the genus is nearly doubled to at least 3.9 mya, and these earliest representatives in North America are as large as specimens from much younger faunas in Arizona. In addition, the expanded population of *G. texanum* from 111 Ranch now includes adults as large as the largest specimens known for the genus (the holotype of *G. arizonae*) (Table 3). For example, the total length of the humerus (390 mm) of an adult individual (MSM P4818) from the 111 Ranch fauna is considerably longer than the humerus (258 mm) of the juvenile individual (F:AM 95737) described by Gillette and Ray (1981) from the same fauna, and longer than the humerus (365 mm) of the holotype specimen (USNM 10536) of *G. arizonae*. With the new specimens described above, it is clear that *Glyptotherium* size was already quite large by the time it had established a population in central Mexico in the early Blancan NALMA and maintained that size or decreased only slightly by the end of the Pleistocene. Instead, if there is any change in overall size, we suspect but cannot fully prove that the trend was larger in the early species (*G. texanum*), to slightly smaller in the Rancholabrean species (*G. floridanum*). McDonald (2005) also suggested that the earliest members of each group of xenarthrans that expanded into North America were generalists, and that later taxa were more specialized with respect to ecology and metabolism. The synonymy of *G. texanum* and *G. arizonae* proposed here and the narrowing of differences that separate *G. texanum* and *G. floridanum* challenge that generalist-to-specialist history.

Cody et al. (2010) postulated earlier dispersal of plants than of animals in the GABI. If correct, the expanding populations of glyptodonts during the GABI might have encountered habitats not altogether different from the habitats they occupied in South America. Pérez-Crespo et al. (2012) concluded that *Glyptotherium* occupied open grassland habitats according to stable isotope analysis, in contrast with the semiaquatic habitat proposed by Gillette and Ray (1981) based in part on faunal associations. Because there is no convincing evidence of glyptodonts other than *Glyptotherium* in the northward expansion during the GABI, we suggest the establishment of a founder population in northern South America or in the Isthmus of Panama that became isolated and underwent relatively rapid morphological change (cladogenesis), perhaps by allopatric speciation in habitats at least partially populated with a biota (plants and animals) with which they had been associated in South America.

Woodburne (2010) included the early occupation of *Glyptotherium* in Central America and Mexico as a possible holding pen scenario (early Blancan NALMA) and considered this part of their history as pre-Great American Biotic Interchange. With subsequent expansion into northern Mexico and southern United States in the late Blancan NALMA, *Glyptotherium* participated in GABI-1, Woodburne's (2010) first wave of South American taxa that expanded into North America during the late Blancan NALMA. The latest Quaternary distribution included the Gulf Coastal Plain and the Atlantic Coastal Plain, with occupation of distal reaches of their drainages in central and northern Mexico. Dispersal of glyptodont populations was probably facilitated by lower sea level and expansion of their habitat during glacial maxima (Rincón et al. 2008), as postulated by Woodburne (2010) for expansion of the Central America biota in general in the Quaternary, with a possibility of limited isolation of populations during interglacials when sea level was higher.

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