

# THE CINGULATES (XENARTHRA) OF THE LEISEY SHELL PIT LOCAL FAUNA (IRVINGTONIAN), HILLSBOROUGH COUNTY, FLORIDA

Kevin F. Downing<sup>1</sup> and Richard S. White<sup>2</sup>

## ABSTRACT

The late early Irvingtonian Leisey Shell Pit local fauna provides a superb record of the diversity of shelled edentates in the southeastern United States during the early Pleistocene. Among the four species of cingulates recognized in the Leisey Shell Pit local fauna, two, the dasypodid, *Dasypus bellus*, and the pampathere, *Holmesina floridanus*, are well represented in other Pleistocene fossil localities in Florida. Fossil material of *D. bellus* and *H. floridanus*, chiefly osteoderms at Leisey 1A, is indistinguishable from comparable material at other Irvingtonian Florida localities except for modest differences in average size. A third cingulate, a large glyptodont, is represented by a small sample of osteoderms, and is tentatively referred to *Glyptotherium arizonae*.

The most notable cingulate in the Leisey Shell Pit local fauna is the thick-armored and relatively large dasypodoid *Pachyarmatherium leiseyi*, here described as a new genus and species. *P. leiseyi* is presently known from isolated osteoderms and postcranial elements, and from a nearly complete postcranial skeleton in a private collection currently unavailable for detailed inspection. Large samples of *Pachyarmatherium leiseyi* osteoderms have been recovered from Leisey 1A and Haile 16A, and several isolated postcranial elements from Haile 16A. This new taxon is readily distinguished from other fossil and living armadillos by characteristics of the carapace, including the thickness and morphology of the carapacial osteoderms, a single, narrow transverse zone of imbrication between the pelvic and scapular bucklers and its unique border and caudal osteoderms. It is distinguished from glyptodonts by its clawed ungual phalanges, free dorsal vertebrae, and diminutive and probable edentulous jaws. The aggregate of skeletal morphology suggests that *P. leiseyi* was a strong, non-fossorial scratch digger and may have been mymercophagus. Although the detailed phylogenetic relationships of *P. leiseyi* are uncertain based upon limited available information, it appears to retain many primitive features of cingulates in its postcranial skeleton and is most closely related to the dasypodoid group. *P. leiseyi* first appeared in the late Blancan in North America, with records from both Florida and South Carolina, and is best known from seven early Irvingtonian localities in peninsular Florida.

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<sup>1</sup> The senior author is an Assistant Professor (Earth and Biological Sciences) at the School for New Learning, DePaul University, 243 S. Wabash Avenue, Chicago IL 60604-2302, U.S.A.

<sup>2</sup> The junior author is a former student of the University of Arizona. Present address: 16606 North Columbus, Catalina, Arizona 85737, U.S.A.

## RESUMEN

La fauna local de fines del Irvingtoniano temprano, proveniente del Depósito de Conchuelas de Leisey, provee un excelente registro de la diversidad de edentados con caparazón en el sureste de los Estados Unidos durante el Pleistoceno temprano. De entre las cuatro especies de cingulados reconocidas en la fauna del Depósito de Conchuelas de Leisey, dos, el dasipódido, *Dasyypus bellus*, y el pampaterio, *Holmesina floridanus*, están bien representados en otras localidades de fósiles del Pleistoceno de Florida. El material fósil de *D. bellus* y de *H. floridanus* en Leisey 1A consiste principalmente de osteodermos, los cuales a parte de modestas diferencias en tamaño medio, son indistinguibles de material comparable proveniente de otras localidades del Irvingtoniano de Florida. Un tercer cingulado, un gran gliptodonte está representado por una pequeña muestra de osteodermos, siendo referido tentativamente como *Glyptotherium arizonae*.

El cingulado más notable de la fauna local del Depósito de Conchuelas de Leisey, es un dasipodidoide relativamente grande y de gruesa caparazón. Este cingulado, *Pachyarmatherium leiseyi*, representa un nuevo género y especie siendo conocido a través de osteodermos aislados, elementos postcraneales y un esqueleto postcraneal casi completo perteneciente a una colección privada actualmente no disponible para una inspección detallada. Se han recuperado grandes muestras de osteodermos de *P. leiseyi* de Leisey 1A y Haile 16A, así como varios elementos postcraneales aislados provenientes de Haile 16A. Esta nueva taxa se distingue fácilmente de otros armadillos fósiles y vivientes en características del caparazón, incluyendo su grosor y morfología de los osteodermos; una sola zona de imbricación angosta y transversa entre los escudos pélvicos y escapulares; y lo singular de sus osteodermos caudales y del borde. Esta especie se distingue de otros gliptodontes por la presencia de garras en las falanges ungueales, por poseer vértebras dorsales libres y mandíbulas diminutas y probablemente edentadas. La morfología esquelética completa sugiere que *P. leiseyi* era de vida no subterránea, fornido, cavador y probablemente mirmecófago. Aunque existe incerteza acerca de las precisas relaciones filogenéticas de *P. leiseyi* en base a lo limitado de la información disponible, parecer ser que esta especie retiene varias características primitivas de cingulados en el esqueleto postcraneal relacionándose más cercanamente al grupo dasipódido. *P. leiseyi* apareció por primera vez en Norte América en el Blancano tardío con registros en Florida y Carolina del Sur, siendo bien conocido desde siete localidades del Irvingtoniano temprano en Florida peninsular.

## INTRODUCTION

The three major groups of North American fossil cingulates, armadillos (Dasypodidae), giant armadillos (Pampatheriidae) and glyptodonts (Glyptodontidae), are represented in the late early Irvingtonian Leisey Shell Pit local fauna. *Dasyypus bellus* is an average-sized armadillo with osteoderms that are identical to other Florida Irvingtonian specimens described by Martin (1974). Leisey 1A specimens of *D. bellus* are distinguished from late Blancan ones described by Robertson (1976) only by their slightly larger size. The pampatheres, or giant armadillos, considered more closely related to the glyptodonts and the eutatine armadillos than to the dasypodid armadillos by Engleman (1985), are represented at Leisey 1A by *Holmesina floridanus*. The specimens, which include a substantial number of non-carapacial elements, are intermediates in the chronocline between the small Blancan *H. floridanus* and the large Rancholabrean *H. septentrionalis*. The Leisey 1A sample is referred to *Holmesina floridanus* following Hulbert and Morgan (1993).

*Pachyarmatherium leiseyi* is a new dasypodoid comparable to the extant armadillo genus *Prionodontes* in size, but with thick osteoderms. *P. leiseyi* is represented by isolated carapacial and caudal osteoderms at Leisey 1A and by additional material from other sites in Florida and South Carolina, including a nearly complete postcranial skeleton in a private collection. *P. leiseyi* appears to have emigrated from South America to North America during the late Blancan from a lineage of poorly known South American dasypodoids. Its temporal and geographic distributions appear to have been restricted to the late Blancan and early Irvingtonian of the southeastern United States, respectively (see Morgan and Hulbert this volume for a discussion of the age of the Leisey and other Florida Plio-Pleistocene faunas).

The glyptodonts at Leisey are represented by the large *Glyptotherium arizonae*. The material referred to *G. arizonae* was not found in the principal bone bed (Leisey 1A), but was limited to the stratigraphically lower shell bed in the Leisey 1 quarry. Gillette and Ray (1981) presented a thorough discussion of *G. arizonae* and the other species of *Glyptotherium* found in North America.

In the report below, we describe the cingulate material recovered from the Leisey Shell Pit vertebrate localities, highlighting its relationship to similar material from other fossil localities in Florida. In addition, for *Pachyarmatherium leiseyi*, we incorporate information provided by a postcranial skeleton currently in a private collection, which was displayed for sale at the 1992 Tucson Gem and Mineral show. This specimen was collected at an undisclosed locality in Charlotte County, Florida, in the late 1980s. Both authors briefly viewed this specimen at the show and the junior author measured and photographed the reconstructed animal.

## ACKNOWLEDGEMENTS

The senior author wishes to thank S. David Webb and Gary S. Morgan of the Florida Museum of Natural History and Richard C. Hulbert, Jr., of Georgia Southern University for their thoughtful insights and reviews during the punctuated metamorphosis of this paper. Both authors wish to thank: Everett Lindsay and Kevin Moodie, Department of Geosciences, University of Arizona, for laboratory space and general consultation; Yar Petryzyn, Department of Evolutionary Biology and Ecology, University of Arizona; Jay Villemarette and Henry Galiano for providing recent comparative material; Gary S. Morgan, Florida Museum of Natural History, for arranging the loan of UF specimens; John A. White, Department of Geosciences, University of Arizona, for a helpful discussion on the use of material held in private collections; James Knight, South Carolina State Museum, Columbia, South Carolina, for notification of the existence of South Carolina specimens of *Pachyarmatherium leiseyi*. Downing examined the Leisey specimens and is responsible for the descriptions of *Dasypus bellus*, *Holmesina floridanus*, and *Glyptotherium arizonae*, as well as the diagnosis and description of *P. leiseyi*. White was principally responsible for recording and integrating additional information from the privately held specimen of *P. leiseyi*. Both authors collaborated in the development of the discussion section of *P. leiseyi*.

## SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope 1889

Suborder CINGULATA Illinger 1811

Superfamily DASYPODOIDEA Cabrera 1929

*Pachyarmatherium* new genus

**Type and Only Known Species.**—*Pachyarmatherium leiseyi* new species.

**Chronologic and Geographic Ranges.**—Late Blancan (late Pliocene) of Florida and South Carolina; early Irvingtonian (latest Pliocene and early Pleistocene) of Florida.

**Diagnosis.**—Interior carapacial osteoderms extremely small, thick; central figure polygonal, convex with no medial depression, displaced towards one edge, larger than peripheral figures; peripheral figures in single row, convex, asymmetric pattern with largest figures opposite central figure, small or absent along edge of displaced central figure, 3-6 in number; hair follicle pits at intersection of groove around central figure and radial grooves, 1-4 in number; surface smooth to weakly punctate; undersurface weakly concave, smooth to weakly striated with several vascular foramina.

**Etymology.**—*Pachyarma*- in reference to the relatively thick osteoderm armor; plus *-therium* for mammal.

**Discussion.**—Follows the description of *P. leiseyi*.

### *Pachyarmatherium leiseyi* new species

**Type Specimens.**—Holotype, UF 64347, interior carapacial osteoderm collected by Mr. Frank A. Garcia 1983. Paratypes UF 81624, near border carapacial osteoderm; UF 67099, 80371, 81807, interior carapacial osteoderms collected by personnel associated with the Florida Museum of Natural History excavations conducted from 1983 to 1984.

**Type Locality.**—Leisey Shell Pit 1A, NW1/4, SE 1/4, SW 1/4 Sec. 15, T32S, R18E, Ruskin 7.5' Quadrangle; Hillsborough County, Florida Bermont Formation.

**Chronologic and Geographic Ranges.**—As for genus.

**Referred Specimens.**—**Leisey Shell Pit 1A:** UF 64396, 67095-67099, 80036, 80037, 80220, 80316, 80317, 80508, 80532, 80615, 80687, 80767, 80892, 80893, 80916, 80959, 81004, 81288, 81622-81623, 81808, 81815, 82001, 82249-82250, 82336-82337, 82457, 82628, 82653-82655, 82770-82771, 82828-82829, 82924, 83103-83109, 83225, 83227, 83427-83428, 83585-83588, 83619-83620, 83679, 83767, 83826, 83856, 83975, 84076, 84291, 84478, 84762-84764, 84915, 84988, 85271-85274, 86163, 86183, 86197, 86327, 86348, 86361, 83674, 86385-86387, 86389, 86395, 86399-86404, 86417, 86432, 86440-86445, 86450-86451, 86456, 86460-86461, 86472-86473, 86482-86485, 86488, 86491-86492, 86500, 86504, 86508-86509, 86513, 86523-86526, 86539-86543, 86665, 86686, 86836, 86854, 87188-87193, 87608, 87968-87972, 87978, 88083, 88151-88152, 88230-88233, 88366-88368, 88411, 88619, 88620, 88704, 132074-132084, 132900, 137649-137650, 142201-142202, 142226 osteoderms. **Leisey Shell Pit 3:** UF 124174, 124175, 124555, 124556 four osteoderms. **Leisey Shell Pit 3A:** UF 142208-142211, 142217 five osteoderms. **Leisey Shell Pit 3B:** UF 132053, 133801 two osteoderms.

**Additional Localities:** **Haile 16A,** Alachua County: UF 95101-95188, 95196-95208, over 250 osteoderms; 135666, left metacarpal II (juvenile); 135667, left metatarsal II; 135668, right calcaneum. **Port Charlotte,** Charlotte County: UF 10322, osteoderm. **Payne Creek Mine,** Polk County: UF 128986, osteoderm; 61319-61322, four osteoderms (casts only). **Apollo Beach,** Hillsborough County: UF 93001-93007, seven osteoderms. **Kissimmee River 6,** Okeechobee County: UF 52673, 52675, two osteoderms. **El Jobean Shell Pit,** Charlotte County: UF 131962, 131963, 131966, three osteoderms. **Dorchester County,** South Carolina: several osteoderms.

**Diagnosis.**—As for genus.

**Etymology.**—*leiseyi*, for Mr. Bud Leisey, in recognition of his generous support of the paleontological field work at the Leisey Shell Pit from 1983 to 1992.

**Description.**—Carapacial osteoderms small and relatively thicker than any known dasypodid. In a sample of 42 osteoderms from Leisey 1A, mean greatest width is 13.8 mm with an observed range of 8.1-22.9 mm, while mean thickness is 8.9 mm with an observed range of 5.5-13.3 mm. The osteoderms are structurally similar to those of glyptodonts, however, they are approximately one third the width and half the thickness of those from *Glyptotherium arizonae* and *G. floridanum*.

Figures on the smooth to weakly punctate external surface of the osteoderms are well preserved and separated by distinct grooves. The arrangement of the figures is similar to that in *Glyptatelus* and *Dasypus bellus* in that the central figure is displaced towards one edge of the scute; it differs from *D. bellus* in that

the peripheral figures are more regular and well defined by the greater groove depth (Fig. 1A). Central figures are approximately one half the osteoderm width, and all those studied were distinctly convex with no medial depressions. The sides of the central figure generally parallel the sides of the less regularly shaped peripheral figures, giving it an overall polygonal appearance. Convex peripheral figures typically number 4 or 5 (observed range: 3 to 6), similar to the condition observed in *D bellus*.

The number and location of hair follicle pits on *Pachyarmatherium leiseyi* are similar to those of dasypodids. Deep pits are located where the groove around the central figure intersects with the radial grooves between peripheral figures. These pits number from one to four, one being the most common. The pits are typically situated at the intersection nearest the largest peripheral figure.

The undersurfaces of the osteoderms show a smooth to weakly striated texture on a slightly concave surface (Fig. 1B). Typically, the undersurface is marked by several small foramina. In side view, the osteoderms reveal their trabecular internal microstructure (Fig. 1C).

A near border osteoderm is represented by UF 81624 (Fig. 1D). It is pentagonal in shape with a moderately conical surface showing little punctation and resembles the bossed posterior border osteoderms of the glyptodont *G. floridanum*. All of its sides appear to have had adjacent osteoderms. It is similar in size to average interior osteoderms. Additional *Pachyarmatherium leiseyi* osteoderms that have been found in other Florida localities, and Dorchester County in South Carolina, show no major differences from those at Leisey 1A.

A large number of osteoderms (>250) from Haile 16A, which had been curated as *G. floridanum* (as juveniles), are here assigned to *P. leiseyi*. These specimens, including some juvenile osteoderms, provide a great deal of additional information about *P. leiseyi* armor. The interior carapacial osteoderms from Haile 16A (Figs. 2A, B) are very similar in character to the Leisey 1A osteoderms, having typically 3 to 5 peripheral figures (observed range 2 to 6) and 1 or 2 hair follicle pits (observed range 0 to 3). In 65 specimens (UF 95101-95165), mean width is 13.6 mm with an observed range of 9.6-18.1 mm, while mean thickness is 7.4 mm with an observed range of 5.0-11.2 mm. This suggests that the Haile specimens are nearly identical to the Leisey 1A specimens in width but slightly thinner. The juvenile interior carapacial osteoderms (Fig. 2C) generally average fewer peripheral figures (typically 3) than the adults. There is usually a single hair follicle pit and, whereas the central figure in the adults was approximately one half the osteoderm width, the central figure in juveniles is even more prominent, approximately two thirds the osteoderm width.

A variation on the normal interior carapacial osteoderm is seen in the Haile 16A specimens UF 95166-95169. The specimens have thicknesses almost as great as their widths and also have convex bottoms. They show one hair follicle pit, two peripheral figures, and a unique central figure which extends beyond the side of the osteoderm forming an overhang.

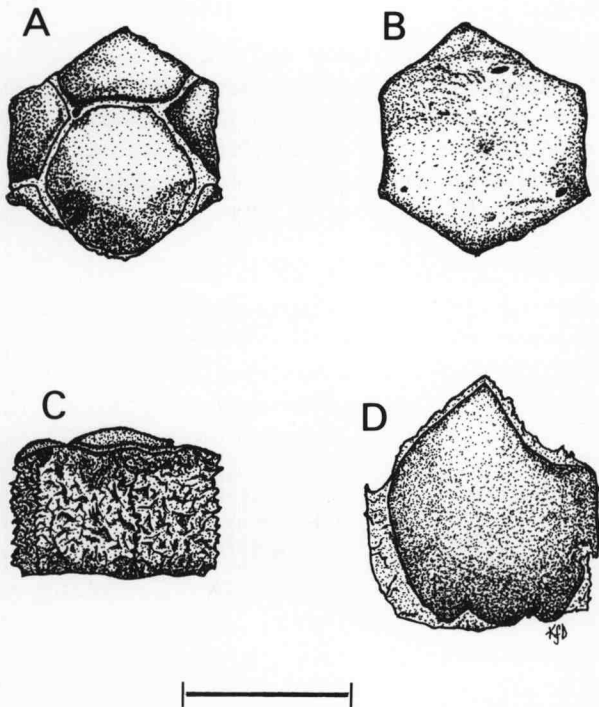


Figure 1. *Pachyarmatherium leiseyi* from Leisey 1A. Carapacial osteoderm (holotype, UF 64347). (A) dorsal surface; (B) undersurface; (C) side; (D) near border osteoderm (paratype, UF 81624) dorsal surface. Scale bar 10 mm in length.

Two different types of *Pachyarmatherium leiseyi* border osteoderms have been identified from Haile 16A. The first group (UF 95177-95183) is relatively large compared to the interior osteoderms. They have from one to two hair follicle pits, two well defined peripheral figures (some have a very small third figure), and in lateral view their rounded sides can be seen (Figs. 2D, E). On the surface of this rounded side there is typically a small furrow. A distinctive small projection juts out near the bottom of the side which abuts more interior osteoderms and presumably helps adjoin them. A juvenile example of this border osteoderm shows few differences from the adult specimens (Fig. 2F).

The second group of border osteoderms are represented by Haile 16A specimens UF 95170-95175, and are characterized by relatively thin wedge-like lateral profiles, two hair follicle pits, three peripheral figures, and a central figure that tends to be large and pentagonal (Figs. 2G, H). A juvenile specimen closely resembles the adult form (Fig. 2). This group of border osteoderms is most likely from the anterior edge of the pelvic buckler.

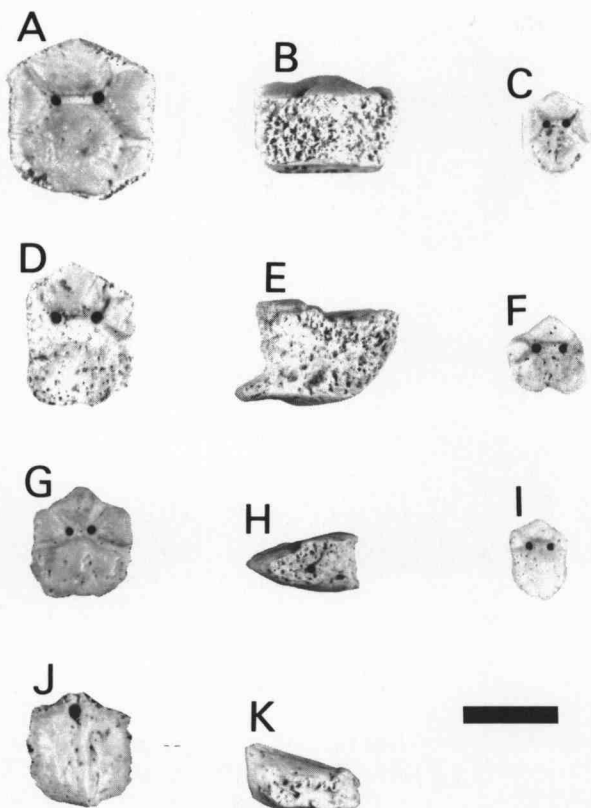


Figure 2. Osteoderms of *Pachyarmatherium leiseyi* from Haile 16A (Irvingtonian). Interior carapacial (UF 95102): (A) dorsal view; (B) lateral view. Juvenile (UF 95200); (C) dorsal view. Carapacial border (UF 95177); (D) dorsal view; (E) lateral view. Juvenile (UF 95183); (F) dorsal view. Carapacial border (UF 95172); (G) dorsal view; (H) lateral view. Juvenile (UF 95176); (I) dorsal view. Caudal osteoderm (UF 95185); (J) dorsal view; (K) lateral view. Scale bar 10 mm in length.

A final type of osteoderm from Haile 16A (UF 95184-95188) is very different from the others. It is characterized by having no central or peripheral figures, a single hair follicle centrally positioned over the thickest edge, and smooth curved surfaces (Figs. 2J, K). The underside of the osteoderm is curved convexly along the length. This osteoderm form most likely represents part of the caudal armor.

Three postcranial elements from Haile 16A are tentatively referred to *Pachyarmatherium leiseyi*: a juvenile left metacarpal II, a left calcaneum (Fig. 3A), a left metatarsal II (Fig 3E). Justification for referring these elements to *P. leiseyi* are presented in the discussion below.



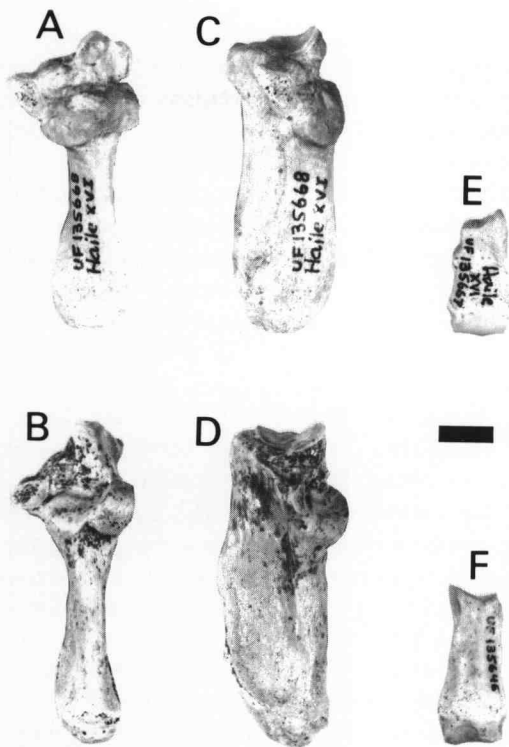


Figure 3. Comparison of *Pachyarmatherium leiseyi* and *Dasypus bellus* postcranial elements from Haile 16A. (A) dorsal, and (C) medial views of right calcaneum of *P. leiseyi*; (UF 135668). (B) dorsal, and (D) medial views of right calcaneum of *D. bellus* (UF 24938). Anterior views of left metatarsal IIs of (E) *P. leiseyi*; (UF 135667) and (F) *D. bellus* (UF 135645). Scale bar 10 mm in length.

**Discussion.**--When osteoderms of *Pachyarmatherium leiseyi* were first examined, they were initially allocated to the Glyptodontidae because of several shared characteristics (e.g., extreme thickness and lack of movable osteoderms). This was the draft interpretation when Webb et al. (1989:105) mentioned this taxon in their discussion of the Leisey site geochronology as "a new, small kind of glyptodont". Hulbert and Morgan (1989) also referred to this species as a miniature glyptodont, probably a new species. In February, 1992, the authors examined a nearly complete, but poorly restored, postcranial skeleton with associated carapace in a private collection on display for sale at the Tucson Gem and Mineral Show. This skeleton provided additional information concerning the morphology of this new dasypodoid. Discussions with G. Morgan (personal communications, 1992) indicated that he and R. Hulbert had also seen and recognized the affinity of this specimen to previously collected material, as it has been offered up for sale in Florida before its display in Tucson and current

restoration. While the type description and diagnosis sections above have been based upon specimens available in museum collections, we have chosen to use the observations made upon the privately held specimen in the discussion which follows. A much more detailed description and analysis needs to be made of this material if and when it becomes available for examination. Table 1 summarizes our preliminary measurements on the postcranial skeleton. It should be emphasized here that the measurements were made on a poorly restored and mounted specimen under less than ideal conditions. Measurements were only taken on elements which had not been restored. We believe them to be accurate enough to provide a good indication as to the size of the various elements listed.

**Armor:** One of the most distinguishing characteristics of *Pachyarmatherium leiseyi* is its carapace. As has already been noted, the osteoderms are extremely thick relative to their small size. The sutures between adjoining osteoderms consist of strongly intermeshing trabecular structures similar to the thick glyptodont carapacial osteoderms (Fig. 4). The associated carapace of the privately-held specimen reveals additional information regarding the dermal armor of *P. leiseyi*. Most notably, its carapace consisted of an anterior scapular buckler and a posterior pelvic buckler whose common border formed a restricted transverse area of imbrication. The anterior buckler overlapped the posterior buckler along a single band of osteoderms with one wedged shaped edge, likely permitting modest flexure of the carapace. Unlike the bands of many dasypodids, which permit both anterior and posterior imbrication and motion between bands of moveable osteoderms, the two respective osteoderm bands involved with the medial carapacial break were tightly integrated and sutured to the rest of the carapace along their remaining four sides (i.e., they were immovable).

Not a single osteoderm analogous to the independently movable bands of pampatheres or dasypodids were recovered with this specimen, while many hundreds of osteoderms (representing approximately 75% of the carapace), including nearly all the edges of the two fixed bucklers, were recovered. While it is possible that all of the movable osteoderms had become disassociated from the specimen during its original burial and/or recovery, the fact that the two fixed portions overlap precisely and that the length of the carapace thus overlapped matches the remainder of the post-cranial skeleton so well, argues for the interpretation that we have proposed here.

Among the recent dasypodids, the number of movable bands in the carapace ranges from a minimum of one (rarely) in *Tolypeutes* to as many as 14 in *Priodontes* (Wetzel, 1985). In *Stegotherium*, a well described pre-Pleistocene armadillo allocated to the Dasypodini by Engleman (1985), the carapace consists of an uncertain number (but at least 20) of movable bands, which are not so clearly differentiated from the immovable osteoderms. In fact, Scott (1903a) was not certain whether any of the pelvic buckler osteoderms were fixed in *Stegotherium*; he does state that a fixed scapular buckler is not present. The

Table 1. Measurements (in mm) of postcrania of *Pachyrmatherium leiseyi*, based on measurements of mounted skeleton in private collection except where indicated.

Scapula:	height	120.00
	height of spine	36.5
Radius:	length	67.0
	distal width	23.0
Ulna:	total length	115.0
	length of olecranon process	57.0
	length of remainder of ulna	58.0
	distal width	29.0
Femur:	length	150.0
	distal width	42.0
	width through trochanter and head	53.5
Patella:	height	30.0
	width	17.0
Tibia:	length	99.5
	distal width	45.0
Calcaneum:	length	56.0
	length (UF135668)	55.0

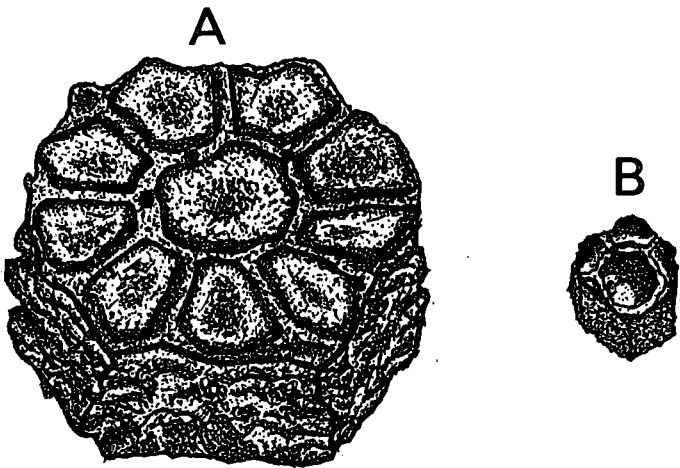


Figure 4. Comparison of interior carapacial osteoderms. (A) *Glyptotherium floridanum*; (B) *Pachyrmatherium leiseyi*. (X 1.00).

structural character of the single area of imbrication on *P. leiseyi* is suggestive of a morphological condition incipient to the development of multiple bands, however, the apparant variability of band numbers in modern forms leaves this hypothesis

equivocal until a broader phylogenetic analysis of cingulates can establish more clearly the patterns and polarity of movable band addition or reduction.

The caudal armor of *P. leiseyi* consists of a series of eight tubes each underlain by a single caudal vertebra. Each tube consists of three rows of osteoderms, the posterior most of which are slightly flared outward and which tend to be pointed, producing a weakly serrate posterior margin. The terminal caudal cone's anterior row of osteoderms is smaller in diameter than the immediately preceding tail section. The cone shows no trace of terminal enlargement. The individual osteoderms of the tail sections do not show a rosette pattern with a central figure as in the carapacial elements. Each has a low border rising to a keel which is oriented from the anterior to the posterior end of the osteoderm.

**Postcrania:** Several general observations can be made about the remainder of the skeleton. The thoracic and lumbar vertebrae are all free, not fused or co-ossified in the dorsal tube and synsacrum as observed in glyptodonts. The digits of both the manus and pes in *Pachyarmatherium* have strong digging claws, all of which are approximately equal in size. There is none of the enlargement of the central digits seen in some of the dasypodids, such as the comparably giant *Priodontes*. The ungual phalanges are not hoof-like, unlike those of glyptodontids, including early forms such as those in the Propalaeophlophorinae group. The ungual phalanges of the manus are slightly narrower and more claw-like than those of the pes.

One of the most exceptional characters of the postcranial skeleton is in the structure of the ulna. In this specimen, the length of the olecranon process to the remainder of the ulna is 57 mm to 58 mm (98%), a higher proportion than that recorded for any other fossorial mammal by Hildebrand (1985). The closest extant cingulate with similar proportions, cited by Hildebrand, is *Euphractus*, a dasypodid armadillo with an olecranon process 95% the length of the remainder of the ulna. While the extreme development of the olecranon process is typically correlated with a digging adaptation, *Pachyarmatherium* shows few of the correlated modifications usually accompanying such development. Neither adaptations for humeral rotation digging nor the extreme development of hooking and pulling digits such as that found in the anteaters or in the dasypodid *Priodontes* are present. *Pachyarmatherium* may have been a more generalized scratch digger, similar to *Dasypus novemcinctus*.

Three postcranial elements from Haile 16A represent a small cingulate and are referred to *Pachyarmatherium*. They are similar in size, but differ in morphology from *Dasypus bellus*, the only other small cingulate in the fauna. They also resemble the corresponding elements of the privately held specimen. A left calcaneum (UF 135668) is nearly the same length as a calcaneum of *D. bellus* (UF 135649), yet differs in the nature of the articular surfaces, particularly the sustentacular facet (Fig. 3A, B). The calcaneum of *P. leiseyi* is also slightly less robust. A left metacarpal II (UF 135666) is from a juvenile individual as

evidenced by the missing and unfused distal epiphysis. It is shorter and wider than the corresponding element in *D. bellus* (UF 135643). The proximal end of this element is more pronounced ventrally as a massive knob dissimilar to the condition observed in *D. bellus*. The prominence located on the dorsoexternal border at midshaft for attachment of the extensor carpi radialis is smaller than that of *D. bellus*, although the extent that this is due to the immaturity of the specimen at hand is unknown. A left metatarsal II (UF 135667) is similar in size and gross morphology to the same element in *D. bellus* (UF 135645), but is considerably shorter and therefore relatively more robust (Figs. 3E, F). The proximal articulation is narrower and is longer dorsoventrally. The median tubercle on the distal (phalangeal) articulation is not as strongly developed as is that of *D. bellus* (UF 135646), and the two halves of the distal articulation located on either side of the median tubercle lie in the same plane, whereas in *D. bellus* the external side is inclined relative to the internal side.

**Skull:** A few fragments of a skull were found along with the postcranial material of the privately held specimen. In so far as we have been able to ascertain, there was no other cingulate material obtained at the locality other than this individual. Therefore we consider it likely that these cranial and jaw fragments are indeed from *P. leiseyi*. One fragment consisted of the parietals and frontals including the dorsal margin of one orbit. The skull fragments indicate a lunate occipital crest comparable to those of *Dasypus novemcinctus*. More significantly, however, are three consequential fragments of the lower jaw. Two fragments are from the left mandible, and while not actually fitting together, are estimated to lack only about 5 mm or less between them. Other than the one small missing intervening portion, that side of the lower jaw is complete. The third fragment represents the anterior end of the right jaw.

The lower jaws appear to have been diminutive like those of *Stegotherium tessellatum*, from the early Miocene of South America, rendered in Scott (1903A). They were probably edentulous, unless the missing portion contained alveoli for very small teeth. However, the ramus of the mandible just adjacent to the missing portion on both sides is thin and blade-like with no trace of a swelling to accommodate alveoli. The mandibular symphysis appears to have been reduced with no evidence of a strong suture between the mandibular rami. In this respect, the mandible matches the condition seen in *Dasypus novemcinctus*. As observed in the dasypodids, there appears to be two mental foramina in each jaw, with the posteriormost being the larger. The coronoid process extends much above the mandibular condyle which in turn is not elevated above the horizontal ramus. This character also agrees with species of *Dasypus*. If the skull material is correctly associated with the remainder of the postcranial skeleton, then *Pachyarmatherium* may have been a more functionally committed myrmecophage than is *Dasypus*, but possibly less so than the anteaters (*Myrmecophaga* and *Tamandua*) or the pangolins (*Manis*). These latter groups are also edentulous and show a reduction of the horizontal ramus, but have a much greater reduction of the

ascending ramus indicating even more pronounced reduction of the masticatory system.

**Phylogenetic Relationships.**—It is evident that *P. leiseyi* shows a combination of features associated with armadillos and glyptodonts. The almost entirely rigid carapace, comprised of thick and sutured osteoderms with deep grooves as well as highly bossed caudal and border ornamentation, is structurally analogous to features usually associated with glyptodonts. On the other hand, osteoderm imbrication permitting flexure of the pelvic and scapular bucklers is a characteristic usually associated with armadillos and giant armadillos. It should be noted, however, that a simple imbricating band near the middle of the length of the carapace, as is observed for *P. leiseyi*, may also have been present, at least in part, in some early glyptodont groups. For example, Scott (1903b) and Hoffstetter (1958) indicate that some primitive glyptodonts, such as those of the subfamily Propalaeohoplophorinae of South America, appear to have had an area of imbricating osteoderms near their lateral margin. The figure ornamentation patterns of *P. leiseyi* carapacial osteoderms are similar in their peripheral figure reduction and central figure displacement to those seen on armadillos such as *Dasypus* and the glyptateline glyptodonts such as *Glyptatelus tatusinus* figured in Hoffstetter (1958). Unlike *Glyptatelus*, *P. leiseyi* central figures are polygonal and have hair follicle locations restricted to groove intersections.

The presence of claws rather than hooves and free dorsal vertebrae in *P. leiseyi*, may be retained primitive features of cingulates seen in other dasypodoids. The diminutive and possibly edentulous partial jaw associated with the *P. leiseyi* skeleton, is suggestive of a derived grade seen in other dasypodids, such as those of the subfamily Stegotheriinae from the Miocene of South America. Early glyptodonts, including members of the Propalaeohoplophorinae and the Glyptatelinae do not show dentary reduction. The character of the jaw, in combination with the other skeletal features, argues for the provisional assignment of this genus to the dasypodoid group. Under this hypothesis, the thickening of the osteoderms observed for *P. leiseyi* may have been derived separately from that of the glyptodontids.

We have refrained from presenting a more detailed phylogenetic analysis, including familial assignment, because of the limited examination of the private specimen and because many critical characters are not preserved. For instance, the skull characters used by Engleman (1985) in his general analysis of the cingulates, such as an ossified bulla, are not available even on the exceptional private specimen. Until the postcranial material mentioned above becomes available, or until other material is discovered, a more rigorous phylogenetic analysis of this pivotal cingulate will not be possible.

**Family DASYPODIDAE Bonaparte 1838***Dasyus bellus* (Simpson 1929)

**Referred Specimens.**--Leisey Shell Pit 1A: UF 64341, 80173, 80560, 80686, 81813, 81814, 81927, 83223, 83224, 83425, 83426, 85332, 83584, 83837, 84852, 86326, 86423, 86439, 86446, 86471, 86664, 87186, 87187, 88702, 132085, 132086, 142203, 142204 immoveable osteoderms; UF 80003, 80891, 81402, 83134, 86388, moveable osteoderms; UF 115730, right tibiofibula. Leisey Shell Pit 3: UF 130011 movable osteoderm. Leisey Shell Pit 3A: UF 142205-142207, 142216, 142220 immovable osteoderms. Leisey Shell Pit 3B: UF 132046 right distal femur.

**Discussion.**--*Dasyus bellus* is represented by both moveable and immoveable osteoderms at Leisey Shell Pit. The immoveable osteoderms are roughly hexagonal with large, weakly convex central figures. The central figures are situated towards one edge of the osteoderms and are bordered by 2-6 irregularly shaped peripheral figures. There are typically 3-4 hair follicle pits situated within the groove that surrounds the central figure, some of which are situated at the intersection of the radial grooves between peripheral figures and the groove that surrounds the central figure. Osteoderm undersides are typically marked by a small central foramen. The moveable (imbricating) osteoderms are rectangular, with convergent rows of hair follicle pits ornamenting the wedge-shaped posterior end.

Osteoderms of *Dasyus bellus* from Leisey do not differ significantly in appearance from those found in the Florida Blancan sites of Haile 15A and Santa Fe River 1B nor from osteoderms at Irvingtonian sites such as Inglis 1A, Haile 16A, and Coleman 2A. Leisey 1A immoveable osteoderm sizes overlap with those from Blancan and early Irvingtonian sites (Table 2). There are few well preserved moveable osteoderms from Leisey 1A, so that little can be concluded about their sizes.

Although the size ranges of the immoveable osteoderms have substantial overlap, the mean values produce a trend towards increasing size for *Dasyus bellus* from the Blancan through the Irvingtonian. This is in agreement with the size increase noted by Martin (1974) for moveable osteoderms. With such a small sample of osteoderms, however, (relative to the hundreds, which vary in size, on an individual carapace), support for a general chronocline increase in size through time, as recorded by osteoderms, is far from conclusive.

**Family PAMPATHERIIDAE Paula Couto 1954***Holmesina floridanus* (Robertson 1976)

**Referred Specimens.**--Leisey Shell Pit 1A: UF 120951, right mandible with four teeth (numbers 5-8); 65890, 86419, 86685, isolated upper 4th, 9th, and

9th teeth, respectively; 67100, maxillary fragment; 67500, partial basicranium (collected away from the main bone bed); 84749, femur; 86488, juvenile femur; 86538, tibiofibula; 65900, juvenile tibia; 83226, astragalus; 86124, metatarsal IV; 86487, metatarsal II; 813636, digit IV ungual phalanx; 86351, partial scapula; 86638, humerus; 85622, partial ulna; 86470, juvenile radius; over 350 isolated osteoderms including 64342-64345, 80888, 80915, 81002, 86411, and 86431. Leisey Shell Pit 1: UF 66422, right mandible with 5th and 9th teeth.

Table 2. Measurements (in mm) of immoveable osteoderms of *Dasyops bellus* from the late Pliocene and early Pleistocene of Florida. N = number of specimens; OR = observed range.

	Thickness			Maximum Width	
	N	Mean	OR	Mean	OR
Blancan					
Haile 15A (UF 24976)	10	3.8	3.5-4.5	9.7	8.3-12.4
Very Early Irvingtonian					
Inglis 1A (UF 24978)	10	4.1	3.6-4.7	11.6	8.4-14.5
Early Late Irvingtonian					
Leisey 1A	8	4.6	3.2-5.5	13.0	11.2-14.9

**Discussion.**—A general trend in pampathere evolution towards increasing size has been well documented and discussed in the literature (Robertson 1976; Kurtén and Anderson 1980; Edmund 1985a, 1985b, 1987; Hulbert and Morgan 1993). The fossils from Leisey 1A agree with this trend and differ predominantly only in size from Blancan and Rancholabrean specimens. Robertson (1976) established that the small Blancan *Holmesina floridanus* (which he described as *Kraglievichia floridanus*) is directly ancestral to the large Rancholabrean *H. septentrionalis*, forming a chronocline. Edmund (1987) quantified this trend in size on the basis of additional material, and placed *K. floridanus* in *Holmesina*. The Leisey 1A material is assigned to *H. floridanus* following Hulbert and Morgan (1993), who demonstrated that the Florida Blancan species is *H. floridanus*, the middle to late Irvingtonian and Rancholabrean species is *H. septentrionalis*, and that early Irvingtonian specimens are intermediate between the two in size but referable to *H. floridanus*.

The partial right mandible, UF 66422, contains the 5th and 9th teeth, and alveoli for all but the first tooth. The two teeth differ only in size from other *Holmesina floridanus* specimens. UF 66422 is slightly larger than a right



Table 3. Measurements (in mm) of mandibles of *Holmesina floridanus* from Leisey Shell Pit and Inglis 1A.

Characters	Leisey 1A UF 66422	Leisey 1A UF 129051	Inglis 1A 20948
Alveolar measurements			
tooth 3: length	10.6	—	9.4
width	6.7	—	6.4
tooth 4: length	13.0	11.6	13.0
width	7.0	7.7	6.3
tooth 5: length	17.6	18.6	15.1
width	9.8	9.9	—
tooth 6: length	17.8	22.4	18.5
width	11.5	11.8	9.2
tooth 7: length	16.8	22.5	17.7
width	10.0	10.9	9.5
tooth 8: length	14.8	—	17.1
width	9.6	—	8.2
tooth 9: length	11.0	—	12.9
width	7.3	—	7.0
Mandible thickness at 7th alveolus	20.5	19.9	19.2

Table 4. Cranial measurements of *Holmesina floridanus* from Leisey Shell Pit.

Anteroposterior length tooth 4 (UF 65890)	13.8
Anteroposterior length tooth 9 (UF 86419)	11.7
Anteroposterior length tooth 9 (UF 86685)	11.4
Partial braincase (UF 67500)	
Transverse diameter between hypoglossal foramina	45.0
Transverse diameter between foramina ovale	46.7
Length of basioccipital from ventral edge of foramen magnum to basioccipital-basisphenoid suture	51.7
Transverse diameter, right facet for occipital condyle	21.9
Transverse inside diameter, occipital condyle	34.0

mandible, UF 20948, found at Inglis 1A, early Irvingtonian (Table 3), and also differs from the Inglis specimen in having two large mental foramina located centrally beneath the second alveolus with a third small foramen located more posteroventrally. UF 20948 has a linear arrangement of all three foramina with the two most anterior foramina beneath the 3rd tooth. Additionally, the masseteric fossa is more restricted on UF 66422.

A second mandible from Leisey, UF 129051, has teeth 5 through 8, but does not preserve as much of the ramus as does UF 66422. The shape of the teeth is similar to the other Leisey mandible and the Inglis jaw, but the measurements of the teeth, especially length, are larger (Table 3).

A basicranium, UF 67500, consists of a large basioccipital and an incomplete auditory bulla with the right condyle and the right squamosal portion of the zygomatic arch preserved (measurements in Table 4). It resembles a more complete skull of *Holmesina septentrionalis* from the Pleistocene of Texas described by James (1957). An isolated upper left 4th tooth, UF 65890 from Leisey 1A, has a reniform occlusal outline. Unlike late Pleistocene specimens, there is an additional concave surface running down the posterior lobe of this tooth. Lastly, a left maxillary fragment, UF 67100, with portions of the 6th and 7th alveoli is slightly more robust than similar Inglis 1A fragments.

Among the elements representing the limbs are a tibiofibula, UF 86535, a juvenile tibia, UF 65900, and a digit IV ungual phalanx, UF 81363. Features of the tibiae agree with those of a large *Holmesina* from the latest Pleistocene at Hornsby Springs (UF 4016). Other than its smaller size, the ungual phalanx shows little difference from a specimen (UF 9336), from Branford 1A (Rancholabrean). The humerus from Leisey 1A, UF 86638, exhibits the typical intermediate size relationship with Blancan and Rancholabrean specimens (Fig 5; Table 5). A Leisey metatarsal IV (UF 86124) has a length of 37.3 mm. A single Blancan example measures 28 mm, Irvingtonian examples average 39 mm, and Rancholabrean examples diminish to an average of 30 mm. (Edmund, 1987). The Leisey example, late early Irvingtonian, fits well within the demonstrated chronocline.

The relative size of moveable and immoveable osteoderms of *Holmesina* is a reasonably good biostratigraphic indicator for Florida Blancan, Irvingtonian, and Rancholabrean sites (Edmund 1985b; Hulbert and Morgan 1993). The Leisey 1A osteoderms fall between Blancan and Rancholabrean specimens and are slightly smaller (Fig. 6) than those at Inglis 1A (earliest Irvingtonian) or Haile 16A (late early Irvingtonian). In a sample size of 19, the average length of moveable osteoderms from Leisey 1A was found to be 78.2 mm with an observed range of 61.5-92.7 mm, while the average width was determined to be 26.4 mm with an observed range of 22.8-29.1 mm. Since there are more than 600 osteoderms on the carapace of *Holmesina* (Edmund 1985b), caution should be employed, as with *Dasyops bellus* osteoderms, when generalizing about evolutionary and

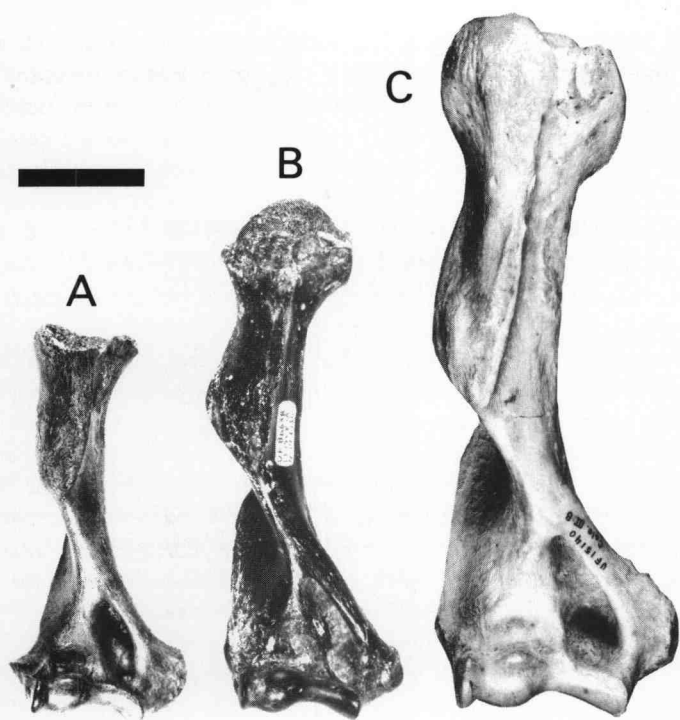


Figure 5. Comparison of *Holmesina* right humeri, anterior view. (A) *H. floridanus*, Santa Fe 1, Blancan (UF 10432); (B) *Holmesina floridanus*, Leisey 1A, Irvingtonian (UF 86638); (C) *H. septentrionalis*, Coleman 3B, Rancholabrean (UF 15140). Scale bar 40 mm in length.

Table 5. Postcranial measurements of *Holmesina floridanus* from Leisey Shell Pit

Femur (UF 84749)	length	225.0
	width at 3rd trochanter	42.3
	diameter of head	24.3
Scapula (UF 86351)	transverse diameter glenoid facet	22.9
Humerus (UF 86638)	length	175.0
Ulna (UF 85622)	width at semi-lunar notch	29.5
Tibiofibula (UF 86538)	diameter of opening	108.0
Astragalus (UF 83226)	length	37.7
MT II (UF 86487)	length	41.4
MT IV (UF 86124)	length	37.3
Ungual phalanx digit IV (UF 81363)	length	28.6

biostratigraphic placement from small samples of osteoderms alone. Hulbert and Morgan (1993), subsequent to the measurements discussed here, have analyzed a greater sample of the Leisey *Holmesina*.

**Family GLYPTODONTIDAE Burmeister 1879**  
**Subfamily GLYPTODONTINAE Trouessart 1898**  
*Glyptotherium arizonae* Gidley 1926

**Referred Specimens.**--Leisey Shell Pit 1: UF 124618-124630, 13 osteoderms, possibly from a single individual; 131976, interior carapacial osteoderm.

**Description.**--A poorly preserved osteoderm (UF 131976) is from the interior of the carapace and is marked by eight peripheral figures, a large central figure, and several hair follicle pits. The series UF 124618-124630 contains four typical interior carapacial osteoderms (124618-124621) with the diagnostic morphology of *G. arizonae*. The size and morphology of these osteoderms matches those from Florida referred to *G. arizonae* by Gillette and Ray (1981). *G. arizonae* is limited to the lower shell bed of Leisey 1 and is not found in the Leisey 1A horizon.

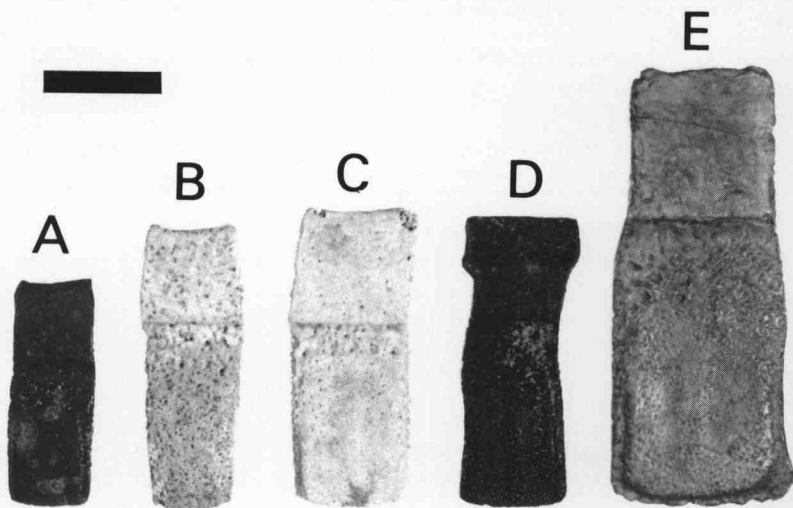


Figure 6. Comparison of *Holmesina* movable osteoderms. (A) Santa Fe 1, Blancan (UF 10431); (B) *H. floridanus*, Haile 15A, Blancan (UF 10902); (C) *H. floridanus*, Inglis 1A, Irvingtonian; (D) *Holmesina floridanus*, Leisey 1A, Irvingtonian (UF 86498); (E) *H. septentrionalis*, Branford 1A, Rancholabrean (UF 9336). Scale bar 30 mm in length.

## SUMMARY

It has been recognized for decades that edentates were an important component of the Pleistocene faunas of Florida (e.g., Holmes and Simpson, 1931). The Leisey Shell Pit 1A local fauna provides a superb record of the diversity of the cingulate edentates in the southeastern United States during the late early Irvingtonian. The relatively high number of cingulates at this time, arguably their peak diversity interval in this region, developed as new immigrants from South and Central America ventured across the improved intercontinental connections during the Pleistocene Epoch. Among the four species of shelled xenarthrans recognized in the Leisey Shell Pit 1A local fauna, *Dasyurus bellus* and *Holmesina floridanus* are very well known from other localities in Florida. The distribution of *Glyptotherium arizonae* included the Gulf Coast and southwestern United States.

The most notable cingulate in the Leisey Shell Pit local fauna is *Pachyarmatherium leiseyi*. *P. leiseyi* is presently known from isolated osteoderms and postcranial elements, and from a nearly complete postcranial skeleton in a private collection currently unavailable for detailed inspection. This new dasypodoid is readily distinguished from fossil and living armadillos by characteristics of the carapace, including its thick osteoderms, a single area of imbrication between the pelvic and scapular bucklers, unique border and caudal osteoderms, and edentulous jaws. Among the many features which distinguish it from the Pleistocene glyptodonts are its much smaller size, osteoderm morphology, free dorsal vertebrae, and presence of claws rather than hooves. The known skeletal morphology suggests that *P. leiseyi* was functionally a strong scratch digger. *P. leiseyi* has not been found in significantly younger localities than Leisey in the southeastern United States, therefore, it may have had a relatively brief presence in North America after its dispersal from South America in the late Pliocene.

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