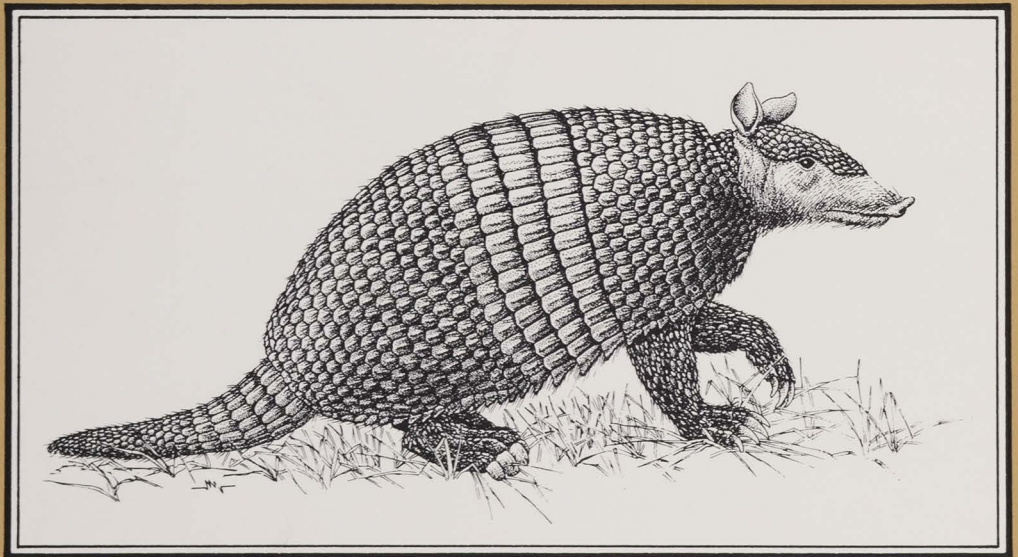


NUMBER 40  
PEARCE-SELLARDS  
SERIES

The Armor of  
FOSSIL GIANT ARMADILLOS  
(*Pampatheriidae, Xenarthra, Mammalia*)

A. GORDON EDMUND



JUNE 1985  
TEXAS MEMORIAL MUSEUM, UNIVERSITY OF TEXAS AT AUSTIN



# Pearce-Sellards Series

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The Pearce-Sellards Series is an occasional, miscellaneous series of brief reports of Museum and Museum-associated field investigations and other research. All manuscripts are subjected to extramural peer review before being accepted. The series title commemorates the first two directors of Texas Memorial Museum, both now deceased: Dr. J. E. Pearce, Professor of Anthropology, and Dr. E. H. Sellards, Professor of Geology, The University of Texas at Austin.

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### ABSTRACT

Fossil giant armadillos are protected by armor consisting of about 800 osteoderms covering the body, head, tail, legs and feet. The body armor is composed of an anterior (pectoral) buckler and a posterior (pelvic) buckler, separated by three transverse bands of imbricating plates. In one phyletic line the pelvic osteoderms are rectangular, rather than polygonal. The surficial ornamentation of the keratin-bearing portion of the osteoderms appears to be conservative and taxonomically characteristic in at least two major phyletic lineages. These characters will be used in a future taxonomic revision.

### SUMARIO

Los prionodontes fosilados (pampaterios) están protegidos por una armadura que consiste en alrededor de 800 láminas del osteodermis que cubren el cuerpo, la cabeza, las piernas y los pies. La armadura corporal está compuesta de un escudo delantero (pectoral) y un escudo trasero (pelviano) separados por tres bandas transversas de láminas imbricadas. En una de las líneas filéticas, las láminas osteodérmicas pelvianas son rectangulares más bien que poligonales. La ornamentación superficial de la parte queratinosa de las láminas osteodérmicas parece conservativa y taxonómicamente característica de por lo menos dos de las más importantes líneas filéticas. Se utilizarán estos caracteres en una futura revisión taxonómica.

### ACKNOWLEDGEMENTS

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### ABBREVIATIONS

HMNS	Houston Museum of Natural Science, Houston, Texas
IFG	Instituto de Fisiografía y Geología, Universidad Nacional del Litoral, Rosario, Argentina
IGM	Instituto de Geología y Mineralogía, Mexico City
MACN	Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina
MLP	División Paleontología Vertebrados, Universidad Nacional de La Plata, Argentina
RHB	Private collection of Roy and Helen Burgess, Venice, Florida
ROM	Department of Vertebrate Palaeontology, Royal Ontario Museum, Toronto
TAMU	Texas A and M collection at the Texas Memorial Museum, Austin, Texas
UF/FSM	University of Florida, Florida State Museum, Gainesville, Florida



## INTRODUCTION

Since their discovery in Brasil in 1838, fossil giant armadillos have been described by numerous authors (Ameghino 1889, Castellanos 1927, 1937, 1946, 1956, Edmund 1984, Hibbard et al., 1978, Hoffstetter 1952, Holmes and Simpson 1931, James 1957, Lund 1839, Moreno and Mercerat 1891, Rovereto 1914), often on the basis of very fragmentary material. Because osteoderms are by far the most common elements in the fossil record, and because they bear valid taxonomic criteria, they are here described in detail prior to a major taxonomic revision by the author. No reasonably complete individuals have yet been found, but composite material adequate for detailed description of typical forms is now on hand.

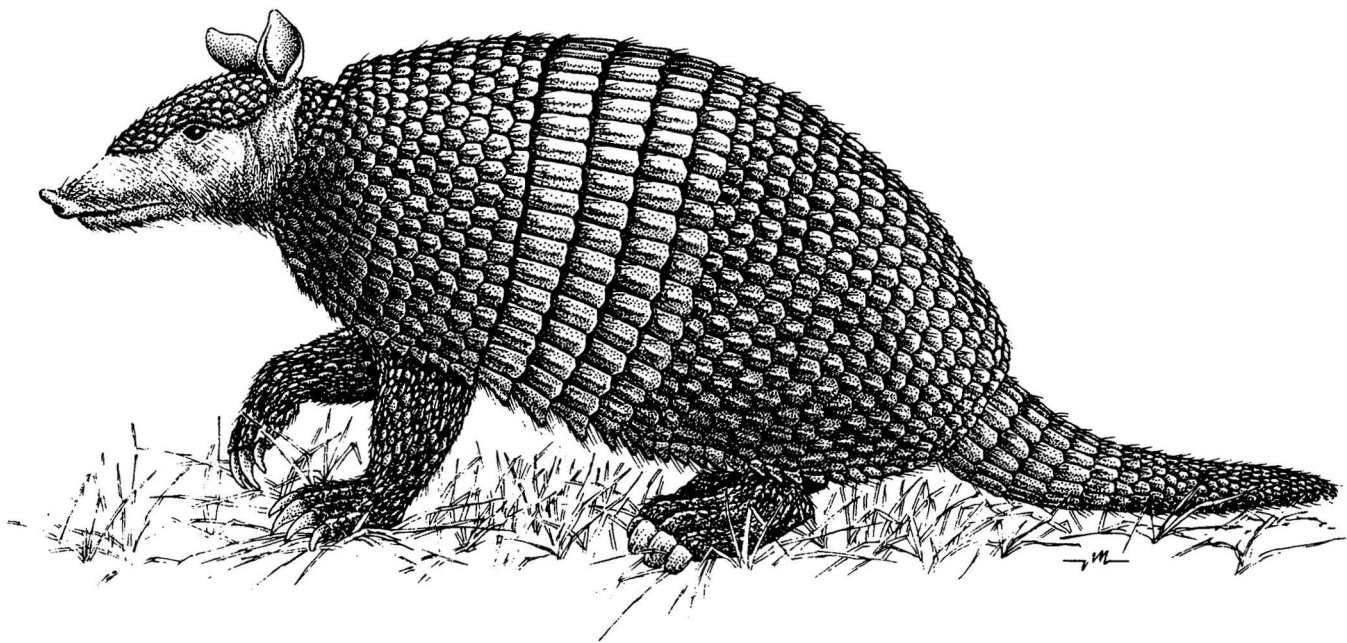


Fig. 1. Restoration of *Holmesina septentrionalis* based on composite material from Florida.

## A GENERAL DESCRIPTION OF THE ARMOR

Pampatheres share with true armadillos (Dasypodidae) and glyptodonts a well developed dermal armor on the head, body, tail and limbs. In the pampatheres and dasypodids the body armor is made flexible by the presence of transverse bands of specially modified overlapping osteoderms. This feature is absent in the glyptodonts, whose carapace constitutes a solidly sutured dome (Gillette and Ray, 1981). In pampatheres and dasypodids the osteoderms of the bucklers are joined by sutures, but even in the giant forms, as in the living *Priodontes*, there was probably a fair amount of flexibility.

As with living dasypodids, the individual dermal plates of pampatheres consist of an underlying osteoderm and a superficial keratinous scute. Unfortunately, in the paleontological literature, the osteoderms are usually referred to as scutes (*placas* in Spanish). To avoid confusion with the keratinous true scute, I propose to use the term osteoderm for the bony part. Only the latter is preserved in the fossil record.

Knowledge of the precise arrangement of osteoderms is limited by the paucity of well-preserved specimens. No single specimen is known in which the osteoderms are *in situ*, even on one side. However, some specimens have been found with various areas intact, or with most of the osteoderms present but disarranged. Also, study of skeletal as well as osteodermal characters indicates that the pampatheres are exceptionally conservative. One example is the *Holmesina* lineage, well known from the late Pliocene to late Pleistocene of Florida. Except for a gradual increase in size, there is no difference in the morphology and ornamentation of the osteoderms.

Similarly the lineage represented by *Vassallia* and *Pampatherium* from Argentina, Uruguay and Bolivia, retains common morphological features in the osteoderms from the later Miocene (Huayquerian) to latest Pleistocene (Ensenadense). Fortunately, the two most nearly complete carapaces known represent the two lineages described above (i.e. *Holmesina* and *Vassallia*). These are, with only the minor differences described below, almost identical in general structure, so that by extrapolation one can describe the complete armor of a generalized pampathere with reasonable confidence.

Although the arrangement and relative size of the osteoderms are probably very similar, the details of surface ornamentation, presumably reflecting the ornamentations of the overlying keratinous scutes, differ considerably between the two taxa (Edmund 1984). The close conformation between osteoderm and scute surface ornamentation was determined for five genera of living dasypodids, *Dasypus*, *Chaetophractus*, *Tolyteutes*, *Zaedyus*, and *Priodontes*. In each case the keratinous surface closely resembles the topography of the underlying osteoderms. Osteodermal ornamentation of pampatheres has been used taxonomically by South American workers in the absence of other skeletal material.

## TYPES AND NUMBERS OF OSTEODERMS

The armor consists of specialized osteoderms covering the head, body, tail and limbs. The total number of osteoderms is unknown, but in the most nearly complete individual, *Holmesina septentrionalis* (RHB 3151), from the late Pleistocene of Florida, they number in excess of 800. The osteoderms are distributed as follows:

Carapace	631
Cephalic	7
Caudal	131
Legs	84
TOTAL	853

In this individual it is obvious that some osteoderms are missing from both the carapace and the cephalic casque. The carapace alone probably consisted of at least 700 components, which explains the relatively high number of osteoderms. In the same individual, we can estimate the girth of the animal. Twenty-eight osteoderms can be arranged in a single transverse row, with a total width of 112 cm. If this represents three quarters of the total girth (the belly being unarmored), the girth measured about 150 cm.

No complete cephalic casque is known. James' (1957) restoration of *Holmesina* shows an extensive casque with about 90 osteoderms, although only three were found in place on the skull. Specimen TAMU 3000 (cf. *Holmesina* sp.) has four osteoderms on the squamoso-parietal areas, and five on the maxilla, suggesting a total of approximately 50 in the complete casque.

The carapace consists of three sections: an anterior (or pectoral) and a posterior (or pelvic) buckler, separated by a flexible mid-section consisting of three transverse rows of imbricating osteoderms (Fig. 1). These imbricating bands slide over each other, as well as under the modified posterior osteoderms of the pectoral buckler and over the modified anterior osteoderms of the pelvic buckler (Fig. 11). The number of imbricating bands (three) is known in only two specimens. One, figures by James (1957), is referred to *Holmesina septentrionalis*. The other, IGM 56-501, although labelled *H. septentrionalis*, is referred by the author to the South American genus *Vassallia* (Castellanos, 1927). This specimen, a mounted carapace and tail, is imperfectly restored, but the presence of three imbricating bands is unquestionable.

The anterior buckler consists of polygonal osteoderms. In some species of pampatheres (see below) the osteoderms of the posterior buckler are also polygonal, whereas in others they are mostly rectangular. The tail is well armored but flexible. Imbricating rings of osteoderms cover the proximal portion, while the remainder is sheathed in osteoderms of random size and arrangement. The osteoderms set into the limbs are small and of random sizes, presumably correlated with the flexibility and vulnerability of the area covered.

## STRUCTURE OF OSTEODERMS

Although osteoderms vary in size and form in different parts of the body, and to a lesser extent between species, they are generally recognized by a common morphology. The following description is of a typical osteoderm from one of the bucklers of *Holmesina* sp. (Fig. 2). It is hexagonal, but longer than wide. The underside is usually slightly concave, relatively smooth, but with a characteristic fibrous appearance which usually is most obvious as a color pattern, although it can sometimes be seen as surficial ornamentation in sharply raking light. Holmes and Simpson (1931) described this as a "fabric-like structure of the corium fibers." The outer surface is perforated by numerous foramina, several of which range from 1 to 2 mm in diameter. These presumably were vascular, for the nourishment of the osteoderm and its overlying scute, and meet the surface at random angles.

The outer surface of a *Holmesina* osteoderm is characteristically ornamented. The outer margin is depressed approximately 1 mm below the remaining surface, forming a band approximately 2 mm wide, herein termed the marginal band. The anterior part of the marginal band is generally wider (about 6 mm in this example) and bears a number of crater-like pits, presumably the site of hair follicles during life.

The remainder of the surface of the osteoderm consists of a sharply defined submarginal band or ridge, a central raised keel or ridge, and a depressed area, or sulcus, separating the two. In the example (Fig. 2), the submarginal band forms an almost complete ring, subparallel to the sides of the osteoderm. In other examples, it may be less sharply defined or even absent. The central keel or ridge in *Holmesina* is long and narrow, being most elevated posteriorly, where it almost meets the marginal band. The sulcus, separating the central area and the submarginal bands, is more or less horse-shoe shaped,

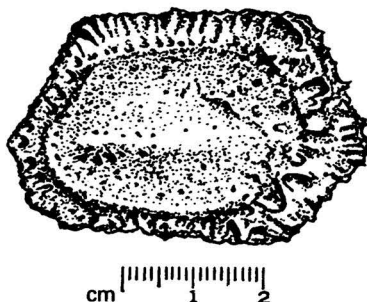


Fig. 2. Typical buckler osteoderm of *Holmesina* sp., FSM/UF 15136, Coleman IIIB, Florida. Dorsal view.

and fairly broad and shallow. In some genera it is narrower and deeper and may divide to form two parallel sulci separated by the central keel or ridge, whereas in others, the sulcus is very shallow or absent.

The area encompassed by the submarginal band, presumably covered by the keratinous scute in life, is coarsely punctate. The marginal area is coarsely rugose, and the lateral edges bear the marks of complex fine sutures. In other genera of pampatheres, notably the lineage represented by *Vassallia* and *Pampatherium*, the ornamentation is far less elaborate. The marginal area is usually reduced, and most of the surface of the osteoderm is flat or slightly raised, sometimes with no trace of a central figure. The distinction between the well-ornamented genera and the feebly-ornamented genera applies equally to the buckler and to the imbricating osteoderms.

A thin section was prepared from a buckler osteoderm of *H. septentrionalis* from Venice, Florida (ROM 4682). Of the average thickness of 9.7 mm, more than 5 mm consists of coarse, thin-walled cancellous bone. The ventral surface is of dense compact bone varying from 1.3 to 1.9 mm in thickness, relatively flat internally and externally. In contrast, the dorsal or exterior surface consists of somewhat less compact bone, heavily convoluted on both dorsal and ventral surfaces. It averages somewhat more than 2 mm in thickness, but is penetrated by sinuses or vessels from the cancellous bone. Clayton Ray (pers. com. 1983) pointed out that the marrow cavity and wall thickness of osteoderms in *Dasybus* vary drastically between winter and summer, reflecting increased hematopoiesis during the warmer season. Presumably the same variation occurred in pampatheres.

## DETAILED DESCRIPTION OF EACH AREA

### Cephalic Casque

In common with other loricates, all pampatheres bore a cap of specialized osteoderms on the upper surface of the skull. A few cephalic osteoderms were preserved in their natural position on the skulls of specimens of *Holmesina* from Texas (TAMU 3000 and HMNS 173) or associated with other specimens, such as *P. typum* (MLP 81-x-30-1). Cephalic osteoderms are morphologically similar to the typical buckler osteoderm described above, but with significant differences. The outline is generally more angular, often with at least one side meeting the next at less than 90°. They are smaller than the buckler osteoderms and only two-thirds as thick. Most characteristic is the ventral surface, which is generally concave and marked with a network of broad (up to 2 mm) but shallow vascular canals (Fig. 3). On the dorsal surface, the marginal band is relatively wide and rugose, and obvious follicle pits are absent. The relief of the sculptural ornamentation is more exaggerated than for a buckler osteoderm of the same species.

### Carapace

The exact shape and outline of the carapace is unknown. The mounted carapace and tail of IGM 56-501, tentatively referred to the genus *Vassallia*, is unreliable for this purpose. It does indicate, however, that the armor covered the top and sides of the animal, and that the bucklers were well rounded over the pectoral and pelvic areas. The emargination in the neck region was much larger than that for the tail. More information on the form of the carapace must await discovery of better specimens, but much can be inferred from isolated or partly associated material.

Figure 1 represents the restoration of a typical pampathere based on the detailed study of osteoderms. It is similar to that of James (1957), representing *Holmesina*, and differs mainly in details of the margins and number of osteoderms.

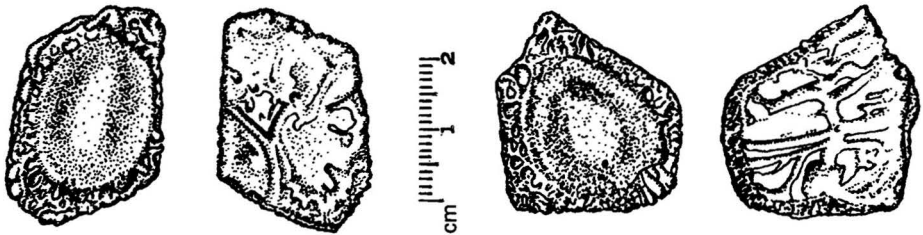


Fig. 3. Two cephalic osteoderms of *Pampatherium typum*, MLP 81-x-30-1. Dorsal and ventral views.

Ameghino (1889) in describing *Chlamydotherium* (= *Pampatherium*) noted that the osteoderms of the posterior buckler are rectangular, whereas those of the anterior are polygonal. Scillato-Yane (pers. com. 1981) confirmed this observation, also on the basis of Argentinian material. The same condition is seen in some living dasypodids (e.g. *Chaetophractus villosus*), but not all (e.g. *Dasyurus novemcinctus* or *D. hybridus*). The following are the only pampathere specimens with significant sections of articulated armor preserved:

*Holmesina septentrionalis* HMNS 173, Texas, imbricating bands and much of the pelvic buckler

*H. septentrionalis* UF/FSM 9336, Florida, patch from anterior midline, pectoral buckler

cf. *Vassallia* sp. IGM 56-501, Mexico, mounted carapace and tail with considerable restoration.

The posterior buckler of specimen HMNS 173 is made up of polygonal plates (Fig. 4), whereas that of IGM 56-501 is made of essentially rectangular plates. Unfortunately, most collections consist of batches of isolated osteoderms, presumably including elements from both anterior and posterior bucklers. All evidence indicates that anterior buckler osteoderms are polygonal.

If the shapes of osteoderms representing a single specimen or species are classified as either polygonal or rectangular (Table 1), it is possible to decide whether or not the posterior buckler was constituted of rectangular plates. The relative numbers of osteoderms in the two bucklers is not known, but a fairly high percentage of rectangular osteoderms (say at least 30%) would certainly indicate a posterior buckler made up of rectangulars. As Table 1 shows, only 11% of the 235 *Holmesina* osteoderms studied are rectangular. This agrees well with the condition seen in the partial *Holmesina* carapace HMNS 173 (Fig. 4). In contrast, *Pampatherium* by definition (Ameghino, 1889) has a posterior buckler composed of rectangular osteoderms. It is interesting to speculate on the reason for Ameghino's arriving at this conclusion, since he had no articulated material. However, the posterior buckler of the closely related genus *Vassallia* is now known from the mounted carapace IGM 56-501 from Mexico, which clearly shows that the anterior buckler is composed of polygonal, and the posterior of rectangular osteoderms. Analysis of the data in Table 1 confirms that there is a high proportion of rectangular plates in mixed lots of *Pampatherium* and *Vassallia*. Indeed it suggests that the posterior buckler had a higher number of osteoderms than the anterior.

TABLE 1

<i>Holmesina</i> sp.	N	% rectangular osteoderms	% polygonal osteoderms
TAMU 3000	15	20	80
ROM 24114	13	8	92
HMNS 173	33	0	100
RHB 3151	44	9	91
UF 9336	30	0	100
ROM 23919 (Ecuador)	50	18	82
ROM 2022 (Peru)	50	18	82
TOTAL	N 235	Av. %11	Av. %79
<i>Pampatherium</i> & <i>Vassallia</i>			
cf. <i>Vassallia</i> sp., USNM Valsequillo, Puebla, Mex.	22	73	27
<i>Vassallia minutum</i> , MLP 69-XII-26-17	13	69	31
<i>P. typum</i> , MACN, mixed lot	29	69	31
<i>P. typum</i> , MLP 69-IX-5-1	29	41	59
TOTAL	N 93	Av. %63	Av. %37



When recording the shape of osteoderms, it is necessary to identify clearly those which are truly rectangular, i.e. those longer than wide and with four major faces set approximately at right angles to each other. Such osteoderms must be distinguished from others which have a generally rectangular aspect, but which, in fact, are actually "squarish," or are irregular pentagons or hexagons. McGowan (1983 pers. com.) suggested using a circumference/area ratio to segregate rectangular osteoderms from all other shapes, since rectangles have the greatest relative circumference. This test was tried on a small sample and agreed well with visual classification of shapes.

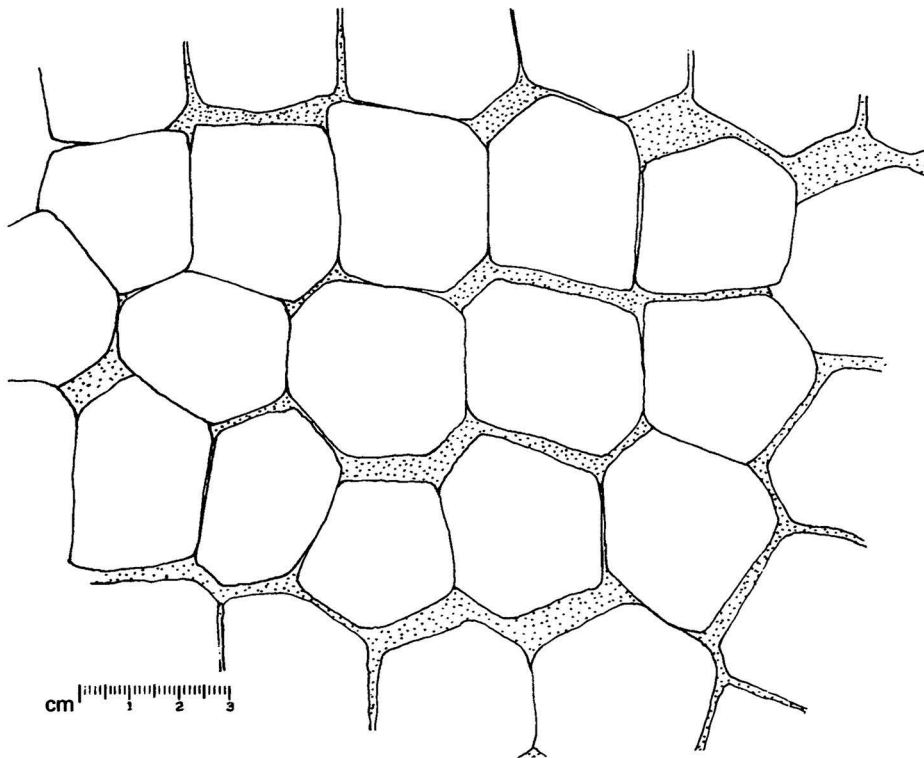


Fig. 4. Diagram of outlines of osteoderms of part of the posterior buckler of *Holmesina* sp., HMNS 173.

Records were kept of the numbers of contact edges on the osteoderms of numerous suites of specimens. There was no significant difference between the number of contacts in the truly rectangular osteoderms and those in the polygons.

Specialized osteoderms can be described for certain areas of the bucklers. Areas of articulated osteoderms at the emargination for the neck are known

for *P. typum* (MLP 81-x-30-1) and for *H. septentrionalis* (several Floridian specimens). The osteoderms in this area are considerably thicker than elsewhere on the carapace, being at their maximum thickness near the rear end of the marginal osteoderm at or near the midline. From this point, they gradually decrease caudad and laterad to the thickness typical of the remainder of the carapace. The size and proportions of the nuchal osteoderms are variable, but all have a peculiar morphology. In outline they are squarish or rectangular, some being wider than long. The dorsal surface bears an ornamented area similar to that of the other buckler osteoderms. The anterior margin then drops fairly sharply to form a smooth-edged lip, usually slightly tilted upward (Fig. 5). The relative sizes of the ornamented area and the depressed marginal lip vary greatly, but the latter makes up about a quarter of the total length of the osteoderm. The rolled-up lip is about 5 mm thick. Between the



Fig. 5. Marginal osteoderm from the nuchal area of the buckler, *Holmesina* sp., FSM/UF 15136, Coleman IIIB, Florida. Dorsal, ventral, and lateral views.

lip and the ornamented area, the surface is rugose, with a transverse row of several follicular pits. Simpson (1931) figured an associated row of seven osteoderms from the "anterior notch of the carapace," but did not describe it in the text. It is not known if other osteoderms were set in the skin of the back of the neck, as is seen in some living dasypodids, nor do we have information on the buckler margin in the caudal region. Simpson (1931) described the "lateral margin of the carapace, both of the bucklers and movable bands" as being "formed by a series of pendant ovoid projections." Marginal osteoderms on the bucklers tend to be only feebly ornamented, are often of irregular shape, and probably projected to some extent beyond the general outline of the body. The keratin-bearing portion carries over the rather wedge-shaped margin to occupy part of the lower (or inner) surface (Fig. 6). The same sort of finished edge is seen in living dasypodids.

The other specialized marginal osteoderms of the bucklers are those bordering the movable bands. The posterior row of osteoderms on the anterior (pectoral) buckler are always rectangular and bear sutural connections with their neighbors, except on the posterior margin, which is thin and smooth.

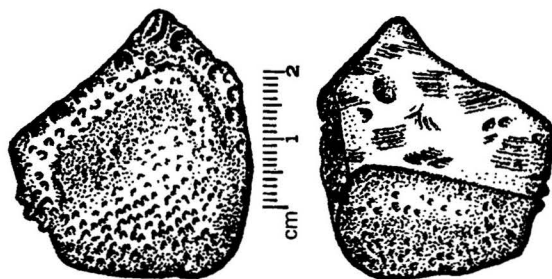


Fig. 6. Osteoderm from the margin of the buckler, cf. *Holmesina occidentalis*, ROM 23919. Upper Pleistocene, Ecuador.

The surficial sculpture is the same as in the other buckler osteoderms but each plate thins gradually from front to rear, where it overlaps a plate from the anterior imbricating band (Fig. 7).

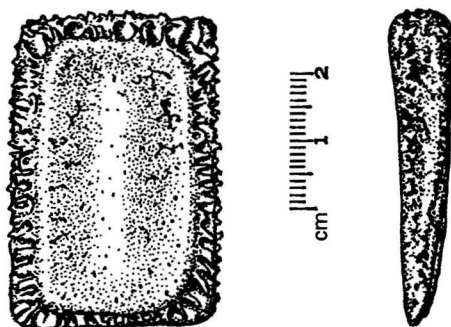


Fig. 7. Osteoderm from the posterior row of the pectoral buckler, *Holmesina* sp., FSM/UF 24935. Dorsal and lateral views.

The osteoderms of the anterior row of the posterior (pelvic) buckler are almost identical with those of the imbricating bands, except that they are generally shorter than the latter, and, of course, are well sutured to the adjacent osteoderms of the buckler. The maximum number of these plates in any single individual is 28, found in *H. septentrionalis*, RHB 3151.

#### Imbricating osteoderms

As mentioned above, the movable bands are adequately preserved in only two specimens. Because of the conservatism of other features in the Pampatheriidae, and because the two specimens represent clearly different lineages, I conclude that all pampatheres possessed only three imbricating bands (Fig.

8). The movable area actually consists of the three transverse bands plus the last row of osteoderms of the pectoral buckler and the first row of the pelvic buckler. There are thus four transverse rings at which flexion occurs. The posterior margin of one osteoderm slides over the specialized, raised, anterior end of the succeeding osteoderms. In life this area was covered, as in living dasypodids, by tough, flexible skin.

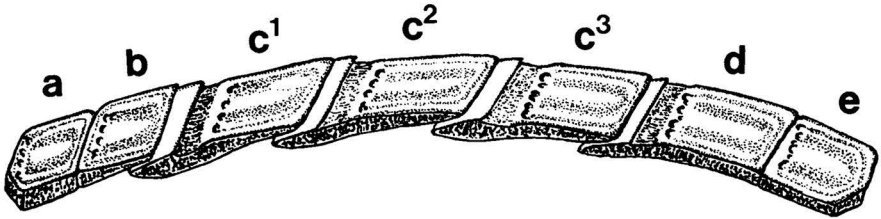


Fig. 8. Diagram showing the relationship of osteoderms in the region of the imbricating bands of a typical pampathere. a, fixed osteoderm of the pectoral buckler; b, posterior osteoderm of the pectoral buckler; c<sup>1</sup> - c<sup>3</sup>, typical imbricating osteoderms; d, anterior osteoderm, pelvic buckler; e, fixed osteoderm, pelvic buckler.

A typical osteoderm from one of the movable bands has a length-width ratio of about 2.5 to 1. The dorsal surface can be divided into three areas: the exposed or ornamented part, a usually depressed rugose area, and a sharply defined raised table at the anterior end (Fig. 9). Ventrally, the osteoderm is generally concave, frequently with the anteroposterior concavity divided into

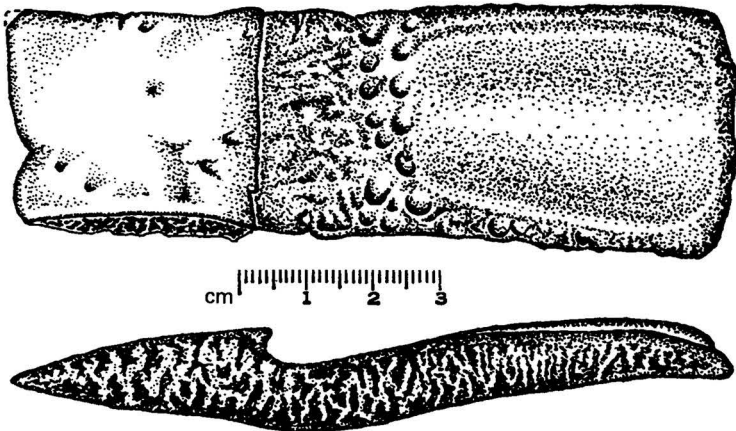


Fig. 9. Imbricating osteoderm of *Holmesina* sp., FSM/UF 15136, Coleman III B, Florida. Dorsal and lateral views.

separate sections beneath the ornamented area and the raised table. The ventral surface has the same fibrous appearance and foramina seen in the buckler osteoderms.

The ornamented area usually occupies more than half of the length of the osteoderm, and bears a surficial sculpturing which appears as a longitudinally stretched version of the ornamentation of a corresponding buckler osteoderm. The posterior margin usually tapers to a fairly thin edge. In very well preserved specimens this edge bears several (up to 10) foramina less than 1 mm in diameter. These may have borne hairs, as in dasypodids, but the foramina in pampatheres are proportionately much smaller than those in the true armadillos.

The ornamented area may be divided from the rugose band by a continuation of the submarginal band, but this is not a constant feature. Usually the rugose area is depressed, with a transverse row of several broad, shallow pits, presumably follicular. The anteroposterior length of the rugose area is variable, even among osteoderms from the same individual, but it is usually wider (transversely) than long. The articular surface, or table, is sharply raised several millimeters above the rugose area, and its surface is usually "flattish" transversely and convex anteroposteriorly. It makes up the anterior quarter to third of the length of the osteoderm. The surface texture resembles that of the ventral surface in being rather fibrous, although in some specimens it appears to be smoother and denser. This may be a function of preservation rather than age.

The marginal osteoderms in the imbricating area are peculiar, presumably correlated with the unusual amount of overlap and movement which would take place in this area during flexion of the carapace. This is well shown in RHB 3151, a specimen of *H. septentrionalis*, in which several marginal imbricating osteoderms from the left side are preserved. These are broad osteoderms with wide articulating areas. They are also accompanied by fused or loosely sutured auxiliary osteoderms (Fig. 10). The lateral osteoderms have

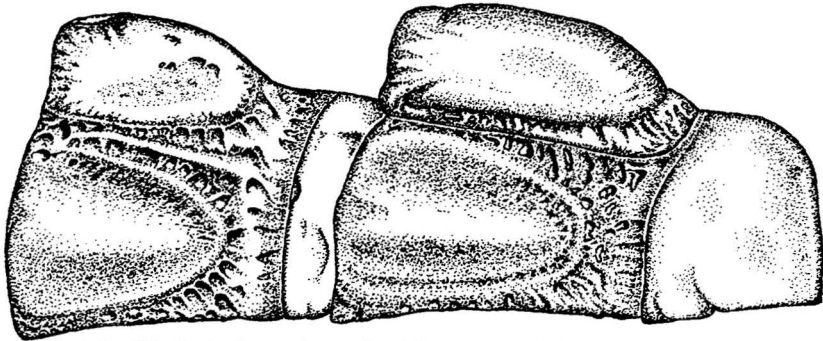


Fig. 10. Osteoderms from the left margin of the imbricating area of *Holmesina septentrionalis*, RHB 3151. Florida.

a finished surface which continues over onto part of the inner (ventral) side. In life this would have borne a sharp horny flange similar to that seen in some living dasypodids (Fig. 11). Such a series of sharp osteoderms would provide excellent protection against carnivores.

Another curious feature of some of the osteoderms in this area is the thick, sutural rear margin, reminiscent of the condition of the anterior row of osteoderms in the posterior buckler. This suggests that there was an additional segment, probably movable, sutured to the posterior margin. Small semilunar, cuneiform osteoderms which would fit in this area have been observed in some lots of isolated osteoderms.

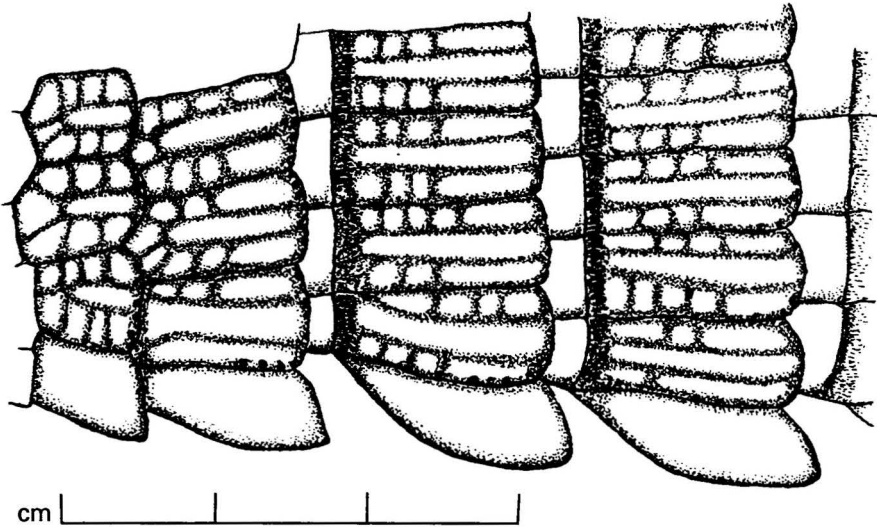


Fig. 11. Osteoderms of the left margin of the living dasypodid *Chaeophractus villosus*, ROM R1114.

#### Caudal armor

Caudal osteoderms are preserved *in situ* in only one known specimen, *P. typum* IFG 705, although good suites of these osteoderms are preserved in other specimens, particularly *H. septentrionalis* UF/FSM 9336 and RHB 3151. The Mexican mounted armor (cf. *Vassallia* sp.) IGM 56-501, includes a tail, but the arrangement of osteoderms is artificial.

Specimen IFG 705 is badly weathered, but represents most of an isolated tail with the osteoderms essentially in place. The two proximal caudal vertebrae are associated with only a few typical caudal osteoderms. The next three vertebrae bear reasonably regular rings of subrectangular osteoderms, fifteen

in the first two rings, twelve in the third. Presumably there were at least two further rings on the more proximal vertebrae, making a total of five rings. The part of the tail distal to the rings is covered with osteoderms which decrease in size and regularity of shape, apparently forming a fairly solidly sutured pavement with larger osteoderms above, smaller ones below. The cross-sectional shape of the tail is generally round, possibly flattened somewhat ventrally. Although the terminations of the neural and haemal spines and transverse processes of the caudal vertebrae are enlarged, no corresponding modification was seen on any caudal osteoderms.

The anterior caudal osteoderms imbricate to some extent, but the provision for movement is not as well developed as in the movable bands of the carapace. The shapes of the osteoderms are quite variable, depending on their position in the tail armor. At least sixty well-preserved caudal osteoderms are known for *H. septentrionalis*, UF/FSM 9336 (Fig. 12). Their shape and pattern are generally distinctive, so that they are unlikely to be confused with other types of osteoderms. Most are concave transversely on the ventral surface, some conspicuously so. The anteroposterior contour is sinuous, with the anterior lip inflected upward (outward) and the posterior half (more or less), saucer-shaped.

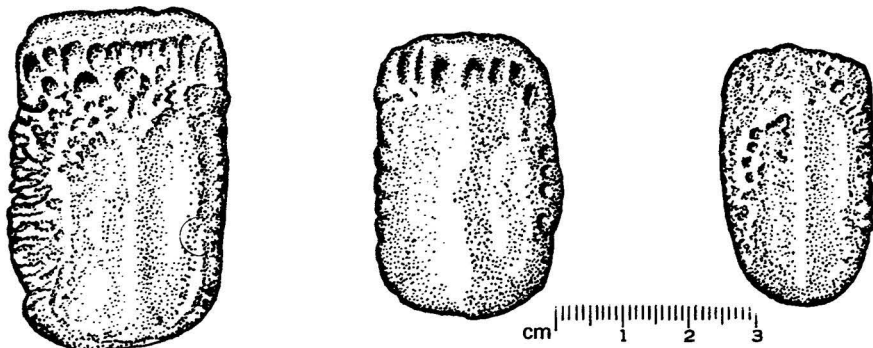


Fig. 12. Osteoderms from the tail of *Holmesina septentrionalis*, FSM/UF 9336.

In dorsal view, the outline is generally rectangular, the anterior margin often broad and straight, and the posterior margin often narrower and more rounded. The anterior margin is thin, often with a relatively smooth, slightly raised lip. Posterior to this is a broad, heavily rugose area which may extend far down the sides of the osteoderm. The posterior part consists mainly of an ornamented area extending in all cases to the rear margin. Presumably this area was covered in life by the keratinous scute.

The single known example of pampathere caudal armor (IFG 705 described above) included five free rings, each containing a single row of osteo-

derms and each associated with a single caudal vertebra. The specimen is inadequate to indicate whether or not the proximal row formed a complete ring. Gillette and Ray (1981) described specimens of North American glyptodonts with up to 12 free rings anterior to the caudal tube. Each ring in these examples, corresponding to one vertebra, consists of two rows of osteoderms. Most, but not all, fossil and living dasypodids also have two rows of osteoderms per caudal ring.

#### Osteoderms of the limbs

During the collecting of UF/FSM 9336, *H. septentrionalis*, numerous small osteoderms were found in close association with the legs and feet. Some are fairly large and rather similar to some caudal osteoderms, especially those labelled "upper hind leg." It is possible that some of these may, in fact, be displaced caudals. Others, labelled "leg" and "front foot," tend to be small, with rounded outlines. Most have a clearly defined end, similar to the anterior end seen in caudal or buckler osteoderms, which can only be regarded as proximal. This end often has a slightly upraised lip, behind which is a transverse, deeply pitted area or band. The remainder of the osteoderm is finely punctate, usually with a median keel in this species. Many of the smallest ones, from the foot, are almond-shaped, with at most only vestiges of any proximal sculpturing (Fig. 13). No other specimens are known in which there is a definite association of osteoderms with limb or podial elements, although isolated elements matching the description above have been found in numerous collections of isolated osteoderms.

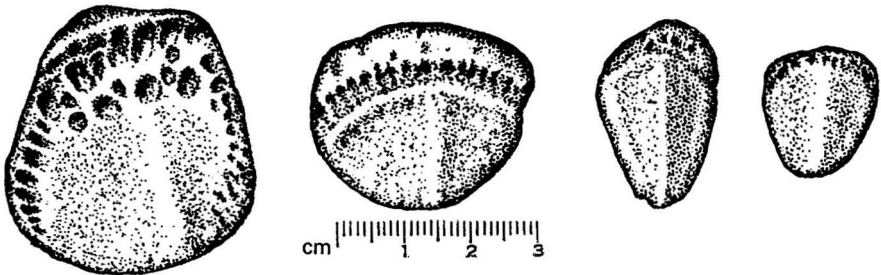


Fig. 13. Osteoderms from the legs and feet of *Holmesina septentrionalis*, FSM/UF 9336.



## CONCLUSIONS

Osteoderms typical of various areas of the body can now be identified with considerable confidence. Despite paucity of articulated or associated material, good suites typical of several taxa are known. Although all osteoderms have an area covered by a keratinous scute with a peculiar ornamentation, only those of the non-marginal areas of the carapace should be used for taxonomic work. At least two major lineages can be detected from the mass of isolated osteoderms in various collections, essentially one with almost featureless osteoderms, and the other with a well-raised submarginal band and a relatively high keeled central figure. In the latter, as typified by the genus *Holmesina*, almost all of the buckler osteoderms are polygonal. In the other lineage, represented by the genera *Pampatherium* and *Vassallia*, the osteoderms of the pelvic buckler are mainly rectangular. A revised taxonomy of pampatheres, based on osteoderms, is in preparation.

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