Article VII.—PLEISTOCENE EXPLORATION AND FOSSIL EDENTATES IN FLORIDA

By Walter W. Holmes and George Gaylord Simpson

TEXT FIGURES 1 TO 21

The purposes of this paper are (1) to record the history of explorations of the West Coast Pleistocene of Florida carried on by Holmes, 1924–1930; (2) to summarize present knowledge of the distribution of the Xenarthra in the United States, and (3) to describe and illustrate xenarthran dermal bones, scutes, and some other remains found in Florida.

PLEISTOCENE EXPLORATION IN FLORIDA

The following is a summary of the Holmes and American Museum work in the Pleistocene of Florida to date, exclusive of the continued examination of prospects and isolated localities by Holmes. The work of each year has taken place chiefly in the latter part of the winter or early spring:

1924—Discovery and reconnaissance of Seminole Field, Station A.

1925—Preliminary work at Station A.

1926—Intensive work at Station A.

1927—Continued intensive work at Station A.

1928—Saber-tooth Cave.

1929—Seminole Field, Station B.

Bradenton Field.

Reconnaissance of whole Florida Pleistocene.

1930—Reconnaissance of part of Everglades and southeast coast.

Renewed work in Bradenton Field.

Extensive investigation of Sarasota County.

With the exception of the general reconnaissance in 1929, all of this work was under the direction of Holmes, and since 1928 has been officially included in the American Museum program. Simpson visited the state in 1929 and 1930. Other workers are mentioned below.

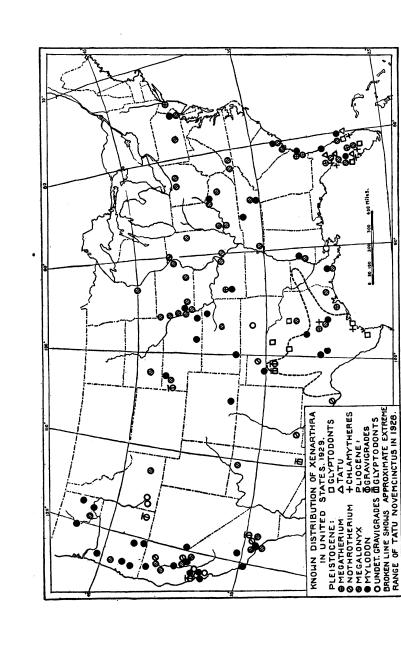


Fig. 1. United States. Outline map with distribution of recent and fossil edentates. In a few cases, as in Florida, individual occurrences are too close together for separate symbols.

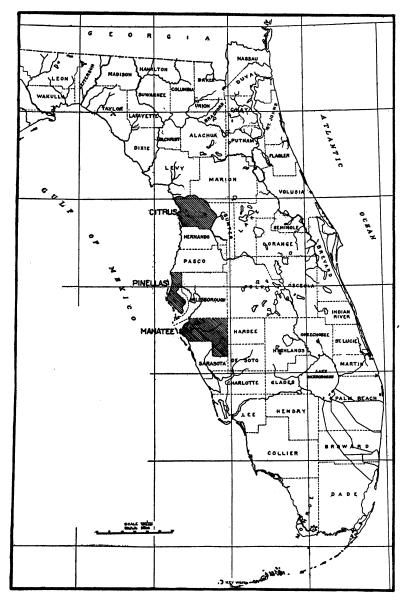


Fig. 2. Florida. Index map showing location of three counties in which most intensive work has been done by Holmes and American Museum parties.

SEMINOLE FIELD

Seminole is an unincorporated settlement located on the west coast of Pinellas County, Florida, about half way between Clearwater and St. Petersburg (Fig. 3). It is the approximate center of five points where Pleistocene fossils have been found by the senior author. This section of the west coast was long inhabited by Seminole Indians who lived there until driven out in the Seminole War, so that the name chosen for the field seems doubly appropriate. Fossils are derived chiefly from two localities in this field, designated Station A and Station B. (Fig 3.)

Station A is about one mile east of the settlement, across the northern end of Boca Ciega Bay, now known as Long Bayou. It is bisected at Joe's Creek by the highway from Seminole Bridge to Pinellas Park. Joe's Creek formerly drained the low-lying watershed to the east and south. About fifteen years ago its general course was followed in digging one of the main canals of a drainage system. This canal is now tidal and in dry seasons drains the windings of the old stream where they extend beyond the straight canal.

In March, 1924, Dr. W. D. Matthew visited St. Petersburg, and Holmes showed him a curious object found on a canal bank. He identified this as a *Chlamytherium* scute, and together we located the field on March 27. Dr. Matthew had to leave that night, but enough had been found to warrant his urgent request for further search. The Seminole Field and Saber-tooth Cave collections in The American Museum of Natural History are the result of his help and of the interest he aroused.

The balance of the first season was spent in surface exploration of miles of drainage canal banks. A few fossils were found at other localities, but not enough to warrant further search save in the Seminole Field.

In October, 1924, Mr. Walter Granger visited the field and located the bone-bearing stratum about three feet below the surface. The work in 1925 was confined entirely to recovering fossils by hydraulic sluicing from the sand dredged from the canal in its construction. It was hoped that this would lead to the most favorable places for working the fossil stratum, but the richer areas were not actually found in this way.

In January, 1926, Mr. H. R. Megathlin took charge of the work, securing much material in place, but more from the old bed of Joe's Creek in the bends outside the canal. Mr. Megathlin continued work until May, 1926, and his efforts contributed greatly to the value of the collection, notably in the discovery of three of the lots of glyptodont scutes to be described below.

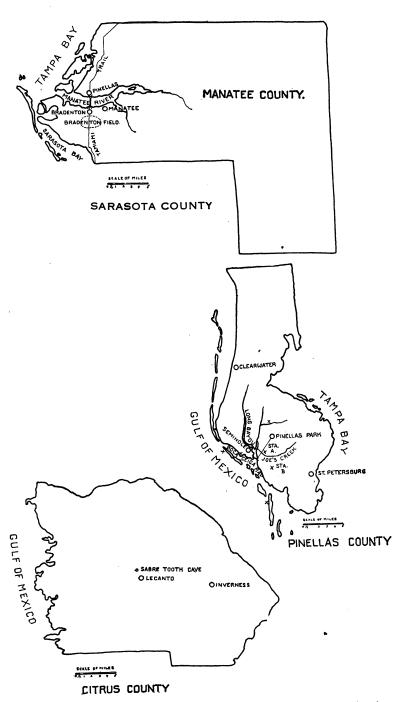


Fig. 3. Maps of Manatee, Pinellas, and Citrus Counties, Florida, showing localities mentioned in the text.

In 1927, Charlie Wilson, a colored man who had been trained in the field for two years, carried on the excavating. The principal object of this final work was to locate the balance of the glyptodont scutes of the third find of the previous year.

The resulting Seminole Field Collection from Station A, one of the richest in variety ever obtained from a single Pleistocene locality, was presented to The American Museum of Natural History, where preliminary identifications were made by W. D. Matthew and H. R. Megathlin. Definitive study of the mammalian fauna was assigned to one of the present authors, who has already published a discussion of it.

In 1928 attention was turned to Saber-tooth Cave, discussed below, but in 1929 work was done at a second locality in the Seminole Field. This locality, Station B, is about two miles south of Station A. The deposit so far examined here is not so extensive as at Station A, being confined to a single area along a canal bank, but a very large amount of excavating was done to cover this area thoroughly. The fauna is more limited than at Station A, the following mammals being so far recognized:

Boreostracon floridanus Holmesina septentrionalis Mylodon sp. Arctodus floridanus Equus complicatus Bison latifrons Parelephas sp.

Edentates occur in the Seminole Field in greater number and variety than at any other locality in Florida, although the material is mostly dissociated. Most of the scutes described below are from this field. The following edentates have been identified:

Tatu bellus Holmesina septentrionalis Boreostracon floridanus Megalonyx cf. wheatleyi Mylodon Iharlani

SABER-TOOTH CAVE

The cave to which this name has been applied is situated about one mile northwest of Lecanto on the property of Mr. D. J. Allen. The town of Lecanto is about ten miles west of Inverness. Although the center of the town is only about thirty-five feet above the level of the

^{&#}x27;Simpson, G. G. 1928. Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. Bull. Amer. Mus. Nat. Hist., LVI, pp. 561-599.

Gulf of Mexico, which lies ten miles to the west, it is surrounded by low rolling hills which give an impression of greater altitude and somewhat suggest southern New England.

The greater part of Citrus and adjoining counties is underlain by the Ocala Limestone of Eocene age, which outcrops in the hills save where these are formed of wind-blown sand. Solution of this limestone has formed a great many sink holes, some of which are without apparent outlet or with fissures too small for entrance by man, while others may be explored for a short distance. A few terminate in underground streams or pools in which blind crawfish live and blind fish are reported to exist, although not seen by the authors.

Saber-tooth Cave is a sink hole, its entrance screened by a clump of trees and brush. At the surface is a funnel-like depression about seventy-five feet in diameter, at the bottom of which are two round perpendicular shafts each 12 feet in diameter and with a wall of about seven feet between them. They extend for about seventeen feet through the limestone and then open into a vaulted chamber.

A few years ago Mr. Allen built a pole-ladder and rescued a pig which had fallen into the cave. Shortly after this Murray Davis with some boy companions entered the cave by means of this ladder and found a tooth which proved to be an upper canine of a Saber-tooth tiger. Hearing of this discovery, Mr. Herman Gunter, Florida State Geologist, visited Davis, who generously gave the tooth to the State Geological Survey.

Holmes' attention was called to this by Mr. Gunter, who pointed out that the cave had not been searched for other fossils. Mr. Gunter promised his coöperation in arranging for scientific exploration of the cave by an American Museum party under the sponsorship of Holmes, and obtained permission for this work from the owner through Mr. John E. King of Lecanto, who also gave other valuable assistance. Mr. D. J. Allen not only made the exploration possible, but gave freely of his time and valuable advice. Mr. Strauss L. Lloyd of Inverness, and Mr. Davis, father of Murray, of Lecanto, also contributed to the success of the expedition, and many others in Lecanto helped, with genuine hospitality and sincere interest.

On February 13, 1928, Carl Sorensen of the American Museum staff began work in the cave, assisted by Charlie Wilson and directed by Holmes. Although not extremely rich in individual specimens (except for remains of about forty cotton rats), the fauna proved to be of great interest and to include many species, four of them previously unknown. It has been described elsewhere.¹

In the Saber-tooth Cave the following edentates occurred:

Tatu bellus Holmesina septentrionalis Megalonyx cf. wheatleyi

Holmesina is represented by well preserved scutes, limb and foot bones. Some of the edentate bones from this locality have been mentioned and figured in the two papers cited.

Bradenton Field

The newly discovered Bradenton Field consists so far as now known of a series of occurrences in Manatee County near Bradenton. The fossils occur in the banks of a drainage ditch which crosses the Tamiami Trail about one mile south of the business section of Bradenton. The bone stratum, like that of the Seminole Field, is a layer of brown sand immediately above the marine Anastasia Formation.

The locality was discovered by Mr. J. E. Moore of Sarasota. It was examined soon after discovery by both of the authors of this paper, and with Mr. Moore's generous coöperation and the permission of the County Commissioners it was worked early in 1929 by Carl Sorensen under the direction of Holmes. This first work was done about 100 yards east of the Tamiami Trail. The resulting collection was remarkable rather for the preservation of individual specimens than for its variety, and included the following species as described elsewhere:²

Neochærus pinckneyi Odocoileus sp. Tanupolama sp.

Parelephas floridanus (Type locality)

During the latter part of 1929, Mr. Moore continued exploration along this canal, finding several other fossil occurrences in the immediate vicinity. These were again visited by both the present authors early in 1930, and an arrangement was made by Holmes for the working of the principal new locality, about a quarter of a mile east of the Tamiami Trail, under the immediate direction of Mr. Moore and for the American Museum. The resulting collection included characteristic

¹Simpson, G. G. 1928. Pleistocene mammals from a cave in Citrus County, Florida. Amer. Mus. Novitates, No. 328.

²Osborn, H. F. 1929. Amer. Mus. Novitates, No. 393, pp. 19–20. Simpson, G. G. 1930. Amer. Mus. Novitates, No. 406, pp. 5–12.

species of the Melbourne fauna and unusually perfect material of the great chlamytheriine armadillo, *Holmesina septentrionalis*, part of which has been described elsewhere.¹

DISTRIBUTION OF EDENTATES IN THE UNITED STATES

One of the most striking peculiarities of the Pleistocene fauna of Florida is the variety of edentates which it includes. Except for the exclusively western *Nothrotherium*, all of the definitely established edentate genera of the Pleistocene of the United States occur in the state, and nowhere else outside of South America is such a large representation of this peculiar Order known ever to have existed. To aid in establishing the significance of this fact, we propose first to sum up very briefly what is known of the occurrence of edentates in this country.

EARLY TERTIARY.—In the Paleocene and Lower Eocene of New Mexico, Wyoming, and Montana, occurs the group Ganodonta or Tæniodonta, aberrant animals paralleling the ground-sloths in several respects, and believed by Wortman to be closely related or ancestral to the latter. Matthew and others, however, consider the relationship to be more distant, and the tæniodonts probably have no great significance for the history of edentates. The Palæanodonta, a group of small mammals from the Lower and Middle Eocene of Wyoming, were, on the contrary, true edentates, although very primitive and not far removed from the Insectivora. They suggest that this stock entered South America from the north, although it later disappeared in North America for a time. Epoicotherium from the Oligocene of Montana is the only probable North American edentate known between the Middle Eocene and the Lower Pliocene. Known only from a skull, it yet strongly suggests the armadillos, although probably only indirectly related to the latter.

PLIOCENE.—At about the beginning of the Pliocene, land connection with South America, long broken, was reëstablished, and members of some of the peculiar groups which had meanwhile been evolving in the southern continent entered North America. In the Snake Creek beds of western Nebraska, Rattlesnake Formation of eastern Oregon, Pinole Tuffs, San Timoteo, and Eden Beds of California, and the Blanco Formation of northwestern Texas, have been found sparse remains of ground-sloths. Very imperfectly known, these appear all to be of the megalony-chid group and suggest that several distinctive genera will eventually be recognized.

Simpson, G. G. 1930. Amer. Mus. Novitates No. 442.

Glyptdonts also appear in North America for the first time in the Pliocene, the oldest now known being Glyptotherium texanum from the Middle Pliocene Blanco Beds of Texas. "Glyptotherium" arizonæ occurs in the Upper Pliocene of southeastern Arizona.

PLEISTOCENE.—The Xenarthran invasion from the south reached its climax in the Pleistocene, the presence of the following genera being definitely established.

Order XENARTHRA
Gravigrada
Megatherium
Nothrotherium
Megalonyx
Mylodon¹
Dasypoda
Tatu
Holmesina
Glyptodontia
Boreostracon
Glyptodonts indet.

No ant-eaters or tree sloths are known ever to have occurred in what is now the United States, nor is there any trace of the Old World manids or of allies of the pseudo-edentate *Orycteropus*.

Of these genera, Megatherium, Mylodon, and Tatu also occur in South America, and in the north they appear to be immigrants in the early Pleistocene or later. Nothrotherium also occurs in South America, but there is some reason to believe that it reached North America earlier than the above genera. Megalonyx evolved in North America from the Pliocene megalonychids. Holmesina is related to Chlamytherium of the South American Pleistocene but was probably derived from one of the Pliocene genera of that continent. The glyptodonts are not well known, but the group apparently did have a distinctive northern deployment even in the Pliocene, and probably several characteristic North American genera will eventually be recognized. The Florida form, Boreostracon, which probably also occurs in Texas, was distinct, but closely allied to Glyptodon proper.

The geologic distribution of these Pleistocene xenarthrans is not clearly known. Of the ground-sloths, at least *Nothrotherium*, *Megalonyx*, and *Mylodon* occurred in the Lower Pleistocene. At least *Megalonyx* and *Nothrotherium*, and possibly also other genera of ground-sloths,

^{&#}x27;Various other genera have been named. Paramylodon and Thinobadistes differ little from Mylodon. Morotherium may be synonymous with Nothrotherium or Megalonyx, or may be partly based on a mixture of the two.

survived to the end of the period or even into the Recent. The glyptodonts and armadillos are associated with an adequately known fauna only in Florida, and here are of doubtful exact age.

The geographic distribution of the known occurrences is shown on the accompanying map. Mylodon and Megalonyx occur throughout the country. Megatherium, so far as known, occurs only east of the 100th meridian and Nothrotherium only west of this line, although both approached it very closely and no doubt their ranges overlapped. The reason for this apparently exclusive distribution is not clear—these two genera are not of similar station of life; Megatherium is the largest, Nothrotherium the smallest of our Pleistocene sloths, and there seems to have been no adequate geographic or environmental barrier between their ranges. Each occurs in association with Mylodon and other widespread genera. The presence of the quite similar Megalonyx can hardly be supposed of have excluded Nothrotherium in the east, for they occur together at several western localities.

At the present time glyptodonts and armadillos are known only from east of the 100th meridian and south of the 35th parallel, but discoveries are few and future work will doubtless extend this range somewhat.

Although belonging to the same genus as our only living edentate, the Florida armadillo *Tatu bellus* is more closely allied to Pleistocene species from Brazil and Argentina and represents an earlier invasion than that of the recent form.

RECENT.—The only recent edentate in the region here considered is Tatu novemcinctus, the nine-banded armadillo. This apparently cannot be considered as a relic of the Pleistocene invasion but is a recent immigrant, possibly crossing the Rio Grande within the last few hundred years. Strecker has shown that in spite of constant human persecution, it has considerably extended its range to the north into the Panhandle region of northwestern Texas and to the east into Louisiana within the last few decades and is still advancing. It furnishes a striking contemporary example of animal migration—the more interesting in the present connection in that its eastward extension suggests the probable route of its Pleistocene ally Tatu bellus in reaching Florida. If not checked by man, it may even repeat the entire event. It will soon reach the Mississippi, but, as it has already crossed the Rio Grande, Red River, and numerous smaller streams, this will not be a permanent barrier. Unfortunately its distribution is somewhat falsified by human transportation—the obvious explanation of reports of its occurrence in Florida.

FOSSIL EDENTATES IN FLORIDA

The occurrence of edentates in Florida is here more exactly given: Megatherium sp.—Archer, Alachua County; Williston, Levy County; Zolfo, Hardee County.

—The material is fragmentary, but not distinguishable from *M. mirabile. Megatherium* has not yet been found in definite association with the widespread "Stratum No. 2" fauna, whether by accident or because of difference in age or facies.

Megalonyx sp.—Saber-tooth Cave, Citrus County; Seminole Field, Pinellas County; Melbourne, Brevard County; Vero, St. Lucie County; Dunnellon, Marion County; Peace Creek, de Soto County.

—At least two species occur, a smaller about the size of M. wheatley i and a larger about the size of M. jeffersoni. The former is present in the Saber-tooth Cave and Seminole Field, the latter at Vero, Melbourne, and Peace Creek.

Mylodon sp.—Seminole Field, Pinellas County; Melbourne, Brevard County; Vero, St. Lucie County; Sarasota, St. John County; Labelle, Lee County.

—The remains of *Mylodon* are mostly fragmentary and somewhat equivocal, but none show definite distinction from *M. harlani*. *Thinobadistes segnis* Hay, from Williston, Levy County, is a mylodont of dubious age and relationship.

Tatu bellus.—Saber-tooth Cave, Citrus County; Seminole Field, Pinellas County; Melbourne, Brevard County; Vero, St. Lucie County; Ocala, Marion County; Sarasota Field, Sarasota County.

Holmesina septentrionalis.—Saber-tooth Cave, Citrus County; Seminole Field, Pinellas County; Melbourne, Brevard County; Vero, St. Lucie County; Withlacoochee River; Hillsborough River; Sarasota Field, Sarasota County (throughout this region); Peace Creek, de Soto County; Bradenton Field, Manatee County.

Boreostracon floridanus.—Seminole Field, Pinellas County; Melbourne, Brevard County; Sarasota Field, Sarasota County; Peace Creek, de Soto County.

—These last three species are readily recognizable even from quite isolated remains, and there appears to be but a single form of each genus represented in Florida.

DERMAL OSSICLES AND SCUTES Mylodon

As is well known, *Megatherium* and *Megalonyx* (as well as *Nothrotherium*) are without dermal ossicles, but the skin of *Mylodon* is thickly studded with these. Some hundreds of ossicles of the latter animal were found in the Seminole Field. They vary in size from about 5 mm. (smaller ones possibly overlooked) to about 40 mm. in maximum diameter. Most of them are from 5 to 13 mm. in thickness. North American

Mylodon ossicles have already been so fully described, that further details will not be given here. The Florida ossicles agree closely with those from Rancho la Brea.

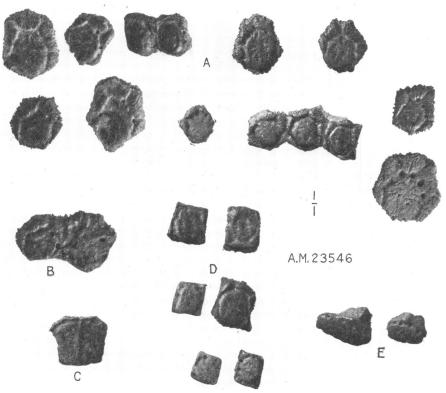


Fig. 4. Tatu bellus Simpson. Scutes from Seminole Field, Station A. A, Buckler scutes. B, Buckler scutes fused after injury. C, Problematic scute, possibly from the casque. D, Leg scutes. E, Marginal scutes. Natural size.

Tatu bellus

This species was defined and briefly contrasted with others of the genus in a recent paper (Simpson, 1928, . . . Seminole Field . . . , op. cit.). Its presence in Florida had been known for some years, being noted at Ocala by Sellards in 1916, but only at Seminole were scutes

¹Merriam, J. C. 1906. Recent discoveries of Quaternary Mammals in southern California. Science, N. S., XXIV, pp. 248-250. Sinclair, W. J. 1910. Dermal bones of *Paramylodon* from the asphaltum deposits of Ranchola Brea... Proc. Amer. Phil. Soc., XLIX, pp. 191-195. Stock, C. 1925. Cenozoic gravigrade edentates of western North America... Carn. Inst. Pub. No. 331, esp. Pl. xxi.

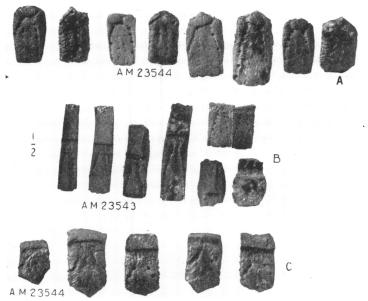


Fig. 5. Tatu bellus Simpson. Scutes from Seminole Field, Station A. A, posterior scutes of anterior buckler. B, Movable ring scutes. C, Anterior scutes of posterior buckler. One half natural size.

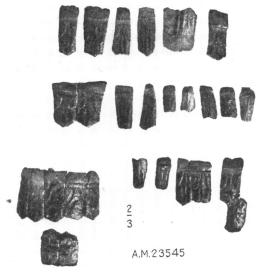


Fig. 6. Tatu bellus Simpson. Caudal scutes from Seminole Field, Station A. Proximal and distal scutes of the biserial rings. Two of the groups (second from upper right, and lower right) consist of two scutes fused after injury. In the lower left is a group of five proximal scutes of a movable caudal ring and another of two distal scutes of the same or an adjacent ring. Two thirds natural size.

found in sufficient abundance to characterize the animal. The available material includes scores of scutes, from all parts of the body, mostly dissociated. (Figs. 4, 5, 6.) Little direct evidence is available as to the arrangement and gross structure of the carapace, but the separate elements are so exactly matched in the recent *Tatu novemcinctus* of Texas (and Southward) and in the Pleistocene *Tatu grandis* of Argentina that there is little doubt that *Tatu bellus* had nearly the same general appearance as these species.

The scutes of armadillos occur in several different parts of the animal: (a) the casque, on the top of the head, (b) the carapace, consisting of anterior (or scapular) buckler, movable rings and posterior (or pelvic) buckler, (c) the caudal tube, and (d) the leg and foot scutes.

We have not been able positively to identify the casque scutes, although we suggest that certain polygonal scutes, relatively thin, overlain by a single scale and with marginal follicles, belong here.

Scutes of the bucklers are very numerous. Except for those which bordered on the movable rings, it is impossible to determine from which buckler isolated scutes are derived, for the general character is the same. For the most part they are between ten and twenty millimeters in maximum diameter. The lower surface is usually rather rough, slightly concave and pierced near its center by from one to three vascular foramina. Away from the margins these scutes are almost invariably hexagonal, although somewhat irregular in outline, and were immovably joined by vertical sutures with numerous interlocking bony spicules. Occasionally two or more are fused together, but only as the result of injury or disease.

The external surface of the buckler scutes is hard and glistening. Each scute is marked by impressed grooves dividing it into a rounded hexagonal main figure and several marginal areas. The larger area, usually called central, is not literally so, as its posterior margin coincides with the posterior margin of the scute. The marginal areas, four or five in number, were continuous with the similar areas of the adjacent scute. Each of these areas was covered, in life, by a horny scale, the grooves making the boundaries of the scales. The marginal or intercalary scales generally crossed the suture between contiguous scutes. The rather complex relationship between scutes and scales is diagrammatically shown in the accompanying figures (Figs. 7, 8). The scale areas are somewhat swollen, and their surfaces are marked by minute,

[&]quot;'Primary scale" = "Hauptschuppe" of Meyer. "Intercalary scales" = "Furchenschuppen" of Meyer.

irregularly radial, anastomosing grooves, presumably vascular. The main or primary scale area is further marked by from four to ten minute punctuations, somewhat vaguely arranged in two anteroposterior rows, which are also clearly of vascular origin. To be sharply distinguished from these small vascular foramina are the much larger and more regular follicles, which occur only in the large, regular grooves—the hairs, in life, necessarily passing between the scales. Each buckler scute has from four to eight follicles, which, in distinction from the recent form.

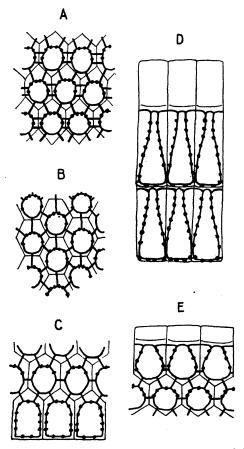


Fig. 7. Tatu bellus Simpson. Diagrams of scute, scale, and hair relationship. Light lines are outlines of bony scutes, heavy lines of horny scales, and black dots are hair follicles. A-B, Internal areas on bucklers. C, posterior edge of anterior buckler. D, Parts of two movable rings. E, Anterior edge of posterior buckler. Approximately two thirds natural size.

are generally along the anterior and lateral margins of the primary scale, with occasionally one on its posterior margin, very rarely any between two intercalary scales. In the central parts of the buckler the intercalary scales are nearly as large as the primary scales. In approaching the lateral margins the disparity increases and the marginal row is composed entirely of primary scales, each covering one scute.



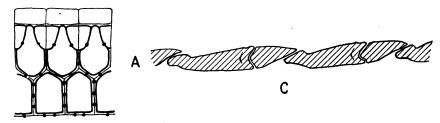


Fig. 8. Tatu bellus Simpson. Diagrams of scute, scale, and hair relationship. In A, light lines are outlines of bony scutes, heavy lines of horny scales, and black dots are hair follicles. A, Segment of one movable caudal ring. B, Vertical longitudinal section through edges of bucklers and through movable rings, showing overlapping relationships of bony scutes; anterior buckler to the left; part of movable rings omitted. C, Similar section through successive caudal rings, showing biserial structure. Not to scale.

The posterior scutes of the anterior buckler are five-sided and elongate. Anteriorly each is suturally united with two normal buckler scutes. Laterally it is united also suturally but less firmly (bony spicules fewer and shorter or else lacking) with its fellows of the same row. Posteriorly it tapers to a straight transverse edge and overlies the anterior part of the first movable ring. The primary scales were separated transversely by long wedge-shaped intercalary scales and abutted anteriorly on a single nearly equidimensional intercalary scale which overlapped the preceding buckler scutes to a slight extent. The margins of the primary scale are marked by five to eight follicles, and, as in the movable bands, the posterior end has two or three nearly horizontal follicles.

The anterior rank of the posterior buckler scutes presents a converse modification, the anterior ends of the scutes being overlain by the tongues of the last movable ring. They had only primary and single intercalary scales, the latter wedged between the former in the same transverse series.

The movable rings are made up of long quadrangular scutes, each divided into a shorter anterior base and a longer posterior tongue. The base was overlain by part of the tongue of the corresponding scute of the preceding ring. The tongue, only, was covered with scales. The latter form a single transverse series on each ring and are wedge-shaped, the primary scales broader posteriorly, the intercalary scales nearly as large and broader anteriorly. The outer surface of the tongue is thus marked by two curving, diverging grooves, each with several very prominent follicles. Between these are two irregular longitudinal lines of minute vascular perforations, and the surface is marked by small anastomosing vascular grooves. The thin posterior end of each scale has from two to four horizontal follicles. The inferior surface has several vascular foramina, generally in a single group beneath the anterior part of the tongue.

The tail was enclosed in a tube made up chiefly, as in *Tatu novem-cinctus*, of a series of movable rings. A few scutes suggest that, also as in the recent form, the rings became indefinite distally and that the tube here was composed of numerous keeled scutes, each with a single scale, slightly movable with respect to all their neighboring scutes. The rings are biseriate, consisting of a proximal and a distal transverse row of scutes, the distal row overlapping part of the proximal row of the following ring. The distal scutes are always covered by a single scale. They have the usual double series of vascular punctuations and have follicles around the edges. The proximal scutes are of two main types: in one (dorsal in *T. novemcinctus*) there are intercalated scales between the anterior parts of the primary scales, while in the other (ventral in *T. novemcinctus*) there was one scale on each scute. Anteroposterior median keels are present on the tail scutes, vague proximally but becoming sharper and more prominent toward the tip of the tail.

The leg and foot scutes are relatively small, mostly quadrangular, and, where closely appressed, were flexibly united by plane, vertical or concave-convex articulations.

The carapace and caudal tube of *Tatu bellus* were subject to frequent injury. A number of the scutes from Seminole show a defacement of their surface features which can be imputed only to injury of the over-

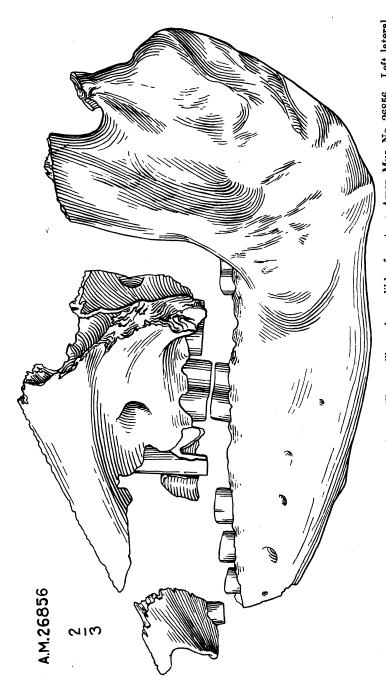


Fig. 9. Holmesina septentrionalis (Leidy). Premaxilla, maxilla, and mandible of neotype, Amer. Mus. No. 26856. Left lateral view. The premaxilla is reversed from the right side. Two thirds natural size.

lying scale and tissues. In other cases a deep pit is seen which represents a healed wound in the bone itself, in some cases with evidence of infection and suppuration. A common result of such injuries was the complete fusion of adjoining plates, which is always accompanied by other evidence of injury or infection and apparently was never normal. No definite case of exostosis in the exoskeleton was found.

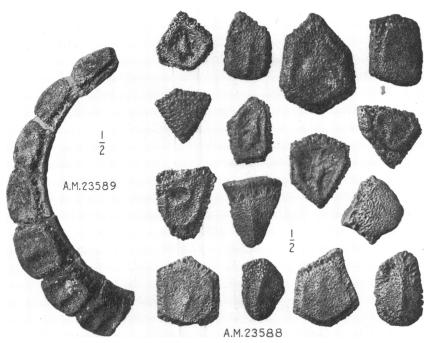


Fig. 10. Holmesina septentrionalis (Leidy). Part of anterior notch of carapace, collected by Moore in Sarasota County. Approximately one half natural size.

Fig. 11. Holmesina septentrionalis (Leidy). Buckler and miscellaneous scutes from Seminole Field, Station A. The upper right and second below it are marginal buckler scutes, that between them, perhaps a casque scute. These and the scutes in the following two figures are selected rather to show all of the types of scutes found than their relative frequency. One half natural size.

Holmesina septentrionalis

The genus *Holmesina* is extinct and nothing approaching a complete carapace has ever been found. Judging from the scutes of the related genus *Chlamytherium*, of which a great number have been described from South America, especially by Lund, Winge, and Lydekker, the general structure was much as in the recent *Euphractus* or *Priodontes*,

although the size was much larger and the number of movable rings is unknown.

The most striking difference from Tatu lies in the fact that the scale pattern and scute pattern were the same: the exposed part of each scute was covered by a single scale of the same shape and nearly the same size (Figs. 10, 11, 12, 13).

The bucklers were formed of rather irregular polygonal plates, four- to seven-sided, averaging about 30 to 40 mm. in diameter and 8 to

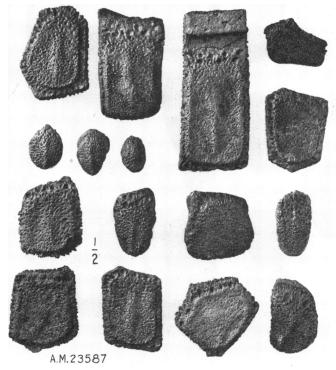


Fig. 12. Holmesina septentrionalis (Leidy). Various scutes from Seminole Field, Station A. One half natural size.

15 mm. in thickness. The inner surface, plane or (usually) concave, shows very clearly the fabric-like structure of the corium fibers, with numerous scattered vascular foramina. The external surface has a depressed marginal area, two to five mm. in width, and a slightly elevated central area which may be plane but more commonly has a vague anteroposterior median ridge flanked by shallow depressions. On some plates,

particularly near the margin in all probability, the ridge is sharper and keel-like. The entire surface is marked by very numerous small punctations which give it a characteristic texture. Around one or more sides, outside the central (scale) area, may be larger openings which in some cases are surely hair-follicles, but in others are too poorly differentiated from the vascular foramina for decision.

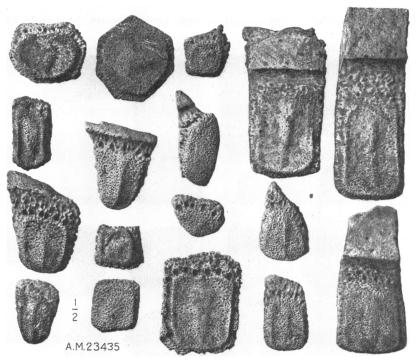


Fig. 13. Holmesina septentrionalis (Leidy). Various scutes from Saber-tooth Cave. One half natural size.

The movable bands are constructed on the same principle as in all true armadillos. The scale-covered part is marked by a definite rounded longitudinal ridge. Anterior to the scale area, between it and the more deeply bedded base, is a group of large punctations, and others may occur around the edges and posterior end. We are uncertain as to the extent to which these may be interpreted as hair follicles.

The lateral margin of the carapace, both of the bucklers and of the movable bands, was formed by a series of pendant ovoid projections.

In addition to variants of the more usual types just described, there

are in the collection a few smaller oval or lanceolate plates, sharply keeled, without marginal areas or sutural surfaces. These may be foot ossicles or they may belong to the tail—tail scutes have not been certainly identified.

Boreostracon floridanus

OCCURRENCE.—From the location of the various groups of remains, from the duplication of parts, and from the apparent individual ages of the different groups of scutes, it is clear that remains of at least six

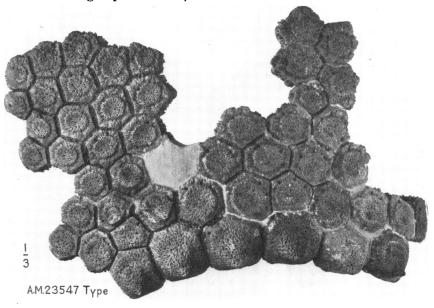


Fig. 14. Boreostracon floridanus Simpson. Type, Amer. Mus. No. 23547, part of glyptodont No. 5 of Seminole Field, Station A. Posterior part of carapace, with six scutes of the posterior notch. One third natural size.

individual glyptodonts were found in the Seminole Field. Additional specimens were found two miles to the west of Station A and on the beach on the Gulf coast three miles to the northwest.

The groups found at Station A were numbered in the order of occurrence, each group apparently representing one individual, but possibly in some cases with admixture of two or more.

No. 1—About 200 scutes found in the bone stratum. An immature individual, the scutes encrusted with lime.

No. 2—About 25 scutes, also from bone stratum. The largest, and presumably the oldest, individual. The largest scute (aside from border or tail scutes) was found here, Fig. 17A. They were badly preserved, mostly nothing but brittle shells.

No. 3—Several hundred scutes and fragments, also from bone stratum. The border scutes of this specimen are sufficiently well represented to have revealed the true character of the Florida glyptodont for the first time. See Fig. 14 B, C.

No. 4—In 1926 were found about 150 scutes in a pocket, secondarily deposited in the old creek bed, outside the limits of the canal, and in the dumps. In 1927 more extensive exploration led to the recovery of many more scutes and of parts of two teeth, the first from Florida. Preservation fair. A young individual of about the age of No. 1. More associated scutes of the nuchal notch add to knowledge of that part. See Fig. 14A.

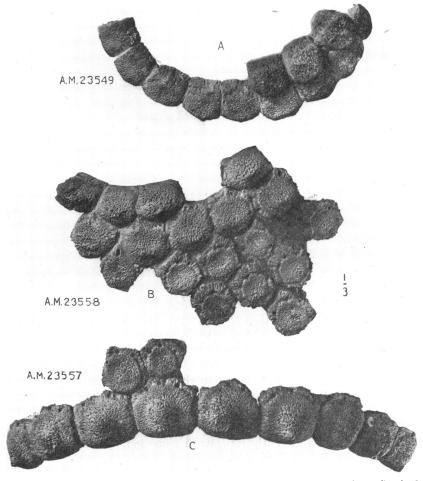


Fig. 15. Boreostracon floridanus Simpson. Parts of carapaces from Seminole Field, Station A. A-B, Segments of anterior notches of two individuals. C, Segment of posterior notch. One third natural size.

No. 5—Many scutes secondarily deposited in the old creek bed about six feet nearer the canal and (although in a younger deposit) three feet lower than No. 3. Their recovery was due to the search for missing parts of No. 3, and it was at first believed from their position and characters that they were scutes of this individual which had been washed out of the Pleistocene stratum and redeposited in the recent stream bed. Laboratory comparison, however, showed some duplication of parts,

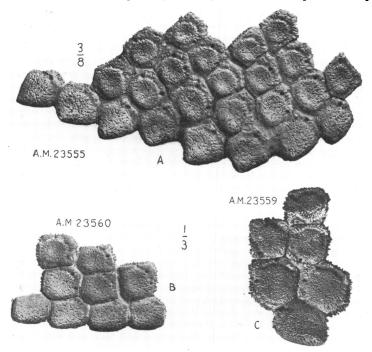


Fig. 16. Boreostracon floridanus Simpson. Parts of carapaces from Seminole Field, Station A. Segments of anterolateral margins of three individuals. One third natural size.

so that Nos. 3 and 5 do include at least two individuals, but possibly somewhat mixed. No. 5 included further welcome groups of associated scutes, among them the large posterior group, which has been made the type specimen. See Fig. 13.

No. 6—Many scutes secondarily deposited near the former creek bed about 100 feet upstream from Nos. 3 and 5. A relatively large individual.

The seventh group of scutes is that from Station B, several hundred scutes¹ apparently of a single large individual. They are splendidly preserved, but were all separated and at present only a few have been associated in groups.

The collection includes a sufficient number of isolated scutes and of associated groups of scutes to form a definite and, we believe, accurate

¹There were probably more than 1000 scutes in the carapace of each individual and more than 250 scutes in the tail.

conception of the structure of the carapace proper. It is rather strange that, with at least seven individuals present and a high percentage of the carapace scutes of these recovered, very few caudal or casque scutes, teeth, or endoskeletal parts were recovered. The six tooth fragments found are all young, corresponding in age more or less to Nos. 1 and 4 among the scutes.

DESCRIPTION OF SCUTES.—The central scutes of this species show a typical pattern which is variously modified in the more marginal regions. These scutes are generally hexagonal, although they may be very irregular and with four to eight sides. The inner surface is concave, with numerous vascular foramina. The usual irregular fabric-like arrangement of the fibres is subordinated to a very marked radial disposition. The dorsal surface, as in the buckler scutes of Tatu (with which there are many striking analogies), is divided by grooves into a nearly circular central area and a number of smaller marginal areas, corresponding to the overlying scales. The area of the primary scale is here truly central, generally somewhat depressed in the center, and strongly punctate (vascular foramina). The marginal areas, which are not always well differentiated from each other, also have vascular openings and are especially marked by a number of irregular radiating vascular grooves. On each plate these areas are generally six to nine in number, and in this central region they generally were separated by marginal grooves (along the sutures) from their neighbors on the next plate. That is, adjacent primary scales were usually separated by a double series of intercalary scales, and here are found only occasionally intercalary scales which cross scute sutures. Follicles, usually two to four in number, occur only between a primary scale and the surrounding intercalary scales and tend to occur only on the anterior and lateral margins of the primary scale.

Toward the borders the central or primary scale area becomes relatively larger and, especially anterolaterally, may touch the posterior margin of the scute. While there are two rows of intercalary scale areas between primary scales in the central part of the carapace, more marginally there is generally but one, the transition between the two conditions being gradual. Hair follicles are somewhat less numerous laterally, usually only one or two on each scute, occasionally none at all.

Along the borders of the carapace the scutes are regularly arranged in transverse rows. In the more central part traces of regularity are discernible, but the segmented arrangement is masked by interpolation of accessory rows and individual scutes. As seen in the accompanying photograph (Fig. 17B), the middle or more posterior lateral scutes may

tend to form definite transverse bands, four scutes in width in the example figured. The anterolateral scutes, unlike most genera of the Glyptodon group, are relatively small, firmly sutured, quite immovable.

Two scutes are occasionally fused, with more or less suppression of the adjacent intercalary scale areas (Fig. 17D). This is an abnormality, however, although not due to disease or injury so far as can be observed.

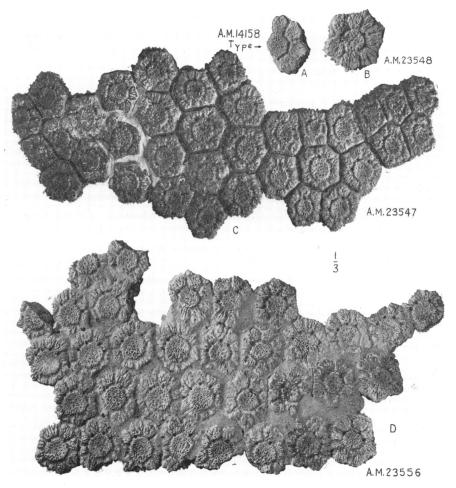


Fig. 17. Boreostracon floridanus Simpson and "Glyptodon petaliferus" Cope. A, "Glyptodon petaliferus," type. B, Boreostracon floridanus, scute most nearly similar to Cope's type. C-D, Boreostracon floridanus, scute most nearly similar to Cope's type. C-D, Boreostracon floridanus, central parts of carapaces. One third natural size.

Normally the scutes are united by open sutures, crossed by numerous long interlocking spicules of bone which hold the scutes firmly together. Even in the oldest individual in our collection, the sutures are still open.

All of the scutes of the marginal row were covered by a single scale each. Those of the nuchal border, or anterior notch (unlike Glyptodon), were without bosses, and the first two rows, at least, of this part were somewhat movable against each other, as in some armadillos (Fig. 14A). The lateral borders are formed by projecting boss-like scutes which are firmly united with each other and the apices of which point backward, downward, and slightly outward. The scutes of the posterior border bear low pointed bosses.

The caudal tube is represented only by relatively few isolated scutes, but so far as these may be relied on, it was built on the same general plan as in *Glyptodon* or *Tatu*, with a number of biseriate rings, terminating in a less definitely segmented and less flexible tube of uncertain length. All caudal scutes are simple, with only one overlying scale. The scutes of the distal row in each ring bear low pointed projections.

Two interesting caudal scutes were found by J. E. Moore in the so-called Sugar Bowl district of Sarasota County. Associated carapace scutes indicate an individual two-thirds or three-quarters the size of the largest Seminole Field animal. These come from the terminal part of the tail, which apparently was tube-like and not divided into definite movable rings. The beak-like posterior projection, prominent on the anterior rings, has flattened out. The more anterior of these two scutes forms a 40° arc of a circle, indicating a ring or row of nine scutes, while the more posterior forms a 60° arc, indicating a row of six scutes. The two rows represented were apparently contiguous and the more anterior overlapped the other. The posterior end of the more distal row shows no sign of contact with other scutes, and nothing indicates the presence of bone beyond this point, which would leave a very small opening at the end of the tail tube, possibly capped by a scale.

HAIR FOLLICLES.—It has been generally assumed that the large pits in the inter-scale grooves of glyptodonts lodged hair follicles. Lydek-ker,¹ however, argues against this. He says, "There is a unique but broken specimen [of *Glyptodon clavipes*] in the Museum [Museo de la Plata] showing here and there the horny epidermal plates in a more or less imperfect state of preservation. Those plates have been converted into a soft chalky-looking substance of about an eighth of an inch in

¹Lydekker, R. 1894. The Extinct Edentates of Argentina. An. Mus. La Plata, Paleontologia Argentina, III, Part II (2), p. 9.

thickness, and, as might have been anticipated, a separate plate covers each disc of the scutes. In the portions of this specimen where the horny plates have disappeared, the groove surrounding the central disc shows the deep pits already alluded to; and since these pits do not penetrate the horny plates, it is evident that they are not, as has often been supposed to be the case, hair pits, and hence they are doubtless vascular. This view is confirmed by Tatusia [Tatu], which is devoid of hairs, although the scutes are penetrated by similar perforations; and it may also be noted that in all the villose armadillos the hairs never penetrate the scutes, but appear in joints between them, or grow from oblique pits in their hinder margins. It is likewise noteworthy that in Glyptodon the pits in the central groove generally occur at the points where the radiating peripheral grooves are given off, and it is therefore probable that each of these grooves marks the course of a blood-vessel."

As Lydekker's view also concerns our interpretation of Tatu bellus and invokes certain misconceptions which, although previously corrected. find some currency even in the most recent literature, we propose to treat it in some detail. Most studies of the hair of armadillos, such as the classic work of de Meijere (1894) or the more recent study of Fernandez (1921), are so taken up with hair-scale relationships that the bony scutes are largely ignored. Römer (1892) showed that the development of the hair follicle and the cornification of the stratum corneum precede ossification in the cutis. The follicles are interstitial with respect to the horny scales (which may, however, fuse in development and obliterate some follicles) but are only indirectly related to the bony scutes. latter, as is very well known and readily ascertainable, do not invariably correspond to the horny scales. The primitive condition may have corresponded with the stated hypothesis of one scute for one scale, but where this occurs in the recent forms it has been shown to be secondary and we know of no paleontological proof that it was an ancestral condition. Ossification begins in numerous centers, and Römer has shown that it spares some or all of the follicles between the scutes (where scute and scale boundary coincide) but may obliterate follicles within the area of a single scute. This it does not always do, however. The follicles of the carapacial region, whether in scute sutures or not, are always surrounded by bone.

In those forms in which scale boundaries transgress scute boundaries, follicles may and very frequently do persist even though completely surrounded by the bone of a single scute. They pierce¹ the outer dense

[&]quot;Pierce" not to be construed actively, as they were there before the bone.

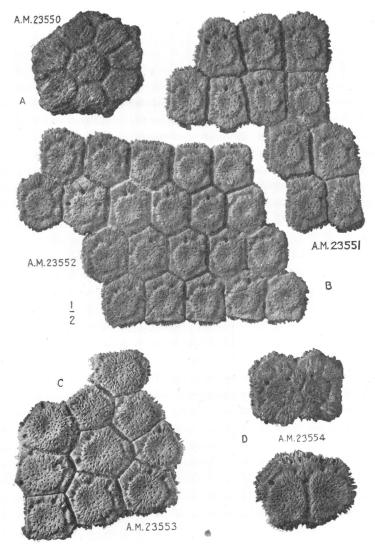


Fig. 18. Boreostracon floridanus Simpson. Scutes from Seminole Field, Station A. A, Unusually large scute. B, Lateral areas showing segmented arrangement. C, Irregularly arranged scutes. D, Two pairs of fused scutes. One half natural size.

bony layer and terminate in the middle cancellous tissue (see "microscopic structure" below). Despite implications or statements to the contrary by Römer, de Meijere, Lydekker, and others, they thus persist in the recent species of *Tatu*. On the belts, for instance, aside from the strong vibrissa-like posterior hairs (also rooted in the bone itself), there

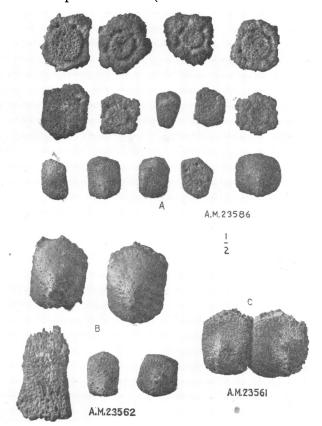


Fig. 19. Boreostracon floridanus Simpson. A, Scutes of young individual. B-C, Caudal scutes. One half natural size.

are numerous but very inconspicuous hairs along all the longitudinal boundaries between the scales, and none of these boundaries coincide with those of the bony scutes.

Thus despite Lydekker's contrary statement, the large pits, even in the recent *Tatu*, which occur only in the grooves *between* scales, do contain the roots of hairs and are quite distinct from the vascular punctations, much more common beneath scales. His statement that hairs never penetrate scutes but appear in joints between them or grow in pits in the hinder border is true only where the scales are practically co-extensive with the scutes. They never penetrate scales. Furthermore his "pits in their hinder borders" are exactly such pits as he supposes elsewhere not to contain hairs.

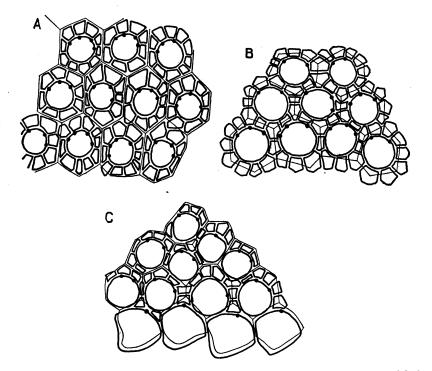


Fig. 20. Boreostracon floridanus Simpson. Diagrams of scute, scale, and hair relationship. Light lines are outlines of bony scutes, dark lines of horny scales, and black dots are hair follicles. A, Part of central area of carapace with intercalary scales generally not crossing margins of scutes. B, Part of carapace with intercalary scales generally crossing scute margins. C, Part of lateral border. Not to scale.

The evidence of his specimen with the scale substance partly preserved is equally inconclusive, for he himself states that the scale boundaries lay along the grooves between the discs, and the trace of hair (naturally of much smaller diameter than its follicle) passing between closely appressed scales could hardly be seen in a "soft chalky-looking substance" in any event.

Polished and thin sections show that the pits which we suppose to have lodged hair follicles are generally larger than the vascular canals or the sinuses of the trabecular bone, with which they communicate by smaller foramina or canals, and are straight or simply and slightly curved, never branched. Vascular canals, on the contrary, are of the same size as the sinuses or, usually, smaller, often irregular or strongly curved, frequently branching.

From their size and arrangement, their relationship to the vascular supply, their invariable localization between the horny scales, and their apparent analogues in *Tatu*, it seems to us positively established that the pits alluded to did lodge hairs in all the glyptodonts.

MICROSCOPIC STRUCTURE

We have not been able to study the histology of our edentate dermal bones in as much detail as the subject deserves, but the examination of several sections of each genus permits a few preliminary remarks. The subject would repay more extensive study than is possible at this time.

Tatu and Holmesina are essentially similar in the structure of their scutes. Each scute is rather clearly divisible into three parts: outer and inner tables and a middle trabecular part. The latter may constitute up to two-thirds of the total thickness in thick shield scutes of Holmesina, but its thickness is normally about half that of the scute or a little less, and it may be quite lacking, as in some of the tail scutes of Tatu. The two tables are usually of about equal thickness. In the tongues of the belt scutes of Tatu, the inner table may be thicker, while in the same part of Holmesina it is usually the outer table which is thicker.

The free surface of the lower table has the fibrous, interlacing, textile-like appearance familiar in dermal ossicles of both reptiles and mammals. In thin section, numerous fibers are seen, approximately parallel to the surface, and occurring in groups which are interlaced in a very complex way, although seldom crossing at right angles. As described above, a few large nearly central vascular canals pierce the bone below. There are also more numerous, but still rather sparse, smaller vascular canals. These canals all run obliquely through the lower table into the sinuses of the trabecular central part, between the fiber groups. The fibers bend around them, and in some cases a few concentric lamellæ occur, but these are often absent, the canals simply appearing as spaces between the interwoven fiber groups. The fibers tend to a radial arrangement toward the margins, which is strongly developed in shield scutes of Tatu, but vague or absent in many other

scutes. Numerous stellate or elongate lacunæ are scattered through the sections. The canaliculi are generally numerous and may be long, branching, and anastomosing.

The outer table is quite unlike the inner in appearance. A fractured surface is not fibrous, but dense and porcelain-like, and the outer surfaces of the scutes are smooth and glistening. In tangential section of the outer part of a shield scute of *Tatu bellus*, the larger part of the bone

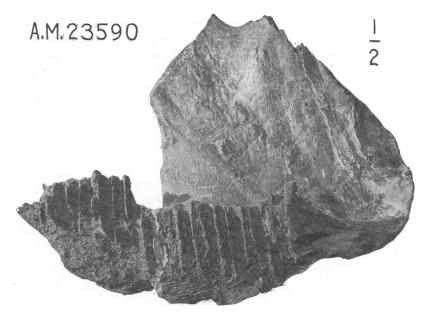


Fig. 21. Boreostracon floridanus Simpson. Part of right lower jaw from Seminole Field, Station B. Internal view, showing broken tooth alveoli. One half natural size.

is not visibly lamellar and has only vague suggestions of fibrils, consisting of a fairly homogeneous ground mass with numerous scattered stellate lacunæ. Around the edges a fairly definite radial fibrous structure is visible, and around the follicle pits and vascular canals, are very distinct haversian lamellæ. In some parts of the section, minute canals slightly greater in diameter than the average lacunæ are seen. These resemble, more nearly than anything else seen in these scutes, true haversian canals, but the development of lamellæ around them is indistinct in our sections.

The cancellous middle part is like that so common throughout the Vertebrata. Large anastomosing sinuses are separated by thin trabeculæ. The bone forming the trabeculæ is definitely lamellar, the fibrils gathered

into sheets approximately parallel to the sinus walls, and many lacunæ are present. Toward the sutural surfaces, however, the bone becomes dense, the vascular spaces become very small and radial in direction, and the surrounding fibrils are also radial, many of them interstitial.

In Boreostracon, like most glyptodonts, the scutes are much more porous and lighter relative to their size than in the armadillos. The inner table is reduced to a thin periosteal layer of interwoven fiber groups, between which pass numerous canals. The latter become larger in passing outward and communicate with the sinuses of the cancellous central layers. Canals and sinuses are surrounded by lamellar bone. The outer table is fairly thick, but it, also, is not sharply distinguished from the trabecular part, and it contains numerous vascular canals. The vertical sutural surfaces are not so dense as in armadillos, and the scutes articulate by long spicules of bone, with prominent radial haversian systems. Spicules of adjacent scutes interlock somewhat as do the bristles of two brushes pressed together.

The dermal ossicles of *Mylodon* are quite unlike those of the loricates. Vascular canals are present and may branch or anastomose to some degree, but real trabecular bone is absent and the canals are relatively few. Around most, but not all, of the canals, the bone is lamellar, haversian-like, but for the most part the fine structure of the ossicles is very dense and homogeneous, consisting of innumerable interlacing fibrillar groups. No definite relation of the fibers to the surface was seen, although a vague concentricity suggests successive stages of growth. In the large ossicles there is some indication of fusion of originally separate smaller parts.

JAWS AND TEETH

Teeth of ground sloths are not uncommon in the Pleistocene of Florida, and some of them have been mentioned elsewhere (Simpson, op. cit., 1928, pp. 11, 12; 1929, p. 578). They differ in no way from more complete remains found elsewhere. A partial jaw of *Tatu bellus* and some teeth have been found (Simpson, 1929, p. 579). The jaw will doubtless be described and figured by Gidley. No important additional material of these groups has been found. A few isolated teeth of *Boreostracon floridanus* are known (Simpson, 1929, pp. 581–582) and a partial lower jaw without teeth is described below.

The dentition of *Holmesina* is fairly well known from a lower jaw described by Sellards, other specimens probably of this genus described

by Cahn' and by Hay,² and especially some fine material from Bradenton described by Simpson³ and attributed.

Boreostracon floridanus

A new specimen of this species, Amer. Mus. No. 23590, from Seminole Field, Station B, includes part of the right lower jaw with the angle, much of the ascending ramus, and the outer sides of the alveoli of the last five teeth and a small part of the preceding one. The teeth themselves are missing except for a few fragments. The most distinctive characters of the jaw itself are the proportions of the part preserved and the character of the postdental canal. The ascending ramus has the same morphologic character as in *Glyptodon*, *Lomaphorus*, etc., but it is decidedly lower and broader anteroposteriorly, a fact which would probably give the complete jaw or skull a very distinctive appearance. The most posterior point of the jaw is directly at the alveolar level rather than above it as in the South American genera.

Immediately behind the last molar is an oval canal, about 13 mm. in antero-posterior and half as much in transverse diameter, running for a distance of about 14 mm. downward and inward at an angle of about 45° to the horizontal. It is covered by a span of bone which buttresses the posterior wall of the last alveolus against the base of the angular region. The true dental foramen was evidently below and quite separate from this and is not preserved.

Some information regarding the teeth is available from the partial alveoli. The chief distinctive point seems to be that on the last five teeth (at least) the posterior lobe extends little if any farther externally than the other lobes and that its external projection is not angulate but blunt or rounded and unusually wide anteroposteriorly.

This additional information adds to the evidence that *Boreostracon* is related to *Glyptodon*, *sens. strict.*, but quite distinct. More complete jaw or skull material may make the resemblance to this genus, rather than another, less striking, since the jaw is less specifically *Glyptodon*-like than are the scutes.

¹Cahn, A. R. 1922. Journ. Mamm., III, pp. 22-24. ²Hay, O. P. 1926. Proc. U. S. Nat. Mus., LXVIII, Art. 24, p. 2. ⁸Simpson, G. G. 1930. Amer. Mus. Novitates, No. 442.