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THE HISTORY AND INTERPRETATION OF SAUROPOD SKIN IMPRESSIONS

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ABSTRACT: Fossilized skin impressions of sauropods provide the only verifiable evidence for interpreting what the outer appearance of these dinosaurs actually looked like when they were alive. Historically, the few rare examples of skin impressions have been largely ignored, misinterpreted, and most often not incorporated into life restorations. Recent discoveries further demonstrate the exclusively reptilian characteristics of their physical appearance. With this new evidence many popular interpretations and controversial concepts of sauropod functional biology are reevaluated.

RESUMO: As impressões da pele dos saurópodes que fossilizaram e chegaram até aos nossos dias, são a única evidência que nos permite conhecer o seu aspecto em vida. Os poucos e raros exemplos conhecidos de impressões de pele foram ignorados, mal interpretados e, na maior parte dos casos, não foram usados nas reconstituições destes animais. Descobertas recentes demonstram que a aparência física dos saurópodes tem, exclusivamente, características reptilianas. Com base nestas novas evidências, muitas interpretações populares e ideias controversas sobre a biologia dos saurópodes são de novo avaliadas.

INTRODUCTION

Sauropods, more commonly referred to as "brontosaurs", are perhaps the most popularly known of all dinosaurs. Their bizarre body proportions consisting of a small head, long neck and tail in essence typify one's very image of the general term "dinosaur".

This is why it is all the more important that pictorial representations or "life depictions" of sauropods reflect the scientific evidence as thoroughly and responsibly as possible. For it is these images, which are popularly used that contribute to our perception of what living dinosaurs must have been like.

Due to a lack of adequate living analogies, the huge body and pillar-like limb structure of sauropods results in them often being referred to as elephantine. While not entirely inappropriate in some applications, this kind of analogy is oversimplified and often results in erroneous depictions of sauropods with a smooth, leathery hide like that of elephants. This kind of skin texture implies a warm blooded mammal-like metabolism, and further contributes to a circular rational. If dinosaurs looked like warm blooded mammals then maybe they truly were endothermic, and conversely if they were endothermic shouldn't they physically look the part? Such erroneous circular thinking has repeatedly influenced not only the general public's concept of what dinosaurs were like, but also that of many professional paleontologists. This mis-perception becomes all the more ironic because physical evidence in the form of fossilized skin impressions has been known since as early as 1852 (MANTELL, 1852).

Largely dismissed by both paleontologists and artists alike, skin impressions of sauropods and other dinosaurs are rarely appreciated for their full significance, and much like trace fossils, are irrationally regarded as being of lesser importance than skeletal remains. But just as fossil footprints represent direct evidence of behavioral activity, fossil skin impressions represent the only direct evidence of what the outer appearance of live dinosaurs truly looked like. In this respect it is worth stressing that complete and partial mummified dinosaur remains are true body fossil remains, sometimes with actual remains of the integument adhering to the textured surfaces that we commonly refer to as "skin impressions" (LOCKLEY, 1992).

Other significant factors associated with skin impressions are that they can also provide physical evidence towards understanding the morphological biology and the metabolism of dinosaurs. In rare examples, fossil skin impressions can and have demonstrated physical characteristics of the soft anatomy which are not otherwise verifiable. This includes indications of body shape and musculature, as well as, and also ornamental features of the epidermis not revealed by skeletal characteristics. These ornamental structures reflect a more elaborate visual appearance, and perhaps functional morphology, that would otherwise remain obscure.

HISTORY OF DISCOVERY

In 1852, S.H. Beckles discovered a large humerus, radius and ulna from Wealden beds of Hastings, England (MANTELL, 1852). Most remarkable though was the fact that portions of the surrounding matrix split apart revealing the actual appearance of the animal's scaly hide. In the same year, G. Mantell exhibited this unique fossil while giving a lecture at the Royal Institution during which he noted the scaly nature of the skin as being composed of hexagonal plates (Fig. 1A).

This initial discovery of a dinosaurs' skin impression occurred so early in the history of paleontology that the animal to which it belongs was not even regarded as a dinosaur, but rather that of a gigantic crocodile. Thus the apparent scalation was not too surprising as it was much as one would have expected for a reptile. It was much later realized that this "gigantic crocodile" was indeed a sauropod dinosaur.

The second notice of this specimen was made by O. C. Marsh during a lecture for the British Association for the Advancement of Science in 1888. The following year, Marsh published a brief account stating that this fossil represented "portions of the osseous dermal covering, the first detected in the *Sauropoda*, known only in the present specimen" (MARSH, 1889). Marsh's use of the term "osseous" is misleading as there is no dermal bone structure preserved in this specimen.

It is also surprising that Marsh gave so brief a description and did not elaborate on it any further in subsequent publications. One may speculate that Marsh may have thought it unnecessary to further state the obvious - that these prehistoric reptiles were covered in scales.

Following Marsh's brief note were repeated claims of finding the first dinosaur skin impressions. These were not of sauropods but that of hadrosaurs. The obscure references made by both Mantell and Marsh to truly the first dinosaur skin discovered were ignored for many years until R.W. Hooley published a more insightful, yet brief paper (HOOLEY, 1917). HOOLEY (1917: 150) noted that "the extent of the epidermal impression is 210 mm long by 200 mm wide. It consists of hexagonal plates. The plates do not overlap". Hooley also noted that the tubercular nature of the skin and variable size gradations were similar to that of the hadrosaur *Trachodon* (*Anatosaurus*). An excellent color photograph of this sauropod skin specimen (Fig. 1A) was published in a popular book by NORMAN & MILNER (1989).

Hooley's most perceptive analysis dealt with the speculation that the tiny (2 to 3 mm) bumps along the surface of the larger individual scales were possible papilliform protuberances relating to the internal structures of the skin between the underlying dermis and epidermis. This interpretation was later confirmed by the present author (see below).

Obscurity befell Hooley's paper and once again claims of discovering the first sauropod skin impressions were made in 1932-33 by (BROWN, 1935). Eighty years had passed since Beckles had discovered the first dinosaur (sauropod) skin! And during these many years the premiere paleo-artist, Charles R. Knight had immortalized the imagery that the public grew to accept for the appearance of these famous long-necked dinosaurian giants (MASSEY-CZERKAS & GLUT, 1982). This vision was strengthened further

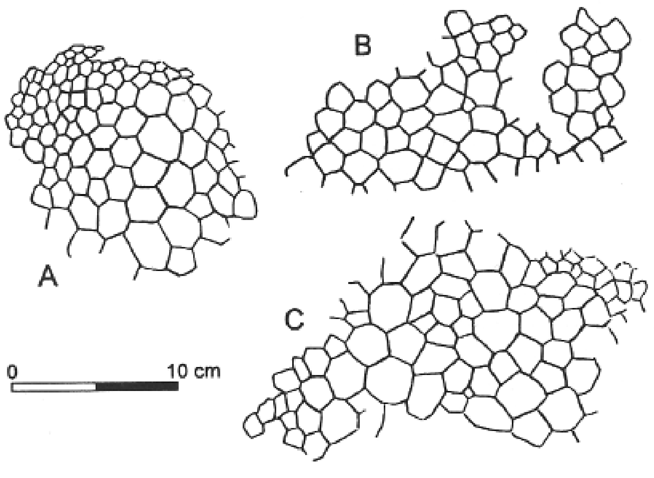

Fig. 1 - Scale patterns of sauropod skin. **A** - the first dinosaur skin discovered. It is from the forelimb. British Museum Nº R. 1870. **B** - Skin possibly from the side of the neck. Corresponds to photo in Figure 2. Specimen is from the Dinosaur National Monument. **C** - Howe Quarry specimen from the belly region, Nº D - 28 - 3. Corresponds to photo in Figure 3. Scale bar is 10 cm.

by numerous other artists and even motion pictures such as silent classic "The Lost World" and the 1933 version of "King Kong".

Beckles, Mantell and even Marsh never had the opportunity to see KNIGHT's (1897) earliest depictions of what at that time was a modern concept of sauropod life restoration. Brilliantly realistic in most respects, Knight's depictions were as believable and authentic as possible in all but one respect. Working under the guidance of famed paleontologists, such as Henry F. Osborn, Knight's imagery of sauropods fell short in not emphasizing the scaly nature of sauropod skin. Consequently, a false perception of sauropods having a smooth skin, composed of tiny scales resembling the leathery hide of elephants, became firmly entrenched in pictorial reconstructions and in everyones imagination.

For over thirty years, indeed ever since, this kind of smooth-skinned imagery of sauropods influenced the public's mind as to what a sauropod should look like. It no doubt had a similar effect on Brown even when he as in the process of finding sauropod skin impressions of his own.

Brown had encountered one of the most amazing dinosaur quarries ever discovered. It was on the Barker Howe ranch located below the Big Horn Mountains near Shell, Wyoming. Not only was the Howe Quarry astonishing in the vast concentration of sauropod skeletons, this quarry was also laden with the greatest quantity of sauropod skin ever discovered.

Brown published only semi-popular articles on the Howe Quarry sauropods with tantalizing, but sparse details regarding the fossilized skin. Illustrating Brown's lack of adequate appreciation for the significance of the rare skin fossils can be readily inferred by Brown's own text (BROWN, 1935) stating "Patches of skin impression, in many cases overlaid by the actual substance of the epidermal covering, were found all over the quarry in such profusion that much of it had to be destroyed in preparing the bones for shipment".

In actuality, only three small fragments, each no bigger than a couple of inches across, and box of even smaller fragments which were later removed from around some distal tail vertebrae are all that Brown saved from destruction. This fact alone reveals a very indifferent attitude towards the importance of skin as an important component of whole animal morphology.

Brown was at least correct in his observation of the epidermal covering being composed of the preserved remains of actual skin material. This is to say that the skin was not just preserved as an impression, but that the actual tissues of the true skin itself had been preserved as a thin carbonaceous layer.

Brown was not so accurate in this description of the scales, particularly in regards to their size. Brown misinterpreted the tiny (2 to 3 mm) bumps as the external surface of the epidermis, thereby suggesting that sauropods had a smooth skin. These tiny bumps, however, reflect the texture of the internal layer between the epidermis and the dermis. The same is true of the English material. Hooley interpreted the fine papilliform texture on the larger scales of Beckles' and Mantell's original piece of sauropod skin.

Since Brown's excavation at the Howe Quarry, only a few additional small patches of sauropod skin were discovered. Three are from the Dinosaur National Monument. One has been illustrated in popular press, but most have not been formally described. The most obvious significant characteristics of these skin impressions is the large size of the scales. The bigger fragment (Fig. 1B, 2) measures 25 x 12 cm and is very similar to that described by Mantell and Hooley. Again, the smallest scales surround the progressively larger scales in the center of what may be interpreted as an ornamental cluster pattern as seen on some hadrosaurs. Presumably, this fragment was associated with cervical vertebrae pertaining to *Barosaurus*. A smaller fragment in the Carnegie collections measures about 8 x 8 cm. It is different in having scales of only moderate size, about 1 cm in diameter, and is in a more uniform pattern.

A possible patch of skin represented by a carbonaceous layer was noted by Charles Gilmore (GILMORE, 1925). It was from between the ribs of the juvenile *Camarasaurus* from the Dinosaur National monument, Carnegie #11,338. No scale pattern was discernible.

Rather ironically, there are three small fragments strikingly similar to those collected by Brown in the collections of Harvard. These were associated with a limb bone discovered near the Howe Quarry. Unfortunately, considerable amounts of skin impressions were observed but not collected.

RECENT DISCOVERIES AT THE HOWE QUARRY

During 1990-91, the Howe Quarry was reopened by Siber and Siber Enterprises, as part of a project of the Aathal Dinosaur Museum in Switzerland. Continuing where Brown had left off, the new excavation revealed numerous additional sauropod bones, both articulated and scattered about. Fortunately, numerous skin impressions were observed during the excavation and great care and effort was made to collect and thoroughly document even the smallest of pieces. Concern regarding the scientific significance of the material led to the authors direct participation. Information was exchanged and a search for new specimens was initiated in the hopes of finding both

Fig. 2 - Photo of large scales on replica of block from Dinosaur National Monument. Same as B of Figure 1. Scale bar is 10 cm.

anticipated, and unexpected material including large scales and ornamental structures like spikes or frills.

During the second field season, the author visited the quarry and examined the various skin impressions still *in situ*. One example was that of a single dermal spine. At this point, it was realized that sauropods looked significantly different than previously believed. Throughout the remaining field season, the discovery of additional spines continued. Several of which were found by fortuitous blows of the pick-hammer which literally popped the surrounding matrix free from the otherwise hidden dermal spines. Finally, in addition to large quantities of skin impressions, most of which were small fragments, no less than 14 dermal spines of varying sizes were identified.

Much of the skin impressions discovered by the Siber excavation at the Howe Quarry are not directly associated with skeletal remains. This not only demonstrates the difficulty in the excavation process but more significantly represents unique preservational conditions resulting from considerable predation. Severed pieces of soft body parts were strewn throughout the quarry apparently by the feeding actions of both large and small theropods. This is further substantiated by numerous shed theropod teeth of various sizes and even theropod footprints (LOCKLEY *et al.*, *in press*) amid the skeletal remains. The pattern of disarticulated remains and articulated body parts provide evidence that these sauropods had been literally torn apart during the feasting. It is unknown whether or not the sauropods were already dead or still alive during the predation.

The sauropods appear to have gathered together in a waterhole during a drought. Similar behavior has been observed among other water dwelling animals such as the hippopotamus (KLINGEL, 1991). The largest sauropods were in the deepest part and were surrounded by smaller individuals.

The waterhole apparently became a deep mud slurry in which the bones and skin were preserved. The undersides of the animals may have had a preservational bias in favor of being preserved due to the fact that they would have already been immersed in the slurry. This would also account for several limbs being preserved upright. It was probably only during the act of predation that the dismemberment of the bones, musculature and skin took place. Apparently, large sections of flesh and hide were carried by theropods to the edge of the waterhole. One such example, that of a skin impression measuring about 25 x 75 cm, was found on the outside perimeter of the quarry isolated from any bones nearby.

The quality of preservation varies considerably with some skin impressions being barely discernible. Individual scales are not always obvious. They vary in size from less than 1 cm to more than 3 cm (Fig. 1C, 3). Unlike most other examples from other dinosaurs, almost all skin impressions from the Howe Quarry are not preserved as just a natural cast of the original skin's external surface. As BROWN (1935) had recognized, the actual epidermis itself appears to have been preserved as a thin carbonaceous layer about 1 or 2 mm thick. Future studies will involve thin sectioning the skin. The external surface has tiny bumps (1 or 2 mm wide) covering each scale. Below the carbonaceous layer are usually larger tubercles (2 to 3 mm wide). These corresponds well with Hooley's interpretation of the tiny papilliform texture being made by the contact layer of the epidermis and the underlying dermis (Fig. 4).

Few sections of skin are reliably associated with bones so as to represent their natural positions. When associated, it generally appears that portions of the lower sides and belly region are preserved with ribs and gastralia. The scales are moderate in size, usually 2 to 3 cm wide. In typical dinosaurian fashion, they are in rosette patterns and non-overlapping. No additional ornamentation, such as diamond shaped clusters like that on some hadrosaurs are discernible.

On one ungual, portions of a nail-like sheath is preserved. It is interesting in that the sheath is not too thick, which demonstrates that size and shape of the claw was not too different from the bone itself.

Of all the skin impressions, the most enlightening are the dermal spines. However they were arranged in life, they dramatically illustrate the reptilian nature of sauropods regarding their true physical appearance (CZERKAS, 1992; Fig. 5 herein). The closest analogy to the dermal spines of sauropods is seen with the spines found on reptiles, such as iguanas, cyclura, and the fleshy lobes along the top of the tail on crocodilians.

Only two small patches of skin (#F-27-29 and #K-27-8) surrounding a few distal tail vertebrae provide direct physical evidence as to how the dermal spines were arranged in life (CZERKAS, 1992; Fig. 6 herein). It is clear that the spines closely followed

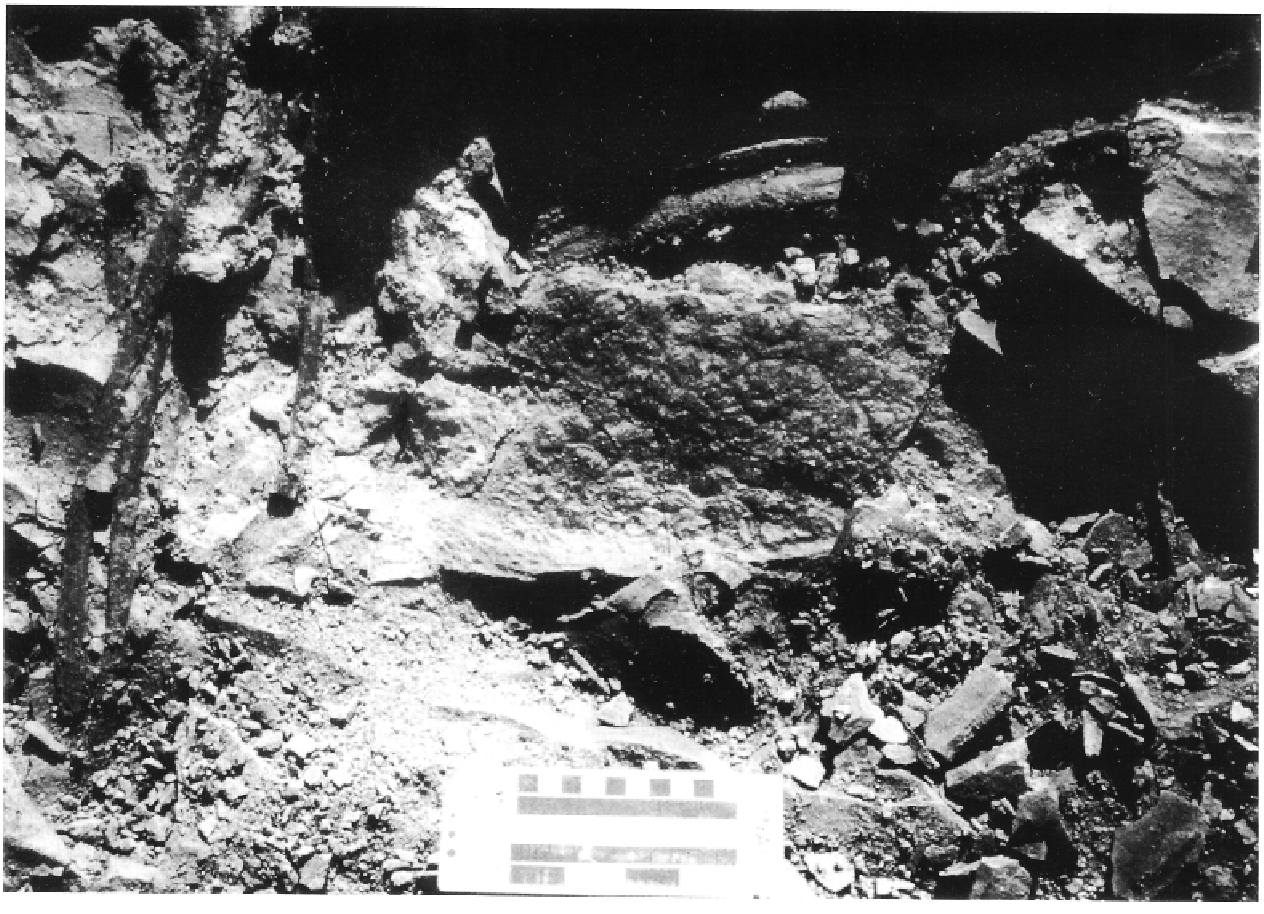

Fig. 3 - Photo of skin *in situ* associated with ribs and gastralia. Same as C of Figure 1. Scale bar is 10 cm.

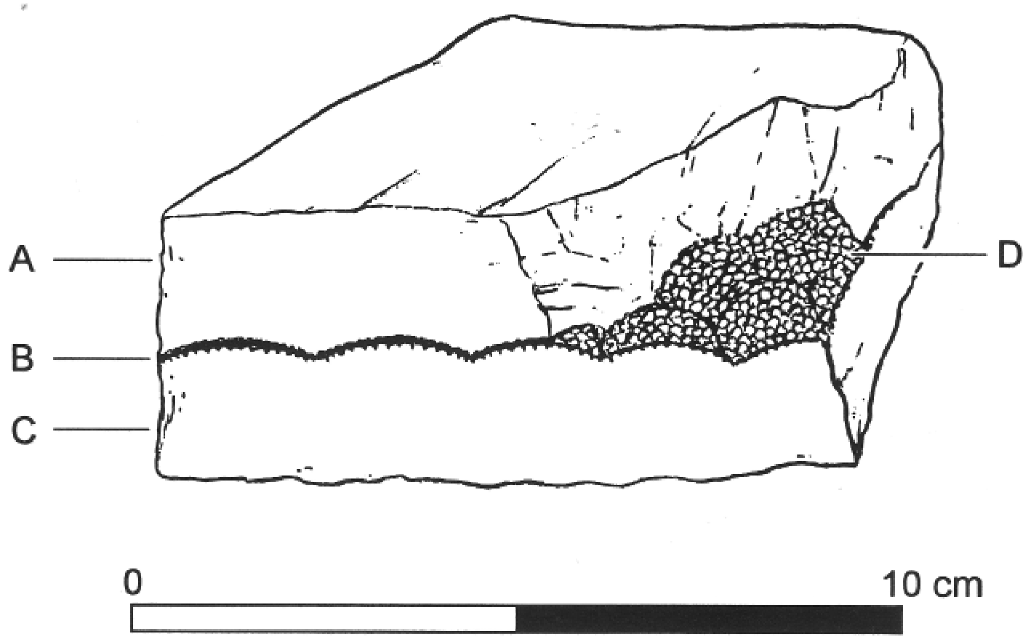

Fig. 4 - Drawing of block with carbonaceous layer of epidermis enclosed on left and large scales exposed on right. **A** - overlying matrix. **B** - cross-section of carbonaceous epidermal layer. **C** - underlying matrix which preserves the papilliform texture of the dermis. **D** - of large scales with epidermis removed and covered with remaining papilliform texture of dermis exposed. Scale bar is 10 cm approximately.

one another on the dorsal median line forming a single row of spines. However, it remains obscure as to exactly how the spines were arranged elsewhere on the body. In lieu of having other dermal spines directly associated with skeletal elements from other regions of the body, this suggests that the most conservative interpretation to account for the larger isolated dermal spines should have them continue anteriorly along the summit of the tail. This would create an ornamental crest of spines along the entire length of the tail with the largest spines near the proximal end.

Without the direct association of bones along with the dermal spines, the proper positioning of the spines elsewhere on the body remains uncertain. There is however, other less definitive evidence which suggest a more extensive and complex arrangement of dermal spines. It is entirely plausible to believe that the single row of spines continued not only for the length of the tail but also along the body and neck as well (CZERKAS, 1992). Analogies with other diverse types of dinosaurs, such as *Ceratosaurus* and hadrosaurs, and numerous extant reptiles (agamids, cyclura and iguanas) add credence to having sauropods portrayed with dermal spines running the length of the neck, back and tail (Fig. 5). Although this interpretation is based upon general patterns seen in other dinosaurs and extant reptiles, it can only be confirmed by the future discovery of more complete skin impressions directly associated with the neck and body.

As preserved, there are no less than three distinct morphologies among the dermal spines. They are all variations of the same pattern, representing progressive differences according to size and probable positioning on the body.

The first morphological grouping is that of small conical spines which are tall, sharply pointed, and compressed laterally. The second type of dermal spines are much larger, but are compressed laterally to a greater extent and are proportionately longer. These two morphologies appear to represent spines from the same continuous row. Their greatest difference being that they become more laterally compressed and longer, becoming fin-like as they increase in height (Fig. 8).

The third morphologically distinct type of dermal spines may not have belonged to the row of spines consisting of the first and second types. This third type is represented by large and small spines which are proportionately much shorter and blunt, rather than pointed (Fig. 9). The large blunt spine (#E-28) is at least 10.5 cm long, and a small blunt spine (#0-26-10) only 6 cm in length. The large spine (#E-28) appears to be asymmetrical with its longitudinal ridge being off center. This suggests a possibility that some spines were not midline structures. This may be analogous somewhat to the large flat, round scales found on ceratopsians (STERNBERG, 1925), or conical spines as seen on *Carnotaurus*

(BONAPARTE, NOVAS & CORIA, 1990). They similarly may have been located on the upper side portions of the neck, body and tails. The upper portions of the limbs may also have been protected by such large, blunt spines.

The lack of thoroughly ossified, well defined bony scute-like structures within the dermal spines helps explain why such details of the large ornamental scalation is rarely preserved. One may consider these non-ossified spines as a precursor to the more thoroughly ossified scutes that are now well known to belong to some sauropods, such as *Saltasaurus* (POWELL, 1992). Conversely, the presence of large scutes on *Saltasaurus* may indicate that less armored forms could still have had similarly large non-ossified scales. And so, it is all the more likely that in addition to a median row of spines, additional blunter spines probably occurred elsewhere on the animal.

It is possible that some ossification within the dermal spines may have occurred resulting in a comparatively small nodule, or nodules inside. Several examples of small bone-like nodules were discovered throughout the quarry, often in groups of three. Each grouping had different size nodules, the largest usually being no more than 2 cm long and the smaller ones being about half as big. Some of these nodules were found near cervical vertebrae. One dermal spine is broken so as to reveal a nodule-like concentration inside which is more dense than the rest of the surrounding matrix.

Currently, there is no way to determine if the tail spines remained in one row as they progress anteriorly, or if they diverged into two rows in a crocodilian fashion.

FUNCTIONAL IMPLICATIONS

It is doubtful that the dermal spines could have had much offensive capabilities. Although when more fully ossified, they may have become more effective as in the case of the tail-clubs of sauropods like *Shunosaurus* and *Omeisaurus*. As defensive structures, the dermal spines may have helped strengthened the hide, thereby preventing easy damage to the skin and deterring attacks.

The ornamental nature of the dermal spines and scalation of sauropod skin inherently played a role in visual recognition. Attractiveness, or sexual dimorphism cannot be discerned. The natural life colors of the skin are not preserved and are not likely to be. However, color patterns in vertebrate skin are in rare instances, known to be preserved (STEWART, 1993) and could be discovered even on dinosaurs. As seen among some living reptiles, one can speculate that the actual color could have varied as a thermoregulatory device to control absorption and reflection of heat from sunlight. The scalation on

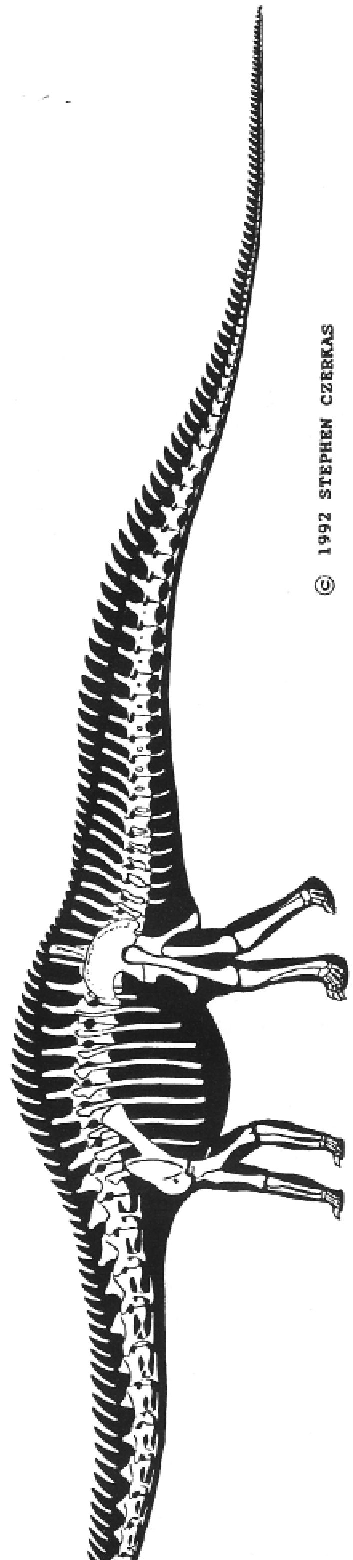

Fig. 5 - Skeleton and body outline of a diplodocid sauropod demonstrating ornamented profile of dermal spines. The total length of the sauropods associated with the dermal spines is approximately 14 m.

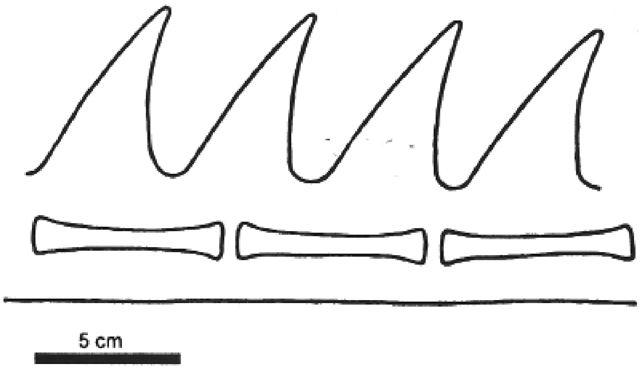

Fig. 6 - Drawing of distal caudal vertebrae with narrow, pointed dermal spines restored. Mass of tail and dermal spines are based on two individual specimens of tails with skin impressions and with isolated spines of similar size. Scale bar is 5 cm (after CZERKAS, 1992).

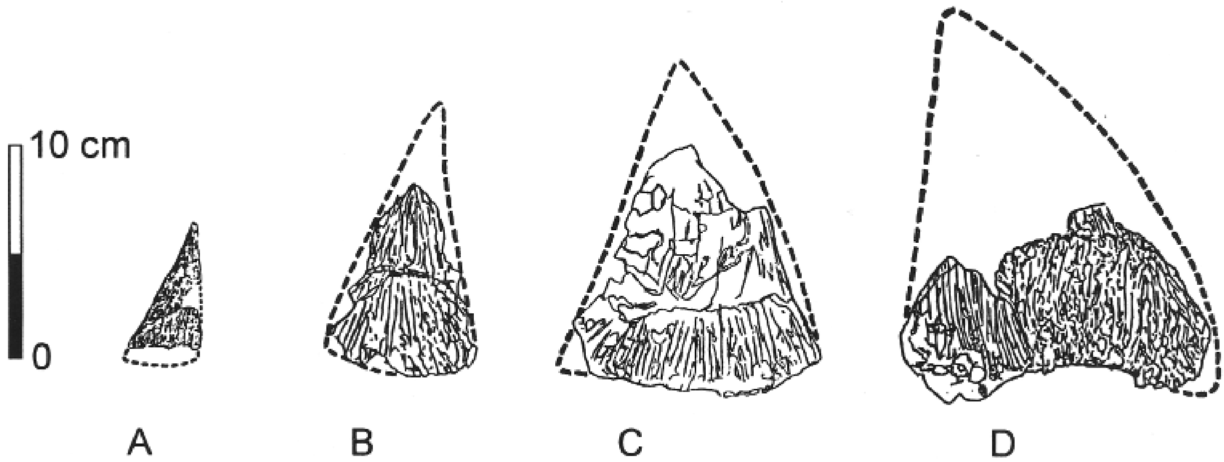

Fig. 7 - Drawings of narrow, pointed dermal spines with suggested outlines restored. Corresponds to figure 8A, B and C. A and B are left lateral views, C and D are right lateral views. Scale bar is 10 cm.

sauropods, and other kinds of dinosaurs, was typically reptilian in regard to its being non-permeable as a water conserving adaptation.

In regards to the metabolism of sauropods, whether warm or cold-blooded, the need to counter the debilitating effects of overheating would necessitate some way for the animal to cool itself. True endothermy would have been dangerously detrimental for giant sauropods (SPOTILLA, 1980) if not totally impossible (WEAVER, 1983). Even as ectothermic inertial homiotherms, high levels of activity would compound the need for heat dispersal. Although often regarded as wholly terrestrial animals, sauropods could have certainly taken advantage of the cooling effects of lakes, rivers and even ocean waters to help disperse excess body heat. It may be more than coincidence that the tail of sauropods, when equipped with the laterally compressed dermal spines, is functionally reminiscent of a crocodilian tail. This suggests that sauropods were adept swimmers when it was necessary. The presence of large, laterally compressed dermal spines on the tail of diplodocids further corroborates previous prophetic interpretations that some sort of "vertical fin" probably existed which aided in the animal's ability to swim (OSBORN, 1889).

INTERPRETING LIFE RESTORATIONS - DISCUSSION AND CONCLUSIONS

Although complete sauropod mummies are not known, we need to rethink our restorations of these famous animals (CZERKAS, 1992). Currently we are dealing with only fragmentary sections of fossilized skin which causes uncertainty in interpretations of the areas that are not preserved. One can anticipate that future interpretations will necessitate additional modifications as new evidence is discovered.

The inference that dermal spines can be attributed to all the varied types of sauropods, may or may not, eventually prove to be warranted. Certainly there must have been variations between different taxa,

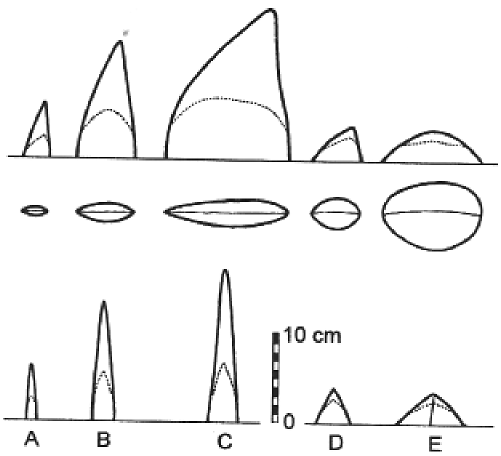

Fig. 8 - Outlines of dermal spines in; top row, left lateral views; middle row, dorsal view; bottom row, anterior view. A, B, and C are median structures which are narrow and pointed. D and E are wide, blunt spines presumed to be from the sides of the animal. Broken lines represent lower portions of spines which are preserved dimensionally, in the round. Scale bar is 10 cm.

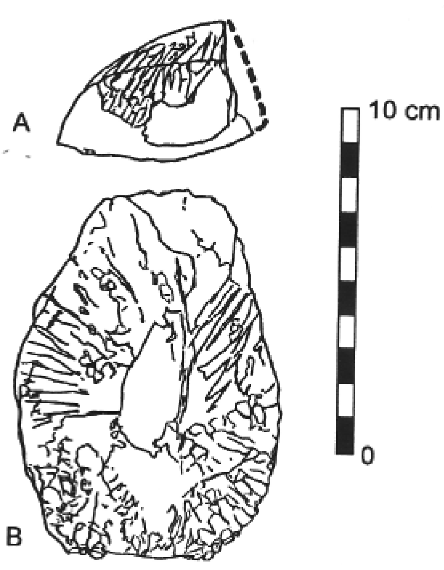

Fig. 9 - Drawings of small and large, blunt dermal spines. A, is in left lateral view, and B is in dorsal view. Corresponds to Figure 8D and E. Scale bar is 10 cm.

with more or less spines, or possibly, none at all. But to portray any sauropods without dermal spines, at least on the tail, falsely implies that evidence exists to the contrary of what has been revealed by the current discovery of dermal spines. Indeed, it may be appropriate to incorporate dermal spines not only on all sauropods but also on their distantly related ancestors, the prosauropods.

Unfortunately in recent years, it has become popular practice to portray sauropods as smooth skinned and rather mammalian. No doubt this has been in response to a broader acceptance of the controversial concept that dinosaurs might be been warm blooded, and therefore should look the part.

Since 1852, the reptilian scaly hide of sauropods has been known, but has been largely ignored. Finally, the reptilian nature of sauropod skin has become indisputable with the discovery of dermal spines on diplodocids thus presenting a new look for sauropods. It is now clear that previous interpretations have been erroneous in either being overly conservative or even contradictory to the available fossil evidence. It is no longer acceptable or accurate to portray sauropods as being smooth skinned animals. Along with including noticeable sacles, and the proper addition of dermal spines ornamenting the generalized body outline, sauropods will be viewed as being more reptilian.

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