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A taphonomic model for the Mesosauridae assemblage of the Irati Formation (Paraná Basin, Brazil)

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ABSTRACT

The Irati Formation (Permian, Paraná Basin, Brazil) is made up of a succession of black bituminous and non-bituminous shales and mudstones with interbedded carbonate layers, which record deposition in marine environments. Mesosaur remains are abundant at several sites in this formation, where they occur preserved in centimetre-thick beds and displaying various degrees of skeletal disarticulation. This paper seeks to establish a model to explain the processes that generated the mesosaurian taphocoenosis in the Irati Formation. Three types o successions containing mesosaur remains were analysed: 1) Carbonate turbidite facies in the State of São Paulo; 2) Carbonate tempestite facies in Rio Grande do Sul; 3) Black shale facies in the State of Paraná. Three taphonomic classes are established: Class I) articulated skeletons; Class II) partially articulated skeletons; Class III) isolated bones (including Class IIIA with complete isolated bones and Class IIIB with fragmented isolated bones). Based upon the sedimentological and taphonomic evidence, a taphofacies model is proposed. The hypothesis here advanced is that all accumulations of mesosaur remains resulted from catastrophic mortality caused by storm events. The basic assumption is that these reptiles died and were buried through the action of successive storms that occurred in the Irati Sea. The taphonomic model points to repeated episodic events of burial, erosion, reworking and redeposition of skeletons and suggests significant time averaging.

KEYWORDS **Taphonomy. Taphofacies. Mesosauridae. Irati Formation. Paraná Basin.**

INTRODUCTION

The mesosaurs (Parareptilia, Mesosauridae; Gauthier et al., 1988; Benton, 1991) were water-dwelling tetrapods that lived during the Permian in the Whitehill-Irati Sea, a large epicontinental sea extending between South America and Africa. In Brazil, the sedimentary successions deposited in the Whitehill-Irati Sea are included in the Passa Dois Group. This stratigraphic unit of the Paraná Basin comprises the Irati Formation, which consists of a succession of black shales and bituminous and non-bituminous siltites, interleaved with carbonate layers (limestones and dolomites). The Irati Formation crops out in the states of Mato Grosso, Goiás, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Figs. 1 and 2).

The Whitehill-Irati sea (Fig. 2) was relatively shallow (maximum depth 200 m) and normally calm, with low salinity, stratified waters where a thermo-oxicline developed. The deeper water layers were colder, denser, more saline, with low oxygen content and rich in hydrogen sulfide. The upper surface waters were warmer, less dense, less saline and well oxygenated. A diversified fauna (mesosaurs, fishes, crustaceans, foraminifera, ostracodes, brachiopods and sponges) inhabited the shallow waters, but the deeper waters were practically barren of life. Car-

FIGURE 1 **Outcrops of the Passa Dois Group (Paraná Basin, Brazil) that includes the Irati Formation. 1: Rio Claro (State of São Paulo); 2: São Mateus do Sul (State of Paraná); 3: Passo de São Borja (State of Rio Grande do Sul).**

bonate facies were deposited mainly in the littoral and nearshore areas, whereas black shales were restricted to the inner basin and generated under anoxic bottom conditions.

Because of its abundance, mesosaur fossil material has long attracted the attention of researchers. Mesosaur remains occur in large quantities, preserved in sediment layers of a few centimetres, indicating a pattern of mass mortality. The skeletons show various degrees of disarticulation ranging from complete specimens, which even preserve their skulls, to isolated and abraded bone fragments. This pattern of preservation also occurs in equivalent permian deposits of South Africa (Oelofsen, 1981), Uruguay (Bossi, 1966) and Paraguay (Beder, 1923). This spectrum of preserved material type suggests a complex taphonomic history involving significant time averaging.

To get better understanding of the processes that resulted in the generation of this taphocoenosis, taphonomic studies were carried out. Data were collected to throw light on the biotic and abiotic factors that influenced the genesis of this taphocoenosis, and to test whether these data were consistent with the hypothesis of catastrophic mortality. This mortality could extend all over the Paraná Basin or at least over very large zones.

The point of departure for this kind of analysis is the principle that the preservational state of each fossil is largely determined by the biostratinomic and diagenetic processes that occurred in the original sedimentary and palaeobiological environment, and/or in its immediate neighbourhood. Therefore, fossil preservation is used in the same way as primary sedimentary structures to reconstruct the environments in which deposition occurred. This kind of study is applicable to the Irati Formation's mesosaur-rich *Lagerstätten* (*sensu* Seilacher, 1970), which occur in different litho- and taphofacies that record deposition in diverse palaeoenvironments.

The material studied consists of 103 specimens belonging to the collection curated by the Universidade Federal do Rio Grande do Sul (UFRGS). They were yielded by calcarenites, calcilutites, siltites and black shales of the Irati Formation, occurring in the Brazilian states of Rio Grande do Sul, Paraná and São Paulo.

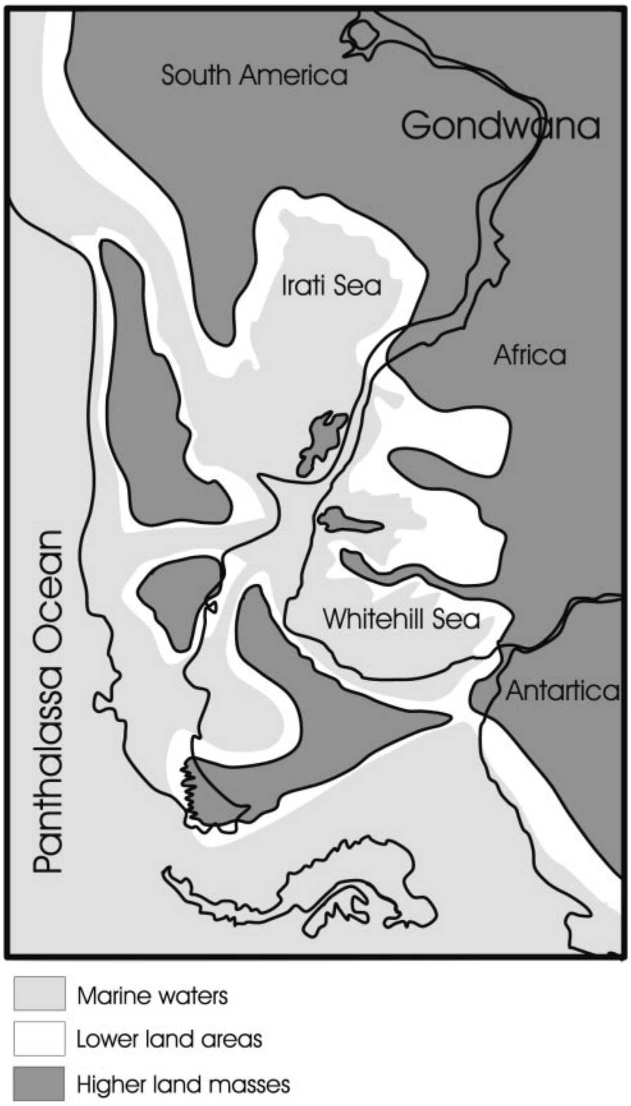

FIGURE 2 **Palaeogeographic reconstruction of the Whitehill-Irati Sea (modified from Lavina, 1991).**

The following information was recorded for each specimen studied (Table 1): a) taxonomic designation (*Mesosaurus, Stereosternum, Brazilosaurus* or undetermined material); b) geographic occurrence; c) lithology; d) preservation state (degree of articulation).

TAPHONOMIC CLASSES

The ordering and classification of the skeletal material according to increasing levels of complexity and completeness resulted in three taphonomic classes defined by the fossil features (e.g., degree of disarticulation, fragmentation, and abrasion). This type of methodology is widely used in vertebrate taphonomic analysis (Dodson, 1971; Gradzinsky, 1970; Holz and Barberena, 1994). Each class represents a stage in the taphonomic history of the considered taphocoenosis. The three preservation classes, that have been set up for the mesosaur fossil assemblage are closely related and can occur together in the same sedimentary level (Fig. 3):

Class I) Articulated skeletons that present complete articulation, with all bones displayed in natural position;

TABLE 1 **Available Mesosauridae material***

São Mateus do Sul (Paraná)	Collection Number
Taxonomic designation: *Mesosaurus* Lithology: black shale Preservation state: articulated skeletons	PV0186P, PV0187P, PV0188P, PV0198P, PV0190P, PV0193P, PV0195P, PV0196P, PV0197P, PV0198P, PV0199P, PV0208P, PV0210P, PV0211P, PV0215P, PV0217P, PV0218P, PV0276P, PV0277P, PV0278P, PV0275P, PV0192P, PV0283P, PV0346P, DGM85-R
Taxonomic designation: *Mesosaurus* Lithology: black shale Preservation state: isolated bones	PV0212P , PV0213P, PV0284P
Articulated skeletons: 89%; isolated bones: 11%	

Rio Claro (São Paulo)	Collection Number
Taxonomic designation: *Stereosternum* Lithology: calcilutite Preservation state: articulated skeletons	PV0170P, PV0171P, PV0172P, PV0174P, PV0175P, PV0176P, PV0180P, PV0181P, DGM542-R, PV0345P
Taxonomic designation: *Brazilosaurus* Lithology: calcilutite Preservation state: articulated skeletons	PV0267P, DGM 539-R
Taxonomic designation: undetermined material Lithology: calcarenite Preservation state: partially articulated skeletons	PV0252P, RI-1, RI-3 ,RI-4, RI-5, RI-6, RI-7, RI-8, RI-9
Taxonomic designation: undetermined material Lithology: calcarenite Preservation state: isolated bones	PV0245P, PV0246P, PV0247P, PV0248P, PV0249P, PV0250P, PV0251P, PV0253P, PV0254P, PV0255P, PV0256P, PV0258P, PV0259P, PV0263P, RI-2
Articulated skeletons: 33%; partially articulated: 25%; isolated bones: 42%.	

Passo de São Borja (Rio G. do Sul)	Collection Number
Taxonomic designation: undetermined material Lithology: calcarenite Preservation state: partially articulated skeletons	PV0219P, PV0221P, PV0267P, PV0268P, Pv0270P, PV0337P
Taxonomic designation: undetermined material Lithology: calcarenite Preservation state: isolated bones	PV0191P, PV0264P, PV0265P, PV0266P, PV0269P, PV0271P, PV0272P, PV0274P, PV0280P, PV0323P, PV0324P, PV0325P, PV0326P, PV0327P, PV0328P, PV0329P, PV0330P, PV0331P, PV0332P, PV0333P, PV0334P, PV0335P, PV0336P, PV0338P, PV0340P, PV0341P, PV0342P, PV0343P, PV0344P, GH052
Taxonomic designation: undetermined material Lithology: siltite Preservation state: isolated bones	PV0273P, PV0281P, PV0282P
Articulated skeletons: 0%; partially articulated: 15%; isolated bones: 85%.	

*** PV: Paleontologia de Vertebrados (Universidade Federal do Rio Grande do Sul); DGM: Divisão de Geologia e Mineralogia (Departamento Nacional de Produção Mineral); RI: private collection.**

skull, vertebral column, ribs, waist and limbs are preserved.

Class II) Partially articulated skeletons, with a rather changing degree of disarticulation in the specimens. There may be cases where the vertebral column and ribs are articulated, or only a segment of articulated vertebrae that are identified as belonging to one individual.

Class III) Disarticulated bones, including complete (Class IIIA) and/or fragmented bones (Class IIIB).

SEDIMENTOLOGICAL CONSTRAINTS

Mesosaur bearing facies were analysed in three significant areas where the Irati Formation and its fossil content had been well studied.

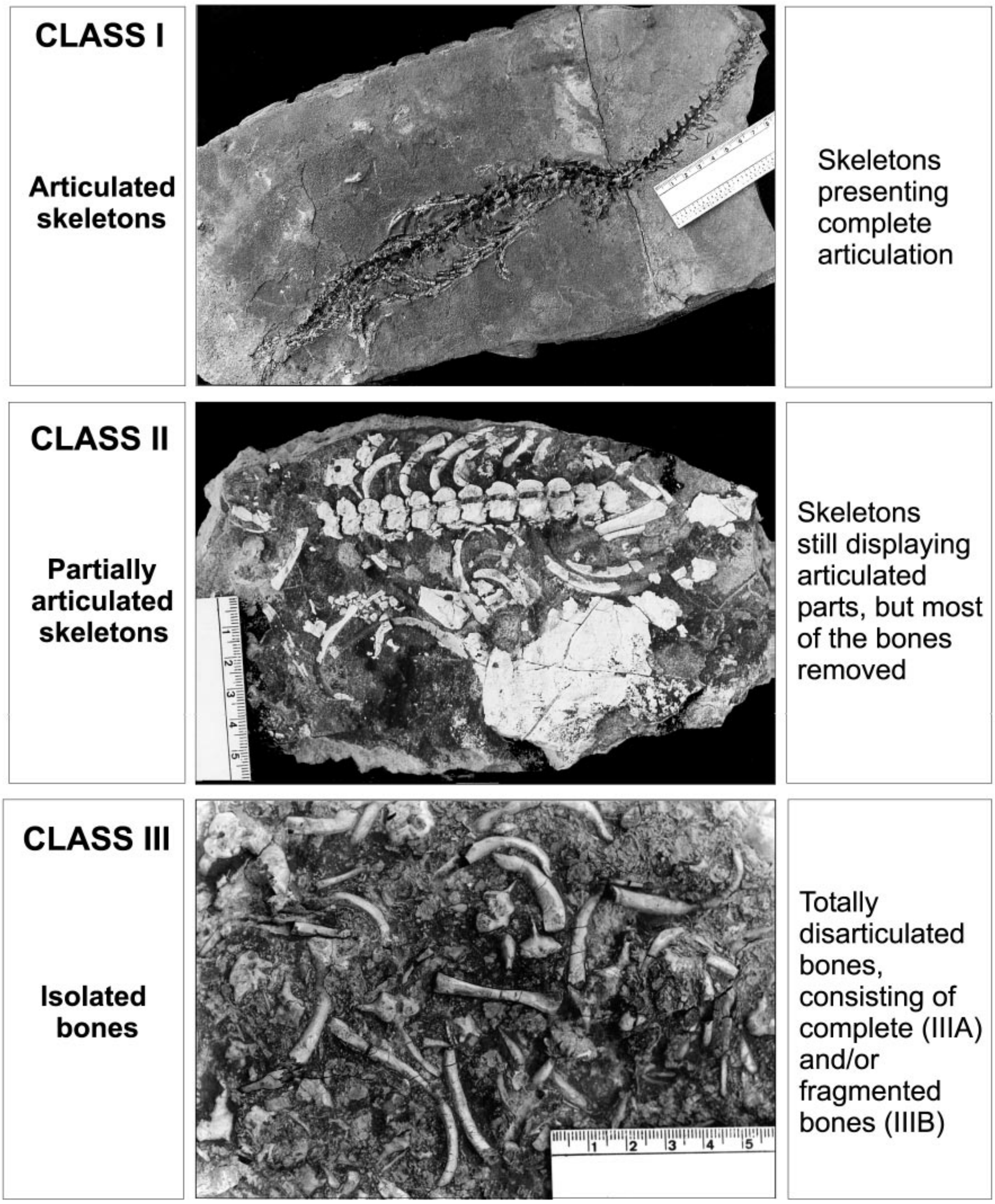

FIGURE 3 **Taphonomic classes established for the different preservational grades presented by the mesosaurs of Irati Fm.**

Tempestite facies with hummocky cross stratification. State of Rio Grande do Sul

The outcrop at Passo de São Borja, in the township of São Gabriel, on the right bank of the Santa Maria River, includes a succession of shales and black siltites, both bituminous and non-bituminous. These fine grained siliciclastic facies interbed an up to 1 m thick carbonate bed. A 10-20 cm thick calcirudite layer occurs at the bottom of this bed, which grades upwards to 20 to 40 cm thick, fine grained calcarenite beds. These calcarenite beds show wave lamination and hummocky cross stratification (HCS) and would correspond to proximal tempestite deposits (Fig. 4; Della Fávera, 1987; Lavina et al., 1989, 1991).

Some partially-articulated mesosaur skeletons (Class II) and many isolated bone fragments (bone-beds; Class IIIA and IIIB) occur in great concentration at the base of the calcarenite beds. Shell-beds made up by crustacean carapaces and silicified tree-trunks occur at the same level.

Distal tempestites, turbidite facies - State of São Paulo

These facies crop out in the township of Rio Claro. A thick dolomite bed occurs at the base of the sequence, which consists mainly of laminated dolomitic calcilutites with undulated lamination. Interleaved with the calcilutites there are dolomitic calcarenite horizons rich in bioclasts (mesosaur bones, crustacean shells, ostracodes, foraminifera and stromatolite clasts). This carbonate facies assemblage (the so-called "dolomitic bank") is overlain by dark-grey and bituminous black shales interbedded with limestones and dolomites ("rhythmic zone"; Fig. 5). Crustacean shell-beds also occur in this facies. According to Lavina (1991) this rhythmic facies, with recurrently associated carbonates and shales, are distal tempestites linked to deposition from turbulent currents induced by storms and deposited below the base-level of the storm wave action.

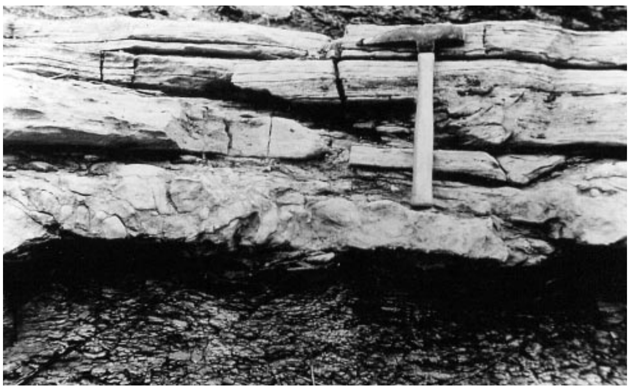

FIGURE 4 **Tempestite facies with hummocky cross stratification (Irati Fm., State of Rio Grande do Sul).**

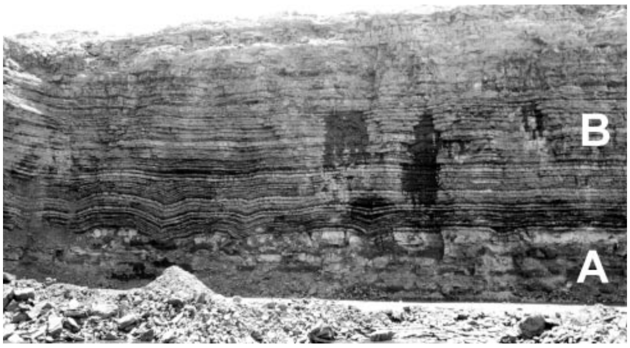

FIGURE 5 **Turbidite facies (Irati Fm., State of São Paulo). A) Lower dolomitic bed. B) Overlying thin bedded rhythmite deposits. The height of this outcrop is about 12 m.**

Most of the articulated mesosaur specimens (Class I) have been collected from the top of the lower dolomitic bed, close to its boundary with the overlying rhythmic facies. Semi-articulated (Class II) and disarticulated (Classes IIIA and IIIB) bone-bed materials occur both at this level and in the rhythmically stratified deposits.

Bituminous shale facies - State of Paraná

This facies occurs near São Mateus do Sul, and includes two beds of black bituminous shale interleaved with a succession of interbedded shales and limestones. Oelofsen and Araújo (1983) have interpreted this facies as representing sedimentation in relatively deep, stratified waters that were anoxic at the bottom. Mostly articulated (Class I) mesosaur remains occur in the upper shale bed, concentrated particularly in a 30 cm layer. Nevertheless, isolated bones (Class III) also occur.

Storm influence on deposition

The key to interpret the triggering events leading to the mesosaur taphocoenosis lies mainly on the facies analysis of carbonate tempestites. The direct evidence of storm action in the past lies in the tempestites (*sensu* Einsele and Seilacher, 1982), i.e. beds that often show undulate lamination and hummocky cross stratification - HCS (Aigner, 1985). According to Brett and Seilacher (1991), the energy generated by storm winds is transformed at the water-atmosphere interface into waves whose orbital movement produces a pattern of oscillating currents in the seabed. Waves and unidirectional bottom currents induced by storms operate simultaneously, thereby producing a hydrodynamic system termed combined flow (Swift et al., 1983). The oscillating flow (waves) tends to diminish with increasing depth, giving place to the unidirectional flow (bottom currents).

The characteristic facies of a storm bed results from wave action that erodes, reworks and remodels bottom sediments, forming the HCS. These structures, proposed by Harms et al. (1975), are considered the most reliable indicators of storm influence in the geological record (Duke, 1985).

The basic mechanism able to produce HCS from a megastorm involves the generation of large waves, which are caused by energy transfer from air to water and then from the water-column to the seabed. These processes cause erosion and suspension of large volumes of sedimentary material (including biogenic particles) next to the coastline. These sediments are transported to offshore zones by geostrophic currents, where they are deposited as tempestite layers.

Einsele and Seilacher (1991) have stated that the biogenic material in tempestites is autochthonous or para-autochthonous. The beds composed of accumulated shells, crustacean carapaces or vertebrate remains are normally consistent evidence of storm action. The tempestites tend to incorporate a large proportion of abraded and fragmented skeletal material because of frequent reworking resulting from storm wave action.

DEFINITION OF TAPHOFACIES

The three taphonomic classes and subclasses of occurrence established for the mesosaur taphocoenosis are grouped into three taphofacies (*sensu* Speyer and Brett, 1986), based on the preservation of the fossils. In theory it is possible to relate consistent patterns of fossil preservation with palaeo-environmental parameters on the base of taphofacies models and their comparative study (Brett, 1995).

Taphofacies 1

Partially articulated skeletons of Class II (15%) and isolated bones (bone-beds) of Class IIIA and IIIB (85%) preserved in carbonate tempestite facies of Passo de São Borja (RS). This taphofacies characterises the shallowest environment (probably ranging from 10 m to 80 m). This would be the zone of tempestite formation with greater turbulence, where the storm effects should be most intense (Della Fávera, 1990). The degree of disarticulation and fragmentation of the bone material in this taphofacies is very accentuated.

Taphofacies 2

Articulated skeletons of Class I (33%), partially articulated skeletons of Class II (25%), and isolated bones (bone-beds) of Class IIIA and IIIB (42%), preserved in the carbonate turbidite facies of São Paulo. In this taphofacies, situated below the base-level of wave action and characterised by distal tempestites, the three taphonomic classes are found, showing that storm effects were quite intense at times. Nevertheless, sometimes the subsequent storms had not sufficient erosive power to re-expose and rework the skeletons.

Taphofacies 3

Articulated skeletons of Class I (89%) and isolated bones of Class IIIA (11%) preserved in the bituminous shale facies of São Mateus do Sul. As originated in the deeper basin environments, this taphofacies show less intense storm effects. Bed disturbance was almost insignificant and is recorded only by some few isolated elements belonging to Class III, which were disconnected from their original skeletons (Class I).

Integration of taphonomic and sedimentological data

The above-mentioned three taphofacies provide both sedimentological and taphonomic evidence that the events generating the taphocoenosis of the Irati Formation mesosaurids may have been severe storms, which left their signature both in the depositional and in the palaeobiological record. In Rio Grande do Sul, the most obvious evidence for storm action are the typical HCS bearing tempestites, which contain mesosaur bone-beds and crustacean shell-beds. In São Paulo, although HCS structures have not been recorded, wave-marks and the limestone-shale rhythms indicate distal tempestites. The crustacean shell-beds and the disarticulated and fragmented mesosaur remains corroborate these facts. In Paraná, however, only the taphonomic evidence remains, since no structures diagnostic of storms occur in the shales. In this case, the taphonomic evidence is the concentration of bones in thin layers and the presence of some isolated bones, which probably were disconnected from their skeletons through the action of storm-generated currents.

TAPHONOMIC INTERPRETATION

Once established the probable cause of the taphocoenosis, we next consider evidences obtained from analyses of specimens constituting the three classes, which yield some inferences concerning the biostratinomic processes operating in the mesosaur assemblage. The analysis of the collected data is organised into five points, discussed below. These data will be considered further on to propose a taphonomic model (Fig. 6).

Mass mortality

Taphonomic evidence

The fossils of the three skeleton classes occur in levels a few centimetres thick and in great abundance, suggesting a mass mortality phenomenon. This leads us to believe that episodic events caused the death of many individuals that were buried together.

Discussion

It is important to emphasise that representation of juvenile individuals in the mesosaur assemblage does not correspond to the pattern expected from a catastrophic mass mortality. Mass mortality phenomena are geologically instantaneous events that provide a "frozen" community at a given time since there is no age selection, as it is in a selective death. Therefore, it would be expected that the number of fossil juveniles would exceed that of adults. Nevertheless, articulated juveniles are extremely rare in the mesosaur taphocenosis and disarticulated juveniles are even scarcer. A bias against more fragile bones is suggested and probably it would result from reworking of the bone material. This reworking would justify the anomalous pattern of population observed.

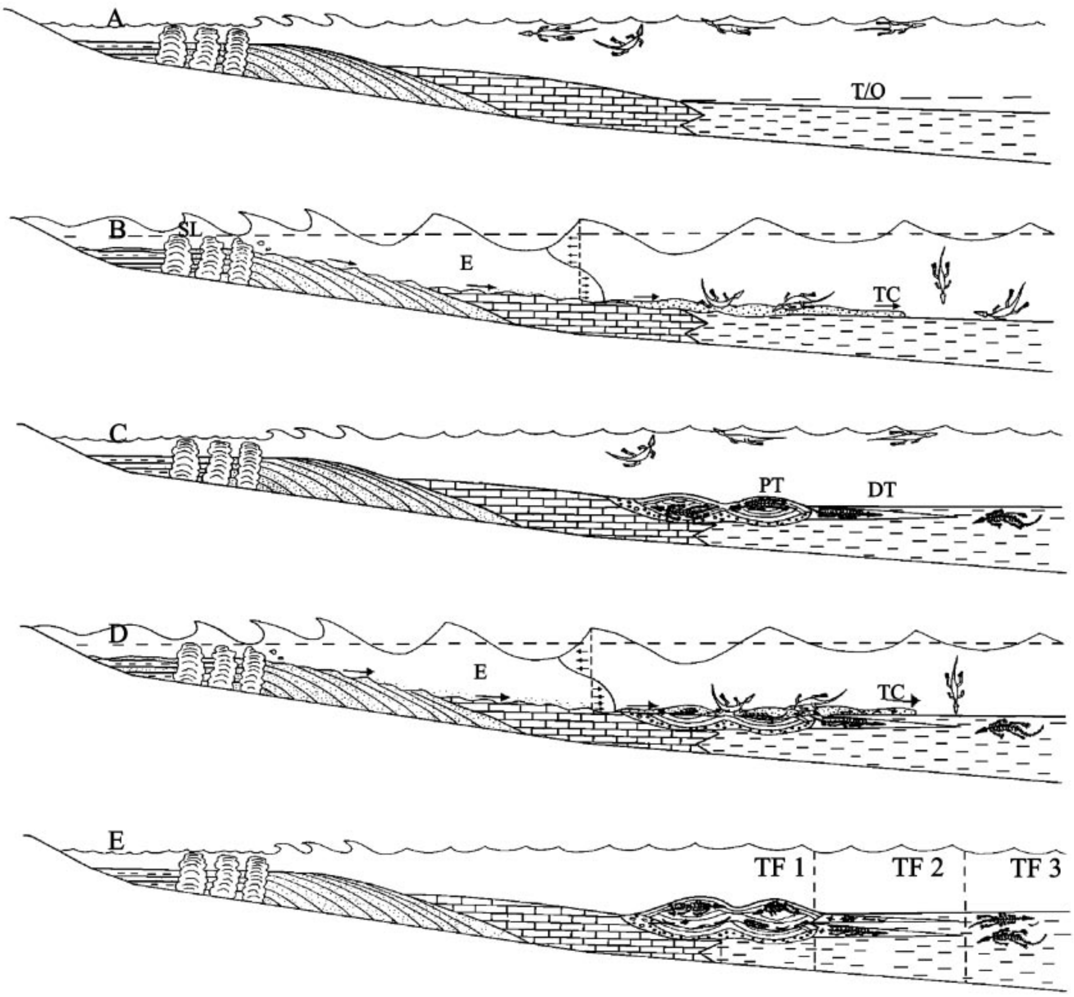

FIGURE 6 **Cartoon showing idealised onshore-offshore sections in the Whitehill-Irati Sea, showing the relation between the different facies and the processes influencing on the formation of mesosaur taphocoenosis. Note the development of carbonate facies in the marginal littoral zones (including stromatolites and bioclastic sands) in opposition to the predominance of fine grained silicilastic deposits in the offshore areas. A to E display a sequence of taphofacies' generation along time. A) Normal conditions with mesosaurs living at the surface waters and water stratification because of the development of a thermo-oxicline (T/O). B) Major storm event affecting the sea (SL) and producing a combined flow (waves and currents); thermo-oxicline break and upwelling of anoxic waters; erosion of previously deposited sediments (E), reworking and suspension of biogenic and sedimentary material; transport to offshore zones by turbiditic currents (TC); mesosaurs dying, reaching the bottom and being buried. C) Normal conditions; proximal (PT) and distal (DT) tempestite deposition at shallow parts of the basin; little bottom disturbance at deeper basin zones. D) New major storm event reworking the previous deposits and associated buried biogenic material that had resulted from B and C; new mesosaurs' carcasses reaching the bottom and being buried. E) Normal conditions: formation of new tempestites overlying the older ones (produced in C). Taphofacies 1 (TF1) - proximal tempestite zone; Taphofacies 2 (TF2) - distal tempestite zone; Taphofacies 3 (TF3) - no tempestite generation.**

Transport and disarticulation

Taphonomic evidence

Proceeding data from the Class I show that mesosaur carcasses did not remain floating after death and did not experience consequent disarticulation in the Whitehill-Irati Sea. Therefore, the animals were buried together.

Discussion

Assuming that skeleton disarticulation tends to be a relatively rapid process, both in air and in water (Hill and Behrensmeyer, 1984), and that the degree of articulation of a carcass is inversely proportional to the time between its death and burial, we can infer a rapid burial for the representatives of the first taphonomic class. Speyer and Brett (1988) have stated that vertebrate skeletons are among the best indicators of rapid burial, because of their tendency to disarticulate rapidly after death.

The first point to consider is the process of necrolysis. Aerobic and anaerobic decomposition processes can act on a cadaver. The former are most rapid and are caused by the action of aerobic bacteria that attack external tissues. The latter occur through the action of anaerobic bacteria that penetrate tissues through the intestine wall, producing decomposition gases. These anaerobic bacteria are the real cause of carcass putrefaction (Weigelt, 1989). Mesosaur carcasses in Class I were buried in an anaerobic environment where anoxic conditions predominated. Such an environment inhibits the action of aerobic bacteria and necrophagous animals practically never occur. Consequently, an articulated skeleton can be preserved longer in an anaerobic than in an aerobic environment. Anoxia retards decomposition but does not prevent it (Allison, 1988). Seilacher et al. (1985) have quoted much evidence that even in anoxic environments, skeletons of certain organisms (i.e. vertebrates, echinoderms and arthropods) cannot be preserved in an articulated state unless covered by at least a thin layer of sediment, as Zangerl and Richardson (1963) (in Allison, 1988) and Davis and Briggs (1998) have demonstrated experimentally. These studies show that anaerobic degradation can be rapid and efficient, causing skeletal disarticulation and even swelling of the carcass, giving a tendency to float. Even where a vertebrate carcass shows no tendency to float and remains on the bottom in still water, the components of the skeleton get disconnected and remain juxtaposed on the sediment. In some cases, small bones are removed by bottom currents (Davis and Briggs, 1998).

We can infer that the mesosaur specimens could have remained exposed at the bottom of the Whitehill-Irati Sea for some time after death, without deteriorating immediately. Nevertheless, the length of time before burial could not have been long, otherwise anaerobic decomposition would have caused the disarticulation of skeletons.

The hypothesis of transport by floating can be rejected, since for a floating carcass to be buried whole it must be transported for a short time only and then must come to rest onshore or in a shallower region. A mesosaur floating far from the coast in relatively deep water would find no place where it could run aground for burial. If it remained buoyant long, the carcass would disintegrate, bones would be lost and transported considerable distances. If they were buried, they would occur in separate regions. In addition, there is a tendency for bodies to be transported towards the shore where the prospects for preservation are very low (Seilacher, 1991), and this is not what is found.

Selection and reworking

Taphonomic evidence

There is no evidence of selection by transport. Bones with signs of fragmentation and abrasion suggest that sediment was reworked after remains were buried.

Discussion

Most of the skeletons in Class II exhibit a general pattern consisting of vertebral segments from the trunk, with or without associated ribs. Such a pattern is attributed to two factors: 1) the fact that these components are the last to be disarticulated in a tetrapod skeleton (Toots, 1965a; Schäfer, 1972; Dodson, 1973; Weigelt, 1989); 2) to pachyostosis, which confers greater resistance to movement. Pachyostotic bones of mesosaurs –ribs and vertebrae (Timm, 1996)– exhibit a greater degree of bony tissue compaction and, consequently, greater density than other bones of the body. It is therefore more difficult to remove vertebrae and ribs than other lighter bones.

Compared with this predominant trend, few other kinds of bones are found that are still articulated. The question arises: What happened to the remaining bones? There are two hypotheses that explain the low incidence of lighter, more fragile bones. First, they could have been transported differentially and deposited at other sites; secondly, and more probably, they could have been worn away.

Amongst the Class II material, many disarticulated bones (Class III) are found near their respective specimens, principally vertebrae and ribs, but also humeri and femurs. This suggests that bones disarticulated from skeletons did not undergo hydraulic selection, but remained near the original skeleton. Moreover, in very rare examples it is possible to find, in association with the pachiostotic bones, quite delicate and fragile bones, such as gastralia and phalanges, although much fragmented. Individual elements of the same skeleton show wide variations in size, shape, density and buoyancy. That is to say, they were not transported all together and under the same flow conditions (Voorhies, 1969; Dodson, 1971).

Another important fact is that signs of fracture and wear are observed, mainly on vertebrae, which in the majority of cases have their neural spines fractured, pointing to some degree of reworking of the material.

It is concluded that the components of Class II, after being buried whole (as in Class I), may have been re-exposed, then experienced reworking and consequent partial disarticulation. During the course of this disarticulation, suspension and redeposition, considerable attrition of bone elements occurred by friction against other biogenic particles also in suspension (e.g. crustacean shells) and against sediment grains, culminating in the total destruction of the most fragile bones and in wearing on others.

These examples from Class II suffered more intensely the effects of storm reworking than specimens of Class I, but these effects were not sufficiently damaging to disarticulate or destroy their skeletons completely. Therefore, to a greater or lesser degree they were preserved partially articulated. The more incomplete an exemplar of this class, the greater the number of reworked episodes, and the more intense was the reworking of its skeleton.

Regarding the samples studied from Class III, it is found that isolated bones show various degrees of wear, ranging from elements that are entirely complete in form and structure, to bone fragments. What is found in the disarticulated bone material of this class as a whole are great quantities of ribs and vertebrae, and to a lesser extent long limb-bones, teeth and bones belonging to pelvic and scapular girdles. The more fragile bones such as abdominal ribs and phalanges occur less frequently. No isolated skull was found. Added to these, much fragmented material was also found but was difficult to identify. If these different types of bone had been transported, they would never have been found together since they have different potentials for hydraulic selection.

Thus, we can clearly deduce that Class III skeletons did not experience total disarticulation before burial, but that previously buried parts experienced later disarticulation because of reworking caused by oscillatory flow. The effects of reworking are evident somewhat on almost all bones as fractures, rounded surfaces, abrasion and total fragmentation of some bones.

From a taphonomic viewpoint, fragmented skeletons are considered more interesting than complete ones, because the nature of their fragmentation can indicate which processes were responsible for their preservation (Behrensmeyer, 1984). Isolated bones and abundant fragments of mesosaurs forming bone-beds, together with the beds of crustacean shells, comprise the palaeontological evidence most directly related to catastrophic mortality caused by storms. When they make up part of a tempestite in association with HCS, there is no doubt at all concerning their origin. The disarticulated material from São Paulo preserved in a turbidite facies and forming distal tempestites, is also found in association with crustacean shells, to a lesser extent.

The greater predominance of vertebrae and ribs compared with other bones runs counter to claims by Reif (1982, in Martill, 1991), who says that storm activity is a determinant factor in the genesis of marine bone-beds, which are indicated by the more resistant bone elements, which in this case are pachyostotic.

The concentrations of Class III bones were produced by various storm events which, because of their “cannibalistic” power, eroded the sediment and biological materials, including skeletons deposited by the preceding storm, so that at any one level bones can be found that are in various stages of reworking. The more fragmented and more abraded isolated bones are those that have experienced more intense reworking as a result of successive storms.

In contrast to this finding, the rare isolated bones of Class I do not show evidence of wear, remaining whole. This can be attributed to their location in the basin, in more distant and deeper waters and below the base-level of storm wave action.

Orientation

Taphonomic evidence

Skeletons in all three classes are distributed chaotically, showing no tendency to alignment by currents causing bottom drag. The mesosaur “orientation” pattern is consistent with that produced by oscillating currents.

Discussion

Another important point of analysis concerns the question of position and orientation of skeletons. In no case is there ever any orientation pattern. The Class I skeletons are found to be deposited at random. There is not a consistent head-tail positioning of the fossils. Specimens are usually found in a dorsal position on the sediment, but some took up a ventral position and others a lateral position (generally only the skull and neck). The limbs are normally found extended, twisted to a greater or lesser extent, spread laterally, below or above the body. Some lateral curvature from tail to neck is observed, and is sometimes quite accentuated.

The question arises here about the nature of bottom currents present in the Irati Sea. Various authors are in agreement about the "day-to-day" calm conditions that prevailed in this vast epicontinental basin. According to Einsele (1992), in present-day meromictic lakes and seas that stratify (e.g. the Black Sea or East Mediterranean), the surface waters are normally characterised by the presence of turbulence and circulation, but the bottom waters are very little affected by currents. Taking present-day epicontinental seas, with stratified water columns, as a model it can be inferred that bottom currents in the Whitehill-Irati Sea must have been weak or even absent, adding to the stagnant water conditions.

Toots (1965b) states that remains of organisms reaching the bed of a water body will assume a preferred orientation determined by the body's centre of gravity, and that a random position cannot result from this process. In the absence of bottom currents, the configuration taken by skeletons would be their position in life, this being their position of greatest stability. Skeletons However, no evidence occurs of an orientation pattern of mesosaur skeletons, because of the absence of currents, or yet of bottom currents, which would have tended to align skeletons. What is observed in these articulated skeletons is a chaotic orientation of the body extremities, apparently without any order. Toots (1965b) observes that absence of orientation in fossils requires special circumstances such as turbidity currents and disturbance of the bottom by wave action. According to Seilacher (1991), where the bottom has little or no oxygen, the effect of storms is felt below the wave base as turbidity currents. In such cases, sediment particles and fossils included in that current are carried in suspension and re-deposited on the bottom by gravity when lateral movement ceases.

One fact that can be verified from the outset is that specimens representing this class are invariably enclosed in fine sediments (calcilutites and shales). The density of their carcasses resulted in them behaving like grains smaller than sand, being drawn into suspension and deposited together with fine sedimentary material.

It is most probable that when the mesosaur carcasses reached the bottom, they were subjected to the action of flows that reoriented them. Orientation of the carcasses is affected by currents, so that disturbances can occur before they are buried by mud. Since deeper environments are more rarely affected by wave-caused erosion (Speyer and Brett, 1988) the skeletons remained articulated.

The analysis of some Class II specimens studied *in situ* in Rio Grande do Sul confirms the action of the oscillatory flows proposed for Class I. When long fossils are affected by oscillatory currents such as waves, their long axes tend to become perpendicular to the flow. Seilacher, 1970 (in Ziegler, 1983) demonstrates the orientation taken by fishes *Semionotus* of the Triassic in the Karoo Basin, their bodies showing alignment perpendicular to the flow direction of oscillatory currents.

In the carbonate tempestitic package of Rio Grande do Sul, many vertebral column segments, and even specimens that are rather more complete, show the same kind of orientation as that acquired by fossilised gymnosperm trunks. This orientation lies following the N-S direction. Knowing that winter storms moved from west to east (Lavina et al., 1991), the orientation shown by the reptile skeletons and by the fossilised trunks fits the model of orientation caused by oscillating storm flow. Therefore, both mesosaur skeletons and trunks were transported together with a huge volume of sedimentary material and deposited in offshore regions, oriented perpendicular to the direction of flow of oscillatory currents produced by some great storm. In South Africa, Oelofsen (1981) suggested that the orientation shown by the fossils was caused by an oscillatory movement of the bottom waters. Like Brazilian mesosaurs, the African ones do not display a consistent head-tail positioning and show a general preferential orientation, perpendicular to the direction of the flow. The author speculated that this oscillatory movement of the waters was caused by an omnipresent factor like a tidal surge. Under a new viewpoint, this tidal surge might be reinterpreted as storm action. Then, storms may have occurred in all parts of the Whitehill-Irati Sea, not only at the Brazilian coast.

Regarding the orientation of isolated (Class III) bones, no pattern seems to exist in any of the facies studied. The chaotic distribution shown for bone elements runs counter to that produced by oscillatory flow action. If bones are oriented only by normal bottom currents, there is a tendency for them to align in the direction of the current (Weigelt, 1989), and this is not verified. The shell-beds of crustacean also show chaotic orientation, reinforcing this conclusion.

Time-averaging

Taphonomic evidence

The various reworking events point to significant time-averaging (geological time involved in generating a taphocoenosis).

Discussion

We take as a starting point the principle that all mesosaurs that were victims of catastrophic mortality caused by storm action occurring at various times in the Whitehill-Irati epoch and in various parts of this vast basin, were buried whole. The animals died during the course of each storm and were buried during the period that it was active. Each subsequent storm event caused the reworking of previously deposited material, generating a fossil assemblage with long time-averaging.

CAUSES OF DEATH

Another fundamental aspect of the taphonomic analysis is investigation of the causes of death of the biocoenosis. All data discussed hitherto are consistent with the hypothesis that storms were the agent causing mass death of mesosaurs in the Irati Formation. How did storm events act on fauna to cause catastrophic mortality?

As a first preliminary hypothesis, the generating process of a tempestite involves the remobilisation of previously deposited sediments, resulting in an increase in suspended material. When storms occur in offshore zones where anoxic bottom conditions occur, a break in the water stratification can take place. The action of large waves turns over the anoxic bottom, bringing into suspension a large volume of fine, toxic sediment, which then reaches the photic zone. The water becomes turbid, changes occur in pH and the level of dissolved oxygen becomes reduced as a consequence of its reaction with the hydrogen sulfide. Lack of oxygen combined with the presence of this sulfide and of trace metals brought from the bottom cause the death of the entire food chain by poisoning the plankton. With the consequent poisoning at all trophic levels of the food chain, animals like the mesosaurs would die though loss of their food source.

When the above-mentioned hypothesis is applied to the mesosaur taphocoenosis, some problems arise. If the death of these animals was caused by this mechanism, it should take place relatively slowly (over a period of days if not longer) and such a large number of complete carcasses would not occur. After the storm ended, conditions of calm would return to the Whitehill-Irati Sea and the mesosaurs, dying gradually through lack of food, would suffer decomposition, transport, action of scavengers and disarticulation. This being so, the cause of death of these animals must have been an integral part of the same event that later buried the carcasses. That is, the animals died during the storms and were buried during the period of its activity. Seilacher (1991) draws attention to this type of problem. This author stated that it was still not possible to understand the mechanisms by which a large number of animals met their deaths in such short time. If they died from being poisoned, it would have to have affected the entire fauna very rapidly and caused immediate death whilst the storm was still active. Lavina (1991) suggested the hypothesis of poisoning by gases through the formation of toxic clouds in the atmosphere near the water surface, as presently occurs in African lakes. This hypothesis appears more coherent, as the mesosaurs were lung-breathers and would die from asphyxiation if they breathed toxic air. Thus, the instantaneous death would allow burial as soon as storm waves ceased, when clouds of suspended sediment would be deposited.

Finally, a third possibility would be death caused by the great turbulence in waters produced by giant waves. As the mesosaurs breathed through lungs, they would die if they were caught up in extreme wave turbulence. Either through being unable to reach the surface to breathe or through ingesting large quantities of water, they might be quickly asphyxiated by large quantities of mud in suspension, which would subsequently cover them. Brongersma-Sanders (1957) mentions mass mortality of fishes, organisms that are highly adapted to aquatic life, through the turbulence of ocean waters during severe storms. This last hypothesis strengthens the deduction that the event causing death was the same as that responsible for burying the carcasses.

CONCLUSIONS. BIOSTRATINOMIC MODEL

After all these considerations, it is possible to propose a model where each of the stages occurred after the mesosaurs death is gathered. The taphonomic evidences discussed above corroborate the storm hypothesis. Moreover, this is reinforced by Oelofsen’s (1981) observations about African mesosaurs. Besides the absence of a preferential head-tail positioning, which can be attributed to oscillatory flow produced by storms, fragmented and abraded disarticulated material from Karoo Basin (“Doros Bone Bed”) show signs of reworking, like Brazilian material. Similar mesosaur bone-beds have been also reported in Uruguay and Paraguay.

The mesosaur taphocoenosis resulted from a multi-episodic taphonomic history beginning with the articulated skeletons of Class I. Later storm events caused death and burial of entire carcasses and simultaneously reworked remains that had been buried by earlier storms. These remains could be reworked repeatedly, until they became the isolated and fragmented parts of Class III.

The storm hypothesis as the catastrophic death agent of the mesosaur assemblage is acceptable for the three taphofacies, since severe storms occurred several times and in many areas of the Whitehill-Irati basin. Thus, the storms that produced the taphofacies 1, probably were not the same that produced the taphofacies 2 or 3. In addition, it is important to emphasise that these taphofacies could express lateral variation of the palaeoenvironmental conditions in the Irati Fm. and were not necessarily in sequence from the shore to offshore zones (Fig. 6).

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