PALAEOECOLOGICAL IMPLICATIONS OF THE DISTRIBUTION OF MESOSAURID REPTILES IN THE PERMIAN IRATI SEA (PARANÁ BASIN), SOUTH AMERICA

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ABSTRACT A reconstruction of the upper Permian Irati sea and conditions in the waterbody is attempted. The reconstruction is based on faunal and facies distributions and the biostratigraphy of the formation. It is deduced that the Irati, like the southern Africa Whitehill Formation is a chronostratigraphic unit and that the mesosaurid reptiles colonised the sea halfway through its existence. The sea itself is seen as a relatively shallow embayment of a central sea arm that occupied a position between Africa and South America. In the Irati embayment (sea), black shales accumulated in the stratified waters of the relatively deeper central areas whilst limestones and dolomites formed in nearshore and generally shallow areas. The accumulation of limestones in the São Paulo-Mato Grosso-Goiás area is a result of the restricted nature of this sub basin.

Transgressive and regressive events caused a horizontal displacement of the shallow and deeper environments and resulted in isochronous facies changes in different parts of the basin. This explains e.g. the vertical displacement of deeper water black shales by shallow water limestones or even silty shales in some outcrops. The lithological changes because it was tied up with palaeoenvironmental changes were accompanied by faunal migrations which is reflected in the fossil-record.

RESUMO A reconstituição de um mar no Permiano Superior do Irati e as condições no corpo da água são tentadas. A reconstituição baseia-se na distribuição de fauna e fácies bem como na bioestratigrafia da formação. Deduz-se que o Irati, assim como a Formação Whitehill da África do Sul, é uma unidade cronoestratigráfica e que os répteis mesossaurídeos colonizaram o mar durante a metade do tempo da existência deste. O mar, em si, é visto como uma baía, relativamente rasa, de um braço de mar central que ocupou uma posição entre a África e a América do Sul. Na baía (mar) do Irati acumularam-se folhelhos pretos nas águas estratificadas de áreas centrais relativamente mais profundas, enquanto calcários e dolomitos se formaram perto da costa e geralmente em áreas rasas. A acumulação de calcários na área de São Paulo-Mato Grosso-Goiás resultou da natureza restrita desta sub-bacia.

Eventos transgressivos e regressivos causaram um deslocamento horizontal dos ambientes rasos e mais profundos que resultaram em mudanças isocrônicas de fácies em diferentes partes da bacia. Isso explica, por exemplo, o deslocamento vertical dos folhelhos pretos de águas mais profundas por calcários de águas rasas ou mesmo folhelhos sílticos em alguns afloramentos. As mudanças litológicas sendo vinculadas às mudanças paleoambientais foram acompanhadas por migrações faunísticas que se refletem no registro fossilífero.

INTRODUCTION The sediments of the Kazanian (?) age (Pinto, 1972) Irati sea cover an immense area (1,700 km²) in the States of Goiás, Mato Grosso, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul. The formation varies from 20 to 40 m in thickness. The sediments extend also into northern Uruguay, where the mesosaurid-bearing Mangrullo Formation outcrops in the Departments of Cerro Largo, Tacuarembó and Rivera, and are present in subsurface also in Artigas, Salto and Paysandú (Mones & Figueiras, 1980). In Paraguay, mesosaurid remains were reported from reddish shaley sandstones near the town of Villarica (Beder, 1923; Harrington, 1956). These sediments from the top of the Tubarão Formation are probably onshore, subaerial in origin.

Outside what is normally considered as the Paraná Basin, mesosaurid remains were also recovered from the pistolithic and oolitic limestones that outcrop in the upper Araguaia River, on the borders of Goiás and Mato Grosso. These sediments, which contain small crustaceans and silicified *Filicolas*, were correlated with similar sediments of the Pedra de Fogo Formation in the Parnaíba and Tocantins basins of Piauí, Maranhão and Bahia (Harrington, 1956). If this cor-

relations can in future be corroborated, the Pedra de Fogo Formation may once have extended across the central Brazilian shield area. It is however at present not possible to tell with certainty how far north the habitat of mesosaurid reptiles extended.

Mesosaurid reptiles were first described from the southern African Karoo basin, Whitehill Formation of the Ecga Group (formerly known as the White Band). A biostratigraphic study of the Whitehill Formation by Oelofsen (1981) has shown it to be a chronostratigraphic unit. Oelofsen (*op. cit.*) postulated that the almost identical Whitehill and Irati Formations were deposited in shallow contemporaneous embayments of a central sea arm that occupied a central position between the African and South American continents. From this a close similarity in the biostratigraphy of the two basins is to be expected.

THE DISTRIBUTION OF THE MESOSAURID GENERA IN THE IRATI FORMATION The presence of mesosaurid reptiles in the Irati sediments was known since 1886, when the first specimen from the limestones of São Paulo was des-

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cribed by Cope as *Stereosternum tumidum*. In 1908, McGregor described a second form from the black bituminous shales of Paraná and referred it to the genus *Mesosaurus*. A third form, *Brazilosaurus sanpauloensis*, from São Paulo, was described by Shikama & Ozaki (1966). It should be noted that several spellings of the species name *Brazilosaurus sanpauloensis* were used in the original description and the spelling adopted here is that of Araújo (1976).

Araújo (*op. cit.*), by means of statistical analysis, could establish beyond doubt that the abovementioned three genera were valid and she listed a number of morphological criteria by which the genera can be distinguished. Among these are differences in the ratio of cranial/cervical lengths, the length and shape of the teeth and differences in the number of cervical and dorsal vertebrae in the presacral vertebral count.

Although of sound and valid nature, as mathematically corroborated by Landim *et al.* (1980), these criteria had one practical disadvantage. It did not facilitate the classification of disarticulated specimens in the absence of cranial material. It is, unfortunately, almost invariably the case in disarticulated specimens that no cranial material can be found as is illustrated by the specimens from the Passo de São Borja outcrops of Rio Grande do Sul, and the African, Haub and Kalahari Karoo basins.

The Passo de São Borja material was, from lack of evidence to the contrary, and in accordance with the then known distribution of the three genera in the Paraná Basin, regarded as *Mesosaurus* (Araújo, 1976). This author therefore concluded, on the strength of the distribution of the different genera, that *Mesosaurus* occurs only in Paraná-Santa Catarina-Rio Grande do Sul area of the basin, which was predominated by black shales. This area was referred to as biozone A. The São Paulo area, which is predominated by limestones in which *Stereosternum* and *Brazilosaurus* occur, was referred to a second biozone, B. On the strength of some palynological datings by Daemon (1974), Araújo considered the sediments and fauna of zone B to be somewhat younger than that of the *Mesosaurus*-bearing beds of zone A.

With some minor exceptions, biozones A and B of Araújo coincide, respectively, with the mesosaurid-bearing carbonaceous black shales of the Santa Catarina-Paraná area and the predominantly limestones facies of the São Paulo-Mato Grosso-Goiás area.

The latter facies was considered to have formed in an isolated basin cut off from the southern sub basin by the activity of the Ponta Grossa Arch.

SEDIMENTARY ENVIRONMENTS IN THE PARANÁ BASIN DURING IRATI TIMES

In terms of palaeoecological environments, the model proposed for the sedimentation of the contemporaneous Africa Whitehill embayment, as advanced by Oelofsen (1981), can with some success also be applied to the Irati.

A shallow water environment during the deposition of the São Paulo (probably also Mato Grosso and Goiás) limestones is suggested by the presence of structures such as ripple marks and erosion cuts in the sediments (Amaral, 1971). In the relatively shallow water, proper mixing resulted which prevented the formation of anoxic bottom conditions. This explains the minor development of black shales in these areas.

To the north, in the Pedra do Fogo Formation, a proper evaporitic sequence developed in an area that was perhaps even shallower more subject to evaporation and less well re-fluxed than the São Paulo-Mato Grosso-Goiás area.

The *Mesosaurus*-bearing black shales of Paraná-Santa Catarina (Zone A of Araújo) in contrast represent sedimentation in relatively deeper, stratified waters with anoxic, highly sulphuretted toxic bottom brines. These reducing conditions resulted in the formation of the highly carbonaceous, pitobituminous oil and black shales of this area.

THE BIO- AND LITHOSTRATIGRAPHY OF THE IRATI FORMATION. GENERAL REMARKS

A study of the general litho- and biostratigraphy of the Irati Formation of different areas of the Paraná Basin reveals some remarkable parallelisms, some of which will be commented on.

From Fig. 1 it is clear that all areas of the basin were colonized by mesosaurid reptiles after roughly one half of the sediments of the formation had been deposited. If a generally constant rate of sedimentation is accepted for the total pack of sediments, it can be inferred that the Irati "sea" was invaded by the mesosaurids about halfway through its existence in time. As the colonization of an area by a group of animals is, in terms of geologic time, instantaneous, the first appearance of the reptiles can be used as a very good isochron.

Another isochron is found in the appearance of the pygocephalid crustacean genus *Pygaspsis* near the top of the formation. Incidentally, it should be pointed out that in the present paper the Tiaraju facies (Figueiredo Filho, 1972) only is considered as the equivalent of the African Whitehill Formation and when we refer to the Irati Formation the upper Valente facies identified in Rio Grande do Sul is not considered part of the formation. The top of the formation is therefore taken at the top of the black shales, more or less 1 m above the *Pygaspsis* range zone.

A third correlatable feature of the biostratigraphic column is the presence of *Liocaris* in the middle limestone layers developed in some areas of the basin.

In terms of lithology and sedimentary environments, the following correlations may be drawn.

The peak development of the thick pack of limestones and dolomites in the middle of the São Paulo facies is followed by a grey siltstone which could be interpreted as the culmination of a period of shallowing and regression in this area. This episode of regression is also documented elsewhere in the deeper areas of the basin, e.g. in Paraná-Santa Catarina by the displacement of the bituminous shales by impure limestones and dolomites with intercalated calcareous and black shales.

The Passo de São Borja outcrops

A preliminar study of the biostratigraphy of the Passo de São Borja outcrops on the Santa Maria River, more or less 40 km SSW of São Gabriel, in Rio Grande do Sul, was made. The presence of disarticulated mesosaurid material from limestone beds intercalated in this outcrop has been known for a long time. Some aspects of the outcrops have already been studied by e.g. Jost & Ferreira Pinto (1970), who concentrated on the lithology, and Amaral (1971), who commented mostly on the calcareous beds. The latter worker noticed the close macroscopic similarity between the pale massive limestones in Passo de São Borja and those in Piracicaba and Laranjal Paulista (São Paulo), even as to the amount and nature of the insoluble residue in hydrochloric acid. Amaral furthermore pointed out the presence of similar gymnosperm spores in the limestones of the two areas and considered this an argument for the correlation of the limestones of the two areas.

Amaral (*op. cit.*) attributed the disarticulated nature of the skeletons in the outcrops to a high energy environment, a conclusion corroborated by the presence of intraformational

lenses of limestone clastic conglomerates in the limestones (Jost & Ferreira Pinto, *op. cit.*). Also associated with the limestone beds abundant fossil wood and *Liocaris* occur, both being absent from the carbonaceous black shales immediately underneath and above the limestones.

The presence of rolled fossil wood and disarticulated skeletal elements, the development of the limestones and the intraformational erosion cuts, which resulted in the limestone conglomerates, we consider conclusive evidence for a relatively shallow, high energy environment. We therefore consider conditions during the deposition of the limestones at Passo de São Borja to be very similar to the conditions of deposition Amaral (1971) visualises for the São Paulo limestones.

The regression which resulted in the deposition of the limestones at Passo de São Borja temporarily terminated the formation of limestone in the shallower parts of the basin and caused the deposition of the gray siltstone in the middle of the formation in the São Paulo area. In the deeper parts of the basin (Paraná-Santa Catarina), the regression temporarily brought an end to the formation of the pirobituminous black shales and impure limestones resulted. The Passo de

São Borja calcareous layers, the impure limestones at São Mateus and the gray siltstone in São Paulo (Fig. 1) are therefore isochronous. This deduction is corroborated by the fortunate fact that the mesosaurid reptiles invaded the basin sometime during this regressive period and thus constitute an independent isochron.

The above mentioned period of shallowing in the basin (regressive phase) was followed by a period of deeper water (transgressive phase). In the Passo de São Borja area the shallow water limestone facies probably shifted westward with the transgression. The position of the coastline in relation to Passo de São Borja can be deduced from the presence of red silty sandstones with mesosaurid material in the south-east of Paraguay (Beder, *op. cit.*; Harrington, *op. cit.*). These sediments were partly subareal in origin as its red colour and coarse clastic nature indicate. Towards the west, in the central Santa Catarina, black shales of the central basin occur. The coastline of the Irati sea (Figs. 2 e 3) running from North to South must have crossed the line between the Santa Catarina central area and the Paraguay onshore sediments somewhere to the West of Passo de São Borja.

Drawing by Jefferson C. Simões

Figure 1 —

Figure 2 — Shoreline of Irati Embayment

Figure 3 —

With the transgressive phase, the shallow water limestone environment was replaced by deep water and the carbonaceous black shale overlying the limestones was formed as a result of the return of reducing conditions. Energyless conditions also returned, for the mesosaurid skeletons in the shale are mostly articulated and fossil wood is absent.

Near the top of the Passo de São Borja section, *Pygaspis* is present whilst the disarticulated remains of mesosaurids in the limestones are associated with vast numbers of *Liocaris*. This corresponds very well with the stratigraphical position of crustaceans elsewhere in the basin and confirms that the Passo de São Borja limestones are situated near the middle of the formation. This could, however, not be established in the outcrop at Passo de São Borja for the base of the formation is not exposed at Passo de São Borja and our observations were hampered by the fact that the river was in flood. Only the top 1 m of an unfossiliferous black shale below the limestones could be seen in one locality. From the sections of Padula (1969), however the conclusion that the limestones occupy a position near the middle of the formation is inevitable.

The presence of mesosaurus, stereosternum and brazilosaurus in Passo de São Borja In a study of the osteology of the Mesosauridae by the first author, differences in the haemal arches of *Mesosaurus* and *Stereosternum-Brazilosaurus* were noticed. This study forms part of a revision of the Mesosauridae and an attempt to unravel the cranial anatomy of the group. The result of this study will be published elsewhere.

The haemal arches of *Mesosaurus* are frail with the two arms of an arch forming a sharp V. In *Stereosternum* and *Brazilosaurus* the haemals are stout, pachyostosed elements with the two arms of an arch arranged in a more rounded U-shape (Fig. 4). This feature now for the first time enabled us to distinguish between the genera *Mesosaurus* and *Stereosternum-Brazilosaurus* in disarticulated post-cranial material. This proved to be very practical, for haemal arches are, due to the large number (± 55) present in each individual, frequently found among disarticulated material.

Figure 4 — Haemal arches: A) of *Mesosaurus*; B) of *Stereosternum*; and C) of *Brazilosaurus*

From our model for the palaeoecological environments and distribution of the mesosaurid genera in the Irati sea or embayment, the shallow limestone facies at Passo de São Borja is predicted to be a duplication of the shallow environment in São Paulo, where *Stereosternum* and *Brazilosaurus* are found. This led to a reexamination of the Passo de São Borja material, which was previously referred to *Mesosaurus* (Araújo, 1976).

Our study of the material in the collection of the Department of Paleontology and Stratigraphy of the Federal University of Rio Grande do Sul, revealed the presence of pachyostosed haemal arches of the *Stereosternum-Brazilosaurus* type. Unpachyostosed ribs indicated the presence of *Brazilosaurus* and pachyostosed ribs of the type common to *Stereosternum* and *Mesosaurus* occur in abundance. Confirmation of the presence of *Stereosternum* was found in a further closer study of the material when two bits of mandible with 4.5 mm long teeth, oval in cross section, were discovered. Araújo (1976) has shown that the teeth in *Mesosaurus* are circular in cross section whereas that of the other two genera are oval. The length of the Passo de São Borja teeth falls within the range for teeth lengths measured in *Stereosternum* by Araújo, whereas the maximum registered length for the teeth in *Brazilosaurus* was only 2.75 mm.

During a subsequent visit to the Passo de São Borja outcrops, frail *Mesosaurus* haemal arches were also found which confirmed the presence of this genus, as was suggested by the presence of heavily pachyostosed ribs.

The new evidence, therefore invalidates the idea of two rigid zones of distribution of fauna and a difference in age for the São Paulo and Santa Catarina-Paraná sediments as was

suggested by Araújo (1976). The general association of *Mesosaurus* with black carbonaceous shale, deep water conditions, and *Stereosternum-Brazilosaurus* with limestone, under shallow conditions, however, still seem to be valid.

CONCLUSIONS AND PREDICTIONS 1. The first conclusion that can be drawn from the new results is that *Mesosaurus*, *Stereosternum* and *Brazilosaurus* were contemporaneous in the Irati embayment. There is, therefore, no evidence to support the suggestion that the Irati sediments formed in isolated sub-basins (Mendes, 1961, 1963; Araújo, 1976). Amaral (1971) observation on the general dip of the sediments which suggested to him the existence of a single basin is confirmed. Although the Ponta Grossa Arch did not isolate the São Paulo sub-basin completely as Araújo (1976) suspected the positive orogeny caused by this feature, probably did cause the relatively shallow and restricted nature of this area. As could be inferred from the litho- and biostratigraphy of the sediments, the first appearance of mesosauroids in the middle of the formation over the whole basin, constitutes a very good isochron. The formation is, therefore, regarded by us as a chronostratigraphic unit.

From the lithology it seems sure that the basin went through an initial period of transgression resulting in deeper water, especially in the central part of the basin. This was followed by a general shallowing of the basin (regressive phase) during which limestone formation over the major part of the basin predominated. The limestones in the central areas, however, never became dominant. The shallowing culminated in the deposition of a gray siltstone in some shallow, possibly nearshore, areas. A major transgressive phase followed and black shales were again deposited. The relatively shallow areas such as the São Paulo embayment now also experienced minor black shale development, which appear as intercalations between the upper calcareous layers.

Differences in the lithostratigraphy especially is the lower part of the column, such as the one noted by Amaral (*op. cit.*) in the boreholes near Guareí (SP), could reflect original differences in bottom topography.

As illustrated by the profiles at Guareí and Angatuba, the transition from Paraná-Santa Catarina deeper water to São Paulo-Mato Grosso-Goiás shallow water probably was in the area between the abovementioned localities.

2. We, like Amaral (1971), consider the limestones as indications of shallow deposition. We visualize a shallow area of limestone sedimentation fringing the black carbonaceous shales of deeper environments towards the center of the basin. In the São Paulo area, the more extensive development of limestones and the presence of clastic sediments (Mezzalana, 1971) indicate extended periods of shallow conditions. Along the western border, in what we consider to be near coastal areas, we expect the limestones to continue as smaller, more restricted units to join up with the limestones in Rio Grande do Sul and Uruguay. Towards the center of the basin, these limestones will interfinger with blue and black shales, which will again interfinger with pirobitumenous shales. Areas of intermediate water depth (southern Rio Grande do Sul, Uruguay) will show an increase in the relative abundance of black shales over carbon-rich black shales.

3. The different forms of mesosauroid reptiles inhabited different paleoenvironments in the Irati sea. These areas can be broadly classified in two recognizable zones (Fig. 2) which, in faunal composition, coincide with zones A and B of Araújo (1976). The biozones were determined by water depth and some anatomical adaptations in the species of mesosauroids can be correlated with this.

Stereosternum and *Brazilosaurus* were shallow water forms and therefore are almost exclusively associated with the shallow water limestones. Of the two, *Brazilosaurus* has virtually no special adaptations to deep aquatic environments as is indicated by the lack of pachyostosis of the ribs. The shallow water limestones, with abundant *Stereosternum*, yield relatively few *Brazilosaurus*, which may be interpreted as representing the fringe of the *Brazilosaurus* population. It is likely that the main population of *Brazilosaurus* frequented the coast and coastal waters. *Stereosternum*, more aquatic in nature and showing intermediate pachyostosis of the ribs, apparently occupied the more offshore, shallow areas of the Irati embayment.

In *Mesosaurus*, the ribs reach the highest degree of pachyostosis, although there is evidence that only some forms (species?) of *Mesosaurus* developed the extremely thick ribs. *Mesosaurus*, as was previously advanced (e.g. Araújo, 1976; Oelofsen, 1981) was probably a filter feeder exploiting organisms in the central areas of the basin. *Mesosaurus* will, as a general rule, be associated with the central areas of the basin and is therefore often present in the black oil shale in great profusion. In spite of the excellent fossilization, no trace of any macroscopic fauna or flora is present in these shales, with the exception of some crustaceans in the upper layers (Fig. 2). Large blooms of planktonic organisms could have provided food for *Mesosaurus* and, upon decaying in reducing bottom waters, would have supplied the organic material and sulphur present in the pirobitumenous shales.

In contrast, *Stereosternum* and *Brazilosaurus* are usually associated with innumerable fossils of e.g. *Liocaris*, on which they probably fed.

Some of the observations that our model is based on was already known to E. de Oliveira and he suggested to Rego (1930) that *Mesosaurus* is characteristic of the bitumenous shales while *Stereosternum* occurs in the limestones. He furthermore suggested that habitat differences led to the anatomical differences and that *Mesosaurus* lived in "muddy" waters whilst *Stereosternum* frequented the clear waters of limestone deposition. Although we do not see the waters of black shale deposition as "muddy" the insight de Oliveira had is surprising and it is a loss to science that it fell into obscurity for so long. It was only after our work has reached completion that the work of de Oliveira was brought to our attention by chance.

4. The exclusive presence of neither *Mesosaurus*, *Stereosternum* or *Brazilosaurus* in any particular part of the basin is to be expected, as some minor overlap in distribution naturally was inevitable. This is, for instance, illustrated in the Passo de São Borja outcrops, where all three genera are present, and by the presence in Paraná black shales of a specimen with the *Stereosternum-Brazilosaurus* presacral vertebral count of 34 (unnumbered specimen in the Von Huene material, Tübingen). This last case (Paraná area) could well be interpreted as a fortuitous straying of a shallow water form to deeper waters. The presence of stray individuals among vast numbers of the species adapted to that particular environment is to be expected and corroborate the coexistence of the different forms in the basin.

In the narrow strip of near coastal limestones all three genera should, however, be present, for *Mesosaurus*, at least twice a year, had to cross this zone somewhere in order to deposit its eggs on land. In this area was the permanent habitat of *Stereosternum*, the majority of fossils will, however, be of this genus. The ratio found e.g. in the Passo de São Borja limestone facies, where *Brazilosaurus* seems to constitute approximately 5% of the fossil material and *Mesosau-*

rus even less, support this view. In the overlying black pirobitumenous shales, *Mesosaurus*, however, again dominates, indicating the return of the deep water "Mesosaurus environment".

The material in Uruguay referred to *Mesosaurus* (Mones & Figueiras, 1980) will, in view of the presence of *Stereosternum* and *Brazilosaurus* in Rio Grande do Sul and the apparently shallow conditions that prevailed in Uruguay, probably be of the latter genera. The "Mesosaurus" material in Paraguay (Beder, 1923; Harrington, 1956) will probably also, on close examination, be *Stereosternum-Brazilosaurus*. By the same argument we could predict that the specimens from the upper Araguaia River, referred to *Mesosaurus* by Harrington (*op. cit.*), would be *Stereosternum* and *Brazilosaurus*. This prediction we were able to put to the test for two specimens from this region were found and examined in the collection of the Museu Nacional in Rio de Janeiro. Although both specimens were catalogued as *Mesosaurus* it turned out that one is *Stereosternum* (3,777-u) and the other *Brazilosaurus* (3,779-u).

5. The absence of the shallow water limestone facies on the eastern fringe of the Irati where deep water pirobitumenous shales predominate refutes the proximity of land in this direction. This supports a direct connection of the African Whitehill and South American Irati basins with each other and the world oceans as was suggested by Oelofsen (1981). The physical form of the Paraná Basin therefore changed drastically from the previous Rio Bonito times, when sediments flowed into the basin from the Ponta Grossa, Curitiba, Florianópolis high areas in the north-east and the Porto Alegre-Uruguay shield in the south-east (Medeiros and Thomaz, 1973; Castro, 1980). Even at this time it seems possible that a connection with the sea towards the east through the Torres syncline was possible. During most of the Irati times, however, no emergent areas between the Ponta Grossa Arch

and the Porto Alegre-Uruguay shield seems to have existed.

It is furthermore possible that the northern Uruguay embayment encircled the Porto Alegre-Uruguay shield area, thus transforming it into an island. The elevation of these "high" areas, as Amaral (1971) also concluded, however, must have been very slight as is indicated by the almost total absence of clastic sediments in the basin.

To the north, the São Paulo-Mato Grosso-Goiás embayment possibly extended across the Central Brazilian shield area and could have resulted in the formation of the evaporitic succession of the Pedra do Fogo Formation. The absence of mesosaurids in the evaporites is probably a result of physiological intolerance to such severe environments. In the stratified water of the Paraná Basin, the mesosaurids inhabited the top, relatively fresh water layers as necotonic organisms and never came in voluntary contact with the bottom brines.

In final conclusion it should be stated that much detail work is still needed before the Irati will be fully understood. We hope that this paper will stimulate such work.

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REFERENCES

- AMARAL, S. E. do — 1971 — Geologia e Petrologia da Formação Irati (Permiano) no Estado de São Paulo. *Bol. IGA São Paulo*, (2):5-81.
- ARAÚJO, D. F. — 1976 — Taxonomia e Relações dos Proganosáuria da Bacia do Paraná. *An. Acad. bras. Ciênc.* 48(1):91-116.
- BEDER, R. — 1923 — Sobre un hallazgo de fósiles Pérmicos en Villarrica (República del Paraguay). *Bol. Acad. Nac. Ci. de Córdoba*, 27:9-12.
- CASTRO, J. C. — 1980 — Fácies, Ambientes e Sequências Depositionais das Formações Rio do Sul e Rio Bonito, Leste de Santa Catarina. In: XXXI Congr. Bras. Geol. Camboriú 1980, SBG. *Anais* 1:283-99.
- COPE, E. D. — 1886 — A Contribution to the Vertebrate Paleontology of Brazil. *Proc. Amer. Phil. Soc.*, 23:7-15.
- DAEMON, R. F. — 1974 — Integração dos Resultados Palinológicos aos de Fauna e Flora de Camadas Fossilíferas do Neopaleozóico da Bacia do Paraná — Implicações Estratigráficas e Paleogeográficas. *Revista Unimar*, Univ. Est. de Maringá, 1(1):25-41.
- FIGUEIREDO FILHO, P. M. — 1972 — Faciologia do Grupo Passa Dois no Rio Grande do Sul. *Rev. Bras. Geol.*, 2(4):216-235.
- GERVAIS, M. P. — 1864 — Description de *Mesosaurus tenuidens*, reptile fossile de l'Afrique. *Mem. Acad. Montpellier Sec. Sci.*: 169-175.
- GERVAIS, M. P. — 1865 — Du *Mesosaurus tenuidens* reptile fossile de l'Afrique Australe. *Acad. Sci. Paris*: 950-955.
- HARRINGTON, H. J. — 1956 — Handbook of South American Geology. *The Geol. Soc. of Amer. Memoir* 65:101-128.
- JOST, H. e FERREIRA PINTO, J. — 1970 — Geologia da Folha Estância da Barra, São Gabriel-Rosário do Sul-R.G.S. Geologia da Folha Suspiro, São Gabriel-Lavras do Sul-R.G.S. *Bol. Esc. Geol.*, (17):7-75.
- LANDIM, P. M. B.; PISANI, J. F. e STURARO, J. R. — 1980 — Um Método para a Representação Gráfica de Dados Multidimensionais em Geociências. In: XXXI Congr. Bras. Geol. Camboriú, 1980, SBG. *Anais* 2:1233-1242.
- MCGREGOR, J. H. — 1908 — On *Mesosaurus brasiliensis* nov. sp. from the Permian of Brazil. In: *Comissão Estudos Minas de Carvão de Pedra do Brasil*. Ed. by I.C. White. National Press, Rio de Janeiro, Parte II:301-336.
- MEDEIROS, R. A. e THOMAZ, F. A. — 1973 — Fácies e Ambientes Depositionais da Formação Rio Bonito. In: XXVII Congr. Bras. Geol. Aracaju 1973, SBG. *Anais* 3:3-12.
- MENDES, J. C. — 1961 — Algumas considerações sobre a Estratigrafia da Bacia do Paraná. *Bol. Paranaense Geogr.* (4/5):3-33.
- MENDES, J. C. — 1963 — Novos Aspectos da Estratigrafia das Camadas Eogondwânicas da Bacia do Paraná. *Eng. Min. Met.* 38(226):189-192. Rio de Janeiro.
- MEZZALIRA, S. — 1971 — Contribuição ao Conhecimento da Geologia de Sub-Superfície e da Paleontologia da Formação Irati, no Estado de São Paulo. *An. Acad. bras. Ciênc.* 43:273-336.
- MONES, A. and FIGUEIRAS, A. — 1980 — A Geopaleontological Synthesis of the Gondwana Five. Selected papers and abstracts of papers presented at the Fifth International Gondwana Symposium. Wellington, New Zealand 47-52.
- OELOFSEN, B. W. — 1981 — An Anatomical and Systematic Study of the Family Mesosauridae (Reptilia; Proganosauria) with Special Reference to its Associated Fauna and Palaeoecological Environment in the Whitehill Sea. Thesis presented for the Degree of Doctor Philosophy at the University of Stellenbosch, South Africa.
- REGO, L. F. M. — 1930 — *A Geologia do Petróleo no Estado de São Paulo*. Serv. Geol. Minér. do Brasil, Boletim n° 46, pp. 1-10.

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