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Unusual environmental conditions preserve a Permian mesosaur-bearing Konservat-Lagerstätte from Uruguay

GRACIELA PIÑEIRO, ALEJANDRO RAMOS, CÉSAR GOSO, FABRIZIO SCARABINO, and MICHEL LAURIN



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The environmental characterization of the Lower Permian mesosaur-bearing strata of the Mangrullo Formation (Paraná Basin, northeastern Uruguay) has been controversial. Historically, marine conditions were suggested for this unit, despite the absence of any normal marine fossils. More recently, some authors have argued for freshwater to brackish settings, inferring fluctuating environmental conditions, which would have generated abrupt changes in the composition of the communities. Mesosaurs are the only tetrapods found in this unit, and they colonized the basin at the time of highest isolation, and apparently increased salinity, coincident with a gradual global rise in aridity. An assemblage of extremely low diversity (the "mesosaur community") developed, with mesosaur reptiles, pygocephalomorph crustaceans, and the vermiform producers of the trace fossil *Chondrites* as the dominant components. This community may have existed under temporary hypersaline, lagoon-like conditions, as suggested by ecological, anatomical and physiological attributes of its member taxa. This interpretation is supported by sedimentological and mineralogical features of the enclosing rocks, also seen in the correlative Brazilian Iratí and South African Whitehill formations. In the Uruguayan deposits, as well as in their Brazilian correlatives, relatively close volcanic events affected the basin. This particular environment, where bottom waters were depleted of oxygen and hypersaline, retarded decay of the carcasses, and precluded the development of bioturbating organism, and together with bacterial sealing, favoured exquisite preservation of the fossils, including soft tissues. This leads us to consider the fossil-bearing strata of the Mangrullo Formation as a Konservat-Lagerstätte, the oldest known for South America.

Key words: Mesosauridae, Pygocephalomorpha, hypersaline environments, "mesosaur community", Konservat-Lagerstätte, Mangrullo Formation, Lower Permian, Uruguay.

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Introduction

The Lower Permian Mangrullo Formation, cropping out in northeastern Uruguay, is part of the Paraná Basin infill (Zalán et al. 1990) that covers parts of Brazil, Argentina, Paraguay, and Uruguay. The Mangrullo Formation, nearly 40 m thick (De Santa et al. 2006a), consists mostly of oil-stained, laminated shale, claystone, and siltstone beds, with lenticular to massive structures and partially silicified limestone beds of variable thickness. Previous studies suggested that these sediments had been deposited in a shallow epicontinental sea of variable salinity (Bossi and Navarro 1991; De Santa Ana 2004) under a low-energy environment that allowed the preservation of articulated, almost complete skeletons of mesosaur reptiles and complete individuals of pygocephalomorph crustaceans (Piñeiro 2006; Piñeiro et al. 2012, in press a, b). The Mangrullo Formation is correlated with the Brazilian Iratí Formation (Paraná Basin) and the South African Whitehill Formation (Karoo Basin), mainly on the basis of the shared mesosaur–pygocephalomorph association (Delaney and Goñi 1963; Daemon and Quadros 1970, Oelofsen and Araújo 1983; Bossi and Navarro 1991; Piñeiro 2006, 2008). This assemblage, here referred as the "mesosaur community", has been described for the Iratí Formation of Brazil as well as for the Whitehill Formation of South Africa (Oelofsen 1981), despite the apparent absence of the trace fossil *Chondrites* in the last

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unit. An Artinskian age has been suggested for the Iratí Formation (Santos et al. 2006; Holz et al. 2010), and by extension, for the Mangrullo Formation.

Key fossils in the Mangrullo Formation are the mesosaurs, basal reptiles (Laurin and Reisz 1995; Modesto 1999a). They differ strongly from other early amniotes in their habitat, being the first with a mostly or fully aquatic lifestyle (Modesto 2006; Canoville and Laurin 2010), which may explain why they are not found in the same basins as other early amniotes. Mesosaurs had a fairly wide distribution in Gondwana, being found in South America (Brazil and Uruguay) and Africa (South Africa and Namibia). Moreover, as mesosaurs had a restricted temporal distribution, they are useful fossil markers for the Gondwanan Permian. Despite several hundred complete mesosaur skeletons in museum collections, many aspects of their anatomy and biology remain uncertain, including their habitat.

Previous environmental studies of the Mangrullo Formation have yielded inconsistent results, particularly concerning salinity. Traditionally, marine conditions were inferred, from environmental studies in the coeval Iratí Formation (e.g., Beurlen 1957; Amaral 1971; De Giovanni et al. 1974; Mezzalira 1980; Oelofsen and Araújo 1983). Fossils are rare in the Mangrullo Formation, including bivalves (Figueiras and Broggi 1968), indeterminate conchostraceans, fragmentary pygocephalomorphs (Bossi and Navarro 1991), silicified wood fragments of Coniferales and Glossopteridales (Crisafulli and Lutz 1995; Zamuner 1996) and palynomorphs (Bossi and Navarro 1991; Beri and Daners 1995; Andreis et al. 1996; Piñeiro et al. 1998). None of these is a good indicator of marine environments because they occur in other environments (Piñeiro 2004). Especially, terrestrial plants occur on the coast, so their remains may be fossilized in any type of aquatic environment (Schultze 2009). Recent field efforts within this unit have yielded numerous new materials, including well preserved, almost complete mesosaur skulls and partial skeletons, very fragmentary actinistians (coelacanths), actinopterygian remains, possible acanthodian trace fossils and various other ichnofossils, well preserved, almost complete pygocephalomorph crustaceans, homopteran and coleopteran insect wings, and well preserved plant remains assigned to the *Gangamopteris* Flora (Pinto et al. 2000; Piñeiro 2004, 2006, 2008). Based on the absence of fully marine taxa, Piñeiro (2004, 2006) inferred freshwater to brackish conditions for the fossiliferous levels, taking also into account similar environments suggested for apparently equivalent pygocephalomorph Laurasian communities (Schram 1981). Nevertheless, a thorough analysis of the depositional environment of the mesosaur-bearing strata of the Mangrullo Formation, including ecological, palaeobiological, and anatomical information from the fossils, as well as geological evidence, leads to a different interpretation. The new hypothesis suggests a hypersaline depositional environment for the oil-shale with the fossils, and this could explain the absence of normal marine fossils, the low diversity of the assemblage, and its exceptional preservation.

Institutional abbreviations.—FC-DPV, Colección de Vertebrados Fósiles, Departamento de Paleontología, Facultad de Ciencias. Montevideo, Uruguay; GMHR, Museo Histórico Regional de Cerro Largo, Colección Geológica, Uruguay; MGT, Museo de Geociencias de Tacuarembó, Uruguay.

Other abbreviations.—HCS, hummocky cross stratification; nof, foramen nariale obturatum.

Geological and ecological setting

Most South American Late Palaeozoic sedimentation is characterized by a glacial event that affected the southwestern region of Gondwana (Chumakov and Zarkov 2002). In Uruguay, the glacial cycle (in the north and northeast of the country) is represented by fluvio-glacial and glacio-lacustrine deposits of the Late Carboniferous to Early Permian San Gregorio, Cerro Pelado and Tres Islas formations (Paraná Basin) (De Santa Ana et al. 2006b). At the beginning of the Early Permian, the retreat of the ice sheets was followed by progressive continental warming and increased aridity, with expansion of deserts through low latitudes (Poulsen et al. 2007). Therefore, the Fraile Muerto and Mangrullo formations overlying the Tres Islas Formation were deposited under the influence of sea-level changes and warmer climatic conditions. At least two transgressive-regressive cycles were recognized during the deposition of those units, generating an extensive water body covering part of south-western Gondwana (De Santa Ana et al. 2006b), which was subsequently affected by intensive drying and hostile conditions.

Deposition of the Mangrullo Formation (see Fig. 1, and locality map in Piñeiro et al. 2012) began at a time of rising sea-levels in a relatively warm-temperate climate resulting from migration of Gondwana away from the South Pole and retreat of the ice. The open coastal barrier may have led to an extensive inflow of saline water, but freshwater contributions from deglaciation may also have been important, even favouring the development of freshwater ponds and allowing sporadic colonization by conchostracean crustaceans.

The inferred estuarine-like, brackish conditions for the lower grey to black mudstone are supported by the biota dominated by actinopterygians, coelacanths, and acanthodians, together with indeterminate bivalve molluscs and bioturbating organisms with soft bodies, including the trace fossil *Chondrites* (Piñeiro 2004) in the highest levels of the lower claystone succession (Fig. 1). The vertebrates are mostly represented by isolated scales and teeth that cannot be identified more precisely. Although some scales were tentatively attributed to the Family Elonichthyidae (Piñeiro 2002) because of their small size and sharp, striated dorsal ornamentation (Stamberg 2006), it is difficult to recognize how diverse the gnathostome fauna was, and even whether each major clade was represented by more than one taxon. The presence of acanthodians similar to *Acanthodes* was inferred from the ichno-

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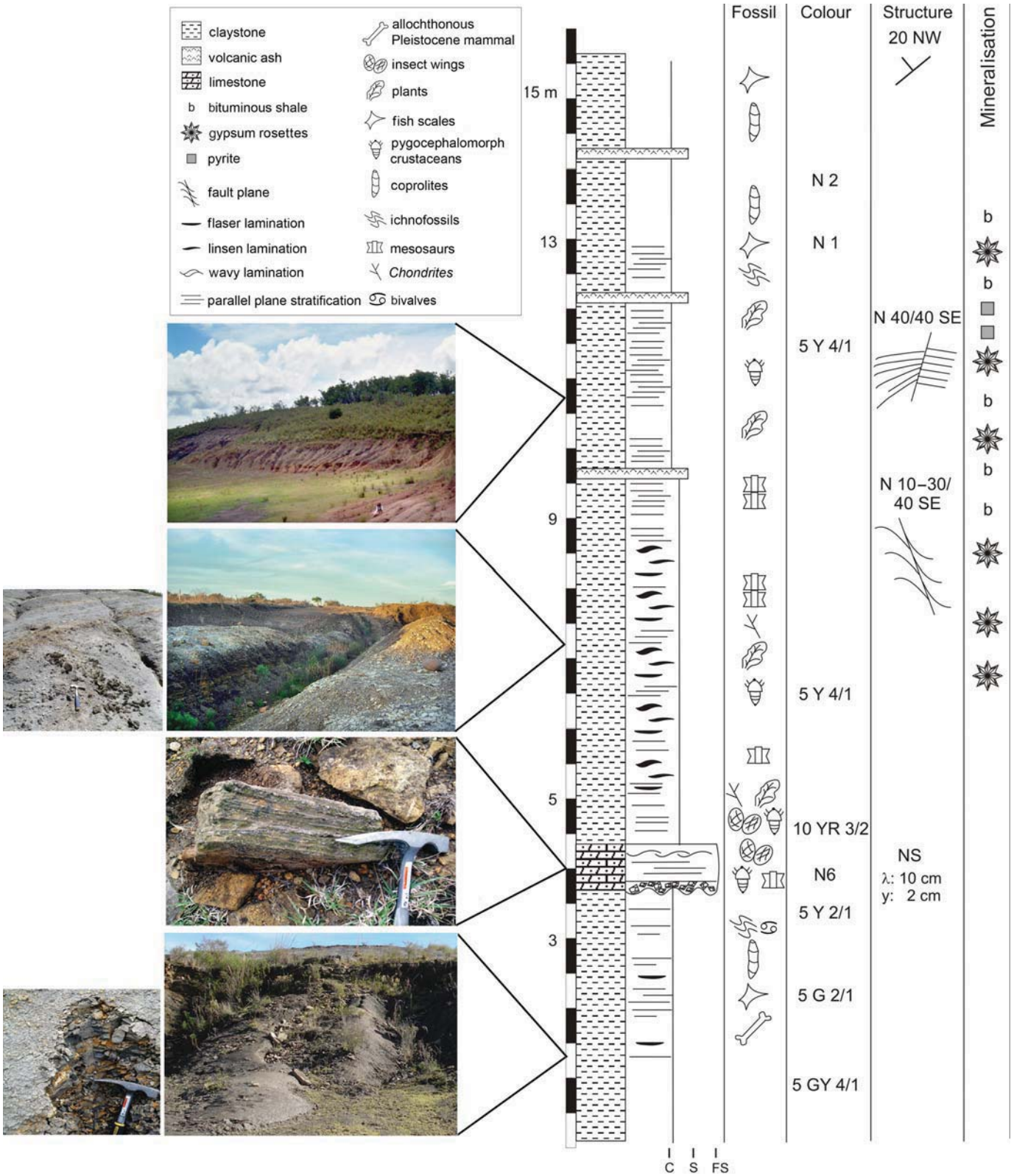


Fig. 1. Generalized stratigraphic section of the Early Permian Mangrullo Formation (Northeastern, Uruguay), showing the various sedimentary facies and their corresponding fossil associations, including the "mesosaur community". Colour codes from standard Munsell Chart. Abbreviations: C, conglomerate; S, silt; FS, fine sandstone.

fossil *Undichna insolentia* (Piñeiro 2006), a Permo-Carboniferous trail consisting of two pairs of in-phase waves and scalloped waves (Anderson 1976). Although our specimen lacks the scalloped wave, the preserved trail displays a pattern that is consistent with the original description (Anderson 1976; see also Trewin 2000). The various *Undichna* species were as-

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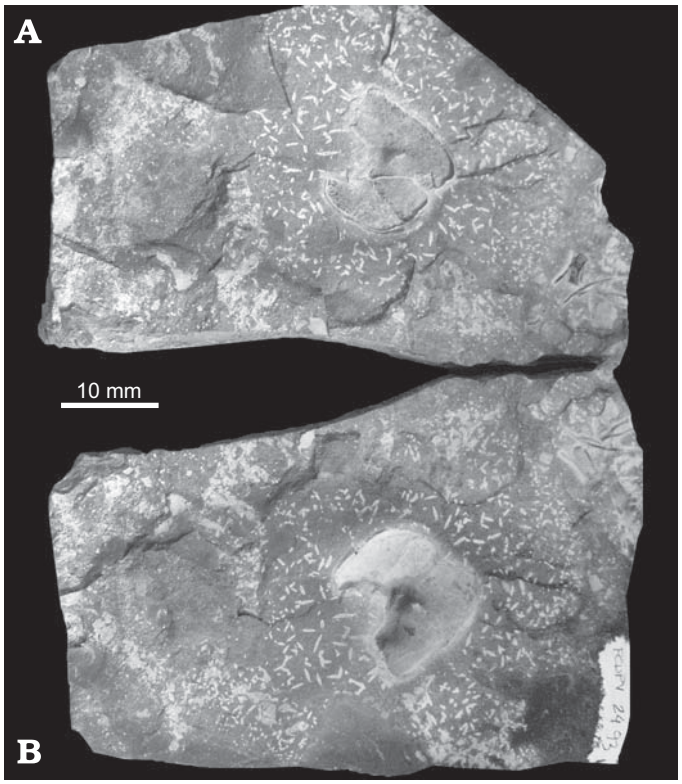


Fig. 2. Mesosaurid scapulocoracoid, FC-DPV 2493, part (**A**) and counterpart (**B**), from the Early Permian Mangrullo Formation (Northeastern Uruguay) preserved in a shale surface highly bioturbated by the trace fossil *Chondrites*.

signed to vertebrates that travelled with their paired fins making contact with the substrate, and acanthodians, elasmobranchs and actinopterygians have been suggested as possible producers (Anderson 1976; Trewin 2000). It should be noted that only actinopterygian and coelacanth body fossils were identified in the lower pelitic levels of the Mangrullo Formation, but no chondrichthyans, which are common in the lower section (Taquaral Member) of the correlative Iratí Formation of Brazil (Chahud et al. 2010). Most Carboniferous and Permian finned vertebrates were described from sequences traditionally interpreted as freshwater or brackish (e.g., Zajíc 2004; Zajíc and Stamberg 2004; Stamberg 2006), but recent works suggest that many of these were actually marine or brackish (Schultze 2009; Laurin and Soler-Gijón 2010), an interpretation corroborated by the marine habitat of the living coelacanth and of the vast majority of extant chondrichthyans (Janvier 1996).

Overlying the mudstone, a decimetric light-coloured limestone layer with ripple-cross-lamination was deposited, indicating wave oscillation in a shallow environment (Piñeiro 2004; De Santa Ana et al. 2006b). This cross-bedding structure suggests that a regressive cycle had started. The connection with the open sea was lost, producing a restricted basin that became progressively shallower (De Santa Ana et al. 2006a), and where evaporitic processes, attested by several layers rich in gypsum rosettes (Fig. 1), may have been favoured by the widespread aridity of the growing Pangaea. Mesosaurs and pygocephalomorph crustaceans first appear in these dolomite and limestone beds (Fig. 1).

The gradual drying of the basin and the stratification of the water column, producing anoxic bottom conditions and increasing salinity by evaporation, may have led to the progressive disappearance of the biota dominated by actinopterygians, coelacanths, and acanthodians, as shown by an interruption in their fossil record before the limestone containing the first mesosaurs and pygocephalomorphs was deposited. The latter taxa dominated the whole regressive cycle, which is represented by the limestone and the overlying oil-stained shale and mudstone; we interpret these as having been deposited in progressively more saline lagoons under the highest restriction of the basin. The oxygen depletion at the bottom prevented colonization by benthic and endobenthic organisms, except for the vermiform producers of the trace fossil *Chondrites* (Fig. 2), which are thought to be opportunist organisms that lived where most other metazoans could not (Bromley and Ekdale 1984).

The initial, transgressive, and free water exchange conditions were reestablished at the top of the unit, where the mesosaur community was no longer present. Actinopterygians and actinistians regained their dominant status and bottom conditions became favourable to colonization by benthic, bioturbating soft-bodied organisms. The affinities of the tracemakers are difficult to determine with certainty because of poor preservation, but *Planolites*, *Arenicolites*, and *Paleophycus*-like structures have been observed (Piñeiro 2002).

Biostratigraphic comparisons with the correlative Iratí Formation of Brazil show some ambiguity in the distribution of taxa, particularly the association of mesosaurs and actinopterygians. However, sedimentologically, both units are very similar. Two members are recognized in the Iratí Formation, the lower Taquaral, represented by siltstone and mudstone beds, and the upper Assistencia Member, predominantly organic-rich shale and intercalated limestone (Santos et al. 2006). These units could be delimited in the Mangrullo Formation (Fig. 1), with comparable evaporitic deposits at the base of the Assistencia Member (Hachiro 2000; Araújo 2001; Holz et al. 2010). However, there is confusion in papers about the Iratí Formation, which indicate several fossiliferous levels each containing a different assemblage; some suggest that a mesosaur-actinopterygian association is present (e.g., Mezzalira 1980), but others do not (e.g., Mussa et al. 1980). Others report only the presence of mesosaurs, crustaceans, actinopterygian scales and other gnathostome remains, ostracods, sponge spicules, etc. in the unit (e.g., Soares 2003 among others), without indicating whether all these taxa coexisted. In a recent, integrative stratigraphic study of the Carboniferous–Permian succession in the Paraná Basin, including the Iratí fossil associations (Holz et al. 2010), actinopterygian remains are mentioned in the Assistencia Member (which also contains mesosaurs), but a mesosaur-actinopterygian association is not specified in this member, which may have accumulated over approximately 1.5 Myr. Thus, a more precise stratigraphic study is needed

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to determine the taxa present in the mesosaur community of the Brazilian Iratí Formation (César Schultz and Flavio Pretto, personal communication 2011).

Biostratigraphic studies of the presumed coeval South African deposits, the White Band, are not much better. The most complete data come from Oelofsen (1981), who delimited several fossiliferous range zones, where apparently mesosaurs and actinopterygians were not found at the same levels. However, the text is not always clear and it cannot be determined if the acme of actinopterygian biodiversity and abundance is stratigraphically coeval with the mesosaur range-zone. On the other hand, evaporitic minerals, such as casts of gypsum rosettes and halite, occur in the Whitehill Formation according to several authors (see Oelofsen 1981, and references therein). Oelofsen (1981) stated that these may indicate periods of increased salinity and formation of bottom brines that excluded colonization by benthic taxa, but that a nearly permanent connection between the Whitehill-Iratí Sea and the open ocean meant that hypersalinity could not persist for long. Besides, saline lacustrine facies were suggested for the Whitehill Formation and equivalent Kalahari basin units, as well as for the Early Permian bituminous deposits of South African and Brazil (Summons et al. 2008). Here, we suggest similar environmental conditions for the Mangrullo Formation, with periods of hypersalinity that are coeval with the mesosaur community.

Ecological evidence for hypersalinity

The mesosaur community features low taxonomic diversity and high abundance of organisms. Mesosaurs are apparently represented by one species (Piñeiro 2006; Morosi 2011; Piñeiro et al. in press b) that are widely distributed in the calcareous and oil-shale levels. Pygocephalomorphs include two, or at most three species (Piñeiro et al. 2011a), but one is dominant, as shown by the high number of specimens from both facies (Piñeiro et al. 2010; Piñeiro et al. 2012). To document the low diversity of the mesosaur community of the Mangrullo Formation, numbers of specimens of all metazoans (except trace fossils) recovered in four field seasons (Table 1) are used to compute the Shannon index, also called the Shannon-Wiener H index, a measure of biodiversity that takes into consideration the number of individuals of each taxon, rather than simply the number of species (Peet 1974; Spellerberg and Fedor 2003). This index is not independent of sample size because its maximal value is ln(N), where N is the number of sampled individuals (Peet 1975). Thus, the Shannon index of the mesosaur community (1.17) has to be compared with other localities with an equivalent sample size (N = 291).

We calculated the Shannon biodiversity index in two ways. In the first, we divided the mesosaur specimens equally between *Stereosternum* and *Mesosaurus*, reflecting

Table 1. Quantitative assessment of the biodiversity of the mesosaur community of the Mangrullo Formation through use of the Shannon index. Numbers of specimens reported include all the finds of four field trips in 2002 to 2004 at the Yaguari Creek locality in the northeast of the Tacuarembó County, Northestern Uruguay. The generic assignment of mesosaurs is unknown for most specimens. If we distribute them evenly into the two genera that may be present, and we discriminate the three (undescribed) pygocephalomorph species, this maximizes the Shannon index and yields a value of 1.173. If we lump all the mesosaur specimens into a single taxon, the Shannon index is only 0.899.

Taxon		Number of specimens (individuals)
Pygocephalomorpha	Species A	156
	Species B	19
	Species C	1
Mesosaurs	*Mesosaurus*	58
	Stereosternum	57
Total		291

Table 2. Semi-quantitative assessment of the biodiversity of the mesosaur community of the Mangrullo Formation (Early Permian of Uruguay) and the Geraldine bonebed (Early Permian of Texas) through use of a simple taxon count. Only body fossils of aquatic metazoans are included. For levels in which scales occur, this is a minimal taxon count because the number of taxa represented by isolated scales in each major clade is unknown. Similarly, the biodiversity represented by ichnotaxa may under-represent the actual biodiversity. These caveats should affect the lower and upper levels of the Mangrullo Formation more than the mesosaur level because more taxa are affected by this potential under-evaluation of the paleobiodiversity; hence, the actual differences in diversity between levels is probably greater than implied by this table.

Formation/Level	Major clade present	Minimal number of species
Mangrullo, Upper actinopterygian level	Actinopterygii	≥1
	level total	≥1
Mangrullo, Mesosaur level	Mesosauria	1
	Pygocephalomorpha	3
	Ichnotaxa	≥1
	level total	≥5
Mangrullo, Lower actinopterygian level	Acanthodii	≥1
	Actinistia	1
	Actinopterygii	≥1
	Bivalvia	1
	Ichnotaxa	≥4
	level total	≥8
Archer City Bonebed	Ostracoda	≥1
	Chondrichthyes	1
	Dipnoi	1
	Osteolepidae	1
	Temnospondyli	3
	Embolomeri	1
	Diadectomorpha	1
	Amniota	4
	Total Geraldine diversity	≥13

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the difficulty of identification from fragmentary specimens that lack diagnostic areas (Modesto 1999a, 2006, 2010). In any case, the taxonomic value of some diagnostic characters has been problematic, even in complete skeletons, and these are currently being reviewed. This procedure maximizes the Shannon index. In the second calculation, we attributed all specimens to Mesosauridae, which minimizes the Shannon index (value of 0.899). Thus, the range of possible values is encompassed by our calculations.

It was not possible to calculate the Shannon index for assemblages below and above the mesosaur community because we cannot determine individuals and taxa from isolated scales. However, it is clear from a simple count of the minimum number of taxa, that the diversity was higher, at least for the lower stratigraphic levels (Fig. 1, Table 2), even though this probably underestimates the number of species. In the upper levels, the diversity appears very low, but it is probably the most underestimated because it was least studied, and the numerous actinopterygian scales and rare teeth may represent several species, rather than one. The ichnotaxa show a reduction in biodiversity in the mesosaur levels. It is also clear that the taxonomic composition of the lower and upper levels is significantly different from that observed in the mesosaur community, and the re-establishment of the actinopterygian community in the uppermost levels of the sequence suggests a coeval basin-wide change in environmental conditions.

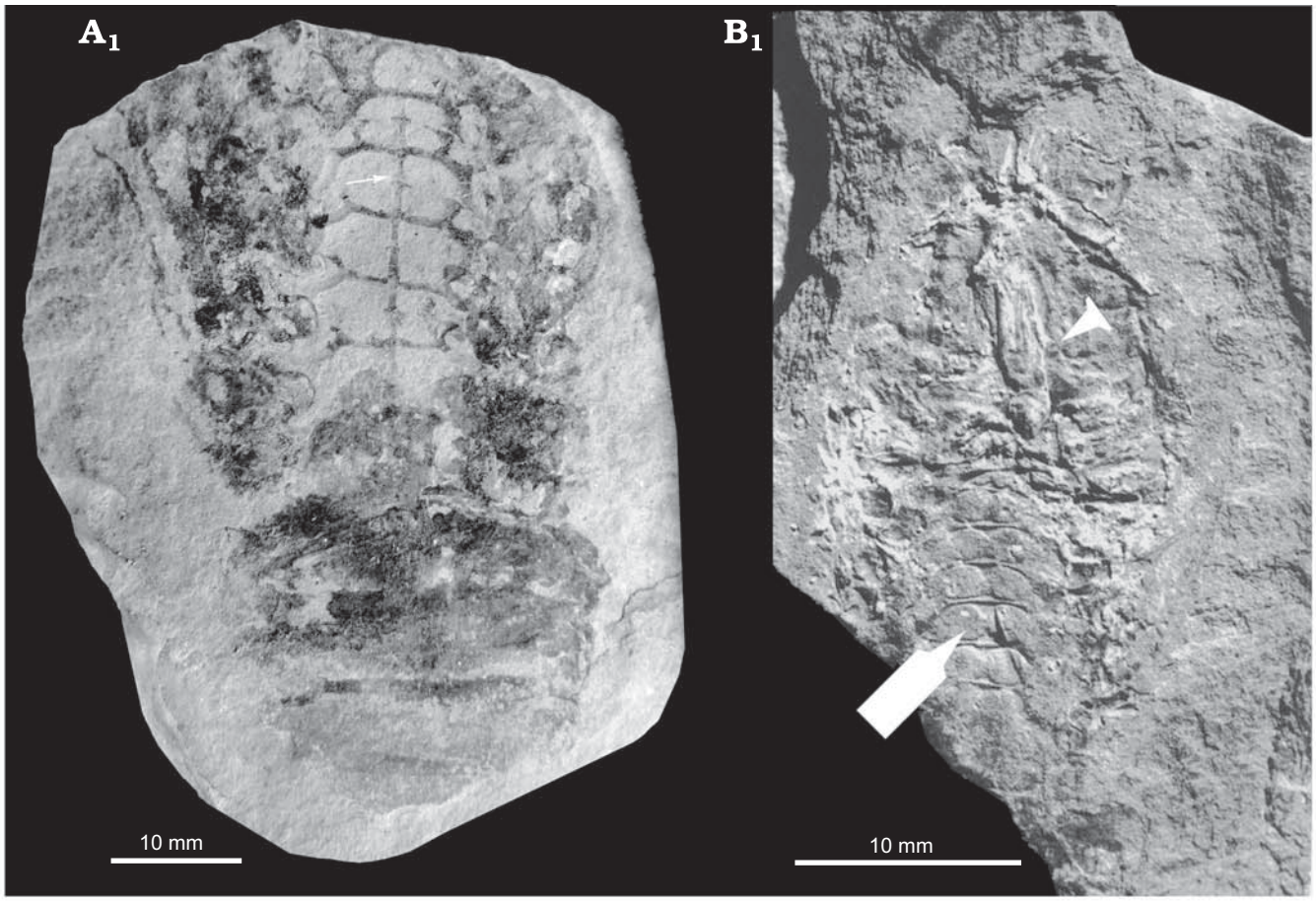
It is hard to evaluate the biological significance of our calculations because the Shannon index has not been computed for many fossiliferous localities, and few papers report the number of specimens of all species from a locality. An exception is Gale et al. (2000), who calculated the Shannon index for marine faunas near the Cenomanian/Turonian boundary, identified only to genus level (specific-level identifications would yield higher Shannon diversity). For levels represented by 100–200 specimens (the highest counted), Gale et al. (2000) report Shannon diversity indices around 2, and some levels with about 80 specimens yielded a similar value. With a maximal value of 1.17, the mesosaur community was clearly depauperate (the Shannon index is a logarithmic measurement, so small variations in that index reflect large biodiversity differences). We compare our results with another locality, the Geraldine bonebed of the Nocona Formation (Early Permian) from Texas. Sander (1987) provided data on numbers of specimens for 84 stegocephalian remains (see SOM: Table 1, Supplementary Online Material at http://app.pan.pl/SOM/app57-Pineiro_etal_SOM.pdf) but did not consider ostracods. Thus, we calculated a Shannon index of 1.40, which can be compared with the same index for the mesosaurs of the Mangrullo Formation alone, whose maximal value (if mesosaur specimens are attributed evenly to both mesosaur taxa) is 0.69 and whose minimal value is 0 (if mesosaur specimens are attributed only to Mesosauridae).

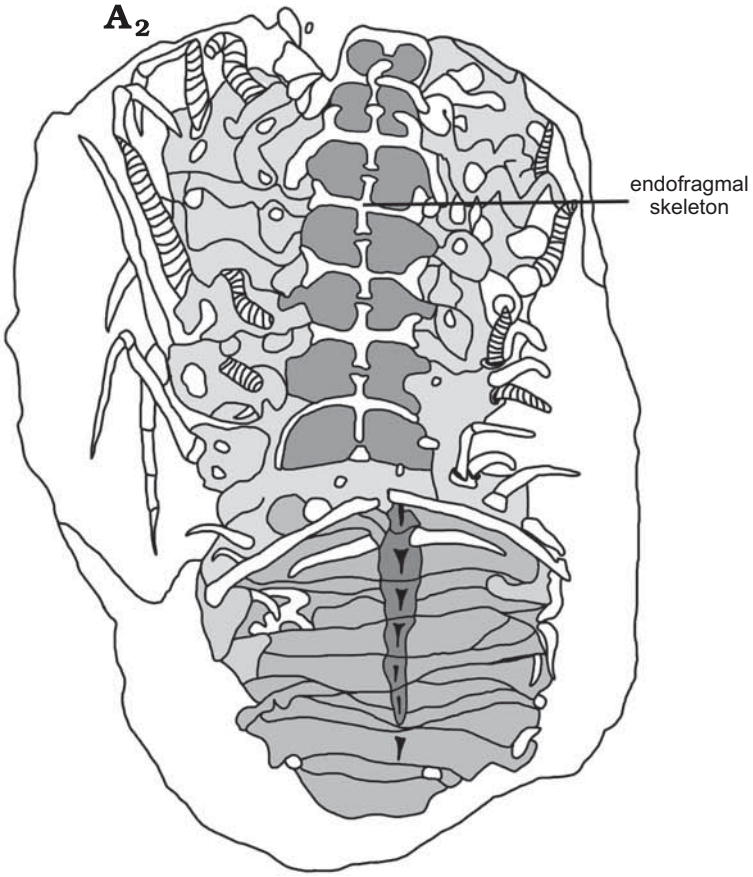
Moderately hypersaline environments today show ecological similarities with the mesosaur community, namely low taxonomic diversity and high abundance of individuals, reflecting the fact that few organisms are capable of tolerating such salinities (Williams 1998). Brackish conditions support similar, but more diverse, communities (Vega-Cendejas and Hernández de Santillana 2004; Peters 2007: 166; Lamptey and Armah 2008). For instance, the Late Devonian (Frasnian) Escuminac Formation, long considered a freshwater environment, is now considered estuarine, and it supports a fair diversity of vertebrates and other metazoans (Schultze and Cloutier 1996; Schultze 2009). Biodiversity in hypersaline conditions depends on salinity: moderately hypersaline ecosystems (salinity 40–100 $g/^{-1}$) are relatively depauperate, mainly including resistant euryhaline taxa (Vega-Cendejas and Hernández de Santillana 2004; Timms 2009), but at higher salinities (≥300 $g/^{-1}$) only microorganisms and small animals survive, including Rotifera, Anostraca, Cladocera, and Copepoda (Timms 2009). In extreme examples, such as the Dead Sea, only microorganisms exist (Buchalo et al. 1998). The low diversity of the mesosaur community is consistent with moderately hypersaline conditions, even though the diversity might have been raised by time-averaging, a consequence of the low sedimentation rates characteristic of oxygen-depleted environments (Stein 1986). Thus, the fossil assemblages of the Mangrullo Formation compare in structure and diversity with those present in coastal lagoons, where there is a range from freshwater to hypersaline environments (Barnes 1989; Timms 2009). These salinity changes reflect closure and opening of the lagoons to the sea. Long periods of isolation result in increased salinity if freshwater inflow is scanty, and this can lead to episodic dramatic loss of biodiversity. Such a scenario may explain the mesosaur community, where all but the most resistant euryhaline inhabitants have disappeared. Conditions were probably not seasonal, as in modern coastal lagoons in which biodiversity peaks far exceed those of the mesosaur community (Lamptey and Armah 2008). For instance, the few actinopterygians in modern hypersaline lagoons mostly inhabit them seasonally, when salinity is near their preferred range (Vega-Cendejas and Hernández de Santillana 2004).

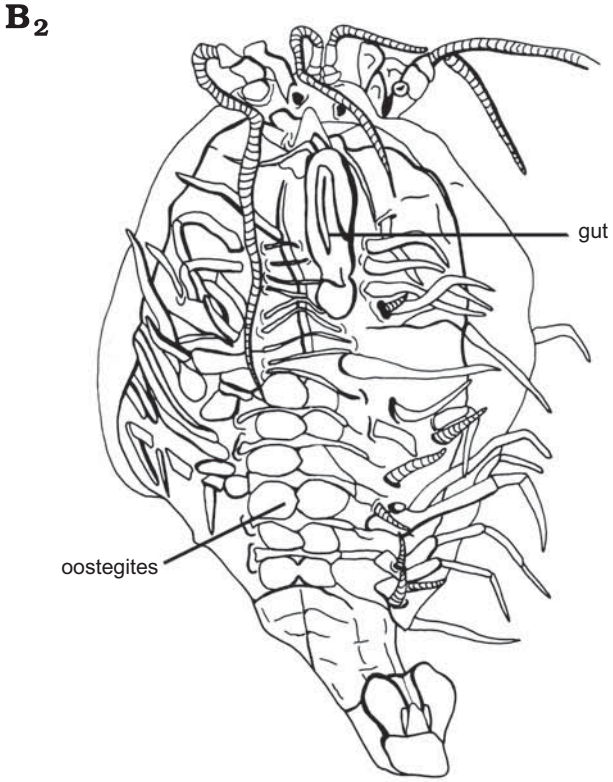
Hypersalinity could also explain the absence of temnospondyls, known from marine deposits from the ?Early Permian Pedra do Fogo Formation in Brazil (Price 1948; Barberena et al. 1985; Cox and Hutchinson 1991). Even though some temnospondyls tolerated brackish or even salt water (Laurin and Soler-Gijón 2001, 2006, 2010; Schultze 2009), there is no evidence that any tolerated hypersaline conditions. Comparison with extant amphibians is relevant because of their similar life history (with larval develop-

Fig. 3. Pygocephalomorph specimens from the Early Permian Mangrullo Formation (Northeastern, Uruguay). **A**. FC-DPI 3732, almost complete individual showing endophragmal skeleton (white arrow). **B**. FC-DPI 3514, almost complete specimen preserving the gut as two sediment-infilled sacs (small white arrow), here interpreted as stomachs and thoracic plate-like structures (thick larger white arrow) suggested to be probable oostegites. Photographs (A_1, B_1), interpretive drawings (A_2, B_2). →

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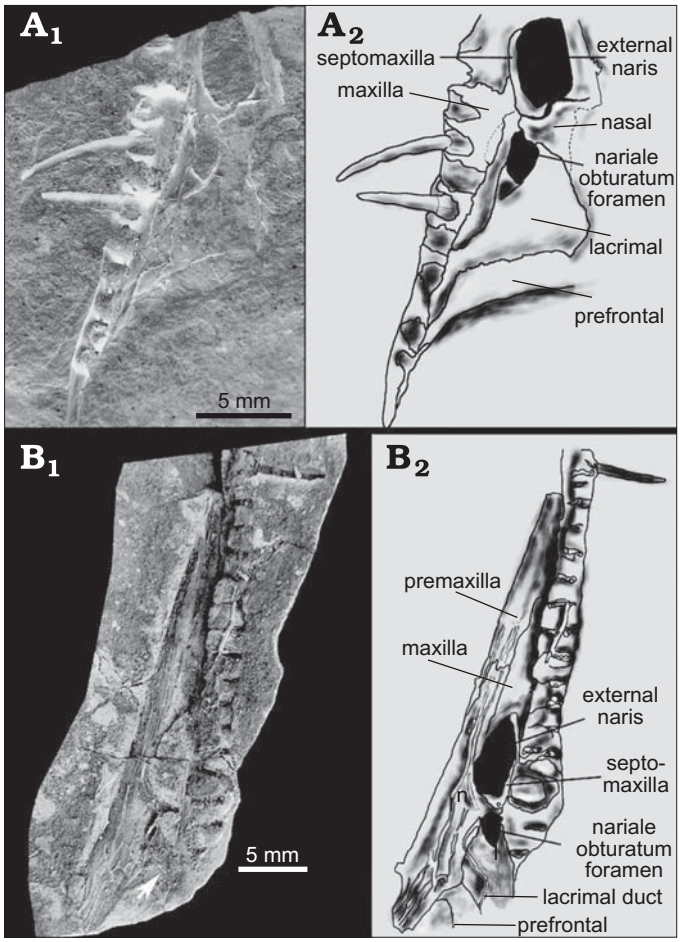


Fig. 4. Mesosaurid partial skulls from the Early Permian Mangrullo Formation (Northeastern, Uruguay) showing the position of the nariale obturatum foramen (nof). **A**. FC-DPV 2254, skull fragment showing the position of the nof related to the external naris and the delimiting bones. **B**. FC-DPV 2104, picture of a skull fragment showing the lacrimal duct emptying into the nof (white arrow on the picture). Photographs (A_1, B_1), interpretive drawings (A_2, B_2).

ment) and physiological characters (like gill breathing in water, presumably permeable skin, etc.). In this group, tolerance to brackish water is rare, tolerance to seawater is even more rare, and a single species is known to tolerate hypersaline water (Schmidt 1957; Laurin and Soler-Gijón 2010). Tolerance to stressful osmotic conditions is more widespread in amniotes because they lack gills and have fairly waterproof skin, facilitating osmotic control. Thus, the low biodiversity of the mesosaur community, and the absence of gill-breathing vertebrates are coherent with the hypothesis that at least these levels of the Mangrullo Formation were hypersaline.

Oxygen availability is another important factor that affects biodiversity, particularly for benthic species. The effects of dropping oxygen rates in aquatic environments can be detected even if the hypoxia lasts only a few weeks (Zettler et al. 2007). Thus, oxygen depletion at the levels that contain the mesosaur community may explain the depauperate endobenthic biota that is restricted to *Chondrites*.

Anatomical and physiological evidence

Pygocephalomorph osmoregulatory strategies.—Stressful environments constrain organisms to adopt several anatomical and physiological adaptive strategies to survive. Tolerance to high salinities depends on osmoregulation or osmoconforming capability (Charmantier and Charmantier-Daures 2001), and crustaceans are among the most adaptable aquatic organisms, being able to survive in a wide range of salinities (Aladin and Plotnikov 2004). Crustacean adaptations to salinity have been studied in adults (Péqueux 1995) and larval and embryonic stages (Charmantier and Charmantier-Daures 2001). These last authors identify three patterns of osmoregulation among crustaceans. Pattern 1 species are osmoconformers in all developmental stages (embryos and adults alike), with little osmoregulatory capability, and can live only in environments where salinity is constant such as normal marine settings. Pattern 2 species have the best osmoregulatory capabilities acquired during embryonic development, and adults are capable of surviving in extremely saline conditions (hypersalinity), as well as in freshwater or brackish environments; these are the only taxa that live permanently in freshwaters. Lastly, pattern 3 species have osmoconformer postembryonic stages (not capable of osmoregulation), but acquire osmoregulation capabilities after metamorphosis. Adults of these species are mesohaline (capable of supporting salinities ranging from 5 to 18 parts per thousand) or euryhaline (able to support a wide range of salinity) and can colonize environments of variable salinity (Charmantier and Charmantier-Daures 2001).

According to this ecological classification, crustaceans can acquire osmoregulatory abilities at different ontogenetic stages (patterns 2 and 3) or never (pattern 1). Anatomical and physiological adaptations present in pattern 2 and 3 species include the development of osmoregulatory organs (e.g., salt pumps) and incubating pouches that provide osmotic protection to the embryos (Charmantier and Charmantier-Daures 2001). However, the presence and function of these structures is difficult to evaluate in extinct crustaceans because gill, gut or maxillary glands are only exceptionally preserved (Briggs and Clarkson 1989).

Pygocephalomorphs are crustaceans from the Late Carboniferous to Early Permian, with Carboniferous taxa restricted to Laurasia and Permian taxa to Gondwana (Brooks 1962; Schram 1981; Pinto 1972; Pinto and Adami 1996; Taylor et al. 1998; Hotton et al. 2002; Piñeiro 2006; Piñeiro et al. 2012; and others). Most pygocephalomorphs inhabited freshwater environments, with some from brackish and coastal near-shore communities (Schram 1981; Briggs and Clarkson 1989). They may even have included marine species, but their unmineralized chitinous skeletons makes preservation in marine conditions rare (Brooks 1962; Briggs and Clarkson 1989). Gondwanan pygocephalomorphs have been considered as marine (Pinto 1971; Oelofsen 1981) or fresh-

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water to brackish (Huene 1940; Piñeiro 2006). Our new evidence suggests that the pygocephalomorphs from the Mangrullo Formation inhabited moderately hypersaline environments. Nearshore marine and highly saline conditions were also claimed for the peculiar Permian Chinese Tylocarididae, pygocephalomorphs that display strongly sclerotized exoskeletons (Taylor et al. 1998).

Two morphological characters of the Mangrullo Formation pygocephalomorphs are consistent with a hypersaline environment. First, the most abundant species has a highly reinforced thoracic region with an endophragmal skeleton (Piñeiro et al. 2012; Fig. 3A). This feature, unknown in other pygocephalomorphs, may be related to buoyancy control in highly saline environments. This increases body density through the development of a heavier skeleton, because unmineralized chitin has a density of 1.425 g/cm^3 (Li et al. 1996), and mineralized chitin would have an even higher density. Second, some pygocephalomorphs appear to have small plate-like structures (oostegites) over the lateral surface of thoracic sternites (Fig. 3B). Oostegites have been described for several pygocephalomorph species as elements that support the incubation pouches or marsupia (Woodward 1907; Brooks 1962; Pinto and Adami 1996). Such structures in crustaceans of ecological groups 2 and 3 (Charmantier and Charmantier-Daures 2001) can protect the embryos in the first stages of development in osmotically hostile environments and eventually reduce the energetic cost of osmoregulation in embryos of ecological group 2.

Oostegites are seen only in specimens from marginal habitats of the Mangrullo Formation, as shown by their association with insect and plant remains, and they were not observed in any of the large number of specimens from the deeper parts of the basin. The latter may have developed a different reproductive strategy, possibly switching from sexual to asexual (e.g., parthenogenesis), as is commonly observed in harsh environments (Browne and MacDonald 1982). These differences between deep-water and shallow-water pygocephalomorphs are consistent with the ecological and environmental conditions suggested above. According to some studies, the co-occurrence of at least two closely related species in the same harsh environment is relatively rare, because food is limited (Moore 1963). Indeed, in this situation, closely related species tend to be seasonally segregated, thus eliminating competition for food and space (Prophet 1963). It is possible that a single species occurred in the main water column, and that more than one colonized the shallower, marginal areas of the Mangrullo Formation, where food may have been more abundant.

Mesosaur adaptations to aquatic (saline) environments. —Mesosaurs are the earliest known aquatic amniotes. They display various characters, such as pachyosteosclerosis, that reflect an aquatic lifestyle (Piñeiro 2004; Modesto 2006, 2010; Canoville and Laurin 2010), but morphologically, the skeleton does not look as specialized as in pelagic marine reptiles. Mesosaurs were obviously not fast swimmers, and

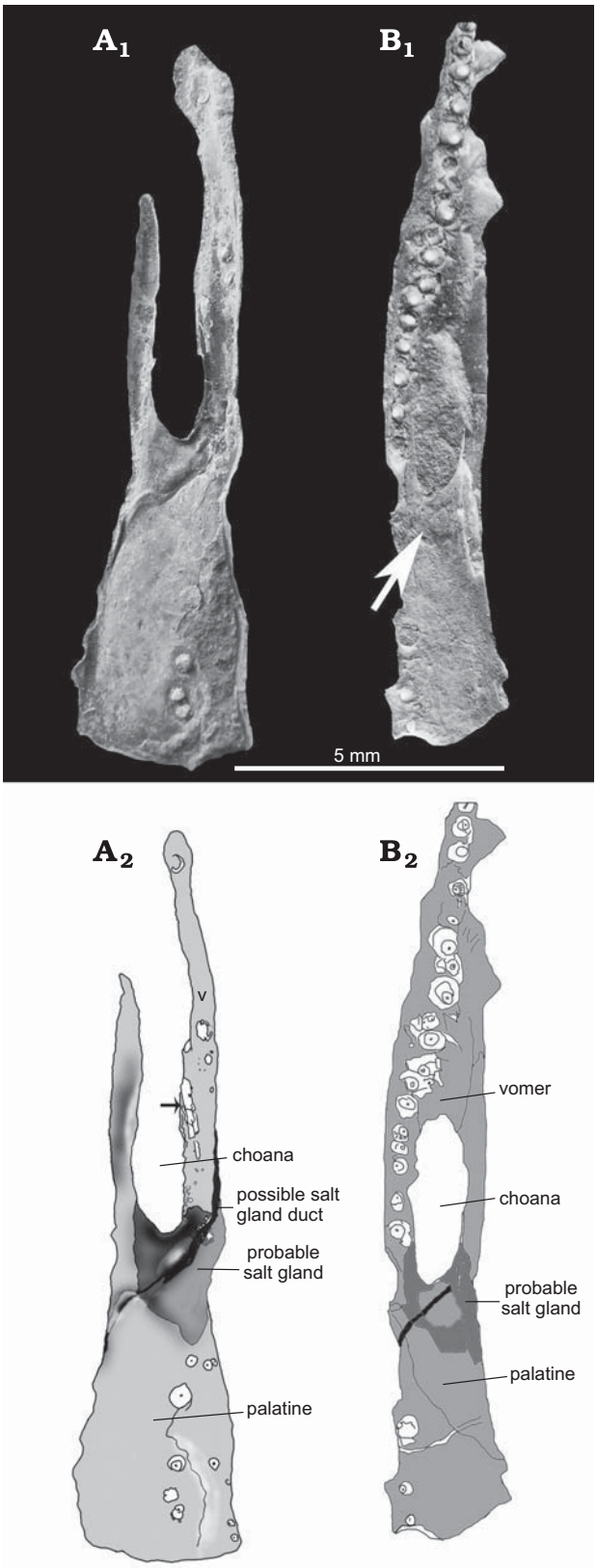


Fig. 5. Mesosaurid palate (FC-DPV 2462) from the Early Permian Mangrullo Formation (Northeastern Uruguay), including palatine and vomer. Part (**A**) and counterpart (**B**). Note the oval area posterior to the choana, probably indicating the presence of a salt gland (see text for additional information). The white arrow marks the posterior boundary of the probable gland. Photographs (A_1, B_1), interpretive drawings (A_2, B_2).

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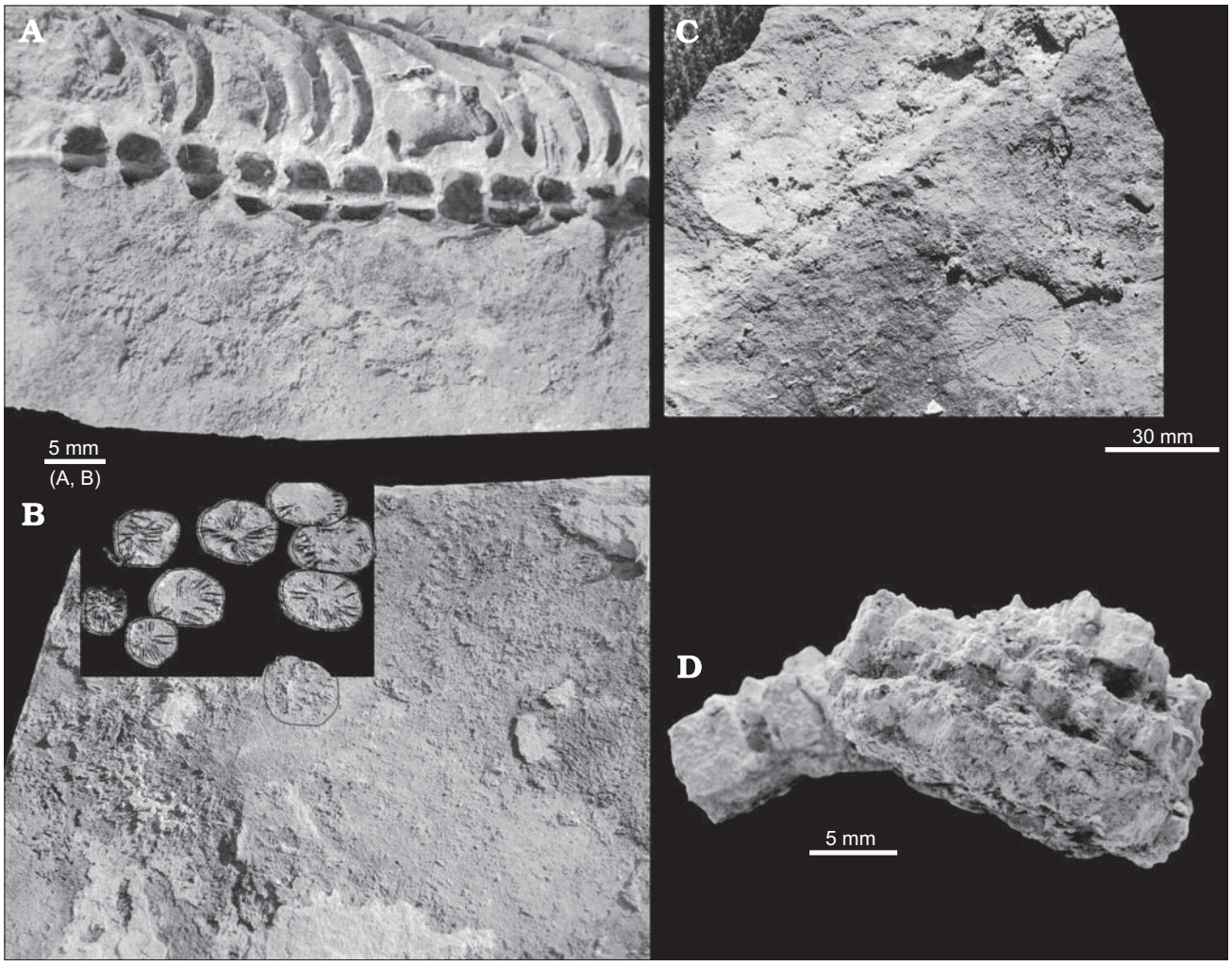


Fig. 6. Gypsum crystals from the Early Permian Mangrullo Formation (Norteastern Uruguay). **A**. FC-DPV 2518, gypsum crystals surrounding a mesosaur skeleton. **B**. GMHR 0001, gypsum crystals associated with oil-shale deposits, with interpretive drawing of crystals in the left corner. **C**. GMHR 0002, impressions of the crystals found in non-bituminous shale. **D**. GMHR 0003, columnar gypsum crystals from bituminous shales.

probably inhabited coastal waters. In fact, this inferred locomotor characteristic, along with their distribution in South America and South Africa, was the main reason to consider mesosaurs as key evidence for the continental drift theory of Alfred Wegener (Du Toit 1927; Wegener 1966); their poor swimming performance seemed to preclude the possibility of crossing the Atlantic Ocean (Romer 1966).

Among the aquatic adaptations of mesosaurs, we will focus on the foramen nariale obturatum (nof, sensu Huene 1941), and their pachyosteosclerosic vertebrae, ribs, and humerus (Canoville and Laurin 2010). The small foramen nariale obturatum is located just behind the external naris (Fig. 4); it is unique to mesosaurs and although it was suggested to be homologous with the anterior maxillary foramen of parareptiles, this hypothesis is not consistent with available evidence (Modesto 2006: 365). Its function has not yet been established. Some authors interpreted it as an osteological indicator of salt glands (Huene 1941), a plausible assumption if mesosaurs had to eliminate excess salt from eating pygocephalomorph crustaceans, as suggested by some workers (e.g., Romer 1974; Raimundo-Silva et al. 1997; Raimundo-Silva 1999). These arthropods were probably isosmotic with seawater, as are most marine metazoans (Schmidt-Nielsen 1979; Buchy et al. 2006). Thus, to avoid dehydration, mesosaurs needed efficient structures to eliminate salt, assuming that their environment was hypertonic. However, studying salt gland form and function in fossils is not easy. Even when the glands are large and well developed, they may not leave any mark on the bones. Thus, they have to be inferred from assumptions about the environment and from anatomical hints. Salt glands are present in several groups of extant aquatic and terrestrial tetrapods, but their anatomy is variable. Thus, reptiles have nasal (many squamates), sublingual and premaxillary (snakes), lingual (crocodiles) as well as lachrymal (turtles) salt glands (Peaker and Linzell 1975; Dunson 1985). Bird nasal salt glands are usually placed in shallow depressions of the frontal bone, dorsally in the skull and between orbits, but they can also be placed below the orbit (Butler 2002).

If mesosaurs developed salt glands, the nof may be rele-

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vant. Several well-preserved moulds of the antorbital area of the skull show that the nof is apparently connected with the orbit through the lachrymal duct (Fig. 4B), as Modesto (2006) noted. This foramen may not be homologous with openings behind the external naris in extinct or extant aquatic or amphibious vertebrates, and its function remains speculative. Its position between the orbit and the external naris and its delimitation by the lacrimal, the nasal and probably a dorsal extension of the maxilla (Fig. 4) places it in the same area as the archosaur antorbital fenestra. This is also of uncertain function, some suggesting that it houses a nasal salt gland (Broom 1913; Ewer 1965), others denying this because of its position at the level of the choana (Osmólska 1985), and others suggesting it was an accessory posterior diverticulum of the nasal cavity housing air sacs (Witmer 1987). In mesosaurs, the nof is placed dorsal to the choana, but there is no visible connection between the two (GP personal observation). Some specimens preserving part of the palate show a roughly oval area anteriorly over the palatine, posteromedial to the choana (Fig. 5, SOM: Fig. 5). This may indicate a salt gland at the level of the nof. It is also possible that a duct, which crosses the presumed position of the gland transversely (Fig. $5B_1$), emptied into the nof. Salt glands in fossil vertebrates have been described recently for the Jurassic metriorhynchid crocodyliform *Geosaurus araucanensis* (Fernández and Gasparini 2008; Fernández and Herrera 2009) in a position equivalent to that inferred for the mesosaur specimen mentioned above (Marta Fernández, personal communication 2010). Thus, if salt glands were present in mesosaurs, a relationship between them and the nof cannot be ruled out, and it is compatible with observations based on the available materials. Thus, the fact that the lacrimal duct empties into the nof raises the possibility that mesosaurs eliminated salt as tears from the nof, which could make sense if mesosaurs inhabited highly saline waters.

Mesosaurs were the earliest known tetrapods with strongly pachyosteosclerotic "banana-shaped" ribs. Pachyostosis is a hypertrophy unrelated to pathological processes (Houssaye 2009) seen as external morphological changes that reflect increased thickness of the cortical bone (Buffrénil and Rage 1993). Osteosclerosis is produced by a reduction in osteoclastic activity in the medullary region, thus producing very compact bone through reduction in diameter of the medullary cavity (Ricqlès and Buffrénil 2001). Pachyostosis and osteosclerosis are common adaptations to increase body density (Ginsburg 1967; Carroll 1982; Taylor 2000; Riqlès and Buffrénil 2001), and the latter is found mostly in taxa inhabiting shallow water (Germain and Laurin 2005; Kriloff et al. 2008; Canoville and Laurin 2010). These adaptations are especially obvious in aquatic amniotes because they breathe largely through their lungs and thus need to be able to dive at a minimal energetic cost with lungs full of air, but even aquatic lissamphibians that breathe through their skin and gills show osteosclerosis (Laurin et al. 2004, 2009), although they lack pachyostosis. If lungs are full of air, the need for such ballast is greater, and it is greater still in saline environments because saline water has a higher density than fresh water.

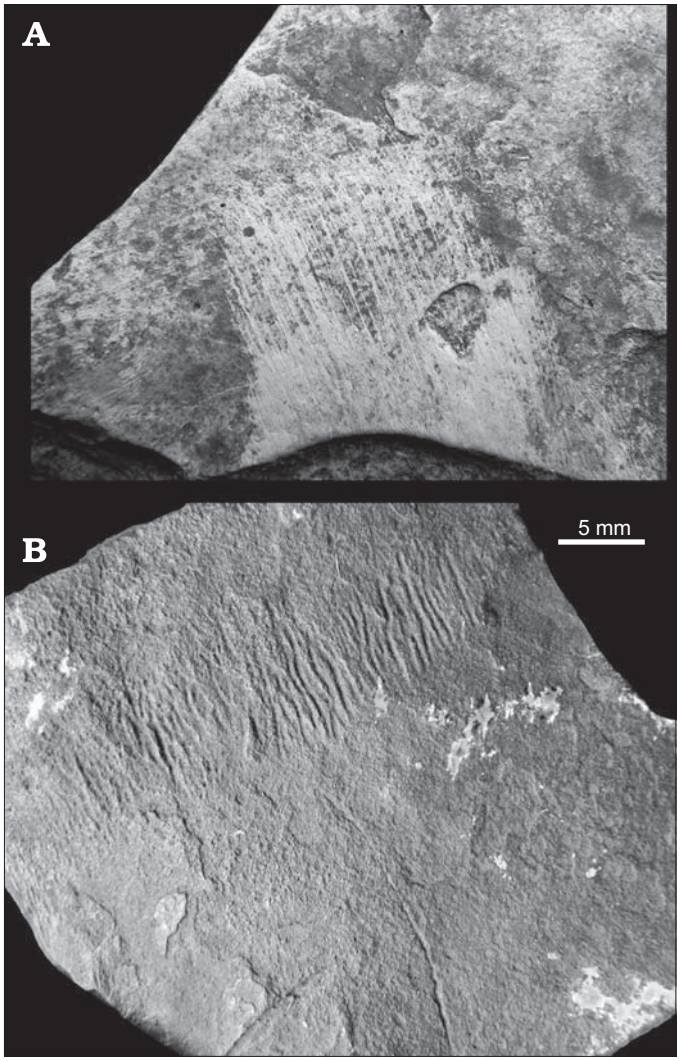


Fig. 7. Carbonization and impressions of filamentous algal mats found in the oil-shale facies of the Early Permian Mangrullo Formation (Northeastern Uruguay). **A**. GMHR 0004. **B**. GMHR 0005.

Pachyostosis has been tentatively related to transitional stages in vertebrate secondary adaptation to aquatic (mainly shallow) environments (Ricqlès and Buffrénil 2001; Houssaye 2009). However, it is not certain how terrestrial were the putative mesosaur ancestors; they may have been amphibious, rather than truly terrestrial (Romer 1974; Canoville and Laurin 2010: fig. 8). If *Brazilosaurus*, the proposed earliest mesosaur (Araújo 1976; Modesto 1996) was not pachyostotic as some authors claimed (Shikama and Ozaki 1966, Araújo 1976; Modesto 1999b), the appearance of pachyostosis in later species may represent either a time lag between their adoption of an aquatic lifestyle and the appearance of pachyosteosclerosis or a response to increasing salinity (and hence, water density) in the basin. Indeed, pelagic extant marine amniotes lack pachyostosis.

Pachyostosis is probably related to habitat depth in aquatic animals. Thus, fully marine animals that consume fast prey and dive deep lack pachyostosis, whereas slow swimmers that live in shallow marine environments display it (Houssaye

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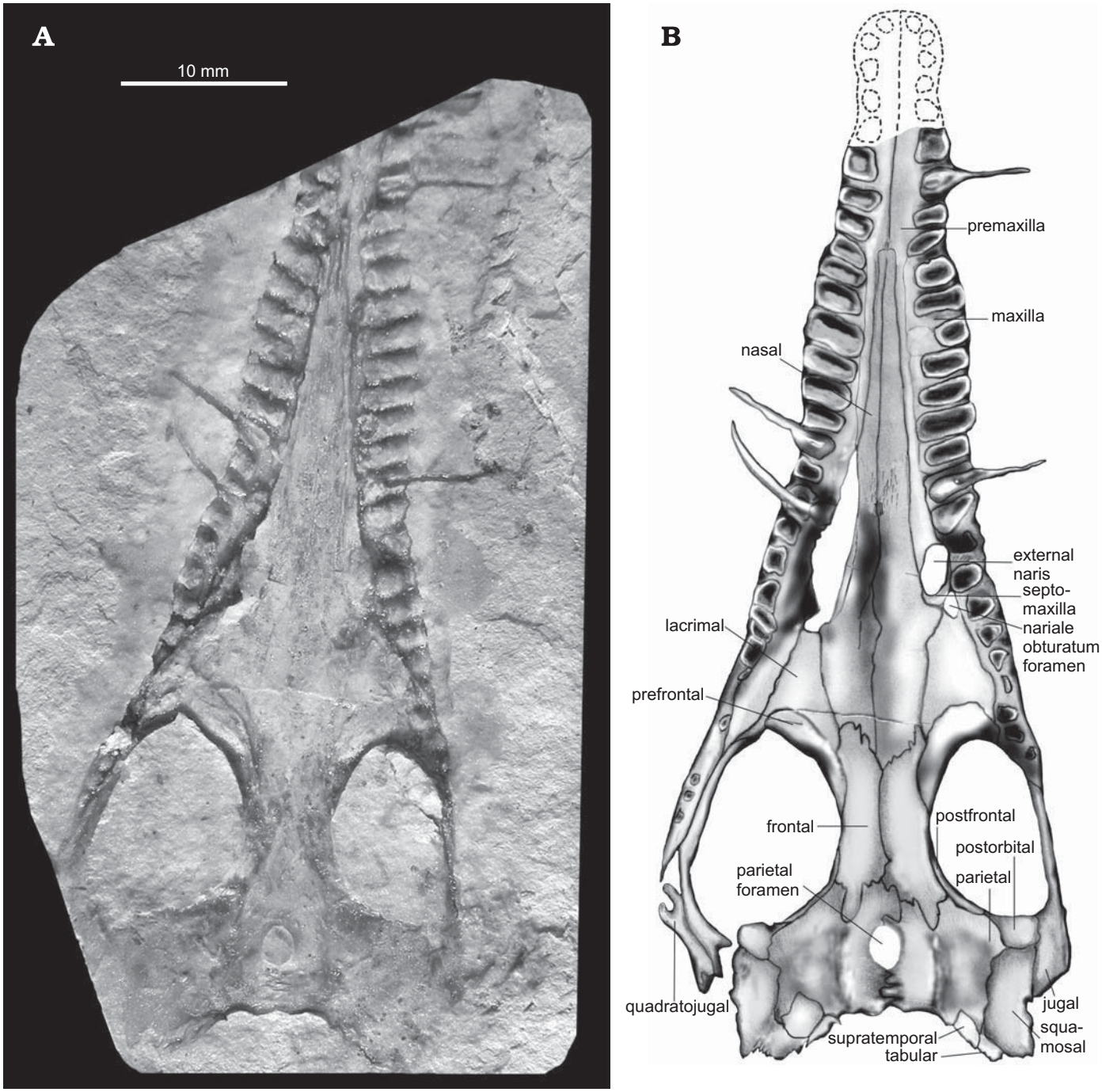


Fig. 8. Almost complete *Mesosaurus tenuidens* skull (FC-DPV 2061) from the Early Permian Mangrullo Formation (Northeastern Uruguay) preserved as an impression of the external surface of the roofing bones in original anatomical position. Photograph (**A**) and interpretive drawing (**B**). Most sutures can be reconstructed and the component bones are clearly delimited, a type of preservation rarely found in mesosaurids.

2009). Although previous work did not exclude the possibility that mesosaurs fed on actinopterygians, this seems improbable from our evidence. Indeed, there is no association between these two groups and, although there are suggestions of the association of actinopterygian and mesosaur remains in the Iratí Formation (e.g., Mezzalira 1980; Soares 2003), these reports are equivocal. On the other hand, pygocephalomorph crustaceans are abundant throughout and may have been an important mesosaur dietary item. For instance, a dark area over the last posterior dorsal vertebrae of a *Brazilosaurus* specimen from Brazil contains tiny fragments of pygocephalomorph carapaces and probably small mesosaur bones, interpreted as putative gastric contents (Raimundo-Silva et al. 1997; Raimundo-Silva 1999). Moreover, two Brazilian isolated coprolites and others associated with the mentioned specimen show disarticulated and poorly preserved carapaces and fragments of cuticle. This reveals that crustaceans must have been at least part of the mesosaur diet.

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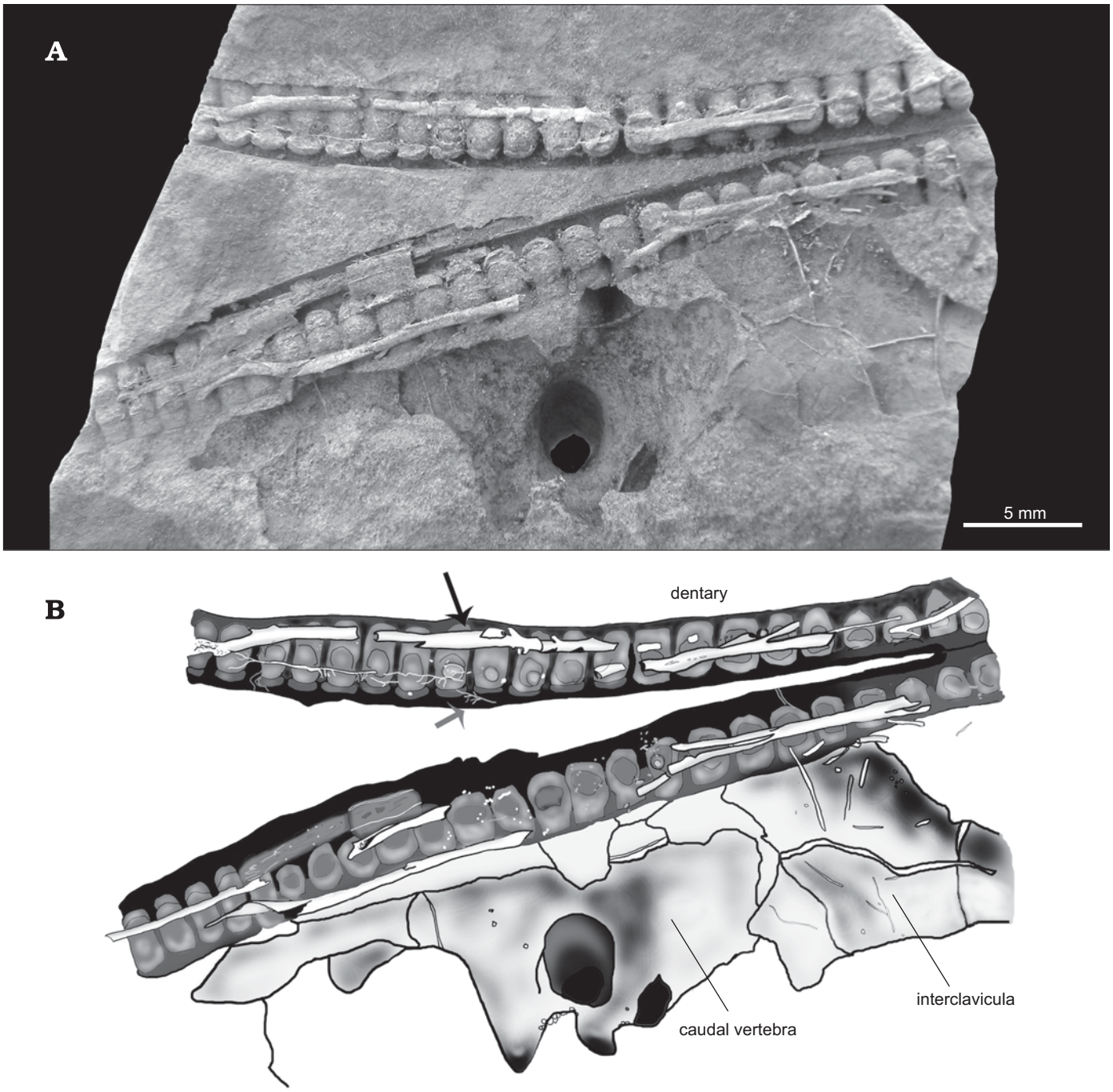


Fig. 9. Exceptional preservation of internal anatomy in *Mesosaurus tenuidens* (FC-DPV 2109) from the Early Permian Mangrullo Formation (Northeastern Uruguay). Photograph (**A**) and interpretive drawing (**B**) of the internal mould of articulated mandibular rami, showing well preserved mandibular nerves, probably the trigeminus ramus, running along the dentary tooth series (black arrow in B), and delicate blood vessels (grey arrow in B).

Mineralogical evidence of aridity and hypersalinity

Permian climates were strongly influenced by the formation of Pangaea. In South America and other regions of southern Pangaea, the Early Permian was characterized by retreating ice sheets and increasing warmth. The accretion of most land masses into a supercontinent increased global aridity, as reported from various parts of the world (e.g., Kessler et al. 2001; Chumakov and Zarkov 2002; Tabor et al. 2008). This climatic change resulted in the formation of evaporites and strongly influenced the distribution of the biota (Chumakov and Zarkov 2002). It also explains the high salinity inferred for the Mangrullo Formation.

The Mangrullo Formation contains evaporite deposits.

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High concentrations of small (diameter, 20–30 mm; height, 1 mm) radial fibrous gypsum and needle crystals are common in outcrops of the oil-shale facies, as well as intercalated centimetric gypsum crystal levels (Figs. 1, 6; see also SOM: Fig. 2, Table 3). Gypsum is a marker of high evaporation associated with aridity in restricted basins (Tucker 1991). Such indicators are seen also in the Iratí Subgroup in Brazil, including evaporitic breccias and radial fibrous gypsum crystals (Hachiro 2000), desiccation marks at some levels, characteristic pollen associations (Vieira et al. 1991; Piñeiro et al. 1998; Preamor et al. 2006), and a high gammacerane index (Wei et al. 2007).

Iron is common in the Mangrullo Formation and at least part of its abundance may be related to a Cretaceous magmatic episode associated with the shales. Alternatively, it may have been introduced into the basin by volcanic events that deposited thin volcanic ashes intercalated with the oil-shale deposits. These ashes have been linked to the Choiyoi magmatism, a volcanic event along the southwest continental margin of South America that affected the Paraná Basin during the Early and Late Permian (280 to 250 Ma), as documented by tuff-rich deposits from Brazil, Uruguay and Paraguay (López-Gamundi 2006; Santos et al. 2006).

Even though the water column remained sufficiently oxygenated to support a depauperate fauna, the near absence of benthic organisms suggests that the bottom waters were strongly depleted of oxygen by sedimentation of high amounts of organic matter (De Santa Ana et al. 2006b), probably from algae. Saline environments (low-grade hypersaline, probable salt content < 20%) such as these often have a high concentration of organic matter that can persist for long periods without being degraded by microorganisms (Larsen 1980). Sulphates are also abundant in the Mangrullo Formation and may have precluded bottom colonization by most grazing animals. Algal mats and bacterial biofilms are common in the fossiliferous levels of the Mangrullo Formation (Fig. 7) and may have protected the skeletons from erosion and decay, and played an important role in the exquisite preservation of soft tissues.

Exceptional fossil preservation

Conditions were favourable to fossil preservation, as shown by soft tissues and delicate structures. Moulds of mesosaur skeletons show exquisite detail of the original structures, and casts (or even digitally enhanced images) give a superb, three-dimensional representation of the anatomy of each bone. Isolated mesosaur skulls from the Mangrullo Formation are the best preserved (Fig. 8) and allow determination of the bones and their sutural relationships. This is hard to do with specimens from elsewhere, which may be whole skeletons, but with crushed skulls and bones displaced from their original anatomical positions (Piñeiro et al. in press b). Exceptional, well preserved embryos and probable hatchling, very small mesosaurids, were also recently described from the Uruguayan Mangrullo Formation, being the oldest known reference of amniotic reproductive biology for the Palaeozoic (Piñeiro et al. in press a).

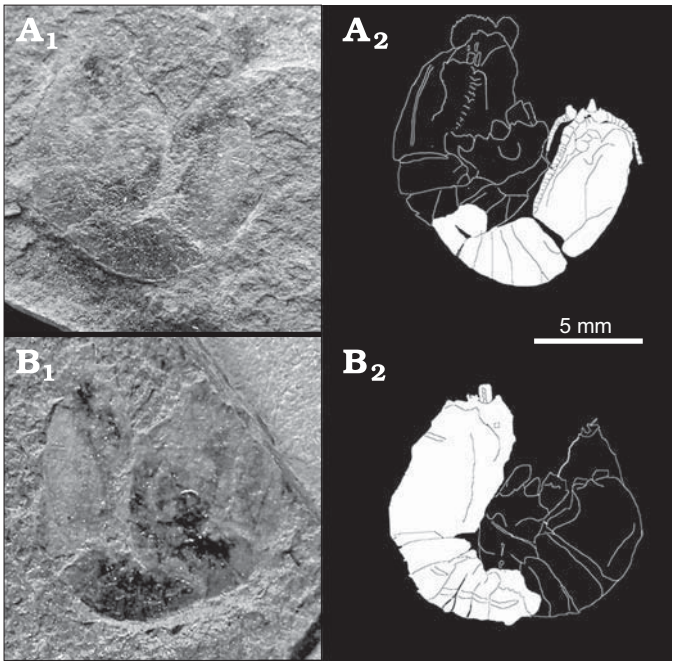


Fig. 10. Possible copula of pygocephalomorph crustaceans (FC-DPI 4468) from the Early Permian Mangrullo Formation (Northeastern Uruguay). Part (**A**) and counterpart (**B**), showing the position of the individuals with respect to each other. Photographs (A_1, B_1) and interpretive drawings (A_2, B_2).

Several mesosaur specimens are preserved as moulds, and remarkably show blood vessels and nerves. These appear to be replaced by calcium phosphate, as suggested by SEM chemical analyses (SOM: Fig. 1, Table 2), which show different mineralogical spectra from the sediment, thus showing that the tubes are not sedimentary infillings. The tubes in different specimens are sufficiently similar in shape and anatomical disposition to suggest the same origin and identity. These networks of tubules are most often found in mandibular remains and are interpreted as the main mandibular nerves (probably the trigeminus ramus) and arteries (Fig. 9; SOM: Fig. 4).

Nerves and bloods vessels are uncommon in the fossil record, since they need special conditions to fossilize. As an example, three-dimensionally preserved muscle, nerve and circulatory tissues in Late Devonian placoderms have been interpreted as phosphatized structures precipitated by microbial infilling (Trinajstic et al. 2007). According to Briggs and Kear (1993), preservation of such delicate tissues requires a drop in pH before decaying, thus triggering early phosphatization. Microbial films protect the carcass from the decay, but may also play an active role in rapid mineralization by creating a favourable micro-environment. All these factors, associated with a poorly oxygenated and hypersaline environment, may explain the preservation of structures that in normal conditions are destroyed a few days after death (Briggs and Kear 1993).

Pygocephalomorphs are represented by well preserved, almost complete individuals. These include preservation of internal anatomy, such as stomach and digestive glands,

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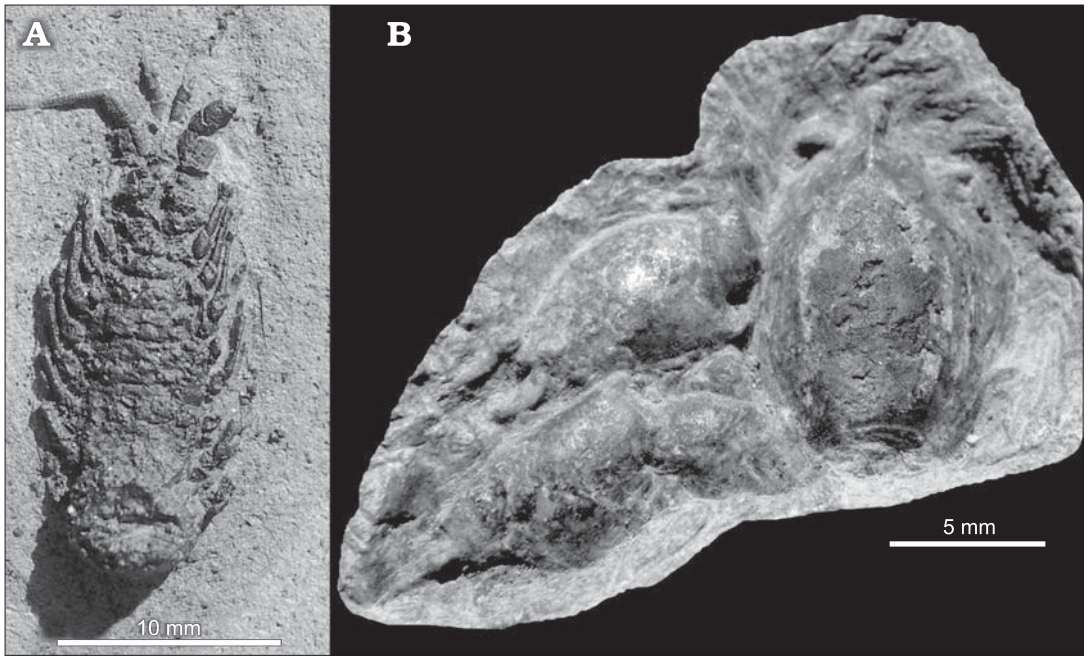


Fig. 11. Almost complete pygocephalomorph specimens from the Early Permian Mangrullo Formation (Northeastern Uruguay). **A**. MGT 1092, a complete individual in ventral view, showing well preserved appendages. **B**. FC-DPI 3306, two small, probably juvenile individuals lie joined to the large carapace of an adult individual.

along with internal structure of the gut (Fig. 3B), as well as copulae or moulting (Fig. 10). These materials will be described in more detail in a forthcoming paper.

Crustaceans that lack mineralized skeletons are uncommon in the fossil record. When preserved, they are not associated with normal marine taxa, suggesting that these environments were not favourable to chitin fossilization (Brooks 1962). Freshwater to brackish or lagoonal (hypersaline) environments may also be more suitable for selective preservation of unmineralized arthropod skeletons (Brooks 1962). Some ancient crustacean communities that included pygocephalomorphs were characterized as near-shore and offshore marine (Schram 1981), but more recent studies suggested that these were more likely brackish, as shown by the absence of more representative marine taxa (Briggs and Clarkson 1989). Spectroscopic analyses of the Uruguayan pygocephalomorphs suggest that the cuticle of most specimens was not mineralized and they may have been preserved by processes allied to precipitation of iron, probably in the form of pyrite (SOM: Fig. 3).

Coprolites and individuals that preserve gut content have been also recovered from the Mangrullo Formation shales, which show small fragments of chitinous pygocephalomorph cuticle associated to small mesosaur bones and unidentifiable materials (Fig. 12). These findings corroborate previous hypotheses which suggested that pygocephalomorph crustaceans were the main item of the mesosaur diet and also support eventual cannibalistic behavior in mesosaurids (Raimundo-Silva et al. 1997; Piñeiro et al. in press a). Therefore, the exceptional preservation of unmineralized, almost complete pygocephalomorph individuals in the Mangrullo Formation was favoured by the environmental conditions. Mineralized specimens come only from the calcareous layer, in which the carapace covering the body segments, as well as the thinner cuticle covering antennae and other appendages are mineralized. As specimens of the same species in other layers are not mineralized, we infer that this is a diagenetic process.

The high density and quality of the fossils, including almost complete skeletons, is consistent with that observed in fossil Lagerstätten. A similar argument was also made for the assemblage containing mesosaur remains in the Brazilian Iratí Formation (Soares 2003). The extremely fine preservation of the mesosaur and pygocephalomorph specimens, including conservation of soft, delicate elements, and aseptic bacterial sealing, further support the recognition of the mesosaur community in the Mangrullo Formation as a Konservat-Lagerstätte (Seilacher 1970, 1990), the oldest in South America, and the second described from that continent (Piñeiro et al. 2010).

Taphonomic context

Taphonomic features of Konservat-Lagerstätten have often been related to catastrophic, geologically instantaneous events that led to mortality of many individuals (Shipman 1975). Mesosaur mortality has been explained by great storms, deduced from hummocky cross stratification (HCS) in the Iratí Formation at the Passo São Borja locality in southern Brazil (Lavina et al. 1991). Such storms probably introduced important chemical and physical changes to the environment that affected the water breathers such as

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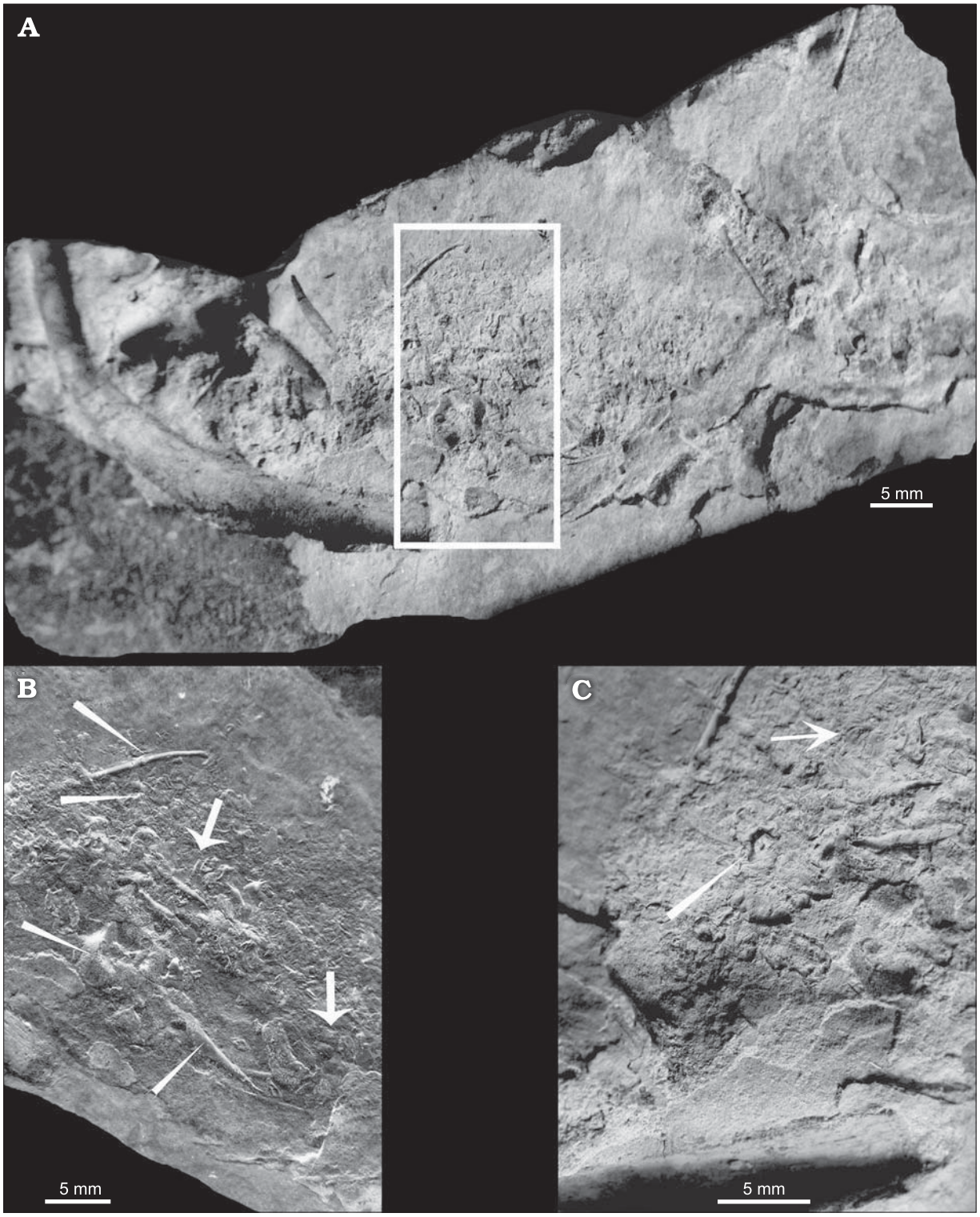


Fig. 12. Partially articulated *Mesosaurus tenuidens* skeleton (FC-DPV 2156) from the Early Permian Mangrullo Formation (Northeastern Uruguay). **A**. General view of a fragment showing an internal mass of elements that are here interpreted as a gastric content. **B**. Close up view of the area delimited by the white rectangle in A, showing some of the identified elements (arrowheads point to small bones, probably from a very young mesosaur; arrows point at pygocephalomorph carapaces and abdominal segments). **C**. Another close up view of A, to show thoracic pygocephalomorph segments preserving part of the endofragmal skeleton (arrowhead) and the remains of a specimen that clearly shows still articulated thoracic and abdominal segments (arrow).

actinopterygians and arthropods, and thus indirectly the mesosaurs, which suffered a reduction of their food sources (Lavina et al. 1991; Soares 2003). Sedimentary settings of the correlative Mangrullo Formation are similar to those of the Passo São Borja locality, having an almost identical stratigraphic arrangement, but no evidence of storms in the

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form of HCS (Piñeiro 2002; 2006). Instead, the deposition of the Mangrullo Formation seems to have occurred in mostly quiet, low-energy environments. Even in the calcareous facies, where asymmetric ripple marks indicate relatively higher-energy environments, like a shore, we found almost entire three-dimensional pygocephalomorph carcasses preserving delicate antennae and antennules, and complete thoraxic appendages (Fig. 11).

Most mesosaur bone beds in the Mangrullo Formation are lenses, which include one to three disarticulated skeletons; the isolated bones display no sign of abrasion or fracture (Piñeiro 2002). Skeletons in the shale layers can be totally or partially articulated, and many are disarticulated but with clear signs that they pertain to the same individual. In this last category, association of two or three individuals is commonly found. Isolated bones are also found, but some are in small slabs and possibly were mechanically separated by water or human action.

Thus, mesosaur remains represent the same three taphonomic categories in Uruguay and in Brazil (Soares 2003), but the taphonomic model and the causes of death seem to differ. Contrary to what may have happened in Brazil, the Uruguayan mesosaur community does not appear to have been affected by catastrophic events. Instead, gradual environmental changes may have caused the extinction of most water-breathing vertebrates and protostomians. We suggest that these changes were associated with episodes of increasing salinity produced by intense evaporation under extended periods of scarce rainfall and occasional volcanic eruptions.

Conclusions

The mesosaur-bearing strata of the Mangrullo Formation were deposited in a hypersaline environment, even though other environments, such as marine, brackish and even freshwater, may have been present at other levels. This probably reflects important variations in salinity in space and time in the basin, as previously suggested (e.g., Bossi and Navarro 1991; Piñeiro 2004, 2006). Variations in the width of the connection to the open sea (probably reflecting transgressive/regressive cycles), the rate of precipitation versus evaporation, and the amount of freshwater input into the basin were probably the most important intrinsic factors influencing salinity, along with the seasonally arid global climates generated by the palaeogeographic configuration of Pangaea.

All this may explain the controversial palaeoenvironmental results obtained from isotopic analysis of dolomitic and limestone levels of the correlative Iratí Formation (De Giovanni et al. 1974), where the data indicate freshwater conditions for some levels and marine environments for others. Similarly, based on their faunal (crustaceans and molluscs) and floral (components of the *Gangamoptheris* flora) compositions, some settings in the Paraná Basin have been interpreted previously as freshwater (e.g., Huene 1940; Beurlen 1957; Mezzalira 1980; Piñeiro 2006), although this is debated (Schultze 2009; Laurin and Soler-Gijón 2010).

We have shown that the mesosaur community from the Mangrullo Formation was not a normal marine biota. Instead, it was probably a highly specialized community that included organisms adapted to live under extreme conditions, especially hypersaline, hypoxic water.

Efforts to resolve the controversial environmental settings of the Mangrullo Formation contribute to the identification of the factors that led to the exquisite and uncommon preservation of its fossils. Such exceptional preservation is observed in the mesosaur community, prompting us to consider the Mangrullo Formation as the oldest Konservat-Lagerstätte in South America.

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