PALEOICHNOLOGICAL ASSEMBLAGE ASSOCIATED WITH *BAURUSUCHUS SALGADOENSIS* REMAINS, A BAURUSUCHIDAE MESOEUCROCODYLIA FROM THE BAURU BASIN, BRAZIL (LATE CRETACEOUS)

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Abstract—The body fossil and ichnological fossil record associated with *Baurusuchus salgadoensis* (Baurusuchidae: Mesoeucrocodylia) in General Salgado County (Adamantina Formation, Bauru Basin, Brazil) is diverse and outstanding with regard to preservation and completeness. Invertebrate ichnofossils, fossil eggs, coprolites, gastroliths and tooth marks on *Baurusuchus* fossils have been identified. The seasonal climate developed in the Bauru Basin during the Late Cretaceous created stressful conditions forcing animals to endure aridity and food scarcity. The Baurusuchidae underwent long arid seasons, probably resorting to intraspecific fighting, scavenging, self-burrowing mounds and stone ingestion. The integration of sedimentology, ichnology and taphonomic data is useful to reconstruct in detail the ecological scenarios under which Late Cretaceous Crocodyliformes survived.

INTRODUCTION

During the opening of the Atlantic Ocean, the continental rupture lead to intracratonic volcanic activity and to the origin of a broad intercontinental depression in Brazil that is known as the Bauru Basin (Fernandes and Coimbra, 1996). This area is located between latitudes 18º S and 24º S, covering part of the present southeastern Brazilian states of Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso, Goiás and Minas Gerais (almost 370,000 km^2). The basin fill is subdivided into two distinctive lithostratigraphic units: the Caiuá Group (Rio Paraná, Goio Erê and Santo Anastácio formations) of Cenomanian-Turonian age and the Bauru Group (Adamantina, Uberaba and Marília formations), of Turonian-Maastrichtian age (Dias-Brito et al., 2001; Paula e Silva, 2003; Paula e Silva et al., 2003).

The Adamantina Formation covers a large portion of the exposed area of the Bauru Basin, across western São Paulo, Minas Gerais, Mato Grosso do Sul (east and south regions) and the southern part of Goiás State. It is composed of fine-grained sandstones and siltstones with intercalations of red, oxidized mudstones of Turonian and Santonian age (Dias Brito et al., 2001). Its deposition took place on an extensive alluvial plain reworked by fluvial systems alongside some shallow ephemeral lakes, under a hot arid or semi-arid seasonal climate (Garcia et al., 1999; Goldberg and Garcia, 2000; Fernandes and Basilici, 2009) (Fig. 1).

The rich fossil record of the Bauru Group yields vertebrate and invertebrate ichnofossils, continental mollusks, arthropods, freshwater fishes, amphibians, squamates, theropod and sauropod dinosaurs, Aves and a diverse fauna of terrestrial and amphibious Crocodyliformes, most of it from the Adamantina Formation (Bertini et al., 1993; Arruda et al., 2004; Carvalho et al., 2005; Vasconcellos and Carvalho 2007; Marinho and Carvalho, 2009). So far, this diverse fauna of Crocodyliformes discovered from the Adamantina Formation comprises at least five distinct groups of Mesoeucrocodylia: Notosuchidae, Sphagesauridae, Candidodontidae, Peirosauridae, Trematochampsidae and Baurusuchidae. This fauna is important for its potential correlation with other Upper Cretaceous basins in South America, Africa, Madagascar and India, and potentially Antarctica, for paleoclimatic, paleoenvironmental, paleogeographical and paleobiogeographical studies (Carvalho et al., 2007).In contrast to the other tetrapod faunal components, the Crocodyliformes are usually found less fragmented, better preserved and commonly associated with a diverse ichnological record, with invertebrate-built structures, egg fragments, coprolites and tooth-marks (Fernandes and Carvalho, 2006; Vasconcellos and Carvalho, 2007; Gracioso and Carvalho, 2009; Souto, 2010; Carvalho et al., in press).This assemblage is particularly useful when dealing with paleoenvironmental and paleoecological reconstructions since there are direct and indirect evidences of paleoenvironmental, taphonomical, paleoecological and paleoethological contexts, normally unavailable with even complete body fossil specimens.

In the present study we developed an integrated approach to the analyses of three fossiliferous Adamantina Formation sites in the Municipality of General Salgado, São Paulo State at the southeast interior of Brazil. These sites yield Baurusuchidae Crocodyliformes complete skeletons, eggs, egg fragments, gastroliths, coprolites, bite-marks and invertebrate ichnofossils.

THE BAURUSUCHIDAE

The Baurusuchidae were medium- to large-sized terrestrial crocodylians, regarded as active cursorial predators based on dental, cranial and postcranial data (Price, 1945; Riff and Kellner, 2001; Vasconcellos et al., 2005; Vasconcellos and Carvalho, 2007; Vasconcellos, 2009) They were first defined by Price (1945), based on the almost complete skull of *Baurusuchus pachecoi* Price, 1945 (Adamantina Formation, Bauru Basin), as crocodylians with elongate, laterally compressed skulls, with extreme similarity to the Eocene Sebecidae *Sebecus icaeorhinus* Simpson, 1937, and thus with a similar paleoecological niche. They have premaxillary and/or maxillary hypertrophied caniniform teeth, and postcaniniform teeth with the theropodomorph or ziphodont condition: laterally compressed and serrated carinae (Langston, 1956; Gasparini, 1972; 1981; Riff and Kellner, 2001; Paolillo and Linares, 2007).

The paleogeographic distribution of Baurusuchidae is restricted to Gondwanaland, specifically South America (Argentina and Brazil) and Pakistan, and their chronostratigraphical range is limited to the Upper Cretaceous (Vasconcellos and Carvalho, 2007). In the Late Cretaceous of Argentina (Southern South America), three genera of Baurusuchidae were described: *Cynodontosuchus rothi* Woodward, 1896, *Penhuechesuchus enderi* Turner and Calvo, 2005 and *Wargosuchus australis* Martinelli and Pais, 2008. They are all from the Neuquén Group, Turonian-Coniacian age (Martinelli and Pais, 2008). Outside South America, *Pabwehshi pakistanensis* Wilson, Malkani and Gingerich, 2001, was found in Pakistan (Pab Formation, Upper Cretaceous, Maastrichtian) (Wilson et al., 2001).Three species of this group are found in the Bauru Basin (Adamantina Formation, Turonian-Santonian, Brazil) — *Baurusuchus pachecoi* Price 1945; *Stratiotosuchus maxhechti* Campos, Suarez, Riff and Kellner 2001; and *Baurusuchus salgadoensis* Carvalho, Campos and Nobre 2005 (Campos et al., 2001; Arruda et al., 2004; Carvalho et al., 2005).

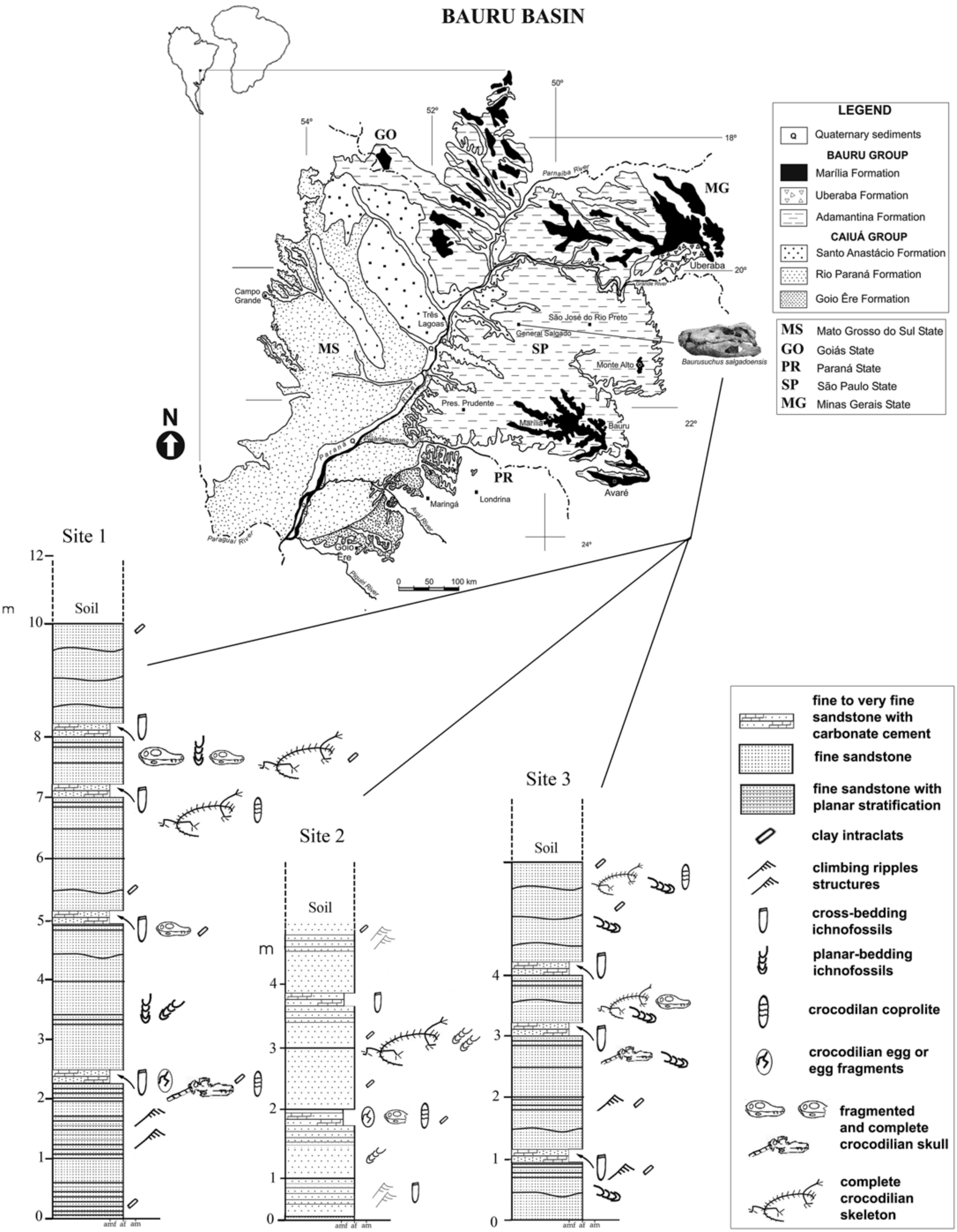

FIGURE 1. Bauru Basin geological map (modified from Fernandes and Coimbra, 1996) and sedimentary profiles from Sites 1, 2 and 3.

Baurusuchus salgadoensis

The description was based on a well-preserved, but slightly deformed, skull and mandible from General Salgado Municipality (São Paulo State, southeast Brazil). Many other specimens were retrieved from nearby sites, some almost complete in a spectacular preservational state, with fully functionally-articulated bone elements and bearing the most delicate bone elements, such as the distal phalangxes and caudal vertebrae, and articulated gasthralia and osteoderms. Some even displayed gastroliths associated with ribs and gastralia, while others have bite marks on their skulls (Arruda et al., 2004; Vasconcellos and Carvalho, 2007) (Fig. 2)

SITES

The outcrops visited and profiled are all located in the vicinity of the Prudêncio e Morais district of the General Salgado municipality, in the northwest of São Paulo State, Brazil. They were exposed by local pluvial erosion and sugar cane cultivation. Their lithostratigraphic context is that of the Adamantina Formation (Upper Cretaceous, Turonian-Santonian) (Fig. 1).

SITE 1: Fazenda Buriti, Prudêncio e Morais District, General Salgado, São Paulo State, Southeast Brazil. Coordinates: 20° 33' 57'' S - 50° 26' 11'' W.

SITE 2: Usina Generalco, General Salgado, São Paulo State, Southeast Brazil. Coordinates: 20º55´82´´S - 50º37´17´´W.

SITE 3: Fazenda RAO-X, Prudêncio e Morais District, General Salgado, São Paulo State, Southeast Brazil. Coordinates: 20° 36' 27'' S - 50° 28' 03, 97'' W.

The body fossil content of crocodylians is abundant with remarkably well-preserved specimens (Fig. 3). Two species have been described from the outcrops: *Baurusuchus salgadoensis*, a Baurusuchidae, and *Armadillosuchus arrudai* Marinho and Carvalho, 2009, a Sphagesauridae. The latter is an omnivorous, medium-sized terrestrial Mesoeucrocodylia closely related to the Notosuchidae (Marinho and Carvalho, 2009).

The Adamantina Formation in General Salgado is characterized by reddish to pale yellow, fine to very fine sandstones, siltstone and mudstones, locally cemented by calcium carbonate horizons (probably aridsol-type paleosol), rare climbing ripple structures, and abundant clay intraclasts, displaying planar to cross-stratified bedding, and sheet or wedge-shaped submetric deposit geometry.The environmental setting of the fine sandstones where the crocodylians of the Bauru Basin (Brazil) were discovered has been interpreted as being deposited by sudden floods on alluvial plains and associated ephemeral shallow lakes, under a dry and hot seasonal climate with alternation of long dry periods and short rainy seasons with widespread floods (Carvalho et al., 2005; 2007; Fernandes and Carvalho, 2006; Vasconcellos and Carvalho, 2006; Fernandes and Basilici, 2009).

The occurrence of almost complete articulated skeletons in such environments, such as those of *Baurusuchus salgadoensis*, suggests these crocodylians could dig large, deep depressions in soft, unconsolidated substrates, like extant "Alligator holes" that allowed for better thermoregulation (Cott, 1961; Richardson et al., 2002; Campbell and Mazzotti, 2004; Palmer and Mazzotti, 2004). These excavated holes provided a source of water during dry periods. This ethological aspect, which probably allowed them to live in more terrestrial and arid environments, is also seen in Cretaceous crocodylians of the Bauru Basin. Freshwater ponds and rivers were scarce, generally drying out during long droughts. This was a very restrictive factor, and the fauna and flora of this region should have been well-adapted to endure these severe environmental conditions (Vasconcellos and Carvalho, 2006).

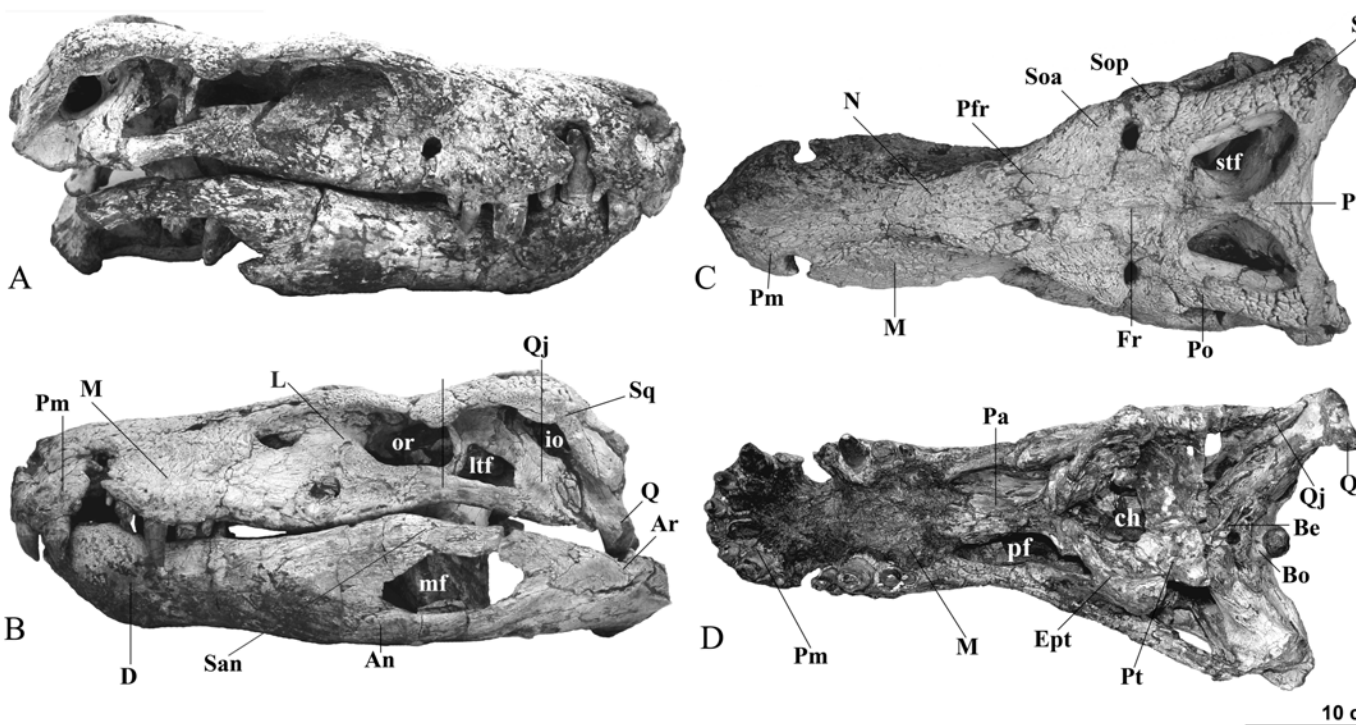

FIGURE 2. Holotype of *Baurusuchus salgadoensis* (MPMA-62-0001-02, from Site 1) in **A**, right lateral view of the skull, **B**, left lateral view, **C**, dorsal view and **D**, palatal view. **Anatomical abreviations: An**, angular; **Ar**, articular; **Be**, basisphenoid; **Bo**, basioccipital; **D**, dentary; **Eoc**, exoccipital; **Ept**, ectopterygoid; **fin**, *foramen incisivum*; **fmg**, *foramen magnun*; **Fr**, frontal; **io**, *incisura otica*; **J**, Jugal; **L**, Lacrymal; **leu**, lateral eustachian foramen; **ltf**, laterotemporal fenestra; **M**, Maxilla; **meu**, medial eustachian foramen; **mf**, mandibular fenestra; **N**, Nasal; **or**, orbit; **P**, Parietal; **Pa**, Palatine; **pf**, palatine fenestra; **Pfo**, Pterygoid foramen; **Pfr**, Prefrontal; **Pm**, Premaxilla; **Po**, Postobital; **Pt**, Pterygoid; **Q**, Quadrate; **Qj**, Quadratojugal; **San**, Surangular; **So**, Supraoccipital; **Soa**, Anterior supraobrital; **Sop**, Posterior supraorbital; **Sp**, Splenial; **Sq**, Squamosal; **stf**, supratemporal fenestra.

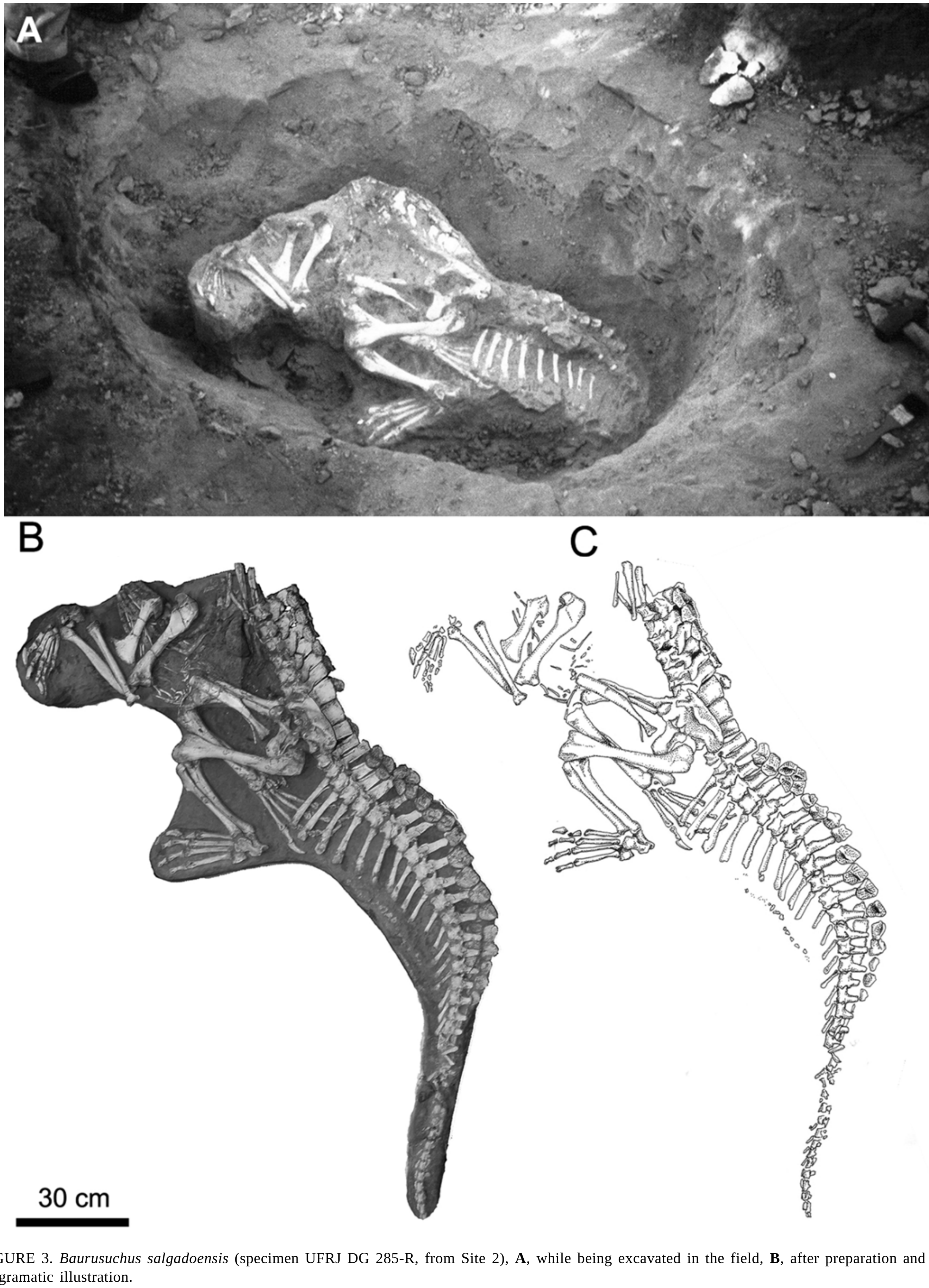

FIGURE 3. *Baurusuchus salgadoensis* (specimen UFRJ DG 285-R, from Site 2), **A**, while being excavated in the field, **B**, after preparation and a **C**, diagramatic illustration.

PALEOICHNOLOGICAL FOSSIL RECORD AND ITS SIGNIFICANCE

Invertebrate Ichnofossils

Planar-bedding Invertebrate Ichnofossils

Among the ichnofossil record, *Taenidium* isp. Heer, 1877 is by far the most common. This meniscate backfill structure, usually considered to be produced by an animal progressing axially through the sediment, is usually directly associated with deposit bedding surfaces bearing a strong reddish color, easily spotted in the field (Fig. 4A). When occurring together with *Baurusuchus* body fossils, *Taenidium* isp. is concentrated were the abdominal and thoracic regions of the specimen would have been. They are particularly abundant around the body remains, been distributed very close to the fossil crocodylians, as a reddish ichnofabric "halo." They are uncommon in cemented strata (Fig. 4D).

Cross-bedding Invertebrate Ichnofossils

Trypanites isp. Bromley, 1972 are rarer, in comparison to *Taenidium*, and commonly associated with cemented horizons. They are narrow, nearly cylindrical, unbranched burrows or borings in hard substrates such as carbonate hardgrounds. Here they usually are filled by a finer sedimentary texture and heavily cemented, carrying this trait as it reaches deeper, coarser beds. They can be fine in structure, with nearly distinguishable walls with a diameter in mm, to burrows with long and well-defined boundaries (Fig. 4B).Their distribution seems to be controlled by cemented horizons. Sometimes *Trypanites* isp. seem to descend from cemented strata directly to crocodylian remains, which occur in massive sandstone bodies (Gracioso and Carvalho, 2009).

In a different location, not one of the sites, a considerably large *Coprinisphaera* isp. Sauer, 1955 has been identified. It was discovered in the same reddish fine sandstones where all other fossils were found, thus in the same lithostratigraphic context, not to say the same depositional setting (Carvalho et al., 2009) (Fig. 4C).

Vertebrate Ichnofossils

Bite Marks

The holotype skull of *B. salgadoensis* (MPMA-62-0001-02: Fig. 5) presents several perforations on both sides. They are asymmetric, present a rough texture and have a preferential axis and shallow grooves along this particular axis. Other, larger perforations are elliptical or slightly round in shape, bearing no grooves.

The smaller ones are located mostly on the left side. They are generally round to elliptical shallow pits nearly 15 mm long on their longer axis, associated with an anteriorly located shallow groove with an anteroposterior direction. Two of them are on the left lateral surface and another one is on the dorsal surface close to the contact between the nasal and frontal bones. The former two are set in a straight line, with their grooves aligned, and are located on the maxilla, close to the anterior margin of the anterior supraorbital. These grooves present unusual texture and rough and longitudinal scars (Fig. 5).

There are larger perforations (more than 15 mm), one on the right lateral surface and two others on the left lateral surface. The largest (25 mm length and 13 mm width), located on the left side, initially considered to be an antorbital fenestra, is deep and elliptical. It is located in the contact between the maxilla and lacrymal, close to the nasal. Although on the lateral surface, the actual opening faces more dorsally than laterally. A small groove with longitudinal scars can be observed posterior to this perforation. The other one on the left surface is smaller (20 mm) and located on the maxilla. It is round and bears concentric scars and a small, triangular, lateroventral groove. The pit on the right side is round, located on the maxilla, close to the tooth row. It is tear-shaped and bears no groove or scar. Most, if not all, seem to display bone remodeling, a signature of cicatrization.

Gastroliths

Outstanding specimens have shown even the most delicate bone structures and even cartilaginous tissue. One of them, UFRJ DG 288-R, has preserved its skull and about 80% of its skeleton. During the removal of the matrix of what should be the specimen's abdominal region, fragments of gastralia were noticed, together with some small, weathered, angular to subrounded clasts, initially recognized as gastroliths. They occur in a restricted cluster, where at least four stones are visible on the surface of the specimen, all of them pebble sized. The texture and fabrics of these rock fragments differ from the surrounding matrix, presenting darker purplish tones (Figs. 6A-C).

In thin section, one of the fragments revealed anisotropic texture, with opaque minerals of euhedric to subhedric habits in abundance. The mineralogical composition presents mainly clay minerals as weathering products; biotite and chlorite are common, the last being the result of hydration of the first. Although highly altered, the low quartz content, small-sized and well-formed crystals suggests mafic composition in a volcanic context, possibly representing a basalt fragment (Vasconcellos et al., 2008b).

Eggs and Egg Fragments

An abundance of isolated, mm-thick egg shell fragments are especially common in the laminated coarser sandstones (Magalhães Ribeiro, 2007). But, at least two Sites (1 and 3) bear nearly complete eggs. They occur as fragments in the same strata as crocodylian remains, but major fragments and better specimens are associated with cemented strata (paleosoil), sometimes immediately next to coprolites (Souto and Magalhães Ribeiro, 2005). One of them, Site 1, has yielded some fragmented but non-transported eggs fragments, one almost complete egg and a probable nidification structure (Fig. 6D).

Coprolites

Among the coprolites collected at the Sites, one sample was particularly impressive (Souto et al., 2005; Souto, 2010). It came from Site 1, partially exposed to the surface, close to and in the same strata as the nidification structure just mentioned. It presents five complete coprolites in an excellent state of preservation, roughly oriented as a group. They are cylindrical in shape, four times longer than wide, white in color, have isopolar extremities and some bear a constriction at the middle portion of their longitudinal axis (UFRJ DG 349-IcV, Fig. 6E). Though they cannot be directly attributed to *Baurusuchus* or *Armadillosuchus*, their morphology is characteristic of crocodylian coprolites (Souto, 2003).

DISCUSSION

The *Taenidium* is the product of invertebrate activity on unconsolidated sediment. Their occurrence in massive sandstones in close association with Baurusuchidae body remains would signify the follow-up events after a flashflood, when a new, unconsolidated sedimentary horizon was deposited together with body fossils of Baurusuchidae, which were carried by the flood or previously immobile in their self-excavated mounds.

The occurrence of *Trypanites* represents a momentary reduction or cessation of sedimentary deposition and the formation of hardgrounds—carbonate-rich paleosols at the sites. These depositional gaps may reflect dry periods where the channels, channel bars and flooded margins were exposed and hard, carbonate paleosols developed. The burrowing invertebrate fauna would colonize these recently consolidated carbonate-rich sediments. Eventually, burrowers would find partially preserved body remains of Baurusuchidae crocodylians, and feast on them.

In continental environments, the ichnogenus *Coprinisphaera* can be produced by several groups of invertebrate organisms, including nematodes, annelids, bivalves, gastropods and arthropods. The authors consider this record to represent a breeding ball constructed and provisioned

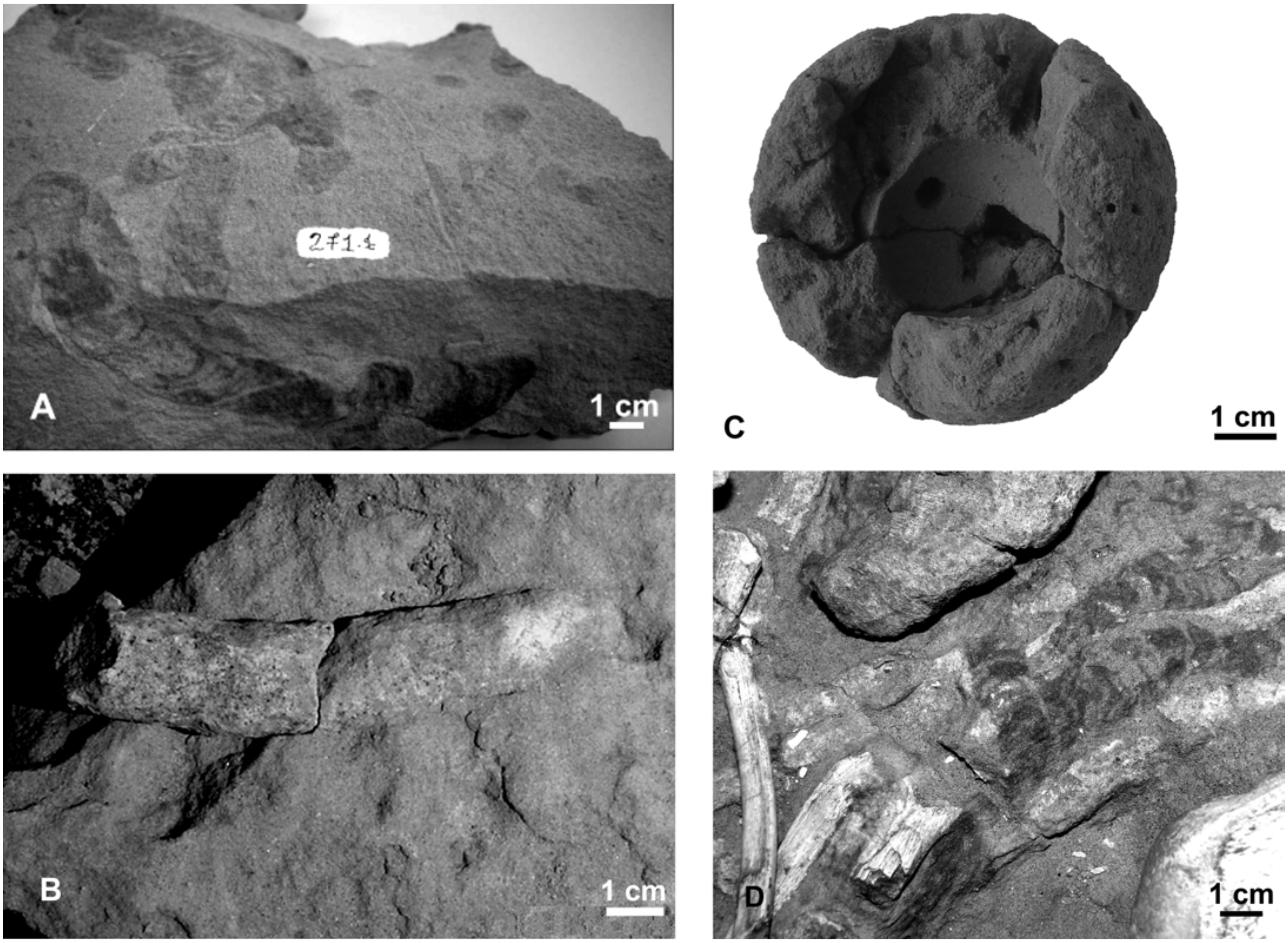

FIGURE 4. Invertebrate ichnofossils found at the General Salgado Sites. **A**, *Taenidium* isp. (UFRJ DG 271-Ic, from Site 3). **B**, *Trypanites* isp. (from Site 1). **C**, *Coprinisphaera* isp (UFRJ DG 521-Ic). **D**, Association of *Taenidium* with *Baurusuchus* ribs (UFRJ DG 285-R, from Site 2).

by adult dung beetles (scarabeids), to conceal and feed larvae. These trace fossils are generally preserved in paleosols and are indicative of a low-humidity plains environmental setting (Genise et al., 2000; Laza, 2006; Carvalho et al., in press) At the General Salgado sites, this provides another evidence of a gap in sedimentary deposition and therefore evidence of seasonality in the humidity.

None of the unusual marks appear to be anatomical or structural in nature, but seem to be bite marks. This interpretation is supported by comparison with numerous studies based on the shape, texture and associated features of bite marks in various taxa (Fiorillo, 1991; Erickson and Olson, 1996; Jacobsen, 1997, 1998; Tanke and Currie, 1995, 1998). The preservation of these marks is favored by the highly resilient nature of the crocodilian skull, especially those taxa with laterally compressed skulls such as the Baurusuchidae (Busbey III, 1995).

The smaller tooth-marks, more circular and shallow, match similar marks observed in the holotype of *Baurusuchus pachecoi* (Stephane Jouve, pers. commun., 2006) and in the tail osteoderms of a Baurusuchidae found at Jales, São Paulo State. The same shape is observed in *B. salgadoensis*—circular to elliptical shallow punctures with delicate grooves following the major axis of the more elliptical marks. These could be associated with Baurusuchidae intraspecific fighting behavior, as suggested by Avilla et al. (2004), due to tooth size and morphology (Riff and Kellner, 2001). However, other predators, such as theropod dinosaurs, could produce these tooth marks, as these animals present tooth variation along their jaws. The hypothesis of a crocodilian producer seems to be highly probable, as head-biting behavior has been observed in extant species (Cott, 1961), and the pattern of toothmarks and associated damage are similar to those observed in extant species attacks (Njau and Blumenschine, 2006).

The large, elliptical and deep toothmarks could be associated with larger archosaurs with more elliptical and ziphodont teeth in cross-section, such as Baurusuchidae crocodylians or Abelisauridae theropods. These dinosaurs are known in the Adamantina Formation, mostly from isolated teeth (Bertini et al.,1993; Candeiro et al., 2006; Vasconcellos et al., 2008a) and some fragmentary remains from Mato Grosso State diagnosed as *Pycnonemosaurus nevesi* Kellner and Campos, 2002. The grooves present in some tooth marks are interpreted as scar or drag marks, due to the action of "strike and-pull back" done by the predator, a particular tactical behavior of attack of animals bearing ziphodont teeth (Colbert, 1946; Busbey III, 1995; Snively and Russell, 2007).

The two types of tooth marks and their probable producers are not mutually exclusive. Both producers could carve independent tooth marks on different occasions. Whether these tooth marks were produced in combat or by predator-prey or scavenging interactions is difficult to determine. On the other hand, this could indicate three scenarios: the **first** with the intraspecific contest among Baurusuchidae crocodylians ; the **second**, *Baurusuchus* falling prey to a medium- to large-sized Abelisauridae theropods (*Pycnonemosaurus*-like) or other Baurusuchidae; and the **third**, *Baurusuchus* received the marks from a scavenger, again probably another Baurusuchidae or a theropod. And, given the dual

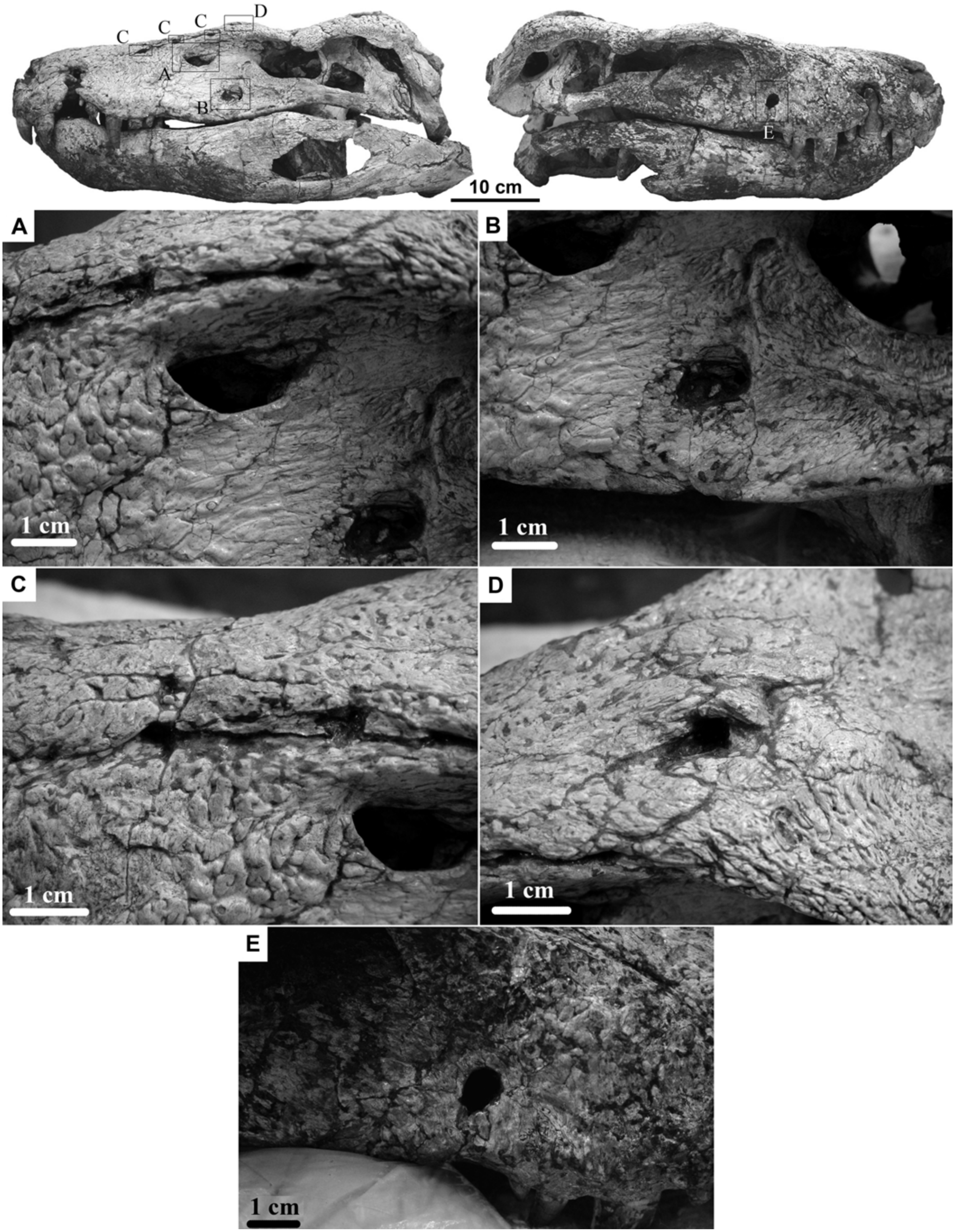

FIGURE 5. Tooth marks in the skull of *Baurusuchus salgadoensis* (holotype,MPMA-62-0001-02, from Site 1) in **A**, left lateral view; **B**, left lateral; **C**, left laterodorsal view; **D**, dorsal view and **E**, right lateral view.

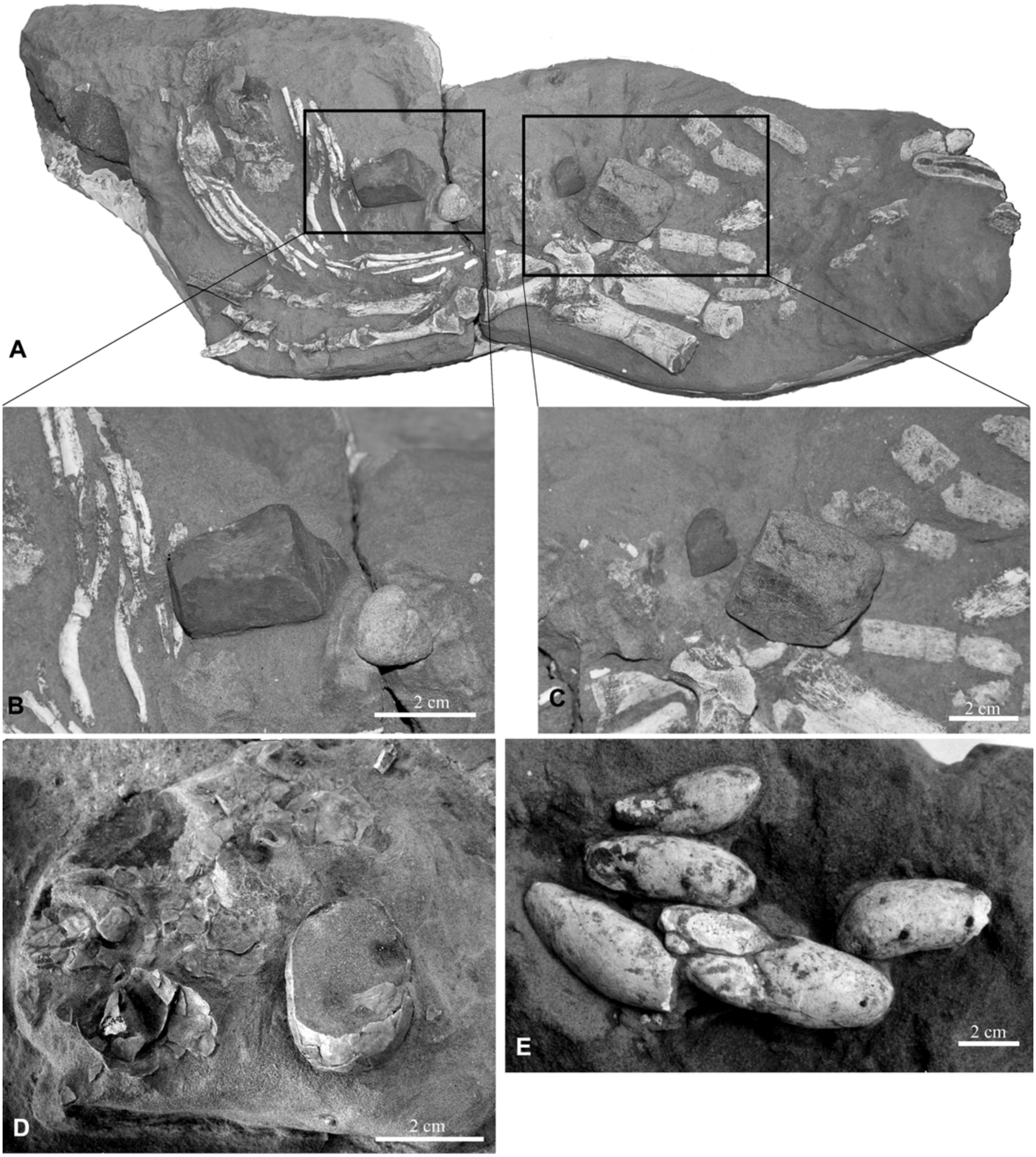

FIGURE 6. Vertebrate ichnofossils found at the General Salgado Sites. **A**, Abdominal region of *Baurusuchus* (UFRJ DG 288-R, from Site 3) bearing preserved gastralia, ribs and a forelimb associated with gastroliths. **B-C**, Magnified view of basalt gastroliths. **D**, Crocodyliformes egg and egg fragments at a nidification structure found at Site 1. **E**, Set of oriented Crocodyliformes coprolites found at site 1 (UFRJ DG 349-IcV).

pattern of tooth marks, two independent scenarios could have occurred, one prior to its death and another after (Vasconcellos and Carvalho, 2007). As described, the wounds display what appears to be cicatrization tissue, which implies the survival of the individual after the attack. This alone excludes the scavenging scenario.

The toothmarks are evidence of an ecological relationship among terrestrial archosaurs (Baurusuchidae-Baurusuchidae or Baurusuchidae-Abelisaridae) during the Late Cretaceous of Bauru Basin. The nature of this relationship is still an open case but probably was one of competition or an attempt of predation. In any case this is the first evidence of ecological interaction among crocodylians and theropods in Brazil.

In extant crocodylians the occurrence of gastroliths is commonly associated with food processing in the stomach, diving ballast, hunger stress and/or supplementary mineral ingestion when under stressful conditions of lack of food or water (Jackson et al., 1974; Henderson, 2003). As Baurusuchidae are characterized as medium- to large-sized, fully terrestrial predator/scavengers based on the skull, axial and appendicular data (Vasconcellos, 2009), the ballast function of gastroliths is excluded.

The extreme climate conditions dominating the Adamantina Formation during the Late Cretaceous long drought periods and short rainy seasons would expose crocodylians from the sites to stressful conditions where famine and mass mortality were common outcomes. These conditions would force the Baurusuchidae to endure or escape. They may have endured by ingesting the basalt rock in search of supplementary minerals or as a hunger-reducing last resort.

The association of complete eggs in what seems to be a nidification structure with a set of oriented coprolites suggests low energy transport or almost no transport. This contrasts with the massive, coarser sandstones in the strata below, where *Baurusuchus* body fossil are usually found with fragmentary isolated coprolites and egg shells. The occurrences of different invertebrate ichnofossils also seem to be controlled by the slight lithology difference. The finer-cemented sandstone beds (paleosols) bear burrows (*Trypanites* isp.) and, in a different locality, even a fully terrestrial ichnogenus (*Coprinisphaera* isp.). The coarser, massive or stratified beds yield meniscate, unconsolidated sediment-related ichnogenera (*Taenidium* isp.).

The cross-stratified/massive sandstone beds represent the successive flood events during the rainy period and preserve the taphocoenoses of the body fossil community (mainly composed of crocodylians) and the biocoenoses of the infaunal invertebrate community. The paleosol beds would represent the periods of dry, hot weather, with little or no sedimentation, where a biocoenosis of a soil burrower invertebrate community would establish itself together with a complete community of crocodylians (evidenced by coprolites, nidification structures and scattered body fossils), and potentially with other archosaurs (such as Abelisauridae theropods) and other vertebrates (thus far unknown).

This scenario would evolve: conditions becoming extremely harsh as aridity increased, reducing water and food supply (either the already scarce vegetation for herbivores or prey to carnivores). In this situation, larger vertebrates, especially the most abundant crocodylian *Baurusuchus*, would resort to survival strategies, employing different methods (omnivory, intraspecific fighting, scavenging, stone ingestion, and eventually, burrowing and aestivation). Death would be a common outcome for these crocodylians, sometimes even those already buried, preserving complete specimens. These could be used as a food supply by hardground burrowers and unconsolidated soil infaunal invertebrates, a conclusion supported by the occurrence of burrows apparently oriented to crocodylian carcasses and the meniscate "halo" around the remains. This group of evidence indicates a biocoenosis/thanatocoenosis for the crocodylians.

CONCLUSION

The paleoenvironmental conditions dominating the Adamantina Formation during the Late Cretaceous are considered mainly arid, marked with strong seasonality, alternating long droughts and short rainy periods, associated with flashflood events.

The puncture marks and grooves on the skull of *Baurusuchus salgadoensis* are toothmarks probably produced by a medium to large archosaur with ziphodont teeth, such as a Baurusuchidae or Abelisauridae theropod dinosaur. Although the actual tooth-mark producer or the paleoecological context in which they were carved cannot be diagnosed precisely, both Baurusuchidae and Abelisauridae are strong candidates, being the largest cursorial predators of that period in terrestrial areas of continental Brazil. This paleoecological relationship among crocodylians and theropods is the first to be identified in Brazil

The ichnofossil record association of complete eggs and coprolites in fine- textured sandstone-cemented paleosol beds alternating with massive/cross-stratified sandstone beds with fragmentary egg shells and coprolite beds suggests a low energy depositional agent to a complete stop of sedimentation during arid periods contrasted with a short, flashflood-dominated season. The invertebrate ichnofossil record apparently supports these extreme, seasonal conditions for the General Salgado Adamantina Formation sites.

These stressful conditions created during the dry season would cause famine and mass mortality, thus forcing animals to endure or escape. The Baurusuchidae underwent the dry seasons, resorting to the behavioral responses of intraspecific fighting, self burial and stone ingestion, but eventually the community partially perished. The integration between sedimentology, taphonomy, and the body fossil and ichnofossil records can be a useful tool in the reconstruction of paleoecological scenarios, building new data on the life, communities, and associated fauna of Cretaceous crocodylians

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Dwarf Caiman. Photo by Jesper Milàn.