DESCRIPTION OF A MULTITAXIC BONE ASSEMBLAGE FROM THE UPPER TRIASSIC POST QUARRY OF TEXAS (DOCKUM GROUP), INCLUDING A NEW SMALL BASAL DINOSAURIFORM TAXON

Descripción de una asociación multitaxones del Triásico Superior de Post-Quarry de Texas (Grupo Dockum), incluyendo un nuevo taxón de pequeño Dinosauriformes basal

Volkan Sarıgül[1], Federico Agnolín[2,3] and Sankar Chatterjee[1]

[1]Museum of Texas Tech University (Box 43191), Lubbock, Texas 79409, USA.
volkansaurus@gmail.com, sankar.chatterjee@ttu.edu
[2]Fundación de Historia Natural Félix de Azara, Departamento de Ciencias Naturales y Antropología, Universidad Maimónides, Hidalgo 775 (C1405BDB), Ciudad Autónoma de Buenos Aires, Argentina. fedeagnolin@yahoo.com.ar
[3]Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Av. Ángel Gallardo 470 (C1405DJR), Ciudad Autónoma de Buenos Aires, Argentina.

AZARA
FUNDACIÓN DE HISTORIA NATURAL

Universidad Maimónides

Abstract. A bone assemblage composed of intermixed small cranial and postcranial fragments from the Post Quarry of Texas, USA, is described. The skeletal elements represent multiple individuals of different taxa, including a partial dorsal column assigned to *Vancleavea campi* and an incomplete dentary referred to a new genus and species of a small-sized basal dinosauriform. Ankylothecodont dental implantation of the dinosauriform dentary bears strong resemblance to silesaurids. A fragmentary archosauromorph braincase is another intriguing element of the assemblage; it displays a striking contrast of a derived otoccipital on a plesiomorphic basioccipital. Poor preservation prevents more conclusive taxonomic assignments for the rest of the skeletal elements. The observed attrition and entangling in this bone assemblage reflect the complexities of the Dockum land tetrapod taphonomy.

Key words. Upper Triassic, Texas, Post Quarry, bone assemblage, Sauria, Dinosauriformes.

Resumen. Una asociación ósea de diminutos fragmentos craneanos y postcraneanos de diferentes individuos es aquí descripto. Los especímenes provienen de la bien conocida localidad fosilífera del Triásico Tardío de Post Quarry, Texas, USA. Los elementos esqueletarios pertenecen a diversos archosauromorfos y saurios, incluyendo una columna vertebral parcial asignable a *Vancleavea campi* y un dentario referido a un nuevo género y especie de pequeño dinosauriformes basal. Implantación anquilotecodonte de los dientes en el dentario indica afinidades fuertes con Silesauridae. Un basicráneo fragmentario de arcosauromorfos constituye un elemento curioso de la asociación. Este ejemplar exhibe un marcado contraste entre un otoccipital muy derivado y un basioccipital con rasgos plesiomórficos. La pobre preservación de la mayor parte de los elementos esqueletarios impide asignaciones taxonómicas más acotadas. El grado de desgaste y la mezcla de esta asociación osteológica reflejan las complejidades de la tafonomía de los tetrápodos terrestres de Dockum.

Palabras clave. Triásico Tardío, Texas, Post Quarry, asociación de elemento óseos, Sauria, Dinosauriformes.

INTRODUCTION

The Post Quarry (MOTT 3624, formerly the Miller Quarry) is perhaps the most productive fossil vertebrate quarry of the Dockum Group of Texas, in terms of numbers and taxonomic diversity. Holotypes of many iconic Dockum vertebrate fossils like temnospondyl *Rileymillerus cosgriffi* Bolt and Chatterjee, 2000, pseudosuchians *Desmatosuchus smalli* Parker, 2005, *Postosuchus kirkparticki* Chatterjee, 1985 and *Shuvosaurus inexpectatus* Chatterjee, 1993, silesaurid *Technosaurus smalli* Chatterjee, 1984 and the controversial *Protoavis texensis* Chatterjee, 1991 were discovered in this famous bonebed, as well as many other specimens referred to temnospondyls, therapsids, phytosaurs, aetosaurs, basal crocodylomorphs and dinosauromorphs (*e.g.*, Chatterjee, 1983; Long and Murry, 1995; Lehman and Chatterjee, 2005; Nesbitt and Chatterjee, 2008; Nesbitt *et al.*, 2009a; Martz *et al.*, 2013; Sarıgül, 2016, 2017a). Although it was noted that the vertebrate fossils recovered from the Post Quarry are usually associated (Lehman and Chatterjee, 2005; Martz *et al.*, 2013), attritional specimens represented by one or few elements also occur as much as the partially complete skeletons. In some cases, as the one introduced here, scattered and damaged elements are intermingled, making attribution of each element to a specific taxon complicated. Such interesting discoveries provide additional data for the taxonomic diversity and taphonomic interpretation of the Post Quarry, a relatively small quarry with an area less than a hundred square meters (Chatterjee, 1985).

Location and Geological Settings

The widely exposed Upper Triassic terrestrial sediments in eastern New Mexico and western Texas, namely the Dockum Group, yield one of the richest Late Triassic land tetrapod faunas in the world. The Post Quarry is located about 15 km south to the
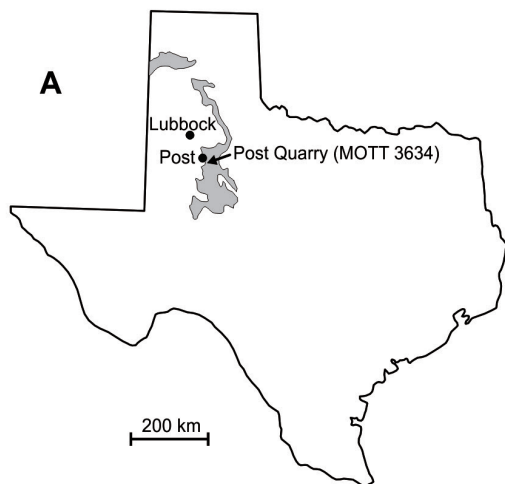

Figure 1 - Field properties of the Post Quarry. **A,** location map of the Post Quarry with the Dockum Group exposures marked in grey (modified after Chatterjee 1991); **B,** a photograph displaying the general view of the quarry and predominant red mudstones (Photo credit: Bill Mueller). The white arrow in the photograph indicates the main fossiliferous horizon of the step-like platform at the lower part of the hill.

town of Post in Garza County, in western Texas (Figure 1A) and placed in the upper part of the lower unit of the Cooper Canyon Formation, referring to a new tri-partite stratigraphic framework established for Garza County (Martz, 2008; Martz *et al.*, 2013). However, this claim is not followed based on the fact that no difference in lithostratigraphy is detected between the previously described Tecovas Formation in Garza County by Lehman and Chatterjee (2005) and the newly demonstrated unit, and thus it is suggested the employment of the former nomenclature (Bill Mueller, personal communication, 2016). Whatever the name is, this basal lithostratigraphic unit is mainly composed of red coloured floodplain mudstones with few intercalating lacustrine deposits and happens to be a direct correlate for the Tecovas Formation in northern Texas and in New Mexico (Figure 1B). The collected tetrapod fossils are not homogeneously dispersed within the fluvial mudstones of this particular quarry;

instead, they are found concentrated in a distinct horizon of ca. 30 cm. in thickness (Figure 1B), except the *Protoavis* specimens which were collected around a meter above (Chatterjee, 1991; Martz *et al.*, 2013).

MATERIALS AND METHODS

Discovery and preparation of the specimens

In the summer of 1993, some delicate fossils within a small mudstone block were found by Soumya Chatterjee, the elder son of Sankar Chatterjee, in the main fossiliferous horizon of the Post Quarry and were jacketed for preparation in the laboratory. This mudstone block yielded tiny and intermingled bone fragments that are poorly preserved, including a partial braincase, an incomplete dentary, few articulated cervical vertebrae associated with an incomplete
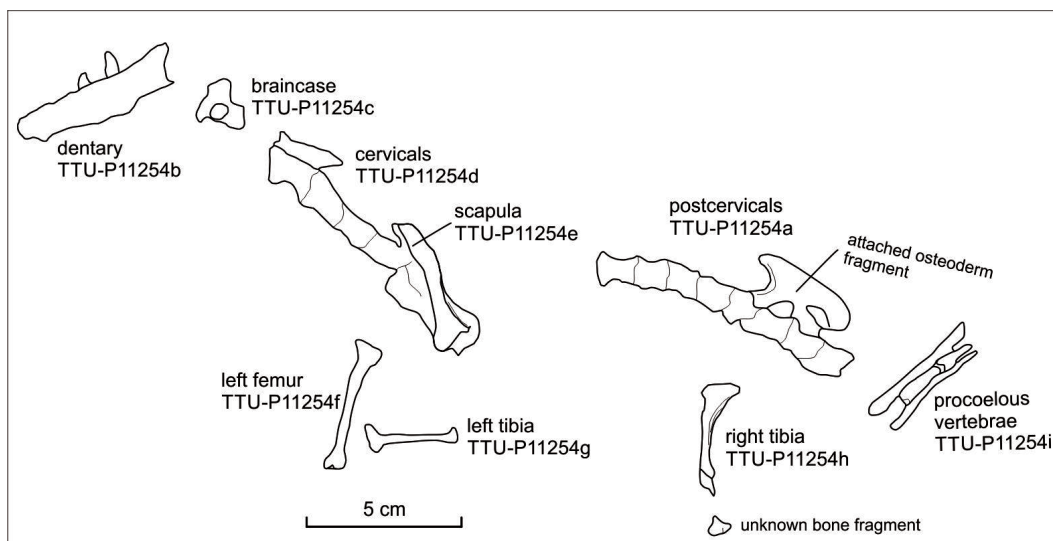

Figure 2 - The original field sketch of the bone assemblage that is redrawn from Sankar Chatterjee's field book and each element is labeled separately with a voucher number in accord with the provided diagnosis. The unknown bone fragment is assumed to be an astragalocalcaneum by Sankar Chatterjee and it is said to be shattered while exposing and now lost.

and distorted left scapula, some articulated postcervical vertebrae with an attached bone fragment, distal end of a left femur, proximal end of a left tibia, distorted right tibia and fibula and two procoelous vertebrae found attached to few fragmentary shafts (Figure 2). These fragments were prepared under a binocular microscope and then the same elements underwent a more elaborate second preparation phase of cleaning and scrapping. Each bone possesses an individual voucher number (TTU-P11254a-i) and is reposited at the Museum of Texas Tech University collections.

Phylogenetic analysis

The phylogenetic analysis here is performed with the aim to elucidate the phylogenetic affinities of TTU-P11254b. We included the specimen within the comprehensive archosaur phylogeny published by Nesbitt (2011) with the modifications by Nesbitt *et al.* (2017) and the re-scoring of *Pisanosaurus* carried out by Agnolin and Rozadilla (2017) (Appendix 1). *Pseudolagosuchus* and *Lewisuchus* are considered as synonymous and fused in a single terminal based on Arcucci, (1997, 1998), and work in progress based on newly collected material (Novas *et al.*, 2015). Character 174 of Nesbitt *et al.* (2017) is modified here as follows:

Character 174: Tooth implantation: (0) free at the base of the tooth; (1) teeth fused to the base by fibrous tissues which form a bulbosity; (2) teeth fused to the base by thin bony ridges.

The resulting data matrix is composed by 419 characters and 93 taxa. The phylogenetic analysis was performed using TNT
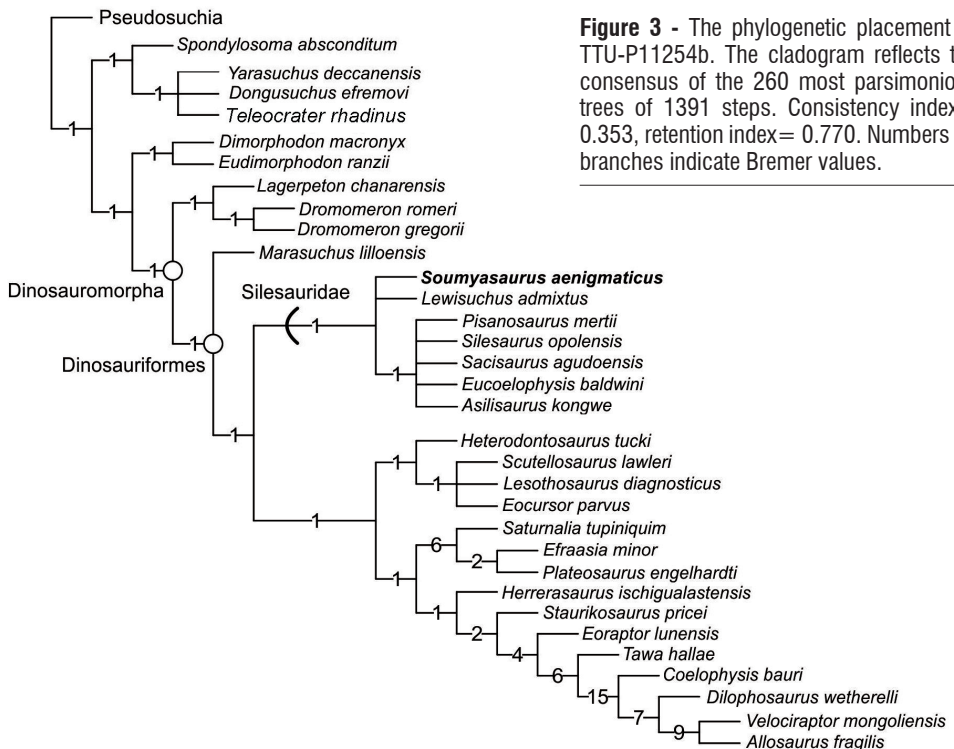

Figure 3 - The phylogenetic placement of TTU-P11254b. The cladogram reflects the consensus of the 260 most parsimonious trees of 1391 steps. Consistency index= 0.353, retention index= 0.770. Numbers on branches indicate Bremer values.

1.1 (Goloboff *et al.*, 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1000 replicates of WAG+TBR, saving 100 trees per replicate. The phylogenetic analysis resulted in the recovery of 260 Most Parsimonious Trees (MPTs), of 1391 steps, with a consistency index of 0.353, and a retention index of 0.770 which are summarized using a strict consensus tree (Figure 3).

We also intend to include the new dinosauriform taxon with the coeval silesaurid *Technosaurus smalli* in a phylogenetic analysis (see scorings of *T. smalli* in Appendix 2). The new dinosauriform taxon and *T. smalli* are both recovered as silesaurids when they are individually included to the analysis. However, it results a more complicated picture when *T. smalli* and the new dinosauriform taxon are included together; both taxa are nested within a polytomy where *Euparkeria capensis* is found as the immediate

outgroup. This situation is attributed to the fragmentary condition of the fossil remains and thus, we opt not to include *Technosaurus* in the phylogenetic analysis performed here.

SYSTEMATIC PALAEONTOLOGY

Sauria McCartney, 1802, sensu Gauthier, Kluge and Rowe 1988
Archosauromorpha Huene, 1946, sensu Benton, 1985
Archosauriformes Gauthier, Kluge and Rowe 1988
Vancleavea campi Long and Murry, 1995
Referred specimen. TTU-P11254a, partial vertebral column and a piece of osteoderm.
Description and remarks. The partially preserved vertebral column comprises seven vertebrae and each vertebra possess shallow lateral excavations on the side,
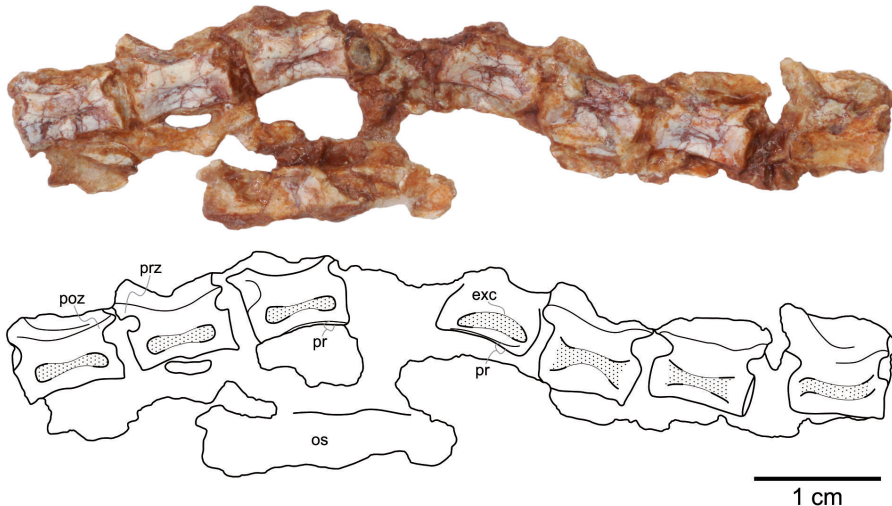

Figure 4 - Partial postcervical vertebrae and attached osteoderm fragment of *Vancleavea campi* (TTU-P11254a). Abbreviations: **exc**, lateral excavations; **os**, attached osteoderm fragment; **poz**, postzygapophysis; **pr**, paramedian ridges; **prz**, prezygapophysis.

a feature shared with many archosauromorphs (Figure 4). Although the specimen is severely compressed mediolaterally, two paramedian ridges are on ventral side are conspicuous on some vertebrae. Presence of two paramedian ridges is an autapomorphy of the dorsal centra of *Vancleavea campi*; however, it is noted that these ridges occur on the caudal vertebrae of *V. campi* as well (*e.g.* Nesbitt *et al.*, 2009b). Concurringly, an independent examination of the specimen concludes that the vertebrae represents part of the postcervical series of *Vancleavea* and the attached unrecognizable piece of bone is an amalgamation of *Vancleavea* dermal armor (Bill Mueller, personal communication, 2015).

Archosauriformes Gauthier, Kluge and Rowe 1988
Dinosauriformes Novas, 1992
Silesauridae Langer, Ezcurra, Bittencourt and Novas, 2010
Soumyasaurus gen. nov.

Etymology. Coined by Sankar Chatterjee to honour his elder son Soumya for his discovery of the specimen.
Type species. *Soumyasaurus aenigmaticus*, sp. nov.; see below.
Diagnosis. As for species, see below.
Stratigraphic and geographic range. As for species, see below.

Soumyasaurus aenigmaticus gen. nov., sp. nov.

Etymology. Species name represents the nature of the specimen, derived from the Latin word "aenigma" that means "enigma or riddle".
Holotype. TTU-P11254, partial left dentary.
Type locality. Post Quarry (MOTT 3624), Garza County, Texas.
Type horizon. Tecovas Formation (or the lower unit of the Cooper Canyon Formation sensu Martz, 2008), collected from the main thin, fossil-rich horizon that is situated about 8 meters below the top of the formation (Martz *et al.*, 2013). The Post Quarry horizon corresponds to Norian (Sarıgül, 2017b).

Diagnosis. A minute silesaurid distinguishable from all other members of the clade except *Asilisaurus kongwe* Nesbitt *et al.*, 2010 by having smooth and conical dentary teeth that have no expansion or curvature above the root. *S. aenigmaticus* differs from *A. kongwe* in having a Meckelian groove restricted to ventral margin of the dentary. Because the anterior portion of TTU-P11254b is not preserved, it remains unknown whether the dorsal margin of the anterior dentary of *S. aenigmaticus* is convex as in that of *A. kongwe*. Similarly, apical sides of the preserved teeth of *S. aenigmaticus* are mostly obliterated and cannot be compared with the teeth of *A. kongwe* that possess weakly serrated carinae at the tip of each crown.

Description and remarks. The dentary fragment is a slender and transversely narrow element with an elliptical cross-section. The lateral side is almost featureless except for the presence of several neurovascular foramina (Figure 5A). Few lingual pits at the alveolar margin are detected on the medial side, and a narrow Meckelian groove runs the length of the dentary on the ventral margin (Figure 5B). Four erupted teeth are preserved, however, there are about 11 closely spaced alveoli, making the dentary tooth count of 15 or more (Figure 5C). Characteristic grooves and foramina implying the presence of a keratinous beak in silesaurids (*e.g.*, Dzik, 2003; Langer and Ferigolo, 2013) are lacking on the edentulous end and this portion is interpreted as the posterior end of the tooth row. The Meckelian groove also tapers towards the counter direction of the edentulous portion, indicating that TTU-P11254b probably represents a left side dentary (Figure 5B-C).
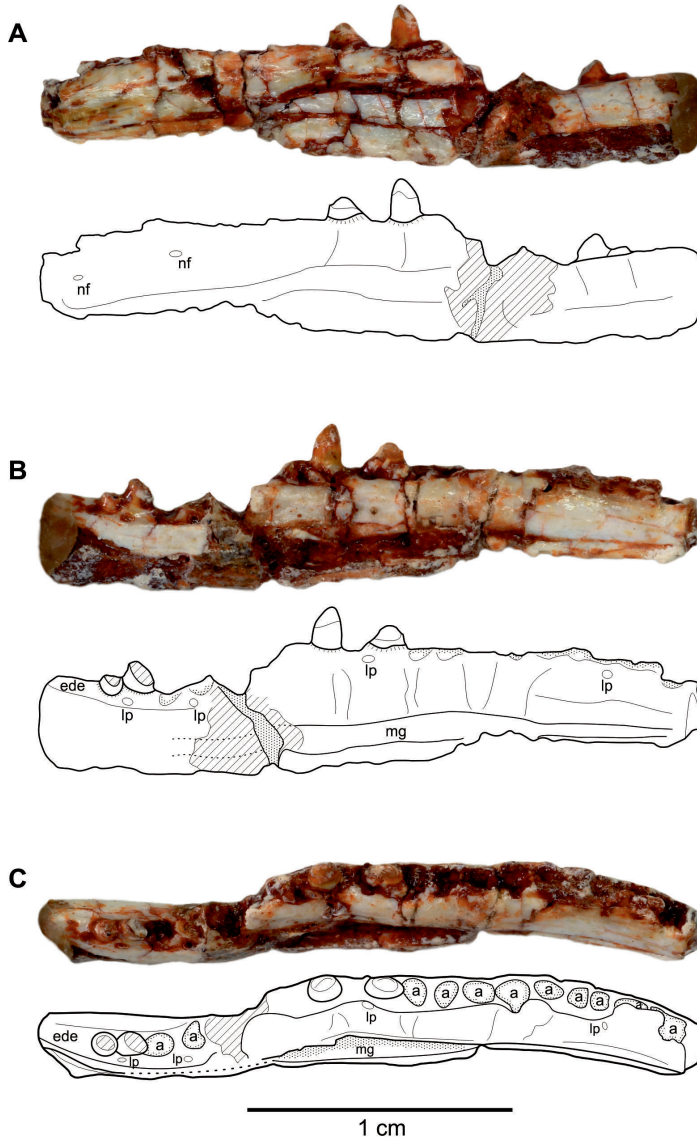
Figure 5 - Incomplete dentary referred to a new basal dinosauriform, *Soumyasaurus aenigmaticus* gen. nov., sp. nov. (TTU-P11254b). **A,** lateral view; **B,** medial view; **C.** dorsomedial view. Abbreviations: **a**, alveolus; **ede**, edentulous portion; **mg**, Meckelian groove; **lp**, lingual pit; **nf**, nutrient foramen. Hatches signify damaged portions.

Presence of ankylothecodont teeth, which means the teeth are fused at the base to the dentary bone (Nesbitt, 2011, character 174) is the main unambiguous synapomorphy shared by *S. aenigmaticus* and Silesauridae. Silesaurid teeth are ankylosed to their sockets by fibrous tissues which creates a collar-like structure around the tooth base as in *Silesaurus*, *Sacisaurus* and *Diodorus* (Dzik, 2003; Kammerer *et al.*, 2012;
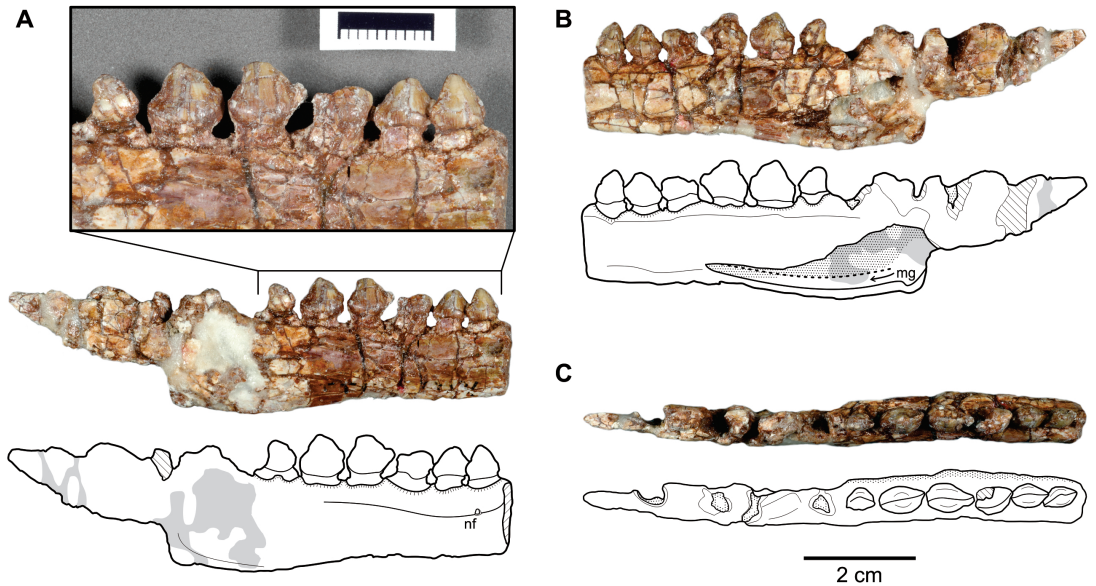
Figure 6 - Dentary of the *Technosaurus smalli* holotype (TTU-P9021). **A,** lateral view; **B,** medial view; **C,** dorsal view. A close-up view of the dentition is provided for the lateral view including a separate 1 cm scale. For abbreviations, see Figure 5

Langer and Ferigolo, 2013), contrasting the condition of other ankylothecodont archosauromorphs where the teeth are strongly attached to their base by bony ridges (*e.g.* Ezcurra, 2014). Another feature shared by *S. aenigmaticus* and other silesaurids except *Asilisaurus kongwe* is the Meckelian groove restricted to the ventral border on the medial side of the dentary (Nesbitt, 2011, character 152; Dzik, 2003; Ferigolo and Langer, 2007; Nesbitt *et al.*, 2010; Kammerer *et al.*, 2012). The anterior tip of the dentary is not preserved; thus, it is not possible to discern whether it is rounded or tapers anteriorly (Nesbitt, 2011, character 155).

Technosaurus smalli is the only other silesaurid described from the same quarry with a holotype consisting of a premaxilla and an incomplete dentary (*e.g.*, Chatterjee, 1984; Nesbitt *et al.*, 2007) (Figures 6A-C). *T. smalli* and *S. aenigmaticus* share the typical silesaurid synapomorphies of having a silesaurid-type ankylosed dentition and a ventrally restricted Meckelian groove. The tip of the dentary is missing in both taxa. Besides the obvious size difference, the major contrast between the two taxa is the dental morphology. The lower jaw dentition of *T. smalli* comprises triangular and possibly tricuspid teeth with unpronounced denticles on the dental edge and faint striations on crown surface; a structure which is clearly different from that of *S. aenigmaticus*.

Dentition of *S. aenigmaticus* is also very different from the other silesaurids with typical leaf-shaped teeth (Dzik, 2003; Kammerer *et al.*, 2012; Langer and Ferigolo, 2013). Although they differ in the position of the Meckelian groove, the dentary teeth of *A. kongwe* probably offers the best comparison for the dentition of *Soumyasaurus* than any other silesaurid in both size and morphology. However, teeth of A. kongwe possess a serrated carina (Nesbitt et al., 2010, Figure 1), but this feature cannot be detected in those of *S. aenigmaticus* since the apical portions of the preserved teeth are either missing or severely damaged.

The inclusion of *S. aenigmaticus* in the data matrix of Nesbitt *et al.* (2017) resulted in its nesting within the basal dinosauriform clade Silesauridae. With the aim to test the robustness of tree topology, Bremer supports are calculated for each node. The support of major archosaur clades, as Ornithodira, Dinosauriformes, and Crurotarsi is relatively low (Bremer support = 1), as previously recognized and discussed by Nesbitt (2011). The clade Silesauridae + *Soumyasaurus* also has a Bremer support = 1. The inclusion of *Soumyasaurus* within Saurischia, sister group to Dinosauria or Theropoda results in a tree of a length of 1392. This implies that a single step may change the position of *S. aenigmaticus*. Thus, *S. aenigmaticus* is attributed to Silesauridae, but with some degree of uncertainty.

Sauria McCartney, 1802, sensu Gauthier, Kluge and Rowe 1988
Archosauromorpha Huene, 1946, sensu Benton, 1985
Gen. et sp. indet.
Referred specimens. TTU-P11254c, partial braincase; TTU-P11254d, cervical vertebrae; TTU-P11254e, left scapula.
Description and remarks. The braincase is poorly preserved, and the intimately fused bones complicate the demarcation of each element. The foramen magnum is obliterated under the collapsed roof of the braincase; the only putative feature visible at this area is a damaged foramen which might be related to a segment of the occipital vein (Figure 7A). The occipital condyle is round in posterior view and the basioccipital probably forms most of the occipital condyle with limited contribution of exoccipitals as in most saurians (Figure 7A). The condylar neck is ventrally constricted at the base, a condition that is also very apparent in lateral view, and then the basioccipital flares again to form a pair of medially well-separated and anteroposteriorly long basal

tubera (Figures 7B-C). Each basal tuber displays slight excavations on the lateral side (Figures 7C-D). The sphenoidal contribution to the basal tubera, if any present, cannot be detected.

The left lateral side comprise a large secondary tympanic opening (*i.e.*, fenestra pseudorotunda) encapsulated by the fused exoccipital-opisthotic complex (oto-occipital or otoccipital), which is dorsolaterally pierced by a foramen that possibly transmitted a segment of the occipital vein, similar to what is identified on the opposite side of the braincase (Figures 7C-D). The bony frame around the fenestra pseudorotunda is a distinguishing character of extant archosaurs, and TTU-P11254c represents few of the fossil examples in which this gracile structure is preserved (Gower and Weber, 1998). The floor of the fenestra pseudorotunda maintains a direct connection between the cranial cavity and the vagus foramen at the occipital side, from where the vagus (X) and accessory (XI) cranial nerves are carried along with the posterior jugular vein (Figures 7C-D). In anterior view, the otic capsule possesses a distinct crescentic groove on its anteromedial border (Figure 7E).

Although the fused exoccipital-opisthotic complex of TTU-P11254c is described in many archosauriforms (*e.g.*, Gower and Sennikov, 1996; Currie, 1997; Gower and Weber, 1998; Gower, 2002), a posterior diversion of the vagus foramen evolved independently in crocodilians by the emergence of a secondary lamina (Klembara, 2005), in neotheropods by the projection of the metotic strut (*e.g.*, Currie, 1995; Sampson and Witmer, 2007; Fiorillo *et al.*, 2009), and possibly in pterosaurs by the posterior ossification of the braincase (*e.g.*, Bennett, 1991; Kellner, 1996). The posterior shift of the vagus foramen in TTU-P11254c is reminiscent to the condition described in neotheropods, where the presence of a well-developed metotic strut results in separation of
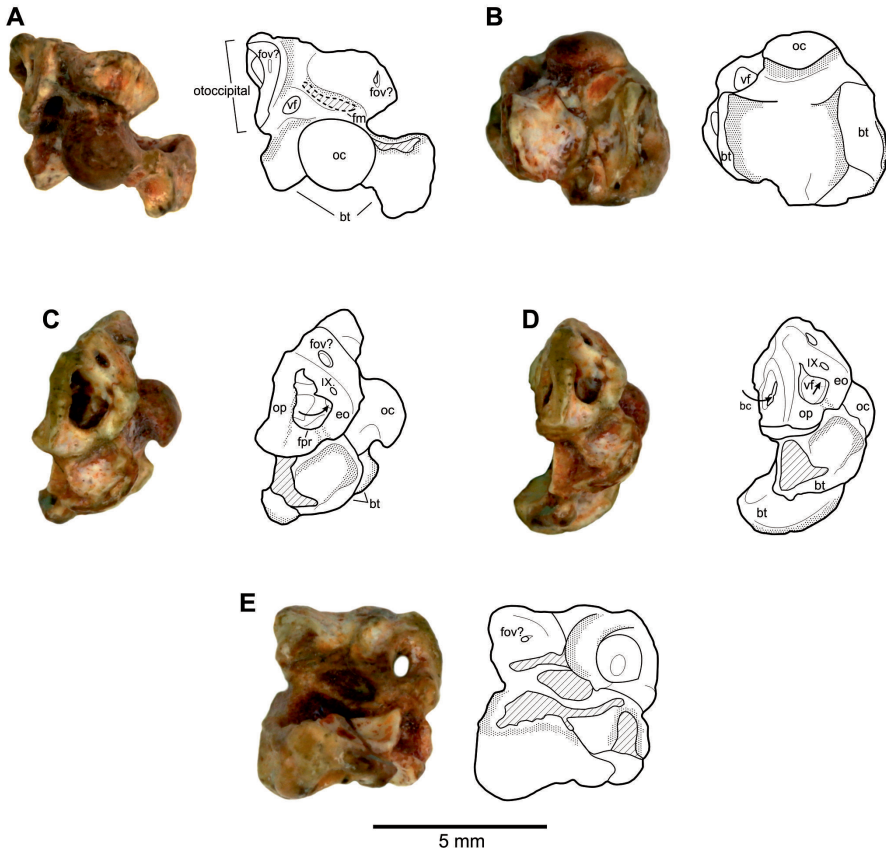
Figure 7 - Partial braincase of an undetermined archosauromorph (TTU-P11254c). **A,** posterior view; **B,** ventral view; **C,** left lateral view; **D,** left ventrolateral view; and **E,** anterior view. Abbreviations: **bc**, brain cavity; **bt**, basal tubera; **eo**, exoccipital; **fm**, foramen magnum; **fov**, foramen for occipital vein; **fpr**, fenestra pseudorotunda; **ic**, crista interfenestralis; **oc**, occipital condyle; **op**, opisthotic; **vf**, vagus foramen; **IX.**, foramen for glossopharyngeal nerve. Hatches signify damaged parts. The arrows refer to the diversion of the vagus foramen.

the vagus nerve. However, this separation results in a laterally diverted transmission instead of a direct one from the endocranial cavity recalls that of non-avian theropods (*e.g.*, McClellan, 1990; Currie and Zhao, 1993; Currie, 1995; Rauhut, 2004; Sampson and Witmer, 2007) rather than that of modern birds like *Rhea* and *Aquila*. It is also noted that the vagus nerve emerges from the occiput via a direct transmission from the braincase floor in one specimen referred to *Troodon* (Fiorillo *et al.*, 2009). Moreover, the upper section of the fenestra pseudorotunda is topologically suitable for being the perilymphatic foramen, and the small foramen situated at the posterior side possibly represents the glossopharyngeal (IX.) nerve foramen. The glossopharyngeal nerve always leaves the braincase laterally from the metotic foramen or the fenestra pseudorotunda; however, a separate exit for this particular nerve is observed in juvenile stages of some modern birds which turned into an ossified notch or a foramen in adult phase as in the subarctic bird genus *Fulmarus* (Walker, 1985).
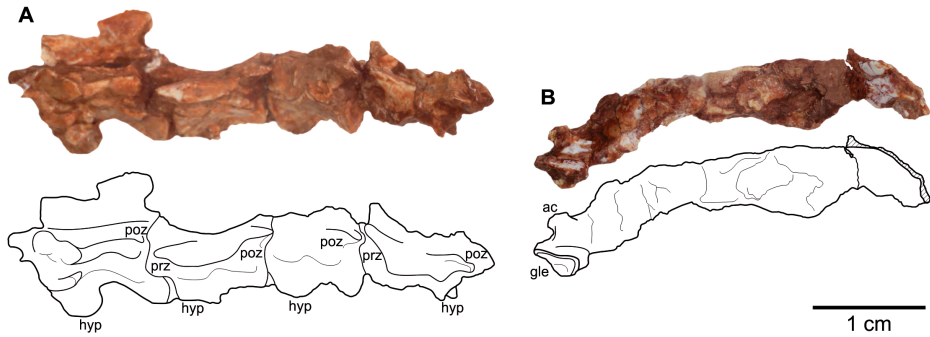
Figure 8 - Cervical vertebrae (TTU-P11254d) and left scapula (TTU-P11254e) assigned to undetermined archosauromorphs. **A,** left lateral view of cervical vertebrae; **B,** lateral view of left scapula. Abbreviations: **ac**, acromion process; **gle**, glenoid fossa; **hyp**, hypapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis. Hatches signify damaged parts.

Although the otoccipital of TTU-P11254c is highly comparable to that of non-avian neotheropods as mentioned above, this portion displays a clear contrast with the plesiomorphic state of the basal tubera. In non-avian theropods, the basal tubera are expanded ventrally and merged at the midline for the most part, if not completely (*e.g.*, Chure and Madsen, 1988, figure 8; Sereno and Novas, 1993; Currie, 1995; Sampson and Witmer, 2007). A possible explanation for either TTU-P11254c represents a new type of theropod or another example of morphological convergence among Triassic archosauromorphs (*e.g.*, Hunt, 1989; Nesbitt and Norell, 2006; Stocker *et al.*, 2016) remains obscure because of the paucity of the available material. Recently, Piechowski *et al.* (2018) have suggested avian-like traits on the braincase of *Silesaurus opolensis* Dzik, 2003 based on ventrally directed paroccipital processes and reconstructed muscle attachments on the occipital side, even though the otoccipital of *S. opolensis* retains the plesiomorphic condition of having a laterally directed metotic foramen. Paroccipital processes of TTU-P11254c are not preserved, but the otoccipital is more derived than that of *S. opolensis* which may indicate a closer relation to avians if TTU-P11254c represents a dinosauriform. Nevertheless, TTU-P11254c might add to the large list of characters interpreted to occur among theropods later in the Mesozoic have already been convergently acquired by archosauromorph taxa during the Triassic.

The cervical vertebrae (TTU-P11254d) and the scapula (TTU-P11254e) bear a close resemblance to archosauromorph bones as well. The preserved cervical centra are anteroposteriorly elongate and transversely compressed, and they have a well-developed ventral keel (Figure 8A). Presence of prominent hypapophyses on the cervicals is a plesiomorphic character that is lost in many archosaur groups (Romer, 1956, Gauthier, 1986), but it is retained in the middle cervical vertebrae of *Postosuchus* spp. and *Rauisuchus* (Nesbitt, 2011, character 192). The scapula is found attached to the cervicals; it possesses a robust and dorsoventrally expanded morphology, differing from what is observed in lepidosauromorphs where the coracoid is the dominant element of the shoulder girdle (Romer, 1956) (Figure 8B). However, the poor preservation of these elements offers any diagnostic features to pinpoint a taxon more inclusive than Archosauromorpha.
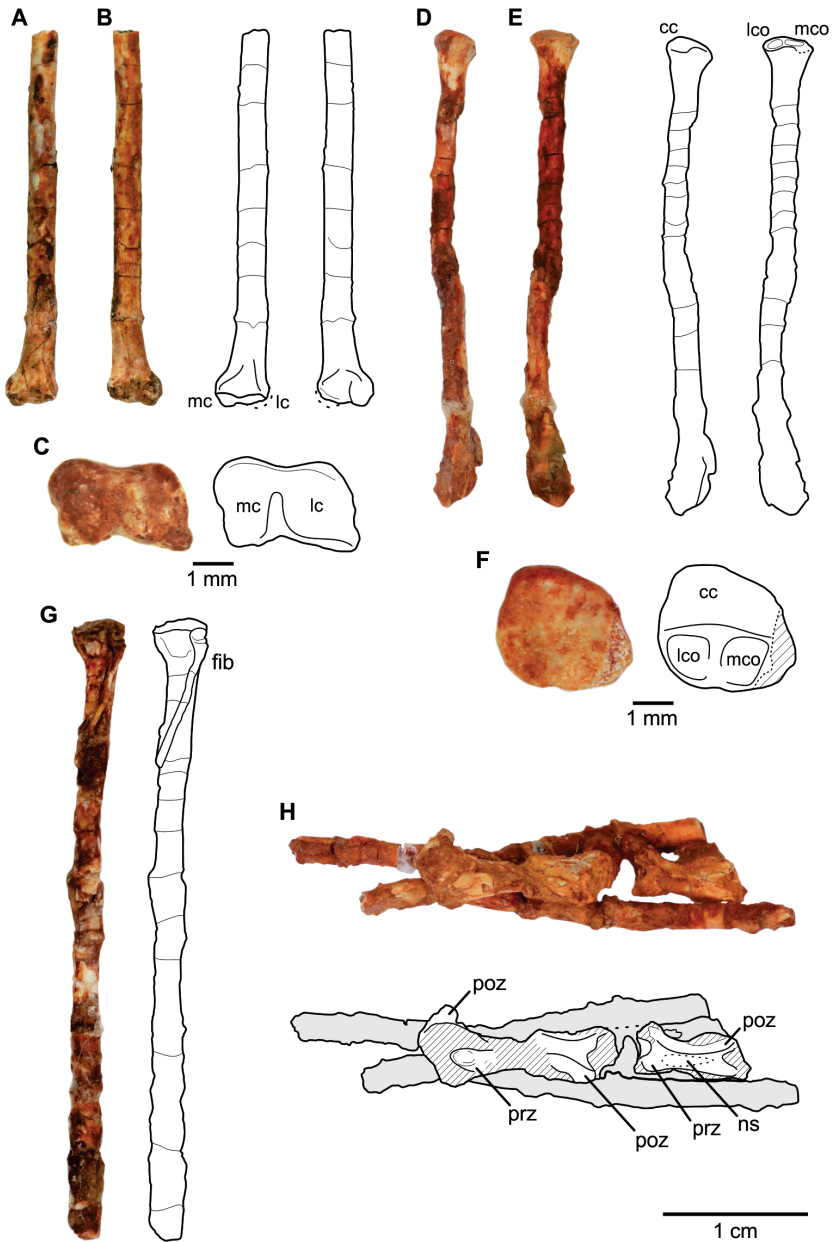
Figure 9 - Limb bones (TTU-P11254f-h) and procoelous vertebrae (TTU-P11254i) found associated with some unrecognizable shafts (colored in grey). **A-C,** left femur (TTU-P11254f) in anterior, posterior and distal views; **D-F.** left tibia (TTU-P11254g) in anterior, posterior and proximal views; **G.** right tibia with attached proximal end of fibula (TTU-P11254h); **H.** two procoelous vertebrae intermingled with few limb bone shafts (TTU-P11254i). Abbreviations: **cc**, cnemial crest; **fib**, fibula; **lc**, lateral condyle; **lco**, lateral cotyle; **mc**, medial condyle; **mco**, medial cotyle; **ns**, damaged neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis. Hatches signify damaged parts. The 1 mm scale is for (**C**) and (**F**).

Sauria McCartney, 1802, sensu Gauthier, Kluge and Rowe 1988

Gen. et sp. indet.

Referred specimens. TTU-P11254f, distal end of a left femur; TTU-P11254g, proximal end of left tibia; TTU-P11254h, a fragmentary right tibia; TTU-P11254i, two procoelous vertebrae and fragmentary undetermined shafts of bones.

Description and remarks. The thin-walled limb bones are extremely long and slender which is reminiscent to that of some basal ornithodirans such as *Scleromochlus* and *Saltopus* (Benton, 1999; Benton and Walker, 2011), as well as that of pterosaurs (Sereno, 1991a). But in a closer look, these limb bones are anatomically inconsistent with that of any typical archosaurian (Figures 9A-G). The distal end of the femur does not bear a tibiofibular crest which is an archosauriform synapomorphy (Nesbitt, 2011, character 322), whereas twin concave facets (*i.e.* cotyles) on the proximal tibia are comparable to that of lepidosaurians like *Clevosaurus* (Fraser, 1988). Moreover, the procoelous state of the two severely damaged vertebrae (Figure 9H) is considered to be a characteristic of a large number of squamates (Romer, 1956), but also of many tanystropheids (Pritchard *et al.*, 2015) and the new basal archosauromorph *Ozimek volans* Dzik and Sulej, 2016. The fragmentary shafts around the procoelous vertebrae are missing both ends but their morphology is identical to that of other described limb bones. Given that the procoelous vertebrae are attributed to the same taxon with the limb bones, these fragments may represent a small-sized lepidosauromorph taxon or a basal archosauromorph related to Sharovipterygidae. A tanystropheid affinity, on the other hand, is less likely since the basal forms possess a sigmoidal femur whereas more derived forms still retain the curvature at the distal end of femur (Pritchard *et al.*, 2015). All these elements are considered as saurian bones due to their incomplete and distorted condition which prevents a more detailed identification.

DISCUSSIONS ON THE SKELETAL ASSOCIATION AND TAPHONOMY

The elements of this particular bone assemblage seem to represent a single individual at first glance since the composing elements were found side-by-side and each bone in the assemblage represents a different skeletal constituent in a misleading in-situ position (Figure 2). Alternatively, the preliminary conclusion by the eldest author that the assemblage is consisted of derived dinosaurian fragments has been also a matter of speculation (see Sarıgül, 2014). Instead, it is realized that the Post Quarry bone assemblage yields an accumulation of various small sized skeletal elements pertaining to multiple individuals of different taxa, after a detailed examination conducted by the first author. The postcervical vertebrae (TTU-P11254a) are ascribed to *Vanclavea campi*, TTU-P11254b represents a new silesaurid taxon *Soumyasaurus aenigmaticus*, whereas remaining elements (TTU-P11254c-i) are too incomplete to be safely referable to a specific taxon more inclusive than Archosauromorpha or Sauria. Among the body elements referred to Archosauromorpha, the braincase (TTU-P11254c) is recently attributed to the same taxon with TTU-P11254b (Agnolin *et al.*, 2016). This assumption is based on the derived otoccipital portion which is endorsed by recent discoveries on the convergently evolved avian-like traits in basal dinosauriform braincases (Agnolin *et al.*, 2016; Piechowski *et al.*, 2018). However, the resulting tree from an additional phylogenetic analysis including both the dentary and the braincase is indistinguishable from that including the dentary alone; thus, the association of these two elements cannot be strictly confirmed. The remaining elements

are too incomplete to be safely referable to a specific taxon more inclusive than Archosauromorpha or Sauria. Future discoveries of more complete specimens or introduction of new viewpoints would bring different and possibly more correct suggestions about the affinity of these elements.

Addressing the taphonomic settings of the Post Quarry provides a better understanding of the perplexity of the TTU-P11254 assemblage. The highly diverse fossil concentration, including both juvenile and adult specimens of different taxa, covering a very small area was initially interpreted as a result of a rapid flood event (Chatterjee, 1985). In contrast, some long-term process of bone concentration was suggested afterwards for the later dispersal of the disarticulated but still associated skeletons with both delicate and robust pieces, of which the long axis of bones are usually found aligned in a certain direction (Lehman and Chatterjee, 2005). Mass mortalities caused by flooding are usually monotaxic or paucitaxic (*e.g.*, Norman, 1987; Mazza, 2015), and as correctly pointed out by Lehman and Chatterjee (2005), neither the mass mortality nor the disarticulation in the Post Quarry is caused by a flooding event. However, a long-term accumulation may not be the case for the Post Quarry since disarticulated skeletal concentrations display evident hydraulic sorting rather than alignment when exposed to strong currents. Based on a study on some modern-day mammals, skeletal components are evaluated under three groups according to their susceptibility to hydraulic transport; lighter bones like ribs and vertebrae are classified under Group I and they were shown to be more easily carried away compared to Group II and III elements, where the former group mainly comprises long bones and the latter is characterized by the skull and mandible as heaviest elements of the skeleton (Voorhies, 1969; Behrensmeyer, 1975). In contrast, the land tetrapod fossil

collection of the Post Quarry includes fairly complete skeletons of *Postosuchus kirkpatricki* (holotype), *Desmatosuchus smalli* (holotype) and *Typothorax coccinarum* Cope, 1875 (*e.g.*, Chatterjee, 1985; Parker, 2005; Martz *et al.*, 2013). Yielding individuals from multiple taxa and representation of each Voorhies group in the Post Quarry assemblage emphasize a pre-mortem gathering of all the different taxa having various sizes and dietary habits and dying at the same place due to an unknown cause. Regardless what the cause of death is, disarticulated state of the skeletons in this autochthonous assemblage suggests that the carcasses were exposed to some physical and chemical degradation before the burial.

This exposure interval was not long enough to induce a considerable loss of skeletal parts as described for the partial skeletons; however, many Post Quarry specimens are represented by a single or few isolated elements, a situation reflecting the complex taphonomy of this quarry. The holotype of temnospondyl *Rileymillerus cosgriffi* is identified based on a skull and lower jaw (Bolt and Chatterjee, 2000); where the holotype of *Shuvosaurus inexpectatus* was originally described based on a fragmentary cranium and mandible as well (Chatterjee, 1993), prior to the complementation with a postcranial skeleton (Long and Murry, 1995). A massive skull and jaws that are almost a meter in length referred to *Leptosuchus* sp. (TTU-P09234; Martz *et al.*, 2013) represents the largest detached piece of a tetrapod fossil of the Post Quarry. These three examples and many other isolated cranial and postcranial fragments of different sizes and shapes (*e.g.*, Chatterjee, 1983; Long and Murry, 1995; Nesbitt and Chatterjee, 2008; Martz *et al.*, 2013; Sarıgül, 2016, 2017a) demonstrate the lack of selective preservation in the Post Quarry taphonomy, concurring with the previous conclusion of the absence of hydraulic sorting. The attritional state

of the skeletons is subject to speculation as well; however, skeletal elements may easily disappear by in-situ factors (*e.g.*, decomposition, scavenging, trampling) or during diagenesis, and the resulting attrition in the Post Quarry can be explained simply by non-preservation.

Although the current activity did not seem to be involved in mortality and disarticulation phases, a gentle flooding like a seasonal inundation of a floodplain, is implied here as the factor that buried the whole assemblage. Such gentle current cannot create sorting in disarticulated skeletons, but it might have been responsible for the preferential orientation of some of the long bones, as well as for the entangling of some lighter bone fragments belonging to different taxa. Indeed, the isolated elements were found in closer association with different bones in some cases. For instance, skeletal consistency of the silesaurid *T. smalli* was resolved after a long examination process and appears to be the closest example to the TTU-P11254 assemblage. Departing from the original diagnosis of Chatterjee (1984), the holotype of *T. smalli* is now restricted to two anterior jaw fragments; whereas the associated posterior jaw fragment now referred to *S. inexpectatus* and the affinity of the other bones remain unresolved (Sereno, 1991b; Hunt and Lucas, 1994; Irmis *et al.*, 2007; Nesbitt *et al.*, 2007; Martz *et al.*, 2013). The entangled condition of the *T. smalli* and TTU-P11254 assemblages may be a result of the burial process. Nevertheless, the limited discussion provided here cannot explain all the taphonomic modes observed in the Post Quarry and a comprehensive study is still needed on the subject.

CONCLUSIONS

A puzzling assemblage of tiny bones from the Post Quarry of Texas represents a multitaxic assemblage, including fragments referred to *Vancleavea campi*, a new basal dinosauriform taxon *Soumyasaurus aenigmaticus* and to various undetermined saurians. Dentary features of *S. aenigmaticus* are quite comparable to what is observed in silesaurids, where the overall tooth morphology resembles to that of *Asilisaurus kongwe* rather to what is observed in *Technosaurus smalli*. It is more difficult to assign the remaining bones due to their fragmentary condition; this is applicable even for the braincase featuring a posteriorly diverted vagus foramen and a possible separate exit for the glossopharyngeal nerve situated on a plesiomorphic basioccipital. The striking combination of plesiomorphic and derived features indicates that such traits were probably more widespread among archosauromorphs than previously thought.

The recognized skeletal inconsistencies and intermixing of different bones in TTU-P11254 assemblage bears close resemblance to another Post Quarry bone assemblage from which *T. smalli* is described, and both assemblages appear to be produced by the same taphonomic processes of the Post Quarry.

we are grateful to the editor and the reviewers for the appraisal of the manuscript.

REFERENCES

Agnolin, F.L. and Rozadilla, S. (2017). Phylogenetic reassessment of *Pisanosaurus mertii* Casamiquela, 1967, a basal dinosauriform from the Late Triassic of Argentina. *Journal of Systematic Palaeontology*. DOI: 10.1080/14772019.2017.1352623.

Agnolin F.L., Sarıgül, V. and Chatterjee, S. (2016). New dinosauriform from the Upper Triassic of Texas and its implications on the origin of the avian-like braincase. *30. Jornadas Argentinas de Paleontología de Vertebrados, Libro de Resúmenes*, p. 71.

Arcucci, A. (1997). Dinosauromorpha. In P. Currie and K. Padian (Eds.) E*ncyclopedia of Dinosaurs* (pp. 179–184). San Diego, USA: Academic Press.

Arcucci, A. (1998). New information about dinosaur precursors from the Triassic Los Chañares Fauna, La Rioja, Argentina. *Gondwana 10: Event Stratigraphy of Gondwana Abstracts, Journal of African Earth Sciences Supplement*, 27(S1), 9-10.

Behrensmeyer, A.K. (1975). The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 146(10), 473-578.

Bennett, S.C. (1991). *Morphology of the Late Cretaceous pterosaur Pteranodon and systematics of the Pterodactyloidea*. University of Kansas, Lawrence (Unpublished Ph.D. thesis), 680 pp.

Benton, M.J. (1985). Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84, 97-164.

Benton, M.J. (1999): *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London B*, 354, 1423-1446.

Benton, M.J. and Walker, A.D. (2011). *Saltopus*, a dinosauriform from the Upper Triassic of Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 101, 285-299.

Bolt, J.R. and Chatterjee, S. (2000). A new temnospondyl amphibian from the Late Triassic of Texas. *Journal of Paleontology*, 74, 670-683.

Chatterjee, S. (1983). An ictidosaur fossil from North America. *Science*, 220, 1151-1153.

Chatterjee, S. (1984). A new ornithischian dinosaur from the Triassic of North America. *Naturwissenschaften*, 71, 630-631.

Chatterjee, S. (1985). *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Philosophical Transactions of the Royal Society of London B*, 309, 395-460.

Chatterjee, S. (1991). Cranial anatomy and relationships of a new Triassic bird from Texas. *Philosophical Transactions of the Royal Society of London B*, 332, 277-346.

Chatterjee, S. (1993). *Shuvosaurus:* A new theropod. *National Geographic Research and Exploration*, 9(3), 274-285.

Chure, D.J. and Madsen, J.H. (1998). An unusual braincase (?*Stokesaurus clevelandi*) from the Cleveland-Lloyd Dinosaur Quarry, Utah (Morrison Formation: Late Jurassic). *Journal of Vertebrate Paleontology*, 18(1), 115-125.

Cope, E.D., 1875, Report on the geology of that part of northwestern New Mexico examined during the field-season of 1874. In *Annual Report upon the geographical explorations west of the 100th meridian [Wheeler Survey], Appendix LL, Annual Report Chief of Engineers for 1875* (pp. 61- 97). Washington, USA: Government Printing Office.

Currie, P.J. (1995). New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology*, 15(3), 576-591.

Currie, P.J. (1997). Braincase anatomy. In: P. Currie and K. Padian (Eds.): *Encyclopedia of Dinosaurs* (pp. 81-85). New York, USA: Academic Press.

Currie, P.J. and Zhao X.-J. (1993). A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences*, 30, 2231-2247.

Dzik, J. (2003). A beaked herbivorous archosaur with dinosaur affinities from the early late Triassic of Poland. *Journal of Vertebrate Paleontology*, 23(3), 556-574.

Dzik, J. and Sulej, T. (2016). An early Late Triassic long-necked reptile with a bony pectoral shield and gracile appendages. *Acta Palaeontologica Polonica*, 61(4), 805–823.

Ezcurra, M.D. (2014). The osteology of the basal archosauromorph *Tasmaniosaurus triassicus* from the Lower Triassic of Tasmania, Australia. *PLoS ONE*, 9(1), e86864.

Ferigolo, J. and Langer, M.C. (2007). A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone. *Historical Biology*, 19(1), 1-11.

Fiorillo, A.R., Tykoski, R.S., Currie, P.J., McCarthy, P.J. and Flaig, P. (2009). Description of two partial

Gauthier, J.A. (1986). Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science* 8: 1–55.

Gower, D.J. and Sennikov, A.G. (1996). Morphology and phylogenetic informativeness of early archosaur braincases. *Palaeontology*, 34(9), 883-906.

Gower, D.J. and Weber, E. (1998). The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. *Biological Reviews*, 73(4), 367-411.

Irmis, R.B., Parker, W.G., Nesbitt, S.J. and Jun, L. (2007). Early ornithischian dinosaurs: the Triassic record. *Historical Biology*, 19(1), 3-22.

Huene, F. (1946). Die grossen Stamme der Tetrapods in den geologischen Zeiten. *Biologische Zentralblatt*, 65, 268-275.

Hunt, A.P. (1989). Cranial morphology and ecology among phytosaurs. In: S.G. Lucas and A.P. Hunt (Eds.), *Dawn of the Age of Dinosaurs in the American Southwest* (pp. 349-354). Albuquerque, New Mexico: New Mexico Museum of Natural History Press.

Hunt, A.P. and Lucas, S.G. (1994). Ornithischian dinosaurs from the Upper Triassic of the United States. In N.C. Fraser and H.D. Sues (Eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (pp. 227-241). Cambridge, Massachusetts: Cambridge University Press.

Kellner, A.W.A. (1996). Description of the Braincase of Two Early Cretaceous Pterosaurs (Pterodactyloidea) from Brazil. *American Museum Novitates*, 3175, 1-34.

Kammerer, C.F., Nesbitt, S.J. and Shubin, N.H. (2012). The first silesaurid dinosauriform from the Late Triassic of Morocco. *Acta Palaeontologica Polonica*, 57(2), 277-284.

Klembara, J. (2005). Ontogeny of the partial secondary wall of the otoccipital region of the endocranium in prehatching *Alligator mississippiensis* (Archosauria, Crocodylia). *Journal of Morphology*, 266, 319-330.

Langer, M.C., Ezcurra, M.D., Bittencourt, J.S. and Novas, F.E. (2010). The origin and early evolution of dinosaurs. *Biological Reviews*, 85, 55-110.

Langer, M.C. and Ferigolo, J. (2013). The Late Triassic dinosauromorph *Sacisaurus agudoensis* (Caturrita Formation; Rio Grande do Sul, Brazil): anatomy and affinities. In S.J. Nesbitt, J.B., Desojo and R.B. Irmis (Eds.), *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin* (pp. 353-392). London: Geological Society Special Publications 379.

Lehman, T.M. and Chatterjee, S. (2005). Depositional setting and vertebrate biostratigraphy of the Triassic Dockum Group of Texas. *Journal of Earth Systems Science*, 114(3), 325-351.

Long, R.A. and Murry, P.A. (1995). Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History and Science Bulletin*, 4, 1-254.

Martz, J.W. (2008). *Lithostratigraphy, chemostratigraphy, and vertebrate biostratigraphy of the Dockum Group (Upper Triassic), of southern Garza County, West Texas*. Texas Tech University, Lubbock (Unpublished Ph.D. thesis), 504 pp.

Martz, J.W., Mueller B.D., Nesbitt S.J., Stocker M.R., Parker W.G., Atanassov M., Fraser N., Weinbaum J. and Lehane J.R. (2013). A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. *Proceedings of the Royal Society of Edinburgh*, 103, 339-364.

Mazza, P.P.A. (2015). Scontrone (central Italy), signs of a 9-million-year-old tragedy. *Lethaia*, 48, 387-404.

McClelland, B.K. (1990). *Anatomy and kinesis of the Allosaurus skull*. Texas Tech University, Lubbock (Unpublished M.Sc. thesis), 122 pp.

McCartney, J. (1802). Preface and Table III. In G. Cuvier (Ed.), *Lectures on Comparative Anatomy* (translated by William Ross), (pp. 353-392). London: T. N. Longman and O. Rees.

Nesbitt, S.J. (2011). The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, 352, 1-292.

Nesbitt, S.J. and Chatterjee, S. (2008). Late Triassic dinosauriforms from the Post Quarry and surrounding areas, west Texas, USA. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 249(2), 143-156.

Nesbitt, S.J. and Norell, M.A. (2006). Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of Royal Society B*, 273, 1045-1048.

Nesbitt, S.J. Irmis, R.B., Parker, W.G., Smith, N.D., Turner, A.H. and Rowe, T. (2009a). Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. *Journal of Vertebrate Paleontology*, 29(2), 498-516.

Nesbitt, S.J. Stocker, M.R., Small, B. and Downs, A. (2009b). The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). *Zoological Journal of the Linnean Society*, 157, 814-864.

Nesbitt, S.J. Sidor, C.A., Irmis, R.B., Angielczyk, K.D.,

Smith, R.M.H. and Tsuji, L.A. (2010). Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, 464, 95-98.

Nesbitt, S.J., Butler, R.J., Ezcurra, M.D., Barrett, P.M., Stocker, M.R., Angielczyk, K.D., Smith, R.M.H., Sidor, C.A., Niedźwiedzki, G., Sennikov, A.G. and Charig, A.J. (2017). The earliest bird-line archosaurs and the assembly of the dinosaur body plan. *Nature*, 544, 484-487.

Norman, D.B. (1987). A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Proceedings of Royal Society of London B*, 230, 215-255.

Novas, F.E. (1992). Phylogenetic relationships of basal dinosaurs, the Herrerasauridae. *Palaeontology*, 35, 51-62.

Novas, F.E., Agnolin, F.L. and Ezcurra, M.D. (2015). Taxonomy of basal dinosauriforms: Evidence provided by a new specimen from the Triassic Chañares Formation, NW Argentina. *V. Congreso Latinoamericano de Paleontología de Vertebrados (Colonia del Sacramento, Uruguay), Libro de Resúmenes*, p. 50.

Parker, W.G. (2005). A new species of the Late Triassic aetosaur *Desmatosuchus* (Archosauria: Pseudosuchia). *Comptes Rendus Palevol*, 4, 327-340.

Piechowski,R., Niedźwiedzki, G. and Tałanda M. (2018). Unexpected bird-like features and high intraspecific variation in the braincase of the Triassic relative of dinosaurs. *Historical Biology*, DOI: 10.1080/08912963.2017.1418339.

Pritchard, A.C., Turner, A.H., Nesbitt, S.J., Irmis, R.B. and Smith, N.D. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. *Journal of Vertebrate Paleontology*, 35(2), e911186.

Rauhut, O.W.M. (2004). Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. *Canadian Journal of Earth Sciences*, 41, 1109-1122.

Romer, A.S. (1956). *Osteology of the Reptiles*. Chicago, USA: University of Chicago Press.

Sampson, S.D. and Witmer, L.M. (2007). Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir*, 8, 32-102.

Sarıgül, V. (2014). *Anatomy of the Late Triassic dinosauromorphs from the Dockum Group of Texas: Their biostratigraphic, paleobiogeographic and evolutionary significance*. Texas Tech University, Lubbock (Unpublished Ph.D. thesis), 300 pp.

Sarıgül, V. (2016). New basal dinosauromorph records from the Dockum Group of Texas, USA. *Palaeontologia Electronica*, 19(2), 1-16.

Sarıgül, V. (2017a). New theropod fossils from the Upper Triassic Dockum Group of Texas, USA, and a brief overview of the Dockum theropod diversity. *Paleobios*, 34, 1-18.

Sarıgül, V. (2017b). New archosauromorph fragments from the Dockum Group of Texas and assessment of the earliest dinosaurs in North America. *Historical Biology*, Advance online publication, DOI: 10.1080/08912963.2017.1333609.

Sereno, P.C. (1991a). Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoirs*, 2, 1-53.

Sereno, P.C. (1991b). *Lesothosaurus*, "fabrosaurids", and the early evolution of the Ornithischia. *Journal of Vertebrate Paleontology*, 11(2), 168-197.

Sereno, P.C. and Novas, F.E. (1993). The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, 13(4), 451-476.

Stocker, M.R., Nesbitt, S.J., Criswell, K.E., Parker, W.G., Witmer, L.M., Rowe, T.B., Ridgely, R. and Brown, M.A. (2016). A dome-headed stem archosaur exemplifies convergence among dinosaurs and their distant relatives. *Current Biology*, 26, 2674-2680.

Voorhies, M.R. (1969). Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Know County, Nebraska. *Wyoming University Contributions in Geology Special Paper*, 1, 1-69.

Walker, A.D. (1985). The braincase of *Archaeopteryx*. In: M.K. Hecht, J.H. Ostrom, G. Viohl and P. Wellnhofer, P. (Eds.), *The Beginnings of Birds: Proceedings of the International Archaeopteryx Conference Eichstätt 1984*, (pp. 123-134). Eichstätt, Germany: Freunde des Juras-Museums

APPENDIX 1. Scorings of *Soumyasaurus aenigmaticus* based on Nesbitt *et al.* (2017) data matrix

Soumyasaurus_aenigmaticus

??
??1?0???????????000?0001????????????????????
??
??
????????????????????????????????

APPENDIX 2. Scorings of *Technosaurus smalli* based on Nesbitt *et al.* (2017) data matrix

Technosaurus_smalli

?????[23]000??
??1?0???????????[01]02011011???????????????
??
??
?????????????????????????????????????