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A new Mastodonsauroid Temnospondyl from the Triassic of Algeria: Implications for the biostratigraphy and palaeoenvironments of the Zarzaïtine Series, northern Sahara

Un nouveau temnospondyle mastodonsauroïde du Trias d'Algérie : implications biostratigraphiques et paléoenvironnementales dans la série de Zarzaïtine, Nord du Sahara

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ABSTRACT

We describe a new species of mastodonsauroid temnospondyl from Algeria, *Stanocephalosaurus amenasensis* nov. sp., on the basis of two exquisite skulls from a Lagerstätte found in the lowermost formation of the Zarzaïtine Series, Illizi Basin, in the area of "La Reculée", In Amenas region, Algeria. The new species is characterized by subtriangular nostrils with concave lateral borders; small orbits; postfrontals posteriorly very wide; very elongate parietals; smoothly concave posterior margin of the skull; ovoid anterior palatal vacuities; very posteriorly pointed choanae; oval interpterygoid fenestrae; and a short anterior extension of the cultriform process of the parasphenoid. *S. amenasensis* is different than the Algerian taxa previously erected by Lehman (1971)–"*Parotosaurus lapparenti*" and "*Wellesaurus bussoni*"–which we consider *nomina dubia*. It enlarges the distribution of the genus in northern Gondwana and supports the Early-Middle Triassic age of the lowermost formation of the Zarzaïtine Series. It also suggests that the local palaeoclimate was very seasonal and these aquatic amphibians died massively in a dewatering sebkha.

Mots clés :
Capitosaures
Lagerstätte
Olénékien
Anisien
Paléoclimat
Mortalité en masse

RÉSUMÉ

Une nouvelle espèce de temnospondyle mastodonsauroïde d'Algérie, *Stanocephalosaurus amenasensis* nov. sp., est décrite sur la base de deux crânes exceptionnellement bien préservés provenant d'un Lagerstätte découvert dans la formation basale de la série de Zarzaïtine, bassin d'Illizi, région de « La Reculée », vers In Amenas, en Algérie. Cette nouvelle espèce est caractérisée par des narines subtriangulaires à bord latéral concave, de petites orbites, des postfrontaux postérieurement très élargis, des pariétaux très allongés,

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un bord concave de la table crânienne, des fenêtres antéropalatales ovoïdes, des choanes très pointues postérieurement, des fenêtres interptérygoïdiennes ovales, ainsi qu'une courte extension antérieure du processus cultriforme du parasphénoïde. *S. amenasensis* est différent des taxons autrefois nommés par Lehman (1971), à savoir « *Parotosaurus lapparenti* » et « *Wellesaurus bussoni* », que nous considérons comme *nomina dubia*. Cette nouvelle espèce élargit la distribution du genre au Nord du Gondwana et confirme l'âge Trias inférieur à moyen de la formation basale de la série de Zarzaïtine. Elle suggère également que le climat local était très saisonnier à l'époque et que ces amphibiens aquatiques sont morts dans une sebkha en cours d'assèchement.

1. Introduction

The Saharian platform, with its almost absent vegetation cover, is a key region for geologists and palaeontologists because many rocks from different ages are outcropping and yield important fossils. This is particularly the case in the Southeast of Algeria, where Triassic rocks from the Illizi Basin yield numerous plants, amphibians (i.e., non-amniotic tetrapods) and reptiles (Aït Ouali et al., 2011; Jalil, 1993; Nedjari et al., 2011). These fossil amphibians, the first ones from the Saharan platform, correspond to temnospondyl remains discovered in the fifties during geological mapping and mining prospections of Algerian-French teams. They come from the base of the Triassic Series of Zarzaïtine and were sampled at the bottom of "La Reculée", a long cliff about 30 km southwest of the city of In Amenas. The fossils comprise cranial and postcranial fragmentary remains attributed to mastodonsauroid temnospondyls by Lehman (1957) on the basis of their medium size and of their ornamentated dermal bones. Later, Lehman (1971) described and erected two taxa, "*Parotosaurus lapparenti*" and "*Wellesaurus bussoni,*" on the basis of very fragmentary material (see Discussion). These "historical" specimens are housed in the MNHN as the "Zarzaïtine collection" (with numbers starting with 'MNHN-ZAR').

Later, Jalil (1993) mostly revised the reptiles of MNHN Zarzaïtine collection. Concerning the amphibians, he followed the taxonomic attribution of Lehman (1971) and proposed an Early to Middle Triassic age for this assemblage based on international non-marine biostratigraphical correlations (Jalil, 1999). Interestingly, Welles (1993) and Jalil (1999) also recognized another amphibian assemblage composed respectively of trematosaurian and brachyopoid fragments that was considered Middle to Late Triassic in age (Jalil and Taquet, 1994). These were the only works undertaken on Algerian temnospondyls so far.

More recently, regular geological and palaeontological fieldwork was conducted in the Illizi Basin by the "Laboratoire de Géodynamique des Bassins Sédimentaires et des Orogènes" of the University of Science and Technology Houari Boumedienne, the "Agence du Service Géologique de l'Algérie", the Société Nationale pour la Recherche, la Production, le Transport, la Transformation et la Commercialisation des Hydrocarbures (SONATRACH), and within the framework of an international collaboration program with the "Centre de Recherches en Paléobiodiversité et Paléoenvironnements" (CNRS, Paris). Palaeontological prospecting, conducted in 2008 and 2009 in the area of "La Reculée", led to the discovery (and systematic excavations) of a new Lagerstätte preserving numerous and exceptionally well preserved temnospondyl specimens Dahoumane, 2011; Nedjari et al., 2010). We refer to Nedjari et al. (2010) and Aït-Ouali et al. (2011) for the complete description of the site including stratigraphy, sedimentology and taphonomy.

The new fossiliferous locality, found in the plain south of "La Reculée" (Fig. 1, GPS coordinates available to qualified researchers by contacting AD), is located at the base of the "Formation 0" (*sensu* Aït Ouali et al., 2011 = "Grès Inférieurs" or "Grès à Stégocéphales" or Lower Sandstone Unit *sensu* Busson, 1971; Groult, 1970), lower section of the Triassic Zarzaïtine Series. This new Lagerstätte yielded numerous temnospondyl specimens, which are exceptionally well preserved in three dimensions: they consist of subcomplete skulls and postcranial elements attributed to capitosauroids (*sensu* Yates and Warren, 2000 = mastodonsauroids *sensu* Damiani, 2001), a widespread group of temnospondyls, which is well diversified (and only known) in the Triassic (Schoch, 2008). This new material is different from the taxa previously described by Lehman (1971). We give here a detailed description and erect a new species, *Stanocephalosaurus amenasensis* nov. sp. on the basis of two well-preserved skulls that we collected and prepared. The material belongs to the Museum of the Faculty of Earth Sciences, Geography and Regional Land Settlement, Alger, where some other elements are still under preparation.

This discovery expands the distribution of the capitosauroid temnospondyl genus *Stanocephalosaurus* towards northern Gondwana and allows interesting biostratigraphic and palaeoenvironmental interpretations.

2. Institutional Abbreviations

MNHN	Muséum national d'histoire naturelle, Paris (France)
UCMP	Museum of Paleontology, University of California, Berkeley (USA)
ZAR	specimens from Zarzaïtine, Museum of the Faculty of Earth Sciences, Geography and Regional Land Settlement, USTHB, Algiers (Algeria)

3. Systematic Palaeontology

Temnospondyli Zittel, 1887–1890

Stereospondyli Zittel, 1887–1890 (*sensu* Yates and Warren, 2000)

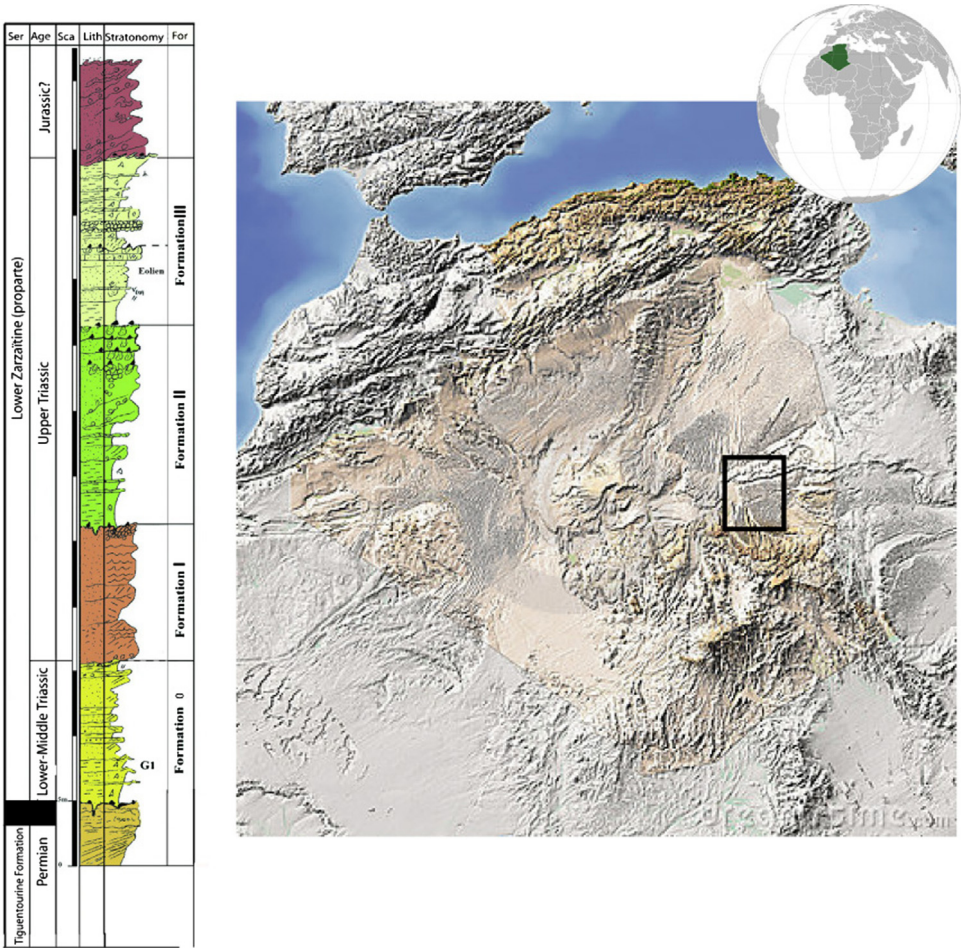

Fig. 1. *Stanocephalosaurus amenasensis* nov. sp. from the Lower/Middle Triassic of Algeria. Geographical and stratigraphical location of the type locality (For: formation number; G1; type locality; Lith: lithology; Sca: scale). The black frame corresponds to the area of "La Reculée" where the type locality is (GPS coordinates are available to qualified researchers by contacting the first author).
Fig. 1. *Stanocephalosaurus amenasensis* nov. sp. du Trias inférieur à moyen d'Algérie. Localisation géographique et stratigraphique de la localité-type (For : numéro de formation ; G1 ; localité-type ; Lith : lithologie ; Sca : échelle. Le cadre noir correspond à l'aire de la Reculée où se situe la localité-type (coordonnées GPS disponibles pour les chercheurs qualifiés en contactant le premier auteur).

Mastodonsauroidea Lydekker, 1885 (*sensu* Damiani, 2001 = "CAPITOSAUROIDS" *sensu* Yates and Warren, 2000)

Paracyclotosauridae Ochev, 1966

Stanocephalosaurus Brown, 1933

Remark—We refer more or less (see below) to Schoch and Milner (2000) and Schoch (2008) for the content of the genus *Stanocephalosaurus*. As these authors did not give a diagnosis of the genus, we propose the following diagnosis:

Diagnosis—the preorbital region is very elongated (proportionally to the postorbital region) and continuously narrowing anteriorly to give a subtriangular and slender snout, which is more or less abbreviated depending on the species; the parietal and postparietal are abbreviated; the postorbital shows an anterolateral extension or "wing" that is more or less anteriorly developed and pointed depending on the species; the choana is elongated.

Type species—*Stanocephalosaurus birdi* Brown, 1933 from the Lower Moenkopi Formation of Arizona, Spathian, Lower Triassic.

Other valid species (from Schoch and Milner, 2000; and Schoch, 2008)—*S. crookshanki* (Mukherjee and Sengupta, 1998) from the Denwa Formation of India (?Middle Triassic); *S. rajareddyi* (Chowdhury, 1970) from the Yerrapalli Formation of India (?Middle Triassic); and *S.* sp. (Watson, 1958) from the Hawkesbury Sandstone of Australia (Lower Triassic).

Questionable species:

- "*Stanocephalosaurus*" *pronus* (Howie, 1970) from the Manda Formation of Tanzania (Anisian, Middle Triassic, Sidor et al., 2013) does not belong to the genus *Stanocephalosaurus* because Schoch (2008) showed, in his phylogenetical analysis of capitosaurs, that it does not form a clade with the type species *Stanocephalosaurus birdi*.

Schoch and Milner (2000) listed two other species that we also consider invalid:

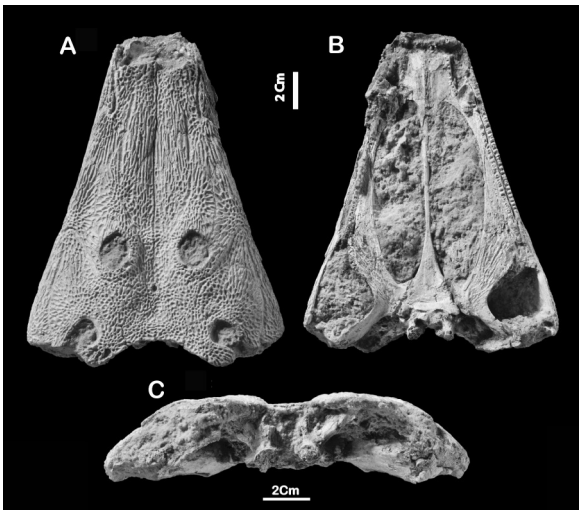

Fig. 2. *Stanocephalosaurus amenasensis* nov. sp. from the Lower/Middle Triassic of Algeria. Photos of the holotype ZAR03 in dorsal (A), palatal (B) and occipital (C) views.
Fig. 2. *Stanocephalosaurus amenasensis* nov. sp. du Trias inférieur à moyen d'Algérie. Photos de l'holotype ZAR03 en vues dorsale (A), palatale (B) et occipitale (C).

- *Stanocephalosaurus* "nov. spec." from the Moenkopi Formation of Arizona (Spathien/Anisian, Lower/Middle Triassic) is mentioned without any reference. According to Schoch (comm. pers., 2014) the material (UCMP uncatalogued) is poor, neither prepared nor described.
- "*Stanocephalosaurus lapparenti*" (Lehman, 1971) from the Zarzaïtine Formation is considered here a *nomen dubium* (see Discussion below).

Stanocephalosaurus amenasensis, nov. sp. (Figs. 1–4)

Etymology—the specific name comes from In Amenas, city of the Illizi Province (Southeast Algeria), the closest to the type locality (Fig. 1).

Holotype—ZAR03, a nearly complete skull lacking the anterior tip of the snout (23 cm estimated length) (Figs. 2–3), but generally less damaged than ZAR04.

Referred specimen—ZAR04, a nearly complete skull (26.5 cm length) slightly weathered on its surface (Fig. 4).

Type Locality and Horizon—"La Reculée" area (Fig. 1), Zarzaïtine district, In Amenas region, southern Algeria; base of the "Formation 0" *sensu* Aït Ouali et al., 2011 (= "Grès Inférieurs" or Lower Sandstone Unit *sensu* Busson, 1971; Groult, 1970), lower section of the Zarzaïtine Series of the Illizi Basin, Lower-Middle Triassic according to Nedjari et al. (2010) and Aït-Ouali et al. (2011).

Diagnosis—*Stanocephalosaurus* showing the following combination of characters: the external nostrils are subtriangular and their lateral borders concave; the orbits are relatively small (orbit length = 10% of the skull length); the postfrontals are very wide posteriorly but narrow anteriorly towards the orbit; the parietals are very elongate (16,5% of the skull length); the posterior margin of the skull table is not angular but smoothly concave; the anterior palatal vacuities are ovoid; the choanae are very posteriorly pointed; and the interpterygoid fenestrae are oval.

4. Description

4.1. Preservation and General Outlines

The specimens ZAR03 and ZAR04 are well-preserved skulls collected in the field. They are almost complete and preserved in three dimensions, i.e. without having been affected by postmortem deformation. Both specimens are almost identical and therefore allow describing in details the cranial anatomy of *Stanocephalosaurus amenasensis* nov. sp:

The skull is naturally flat and subtriangular in general outline, as is the case in many mastodonsauroid temnospondyls (Damiani, 2001). The lateral margins of the skull are straight and the preorbital width regularly decreases anteriorly. The tip of the snout (preserved in ZAR04) is rounded, a typical character seen within the genus *Stanocephalosaurus*. The skull roof bones show a honeycombed ornamentation that is typical for temnospondyls and other stegocephalians (Buffrénil et al., 2015). This ornamentation consists, in the center of the dermal bones, of deep (1–2 mm) and polygonal alveoli, which turn into subtriangular and straight ridges towards their periphery. Wide (4 mm) and deep (2 mm) dermo-sensory canals are also present on the dorsal side of the skull roof. They are particularly well marked on ZAR04: the circumorbital canal runs on the prefrontal, postorbital and jugal, whereas the supranarial canal runs on the nasal and anterior half of the prefrontal. These dermo-sensory canals are linked with an aquatic lifestyle (Steyer, 2003; and see Discussion section).

The preorbital region of the skull is very flat and elongated (up to 16.5 cm in ZAR04), a typical stereospondyl character (Yates and Warren, 2000). The cranial sutures are well visible. The relatively strong degree of ossification of the cranial bones, as well as their well-ornamented external surface suggest an adult individual age for both ZAR03 and ZAR04 (see Steyer, 2000 for temnospondyl ontogeny). The skull ZAR04 is longer and with a relatively stronger degree of ossification than ZAR03: we therefore consider ZAR04 ontogenetically older than ZAR03.

4.2. Skull roof

The skull roof is longer than wide. Its maximum width (16 cm in ZAR03, 17 cm in ZAR04) is reached at the level of the quadratojugal.

The orbits are subcircular (5×5 cm in ZAR03; 2.6×2.5 cm in ZAR04), a common shape found in other paracyclotosaurids. However, these orbits are very small, their length reaching only 10% of the skull length (measured from the posterior end of the mesial suture to the tip of the snout). As the other *Stanocephalosaurus* show proportionally larger orbits, we consider this feature diagnostic of *S. amenasensis* nov. sp.

The external nares, well visible on ZAR04, are elongate and ovoid (24×12 mm), as in other *Stanocephalosaurus* species (they are rounded in *Paracyclotosaurus*). Their mesial margin is curved whereas their lateral margin is straight.

The nasal, frontal and prefrontal bones are very elongated, with the frontal reaching the orbit. The tip of the

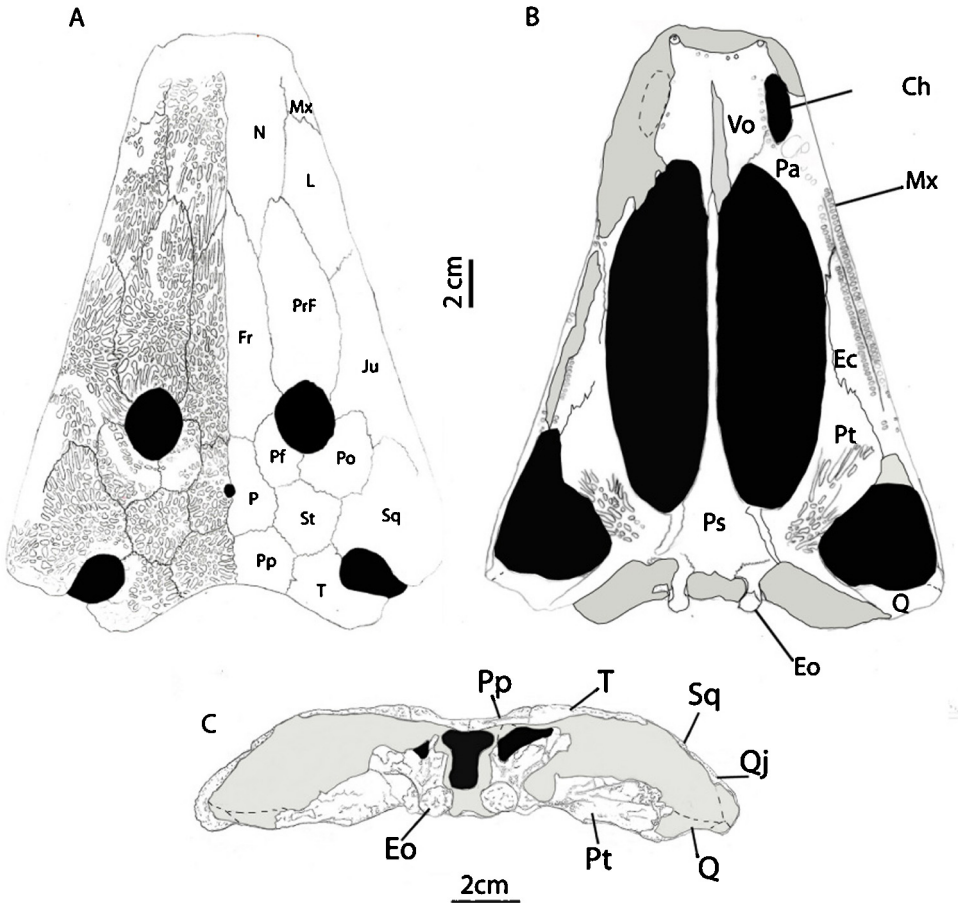

Fig. 3. *Stanocephalosaurus amenasensis* nov. sp. from the Lower/Middle Triassic of Algeria. Interpretative drawings of the holotype ZAR03 in dorsal (A), palatal (B) and occipital (C) views. Abbreviations: Ch: choana; Eo: exoccipital; Ec: ectopterygoid; Fr: frontal; Ju: jugal; La: lacrimal; Mx: maxilla; N: nasal; P: parietal; Pl: palatine; Pf: postfrontal; Po: postorbital; Pp: postparietal; PrF: prefrontal; Ps: parasphenoid; Pt: pterygoid; Q: quadrate; Qj: quadratojugal; Sq: squamosal; St: supratemporal; T: tabular; Vo: Vomer. Only the sutures visible directly on the specimen have been drawn.
Fig. 3. *Stanocephalosaurus amenasensis* nov. sp. du Trias inférieur à moyen d'Algérie. Dessins interprétatifs de l'holotype ZAR03 en vue dorsale (A) : palatale (B) et occipitale (C) (Ch : choane ; Eo : exoccipital ; Ec : ectoptérygoide ; Fr : frontal ; Ju : Jugal ; La : lacrimal ; Mx : maxillaire ; N : nasal ; P : pariétal ; Pl : palatin ; Pf : postfrontal ; Po : postorbitaire ; Pp : postpariétal ; PrF : préfrontal ; Ps : parasphénoïde ; Pt : ptérygoïde ; Q : carré ; Qj : quadratojugual ; Sq : squamosal ; St : supratemporal ; T : tabulaire ; Vo : Vomer). Seules les sutures visibles directement sur le spécimen ont été dessinées.

frontal is very pointed and tapers anteriorly to the posterior part of the nasal, as in other *Stanocephalosaurus* species (the fronto-nasal contact is almost straight and transverse in *Paracyclotosaurus*). The prefrontal has a convex lateral border, as in *S. crookshanki* (Mukherjee and Sengupta, 1998). The jugal also reaches the orbit margin, separating the prefrontal from the postorbital. The postorbital is relatively wide, with an anterolateral corner entering the jugal, again as in other *Stanocephalosaurus* species. The postfrontal is relatively small, but with an unusual shape: it is very wide posteriorly but narrow anteriorly towards the orbit. As the bone is different in the other *Stanocephalosaurus* species, we consider this peculiar shape as diagnostic of *S. amenasensis* nov. sp. The parietal is longer than the supratemporal. It is a very elongate bone, reaching 16.5% of the skull length, a character also considered diagnostic of *S. amenasensis* nov. sp. For comparison, the parietal only reaches 11.4% of the skull length in *S. crookshanki*; 10% in *S. rajareddyi*; 8.7% in "*Stanocephalosaurus*" *pronus*; and 10% in "*P. lapparenti*". The supratemporal of *S. amenasensis* nov. sp. is rhombic, not involved in the otic notch composition, and slightly longer than the postparietal. Consequently, the parietal is also longer than the postparietal, as it is also the case in *S. crookshanki* (the parietal is shorter than the postparietal in *Paracyclotosaurus*). The pineal foramen is rounded, its diameter represents 2.17% of the skull length. It is located in the mid-length of the interparietal suture. The posterior margin of the skull, composed of the postparietal and tabular bones, is concave but not semi-circular, contrary to *Paracyclotosaurus* and other *Stanocephalosaurus* species. This concave posterior margin of the skull table is therefore considered as diagnostic.

In *S. amenasensis* nov. sp., the tabular is expanded laterally rather than posterolaterally, i.e. with an angle lower than 120° from the median axis, as is the case in *S. crookshanki* and *S. rajareddyi*. This lateral extension forms a robust tabular horn with an enlarged posterior extremity, drawing an almost closed and circular otic notch, as in other paracyclotosaurids. The suture of the quadratojugal with the squamosal is not clearly visible but seems laterally

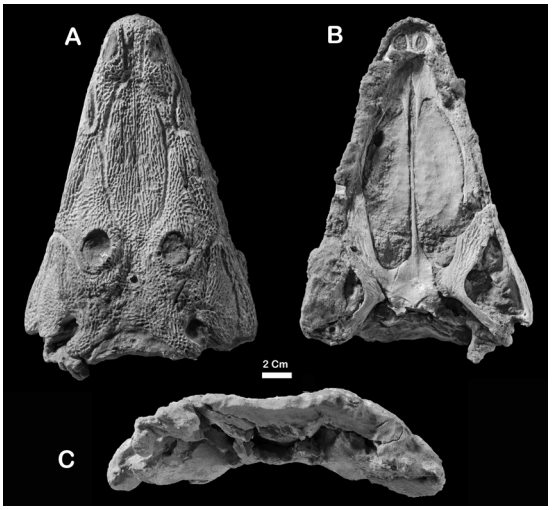

Fig. 4. *Stanocephalosaurus amenasensis* nov. sp. from the Lower/Middle Triassic of Algeria. Photos of the referred specimen ZAR04 in dorsal (A), palatal (B) and occipital (C) views.
Fig. 4. *Stanocephalosaurus amenasensis* nov. sp. du Trias inférieur à moyen d'Algérie. Photos du spécimen de référence ZAR04 en vues dorsale (A), palatale (B) et occipitale (C).

oriented near the posterior margin of the quadratojugal, thus suggesting a relatively narrow bone. This is another difference between *S. amenasensis* nov. sp. and the other species of *Stanocephalosaurus* which possess a large, well developed quadratojugal.

4.3. Palate

The palate is subtriangular in general outline. It is highly fenestrated by large paired interpterygoid and subtemporal fenestrae.

The interpterygoid fenestrae are elongate and ovoid (12 cm in length in ZAR03 and 13.6 cm in ZAR04). Their maximum width (3.5 cm in ZAR03 and 4 cm in ZAR04) is comprised in their first half. The lateral margin of the interpterygoid fenestrae is much more convex than their mesial margin. These fenestrae are separated by the cultriform process of the parasphenoid, a very thin bony blade that is very narrow and straight, as in other *Stanocephalosaurus* species (it is more robust in *Paracyclotosaurus*). However, the anterior extension of this cultriform process is shorter in *S. amenasensis* nov. sp. than in its relatives. It is also slightly more robust in ZAR04 than in the younger ZAR03. Posteriorly, the cultriform process turns into a thin parasphenoid plate that is elongate and subtriangular. The central region of the parasphenoid plate is slightly ornamented on its ventral side.

ZAR04, which preserves the anterior tip of the palate, clearly shows two separated anterior palatal vacuities that are almost rounded but longer than wide. Paired anterior palatal vacuities are also known in *S. crookshanki* but not in the other *Stanocephalosaurus* species where this palatal region is known.

The vomer bears two denticle rows, as is the case in the other *Stanocephalosaurus* species: a transversal denticle row is located between the vomerian fangs, whereas a longitudinal denticle row is running along the inner margin of the choana.

The choana is narrow and elongate. The suture between the ectopterygoid and the palatine is well visible. That between the parasphenoid and the pterygoid is well open, particularly on ZAR03.

In ventral view, the pterygoid has a tri-radiate shape that is typical for temnospondyls. Its medial ramus is very short and shares a long suture with the parasphenoid, a character often found in stereospondyls (Yates and Warren, 2000). The quadrate ramus of the pterygoid is very slender and twists vertically in a thin blade running posteriorly. The palatal ramus is very robust and widens anteriorly. Its ventral surface is well ornamented, with a honeycombed pattern reminiscent of that visible on the dorsal surface of the skull roof bones. Both the palatal and quadrate rami of the pterygoid draw the inner margin of the subtemporal fenestra. Together with its very straight external margin given by the quadratojugal, this subtemporal fenestra has an almost rhombic shape (5×4 cm in ZAR03, 4×6 cm in ZAR04).

4.4. Occiput and braincase

The occiput is better preserved on ZAR03 than on ZAR04. In both cases, it is relatively wide and naturally flat.

The occipital condyles are very small (6% of the skull posterior width) and ovoid in posterior view. They are extended posterolaterally, as is the case in "*Stanocephalosaurus*" *pronus* (they are extended posteromesially in *Paracyclotosaurus davidi* Watson, 1958). The distance between the condyles is substantial (almost 20% of the skull posterior maximum width). The horizontal branch of the exoccipital (reaching the condyle) is narrow and elongate posteriorly, whereas its vertical branch (reaching the tabular) is robust.

The foramen for the glossopharyngeal and vagus nerves is visible on ZAR03 in occipital view: it is rounded and very small.

The magnum foramen is T-shaped, with a naturally flattened dorsal region and a wide ventral region separated by the occipital condyles (Fig. 3 C).

The posttemporal fenestra is triangular. It is relatively well open, large and high in occipital view.

4.5. Dentition

Both marginal and inner teeth are very small (2.5 mm in bottom section anteriorly and 0.8 mm posteriorly). The marginal dentition is composed of small and numerous teeth, which are compressed perpendicularly to the skull margin, a typical stereospondyl feature (Yates and Warren, 2000). These marginal teeth, present on both the premaxilla and maxilla, are vertically curved. At least 42 maxillary teeth and alveoli are counted in ZAR03. Unfortunately, the preservation of ZAR04 does not allow a precise counting for the premaxillary teeth.

The palatal teeth are straight and conical. The palatine fangs are typical for the capitosaurian temnospondyls (Schoch and Milner, 2000): here, they are the largest (7 mm in bottom section) and highest (9.5 mm) teeth of the whole

dentition and have rounded sections and alveoli. Except for these fangs, the palatal and marginal teeth have similar diameters. Posterior to the fangs, the palatine also bears at least 13 teeth and alveoli that are aligned in a row with the ectopterygoid teeth posteriorly. This ectopterygoid tooth row, with at least 33 teeth and alveoli counted on ZAR03, is more than twice as long as the palatine tooth row. This palatine-ectopterygoid straight tooth row is parallel and similar to the maxillary tooth row.

Tooth rows are also present on the vomer: both the longitudinal and transversal vomerine tooth rows bear small and conical teeth of similar height and diameter. Yet, the transvomerine tooth row is bordered by larger teeth.

5. Discussion

5.1. Status of the Algerian material of Lehman (1971) and comparisons

In 1971, Lehman described and erected "*Wellesaurus bussoni*" and "*Parotosaurus lapparenti*" from the Lower Sandstone Member of the Triassic Zarzaïtine Series. These taxa are based on very poorly preserved skulls coming from the "site 5005" near Gour Laoud, a locality that is different than the type locality of *S. amenasensis*: the "site 5005" is indeed above, in the stratigraphic section (but still in the "Formation 0"), and located 50 km east from the type locality, near the Lybian border.

- The holotype of "*W. bussoni*" is a very fragmentary skull (MNHN-ZAR30) of uncertain affinity: according to Schoch and Milner (2000, p. 161), it could be synonymous with "*P. lapparenti*", a hypothesis not followed by Jalil (2001) who noted two differences between these taxa. However, these differences, which concern the extension of the tabular and the position of the mandibular condyle on the quadrate, may be related to ontogeny (Steyer, 2003). Our proper observations suggest that the specimen MNHN-ZAR30 shows proportions similar than those of "*P. lapparenti*", and that its smaller size may reflect a possible juvenile age.
- "*P. lapparenti*" is based on two specimens that Lehman (1971) named "Spécimen A" (Pl. II-III) and "Spécimen B" (Pl. IV). These specimens (now numbered MNHN-ZAR31 and MNHN-ZAR32, respectively) should be considered as syntypes according to the International Code of Zoological Nomenclature, as proposed by Schoch and Milner (2000). However, these authors assigned "*P. lapparenti*" to "*Stanocephalosaurus* as *S. lapparenti*" based on the following diagnosis; "anterior palatal opening completely subdivided; preorbital region much elongated and slender" (Schoch and Milner, 2000, p. 146), but without examining the type material of Lehman. Ruta et al. (2007) followed this opinion but without testing it, because they did not consider all the *Stanocephalosaurus* species in their phylogeny. Jalil (2001) considered "*P. lapparenti*" close to *Mastodonsaurus* but without testing this idea in a phylogeny.

"*P. lapparenti*" is therefore problematic. It has been placed in various groups according to different authors: for example, Morales (1987), and Jalil and Taquet (1994) considered it as a Benthosuchidae *sensu lato*; Maryanska and Shishkin (1996), and Damiani (2001) as an Heylerosauridae; and Shishkin (1980), and Milner et al. (1990) as a Mastodonsauridae *sensu stricto*. Our reexamination of the type material of Lehman did not yield additional diagnostic characters. Lehman (1971, p. 83) gave a diagnosis of "*P. lapparenti*" ("*Parotosaurus* with elongated snout and vomerian plate; large orbits compared to the other *Parotosaurus* species; paired anterior palatal fossae") based on doubtful characters: for example, the orbits are not preserved on the syntypes. Moreover, the only characters that are consistent with the diagnosis of Schoch and Milner (2000), i.e. paired anterior palatal fenestrae and an elongated snout, are highly variable within Mastodonsauroids. For all these reasons, and pending a complete redescription of the type material of Lehman, we consider "*P. lapparenti*" as *nomun dubium*.

In any case, *S. amenasensis* shows several clear morphological differences with "*P. lapparenti*": its external nostrils are more pointed anteriorly and their medial borders are not concave (*contra* their lateral borders, Fig. 4); its quadratojugals are less posteriorly extended; its choanae are not rounded posteriorly but pointed; the ventral surface of its parasphenoid plate is not concave but flattened; its cultriformis process is more slender; and the quadrate branches of its pterygoids are more laterally directed.

5.2. Biostratigraphic and palaeoenvironmental implications

Stanocephalosaurus amenasensis described here brings interesting implications:

- Concerning the age of the "Formation 0" of the Zarzaïtine Series that yielded the material, it is interesting to note that the genus *Stanocephalosaurus*, as defined above, was relatively widespread throughout Pangea during Triassic times. More precisely, the fact that all the species of *Stanocephalosaurus* are known from the Early or Middle Triassic suggests that Formation "0" may be also of Early and/or Middle Triassic age. This hypothesis is congruent with the age proposed by Jalil (1993, 1999, 2001), Jalil and Taquet (1994), Nedjari et al. (2010), and Aït-Ouali et al. (2011) but neither with the Middle-Late Triassic age proposed by Lehman (1971), nor with the Middle Triassic age only (Anisian-Ladinian) suggested by Bourquin et al. (2010), who under-estimated the thickness of the lower section ("Formation 0" *sensu* Nedjari et al., 2010) of the Zarzaïtine Series (2.5 m for these authors instead of 11 m according to our interpretation or 50 m according to Busson and Cornée, 1989).
- Concerning the palaeoenvironment associated to *Stanocephalosaurus amenasensis*, it is interesting to note that the way of life of the capitosaurian amphibians is often debated: for example, Mukherjee et al. (2010), based on histological observations and recognition of Lines of Arrested Growth (LAGs) in the bone structure, suggest that capitosaurians may have lived in semi-arid environments characterized by strong seasonal rains. This is particularly the case of paracyclotosaurids

Fig. 5. *Stanocephalosaurus amenasensis* nov. sp. from the Lower/Middle Triassic of Algeria. *In vivo* reconstruction in the sebkha turning into a pond. Courtesy of Alain Bénéteau (2015).
Fig. 5. *Stanocephalosaurus amenasensis* nov. sp. du Trias inférieur à moyen d'Algérie. Reconstitution *in vivo* dans une sebkha en cours d'assèchement. Avec l'aimable autorisation d'Alain Bénéteau (2015).

which may have lived in water pools, shallow lakes and/or rivers, while maintaining the ability to move on land, from one habitat to another (Mukherjee et al., 2010). The new Algerian species clearly shows dermo-sensory canals running on the skull roof and indicating an aquatic lifestyle (Steyer, 2003; Warren, 2000). *Stanocephalosaurus amenasensis* was discovered in a gypsum layer corresponding to the infilling of a salt lake, which probably represents the last stage of evolution of an alluvial plain under a strong seasonal climate (Nedjari et al., 2010). This salt lake shows that the paleoenvironment of *S. amenasensis* was not typical freshwater. This suggests that the species was euryhaline, as it may be the case in numerous temnospondyls (Laurin and Soler-Gijon, 2010; Steyer, 2002). Several adult individuals were discovered in situ and massively. This accumulation probably occurred during a dry season, when the water level of the sebkha decreased and turned into a pond (Fig. 5). The fact that no larval and juvenile individuals have been found suggests that bigger adult individuals may eat them in the pond. The exceptional preservation of these adults was possible thanks to a gypsum crust, which ended the drying cycle of the pound and protected the bones from atmospheric degradation. The fact that only *S. amenasensis* has been found in this Lagerstätte suggests a rather extreme paleoenvironment. Combined with the presence of gypsum, this paleoenvironment could be hypersaline, as is the case of the Permian Lagerstätte of Mangrullo, Uruguay, which yields mesosaurs (Piñeiro et al., 2012).

6. Conclusion

Stanocephalosaurus amenasensis is a new species of capitosaurian temnospondyl from the Triassic of the Algerian Sahara. It does not come from the same site that yielded "*Parotosaurus lapparenti*" and "*Wellesaurus bussoni*" erected by Lehman (1971), which we consider *nomina dubia*. This new species shows diagnostic characters: subtriangluar external nostrils with concave lateral borders (Fig. 4); small orbits; posteriorly wide postfrontals; elongate parietals; concave posterior margin of the skull table; ovoid anterior palatal vacuities; posteriorly pointed choanae; and oval interpterygoid fenestrae. *Stanocephalosaurus amenasensis* enlarges the distribution of the genus in northern Gondwana and illustrates the great palaeontological richness and potential of the Illizi Basin of southern Algeria. Given the stratigraphic distribution of the other *Stanocephalosaurus* species, this Algerian taxon confirms the Early-Middle Triassic age of the lowermost formation of the Zarzaïtine Series, and partly illustrates the

important faunal recovery after the Permian mass extinction events.

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