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Comment on "Depositional palaeoenvironments in a tide-influenced delta plain with amphibian and Cycadophyta remains – the Triassic Zarzaitine Formation (Algerian eastern Sahara)" S. Mazrou, Y. Lasnami, J. Amer, A. Boutaleb (2024): Geologos 30, 3 (2024): 209–229"

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1. Introduction

In their recent paper Mazrou et al. (2024) discussed the palaeoenvironmental evolution of the Triassic succession in the Zarzaïtine region and the palaeoecology of amphibian (temnospondyls) and Cycadophyta. However, in our opinion, the paper under discussion exhibits significant methodological weaknesses and interpretative errors on sedimentology and palaeoecology of temnospondyls. This strongly affects the validity of interpretations and conclusions. Furthermore, the use of previous work and data are often neglected or poorly exploited.

In our comment, we will analyse the work of Mazrou et al. (2024) and demonstrate that: *(1)* the authors often follow a flawed methodology and present false interpretations and often unfounded conclusions; *(2)* this work, in our opinion, does not always correspond to the scientific standards and rules. The aim of this comment is to avoid misleading researchers who may use these data.

2. Points of discussion

2.1. Exploitation of previous scientific works

In the work of Mazrou et al. (2024), significant previous results have been overlooked, and the exploitation of certain other works has been inadequately addressed. For example:

These authors declare "Apart from the lithostratigraphical study and research into the vertebrate fauna, any sedimentological and palaeoenvironmental analyses of deposits of the Triassic Zarzaïtine Formation were not carried out until now" (p. 210–211), which is not true. As a matter of fact, there were previous sedimentological studies of the Lower Zarzaïtine Formation that have been conducted, some of which were published (e.g. Busson, 1972; Aït Salem et al., 1998; Bourquin et al., 2010; Aït Ouali et al., 2011) and some unpublished works that have been carried out the last decades comprising PhD thesis and magisterial memoirs (e.g. Hammouche, 2006; Taib Cherif, 2011; Dahoumane, 2011).

Some reproduced texts and/or ideas that have been taken from the work of Nedjari et al. (2010) have been detected in the work without citing any references and thus claim ownership, for example Mazrou and co-authors attest that ''Zarzaïtine region constitutes the only place in Algeria where the Triassic is known at outcrop'' (p. 211). This idea was taken from Nedjari et al. (2010; p. 4) but this information was deformed. In fact, the Zarzaïtine area is the only Triassic outcrop in the Saharan platform and not in the whole Algeria (several outcrops are known in the northern part of Algeria: e.g. Durand Delga & Tefiani, 1994; Belhaï, 1998; Meddah et al., 2007; Ferhat & Aït Ouali, 2017).

In their paper, the authors state that the hercynian unconformity was discovered and observed for the first time during their fieldwork (p. 212), whereas these same outcrops (Hercynian unconformity) are well known and have already been reported then described by the previous authors, see Nedjari et al. (2010; p. 5); Bourquin et al. (2010; p. 382 and fig. 6); Aït Ouali et al. (2011; p. 15, 16).

For the illustration of temnospondyl *Stanocephalosaurus amenasensis,* Mazrou et al. (2024) have used a simple picture without citing any reference. It should be noted that this taxon was illustrated *in vivo* reconstruction by Alain Bénéteau from the MNHN team (*Muséum National d'Histoire Naturelle*, Paris) in Dahoumane et al. (2016, p. 925, fig. 5), which shows the true anatomical characteristics of this species.

2.2. Stratigraphy

The "figure 1-A" of Mazrou et al. (2024) illustrating the Triassic stratigraphic column does not represent the stratigraphy of the whole Zarzaïtine region, this stratigraphic section used in this paper does not come from the work of Nedjari et al. (2010) but it is extracted from the work of Dahoumane et al. (2016; fig.1) and is representative of the *Reculée* area only. Dahoumane et al. (2016) have subdivided the outcrops of the Triassic of the *Reculée* area into four (04) Formations (i.e. formations 0, 1, 2, and 3). This lithostratigraphic subdivision is different from the subdivision proposed by Nedjari et al. (2010).

On this same figure, the ages indicated on the left of the measured section and highlighted in red, as it is indicated in the work of Mazrou et al. (2024), do not match neither with the ages attributed by Aït Ouali et al. (2011), nor with those indicated in the work of Carpentier et al. (2016) cited by Mazrou et al. (2024). In fact, the work of Carpentier et co-authors focuses on the deposits of the southern Tunisian basins and their correlation with the deposits of Berkine basin located further north of the Zarzaïtine outcrops, and they have not attributed any ages to the vertebrate fauna discovered in Algeria, but they have simply summarized the results of Jalil (1999) and reported by Bourquin et al. (2010).

Additionally, regarding the ages of the Formations at the *Reculée* area, Mazrou et al. (2024) misquote the results put forward by Aït Ouali et al. (2011). These latter attribute an Early to Middle Triassic age to Formation I, and a Late Triassic age to Formation II, III, IV, not as it is indicated by Mazrou et al. (2024). It is important to note that an Early to Middle Triassic age was initially suggested by Jalil & Taquet (1994) based on vertebrate remains collected by petroleum geologists in the Gour Laoud area, located 45 km to the east. However, they did not specify the exact stratigraphic position for this material. The Early to Middle Triassic age was later confirmed by Dahoumane et al. (2016), based on the *S. amenasensis* Lagerstätte discovered at the base of the *Reculée* succession (Formation 0 *sensu* Dahoumane et al., 2016). The rest of the succession (Formations 1–3) are attributed to the Later Triassic.

2.3. Sedimentology

The palaeoenvironmental evolution of the Triassic succession in the Zarzaïtine region has been studied in detail by Bourquin et al. (2010). Their work provides a comprehensive facies inventory and facies association analysis, supported by photographic illustrations, and proposes a palaeoenvironmental interpretation, including braided rivers within an arid to humid alluvial plain, low-sinuosity rivers in a humid alluvial plain, lacustrine deposits, and marginal sabkha environments. A similar interpretation was proposed by Aït Ouali et al. (2011). Mazrou et al. (2024) claim to have studied two geological sections located 47 km apart but only present a synthetic lithological log of the Zarzaïtine Formation. This raises concerns about their ability to assess lateral facies variations and thickness changes, which are crucial in such sedimentary environments. In contrast, Bourquin et al. (2010) logged 17 detailed vertical profiles (scale 1/100) within a 25 km transect, allowing a robust interpretation of facies distributions. A palaeogeographic interpretation based on only two sections, with such a large separation, risks leading to highly erroneous conclusions.

Mazrou et al. (2024) describe a facies association (FA1) interpreted as an intertidal mixed flat with vertebrate remains, dominated by *Skolithos* ichnofacies. However, their ichnological identification is incorrect. The described ichnogenera (*Arenicolites*, *Monocraterion*, *Skolithos*, *Ophiomorpha*, and *Thalassinoides*) actually correspond to rootlet traces (see ichnology section), completely altering the palaeoenvironmental interpretation. This issue was previously reported by Bourquin et al. (2010) and Aït Ouali et al. (2011) but has been ignored.

The interpretation of FA1 as including "minor sandy and low-energy tidal channels, as well as oriented flat sandstone bodies representing tidal creeks" (p. 217) is poorly substantiated. There is no evidence of key tidal indicators such as: tidal ravinement surfaces at the base of channels, tidal dune facies within channels (Gingras et al., 2012), or inclined heterolithic stratification resulting from lateral accretion (Thomas et al., 1987). Additionally, tidal-dominated delta facies typically contain heterolithic, mud-rich sandstones of moderate intensity and diversity of trace fossils (Tonkin, 2012), which do not match the facies described in FA1.

The facies association FA2 is linked to an outcrop of 10 m thick (Mazrou et al., 2024, figs. 7, 8, 9), yet the exact location of this outcrop (Edjeleh section?) is not specified. The authors interpret these deposits as a tide-influenced deltaic environment (distributary channels and interdistributary areas). While we do not challenge this interpretation outright, the major issue lies in their generalization of this model across the entire study area. This is problematic as previous studies, such as Aït Ouali et al. (2011), do not report these facies in the region. Furthermore, our field observations confirm their absence.

Several 'significant methodological errors' or 'misinterpretations' have been made, including:

Incorrectly incorporating reactivation surfaces within facies descriptions;

Misinterpreting recent desiccation polygons on sandstone bed interfaces (Mazrou et al., 2024, fig. 11C) as Triassic features;

Desiccation cracks indicate just a subaerial exposure (Tucker, 2003; Stow, 2010; Collinson & Mountney, 2019) ant not hot and semi-arid climate, also, braided rivers are not typical of arid zones as it is mentioned in the paper;

Misunderstanding tidal cycle periodicity: In a 28-day lunar cycle, there are two spring-neap cycles (Collinson & Mountney, 2019). However, the authors erroneously state that "the first dunes form during a spring tidal cycle (every 14 days) and the second ones during a neap tidal cycle";

Incorrect identification of neap and spring tide periods in fig. 9B: The thick, lighter-coloured sandstone laminae correspond to spring tides, while the thin, mud-draped (relatively well developed) sandstone laminae represent neap tides.

In the fig. 10c (Mazrou et al., 2024), the mud clasts incorporated within the cross-stratified sandstones have been misinterpreted as mud drape (Fig. 1D). As reported by Collinson & Mountney (2019) "mudflakes, derived from desiccated and fragmented surface mud layers, may become mixed with sand deposits".

A major flaw in this study is the omission of key facies documented in prior works (Bourquin et al., 2010; Aït Ouali et al., 2011), despite their prominence in the field. These include for example: aeolian dune sandstone facies (Fig. 1A), climbing current ripples with rootlet traces (Fig. 1B), conglomerate facies (Fig. 1B), sandy dolomite and discontinuous gypsum layers, various types of palaeosoils such as dolocrete, silcrete (Fig. 1C).

The authors are wrong about marine conditions, as no marine fauna was found, such as Mollusca. The sediments of the *Reculée* area were formed in the freshwater environments such as: braided rivers, low-sinuosity rivers and floodplain lakes (Bourquin et al., 2010; Aït Ouali et al., 2011). The lagerstätte of amphibian remains was formed after the freshwater reservoir in which they lived dried up. This is evidenced by ichnofossils, which are presumably traces of plant roots and desiccation cracks. This evidence suggests the development of palaeosoils on the surface of a dried-up body of water.

2.4. Trace fossils

One of the peculiar aspects of the paper by Mazrou et al. (2024) is the erroneous interpretation of trace fossils. Based on the photographs presented in the sixth figure, the biogenic structures identified by these authors as *Thalassinoides*, *Skolithos*, *Monocraterion*, *Arenicolites*, and *Ophiomorpha* are, in fact, root traces (rhizoliths *sensu* Klappa, 1980). Rhizoliths, which are considered plant trace fossils (Gregory et al., 2006), encompass calcareous and ferruginous rhizoliths (*sensu stricto*), rhizoconcretions, rhizomorphs, root casts, and possibly some of their moulds. It is noteworthy that several previous studies, overlooked by Mazrou et al. (2024), such as those of Bourquin et al. (2010), Aït Ouali et al. (2011), and Arbey et al. (2011), had identified these structures as rhizoliths.

The *Reculée* rhizoliths consist of cylindrical to conical root traces, circular in cross-section, ranging from a few centimetres to 1.5 metres in length. These are vertical structures with horizontal ramifications and carbonate concretions, exhibiting downward

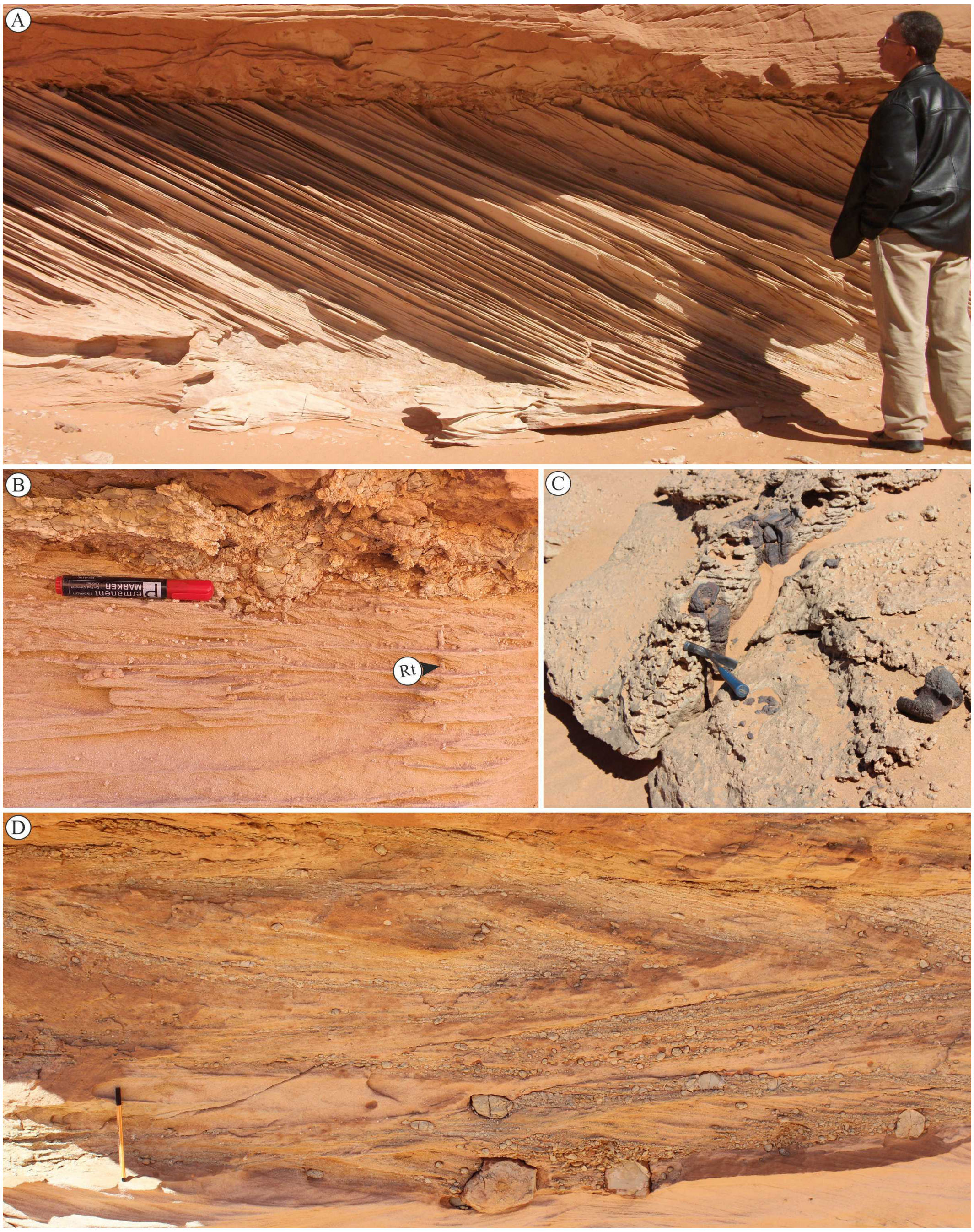

Fig. 1. Examples of the neglected facies at the *Reculée* area. **A –** Cross-stratified aeolian dune sandstone facies; **B –** Climbing current ripples with rootlet traces (Rt) truncated by ravinement surfaces at the top and overlain by mud clasts conglomerate; **C –** Silcrete bearing ferruginised tubular-like forms; **D –** Incorporated mud clasts in a cross-stratified sandstone bed.

bifurcations with progressively smaller diameters. Additionally, *Facies B* described by Bourquin et al. (2010) contains vertical roots connected to a network of horizontal root traces. Most rhizoliths are unfilled, featuring thin external walls. A photograph in Figure 6C of Mazrou et al. (2024) illustrates concentric internal structures in cross-section, which are characteristic of root traces (Klappa, 1980; Ekdale et al., 1984).

The main criteria for attributing the biological structures reported by these authors to rhizoliths rather than bioturbation structures are summarised in Table 1.

The exclusive presence of rhizoliths as trace fossils defines a characteristic ichnofacies, the 'Rhizo-

Table 1. Selected criteria for distinguishing rhizoliths from invertebrate burrows (from Klappa, 1980; Ekdale et al., 1984). The size has been excluded, since it is no longer considered a valid ichnotaxobase (Bertling et al., 2022).

Criteria	Rhizoliths	Invertebrate burrows	The *Reculée* examples
Shape	Cylindrical to conical, circular in cross-section	Highly variable	Cylindrical to conical, circular in cross-section
Branching	Downward bifurcations with decreasing diameters of second, third, and fourth order branches	Downward bifurcating burrows tend to show uniform diameters	Structures in photos 6A-B of Mazrou et al. (2024) (*highly cemented with post-depositional calcitic cement*) show downward bifurcations with decreasing diameters
Orientation	Variable, although most are vertical branching systems or horizontal ramifying networks	Highly variable ranging from simple vertical shafts to highly patterned horizontal networks	Mostly vertical structures with horizontal ramifications
Internal structures	Presence of contained root material, carbonised films	Presence of menisci, spreiten, fecal pellets, etc.	One photo in 6C of Mazrou et al. (2024) shows in the cross-section a concentric internal structure
External features	Few external features recognised, however, tubules, rootlets can be preserved; often associated with slickensides	Annulations, striations, scratch marks, etc.	Some external features such as small calcitic nodules and rootlets

lith ichnofacies', which signifies subaerial exposure and the presence of diverse vegetation types (Melchor et al., 2012). Rhizoliths and root systems also serve as indicators of drainage conditions in soils and palaeosoils (Genise et al., 2016). The use of the Rhizolith ichnofacies as a palaeoenvironmental indicator, characteristic of terrestrial environments (e.g., fluvial systems), is thus supported by the presence of various types of root traces, as exemplified by the *Reculée* section (Melchor et al., 2012). This ichnofacies adheres to a practical criterion within the ichnofacies model, accommodating the recurring occurrence of palaeosoils that host rhizolith assemblages exclusively and show no evidence of invertebrate traces. Building upon this framework, the following sections critique the misattributions of other ichnogenera by Mazrou et al. (2024).

Rhizoliths can be mistaken for certain *Skolithos* ichnospecies; however, the confusion with other invertebrate structures such as *Ophiomorph*a and, particularly, *Thalassinoides* is less justifiable. The rhizoliths identified by Mazrou et al. (2024) as *Skolithos* do not exhibit the defining characteristics of the latter, which should be straight burrows with homogeneous fill (Knaust et al., 2018; Sedorko et al., 2024). The so-called *Skolithos* (and/or *Monocraterion*) structures described by Mazrou et al. (2024) are exichnial, featuring a wall and a concentric internal structure. These features are typical of plant remains, such as roots.

The diagnosis of *Thalassinoides* by Myrow (1995) is as follows: "Horizontal, branching framework of smooth-walled, unlined burrows, lacking vertically oriented offshoots. Burrow diameter consistent within individual specimens; constrictions or swellings at both junctions and inter-junction segments are notably absent". Except for the possible presence of branching, none of the other diagnostic characteristics of the ichnogenus *Thalassinoides* are present in the structures illustrated by Mazrou et al. (2024, Figure 4A–B).

Ophiomorpha is defined based on a combination of two ichnotaxobases: *(i)* the overall burrow morphology; and *(ii)* the presence of a lining with knobs (Knaust, 2025). The diagnosis of this ichnogenus, as provided by Kennedy & MacDougall (1969), Frey et al. (1978), and Knaust (2025), is as follows: "Three-dimensional burrow system with shafts and networks of tunnels, branching dichotomously at acute or right angles, often swollen at the point of branching; tunnels internally smooth, externally lined with knobs whose shape may be discoid, ellipsoid, mastoid, bilobate or irregular; burrow fill passive or active". Neither the overall burrow morphology nor the lining with knobs of the structures described by Mazrou et al. (2024) are consistent with *Ophiomorpha*. These structures exhibit a pottery-like shape with a carbonate wall. What Mazrou et al. (2024) interpret as pellets are, in fact, nodules likely related to calcite crystallisation.

In the Methodology section of the paper under discussion it is stated that the authors have identified the trace fossils based on their standard characteristics and morphological criteria, following the work of Bertling et al. (2006), with a particular focus on "...branching or non-branching and type of burrow infill and wall characteristics". However, in their text, they did not adhere to the valid ichnotaxobases proposed by these authors. If they had followed these criteria, they would not have confused rhizoliths with invertebrate burrows.

Another critical oversight in the Methodology section occurs when Mazrou et al. (2024) state: "Around forty examples of burrows (ichnogenera Monocraterion and Skolithos) have been recorded at both sites, reflecting palaeocurrent orientations" (p. 212). In this statement, they demonstrate a lack of understanding of ichnological principles, particularly the palaeoenvironmental and palaeoecological implications of invertebrate trace fossils. Perhaps the most well-known and common trace fossil, the ichnogenus *Skolithos*, from which the *Skolithos* ichnofacies is named, has become a palaeocurrent indicator? How can a simple vertical, unbranched burrow, produced by suspension feeders, provide palaeocurrent information? The erroneous idea of using trace fossils in the interpretation of the palaeocurrent direction is not based on scientific approach or on bibliographical references in the field of ichnology.

2.5. Palaeontology and environmental implications of Temnospondyls

Upon reviewing the authors' work, several issues related to nomenclature and formatting have been observed and highlighted. The lack of adherence to established standards and conventions leads to the non-accuracy and non-consistency of the work. For example, in their paper the authors use the term "Stegocephalian" to refer to the Temnospondyl group, which is problematic, because it is an outdated classification. Also, throughout the entire paper, the authors have repeatedly neglected to follow the International Code of Zoological Nomenclature in their formatting of genus and species names, as well as ichnogenus names. For instance, the species name "Stanocephalosaurus amenasensis" and ichnogenus names such as "Skolithos" and "Diplocraterion" should be italicized. In addition, in the citation "*Stanocephalosaurus amenasensis* (Dahoumane et al., 2016)," it is important to note that the names of the authors should not be enclosed in parentheses, because the use of parentheses in this context typically indicates that the genus name has been revised, which is not the case here for *S. amenasensis* since the genus name remains unchanged.

In discussing the determining of *Stanocephalosaurus amenasensis*, it is stated that the identification of the new species was based on the study and examination of one single skull, contradicting the original paper which clearly indicates that the species was identified based on the study of two skulls, Holotype-ZAR03 and referred specimen-ZAR04 (Dahoumane et al., 2016). Moreover, Mazrou and co-authors claim that the *S. amenasensis* Lagerstätte has been 'rediscovered' during their field campaign, which is not true, because this same deposit was first discovered by Nedjari et al. (2010), then has been thoroughly investigated by Dahoumane et al. (2016) that led to the determination of a new species, and later by Arbez et al. (2017) for an endocranial structure study on a specimen of the new determined species *S. amenasensis*.

Furthermore, the authors appear to have misinterpreted the findings of Nedjari et al. (2010) and Dahoumane et al. (2016), as the remains of *Stanocephalosaurus amenasensis* were actually discovered in gypseous sand overlain by a gypseous crust, which allows the excellent preservation of this deposit. However, according to Mazrou et al. (2024) these amphibians are not epigenised in gypsum, otherwise, the gypsum would have completely weakened the bones and thus prevent a proper preservation of the Lagerstätte. This is also not true, as this type of preservation has already been reported elsewhere in the world in the Permian Lagerstätte of Mangrullo, Uruguay, which yields Mesosaurs (Piñeiro et al., 2012). This has already been mentioned in the work of Dahoumane et al. (2016).

Concerning the lifestyle of Temnospondyls, the authors argue that this amphibian group lived in a marine environment based on the work of Warren (2000), Damiani & Jeannot (2002), Steyer (2002, 2003), and Dahoumane et al. (2016). In fact, these works and others (i.e. Schoch, 2008; Fortuny et al., 2011, 2016; Scheyer et al, 2014; Rinehaty et al., 2023) attest that temnospondyls spanned a wide range of ecological niches, in both terrestrial and aquatic realms ranging from fresh, brackish and even coastal marine environments.

The remains of temnospondyls are generally preserved in Triassic continental deposits such as in fluvial and lacustrine environments in several regions of the world, for example: Germany (Württemberg, Kupferzell), Morocco (Argana Basin); Iberian Peninsula; Eastern European platform; America (New Mexico in the Moenkopi Formation); Brazil (Parana Basin); Tanzania (Ochev & Shishkin, 1989; Schoch & Milner, 2000; Fortuny et al., 2011; Eltink et al., 2015; Rinehart et al., 2015; Dias-da-Silva & Dias, 2013 in Nonsrirach et al., 2021; Schoch et al., 2022). The fact that temnospondyls were found in a marine environment in the Karoo Basin is not in contradiction with what is already known about the lifestyle of these tetrapods, and it does not exclude their very widespread presence in continental environments such as lakes and rivers.

Dahoumane et al. (2016) clearly identified the presence of the sensory canal in the *Stanocephalosaurus amenasensis*. The occurrence of this feature implies the presence of these organisms in aquatic environments; however, it does not exclude their semi-aquatic lifestyle. According to Morkovin (2024), capitosauroids, which in general have more "terrestrial" features, show significant development of the lower levator of the scapula, which was involved in head support, indicating a lifestyle associated with benthic shallow waters or shorelines. These data are also in agreement with the established ideas (Watson, 1919; Ochev, 1966) about these animals as 'living traps' using the ambush method of hunting. It is also important to note that Mukherjee et al. (2010), based on histological observations and the identification of Lines of Arrested Growth (LAGs) in the bone structure, propose that capitosaurians may have inhabited semi-arid environments with strong seasonal rainfall. This is especially true for paracyclotosaurids, which may have lived in water pools, shallow lakes, and/or rivers, while retaining the ability to move between habitats on land (Mukherjee et al., 2010).

From a climate perspective, several temnospondyls have been reported from continental deposits under semi-arid climates, e.g. the Parana Basin in Brazil (Eltink et al., 2015). Moreover, Schoch et al. (2022) reported another association, similar to the *S. amenensis* Lagerstätte, found in sebkha-type lakes setting from the Kupferzell region in Germany. A palaeoecological simulation model has been developed by Moreno et al. (2024) in which they exhibit the preference of the Triassic Capitosauria group for warmer temperatures and low precipitation.

The authors note the presence of fish remains (hybodont sharks teeth and spines) in these sediments (e.g. Busson & Cornée, 1989; Fabre, 2005). It is important to note that this fauna was collected in the Gour Laoud locality, 45 km from *Reculée* section where the temnospondyls *Stanocephalosaurus amenasensis* Lagerstätte is located.

The authors ascribe the ferruginised tubular-like forms described by Arbey et al. (2011) as Thallophyta to Bennettitales and cycads, on the basis of a simple morphological comparison made in the field. Although, the same authors have criticised the work of Arbey et al. (2011) for not having carried out a systematic study or provided any section for viewing the cellular structure of the plant tissue. Additionally, they claim to have identified seeds, but there is no photographic evidence to support their interpretation.

3. Discussion and concluding remarks

Mazrou et al. (2024) fail to integrate previous findings and do not position their work within a scientific continuum. Their study is marked by methodological shortcomings, weakly supported interpretations, and fundamental errors in palaeontology, ichnology and facies analysis. A more rigorous approach, building upon existing data, is necessary to provide meaningful and scientifically valid conclusions on the sedimentology of the Zarzaïtine region. Numerous texts and/or ideas from previous works have been reproduced in Mazrou et al. (2024) without proper citation, thereby implying authorship. This constitutes a breach of the principles of scientific rigor and ethics.

References

Aït Ouali R., Nedjari A., Taquet P., Bitam L., Tayeb Cherif L. & Bouras R., 2011. Le Zarzaïtine inférieur (In Aménas, Sahara algérien): derniers développements dans une série du Trias pro parte. *Mémoire du Service Géologique de l'Algérie* 17, 9–26.

Arbey F., Nedjari A., Aït Ouali R., Bitam L., Bouzidi W. & Kedadra B., 2011. Découverte de peuplements diversifiés de « thallophytes », champignons, algues, de grande taille, dans les séries continentales triasiques et jurassiques d'In Aménas. *Mémoire du Service Géologique de l'Algérie* 17, 27–65.

Belhaï D., 1998. The Paleozoïc formation of Chenoua massif (Algeria) Stratigraphic and structural analysis, *IGCP Project N° 276 Newsletter* 6, 72–77.

Bertling M., Braddy S.J., Bromley R.G., Demathieu G.R., Genise J., Mikuláš R., Nielsen J.K., Nielsen K.S.S., Rindsberg A.K., Schlirf M. & Uchman A., 2006. Names for trace fossils: a uniform approach. *Lethaia* 39, 265–286.

Bertling M., Buatois L.A., Knaust D., Laing B., Mángano M.G., Meyer N., Mikuláš R., Minter N.J., Neumann C., Rindsberg A.K., Uchman A. & Wisshak M., 2022. Names for trace fossils 2.0: theory and practice in ichnotaxonomy. *Lethaia* 55, 1–19.

Bourquin S., Eschard R. & Hamouche B., 2010. High-resolution sequence stratigraphy of Upper Triassic succession (Carnian-Rhaetian) of Zarzaïtine outcrops (Algeria): A model of fluvio-lacustrine deposits. *Journal of African Earth Sciences* 58, 365–386.

Carpentier C., Hadouth S., Bouaziz S., Lathuiliere B. & Rubino J.L., 2016. Basin geodynamics and sequence stratigraphy of Upper Triassic to Lower Jurassic deposits of Southern Tunisia. *Journal of African Earth Sciences* 117, 358–388.

Collinson J.D., Mountney N.P. & Allen J.R.L., 2019. *Sedimentary Structures*. 4th Edition. Edinburgh: Dunedin Academic Press, 352 pp.

Dahoumane A., Nedjari A., Aït-Ouali R., Taquet P., Vacant R. & Steyer J.S., 2016. A new mastodonsauroid temnospondyl from the Triassic of Algeria. Implications for the biostratigraphy and palaeoenvironments of the Zarzaïtine Series, northern Sahara. *Comptes Rendus Palevol* 15, 918–926. DOI: 10.1016/j.crpv.2015.09.005.

Durand Delga M. & Téfiani M., 1994. *Problèmes posés par le Trias des zones internes des Maghrébides et des Cordillères bétiques*. [In :] Dercourt J., Téfiani M. & Vila J.M (Eds) : Trias ’93. Mémoires du Service Géologique de l’Algérie 6, 41–56.

Ekdale A.A., Bromley R.G. & Pemberton S.G., 1984. *Ichnology – The Use of Trace Fossils in Sedimentology and Stratigraphy*. SEPM, Tulsa, 15, 317pp.

Eltink E., Dias E.V., Dias-da-Silva S., Schultz C.L. & Langer M.C., 2015. The cranial morphology of the temnospondyl Australerpeton cosgriffi (Tetrapoda: Stereospondyli) from the Middle-Late Permian of Paraná Basin and the phylogenetic relationships of Rhinesuchidae. *Zoological Journal of the Linnean Society* 176, 835–860. https://doi.org/10.1111/zoj.12339

Ferhat M. & Ait Ouali R., 2017. New data on the Lower Mesozoic basal series of the Traras Mounts (Tlemcen, northwestern Algeria). *Arabian Journal of Geosciences* 10, DOI10.1007/s12517-017-3097-7

Fortuny J., Galobart A. & De Santisteban C., 2011. A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria, *Acta Palaeontologica Polonica* 56, 553–566. http://dx.doi.org/10.4202/app.2010.0025

Fortuny J., Marcé-Nogué J., Steyer J.S., de Esteban-Trivigno S., Mujal E. & Gil L., 2016. Comparative 3D analyses and palaeoecology of giant early amphibians (Temnospondyli: Stereospondyli). *Scientific Reports* 6, 30387. DOI: 10.1038/srep30387

Frey R.W., Howard J.D. & Pryor W.A., 1978. *Ophiomorpha*: its morphologic, taxonomic, and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 23, 199–229.

Genise J.F., Bedatou E., Bellosi E.S., Sarzetti L.C., Sánchez M.V. & Krause J.M., 2016. *The Phanerozoic four revolutions and evolution of paleosol ichnofacies*. [In:] Buatois L.A. & Mángano M.G. (Eds): The trace fossil record of major evolutionary events. Topics in geobiology. Springer, New York, 301–370.

Gingras M.K., MacEachern J.A. & Dashtgard S.E., 2012. The potential of trace fossils as tidal indicators in bays and estuaries. *Sedimentary Geology* 279, 97–106.

Gregory M.R., Campbell K.A., Zuraida R. & Martin A.J., 2006. Plant Traces Resembling *Skolithos*. *Ichnos* 13, 205–216.

Jalil N.E., 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. *Journal of African Earth Sciences* 29, 219–226.

Jalil N.E. & Taquet P.H., 1994. Les vertébrés triasiques de la série de Zarzaïtine (Algérie). Liste faunique et implications stratigraphiques The Triassic vertebrates of the Zarzaïtine serie (Algeria). *Mémoire du Service Géologique d’Algérie* 6, 99–104.

Kamoun F., Peybernès B., Ciszak R. & Calzada S. 2001. Triassic palaeogeography of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 172, 223–242.

Kennedy W.J. & MacDougall J.D.S., 1969. Crustacean burrows in the Wealden Clay (Lower Cretaceous) of South-Eastern England and their environmental significance. *Palaeontology* 12, 459–471.

Klappa C.F., 1980. Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology* 27, 613–629.

Knaust D., 2025. The ichnogenus *Ophiomorpha* Lundgren, 1891: Taxonomy and environmental distribution. *Earth-Science Reviews* 261, 104988.

Knaust D., Thomas R.D.K. & Curran H.A., 2018. *Skolithos linearis* Haldeman, 1840 at its early Cambrian type locality, Chickies Rock, Pennsylvania: Analysis and designation of a neotype. *Earth-Science Reviews* 185, 15–31.

Lehman J.P., 1971. Nouveaux vertébrés du Trias de la série de Zarzaïtine. *Annales de Paléontologie (Vertébrés.)* 57, 71–93.

Mazrou, S., Lasnami Y., Amer J. & Boutaleb A., 2024. Depositional palaeoenvironments in a tide-influenced delta plain with amphibian and Cycadophyta remains – the Triassic Zarzaitine Formation (Algerian eastern Sahara). *Geologos* 30, 209–229.

Meddah A., Bertrand H. & Elmi S., 2007. La province magmatique de l’Atlantique central dans le bassin des Ksour (Atlas saharien, Algérie). *CR Geosci* 339, 25–26.

Melchor R.N., Genise J.F., Buatois L.A. & Umazano A.M., 2012. *Fluvial environments*. [In:] Knaust D. & Bromley R.G. (Eds): Trace Fossils as Indicators of Sedimentary Environments. Developments in sedimentology. Elsevier, Amsterdam, 329–378.

Moreno R., Dunne E.M., Mujal E., Farnsworth A., Valdes P.J. & Schoch R.R., 2024. Impact of environmental barriers on temnospondyl biogeography and dispersal during the Middle Late Triassic. *Palaeontology* 67, 1–18.

Morkovin B.I., 2024. Structural features of the muscular crests of the Parasphenoid in Early Triassic Capitosauromorphs (Amphibia: Capitosauromorpha) of the East European Platform as a reflection of adaptive differences. *Paleontological Journal* 58, 1291–1300. DOI: 10.1134/S0031030124601130

Mukherjee D., Ray S. & Sengupta D.P., 2010. Preliminary observations on the bone microstructure, growth patterns and life habits of some Triassic temnospondyls from India. *Journal of Vertebrate Paleontology* 30, 78–93. doi: 10.1002/spp2.1263

Myrow P.M., 1995. *Thalassinoides* and the enigma of Early Paleozoic open-framework burrow systems. *Palaios* 10, 58–74.

Nedjari A., Aït Ouali R., Bitam L., Steyer J.S., Taquet Ph., Vacant R. & Kedadra B., 2010. Découverte d’un nouveau gisement de Stégocéphales d’une conservation exceptionnelle dans le Trias d’In Amenas (Bassin d’Illizi, Algérie) [Discovery of a new deposit of Stegocephali of exceptional preservation in the Triassic of In Amenas (Illizi Basin, Algeria)]. *Bulletin du Service Geologique National* 21, 211–228.

Nonsrirach T., Manitkoon S. & Lauprasert K., 2021. First occurrence of brachyopid temnospondyls in Southeast Asia and review of the Mesozoic amphibians from Thailand. *Fossil Record* 24, 33–47. https://doi.org/10.5194/fr-24-33-2021

Ochev V.G., 1966. *Sistematika i filogeniya kapitozavroidnykh labirintodontov (Systematics and Phylogeny of Capitosauroid Labyrinthodonts),* Saratov: Izd. Saratov. Univ. 184 pp.

Ochev V.G. & Shishkin M.A., 1989. On the principles of global correlation of the continental Triassic on the tetrapods: *Acta Palaeontologica Polonica* 34, 149–173.

Piñeiro G., Ramos A., Goso C., Scarabino F. & Laurin M., 2012. Unusualenvironmental conditions preserve a Permian mesosaur-bearing Konservat-Lagerstätten from Uruguay. *Acta Palaeontologica Polonica* 57, 299–318.

Rinehart L.F., Lucas S.G. & Schoch R.R., 2015. Eocyclotosaurus appetolatus, a new cyclotosaurid amphibian from the Middle Triassic (Perovkan) Moenkopi Formation of New Mexico, U.S.A., *Journal of Vertebrate Paleontology* 35, e929140, DOI: 10.1080/02724634.2014.929140.

Rinehart L.F., Lucas S.G., Hunt A.P. & Heckert A.B., 2023. Skull and jaw shape as indicators of trophic guild association in temnospondyl amphibians and other aquatic predators. *New Mexico Museum of Natural History and Science Bulletin* 94, 585–609.

Scheyer T.M., Romano C., Jenks J. & Bucher H., 2014. Early Triassic marine biotic recovery: The predators' perspective. *Plos One* 9, e88987. doi:10.1371/ journal.pone.0088987

Schoch R.R., 2008. The Capitosauria (Amphibia): characters, phylogeny,and stratigraphy. *Palaeobiodiversity* 1, 189–226.

Schoch R.R. & Milner A.R., 2000. *Handbuch der Paläoherpetologie: Teil 3B, Stereospondyli.* Pfeil, Munich, 219 pp.

Schoch R.R., Seegis D. & Mujal E., 2022. The Middle Triassic vertebrate deposits of Kupferzell (Germany): palaeoenvironmental evolution of complex ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* 603, 111181.

Sedorko D., Knaust D., Junior M.N., de Barros G.E.B., Ribeiro V., Sousa F.N., Ghilardi R.P. & Borghi L., 2024. *Skolithos* piperock from the Lower Devonian storm beds. *Palaeogeography, Palaeoclimatology, Palaeoecology* 656, 112604.

Steyer J.S., 2003. A revision of the early Triassic "capitosaurs" (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. *Journal of Vertebrate Paleontology* 23, 544–555.

Stow D.A.V., 2010. *Sedimentary Rocks in the Field (a colour guide).* Manson Publishing, 323 pp.

Thomas R.G., Smith D.G., Wood J.M., Visser J., Caverley-Range E.A. & Koster E.H., 1987. Inclined heterolithic stratification: terminology, description, interpretation and significance. *Sedimentary Geology* 53, 123–179.

Tonkin N.S., 2012. Deltas. [In:] Knaust D. & Bromley R.G. (Eds): Trace fossils as indicators of sedimentary environments. *Developments in Sedimentology*, 64, 507–528.

Tucker M.E., 2003. *Sedimentary Rocks in the Field*. 3rd Edition, John Willey & Sons, Chichester, 236 pp.

Warren A.A., 2000. *Secondarily aquatic temnospondyls of the Upper Permian and Mesozoic*. [In:] Heatwole H. & Carroll R.L. (Eds): Amphibian biology, Paleontology. Surrey Beatty & Sons 4, 1121–1149.

Watson D.M.S., 1919. The structure, evolution and origin of the Amphibia. The 'orders' Rhachitomi and Stereospondyli, *Philosophical Transactions of the Royal Society of London Ser. B* 209, 1–73.

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