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First occurrence of temnospondyls from the Permian and Triassic of Turkey: Paleoenvironmental and paleobiogeographic implications

Premiers temnospondyles du Permien et du Trias de Turquie : implications paléoenvironnementales et paléobiogéographiques

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ABSTRACT

Permian and Triassic tetrapods are very rare in Turkey. Yet this group bears important paleoenvironmental and paleogeographical signals to better understand Pangean models, and especially the geodynamic history of the Permian and Triassic in Turkey, which remains highly debated. Here we present and describe the first temnospondyls from Turkey (SE Anatolia) which consist of a Middle Permian branchiosaurid and an Early Triassic stereospondyl. The branchiosaurid is the first representative of its group in Gondwana and the first from the Middle Permian: it therefore brings important paleogeographic implications and supports the hypothesis that anamniotic tetrapods may have used trans-Pangean migration routes between Europe and Gondwana. It also brings new data to the debated depositional environment of the Permian of SE Anatolia. The Triassic stereospondyl represents one of the few tetrapods known from paleoequatorial areas and confirms a relatively rapid faunal turnover of the anamniotic fauna after the Permian-Triassic mass extinction.

RÉSUMÉ

Les tétrapodes du Permien et/ou du Trias sont très rares en Turquie. Cependant, il a été montré que ce groupe est porteur d'un signal paléoenvironnemental et paléogéographique important, aidant à mieux comprendre les modèles de Pangée, et plus particulièrement l'histoire géodynamique de la Turquie qui demeure très débattue au cours du Permien et du Trias. Nous présentons et décrivons ici les premiers temnospondyles découverts en Turquie (SE d'Anatolie) ; un branchiosauridé du Permien moyen et un stéréospondyle du Trias inférieur. Le branchiosaure à lui seul est le premier représentant du groupe au Gondwana, et le premier datant du Permien moyen : il apporte donc des informations paléogéographiques importantes et confirme que les tétrapodes anamniotiques auraient emprunté des voies de migration trans-pangéennes entre l'Europe et le Gondwana. Il apporte également des

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données nouvelles concernant l'environnement de dépôt du Permien du Sud-Est d'Anatolie. Le stéréospondyle du Trias, quant à lui, représente un des rares tétrapodes connus dans la zone paléoéquatoriale de l'époque et confirme que le renouvellement faunique des tétrapodes anamniotiques s'est effectué assez rapidement après la grande crise Permien-Trias.

1. Introduction

Permian and Triassic rocks from Turkey remain virtually unexplored by vertebrate paleontologists. The Permian and Triassic tetrapod remains known from Turkey consist only of Permian tetrapod footprints from the North of the country (Gand et al., 2011) and Triassic phytosaurian, lungfish and chondrichthyan teeth from the South (Buffetaut et al., 1988; Monod et al., 1983; Thies, 1982). Yet the Permian and Triassic Systems are key for understanding the highly debated geodynamic history of the country: during the Permian and Triassic, according to various models, Turkey consists either of two plates widely separated by the Paleotethys Ocean – one plate belonging to Euramerica and the other to Gondwana (according to Scotese, 2001, Ziegler, 2001, and Ziegler et al., 1997), or of a single assemblage, possibly an isthmus, more or less isolated in the Paleotethys Ocean (Heckert and Lucas, 1999). Moreover, the depositional paleoenvironments of Turkish geological formations are still much debated: for example, the Permian of SE Turkey is considered to represent either marine or freshwater paleoenvironments (e.g., Bozdoğan and Ertug, 1997; Fontaine, 1981).

Here we report and describe new tetrapod remains from the Permian and Triassic of southeastern Anatolia (Fig. 1): although fragmentary, these fossils represent the first occurrences of temnospondyls in the country and are important to better understand the complex tectonic history of Turkey as well as its paleoenvironmental evolution during the Paleozoic-Mesozoic transition. These fossils also clearly show the potential of Turkey in terms of vertebrate paleontology, paleoenvironments and paleobiogeography.

2. Material and geological setting

The specimens were collected in 2009 and 2010 by IH in the Hazro area, southeastern Anatolia, during detailed stratigraphical fieldwork in the Paleozoic-Mesozoic local successions (Denayer and Hoşgör, 2014; Gourvennec and Hoşgör, 2012; Hoşgör and Kostak, 2012; Hoşgör and Stamberg, 2014; Hoşgör et al., 2012). The fossil remains are stored in the IPS (Institut Català de Paleontologia Miquel Crusafont of Sabadell, Spain) collections and consist of two temnospondyl remains coming from two different stratigraphic levels of different estimated ages:

- an almost complete but weathered branchiosaurid skeleton from the Middle Permian Kaş Formation of the Tanin Group (IPS-83195, Fig. 2);
- a large skull roof bone, possibly a postparietal, of a large stereospondyl (IPS-83862, Fig. 3) from the Early Triassic Uludere Formation of the Çığlı Group.

Both remains were recovered from southeastern Anatolia. The rocks of this area belong to two major tectonic units:

- the autochthonous units that include Palaeozoic and Mesozoic sequences belonging to the Arabian Plate;
- the allochthonous units that include Late Cretaceous and Paleogene sequences belonging to the Anatolian Plate and the Bitlis-Zagros suture zone.

The fossils described here come from the autochthonous units. The autochthonous sequences of the foreland area, the folded belt and of the foothill structure belt form the so-called "Border Fold Zone" (Fontaine et al., 1980) located approximately 75 km northeast of the city of Diyarbakır (Fig. 1). This zone is characterized by an 80 km long WNW-ESE trending anticline, rising up at the southern edge of the foothill structure belt (Kellog, 1960; Lebkuchner, 1976; Tolun, 1951). The main autochthonous lithostratigraphic units are briefly reviewed here to provide a framework for the later lithofacies and paleoenvironmental discussion (see also Tolun, 1960; Yılmaz and Duran, 1997 for details): the Late Paleozoic (Permian) and Early Mesozoic (Triassic-Early Jurassic) successions in southeastern Anatolia consist of 13 formations forming three groups; namely the Tanin Group (Middle-Late Permian), the Çığlı Group (Early Triassic) and the Cudi Group (Middle Triassic to Early Jurassic), containing carbonated, clastics and evaporitic rocks of economic importance because they host hydrocarbon reservoirs (Altınlı, 1954; Kellog, 1960; Perinçek, 1990; Schmidt, 1964; Yılmaz and Duran, 1997). The Permian and Triassic rocks from the Hazro area, which yielded the fossils, are:

- the Permian deposits, which rest unconformably on the Carboniferous, belong to the Tanin Group (Perinçek, 1990). This group is subdivided into the Kaş and Gomaniibrik formations. The latter was previously dated to the Tatarian (Late Permian) according to palynomorph and foraminiferous assemblages (Bozdoğan et al., 1987; Köylüoğlu and Altiner, 1989), but recent investigations show that the Gomaniibrik Formation comprises three lithological members (carbonates at the bottom and top members, siltstones and sandstones with a few coal layers at the middle member, see Gümüş et al., 1992; Schmidt, 1964; Yılmaz and Duran, 1997), which recorded

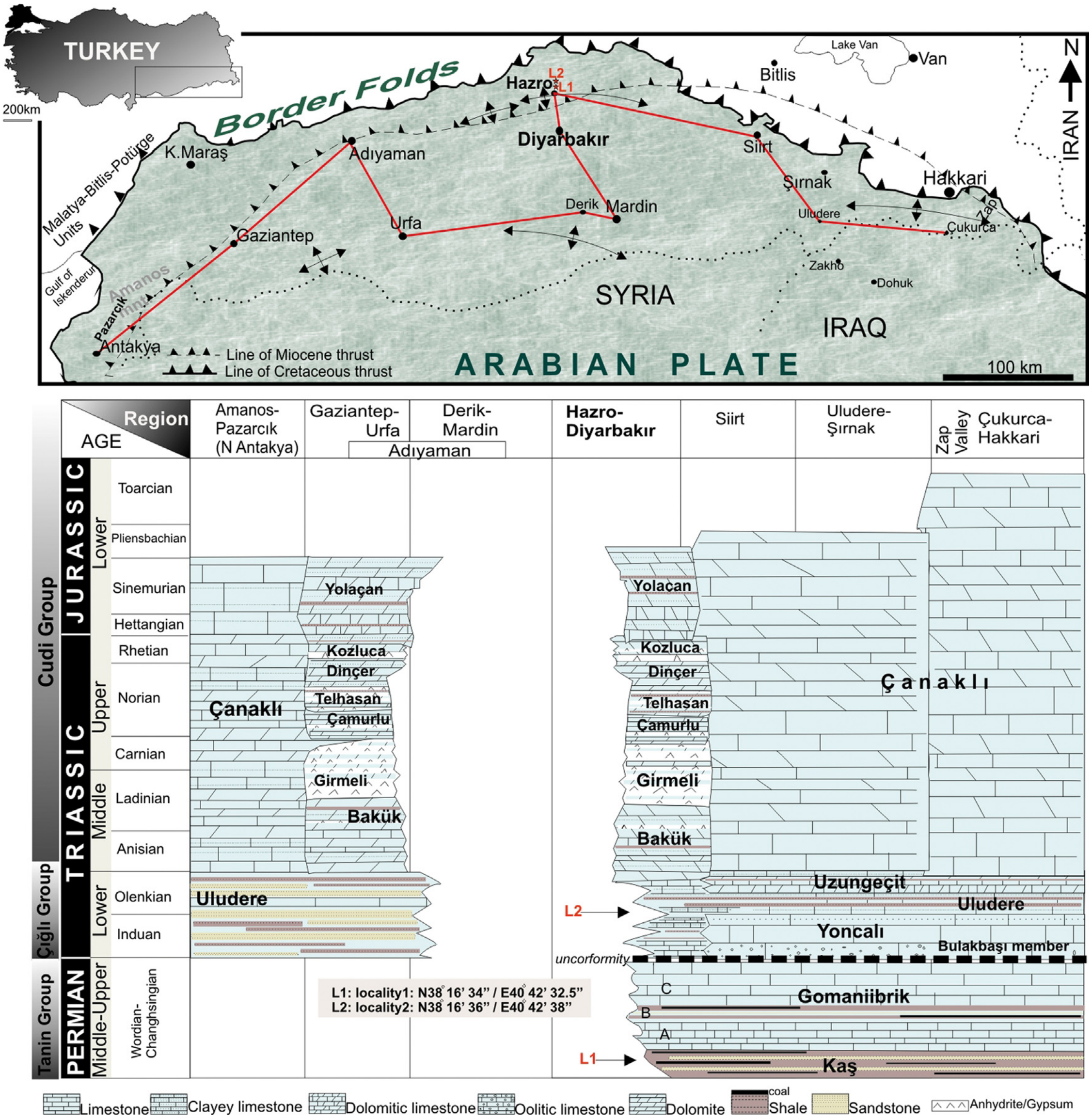

Fig. 1. (Color online.) General Permian-Early Mesozoic lithostratigraphic columns of the northern margin of the Arabian plate – SE Turkey parts based on Çoruh et al., 1997 and Hoşgör and Stamberg, 2014. Red line traces the localities where the stratigraphic columns were performed. Temnospondyl localities are marked by a red star. L1 correspond to the Permian locality and L2 the Triassic locality.

Fig. 1. (Couleur en ligne.) Colonnes lithostratigraphiques de la marge septentrionale de la plaque Arabique – Sud-Est de la Turquie d'après Çoruh et al., 1997 et Hoşgör and Stamberg, 2014. La ligne rouge entoure les localités dans lesquelles les colonnes stratigraphiques ont été levées. Les localités à Temnospondyles sont marquées d'une étoile rouge. L1 correspond à la localité permienne et L2 à la localité triasique.

four foraminiferous biozones comprising the biomarkers *Fusulinina* and *Miliolina*: based on these data, the bottom and middle members are dated from the late Middle Permian (Capitanian) whereas the upper member is dated up to the Changhsingian (Hoşgör and Stamberg, 2014; Stolle, 2007) without an unconformity at its base. The Kaş Formation is a clastic unit which consists of an alternation of sand- and siltstones, dark claystones and marls (Bozdoğan and Ertug, 1997; Bozdoğan et al., 1987). Numerous coal layers are intercalated in the siltstones. The branchiosaur described below was found in a siltstone level of the Kaş Formation (GPS: N 38°16′34″, E 40°42′32.5″), recently dated as Wordian according to the palynomorph assemblages (Stolle, 2007);

- the Early and Middle Triassic deposits, which cover large areas of the northern Arabian platform (Sadooni and Alsharhan, 2004): they are continuous with the sedimentary cycle that began during the Late Permian and that is controlled by the Mardin, Khleissia and Rutbah highs. During the Early to Middle Triassic, deposition in southeastern Turkey, northern Iraq and northwestern Syria was characterized by clastic and carbonated sequences

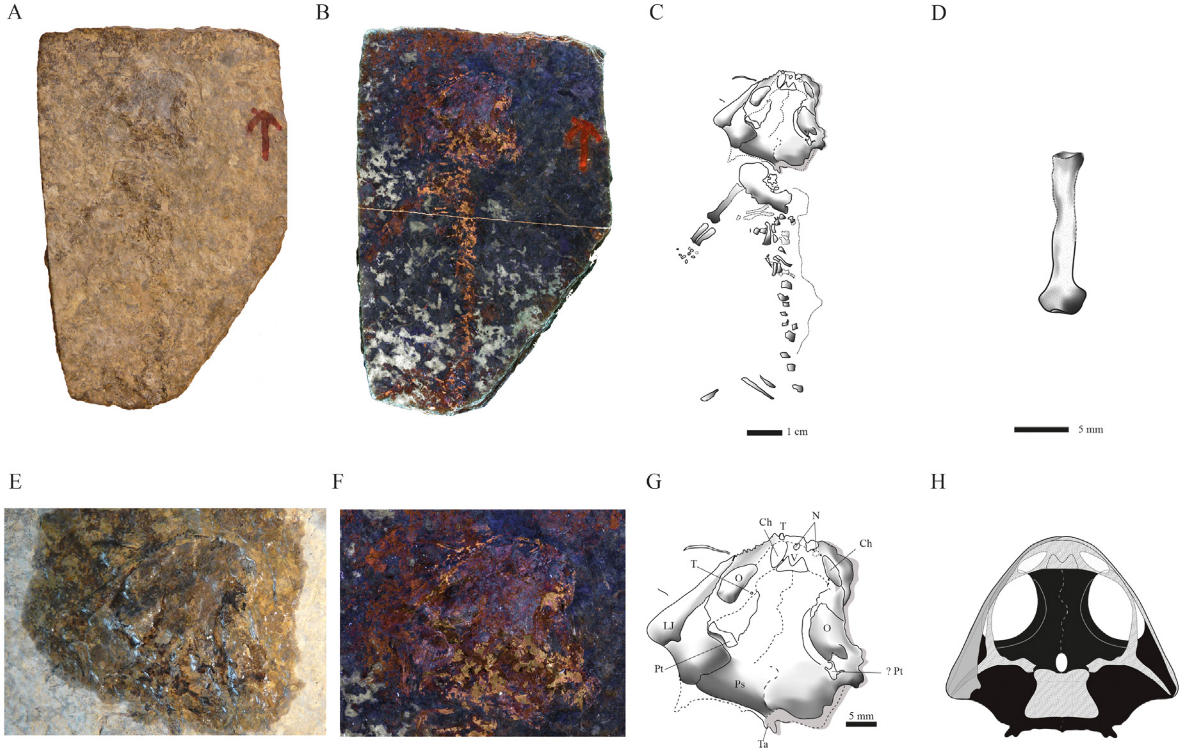

Fig. 2. (Color online.) Permian branchiosaurid. A. Photo of the specimen in normal light. B. Photo under UV light. C. Interpretative drawing of the specimen. D. Detail of the preserved humerus. E. Detail of the skull under normal light. F. Detail of the skull under UV light. G. Interpretative drawing of the skull. H. Reconstruction of the skull in ventral view. Abbreviations: Ch: choana; LJ: lower Jaw; N: naris; O: orbit; Ps: parasphenoid; Pt: pterygoid; T: tooth; Ta: Tabular; V: vomer.

Fig. 2. (Couleur en ligne.) Branchiosauridé permien. A. Photo en lumière naturelle. B. Photo en lumière UV. C. Dessin interprétatif de l'échantillon. D. Détail de l'humérus préservé. E. Détail du crâne en lumière naturelle. F. Détail du crâne en lumière UV. G. Dessin interprétatif du crâne. H. Reconstitution du crâne en vue ventrale. Abréviations : Ch : choana ; LJ : mâchoire inférieure ; N : naris ; O : orbite ; Ps : parasphénoïde ; Pt : ptérygoïde ; T : dent ; Ta : tabulaire ; V : vomer.

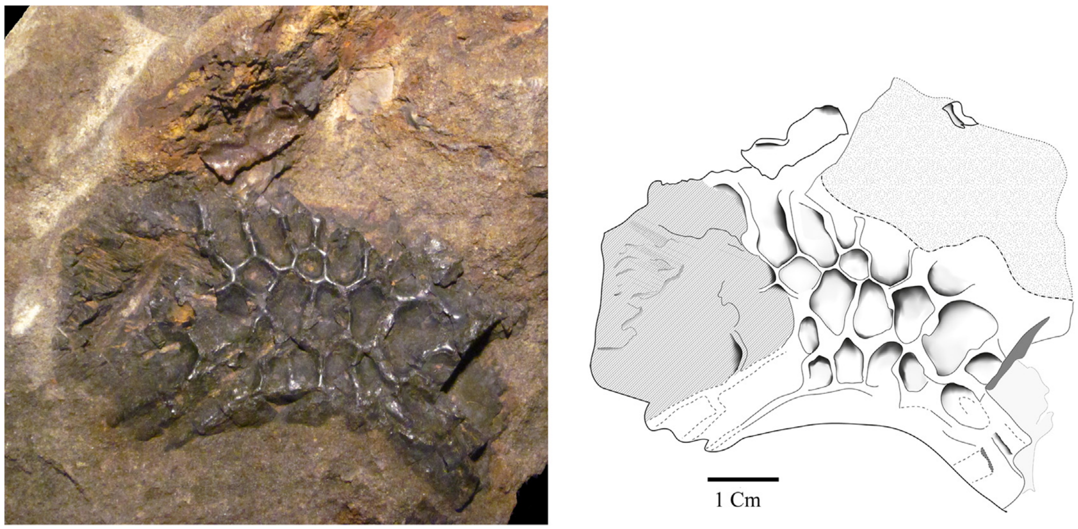

Fig. 3. (Color online.) Triassic stereospondyl. A. Photo. B. Interpretative drawing.

Fig. 3. (Couleur en ligne.) Stéréospondyle triasique. A. Photo. B. Dessin interprétatif.

as well as shallow marine deposits of restricted shelf, lagoonal and tidal-flat origin. These deposits typically show a large variation in facies and cover both shallow marine and deeper marine settings, from inner shelves to interplatform basins. The large stereospondyl bone described below was found in a shale level of the Uludere Formation (GPS: N 38°16′36′′, E 40°42′38′′), dated as Early Triassic according to Çoruh et al. (1997).

3. Permian Branchiosaurid

Preservation – The specimen IPS-83195 is preserved in ventral view on a laminated grey siltstone slab (Fig. 2). It is weathered but subcomplete and articulated, preserving part of the skull, the right forelimb, right partial femur and most of the vertebral column. The pelvic area is obscured by the matrix and the tail is unfortunately not preserved.

Stratigraphic age – Wordian, Middle Permian (Stolle, 2007), Kaş Formation, Tanin Group of the Hazro area, southeastern Anatolia, Turkey.

Ontogenetic age – The degree of ossification of the bones, the relatively large size of the specimen (whose maximum length from the snout to the posterior preserved vertebrae is 100.87 mm) for a branchiosaur, as well as the fact that the ribs show slightly enlarged distal ends, suggest an adult age for the specimen.

Description and comparison

Skull – The general skull shape is subparabolic with a well rounded snout. The skull length is of 27.63 mm, i.e. less than 25% of the estimated total body length. The orbits, as preserved, are elongated and ovoid. They are relatively large compared with the skull size, and dorsally oriented. The interorbital distance is of 8.31 mm. The right nostril is elongated ovoid. The skull table is very short and wide (12 mm × 34 mm), suggesting small supratemporals and parietals, although no sutures of these bones are visible. The left tabular horn is partly preserved and shows a long and deep groove.

The general body size of the specimen is characteristic of a large branchiosaurid temnospondyl or a discosauriscid seymouriamorph, but its subparabolic skull, with a well rounded snout, suggests a branchiosaurid attribution (the skull of the discosauriscids is rather triangular with a relatively pointed and sharp snout: see Klembara, 1997; Klembara and Janiga, 1993). Other dissorophoids such as amphibamids have proportionately larger skulls whereas small skull proportional with the rest of the body fits with branchiosaurids. Large dorsal orbits are also typical for branchiosaurids.

Palate – The outline of the right choana is visible close to – but does not overlap – the nostril: this choana is clearly larger than the nostril. The left choana, better preserved, is elongated, as in *Melanerpeton* or *Apateon*. The vomeral plates are wide and short, with wide posterior margins. The posterior part of the vomers is slightly elevated from the palatal view. They resemble two connected triangles, suggesting that the anterior part of the vomers formed a single unpaired depression. The right pterygoid, which is partly preserved, contacts the right parasphenoid but is still embedded in the matrix in its posterior part. The left pterygoid is also partly preserved: its posterior region shows its sutural zone with the parasphenoid plate. The parasphenoid plate is roughly quadrangular without any evidence of denticles or pits. It shows great developed and concave lateral margins ("the parasphenoid wings") which are also present in amphibamids and other branchiosaurids. The cultriform process of the parasphenoid is not preserved as it is often a fine and fragile road-like element.

The palatine and ectopterygoid are badly damaged on the right side. Yet this right palatine seems expanded and contacts the vomer and pterygoid.

Dentition – The base of a small tooth of 0.9 mm of diameter is preserved in the anterior part of the palatine. A section of the premaxilla-maxilla tooth row is visible along the anterior margin of the skull. Only one tooth is fully preserved, close to the right nostril: it is conical and probably monocuspid. The other upper teeth preserve only their internal moulds: they seem uniform in size and shape. Posterior upper teeth are also visible in the anterior margin of the left orbit, but they are partly masked by the coronoid which shifted and get fossilized in this area.

Mandible – The posterior region of the right mandible is preserved and still articulated with the posterior part of the skull. This articular region is slightly anterior to the occipital articulation, a condition generally seen in adult branchiosaurids rather than in adult amphibamids. The jaw suspensorium is short with the jaw hinge ahead of the level of the occiput. This pattern, associated with such a skull length, fits with a large branchiosaurid identification (as showed by *Melanerpeton* or *Leptorophus*) but not with an amphibamid identification (*Amphibamus*, *Platyrhinops* or *Tersomius* have the same size as that of the Turkish specimen but their jaw suspensorium is well behind the level of the occiput, Milner, pers. comm. 2014). The anterior part of the coronoid series is present near the right orbit: unfortunately its poor preservation prevents any description and size estimation.

Postcranial skeleton – The postcranial skeleton is relatively well preserved except for its pectoral region. The right humerus is subcomplete and relatively elongate: it reaches 14.72 mm in length and 2.7 mm in diaphyseal width. The presence and morphology of a long and slender humerus is of particular interest because it is unusual in Paleozoic amphibian-grade tetrapods and only found in the temnospondyl families Amphibamidae and Branchiosauridae (i.e., it is not found in any other known temnospondyl, seymouriamorph or lepospondyls). The right radius and ulna measure respectively 7.36 mm and 7.15 mm in length. The metacarpals and phalanges are poorly preserved and slightly disarticulated. Some neural arches are visible: they are subrectangular in shape (3.15 mm × 2.15 mm in average). At least sixteen vertebrae are preserved, but it is not sure whether more vertebrae were originally present or not. The preserved ribs are rather straight than curved, with slightly enlarged distal ends. The anterior ribs are larger than those further back. This pattern, and its associated musculature, are indicative of a body undulation during locomotion as known rather in branchiosaurids than in amphibamids where the anterior ribs are tiny and not involved in the body undulation. A long bone (11.44 mm in minimum length × 1.3 mm in diaphyseal width), badly preserved, is assigned to a right femur based on its general morphology and position. A grey line is visible along the left side of the vertebral column: it is interpreted as the external outline of the dermis.

Taxonomic and paleogeographic implications – The shape of the skull and orbits, their relative position on the skull roof, the shape of the snout, the skull size proportional to the rest of the body and particularly the long humerus allow us to refer the specimen with confidence to a dissorophoid temnospondyl. However, although subcomplete, the weathering condition of the skeleton precludes any further generic and specific identification, and a juvenile condition of the specimen cannot be discarded completely. Dissorophoids are small temnospondyls with derived skull morphology. They lived in various habitats from aquatic to terrestrial environments, and are known from the Late Carboniferous of North America and Europe to the Early Triassic of South Africa (with only one representative; *Micropholis* from the Karoo Basin). They correspond therefore to one of the rare surviving group of the Permo-Triassic mass extinction events. Although the specimen described above does not preserve all the synapomorphies of the branchiosaurids as stated by Schoch and Milner (2008), the jaw suspensorium morphology and pattern as well as the rib morphology indicate that the most plausible hypothesis is that this specimen corresponds to an adult branchiosaurid. The branchiosaurids are known in the Late Carboniferous and/or Early Permian of central and western Europe (Czechia, Germany, France, Sardinia, e.g., Schoch and Milner, 2008; Werneburg, 2009; Werneburg et al., 2007), and in the undifferentiated Permo-Triassic of Russia (Werneburg, 2009). Possible branchiosaurids have been also reported in the Late Carboniferous of North America (e.g., Hunt et al., 1996; Hunt et al., 2002; Werneburg and Lucas, 2007). Interestingly, the Turkish branchiosaurid described here is the first from Gondwana and the first known from the Middle Permian. It therefore greatly enlarges in space and time the distribution of the group which was previously restricted to Euramerica, if not Europe only. The Russian Triassic branchiosaurid (*Tungussogyrinus bergi*) already suggested a migration of the group towards northern latitudes (Werneburg, 2009). The new Turkish branchiosaurid from the Middle Permian also suggests another complementary migration of the group from Europe to Gondwana (Fig. 4). This possible southern migration may have been triggered by peculiar climatic conditions starting from the Late Carboniferous and/or Early Permian. This biogeographic hypothesis supports the scenario of trans-Pangean overland migration routes used by other anamniotic tetrapods (temnospondyls, lepospondyls) during the Permian (Germain, 2010; Sidor et al., 2005; Steyer and Jalil, 2009), although the hypothesis cannot be discarded that these migrations also passed through a narrow oceanic basin to reach the Anatolian plate. It has been shown that some temnospondyls may have inhabited and tolerated brackish or saltwater environments (e.g., Laurin and Soler-Gijón, 2010). This could also be the case for the Turkish branchiosaur which may therefore have used both types of routes, overland and/or marine.

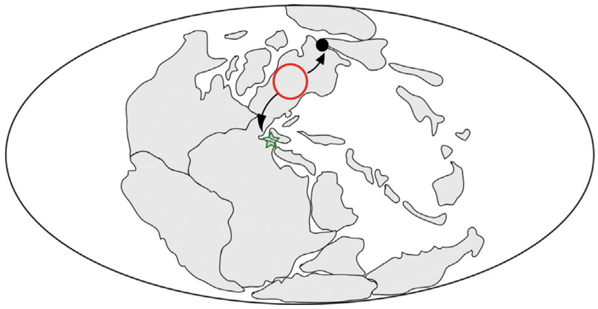

Fig. 4. (Color online.) Permian paleomap with the Central and Western Europe distribution of branchiosaurids (red circle) and the possible migration routes through Pangea. Star corresponds to the studied area.

Fig. 4. (Couleur en ligne.) Paléocarte du Permien, avec la répartition des Branchiosaures en Europe centrale et occidentale (cercle rouge) et les itinéraires possibles de migration à travers la Pangée. L'étoile correspond à la zone étudiée.

4. Triassic Stereospondyli

Preservation – The specimen IPS-83862 consists of an isolated, large and thick partial bone (65 mm × 38 mm × 7.11 mm thick) (Fig. 3). This bone is well ornamented and has been prepared mechanically from its sedimentary matrix. The matrix is a sandstone block from the Triassic Uludere Formation. A portion of the ornamented surface of the bone is weathered, whereas most of its natural borders are broken. Although not complete, this large bone preserves a natural outline that is regularly concave and allows its assignment (see below). Unfortunately no sutures are visible.

Stratigraphic age – Early Triassic, Uludere Formation, Çığlı Group of the Hazro area, southeastern Anatolia, Turkey.

Ornamentation and identification – This partial bone shows a strong honeycombed ornamentation that consists of polygonal ridges. These ridges are 1.2 mm high. They border large polygonal pits (up to 4.5 × 8.5 mm in size) on most of the ornamented surface of the bone. At least two pits are relatively small and round compared with the others: they lie near the middle of the bone and suggest a probable ossification center (e.g., Steyer, 2003). The other pits are more radially elongated, especially toward the periphery of the bone where they turn into subpolygonal grooves. The ornamentation is not as honeycombed in other vertebrates, but typical for temnospondyls: it is found on the external surface of the dermal bones, either on the skull roof or on scapular elements. The average height of the ridges, as well as the thickness of this large dermal bone, suggest an adult individual.

Description and comparison – The bone as preserved is subrectangular and flat (65 mm × 38 mm in dorsal view and 7.11 mm thick). Most of its natural outlines are broken except one, which is regularly concave. This concave outline, as well as the location of the possible ossification center, suggests that this dermal bone belongs to the skull roof, not to a scapular element. The large curvature degree of the natural outline, the relative size of the bone and the orientation of the ornamental ridges suggest that this outline is not bordering the orbits but the posterior region of

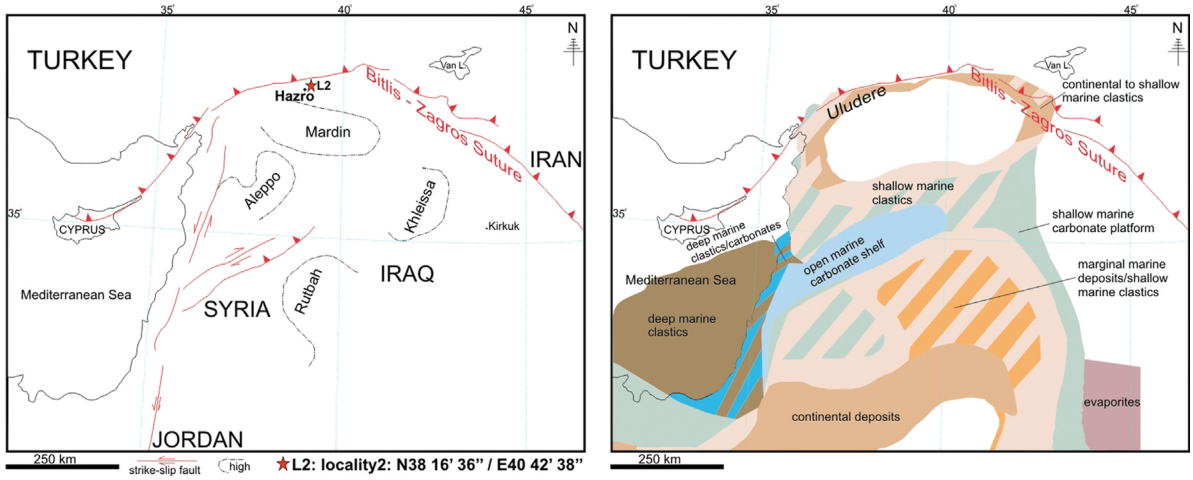

Fig. 5. (Color online.) Structural interpretation of the northern Arabian Plate and Paleofacies of the Early Triassic, based on Ziegler, 2001. Note the Hazro area and the Uludere formation where the Triassic temnospondyl was recovered, indicated by a red star the Triassic locality (L2).

Fig. 5. (Couleur en ligne.) Interprétation structurale de la plaque Arabique nord et des paléofaciès du Trias inférieur, d'après Ziegler, 2001. A noter la région d'Hazro et la formation d'Uludere, dans lesquelles le temnospondyle triasique a été échantillonné ; la localité (L2) est indiquée par une étoile rouge.

the skull roof. In other words, this bone is bordering the skull table or an otic notch of a large, adult temnospondyl. The thickness of the bone and its strong polygonal ornamentation suggest a stereospondyl temnospondyl, fitting with the Triassic age of the specimen. In dorsal view, the nodal points of the bone are not elevated with respect to the sculptural ridges as present in other stereospondyls (Witzmann et al., 2010). The ventral side of the bone was also prepared: it is flattened with no evidence of crista or crest, as visible usually on the tabular bone. We therefore interpret this element as probably corresponding to a left postparietal bone of a medium-large sized stereospondyl, possibly of a 70 cm long skull. A more precise identification seems risky: the relative thickness of the bone resembles that of metoposaurs, whereas the dermal sculpturing pattern of the bone suggests a capitosaurian affinity, particularly to mastodonsaurids (e.g. *Mastodonsaurus 'Heptasaurus' cappelensis* recovered also from the Early Triassic, Schoch, 1999).

Paleogeographical and paleoenvironmental implications – As for the Permian branchiosaurid described below, this second temnospondyl specimen from Turkey breaks records: it is the first tetrapod from the Early Triassic of the Arabian plate and one of the few tetrapods from paleoequatorial areas (Sun et al., 2012) (Fig. 5). Other Triassic tetrapods from adjacent regions are known from the Middle Triassic (Early Anisian) of Jordan and Negev (Israel): they consist respectively of a trematosauroid lower jaw (Schoch, 2011) and a palate of another probable trematosauroid previously assigned to a metoposaurid or a placodont ("*Negevodus ramonensis*", see Schoch, 2011 for a review). Other tetrapods are also known from the Late Anisian of Israel (Negev); they are placodonts and nothosaurs (Rieppel et al., 1997, 1999). At least, the tetrapods from the Late Triassic of this part of the world only consist of a small capitosauroid mandible from northern Ethiopia (Warren et al., 1998) and a partial trematosaurid skull from Pakistan (*Aphaneramma kokeni*). This first occurrence of a stereospondyl in the Early Triassic of Turkey therefore greatly enlarges the distribution of the group and confirms that the faunal turnover of the Permian-Triassic mass extinction occurred relatively quickly, at least for anamniotic tetrapods.

5. Conclusion

The fossil anamniotic tetrapods described here suggest that the Anatolian peninsula has an important potential to better understand the evolution of paleoecosystems during the Permian and Triassic times. This could be due to its paleogeographic key position which recorded faunal connections between Euramerica and Gondwana. These recent discoveries also increase the Permian and Triassic vertebrate paleobiodiversity of Anatolia which remains unfortunately poorly explored: apart from the temnospondyls described here, only actinopterygians and tetrapod footprints have been reported in the Permian (Gand et al., 2011; Hoşgör and Stamberg, 2014); and phytosaurs, lungfish and chondrichthyans in the Triassic (Buffetaut et al., 1988; Monod et al., 1983; Thies, 1982). This confirms that Turkey has a great paleontological potential to help us understand Permian and Triassic climatic models as well as the possible migration routes used by tetrapods through Permian and Triassic Pangea.

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