


New insights into the evolution of temnospondyls

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Received: 15 March 2019 / Accepted: 27 March 2019 / Published online: 26 April 2019
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1 On the interest of these species

The term “Temnospondyli” was originally coined in 1887–1890 by the German paleontologist Karl Alfred von Zittel (1839–1904) to define fossil amphibians with very peculiar vertebrae (*spondylus* in Greek) composed of several (*temno* in Greek) elements, namely the inter-, the neuro- and the pleuro-centrum. Since Zittel, our understanding of this group has evolved thanks to many other paleontologists over the world who excavated and revealed (*they are still doing it!*) the intriguing nature and the hidden questions of these enigmatic amphibians. Today, the temnospondyls still remain one of the most challenging groups, which allows to better understand “(on) the origin of species” (Darwin 1859). Temnospondyls are indeed of great interest for the sciences of evolution because:

- They show a high diversity (+290 species described and gathered in about 200 genera, see, e.g., Schoch 2013) together with a wide disparity and a huge range of sizes (from a few centimeters to more than 5 m in adult body length);
- They are sometimes fossilized and delicately preserved during their larval or juvenile grow stage, i.e. not only during their adult stage, making them very important for studies dealing with ontogeny-phylogeny (e.g., Steyer 2000) or, in a wider range, evo-devo (e.g., Sanchez et al. 2010);
- They may include the Lissamphibia; i.e. the modern amphibians represented today by the Anurans (frogs

and toads), the Caudata (salamanders and newts) and the more discrete Gymniophiona (limbless caecilians), the origin(s) of which remain(s) very controversial (e.g., Ruta and Coates 2007; Pardo et al. 2017, and references therein);

- They are very abundant in Paleozoic and early Mesozoic continental layers: they correspond to the most diverse group of early tetrapods (e.g., Schoch and Milner 2014; Ruta et al. 2007) and show a striking capacity to survive mass extinctions, particularly to the greatest Permian one (e.g., Ruta and Benton 2008; Fortuny et al. 2016).

The interest of temnospondyls resides also in the fact that their phylogenetic position varies considerably within early tetrapods: for example, they were historically considered as members of the “Labyrinthodontia”, an inclusive group of fossil amphibians named after their infolding and labyrinthous tooth structure (plicidentine), but since, some authors realized that this plicidentine is a convergent character also present in lepospondyls, marine reptiles and teleostean fish (e.g., Germain et al. 2016), and that Labyrinthodontia is a polyphyletic group which must be abandoned. Moreover, considering also extant taxa in the phylogenetic analyses, temnospondyls may be closely linked to lissamphians, as mentioned above: they could therefore solve the major problem of the very debated origin of modern amphibians.

Temnospondyls appeared during the Early Carboniferous as shown by its oldest members such as *Balanerpeton* (Milner and Sequeira 1993). Their intra-relationships have been largely discussed and they are still unclear for some groups (e.g., Milner 1990; Yates and Warren 2000; Schoch 2013). Consensually, the basal temnospondyls are the edopoids, ‘dendrerpetodontids’ and Rachitomi (sensu Schoch 2013) whereas the advanced ones correspond to the Eryopiformes (eryopids + stereospondylomorphs) (e.g., Schoch 2013; Yates and Warren 2000). The Rachitomi are of special interest because they include the dissorophoid amphibamids (e.g. *Amphibamus*, *Doloserpeton* and *Geroatrachus*), which are considered as potential ancestors of

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lissamphibians. For this reason, the amphibamids are in the centre of intensive discussions (e.g., Anderson et al. 2008; Marjanović and Laurin 2019, and references therein). The Eryopiformes, particularly the stereospondylomorphs, include the largest individuals in adult body size. During the Permian mass extinction, the stereospondylomorphs as well as the whole temnospondyls decreased in term of species number (e.g., the rhinesuchids) and some of them got extinct (e.g., the ‘archegosauroids’) (e.g., Witzmann 2005; Schoch 2013) but they re-radiated from the Early Triassic on (Ruta and Benton 2008). This important faunal turnover during the Permo-Triassic transition demonstrates the importance of temnospondyls to understand the impact of Permian mass extinction on the whole Pangea. The stereospondylomorphs, particularly the stereospondyls, re-flourished during the Early–Middle Triassic because they quickly occupied empty ecological niches related to both fresh- and brackish-waters: gigantic plagiosaurids, capitosaurids and trematosaurids were present, with adult body sizes up to 5 m (e.g. *Mastodonsaurus*). Some giants persisted during the Late Triassic (e.g., metoposaurids, capitosauroid cyclostosaurids, see Sulej 2007; Gee et al. 2017 and references therein) but they may have encountered competition with the flourishing neosuchian crocodylomorphs in non-marine ecosystems (Fortuny et al. 2016). Finally, the last (i.e., stratigraphically youngest) occurrence of a temnospondyl is that of an early Cretaceous brachyopoid from Australia (Warren 2000), which however did not mean the whole extinction of the group if we consider lissamphibians as part of the temnospondyl clade—*temnospondyls may be not dead!*

In order to create an exchange platform where temnospondyl workers could interact and discuss, we (JF and JSS), together with Thomas Arbez, organized in 2016 an international symposium during the XIVth Annual Meeting of the European Association of Vertebrate Palaeontologists held in Haarlem (The Netherlands) and entitled “Early Tetrapods Awaken”. This symposium aimed to offer to the scientific community an occasion for positive research interactions and to discuss the state of the art of early tetrapods using taxonomy, phylogeny, paleobiogeography, paleobiology, and including various topics such as the fish-tetrapod transition, the lissamphibian origin(s), the temnospondyl and lepospondyl evolution, their associated paleoenvironments and ichnofossils. A total of 16 abstracts (15 oral presentations and one poster) were presented. Authors from six different countries presented their results on various subjects such as Devonian–Carboniferous vertebrates, Permian and Triassic temnospondyls, or lissamphibian origin(s). During this successful symposium, the idea to publish an international special volume in a SCI ranked-journal naturally emerged. After fruitful discussions with colleagues and the excellent feedbacks we received, we decided to open the contributions not only to the symposium participants but also to the

whole “international temnospondyl community”: the aim was to highlight the increasing knowledge we have on the great diversity and disparity of temnospondyls from a wide range of perspectives and multidisciplinary approaches, i.e. investigating both body- and ichno-fossils with different techniques and methodologies.

2 Temnospondyls in space–time

This special volume includes seven contributions that cover a wide range of data, from recent discoveries to precise re-descriptions of both body- and ichno-fossils and using various methodologies. Many contributions are focused on stereospondylomorphs, particularly Triassic stereospondyls. This special volume is subdivided in three different sections:

- The first section deals with stereospondylomorphs and starts with a contribution providing an interesting new phylogeny of the group, with new ideas on the origin of stereospondyls and paleobiogeographic implications (Eltink and Schoch 2019): this is a long-awaited article revising previous phylogenetic analyses and naming new sub-clades on the basis of a re-evaluation of previous hypotheses. The following contribution is a re-description of the stereospondyl *Angusaurus* (Early Triassic of Russia) on the basis of a (so far) unpublished exquisite specimen, and a new phylogenetic analysis of trematosaurids (Fernández-Coll et al. 2019). The exquisite specimen preserves its endocranial region, which has been explored thanks to a micro-CT scan: this work contributes therefore the new trend using computed tomography on temnospondyls (e.g., Maddin et al. 2010; Arbez et al. 2017)—although endocranial reports had already been explored by few pioneers (e.g., Säve-Söderbergh 1936). The three following contributions deal with Late Triassic stereospondyls: Konietzko-Meier et al. (2019) provide a very detailed morphological and histological analysis of an interesting temnospondyl humerus from the Rhaetian (Late Triassic) of Germany. They attribute it to a possible capitosauroid cyclostosaurid—which could be therefore one of the youngest capitosauroids. As previously mentioned, during the Late Triassic the capitosaurids share nonmarine environments with other groups such as the metoposaurids. The latter are the topics of the contributions of Gruntmeier et al. (2019) and Chakravorti and Sengupta (2019) who used different approaches (taxonomy, paleobiology, etc.) and multiple taxa to investigate this enigmatic group: Gruntmeier et al. (2019) present a detailed morphological description of the mandibular sutures in the European genus *Metoposaurus* thanks to histological thin sections. Based on a comparison of mandibular suture patterns with previous

works based on other approaches (e.g., Fortuny et al. 2017; Konietzko-Meier et al. 2018), they suggest that a biomechanical loading regime was involved when these animals fed. Chakravorti and Sengupta (2019) gave an important systematic revision of the Indian metoposaurids based on a detailed re-description and morphometric analyses compared with many taxa from different continents and countries. They erect a new Indian genus and propose a new framework for future analyses.

- The second section comprises an original article focusing on geometric morphometrics to elucidate evolutionary processes: Pérez-Ben and Gómez (2019) indeed use temnospondyls as case-studies to deep on their cranial evolution. They interestingly suggest that intraspecific variation may not play a key role in temnospondyl evolution and authors discuss its evolutionary implications.
- Finally the third section deals with ichnites which correspond to abundant and well-known (but not necessarily understood) temnospondyl indirect remains from different parts of the world: Marchetti (2019) indeed reports a very peculiar and interesting fossil preservation consisting of large manual undertracks from the Early Permian of France, which are better preserved than on the corresponding trampled surface and underlying layers.

3 The future(s) of temnospondyls

Temnospondyls have a very extended and abundant fossil record; they offer an exceptional window to generate new working hypotheses and to better understand evolution. They had a so large distribution in time and space, and they were so abundant in continental ecosystems that they are of great interest to perform paleoenvironmental reconstructions during crucial periods such as the end Permian mass extinction, the end Triassic mass extinction, or the Carnian Pluvial Episode. Temnospondyls allow a better understanding of how life reacts and survives ecosystem changes.

Today, the “classical” paleontological analyses [e.g., anatomical (re)descriptions, systematics, phylogeny] are boosted by modern technologies (e.g., microtomography, 3D models, photogrammetry, geometric morphometrics) to push together the limits of sciences. New integrative and multidisciplinary approaches, particularly paleobiological perspectives, are (and will be) in the center of debates to test new working hypotheses and ideas. Some approaches replace the temnospondyls as alive organisms of the past, interacting with others in their paleoenvironments. As temnospondyls crossed time and extinctions, they represent a key group to better understand the evolution of species and the role of extinctions. In other words, temnospondyls deserve more attention because they provide valuable lessons from the

past, especially since life evolution, the global warming or the sixth extinction are nowadays fundamental topics.

Acknowledgements We are very grateful to all the contributors because without their interest, enthusiasm and perseverance, this special volume would not exist. We acknowledge all the participants of our symposium “Early Tetrapods Awaken” of the 14th Annual Meeting of the European Association of Vertebrate Palaeontologists held in Haarlem (The Netherlands). Our special thanks go to the chief-editors of Journal of Iberian Geology (Jose Lopez-Gomez and Javier Martín-Chivelet) and associate editor (Laura Domingo) for their positive feedback and useful discussions that render this special volume possible. This research paper is a contribution to the CERCA program (Generalitat de Catalunya). J.F. was supported by the research project CGL2017-82654-P of the Ministerio de Ciencia e Innovación and Ministerio de Economía, Industria y Competitividad, respectively, and the European Regional Development Fund of the European Union. J.F. is member of the consolidated research group 2017 SGR 86 GRC of the Generalitat de Catalunya.

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