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Dienerian (Early Triassic) ammonoids from the Northern Indian Margin



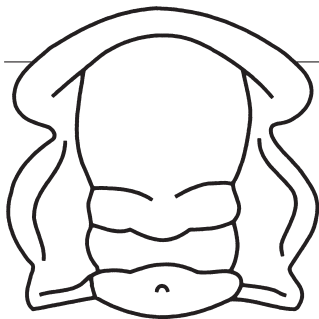
David Ware, Hugo Bucher, Thomas Brühwiler,
Elke Schneebeili-Hermann, Peter A. Hochuli[†],
Leopold Krystyn, Ghazala Roohi, Khalil Ur-Rehman
and Amir Yaseen

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- Cover picture:** *Gyronites plicosus* Waagen, 1895 (Nammal Nala, Salt Range, Pakistan, Pl. 5, Figs 7-9), *Ambites lilangensis* (Krafft, 1909) (Mud Bottom section, Spiti, India, Pl. 6, Figs 11-12) and *Koninckites vetustus* Waagen, 1895 (Nammal Nala, Salt Range, Pakistan, Pl. 14, Figs 18-21), three examples of ammonoids characteristic of the early, middle and late Dienerian, respectively.



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by David Ware, Hugo Bucher, Thomas Brühwiler,
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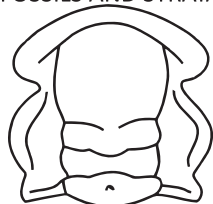
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Foreword

Dienerian (Early Triassic) ammonoids and the Early Triassic biotic recovery: a review

DAVID WARE AND HUGO BUCHER

FOSSILS AND STRATA



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It has been estimated that about 90% of all marine species disappeared during the end-Permian mass extinction (Raup & Sepkoski 1982). It is the biggest known biodiversity crisis in the history of Phanerozoic life, and it led to the replacement of typical Palaeozoic faunas by typical modern communities (Sepkoski 1984). The recovery which followed in the Early Triassic is an intensively studied topic. This recovery is traditionally considered as delayed in comparison with other mass extinctions (Erwin 1998, 2006) as several major marine clades such as corals (Stanley 2003), foraminifers (Tong & Shi 2000) or radiolarians (Racki 1999) recovered only in the late Spathian (Early Triassic) or in the Anisian (Middle Triassic), ca. 5 My after the Permian–Triassic boundary. This delay is interpreted as the consequence of persisting anoxic conditions (Wignall & Twitchett 2002) and unstable environmental conditions during the entire Early Triassic (Payne *et al.* 2004). However, several recent studies suggest a more complex scenario, with pulses of recovery interrupted by periods of additional extinctions. For example, conodonts (Orchard 2007; Goudemand *et al.* 2008) first underwent an important turnover at the Griesbachian–Dienerian boundary, followed by an explosive radiation in the early–middle Smithian, a dramatic extinction in the late Smithian, and another radiation during the early Spathian. Ammonoids also recovered very fast compared to other groups, reaching pre-extinction levels of diversity already during the Smithian (Fig. 1; Brayard *et al.* 2009). Hofmann *et al.* (2014) showed that benthic ecosystems started to recover already in the

Griesbachian, but this recovery has been interrupted by a return to harsh environmental conditions (e.g. anoxia, warm temperatures) during the Dienerian. Recovery of the benthos resumed during the Smithian. Based on palynological and carbon isotopes analysis, Hermann *et al.* (2011a,b, 2012a,b) and Schneebeli-Hermann *et al.* (2012, 2015) contradicted the idea of persistent widespread anoxia and showed that this anoxia was restricted to the middle–late Dienerian and late Smithian. Late Permian and Early Triassic ecological crises of terrestrial plants also immediately predate extinction crises of marine organisms, and the Dienerian diversity low is no exception as documented by Hochuli *et al.* (2016).

Many studies addressing the recovery are based on insufficiently resolved age controls. The construction of a detailed time-scale for the Early Triassic is the cornerstone on which any study addressing this biotic recovery must be based. Ovtcharova *et al.* (2006) and Galfetti *et al.* (2007) established a duration of ca. 4.5 Myr for the Early Triassic and showed that the four Early Triassic ages were of very uneven duration, the Spathian representing more than half of this interval (Fig. 2). Galfetti *et al.* (2007) obtained a maximal duration of ca. 1.4 ± 0.4 Myr for the Griesbachian–Dienerian time interval. No duration of the Dienerian alone is available, but it can be reasonably assumed that it is <1 Myr. A new generation of high-resolution U–Pb ages for the Permian–Triassic boundary (Burgess *et al.* 2014) and for the Early–Middle Triassic boundary (Ovtcharova *et al.* 2015) indicate a duration of 4.83 ± 0.19 Myr

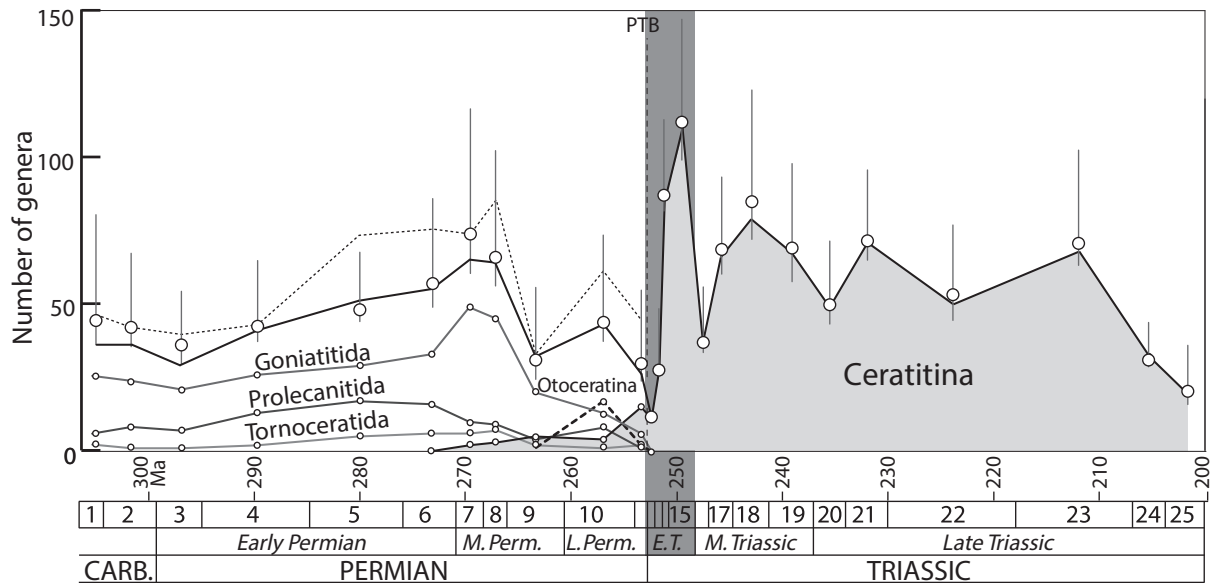


Fig. 1. Total generic richness (black bold line, all ammonoids; grey lines, major ammonoid groups) and mean Chao2 estimate of the overall generic richness with its 95% confidence interval (large circles with vertical bars). The Early Triassic is highlighted in dark grey. PTB, Permian–Triassic boundary; 1, Kasimovian; 2, Gzhelian; 3, Asselian; 4, Sakmarian; 5, Artinskian; 6, Kungurian; 7, Roadian; 8, Wordian; 9, Capitanian; 10, Wuchiapingian; unlabelled successive intervals, Changhsingian, Griesbachian, Dienerian, Smithian; 15, Spathian; 16, Early Anisian; 17, Middle Anisian; 18, Late Anisian; 19, Ladinian; 20, Early Carnian; 21, Late Carnian; 22, Early Norian; 23, Middle Norian; 24, Late Norian; 25, Rhaetian. Modified after Brayard *et al.* (2009).

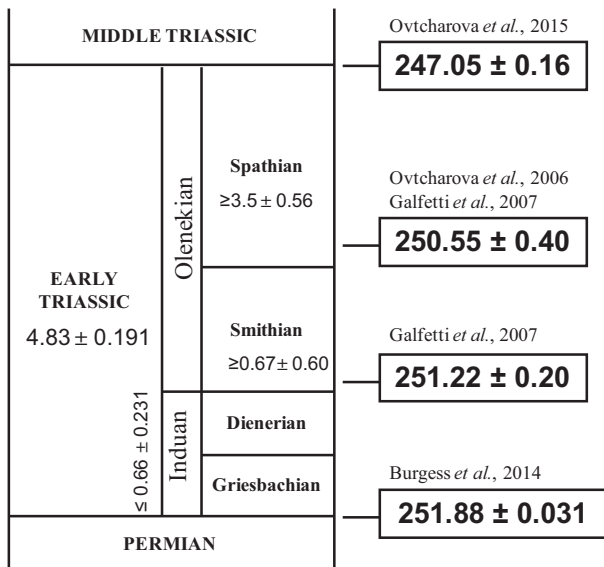


Fig. 2. Lower Triassic stage and substage subdivision (Ogg 2012) calibrated with recently published radiometric ages from South China.

for the Early Triassic. However, the respective duration of each of the four Lower Triassic substages may not be significantly changed because these new U-Pb ages are consistently younger than those of the previous generation.

Brayard & Bucher (2008) proposed a new detailed biostratigraphical scheme based on ammonoids for the Smithian of South China. Brühwiler *et al.* (2010a) constructed the most highly resolved biostratigraphical scheme for the Smithian based on ammonoids from the Northern Indian Margin. This work showed that ammonoids underwent an explosive radiation in the early Smithian, with constant high diversity associated with extremely high turnover rates throughout the middle Smithian and a major extinction in the late Smithian. This extinction could not be detected by Brayard *et al.* (2009) due to the coarser time-scale of this study. Conodonts also suffered from a drastic extinction in the late Smithian.

The stage subdivisions of the Lower Triassic are a subject of debate (Fig. 2). In the latest version of The Geologic Time Scale (Ogg 2012), the twofold subdivision of the Lower Triassic introduced by Kiparisova & Popov (1956), with the Induan and Olenekian, is endorsed. The four stages defined by Tozer (1965) are then considered as substages, the Induan being subdivided into Griesbachian and Dienerian, and the Olenekian into Smithian and Spathian. This twofold scheme is however strongly criticized (e.g. Shevyrev 2006), mainly as it does not reflect the end Smithian crisis, the most important extinction event known for both ammonoids and conodonts within the entire Triassic in every locality where this question has been addressed (e.g. Stanley

2009; for ammonoids: Brayard *et al.* 2006; Brühwiler *et al.* 2010a; Brayard & Bucher 2015; for conodonts: Orchard 2007; Chen *et al.* 2013; Komatsu *et al.* 2016). Moreover, having the Induan defined in the Tethyan realm and the Olenekian in the Boreal Realm makes the correlation of this stage boundary across such a broad palaeolatitudinal range an arduous task. Tozer (1965) provided a broad definition of the Dienerian–Smithian boundary (corresponding to the Induan–Olenekian boundary), explaining that it was probable that in Canada, the oldest known Smithian fauna may be younger than typical Smithian faunas from other areas. Krystyn *et al.* (2007a,b) proposed the Mud section (Spiti valley, India) as a GSSP candidate for this boundary. They based their definition of the boundary on the first occurrence of the conodont *Novispathodus waageni* (Sweet 1970) *sensu lato*. However, Brühwiler *et al.* (2010b) demonstrated the presence in the same section of ammonoid genera typical of the Smithian below the boundary as defined by Krystyn *et al.* (2007a,b) and thus proposed to use the first occurrence of *Flemingites bhargavai* Brühwiler *et al.* (2010b) as the index fossil for this boundary.

Tozer (1965, 1994) originally subdivided the Dienerian of Canada into two parts (lower and upper), each composed of one zone (the *Proptychites candidus* Zone and the *Vavilovites sverdrupi* Zone), and with the second one being further subdivided into three subzones. However, this zonation is based on scattered occurrences of the faunas, often without superpositional information (a fact which can be checked in the list of localities provided in Tozer 1994). Other zonations have been proposed for Northern Siberia (Dagys & Ermakova 1996) and Primorye, Russia (Shigeta & Zakharov 2009), but uncertainties in correlating these persist. Based on material from Nepal, a biozonation has been proposed by Waterhouse (1994, 1996) for the northern Gondwana margin. Unfortunately, this Nepalese material is poorly preserved and does not allow constructing a robust taxonomy (see Gaetani *et al.* 1995). Jenks *et al.* (2015) presented a review of the biostratigraphy of Triassic ammonoids and mentioned that Dienerian ammonoid faunas were still poorly known and in need of an extensive revision.

The Northern Indian Margin has long been recognized as a key area for the study of Early Triassic ammonoids and the establishment of the Early Triassic time-scale. During the Early Triassic, it was situated in southern Tethys, at a palaeolatitude of ca. 40°S (Fig. 3). The very first Dienerian ammonoids were discovered in the Salt Range by Andrew Fleming in the mid-19th century, and this material was described by de Koninck (1863). Waagen (1895)

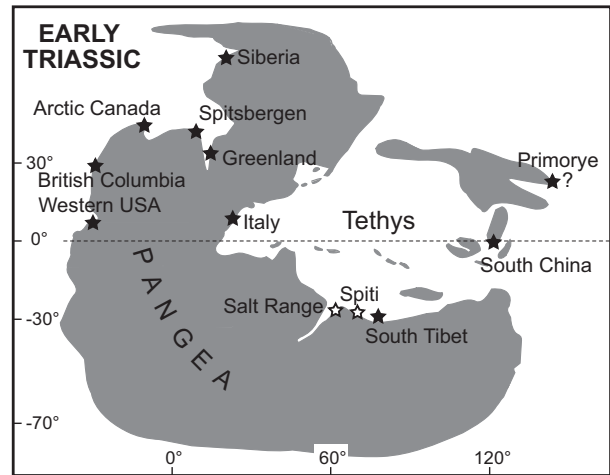


Fig. 3. Simplified palaeogeographical map of the Early Triassic with the palaeopositions of the studied localities (white stars) and of other localities mentioned in the text (black stars). Modified after Brayard *et al.* (2006).

conducted the most impressive and exhaustive study on Early Triassic ammonoids from the Salt Range. Diener (1897) and von Krafft & Diener (1909) published two monographs describing ammonoids from the Early Triassic of the Indian Himalayas, many of them from the Spiti Valley. The very first ammonoid biozonation of the Lower Triassic has been published by Mojsisovics *et al.* (1895) based on these two regions. They recognized only two zones in what we consider here as Dienerian, and this biozonation did not change in the absence of any subsequent detailed work on Dienerian ammonoids of the Salt Range and Spiti. For the Salt Range, Noetling (1905) and Spath (1934) added a few species and proposed slightly different classifications. Griesbachian ammonoids were first discovered by Schindewolf (1954) in the Salt Range. Kummel provided a detailed history of the stratigraphical and palaeontological investigations on the Permian and Triassic of the Salt Range (Kummel 1966; Kummel & Teichert 1966, 1970). He also mentioned that he collected numerous Dienerian ammonoids and that he intended to publish this material later on, a task he unfortunately never completed. Since Kummel's work, only two contributions on Early Triassic ammonoids from the Salt Range were published. The works by Guex (1978) and by the Pakistani-Japanese Research Group (PJRG 1985) only include scarce material of Griesbachian and Dienerian ages. Concerning ammonoids from the Indian Himalayas, only Bando (1981) described a few ammonoids from Kashmir, and Krystyn & Orchard (1996) and Krystyn *et al.* (2004, 2007a,b) gave some details concerning ammonoid biostratigraphy of Spiti, but without any description of ammonoids. A few poorly preserved

ammonoids from South Tibet were also described by Wang & He (1976), and Dienerian ammonoids from Nepal were described by Waterhouse (1996). Outside the Northern Indian Margin, well-preserved Dienerian ammonoid faunas have been studied from British Columbia and Arctic Canada (e.g. Tozer 1994), the Verkhoyansk basin (Siberia, e.g. Dagys & Ermakova 1996), Primorye (Russia, e.g. Shigeta & Zakharov 2009), South China (e.g. Brühwiler *et al.* 2008) and Nevada (Ware *et al.* 2011).

Present work

The two articles included in this volume re-investigate the taxonomy of Dienerian ammonoids from the Salt Range (Pakistan) and Spiti (India). The data presented in the two contributions form the basis of the biochronology and diversity study published by Ware *et al.* (2015).

From 2007 to 2010, the research group at the University of Zürich carried out intensive fieldwork in the Salt Range and in Spiti. Bedrock-controlled high-resolution sampling (i.e. sampling ammonoids bed-by-bed, with the drawing and measuring of each section) of several sections in these regions was performed to revise the Dienerian ammonoid taxonomy and build a new, highly resolved biostratigraphical scheme. Whenever permitted by the sample size, great care was taken to integrate ontogenetic changes and intraspecific variation within the definition of species, in contrast to the traditional typological approach. Hence, the number of resulting valid taxa is more conservative and more robust than that of previous work.

The first article of this volume mainly addresses Dienerian ammonoids from the Salt Range. As the Salt Range is the type locality of most Dienerian ammonoid taxa, it was the region where the most intensive fieldwork was done, and where the most abundant material was found. Hence, this article includes an in-depth revision of Dienerian ammonoid taxonomy, including emended diagnoses of families, genera and species whenever possible. It also includes the description of the few rare Griesbachian ammonoids found in this region. The second article addresses Dienerian ammonoids from Spiti (Himachal Pradesh, India) and their comparison with the Salt Range.

Definitions of stages and substages

In the present work, the stage and substage subdivision of the Lower Triassic follows the

recommendations of Ogg (2012), lowering the rank of the four Lower Triassic stages of Tozer (1965) to that of substage. The Induan stage is then subdivided into the Griesbachian and Dienerian substages, and the Olenekian into the Smithian and Spathian. There is however presently no consensus regarding the definitions of the substage boundaries relevant for the present work (the Griesbachian–Dienerian and Dienerian–Smithian boundaries).

The problem of the Dienerian–Smithian boundary was already briefly discussed. Here, the definition proposed by Brühwiler *et al.* (2010b) is adopted, the base of the Smithian being then defined by the first occurrence of *F. bhargavai* and its co-occurring species characterizing UA-Zone SM-1 (Brühwiler *et al.* 2010a). This zone has been recognized in every section described herein.

The Griesbachian–Dienerian boundary is problematic and less well documented. It was originally defined by Tozer (1965) with the first occurrence of ‘Meekoceratidae’ (i.e. Gyronitidae). In Spiti, Krystyn & Orchard (1996) placed this boundary within the Lower Limestone Member, considering the fauna from the upper part of this interval (their *Pleurogyronites planidorsatus* Zone) as typically Dienerian, based on the presence of abundant Gyronitidae, the absence of the typically Griesbachian *Ophiceras* and the occurrence of the conodont *Sweetospathodus kummeli* (Sweet 1970). In Spiti, this definition of the boundary coincides generally with a minor facies change, with the appearance of thin shale intervals and less massive, finer grained limestones than in the lower part of the Lower Limestone Member. This definition of the Griesbachian–Dienerian boundary was subsequently questioned by Krystyn *et al.* (2004), who considered these beds as late Griesbachian but proposed to use instead the Gangetian substage for the whole Lower Limestone Member. Krystyn *et al.* (2004) also reported some rare Gyronitidae (listed under the genus name ‘*Pleurogyronites*’) associated with typical Griesbachian *Ophiceras* in the bed just below the Griesbachian–Dienerian boundary as defined by Krystyn & Orchard (1996). The same ammonoid association is here documented in the Salt Range (Ware *et al.* 2018) where it is interpreted as condensation. However, both Krystyn & Orchard (1996) and Krystyn *et al.* (2004) reported exclusively Griesbachian conodonts in this bed, thus questioning the condensed nature of this association. The definition of the Griesbachian–Dienerian boundary is thus still problematic, and more expanded sections spanning this boundary are necessary to solve this question. Here, we decided to place the Griesbachian–Dienerian

boundary in agreement with the definition of Krystyn & Orchard (1996). This definition can easily be applied both in the Salt Range and in Spiti, the first Dienerian faunal association corresponding in both cases to the *Gyronites dubius* Regional Zone (equivalent of UA-Zone DI-1 of Ware *et al.* 2015).

Biochronology: the Unitary Association Method and terminology

Following the recommendations of Monnet *et al.* (2015), the construction of the biochronological scheme is here based on the Unitary Association Method of Guex (1991) and Guex *et al.* (2016). As already mentioned, the two papers presented in this volume constitute the base of the biozonation established by Ware *et al.* (2015). As the present work is only the first step in building this biozonation, we here present the construction of ‘Regional Zones’, which are then used to construct ‘Unitary Association Zones’ of Ware *et al.* (2015). Regional Zones correspond to ‘Unitary Association Zones’ built for only one basin, without addressing the lateral reproducibility of these zones outside of the studied basin. Regional Zones are customarily termed ‘beds’ by previous authors (e.g. Brayard & Bucher 2008; Brühwiler *et al.* 2012). Here, the term ‘Regional Zone’ is preferred to avoid any confusion with the term ‘beds’ as it was used in Spiti by previous authors to designate small lithological subdivisions of the different units within the Mikin Formation (e.g. the ‘*Otoceras*’ and ‘*Meekoceras*’ beds of von Krafft & Diener 1909; ‘*Gyronites*’ beds of Krystyn & Orchard 1996). The term ‘Local Maximal Horizon’ designates maximal associations of species as directly observed within each section.

In the two papers presented here, the list of characteristic species and pairs of species is given for each regional zone. A species is said to be characteristic if and only if its range is equal to the zone. A pair of species is said to be characteristic if and only if the overlapping part of their ranges is equal to the zone. Additionally, the number of specimens of each species within each zone is indicated in brackets. This latter information gives an idea of the robustness of the different species ranges. When a species is restricted to one regional zone but represented only by a few rare specimens, its relevance for correlations must be *a priori* taken with caution as its stratigraphical range is likely to be longer. On the other hand, a species represented by many specimens and restricted to one regional zone provides *a priori* more robust information.

Each regional zone presented here is named after the most abundant of the species whose range is strictly restricted to the corresponding zone. Formal ‘Unitary Association Zones’ for the Dienerian of the Northern Indian Margin were constructed by Ware *et al.* (2015), and their correlation with each regional zones described herein is systematically provided here.

References

- Bando, Y. 1981: Lower Triassic ammonoids from Guryul Ravine and the spur three kilometres north of Barus. In Nakazawa, K. & Kapoor, H.M. (eds): *The Upper Permian and Lower Triassic Faunas of Kashmir. Palaeontologia Indica*, Vol. 46, 135–178. Geological Survey of India, Calcutta (India).
- Brayard, A. & Bucher, H. 2008: Smithian (Early Triassic) ammonoid faunas from northwestern Guangxi (South China): taxonomy and biochronology. *Fossils and Strata* 55, 179 pp.
- Brayard, A. & Bucher, H. 2015: Permian–Triassic extinctions and rediversifications. In Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds): *Ammonoid Paleobiology: From Macroevolution to Paleogeography*, 465–473, 628 pp. Topics in Geobiology 44, Springer Verlag, Berlin and Heidelberg.
- Brayard, A., Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S. & Galfetti, T. 2006: The Early Triassic ammonoid recovery: paleoclimatic significance of diversity gradients. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239, 374–395.
- Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T. & Guex, J. 2009: Good genes and good luck: ammonoid diversity and the end-permian mass extinction. *Science* 325, 1118–1121.
- Brühwiler, T., Brayard, A., Bucher, H. & Guodun, K. 2008: Griesbachian and Dienerian (Early Triassic) ammonoid faunas from Northwestern Guangxi and Southern Guizhou (South China). *Palaeontology* 51, 1151–1180.
- Brühwiler, T., Bucher, H., Brayard, A. & Goudemand, N. 2010a: High-resolution biochronology and diversity dynamics of the Early Triassic ammonoid recovery: the Smithian faunas of the Northern Indian Margin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297, 491–501.
- Brühwiler, T., Ware, D., Bucher, H., Krystyn, L. & Goudemand, N. 2010b: New Early Triassic ammonoid faunas from the Dienerian/Smithian boundary beds at the Induan/Olenekian GSSP candidate at Mud (Spiti, Northern India). *Journal of Asian Earth Sciences* 39, 724–739.
- Brühwiler, T., Bucher, H., Ware, D., Schneebeli-Hermann, E., Hochuli, P.A., Roohi, G., Rehman, K. & Yaseen, A. 2012: Smithian (Early Triassic) ammonoids from the Salt Range, Pakistan. *Special Papers in Palaeontology* 88, 1–114.
- Burgess, S.D., Bowring, S. & Shen, S.-Z. 2014: High-precision timeline for Earth’s most severe extinction. *Proceedings of the National Academy of Sciences of the United States of America* 111, 3316–3321.
- Chen, Y., Twitchett, R.J., Jiang, H., Richoz, S., Lai, X., Yan, C., Sun, Y., Liu, X. & Wang, L. 2013: Size variation of conodonts during the Smithian–Spathian (Early Triassic) global warming event. *Geology* 41, 823–826.
- Dagys, A.S. & Ermakova, S. 1996: Induan (Triassic) ammonoids from North-Eastern Asia. *Revue de Paléobiologie* 15, 401–447.
- de Koninck, L.G. 1863: Description of some fossils from India, discovered by Dr. A. Fleming, of Edinburgh. *The Quarterly Journal of the Geological Society of London* 19, 1–19.
- Diener, C. 1897: Part I: the Cephalopoda of the lower trias. *Palaeontologia Indica, Series 15. Himalayan fossils* 2, 2, 1–181.
- Erwin, D.H. 1998: The end and the beginning: recoveries from mass extinctions. *Trends in Ecology & Evolution* 13, 344–349.

- Erwin, D.H. 2006: *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago*, 296 pp. Princeton University Press, Princeton (USA).
- Gaetani, M., Balini, M., Garzanti, E., Nicora, A., Tintori, A., Angiolini, L. & Sciunnach, D. 1995: Comments on Waterhouse, J.B., 1994. The Early and Middle Triassic ammonoid succession of the Himalayas in western and central Nepal. Part 1. Stratigraphy, classification and Early Scythian ammonoid systematics. *Palaeontographica*, Abt. A, 232(1-3): 1–83. *Albertiana* 15, 3–9.
- Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Brühwiler, T., Goudemand, N., Weissert, H., Hochuli, P., Cordey, F. & Guodun, K. 2007: Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. *Earth and Planetary Science Letters* 258, 593–604.
- Goudemand, N., Orchard, M., Bucher, H., Brayard, A., Brühwiler, T., Galfetti, T., Hochuli, P.A., Hermann, E. & Ware, D. 2008: Smithian-Spathian boundary: The biggest crisis in Triassic conodont history. *Abstracts with Program, Geological Society of America* 40, 505.
- Guex, J. 1978: Le Trias inférieur des Salt Ranges (Pakistan): problèmes biochronologiques. *Eclogae Geologiae Helvetica* 71, 105–141.
- Guex, J. 1991: *Biochronological Correlations*, 252 pp. Springer, Berlin.
- Guex, J., Galster, F. & Hammer, Ø. 2016: *Discrete Biochronological Time Scales*, 160 pp. Springer, Cham, Heidelberg, New York, Dordrecht, London.
- Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D. & Roohi, G. 2011a: Terrestrial ecosystems on North Gondwana following the end-Permian mass extinction. *Gondwana Research* 20, 630–637.
- Hermann, E., Hochuli, P.A., Méhay, S., Bucher, H., Brühwiler, T., Ware, D., Hautmann, M., Roohi, G., ur-Rehman, K. & Yaseen, A. 2011b: Organic matter and palaeoenvironmental signals during the Early Triassic biotic recovery: the Salt Range and Surghar Range records. *Sedimentary Geology* 234, 19–41.
- Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D., Weissert, H., Roohi, G., Yaseen, A. & ur-Rehman, K. 2012a: Climatic oscillations at the onset of the Mesozoic inferred from palynological records from the North Indian Margin. *Journal of the Geological Society, London* 169, 227–237.
- Hermann, E., Hochuli, P.A., Bucher, H. & Roohi, G. 2012b: Uppermost Permian to Middle Triassic palynology of the Salt Range and Surghar Range, Pakistan. *Review of Palaeobotany and Palynology* 169, 61–95.
- Hochuli, P.A., Sanson-Barbera, A., Schneebeil-Hermann, E. & Bucher, H. 2016: Severest crisis overlooked – worst disruption of terrestrial environments postdates the Permian-Triassic mass extinction. *Scientific Reports* 6, 28372. <https://doi.org/10.1038/srep28372>.
- Hofmann, R., Hautmann, M., Brayard, A., Nützel, A., Bylund, K.G., Jenks, J., Vennin, E., Olivier, N. & Bucher, H. 2014: Recovery of benthic marine communities from the end-Permian mass extinction at the low-latitudes of Eastern Panthalassa. *Palaeontology* 57, 547–589.
- Jenks, J.F., Monnet, C., Balini, M., Brayard, A. & Meier, M. 2015: Biostratigraphy of Triassic ammonoids. In Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds): *Ammonoid Paleobiology: From Macroevolution to Paleogeography*, 277–298, 628 pp. Topics in Geobiology 44, Springer Verlag, Berlin and Heidelberg.
- Kiparisova, L.D. & Popov, Y.N. 1956: Subdivision of the lower series of the Triassic system into stages. *Doklady Academy Sciences U.S.S.R.* 109, 842–845 [In Russian].
- Komatsu, T., Takashima, R., Shigeta, Y., Maekawa, T., Tran, H.D., Cong, T.D., Sakata, S., Dinh, H.D. & Takahashi, O. 2016: Carbon isotopic excursions and detailed ammonoid and conodont biostratigraphies around Smithian-Spathian boundary in the Bac Thuy Formation, Vietnam. *Palaeogeography, Palaeoclimatology, Palaeoecology* 454, 65–74.
- Krafft, A. von & Diener, C. 1909: Lower Triassic Cephalopoda from Spiti, Malla, Johar, and Byans. *Palaeontologia Indica* 6, 1–186.
- Krystyn, L. & Orchard, M.J. 1996: Lowermost Triassic ammonoid and conodont biostratigraphy of Spiti, India. *Albertiana* 17, 10–21.
- Krystyn, L., Balini, M. & Nicora, A. 2004: Lower and Middle Triassic stage and substage boundaries in Spiti. *Albertiana* 30, 40–53.
- Krystyn, L., Bhargava, O.N. & Richoz, S. 2007a: A candidate GSSP for the base of the Olenekian Stage: Mud at Pin Valley; district Lahul & Spiti, Himachal Pradesh (Western Himalaya), India. *Albertiana* 35, 5–29.
- Krystyn, L., Richoz, S. & Bhargava, O.N. 2007b: The Induan-Olenekian Boundary (IOB) in Mud – an update of the candidate GSSP section M04. *Albertiana* 36, 33–45.
- Kummel, B. 1966: The Lower Triassic formations of the Salt Range and Trans-Indus Ranges, West Pakistan. *Bulletin of the Museum of Comparative Zoology* 134, 361–429.
- Kummel, B. & Teichert, C. 1966: Relations between the Permian and Triassic formations in the Salt Range and Trans-Indus ranges, West Pakistan. *Neues Jahrbuch für Geologie Paläontologie. Abhandlungen* 125, 297–333.
- Kummel, B. & Teichert, C. 1970: Stratigraphy and paleontology of the Permian-Triassic boundary beds, Salt Range and Trans-Indus Ranges, West Pakistan. In Kummel, B. & Teichert, C. (eds): *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*, 1–110. Special Publication of the Department of Geology, Vol. 4, University of Kansas, Lawrence.
- Mojsisovics, E.V., Waagen, W. & Diener, C. 1895: Entwurf einer Gliederung der pelagischen Sedimente des Trias-Systems. *Sitzungsberichte der Akademie der Wissenschaften in Wien (I)* 104, 1271–1302.
- Monnet, C., Brayard, A. & Bucher, H. 2015: Ammonoids and quantitative biochronology – a unitary association perspective. In Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds): *Ammonoid Paleobiology: From Macroevolution to Paleogeography*, 277–298, 628 pp. Topics in Geobiology 44. Springer Verlag, Berlin and Heidelberg.
- Noetling, F. 1905: Die asiatische Trias. In Frech, F. (ed.): *Lethaea Geognostica, Das Mesozoicum* 107–221, 623 pp. Verlag der E. Schweizerbart'schen Verlagsbuchhandlung (E. Nägele), Stuttgart, Germany.
- Ogg, J.G. 2012: Triassic. In Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (eds): *The Geologic Time Scale 2012*, 681–730, 1144 pp. Elsevier, Amsterdam.
- Orchard, M.J. 2007: Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252, 93–117.
- Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A. & Guex, J. 2006: New Early to Middle Triassic U-Pb ages from South China: calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. *Earth and Planetary Science Letters* 243, 463–475.
- Ovtcharova, M., Goudemand, N., Hammer, Ø., Guodun, K., Cordey, F., Galfetti, T., Schaltegger, U. & Bucher, H. 2015: Developing a strategy for accurate definition of a geological boundary through radio-isotopic and biochronological dating: the Early-Middle Triassic boundary (South China). *Earth Science Reviews* 146, 65–76.
- Pakistani-Japanese Research Group 1985: Permian and Triassic systems in the Salt Range and Surghar Range, Pakistan. In Nakazawa, K. & Dickins, J.M. (eds): *The Tethys, Her Paleogeography and Paleobiogeography from Paleozoic to Mesozoic*, 221–312, 317 pp. Tokai University Press, Tokyo.
- Payne, J.L., Lehrmann, D.J., Wei, J.Y., Orchard, M.J., Schrag, D.P. & Knoll, A.H. 2004: Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* 305, 506–509.
- Racki, G. 1999: Silica-secreting biota and mass extinctions: survival patterns and processes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 154, 107–132.

- Raup, D.M. & Sepkoski, J.J. 1982: Mass extinctions in the marine fossil record. *Science* 215, 1501–1503.
- Schindewolf, O.H. 1954: Über die Faunenwende vom Paläozoikum zum Mesozoikum. *Zeitschrift der Deutschen Geologischen Gesellschaft* 105, 153–182.
- Schneebeli-Hermann, E., Kürschner, W.M., Hochuli, P.A., Bucher, H., Ware, D., Goudehand, N. & Roohi, G. 2012: Palynofacies analysis of the Permian–Triassic transition in the Amb section (Salt Range, Pakistan): implications for the anoxia on the South Tethyan Margin. *Journal of Asian Earth Sciences* 60, 225–234.
- Schneebeli-Hermann, E., Kürschner, W.M., Bomfleur, B., Hochuli, P.A., Ware, D., Roohi, G. & Bucher, H. 2015: Vegetation history across the Permian–Triassic boundary in Pakistan (Amb section, Salt Range). *Gondwana Research* 27, 911–924.
- Sepkoski, J.J. 1984: A kinetic-model of Phanerozoic Taxonomic Diversity. 3. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Shevryev, A.A. 2006: Triassic biochronology: state of the art and main problems. *Stratigraphy and Geological Correlation* 14, 629–641.
- Shigeta, S. & Zakharov, Y.D. 2009: Cephalopods. In Shigeta, Y., Zakharov, Y.D., Maeda, H. & Popov, A.M. (eds): *The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia*, 44–140, 218 pp. National Museum of Nature and Science Monographs 38, Tokyo.
- Spath, L.F. 1934: *Catalogue of the Fossil Cephalopoda in the British Museum (Natural History), Part IV: The Ammonoidea of the Trias*, 521 pp. The Trustees of the British Museum, London.
- Stanley, G.D. 2003: The evolution of modern corals and their early history. *Earth-Science Reviews* 60, 195–225.
- Stanley, S.M. 2009: Evidence from ammonoids and conodonts for multiple Early Triassic mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 106, 15264–15267.
- Sweet, W.C. 1970: Uppermost Permian and Lower Triassic Conodonts of the Salt Range and Trans-Indus Ranges, West Pakistan. In Kummel, B. & Teichert, C. (eds): *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*, 207–275. Special Publication of the Department of Geology, Vol. 4, University of Kansas, Lawrence.
- Tong, J. & Shi, G.R. 2000: Evolution of the Permian and Triassic foraminifera in south China. In Yin, H., Dickins, J.M., Shi, G.R. & Tong, J. (eds): *Permian-Triassic Evolution of Tethys and Western Circum-Pacific. Developments in Palaeontology and Stratigraphy*, 291–307, 392 pp. Elsevier, Amsterdam.
- Tozer, E.T. 1965: Lower Triassic stages and Ammonoid zones of Arctic Canada. *Paper of the Geological Survey of Canada* 65-12, 14 pp.
- Tozer, E.T. 1994: Canadian Triassic ammonoid faunas. *Bulletin of the Geological Survey of Canada* 467, 1–663.
- Waagen, W. 1895: Salt Ranges fossils. vol. 2: fossils from the Ceratites formation – Part I – Pisces, Ammonoidea. *Palaeontologia Indica* 13, 1–323.
- Wang, Y.G. & He, G.X. 1976: Triassic ammonoids from the Mount Jolmo Lungma region. In Xizang scientific expedition team of Chinese Academy of Science (ed.): *A Report of Scientific Expedition in the Mount Jolmo Lungma region (1966–1968)*, 223–502. Palaeontology, fascicule 3. Science Press, Beijing [In Chinese].
- Ware, D., Jenks, J.F., Hautmann, M. & Bucher, H. 2011: Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and palaeoceanography. *Swiss Journal of Geoscience* 104, 161–181.
- Ware, D., Bucher, H., Brayard, A., Schneebeli-Hermann, E. & Brühwiler, T. 2015: High-resolution biochronology and diversity dynamics of the Early Triassic ammonoid recovery: the Dienerian faunas of the Northern Indian Margin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 440, 363–373.
- Ware, D., Bucher, H., Brühwiler, T., Schneebeli-Hermann, E., Hochuli, P.A., Roohi, G., Rehman, K. & Yaseen, A. 2018: Griesbachian and Dienerian (Early Triassic) ammonoids from the Salt Range, Pakistan. *Fossil and Strata* 63, 13–175.
- Waterhouse, J.B. 1994: The Early and Middle Triassic ammonoid succession of the Himalayas in western and central Nepal. Part 1. Stratigraphy, classification and Early Scythian ammonoid systematics. *Palaeontographica, Abteilung A* 232, 1–83.
- Waterhouse, J.B. 1996: The Early and Middle Triassic ammonoid succession of the Himalayas in western and central Nepal. Part 2. Systematic studies of the Early Middle Scythian. *Palaeontographica Abteilung A* 241, 27–100.
- Wignall, P.B. & Twitchett, R.J. 2002: Extent, duration, and nature of the Permian–Triassic superanoxic event. *Geological Society of America, Special Paper* 356, 395–413.

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