

FOSSILS AND STRATA

*An international monograph
series of palaeontology and
stratigraphy*

Number 63 • December 2018



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

WILEY

Dienerian (Early Triassic) ammonoids from
the Northern Indian Margin

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

Acknowledgement

Financial support for the publication of this issue of
Fossils and Strata was provided by the Lethaia Foundation

Contents

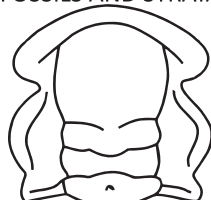
Present work	6
Definitions of stages and substages.....	6
Biochronology: the Unitary Association Method and terminology.....	7
References	7

Foreword

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

DAVID WARE AND HUGO BUCHER

FOSSILS AND STRATA



THE LETHAIA FOUNDATION

It has been estimated that about 90% of all marine species disappeared during the end-Permian mass extinction (Raupe & 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 Schneebeil-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

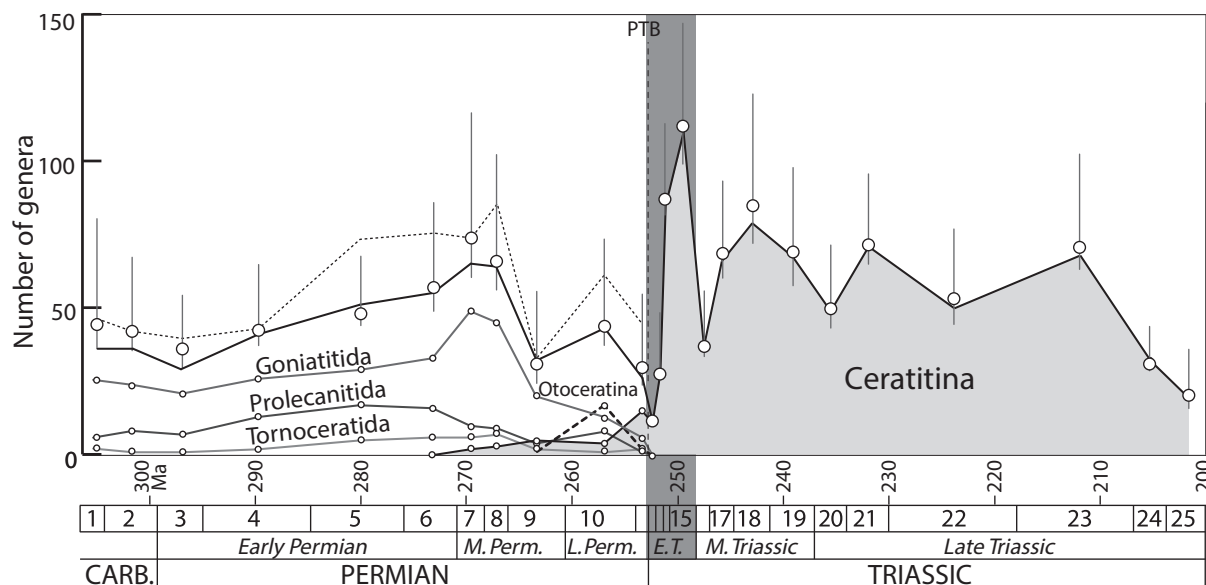


Fig. 1. Total generic richness (black bold line, all ammonoids; grey lines, major ammonoid groups) and mean Chao2 estimate of the overall generic richness with its 95% confidence interval (large circles with vertical bars). The Early Triassic is highlighted in dark grey. PTB, Permian–Triassic boundary; 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).

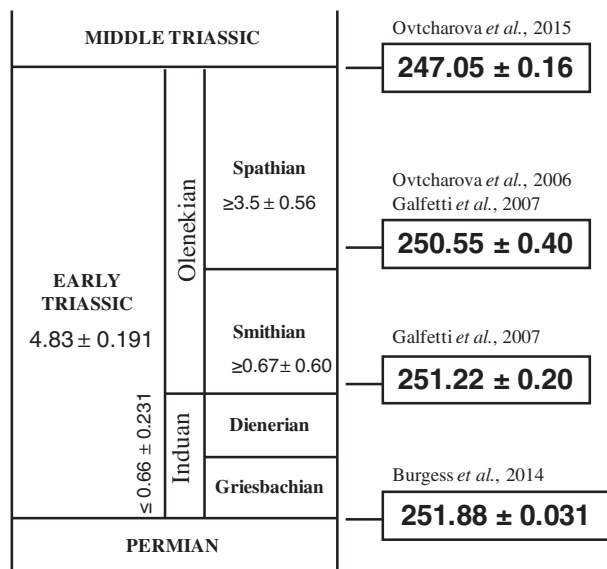


Fig. 2. Lower Triassic stage and substage subdivision (Ogg 2012) calibrated with recently published radiometric ages from South China.

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)

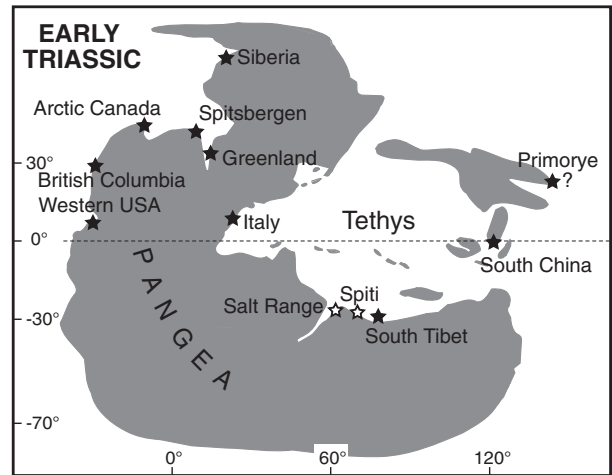


Fig. 3. Simplified palaeogeographical map of the Early Triassic with the palaeopositions of the studied localities (white stars) and of other localities mentioned in the text (black stars). Modified after Brayard *et al.* (2006).

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. & Dickinson, 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., Goudemand, 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.

Griesbachian and Dienerian (Early Triassic) ammonoids from the Salt Range, Pakistan

by

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

Acknowledgements

Financial support for the publication of this issue of
Fossils and Strata was provided by the Lethaia Foundation

Contents

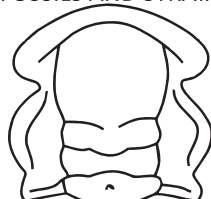
Introduction	13
Geological framework	14
Stratigraphy	14
Lithology and ammonoid preservation	14
Present work	16
Biostratigraphy	19
General subdivisions	19
Griesbachian ammonoid faunas	19
<i>Hypophiceras</i> cf. <i>H. gracile</i> Regional Zone	20
<i>Ophiceras connectens</i> Regional Zone	21
<i>Ophiceras sakuntala</i> Regional Zone	21
Early Dienerian ammonoid faunas	21
<i>Gyronites dubius</i> Regional Zone	23
<i>Gyronites plicosus</i> Regional Zone	23
<i>Gyronites frequens</i> Regional Zone	24
Middle Dienerian ammonoid faunas	25
<i>Ambites atavus</i> Regional Zone	27
<i>Ambites radiatus</i> Regional Zone	28
<i>Ambites discus</i> Regional Zone	28
<i>Ambites superior</i> Regional Zone	29
<i>Ambites lilangensis</i> Regional Zone	29
Late Dienerian ammonoid faunas	29
<i>Vavilovites</i> cf. <i>V. sverdrupi</i> Regional Zone	30
<i>Kingites davidsonianus</i> Regional Zone	30
<i>Koninckites vetustus</i> Regional Zone	30
<i>Awanites awani</i> Regional Zone	31
Conclusion	31
Systematic palaeontology by D. Ware and H. Bucher	31
Classification	31
The population approach: intraspecific variability and convergences	31
Suture lines	32
Ontogeny and growth allometry	33
Systematic descriptions	34
Superfamily Xenodiscaceae Frech, 1902	34
Family Xenodiscidae Frech, 1902	34
Genus <i>Hypophiceras</i> Trümpy, 1969	34
<i>Hypophiceras</i> aff. <i>H. gracile</i> (Spath, 1930)	34
Superfamily Meekocerataceae Waagen, 1895	36
Family Ophiceratidae Arthaber, 1911	36
Genus <i>Ophiceras</i> Griesbach, 1880	36
<i>Ophiceras connectens</i> Schindewolf, 1954	36
<i>Ophiceras sakuntala</i> Diener, 1897	36
Genus <i>Kyoktites</i> n. gen.	37
<i>Kyoktites hebeiseni</i> n. sp.	37
<i>Kyoktites</i> cf. <i>H. hebeiseni</i> n. sp.	37
Genus <i>Ghazalaites</i> n. gen.	38
<i>Ghazalaites roohii</i> n. sp.	38
Ophiceratidae? n. gen. A n. sp. A	39
Ophiceratidae? gen. et sp. indet.	39
Family Gyronitidae Waagen, 1895	40
Genus <i>Gyronites</i> Waagen, 1895	40
<i>Gyronites frequens</i> Waagen, 1895	41
<i>Gyronites dubius</i> (von Krafft, 1909)	44
<i>Gyronites rigidus</i> (Diener, 1897)	45
<i>Gyronites plicosus</i> Waagen, 1895	46
<i>Gyronites sitala</i> (Diener, 1897)	48
<i>Gyronites schwanderi</i> n. sp.	48
Genus <i>Ambites</i> Waagen, 1895	49
<i>Ambites discus</i> Waagen, 1895	51
<i>Ambites atavus</i> (Waagen, 1895)	53
<i>Ambites tenuis</i> n. sp.	55
<i>Ambites radiatus</i> (Brühwiler, Brayard, Bucher & Guodun, 2008)	56
<i>Ambites bojeseni</i> n. sp.	57
<i>Ambites subradiatus</i> n. sp.	58
<i>Ambites?</i> sp. indet.	59

<i>Ambites superior</i> (Waagen, 1895)	60
<i>Ambites lilangensis</i> (von Krafft, 1909)	62
<i>Ambites bjerageri</i> n. sp.	63
<i>Ambites</i> cf. <i>A. impressus</i> (Waagen, 1895)	64
Family Paranoritidae Spath, 1930	65
Genus <i>Vavilovites</i> Tozer, 1971	66
<i>Vavilovites</i> cf. <i>V. sverdrupi</i> (Tozer, 1963)	66
Genus <i>Koninckites</i> Waagen, 1895	67
<i>Koninckites vetustus</i> Waagen, 1895	67
<i>Koninckites khoorensis</i> (Waagen, 1895)	69
Genus <i>Radioceras</i> Waterhouse, 1996	74
<i>Radioceras truncatum</i> (Spath, 1934)	74
Genus <i>Pashtunites</i> n. gen.	76
<i>Pashtunites krafftii</i> (Spath, 1934)	76
Genus <i>Awanites</i> n. gen.	77
<i>Awanites awani</i> n. gen. et n. sp.	78
Genus <i>Koiloceras</i> Brühwiler & Bucher, 2012	78
<i>Koiloceras sahibi</i> n. sp.	79
Family Flemingitidae Hyatt, 1900	80
Genus <i>Xenodiscoides</i> Spath, 1930	80
<i>Xenodiscoides?</i> sp. indet.	80
Genus <i>Shamaraites</i> Shigeta & Zakharov, 2009	80
<i>Shamaraites?</i> sp. indet.	80
Family Proptychitidae Waagen, 1895	80
Genus <i>Bukkenites</i> Tozer, 1994	81
<i>Bukkenites sakesarensis</i> n. sp.	81
Genus <i>Proptychites</i> Waagen, 1895	83
<i>Proptychites lawrencianus</i> (de Koninck, 1863) <i>sensu</i> Waagen, 1895	83
<i>Proptychites oldhamianus</i> Waagen, 1895	85
<i>Proptychites wargalensis</i> n. sp.	85
<i>Proptychites ammonoides</i> Waagen, 1895	86
<i>Proptychites</i> cf. <i>P. pagei</i> Ware, Jenks, Hautmann & Bucher, 2011	88
Family Mullericeratidae Ware, Jenks, Hautmann & Bucher, 2011	88
Genus <i>Mullericeras</i> Ware, Jenks, Hautmann & Bucher, 2011	88
<i>Mullericeras spitiense</i> (von Krafft, 1909)	89
<i>Mullericeras shigetai</i> n. sp.	90
<i>Mullericeras indusense</i> n. sp.	92
<i>Mullericeras niazii</i> n. sp.	92
Genus <i>Ussuridiscus</i> Shigeta & Zakharov, 2009	93
<i>Ussuridiscus varaha</i> (Diener, 1895)	94
<i>Ussuridiscus ensanus</i> (von Krafft, 1909)	95
<i>Ussuridiscus ventriosus</i> n. sp.	96
<i>Ussuridiscus ornatus</i> n. sp.	97
<i>Ussuridiscus?</i> sp. indet.	98
Family incertae sedis	98
Genus <i>Kingites</i> Waagen, 1895	98
<i>Kingites davidsonianus</i> (de Koninck, 1863)	99
<i>Kingites korni</i> Brühwiler, Ware, Bucher, Krystyn & Goudemand, 2010a	100
Superfamily Sagecerataceae Hyatt, 1884	101
Family Hedenstroemiidae Hyatt, 1884	101
Genus <i>Clypites</i> Waagen, 1895	101
<i>Clypites typicus</i> Waagen, 1895	101
Genus <i>Pseudosageceras</i> Diener, 1895	103
<i>Pseudosageceras simplelobatum</i> n. sp.	103
Superfamily incertae sedis	105
Family incertae sedis	105
Genus <i>Subacerites</i> n. gen.	105
<i>Subacerites friski</i> n. sp.	105
Gen. et sp. indet.	106
Acknowledgements	106
References	106
Plates 1 to 33	110

Griesbachian and Dienerian (Early Triassic) ammonoids from the Salt Range, Pakistan

DAVID WARE, HUGO BUCHER, THOMAS BRÜHWILER, ELKE SCHNEEBELI-HERMANN, PETER A. HOCHULI,[†] GHAZALA ROOHI, KHALIL UR-REHMAN AND AMIR YASEEN

FOSSILS AND STRATA



THE LETHAIA FOUNDATION

Ware, D., Bucher, H., Brühwiler, T., Schneebeli-Hermann, E., Hochuli, P.A., Roohi, G., Ur-Rehman, K. & Yaseen, A. 2018: Griesbachian and Dienerian (Early Triassic) ammonoids from the Salt Range, Pakistan. *Fossils and Strata*, No 63, pp. 13–175. doi: 10.1111/let.12273

Intensive and bedrock controlled sampling of four areas (Nammal Nala, Chiddru, Amb and Wargal) in the Salt Range yielded abundant well-preserved Griesbachian and Dienerian (Early Triassic) ammonoids. This material allows establishing a new, high-resolution biostratigraphical frame and an extensive revision of the taxonomy. The Griesbachian is represented by (in ascending order) the *Hypophiceras* cf. *H. gracile* Regional Zone, the *Ophiceras connectens* Regional Zone and the *Ophiceras sakuntala* Regional Zone. The Dienerian comprises 12 distinct regional zones leading to a three-fold subdivision into lower, middle and upper Dienerian. The lower Dienerian, based on the occurrence of the genus *Gyronites*, can be divided into the *Gyronites dubius* Regional Zone, the *Gyronites plicatus* Regional Zone and the *Gyronites frequens* Regional Zone, in ascending order. The middle Dienerian, based on the occurrence of the genus *Ambites*, can be divided into five zones: the *Ambites atavus* Regional Zone, the *Ambites radiatus* Regional Zone, the *Ambites discus* Regional Zone, the *Ambites superior* Regional Zone and the *Ambites lilangensis* Regional Zone. The upper Dienerian, whose base is defined by the earliest representatives of *Paranoritidae*, can be divided into four zones: the *Vavilovites* cf. *V. sverdrupi* Regional Zone, the *Kingites davidsonianus* Regional Zone, the *Koninckites vetustus* Regional Zone and the *Awanites awani* Regional Zone. Correlations with basins outside the Northern Indian Margin are difficult because of the scarcity of such highly resolved studies on Dienerian ammonoids. Emended diagnoses and detailed synonymy lists are provided for most previously known taxa. In addition, five new genera (*Kyoktites*, *Ghazalaites*, *Pashtunites*, *Awanites* and *Subacerites*) and 18 new species (*Kyoktites hebeiseni*, *Ghazalaites roohii*, *Gyronites schwanderi*, *Ambites tenuis*, *Ambites bojeseni*, *Ambites subradiatus*, *Ambites bjerageri*, *Awanites awani*, *Koiloceras sahibi*, *Bukkenites sakesarensis*, *Proptychites wargalensis*, *Mullericeras shigetai*, *Mullericeras indusense*, *Mullericeras niazii*, *Ussuridiscus ventriosus*, *Ussuridiscus ornatus*, *Pseudosagoceras simplelobatum* and *Subacerites friski*) are described. □ *Ammonoidea*, *biostratigraphy*, *Dienerian*, *Early Triassic*, *Salt Range*, *Pakistan*.

David Ware [david.ware@mfn-berlin.de], Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43 10115 Berlin, Germany; Hugo Bucher [hugo.fr.bucher@pim.uzh.ch], Thomas Brühwiler [bruehwiler@pim.uzh.ch], Elke Schneebeli-Hermann [elke.schneebeli@pim.uzh.ch] and Peter A. Hochuli [peter.hochuli@pim.uzh.ch], Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Strasse 4 CH-8006 Zürich, Switzerland; Ghazala Roohi [roohighazala@yahoo.com], Khalil Ur-Rehman [reman_geol@yahoo.com] and Amir Yaseen [geologistgeologist@yahoo.com], Earth Science Division, Pakistan Museum of Natural History, Garden Avenue Shakarparian, Islamabad 44000, Pakistan; manuscript received on 27/10/2015; manuscript accepted on 11/08/2017.

Introduction

The biotic recovery following the end-Permian mass extinction is an intensively studied topic, for which high accuracy and high precision time control is of paramount importance. Nekto-pelagic clades such as ammonoids and conodonts recovered very quickly compared to other marine clades (e.g. Brayard *et al.* 2006, 2009; Orchard 2007) and play the leading roles in dating of Lower Triassic marine sedimentary rocks. However, many studies addressing the recovery are based on insufficiently resolved palaeontological age

controls. This is particularly the case for the Dienerian, where ammonoids and biochronology are still poorly understood (Jenks *et al.* 2015). A review of the current knowledge of Griesbachian and Dienerian ammonoids from the Salt Range is given in the foreword of this volume (Ware & Bucher 2018) to which the reader is referred. From 2007 to 2010, our research group carried out intensive field work in the Salt Range and the Surghar Range. Palynological and carbon isotope records have been recently published by Hermann *et al.* (2011a,b, 2012a,b) and Schneebeli-Hermann *et al.* (2012), oxygen isotopes from biogenic

phosphates by Romano *et al.* (2013), Smithian ammonoids by Brühwiler *et al.* (2012) and bivalves of Smithian and Spathian ages by Wasmer *et al.* (2012).

The present work focuses on Griesbachian and Dienerian ammonoids from four different areas in the Salt Range. It is based on abundant and well-preserved material sampled bed by bed. This new material provides the basis for a comprehensive revision of the taxonomy and biostratigraphy of Griesbachian and Dienerian ammonoids in the Salt Range, where all relevant sections are found. Because of the incomparable quality of the Dienerian ammonoid record of the Salt Range, this taxonomic and biostratigraphical re-investigation is an essential contribution to the Lower Triassic ammonoid zonation of the Northern Indian Margin and to the understanding of the Early Triassic biotic recovery.

Geological framework

The Salt Range constitutes a long and narrow mountain range, approximately 150 km SSW of Islamabad, Pakistan (Fig. 1B,C). The southern limit of the Salt Range defines the Himalayan main frontal thrust, which exposes a northern Gondwanan rift margin succession ranging from the Cambrian to the Cenozoic. It typically consists of a stack of tectonic slices with a south vergence, thus repeatedly exposing Triassic rocks of the Mianwali, Tredian and Kingriali formations (Gee 1980–1981). During the Early Triassic, the Salt Range was situated in the southern Tethys on the northern Gondwana margin, at a palaeolatitude of ca. 30 °S (Fig. 1A).

Stratigraphy

In the Salt Range, Lower Triassic sedimentary rocks are referred to the Mianwali Formation (Kummel & Teichert 1966). This 120 m thick formation is composed of limestone and siliciclastic sedimentary rocks. It unconformably rests on the Changhsingian (Upper Permian) Chiddru Formation. In the eastern part of the Salt Range, the Mianwali Formation is truncated by post-Cretaceous erosion and directly capped by Paleocene marine sedimentary rocks. In the western part, it is overlain by the Middle Triassic Tredian Formation.

The Griesbachian and Dienerian are represented by three units of the Mianwali Fm: the Kathwai Member (which is further subdivided into a dolomitic unit and a limestone unit), the Lower Ceratite Limestone and the lower part of the Ceratite Marls. The thickness of each of these units is highly variable throughout the Salt Range. Their boundaries are

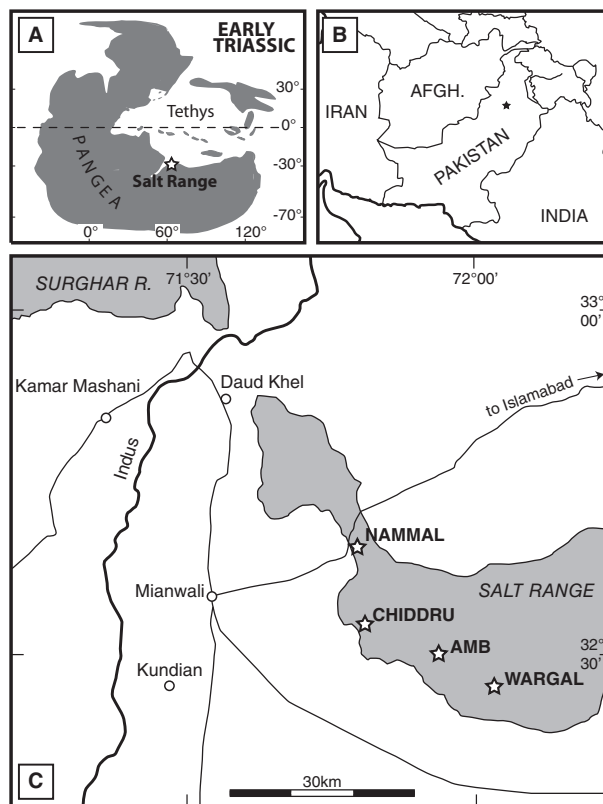


Fig. 1. A. Palaeogeographical map of the Early Triassic with the palaeoposition of the Salt Range (modified from Brayard *et al.* 2006). B. Map of Pakistan with position of the studied area (black star). C. Location map of sampled sections in the Salt Range (modified after Brühwiler *et al.* 2012).

here demonstrated to be diachronous across the different tectonic slices, thus suggesting that these thrusts might correspond to inverted Triassic normal faults. As a typical example among many others, Brühwiler *et al.* (2012) documented that the Dienerian–Smithian boundary coincides with the Lower Ceratite Limestone–Ceratite Marls boundary in Chiddru, whereas it is found within the lower third (ca. 7 m above the base) of the Ceratite Marls in Nammal. Most previous works (e.g. Mojsisovics *et al.* 1895; Spath 1934; Guex 1978; PJRG 1985) did not recognize this diachronism, and assumed that lithological boundaries are synchronous throughout the Salt Range and the Surghar Range.

Lithology and ammonoid preservation

Despite differences in thicknesses and ages in the different sections, the three units studied here show remarkably uniform facies throughout the Salt Range. Detailed lithological descriptions of these units were already published in Kummel & Teichert (1970) and in Hermann *et al.* (2011b). Therefore, only a summary of the lithological succession is given here, along with additional observations

pertaining to the taphonomy and preservation of ammonoids.

Kathwai Member, dolomitic unit. – The dolomitic unit of the Kathwai Member (2–3.5 m thick) consists of a few massive beds of sandy dolomite. Fossils are very rare in this unit and are usually only represented by broken and unidentifiable shells. Only one ammonite (*Hypophiceras* aff. *H. gracile*) was found in this unit, in Nammal Nala. It occurred in a small lens rich in bivalves within a massive dolomitic bed.

Kathwai Member, limestone unit. – The limestone unit of the Kathwai Member (0.5–5 m thick) consists mostly of calcareous glauconitic sandstone beds alternating with thin beds of shale. Although fossils are not rare, they are generally very poorly preserved. Some beds contain accumulations of rhynchonellid brachiopods and echinid spines. Ammonites are rare, and usually represented only by extremely poorly preserved specimens. Identification, even at the genus level, is impossible. Therefore, they have not been included in the present study. The only exception is in Chiddru, where few, better preserved specimens assigned to *Ophiceras connectens*, were found at the base of this unit.

Lower Ceratite Limestone. – The Lower Ceratite Limestone (1–3 m thick) consists of thin, hard, coarse-grained coquinooid limestone beds. Glauconite and iron oxides are locally very abundant. Although very frequent, the fossils are mostly fragmented, and generally very difficult to prepare mechanically. The coarse grained sparitic matrix often crosses the shell boundaries. Ammonoids are very unevenly distributed, often imbricated and accumulated in lenses within the different layers of the Lower Ceratite Limestone. The body chambers of small specimens are generally broken, while large specimens (Proptychitidae) are represented by incomplete phragmocones, the upper side of outer whorls being corroded or eroded (see Pl. 21, figs 38, 39 for a good example). Phragmocones are often completely recrystallized, hence suture lines are only occasionally preserved. Considering the abundance of glauconite and the facies, the Lower Ceratite Limestone may be affected by condensation. However, in the absence of similar studies in sections where the Lower Ceratite Limestone is expanded, palaeontological condensation cannot be demonstrated. Only the second bed of the Lower Ceratite Limestone in Nammal is recognized as condensed. It contains both *Ophiceras sakuntala* and *Gyronites dubius*, an association of genera which has not been documented in any other section. Moreover, the species *Gyronites dubius* has also been

found in Amb, without any co-occurring representative of *Ophiceras*. In Nammal Nala, the two uppermost beds of the Lower Ceratite Limestone are different, being composed of fine grained limestone. The penultimate bed is only 1–2 cm thick, locally absent, and contains numerous and nearly complete ammonoids, some bivalve fragments and abundant fish scales and teeth. Ammonoids are accumulated at the top of the bed, often encrusted by worm tubes and only partially covered by a very thin limestone layer (Pl. 3, figs 1, 2). The last bed is ca. 7 cm thick and composed of fine-grained limestone with locally abundant, nearly complete but strongly recrystallized ammonoids. Its surface is encrusted by centimetric iron oxide concretions, indicating a stop in sedimentation.

Ceratite Marls. – The Ceratite Marls are composed of a ca. 30 m thick succession of marls with intercalated limestone and sandstone beds. Limestone beds are abundant at the base, while sandstone beds become gradually more abundant in the upper half of the Ceratite Marls. In the lower third, ammonoids are very abundant and well preserved in numerous limestone beds and lenses. The thickness of these beds is variable. Many of these beds show imbrication and size sorting of shells, indicative of bottom currents. A typical example of this facies is shown in Figure 2, with small imbricated, both complete and broken ammonoids accumulated at the base of the bed. The body chambers are generally partially broken. Large specimens (all belonging to Proptychitidae) often have their venter abraded. For example, the specimen illustrated on Plate 25, figures 10–14 is a complete phragmocone, the body chamber of which is missing, and whose venter has been abraded on almost the entire last preserved volution. In the Dienerian part of the Ceratite Marls, involute shells often have their narrow umbilicus encrusted by bivalves on both sides, similar to the ones already observed by Ware *et al.* (2011) in Dienerian ammonoid assemblages from Nevada. These bivalves may occasionally induce an irregular coiling of the umbilicus, thus indicating *in vivo* encrusting of epizoans. These bivalves are sometimes also present on the flanks of the whorl and, where overlapped by the body chamber, they are lined by a dorsal shell layer. Usually, only their cemented valve is preserved. The bivalves visible on the ammonoid figured on Plate 25, Figure 10, were described in detail by Hautmann *et al.* (2017), together with similar specimens from the Dienerian of Spiti (India) and the Griesbachian of Greenland. They identified them as *Liostrea* sp. ind., belonging to the sub-family Grypheinae and representing the oldest known representative of

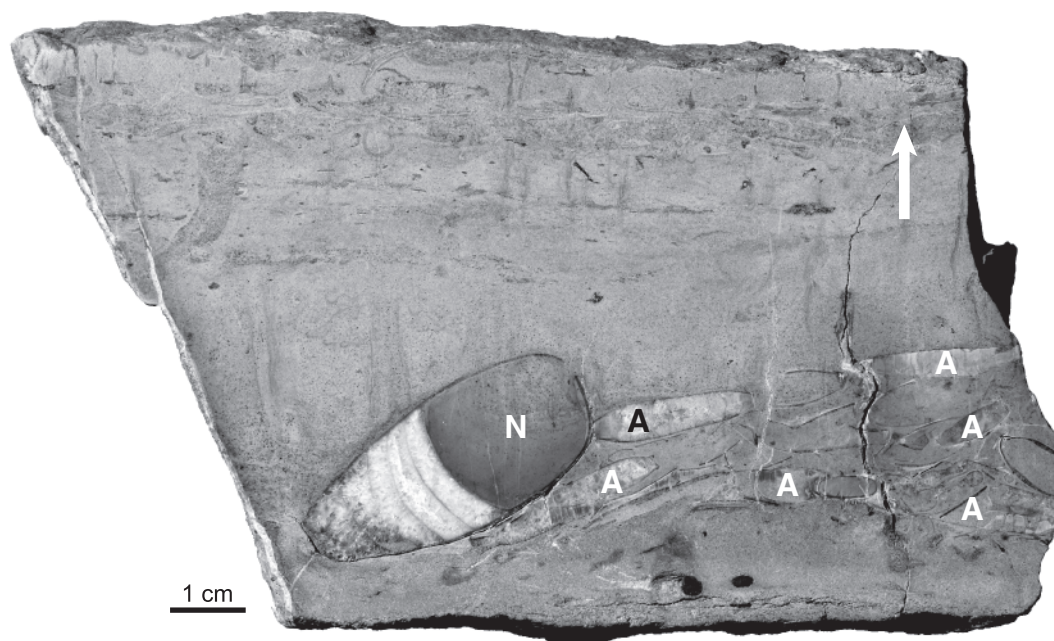


Fig. 2. Polished section of a bed belonging to the *Ambites lilangensis* Regional Zone (Nam100 and equivalents) from Nammal Nala, showing the typical facies of limestone beds at the base of the Ceratite Marls, with an accumulation of imbricated shells at its base with a nautiloid (N), several imbricated complete and broken ammonoids (A), and bioturbation increasing towards the top of the bed. Natural size, arrow indicates top of bed. Specimen PIMUZ30235.

Ostreidae. Besides this specimen, they are not well enough preserved to be formerly identified, but since no other coeval bivalve taxa are known to encrust ammonoids *in vivo*, they can reasonably be assumed to belong to the same taxa. It cannot be excluded that some of the intraspecific variability of the umbilical width observed on these involute shells is a consequence of the presence of these epizoans, but as no fauna without these encrusting bivalves could be found for comparison, this hypothesis cannot be tested. The presence or absence of bivalves in the umbilicus has therefore not been taken into account in the taxonomical analyses, except when they induced an obvious pathological coiling of the ammonoid shell. Such *in vivo* encrusting bivalves have so far not been recorded in older or younger ammonoid faunas in the Salt Range, even in early Smithian faunas which are found in similar facies. It is possible that this unusual high frequency of epizoans was caused by the coeval oxygen-poor water-sediment interface, but alternative hypotheses are also conceivable (see Hautmann *et al.* 2017, for details).

Hermann *et al.* (2011a,b, 2012a,b) and Schnee-beli-Hermann *et al.* (2012) proposed a detailed palaeoenvironmental reconstruction based on several sections (including the ones studied here) throughout the Salt Range and Surghar Range. These studies documented that in Nammal, the middle to

late Dienerian record a local peak of oxygen depletion, unlike previous (Griesbachian to early Dienerian) and subsequent (early and middle Smithian) time intervals. Romano *et al.* (2013) showed that temperature also peaked during the middle and late Dienerian (phase Ib of Romano *et al.* 2013).

Present work

The ammonoids presented in this study were collected in four different areas (Fig. 1C): Nammal Nala, Chiddru, Amb and Wargal, during four field work seasons from 2007 to 2010. Several sections were measured and sampled within a couple of square kilometres in each of these areas. Following recommendations of Guex (1991), a composite section for each area with the position of the samples was constructed based on lithological correlations. Therefore, several samples (each with a distinct number) may have been obtained from the same layer.

Nammal Nala

Nammal Nala is a narrow canyon situated about 5 km east of the village of Musa Khel (ca. 25 km ENE of Mianwali). This area was previously studied by Kummel (1966), Kummel & Teichert (1966, 1970), Guex (1978) and the Pakistani-Japanese Research Group (1985). The Lower Triassic

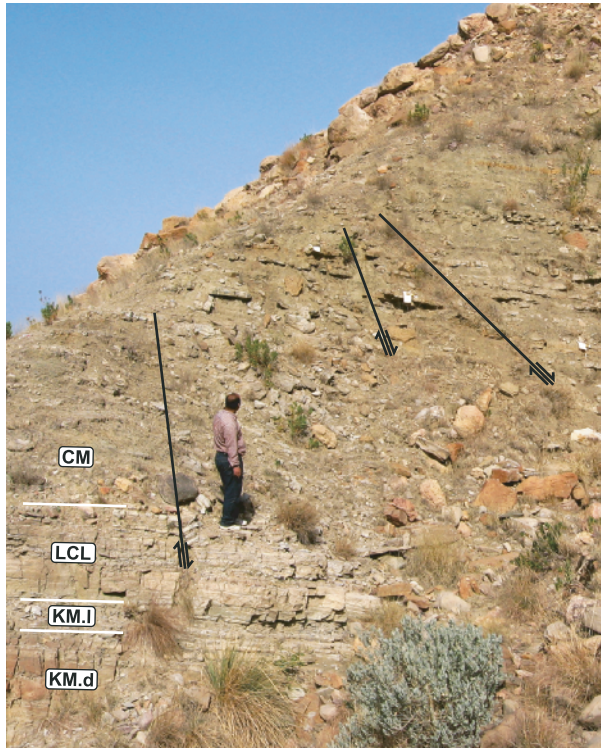


Fig. 3. Section near the entrance of Nammal Nala (N32°39'27.6", E71°47'29.2"). KM.d: Kathwai Member, dolomitic unit; KM.l: Kathwai Member, limestone unit; LCL: Lower Ceratite Limestone; CM: Ceratite Marls. Note the presence of small normal faults (black lines).

Mianwali Formation is beautifully exposed and repeated by faulting. All the exposures reported here are from the northern side of the canyon, which is in part illustrated in Figure 3. A composite section with the ammonoid distribution is given in Figure 4. The most complete Griesbachian and Dienerian sequence of the Salt Range was found in Nammal Nala, especially for the base of the Ceratite Marls, where ammonoids are very abundant and well preserved. This canyon is also very easily accessible, thus allowing intensive sampling. The vast majority of the ammonoids (about 1200 specimens) described here come from Nammal Nala.

Chiddru

The sections studied in Chiddru are situated in a valley about 2.5 km east of the village (ca. 25 km ESE of Mianwali). Several sections were sampled in 2008 and 2010, but the best ones for the Dienerian were already described by Kummel (1966) and Kummel & Teichert (1966, 1970), especially the one on the west side of the valley (Fig. 5). A composite section showing ammonoid distribution is given in Figure 6. In this area, the Kathwai Member and Lower Ceratite Limestone are much

thicker than in other areas, and Dienerian faunas are restricted to the Lower Ceratite Limestone. The base of the Ceratite Marls is already early Smithian in age (Brühwiler *et al.* 2012). In the Lower Ceratite Limestone, ammonoids are abundant but generally broken and poorly preserved. Specimens well enough preserved for identification are rather rare. Despite intensive sampling, only ca. 50 specimens could be included in this study. However, this area is very important for the Dienerian, since it is the type locality of *Koninckites vetustus*, the type species of *Koninckites*. This area has been known since the beginning of the geological investigations in the Salt Range, and has been included in every study dealing with the Early Triassic of this region.

Amb

Amb is a small village situated ca. 35 km east of Mianwali. Three different outcrops were sampled during one field trip (2010) in the valley just south of the village, the best section being situated about 1 km south-east of the village (Fig. 7). A composite section showing the ammonoid distribution is given in Figure 8. The Kathwai Member and Lower Ceratite Limestone have thicknesses similar to those of Nammal, but the Dienerian part of the Ceratite Marls is thinner, with fewer limestone beds. Although often broken, ammonoids from the Lower Ceratite Limestone are very abundant and better preserved than in Nammal. In the Ceratite Marls ammonoids are rather rare, usually strongly recrystallized and difficult to prepare. A total of about 120 specimens from Amb could be included in this study. This locality is the type locality of the type species of the genus *Ambites* (*Ambites discus*). Since the pioneer work of Waagen (1895), the Early Triassic ammonoid fauna of Amb have not been studied.

Wargal

The sections near Wargal are situated in a syncline about 2.5 km west of the village, along Munta Nala. Although the Kathwai Member and Lower Ceratite Limestone are thicker than in Amb, and the Ceratite Marls thinner, the two sections are very similar. We spent only 3 days in this locality, mostly to collect specimens of the genus *Prionolobus*, as it is the type locality of its type species *Prionolobus atavus* and of *Prionolobus rotundatus*. About 100 specimens were collected, mostly in the Lower Ceratite Limestone and at the very base of the Ceratite Marls, easily accessible in the section previously described by

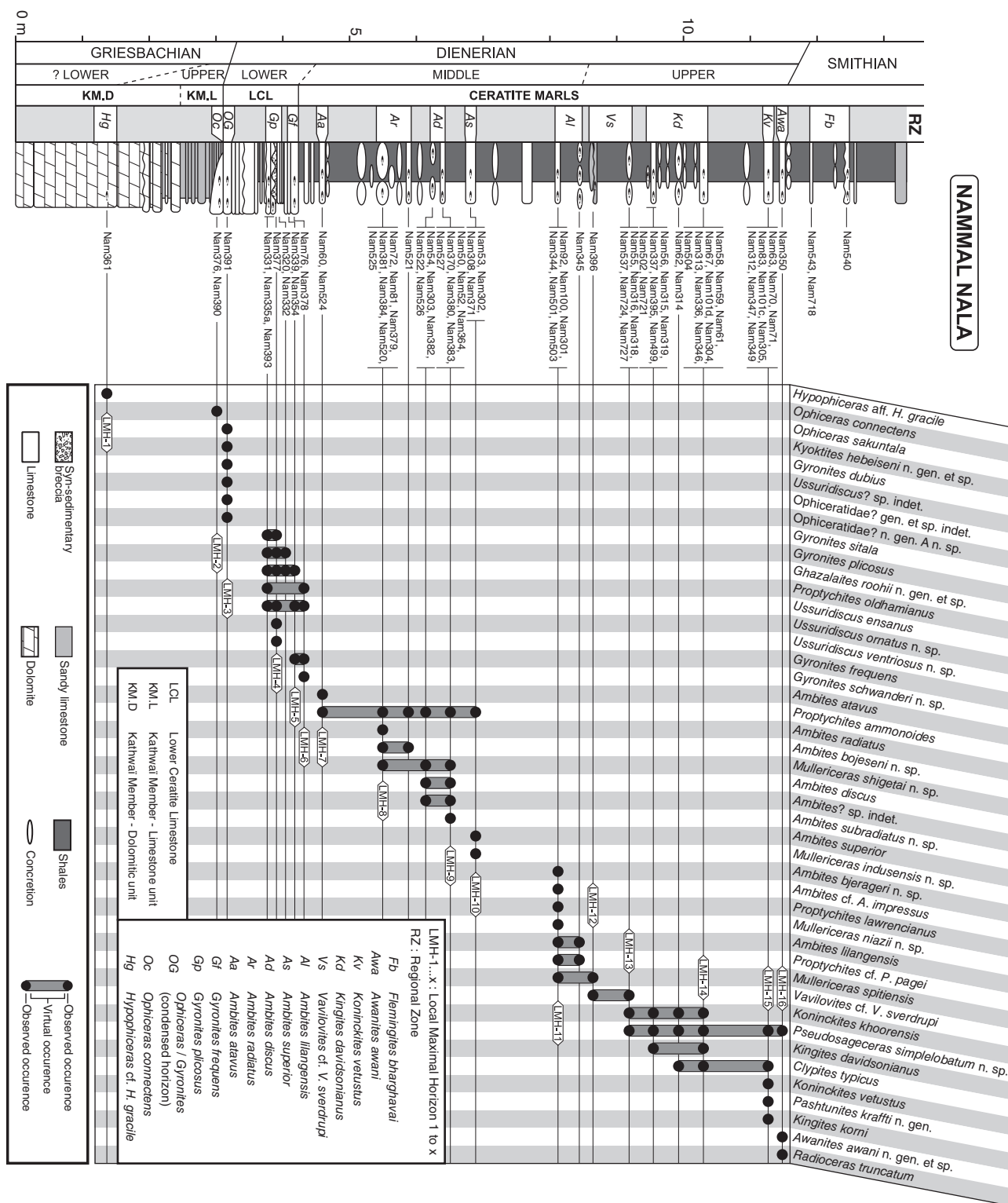


Fig. 4. Composite section of Nammal Nala: lithostratigraphy, ammonoid occurrences and biostratigraphy. Faunal content of NAM543, NAM718 and NAM540: see Brühwiler et al. (2012).

Kummel (1966) and Kummel & Teichert (1966, 1970), and illustrated here in Figure 9. Only the upper part of the lower third of the Ceratite Marls was sampled in another nearby tributary, where a

Koninckites vetustus fauna (sample War104) was found. A composite section showing the ammonoid distribution is given in Figure 10. As in Amb, ammonoids from the Lower Ceratite Limestone are



Fig. 5. Section above the village of Chiddru (N32°32'59.7", E71°47'55.9") on the West side of the gorge, previously described by Kummel & Teichert (1966, 1970) and Kummel (1966). Hammer highlighted for scale. Chiddru Fm., Chiddru formation; KM, Kathwai Member; LCL, Lower Ceratite Limestone; CM, Ceratite Marls.

abundant and rather well preserved, but they are also abundant and well preserved in the Ceratite Marls. This area has been investigated first by Waagen (1895) and later by Kummel (1966) and Kummel & Teichert (1966, 1970).

Biostratigraphy

The extensive bedrock controlled sampling on which the present work is based allows the recognition of a total of 15 regional zones: three from Griesbachian and 12 from Dienerian (Figs 11, 12). The resulting zonation is new with improved resolution. Previously, only three zones were recognized from the Salt Range (Guex 1978; Pakistani-Japanese Research Group 1985), and two zones and four subzones were established in the Dienerian succession of Canada (Tozer 1965, 1994). A preliminary version of this zonation was published in Romano *et al.* (2013). This regional zonation served as base for the construction of the formal biozonation for the Dienerian of the Northern Indian margin palaeoprovince of Ware *et al.* (2015).

The different regional zones are described herein and their correlation with ammonoid zonation from other basins is discussed. Synthetic range charts for Griesbachian and Dienerian ammonoid species and genera from the Salt Range are given in Figures 13 and 14, respectively. Technically, most of these regional biozones correspond directly to local maximal horizons, except for the *Gyronites plicatus* Regional Zone, the *Gyronites frequens* Regional Zone and the *Vavilovites* cf. *V. sverdrupi* Regional Zone

(see below). It should be noted that correlation of this new biozonation with previous ones (e.g. Mojsisovics *et al.* 1895; Guex 1978; Pakistani-Japanese Research Group 1985) cannot be provided because the undetected diachronicity of the different lithostratigraphical units led to mix ammonoid faunas of different (late Griesbachian to early Smithian) ages for the Lower Ceratite Limestone. The age distribution of the Lower Ceratite Limestone varies geographically, this unit being upper Griesbachian to lower Dienerian in Nammal Nala, lower Dienerian to lower middle Dienerian in Amb and Wargal, and Dienerian to lowermost Smithian in Chiddru. These results contrast with the previous age assignment of the Lower Ceratite Limestone to one single zone, namely the *Gyronites frequens* Zone.

For each regional zone, the list of co-occurring species is given, and the characteristic species and pairs of species are indicated in braces. Additionally, the number of specimens of each species in each zone is given in brackets.

General subdivisions

The stage and sub-stage subdivision of the Lower Triassic and their definitions were already discussed in the foreword (Ware & Bucher 2018; this volume). Tozer (1965) subdivided the Griesbachian and the Dienerian into two parts (lower and upper) each, a scheme which has been followed by every author since. Because of the paucity of Griesbachian faunas in the Salt Range, this twofold subdivision cannot be assessed here. However, for the Dienerian, the much higher resolution subdivisions obtained in this study leads to a threefold subdivision of the Dienerian (lower, middle and upper). The lower Dienerian is characterized by the occurrence of the genera *Gyronites* and *Ussuridiscus*, the middle Dienerian by the co-occurrence of the genera *Ambites* and *Mullericeras*, and the upper Dienerian by the appearance of *Paranoritidae* and *Sagecerataceae*.

Griesbachian ammonoid faunas

Griesbachian ammonoids are very rare and generally poorly preserved in the Salt Range. Moreover, Griesbachian ammonoids from other regions of the Northern Indian Margin have not been investigated in detail since the work of Diener (1897) and von Krafft and Diener (1909). A new biozonation for the Griesbachian of Spiti Valley (Indian Himalayas) has been attempted by Krystyn *et al.* (2004), but without explanation or illustration of the taxonomic definitions, thus making this scheme difficult to apply or to test in other areas. As a consequence, the three

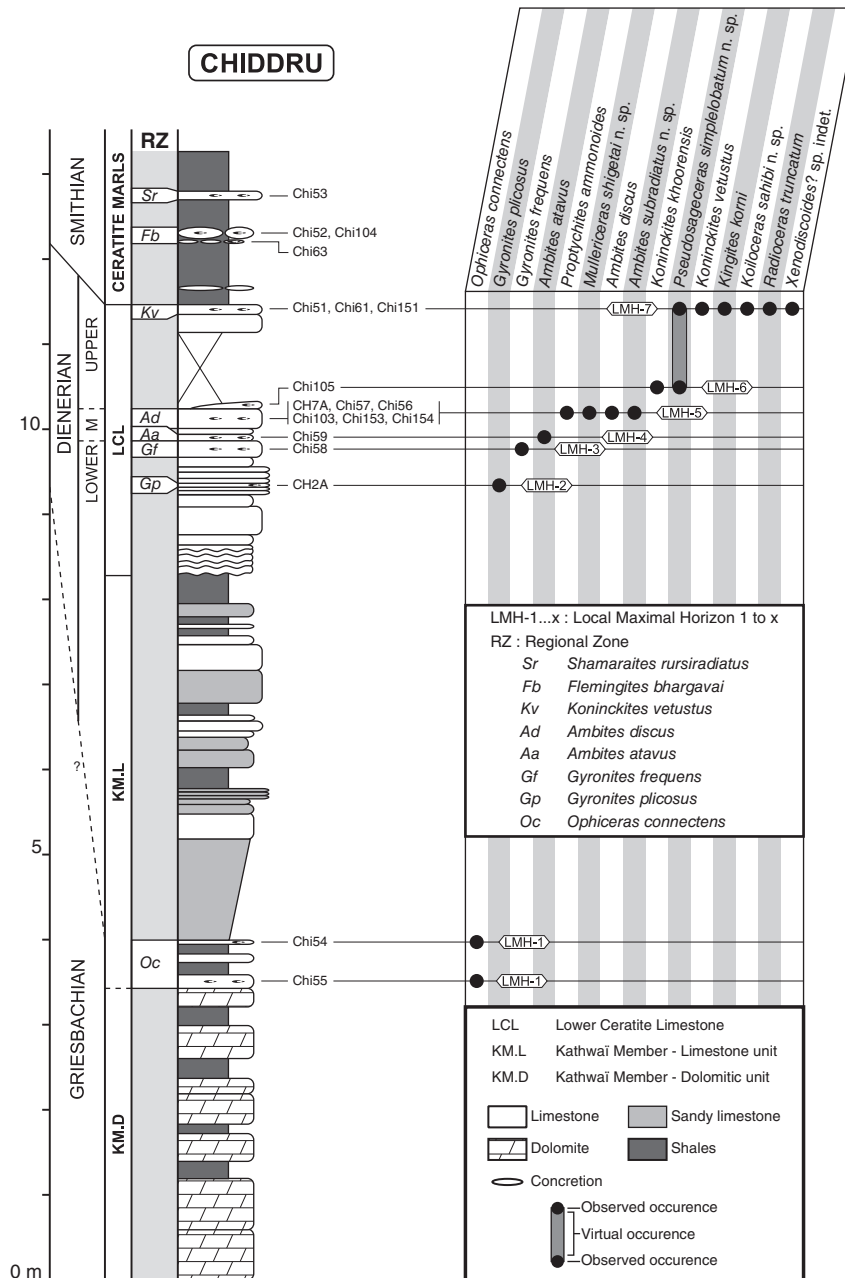


Fig. 6. Composite section of Chiddru: lithostratigraphy, ammonoid occurrences and biostratigraphy. Faunal content of CHI63, CHI52, CHI104 and CHI53: see Brühwiler *et al.* (2012).

Griesbachian regional biozones described here cannot be correlated with confidence.

Hypophiceras cf. *H. gracile* Regional Zone

Co-occurring species. – *Hypophiceras* cf. *H. gracile* ($n = 1$).

Occurrence in the investigated sections. – This zone is here based on a single specimen found in the dolomitic unit of the Kathwai Member in Nammal Nala.

Correlation. – Although species assignment remains uncertain, identification at the genus level of this single specimen is very robust. The genus *Hypophiceras* is known in the Arctic (Siberia, Arctic Canada and NE Greenland), where it occurs together with lower Griesbachian taxa. However, Kummel (1970) reported one specimen from the Kathwai Member of Kathwai, which may be conspecific with ours, and correlated this bed on the basis of lithology with the *Ophiceras connectens* Zone of Chiddru (upper Griesbachian). In the absence of additional material, and



Fig. 7. Section about 1 km south-east of the village of Amb (N32°29'48.1", E71°56'20.6"). Scale indicated by a geologist (circled) in the middle of the view. KM.d: Kathwai Member, dolomitic unit; KM.l: Kathwai Member, limestone unit; LCL: Lower Ceratite Limestone; CM: Ceratite Marls.

considering that this correlation is exclusively based on lithology, this zone is here kept separate from the subsequent *Ophiceras connectens* regional Zone. Additional work on the Griesbachian of the Tethys is necessary to decipher whether the genus *Hypophiceras* is restricted to the lower Griesbachian or if it ranges up into the upper Griesbachian. This zone corresponds to the horizon MH-G1 in Romano *et al.* (2013).

Ophiceras connectens Regional Zone

Co-occurring species. – *Ophiceras connectens* ($n = 13$).

Occurrence in the investigated sections. – This zone has been identified in Nammal Nala (base of the Lower Ceratite Limestone) and in Chidru (base of limestone unit of the Kathwai Member) and only yields poorly preserved specimens of *Ophiceras connectens*.

Correlation. – This species was considered as a synonym of *Ophiceras tibeticum* by Waterhouse (1994), who thus treated this fauna as an equivalent of the Himalayan *Ophiceras tibeticum* zone of late Griesbachian age. Acceptance or rejection of this treatment requires revision of the taxonomy of Ophiceratidae and of the Himalayan Griesbachian faunal succession. This zone corresponds to the horizon MH-G2 in Romano *et al.* (2013).

Ophiceras sakuntala Regional Zone

Co-occurring species. – *Ophiceras sakuntala* ($n = 4$).

Occurrence in the investigated sections. – This regional zone has only been recognized in the condensed layer at the base of the Lower Ceratite Limestone in Nammal Nala.

Correlation. – *Ophiceras sakuntala* also occurs in Shalshal Cliff in the central Himalayas, where it was originally described by Diener (1897). This condensed layer corresponds to the horizon MH-G3 in Romano *et al.* (2013).

Remarks. – Because this layer yields both late Griesbachian and earliest Dienerian taxa (LMH-3, Fig. 4), the natural association of species belonging to this regional zone is obscured.

Early Dienerian ammonoid faunas

Early Dienerian ammonoids from the Salt Range are abundant and usually quite well preserved, but can be difficult to mechanically separate from the matrix. They are all found in the Lower Ceratite Limestone, an interval characterized by low accumulation and sedimentation rate. The lower Dienerian biostratigraphical record must be treated with caution with respect to potential hiatuses and condensed deposition. The Salt Range nevertheless provides the most

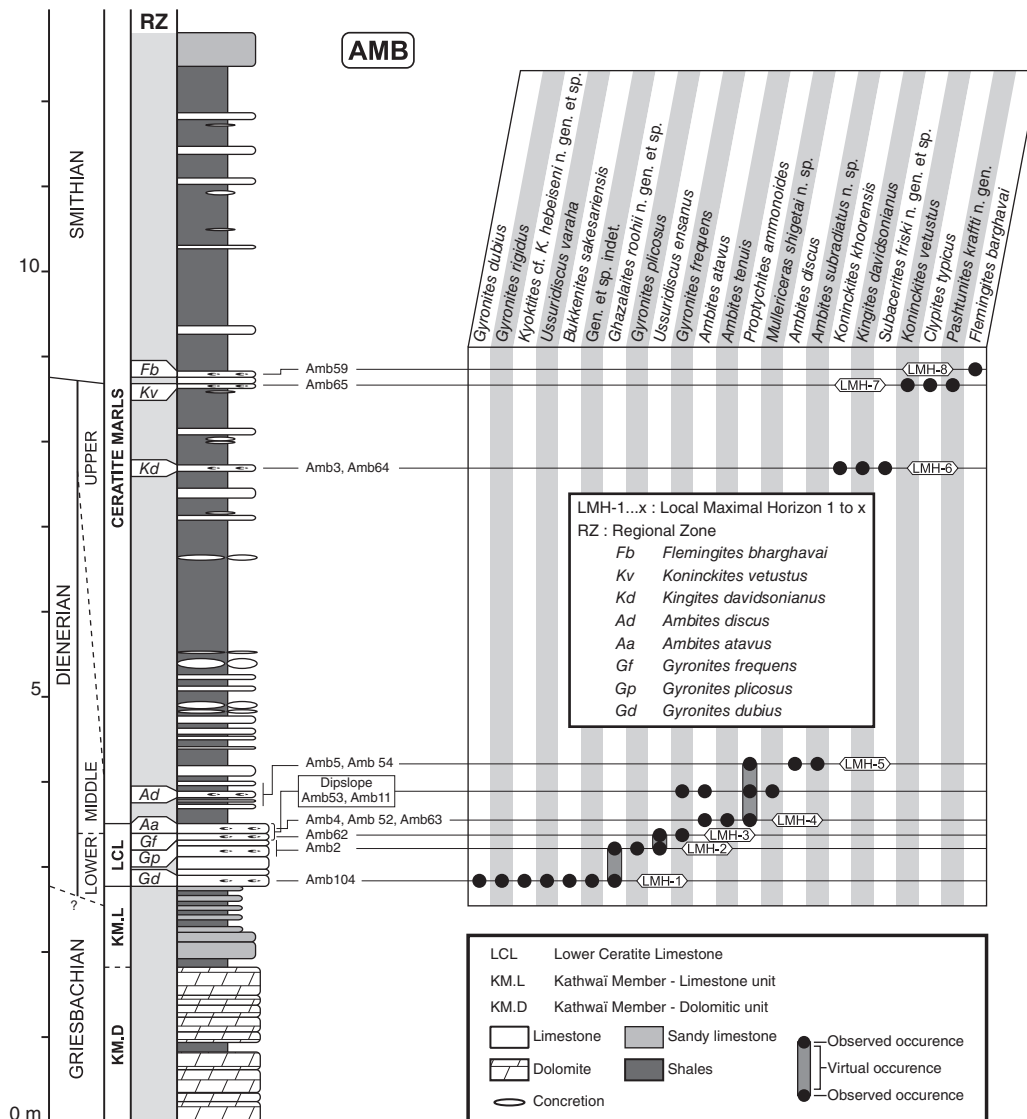


Fig. 8. Composite section of Amb: lithostratigraphy, ammonoid occurrences and biostratigraphy. AMB53 and AMB11 were collected on a dipslope formed by the two uppermost beds of the Lower Ceratite Limestone, without any further distinction.

expanded and diverse faunal succession for the early Dienerian worldwide. A likely case of condensation is found at the base of the Lower Ceratite Limestone in Nammal Nala, where *Gyronites dubius* of earliest Dienerian age occurs together with the late Griesbachian *Ophiceras sakuntala* (LMH-3, Fig. 4).

The lower Dienerian is best characterized by the genus *Gyronites*. In the Salt Range, the genus *Ussuridiscus* is also restricted to the lower Dienerian, but in Primorye, its type species *Ussuridiscus varaha* is found in four consecutive beds belonging to three different zones (Shigeta & Zakharov 2009), ranging from the upper Griesbachian to the middle Dienerian, whereas it is restricted to a single zone in the Salt Range. Its presence in the upper Griesbachian is uncertain, as its occurrence in this substage is based

on bed 1009 of Shigeta and Zakharov (2009, fig. 15), which yielded a poorly preserved specimen assigned to *Lytophiceras*? sp. indet. However, the presence of *Ussuridiscus varaha* in the middle Dienerian is confirmed by its association in bed 1013 of Shigeta & Zakharov (2009) with '*Ambitoides*' *fuliginatus* (here re-assigned to *Mullericeras*), *Proptychites ammonoides* and '*Gyronites*' (here re-assigned to *Ambites* on the basis of the bottleneck shape of the venter). The *Gyronites subdharmus* Zone, which Shigeta and Zakharov (2009) assigned to the upper Griesbachian, contains the genus *Gyronites* and therefore likely correlates with the lower Dienerian as described here. However, *Gyronites subdharmus* is absent in the Salt Range, so a correlation at the species level cannot be made. Krystyn *et al.* (2004) placed their