

# Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery

RICHARD HOFMANN, MICHAEL HAUTMANN, MARTIN WASMER, and HUGO BUCHER



Hofmann, R., Hautmann, M., Wasmer, M., and Bucher, H. 2013. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica* 58 (1): 149–173.

The Spathian (late Early Triassic) Virgin Formation of south-western Utah (USA) yields a comparatively diverse benthic fauna that flourished ~2 Ma after the end-Permian mass extinction. In this study, we present quantitative palaeoecological data, which are analysed in the context of depositional environments. This integrated approach helps to discriminate between effects of the end-Permian mass extinction event and local environmental factors on alpha diversity and ecological structure of the Virgin Fauna. Shallow subtidal environments yield the highest species richness and lowest dominance values as recorded in two benthic associations, the *Eumorphotis ericius* Association and the *Protogusarella smithi* Association, both of which contain 20 benthic species (bivalves, gastropods, brachiopods, echinoderms, and porifers). Tidal inlet deposits yield a low diverse fauna (*Piarorhynchella triassica* Association) with a very high dominance of filter feeders adapted to high energy conditions. Another comparably low diverse fauna is recorded by the *Bakevella exprorecta* Association, which occurs in deposits of the offshore transition zone, most likely reflecting unconsolidated substrates. A single sample containing five bivalve species (*Bakevella costata* Assemblage) is recorded from a marginal-marine setting. The Virgin fauna yields a bulk diversity of 30 benthic species (22 genera) of body fossils and 14 ichnogenera and, thus, represents the most diverse marine bottom fauna known so far from the Early Triassic. Our results suggest that oceanographic conditions during the early Spathian enabled ecosystems to rediversify without major abiotic limitations. However, taxonomical differentiation between habitats was still low, indicating a time lag between increasing within-habitat diversity (alpha diversity) and the onset of taxonomical differentiation between habitats (beta diversity). We suggest that taxonomical habitat differentiation after mass extinction events starts only when within-habitat competition exceeds a certain threshold, which was not yet reached in the Spathian of the investigated area. This interpretation is an alternative to previous suggestions that the prevalence of generalistic taxa in the aftermath of mass extinction events reflects protracted environmental stress. The onset of increasing beta diversity is a potential criterion for distinguishing two major recovery phases, the first ending with habitat saturation and the second ending with the completion of ecosystem differentiation.

Key words: Biotic recovery, mass extinction, palaeoecology, diversity, Early Triassic, Spathian, Virgin Formation, USA.

Richard Hofmann [richard.hofmann@pim.uzh.ch], Michael Hautmann [michael.hautmann@pim.uzh.ch], Martin Wasmer [martin.wasmer@gmail.com], and Hugo Bucher [hugo.fr.bucher@pim.uzh.ch], Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland.

Received 27 April 2011, accepted 13 December 2011, available online 16 December 2011.

Copyright © 2012 R. Hofmann et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

The end-Permian mass extinction is widely accepted as representing the most devastating biotic crisis in the history of metazoan life (Erwin 1993). Besides the study of the causes and mechanism of the extinction itself, the ensuing recovery interval has attracted considerable attention since the early 1990s. The paramount questions addressed in post-extinction research are, in particular, how biota and ecosystems respond to large environmental perturbations, how rapidly ecosystems can recover and how evolutionary processes proceed in vacated ecospace.

An important but largely neglected tool in reconstructing recovery processes is that of quantitative palaeoecological studies. Although the Virgin Formation (or Virgin Limestone Member in most other studies) and related strata of the western USA have been studied in various aspects (e.g., Poborski 1954; Schubert and Bottjer 1995; Boyer et al. 2004; Pruss and Bottjer 2004; Pruss et al. 2007; McGowan et al. 2009; Pruss and Payne 2009; Mata and Bottjer 2011), very little palaeoecological community data were presented. The hitherto most comprehensive study of the Virgin palaeoecology is that of Schubert and Bottjer (1995), which, however, focused on broad patterns throughout the entire Early Triassic of the west-

ern USA and was based on genus identification only. Although their Spathian samples exhibit the highest generic diversity and most advanced trophic structure among all Early Triassic faunas analysed, Schubert and Bottjer (1995) still concluded that the entire Early Triassic of the western USA was dominated by depauperate benthic communities reflecting a considerably delayed recovery. Schubert and Bottjer (1995: 28) suggested that this pattern largely results from the extraordinary magnitude of the end-Permian mass extinction and from intrinsic, ecological effects. Another mechanism that has been invoked to explain the putatively protracted Early Triassic recovery is that adverse environmental conditions persisted well beyond the actual extinction interval and inhibited re-diversification in the marine realm (Hallam 1991). This model was subsequently advocated by many investigators studying Lower Triassic sections from the USA (e.g., Wignall and Hallam 1992; Boyer et al. 2004; Pruss and Bottjer 2004; Mata and Bottjer 2011) as well as other palaeogeographic regions (e.g., Twitchett and Wignall 1996). However, recent studies have challenged several key aspects of this model, such as the universality of small body sizes in the Early Triassic (Brayard et al. 2010, 2011a), the existence of global shallow marine anoxia (Heydari et al. 2008), and a delayed recovery in general (Brayard et al. 2009, 2011b; Hautmann et al. 2011, Hofmann et al. 2011).

The Virgin Formation has been repeatedly studied for more or less representative palaeoecological proxies such as trace fossils (Pruss and Bottjer 2004; Mata and Bottjer 2011), shell bed architecture (Boyer et al. 2004), and microbially induced sedimentary structures (Pruss et al. 2005). All of these studies conclude that strata from this time interval in the western USA record unusual and harsh environmental conditions, such as alkaline and anoxic waters permanently (Boyer et al. 2004) or repeatedly (e.g., Pruss and Bottjer 2004) affecting shallow marine habitats and, thereby, inhibiting ecosystems from taxonomical and ecological restoration.

A study to assess the faunal heterogeneity and the recovery status of the Virgin fauna was recently provided by McGowan et al. (2009). Their data suggest that Virgin communities actually lack typical traits of post-extinction faunas such as pronounced small shell size, faunal homogeneity, low diversity and high abundances of single taxa but are comparable to faunas of the central European Muschelkalk, which were not subjected to any form of abiotic stress related to the mass extinction. Furthermore, this survey was the first to provide quantitative data on the species level and it reported an unexpectedly high bulk diversity of benthic taxa (37 species and 30 genera), including bivalves, gastropods, brachiopods, and echinoderms, which considerably exceeds the 18 genera of benthic organisms reported by Schubert and Bottjer (1995) from their Virgin localities. Hautmann et al. (2012) restudied the material of McGowan et al. (2009) and identified as many as 28 bivalve species belonging to 18 genera.

This paper presents a palaeoecological analysis of the Virgin fauna from south-western Utah based on quantitative species distribution, which is discussed in the context of

depositional environments. This integrated approach helps to distil unequivocal recovery signals from “noise-variation” merely reflecting the environmental heterogeneity of shallow-marine environments and local environmental stress unrelated to actual recovery trajectories. Additionally, it allows the identification of the degree of faunal heterogeneity between adjacent habitats along environmental gradients and, thereby, the assessing of the role of beta diversity in the post-extinction diversity increase.

*Institutional abbreviations.*—PIMUZ, Paläontologisches Institut und Museum collection, University of Zürich, Switzerland.

## Material and methods

Fieldwork was conducted by in October 2009 (by RH) and August 2010 (RH and MW) in the area of St. George and Hurricane in south-western Utah, USA. Bed-by-bed logging and documentation was undertaken at three sections in the Beaver Dam Mountains area west of St. George and at five sections along the “Honeymoon Trail”, east of Hurricane (Fig. 1). This main body of data was complemented by additional observations from some single outcrops in the research area. At the studied sections, fossiliferous beds were chosen for quantitative sampling of macrofossils. The greater part of fossil material was identified and counted in the field but reference samples were taken for lab preparation and further taxonomic identification. Benthic fossils from Lower Triassic successions are notorious for their poor preservation (Schubert and Bottjer 1995; Fraiser and Bottjer 2005; Hautmann and Nützel 2005) with mostly internal and re-crystallised moulds being preserved. However, the material investigated herein is excellently preserved by Early Triassic standards and poses few problems with its taxonomic identification. Crucial taxonomic criteria are readily observable on well preserved, primarily calcitic shells of epifaunal bivalves. Internal moulds of mostly aragonitic infaunal bivalves are morphologically distinct and show no evidence of notable deformation.

The applied sampling procedure varied with respect to the sedimentary rock type and available outcrop area. Surface collections were performed mostly on shale intervals. All other samples, extracted from discrete limestone beds, were representatively sampled and mechanically decomposed for fossil collection. Each collection was performed either until it yielded more than 100 specimens or until further sampling revealed no new finds of taxa. In some cases, sampling was limited by unsuitable outcrop conditions. Beds showing evidence of strong reworking, such as pronounced gradation and size sorting, were not included in the analysis. Trace fossils were documented in the field and integrated in ecological interpretations. Identification of the sedimentological facies is based on field observations. The taxa counted include bivalves, gastropods, ammonoids, brachiopods, and sponges. The abundance of echinoderms was roughly estimated but not quanti-

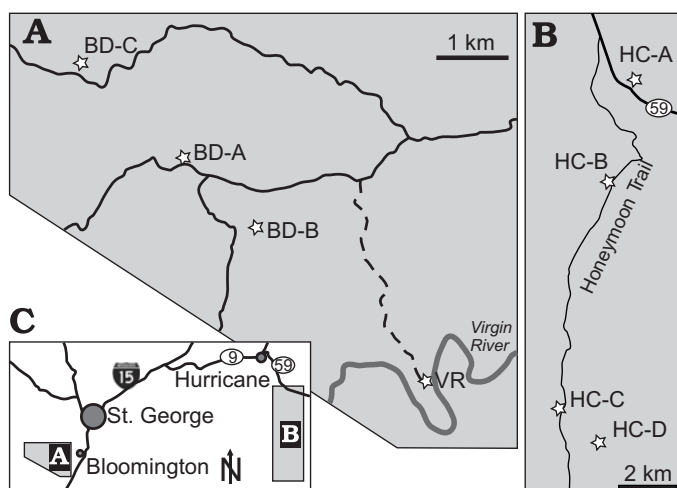


Fig. 1. Localities of the sections mentioned in the text. **A.** Beaver Dam Area (samples BD and VR). **B.** Hurricane Cliff Area (samples HC). **C.** Overview map depicting the position of the study areas (**A** and **B**) around St. George, south-western Utah.

fied and their occurrences, as well as counts of trace fossils, were not considered in the cluster analyses. Most of the echinoderms were recorded by isolated plates and ossicles, which makes it impossible to estimate numbers of specimens in a given sample. Trace fossil counts are problematic, because they do not correspond with the actual abundances of their trace makers in a palaeocommunity.

Identification of bivalve taxa follows Hautmann et al. (2012).

Faunal abundance data were analysed with the software package PAST (Hammer et al. 2001). Cluster analysis was performed in order to generate groupings of samples and species on the basis of their occurrences and abundances. Most comprehensible clusters were obtained using the paired group method implanted in PAST (UPGMA, unweighted paired group with arithmetic mean) together with the Morisita index of similarity (Morisita 1959). The UPGMA algorithm (Sokal and Michener 1958) is generally recommended for taxa-in-sample data sets (Hammer and Harper 2006). The Morisita index is found to be useful in ecological studies of Recent environments (e.g., Wolda 1981) but is recommended for palaeoecological data as well (Hammer and Harper 2006). The advantage of the Morisita index is that it is relatively insensitive to different sample sizes and tends to smoothen high abundances of single taxa. Samples that constitute the most resolved clusters were merged to represent one association. A comparative analysis using the Bray-Curtis similarity index (Bray and Curtis 1957), which is more sensitive to high abundances (Hammer and Harper 2006), yield essentially the same clusters, the only difference being that two samples of two adjacent associations are interchanged. Bootstrapping ( $n = 1000$ ) was used in order to provide a measure for robustness of clustering. Bootstrap values indicate the percentage of re-sampled replicates (random modifications of the original abundance matrix) that confirm the nodes of the computed dendrogram.

Adopted from extant ecosystem research, diversity indices are widely used in palaeobiological studies (Bambach 1977; Sepkoski 1988). Alpha (within-habitat) diversity represents the number of species in one assemblage or association which is assumed to represent the relic of a community (sensu Whittaker 1972). Beta (between-habitat) diversity expresses the taxonomic differentiation between communities or along environmental gradients (Whittaker 1972). Dominance index is defined as  $D = \sum \left( \frac{n_i}{n} \right)^2$ , where  $n$  is the number of individuals of taxon  $i$  (as used in PAST; Hammer et al. 2001).  $D$  is high when very few taxa or a single taxon dominates a community, and  $D$  is low when many taxa are present in similar abundances. The trophic nucleus of an association is defined by those taxa that contribute to 80% of the total specimen number per association (Neyman 1967).

## Geological background

**Notes on the stratigraphic nomenclature.**—The stratigraphic nomenclature of Spathian deposits of the western USA, usually referred to as Virgin Limestone Member (e.g., Schubert and Bottjer 1995; Pruss and Bottjer 2004; Mata and Bottjer 2011), remains somewhat unclear. Poborski (1954) recommended abandoning the somewhat misleading term “limestone” (the Virgin is mainly composed of siltstone). Furthermore, the “Virgin Limestone” has been raised into formational rank and, consequently, the Moenkopi Formation into group status (Poborski 1954). Recently, this concept found agreement from Lucas et al. (2007) and Godspeed and Lucas (2007). Additionally, Lucas et al. (2007) emended the stratigraphic scheme of Lower Triassic Rocks in the western USA by assigning all marine strata to the Thaynes Group and all non-marine deposits to the Moenkopi Group. Although this procedure appears reasonable, problems may arise because the distinction between marine and non-marine facies can be equivocal. Unquestionably, Virgin-type strata represent mostly shallow and marginal marine wedges that are equivalent to the fully marine Thaynes Group, but in the investigated area, no typical Thaynes lithology is developed, and Virgin-type strata are exclusively found in south-western Utah and eastern Nevada. Therefore, we follow Poborski (1954) in treating Virgin-type deposits of south-western Utah as the Virgin Formation of the Moenkopi-Group (Fig. 2). This view seems to be the most applicable solution according to articles 24 and 25 of the North American Stratigraphic Code (NACSN 2005).

**Geological setting and stratigraphy.**—During the Early Triassic, much of the western USA was part of an epicontinental marine basin connected to the Panthalassic Ocean to the west (Fig. 3). The depot centre was presumably situated in an area stretching from the northwestern part of Utah towards central and western Nevada (Blakey 2011). In



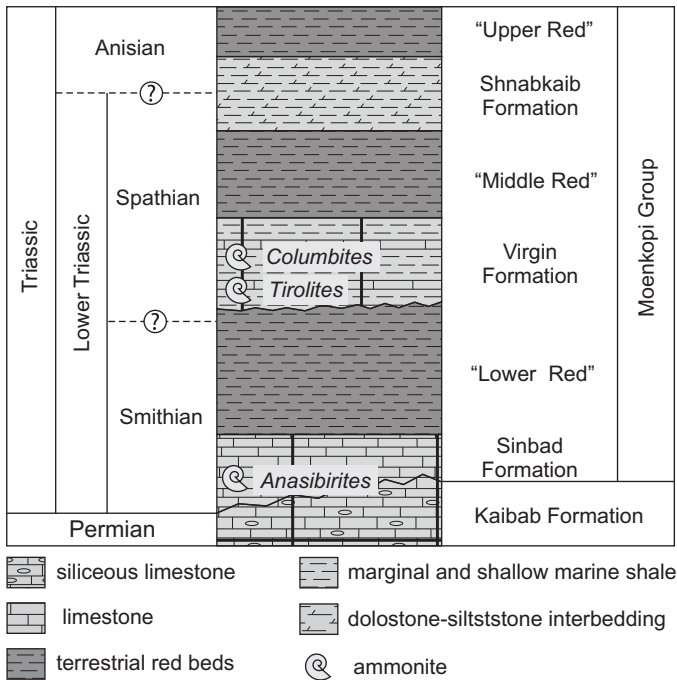


Fig. 2. Lithostratigraphic column of the Moenkopi Group in the investigated area. Thickness of lithostratigraphic units and the position of ammonite markers are schematic and not to scale. Presence of *Anasibirites* after Lucas et al. (2007), *Tirolites* after Poborski (1954), and *Columbites* after Bucher in Hautmann et al. (2012).

the course of several transgressions and regressions, shore-lines shifted considerably over the area, but the approximate maximum extent of marine strata during the Early Triassic is documented in south-western and south-central Utah, with marine tongues transgressing over terrestrial and marginal marine red beds during Smithian (Sinbad or Timpoweap Formation) and Spathian (Virgin Formation) times. The lower contact of the Virgin Formation to the underlying “Lower Red” is marked by an unconformity, which represents either a gap in sedimentation accompanied by erosion, or truncation during shoreline retreat. The heterogeneity of the earliest Virgin-type deposits within short distances, however, suggests that the initial Virgin transgression drowned a considerable land relief. The transition to the overlying “Middle Red” has not been observed. At all the localities studied, the contact between the Virgin Formation and the “Middle Red” was concealed, or the Virgin Formation represented the top of local sections. In the type area, the Virgin Formation is mainly composed of calcereous siltstone, claystone, calcarenite and bioclastic grainstone. These lithotypes generally represent deposits of shallow subtidal and intertidal environments including open and protected marine systems of a tropical to subtropical setting, under arid climate (Reif and Slatt 1979).

Based on lithostratigraphic considerations, the Virgin Formation has been generally assumed to be Spathian in age (Reeside and Bassler 1922). Poborski (1954) mentioned the presence of the ammonite *Tirolites spinosus* in the middle part of the formation. Unfortunately, no figures were presented, but other workers (e.g., Bissell 1973) confirmed this

identification. *Tirolites* is a common ammonite genus of lowermost Spathian strata worldwide and a characteristic element of the first two Spathian ammonite zones (e.g., Galfetti et al. 2007; Guex et al. 2010). Recent fossil collections (McGowan et al. 2009) yielded an ammonoid specimen from middle part of the Formation, which has been identified as *Columbites parisianus* (Bucher in Hautmann et al. 2012), suggesting a late Early Spathian age (Guex et al. 2010). The *Tirolites/Columbites*-beds from China were calibrated with zircon U-Pb data, which indicate an age of  $250.6 \pm 0.5$  Ma for this ammonite zone (Ovtcharova et al. 2006), approximately 2 Ma after the main extinction (Mundil et al. 2004).

## Sedimentary environments of the Virgin Formation

**Beaver Dam Mountains (sections BD-A, BD-B, and VR)** (Fig. 4).—In this area, the Virgin Formation attains a thickness of 34 m and is mainly composed of calcareous siltstone and shale, interbedded with distinct ledge-forming limestone beds. As exposed in the sections BD-A (Fig. 4A) and BD-B (Fig. 4B), the base of the Virgin is composed of ca. 2 m thick,

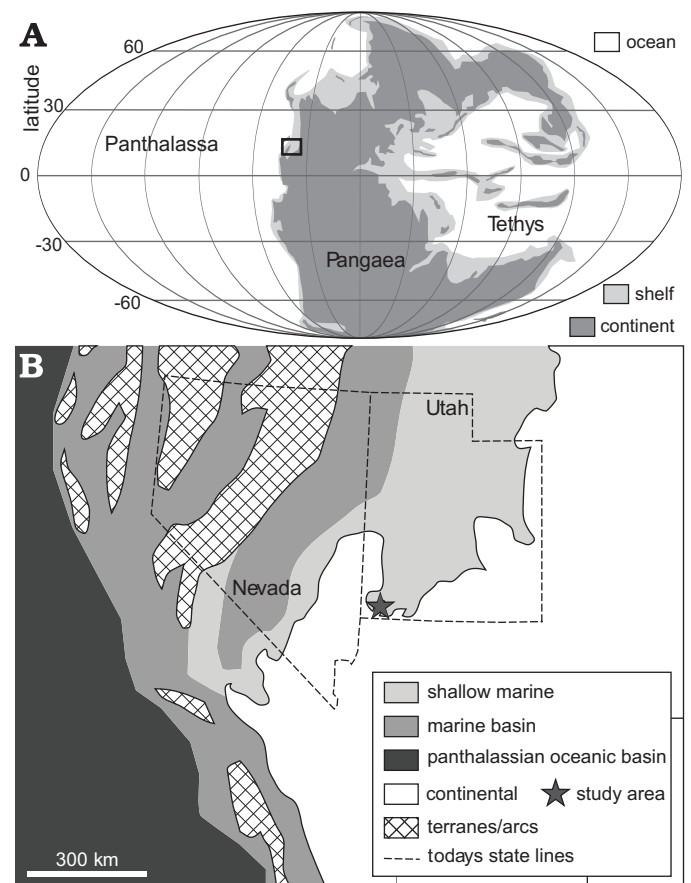


Fig. 3. Palaeogeographic restorations after Blakey (2011). **A.** Global palaeogeography of the Early Triassic. **B.** Early Triassic palaeogeography of the western USA.

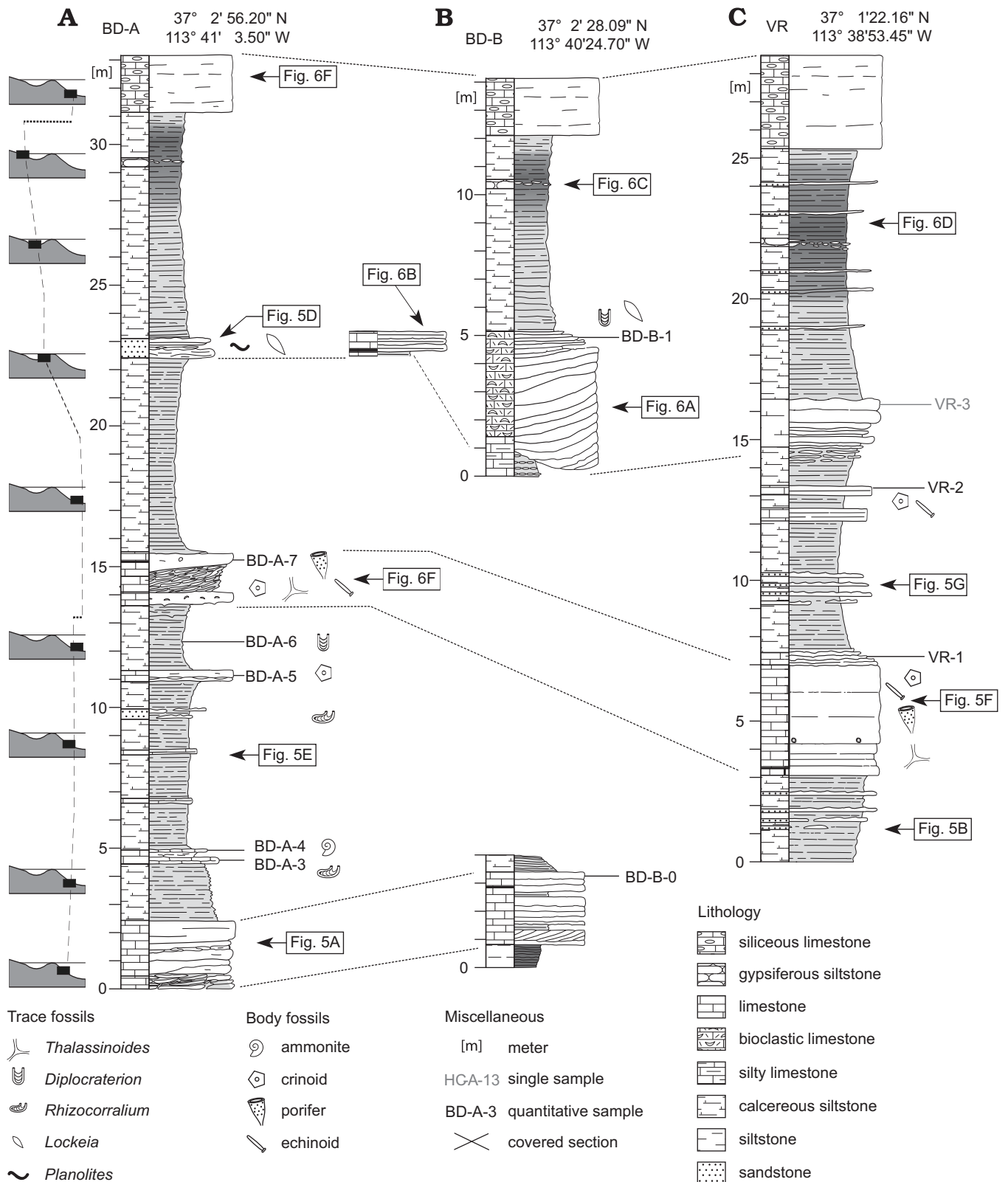
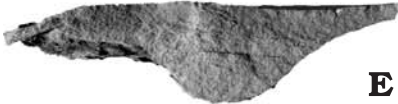
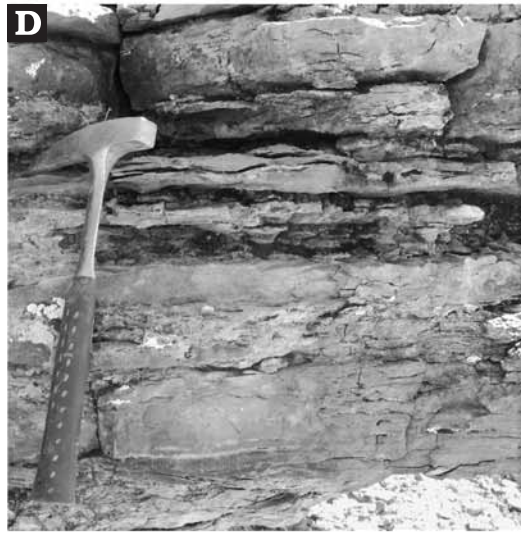


Fig. 4. Stratigraphic sections shown as weathering profile of the Spathian, Lower Triassic in the Beaver Dam Mountains area, Utah, USA. Bathymetric interpretation on the left. Locality map see Fig. 1B. A. Section BD-A. B. Section BD-B. C. Section VR.

mainly through cross-bedded and occasionally planar-bedded, sandy packstone and grainstone (Fig. 5A). These beds are interpreted as shallow subtidal bars of the shoreface zone. These

are succeeded by 12 m of maroon siltstone interbedded with thin limestone layers (BD-A) or massive and ripple cross-laminated, very fine-grained sandstone (VR; Fig. 5B). This points







to alternating suspension fall out under quiet water conditions and the activity of waves and currents. Accordingly, this interval is interpreted as deposits of the lowermost shoreface to offshore transition zone. Short transgressive events lead to the rhythmic deposition of discrete limestone beds. Evidence for erosional events possibly caused by minor storms is provided by the presence of small guttercasts (Fig. 5E) within the siliclastic intervals (Myrow 1992).

A second prominent unit of massive, silty and sandy limestone is observed in the middle part of the section BD-A (Fig. 5C) and within the lower half of section VR (Fig. 5F). These limestone beds record a transgressive event leading to a decline in siliclastic input. The presence of sponges in these beds suggests low detrital input, too. The amalgamated character of these massive limestone beds and the concentration of comparably large sponge fragments at the base of this interval suggest that these beds were deposited under storm influence in the lower shoreface zone. The beds are overlain by bluish-grey, highly calcareous siltstone interbedded with thin limestone beds (Fig. 5G). This siltstone interval is ca. 7 m thick and represents deposits of lower shoreface and offshore transition zone, similar to the lower siltstone beds with few limestone and rippled sandstone beds.

In the section BD-A and VR, this interval is overlain by a 1 to 1.5 m thick sequence of ripple cross-laminated, slightly calcareous sandstone showing flaser bedding and mud drapes (Fig. 5D). These sandstone beds most likely record tidal flat deposits of the lower intertidal zone. The same stratigraphic level in the BD-B section is represented by an up to 5 m thick succession of large scale through cross-bedded, bioclastic grainstone (Fig. 6A). These beds are incised into the underlying siltstones and show a channel-like morphology pinching out towards NW and SE, giving rise, laterally and horizontally to thin beds of parallel cross and planar bedded, bioclastic grainstone (Fig. 6B). These lithotypes are interpreted as tidal inlets deposits representing lateral equivalents of the tidal flat recorded in section BD-A and VR.

In all sections of the Beaver Dam Mountains area, the succeeding interval is composed of purple to reddish siltstone, occasionally interbedded with thin sandstone beds (Fig. 6D). In the upper third of this interval, gypsiferous levels are observed within red, massive to finely laminated siltstone (Fig. 6C). This succession is interpreted as upper intertidal mudflat deposits grading into a supratidal plain with possible early pedogenetic caliche horizons (Fig. 6D). This level is overlain by ca 0.5 m of yellow and bluish-grey, highly calcareous siltstone, once again, recording marine conditions (Fig. 6D). The top of the Virgin Formation is capped by massive, slightly siliceous, recrystallised lime-

stone with a thickness of 2–3 m (Fig. 6F). This unit is difficult to interpret because of the absence of macrofossils and indicative sedimentary structures.

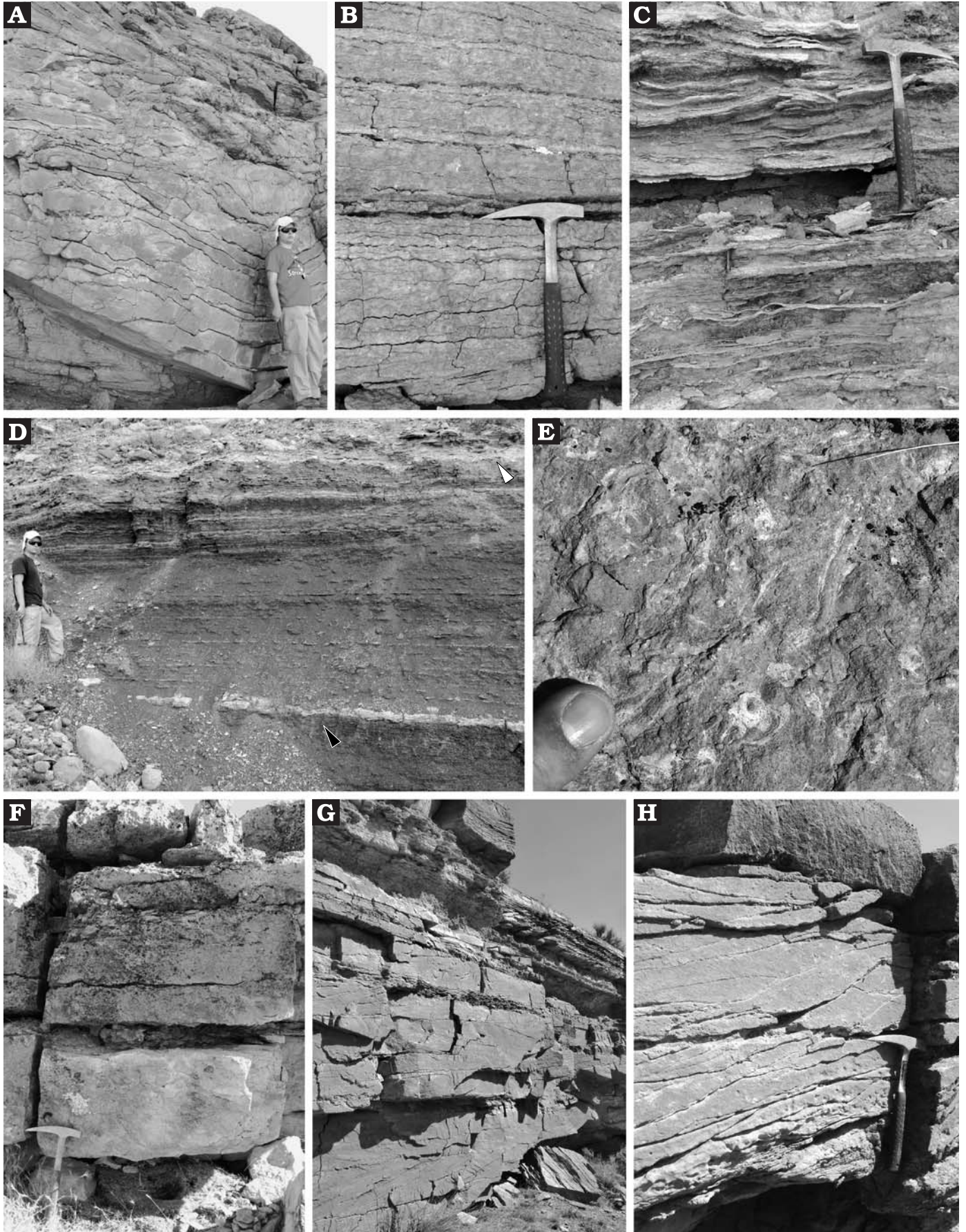
**Hurricane Cliff (sections HC-A, HC-B, HC-C, HC-D)** (Fig. 7).—In the sections cropping out east of the Hurricane Cliff, the Virgin Formation is up to 20 m thick, but as in the case of section HC-C, the base varies considerably, which leads locally to increased cumulative thicknesses. The lithological succession is variable and in particular the lowermost carbonate-dominated unit is different in some sections. These sections are treated separately in the following paragraphs.

**HC-A** (Fig. 7A).—Here, the base is developed as a 5 m thick succession of sandy limestone (Fig. 6G). The lower part is dominated by up to 1 m thick sets of cross-bedded grainstone alternating with thin planar-bedded, silty grainstone beds, which are highly bioturbated. Herring bone cross-stratification (Fig. 6G) and occasionally mud-drapes and sigmoidal cross bedding are frequently observed. All of these sedimentary structures suggest a strong tidal influence with alternating high energy flow regime and slack water periods and alternating current directions (Kreisa and Moiola 1986). These limestone beds alternate with thin, highly bioturbated horizons (Fig. 6E). The upper part of this lower limestone is dominated by thinly bedded, slightly heterolithic, silty limestone. The top is capped by trough cross-bedded grainstone (Fig. 6H). This complex is interpreted as tidal channel deposits or small scale tidal inlets of the lowermost intertidal to shallow subtidal zone.

These beds are overlain by a succession of bluish-grey, calcareous siltstone and fine-grained sandstone which most likely record the deposition around the upper offshore transition and the lower shoreface. This interval is followed by 50 cm of alternating laminated siltstone and ripple cross-laminated, fine-grained sandstone showing flaser bedding and slight bioturbation (lowest bed in Fig. 8A). The following 1.5 meters are composed of maroon, very finely-laminated, slightly heterolithic siltstone beds (Fig. 8A). This whole siliclastic dominated interval most likely represents a shallowing-upward succession ranging from lower shoreface zone to an intertidal succession that includes sand-dominated mixed flat deposits of lower intertidal zone and deposits of upper intertidal mudflats (Klein 1971).

At 8.5 m, 2 meters of bluish grey siltstones, similar to those in the lower part of this fine-grained interval occur. The base of this siltstone is slightly irregular (Fig. 8A). A 30 cm thick bed of massive and ripple cross-laminated sandstone and siltstone is intercalated within this siltstone interval. This siltstone-dominated part of the section is capped by ca. 1 m

← Fig. 5. Sedimentary facies of the Spathian, Lower Triassic in the Beaver Dam Mountains area, Utah, USA. **A.** Subtidal bars composed of trough cross-bedded grainstone at the base of the Virgin Formation at section BD-A. **B.** Claystone interbedded with thin beds of fine-grained sandstone deposited in the offshore transition. Base of section VR. The height of the exposure is 1.80 m. **C.** Ledge of sandy and silty limestone deposited in the lower shoreface. Lower part of section BD-A. **D.** Fine-grained sandstone showing flaser bedding of the sand flat facies. Upper part of Section BD-A. Hammer for scale. **E.** Cross sectional view of a gutter cast from the lower siltstone interval of section BD-A. **F.** Massive, amalgamated grain, and packstone of the lower shoreface. Lateral equivalent to the bed shown in Fig. 5C. Section VR. Height of exposure is 4 m. **G.** Interbeddings of calcareous siltstones and thin limestone. Section VR. The hammer is 35 cm long.





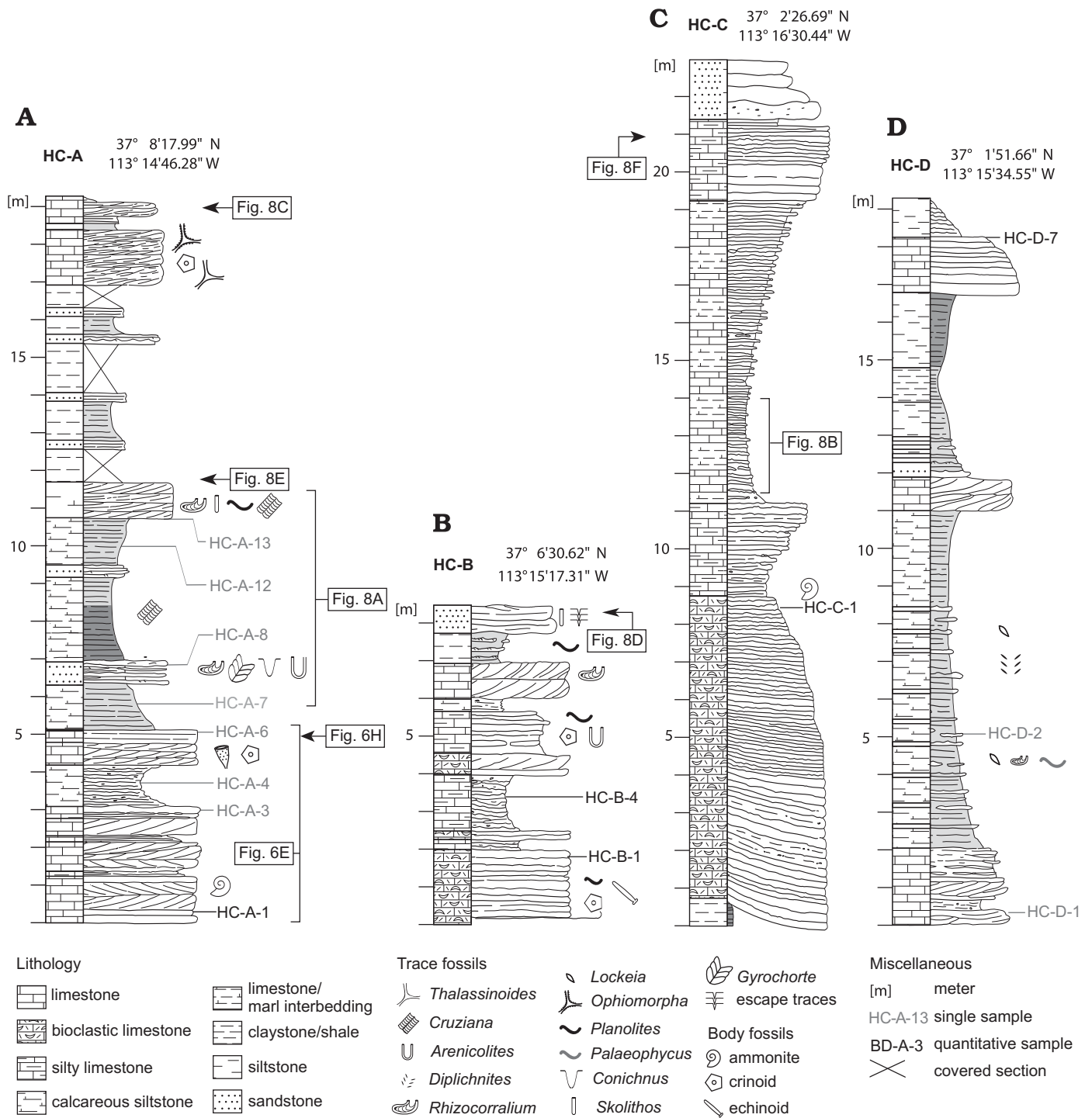


Fig. 7. Stratigraphic sections shown as weathering profile of the Spathian, Lower Triassic in the Hurricane Cliffs area, Utah, USA. See Fig. 1B for locality map. A. Section HC-A. B. Section HC-B. C. Section H-C. D. Section HC-D.

← Fig. 6. Sedimentary facies of the Spathian, Lower Triassic in the Beaver Dam Mountains and the Hurricane Cliffs area, Utah, USA. A. Large scale trough cross-bedded grainstone of the tidal inlet facies at section BD-B. B. Lateral equivalent of the same bed as in A showing parallel bedding of skeletal grainstone. Hammer for scale. C. Gypsiferous siltstone of the supratidal and continental red bed facies in the upper part of section BD-B. D. The same interval as shown in C at the section VR. The black arrow head points to a discrete horizon characterised by nodular gypsum. In the upper part (white arrow head), marine calcareous siltstones mark a short transgression at the close of the marine Virgin deposition. E. Highly bioturbated bedding plane dominated by *Palaeophycus* observed in the basal limestone unit of Section HC-A. F. Siliceous limestone capping the section BD-A. Hammer for scale. G. Basal limestone unit of the section HC-A showing abundant and various types of cross bedding. Height of exposure is 5 m. H. Top of the basal limestone unit at section HC-A showing trough cross-stratified grainstone beds. The hammer is 35 cm long.

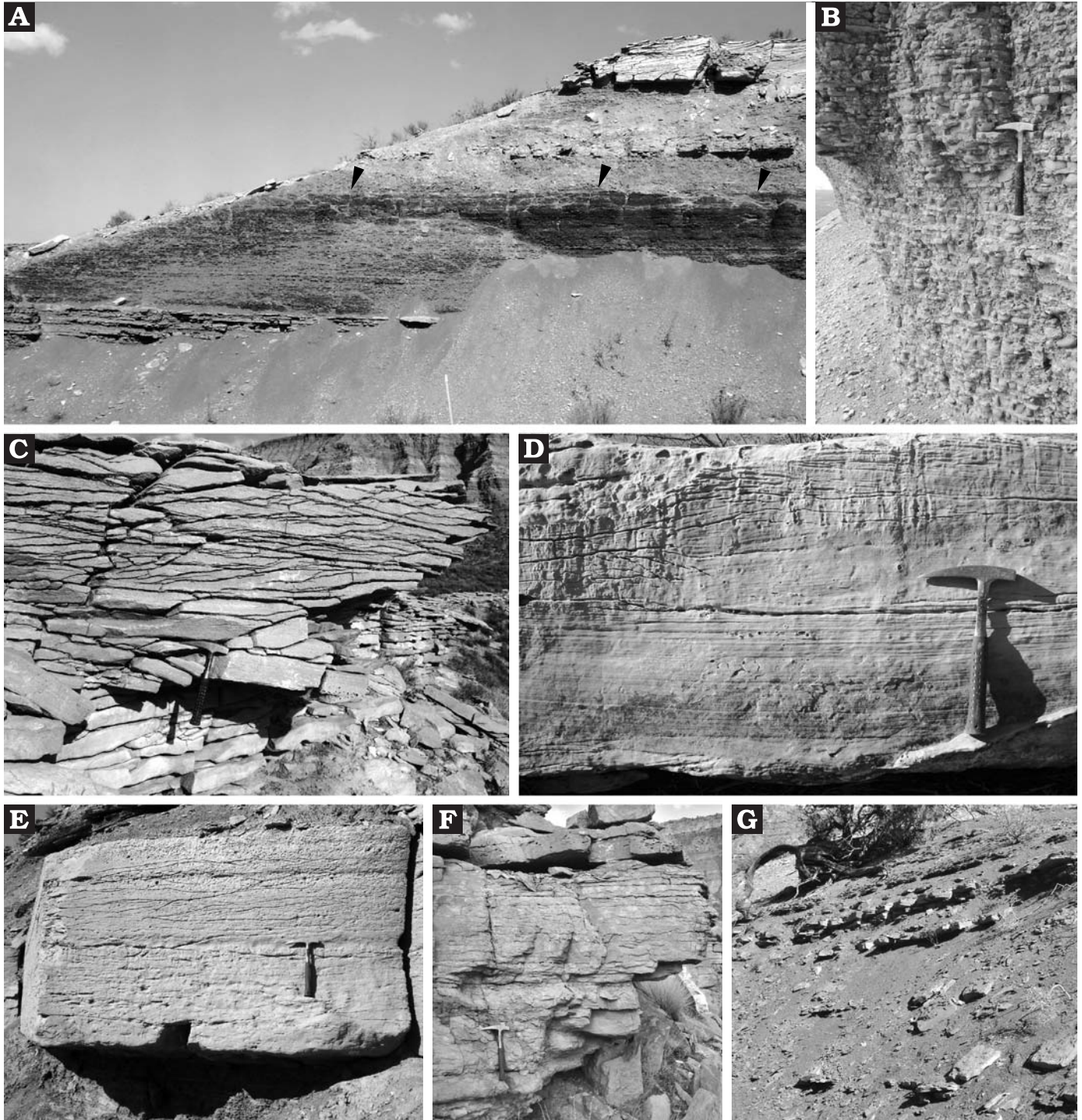


Fig. 8. Sedimentary facies of the Spathian, Lower Triassic in the Hurricane Cliffs area, Utah, USA. **A.** Middle part (~6–12 m) of the Virgin Formation at section HC-A showing the transition between lagoonal and intertidal siltstone to the overlying open marine siltstone. The black arrow heads point to the transgressive surface. Height of exposure is 6 m. **B.** Alternating marls and limestone in the middle part of the section HC-C interpreted as channel fill of the tidal inlet complex. **C.** Trough cross-bedded, highly sandy limestone of the upper shoreface capping the section HC-A. **D.** Hummocky cross-bedded sandstone with *Skolithos* isp. forming the top of section HC-B. **E.** Sandy limestone of the shoreface in the middle part (11 m) of section HC-A. **F.** Parallel stratified grainstone beds forming the topmost beds of HC-C. **G.** Lagoonal siltstone of the lower part of section HC-D. Height of exposure is 3 m. The hammer is 35 cm long.

thick, trough cross-bedded sandy packstone (Fig. 8E). The remaining part of the section is composed of alternating grey siltstone intercalated with some thin fine-grained sandstone. The top is composed of trough cross-bedded sandy limestone

(Fig. 8C). The fine-grained intervals in this upper part are largely covered, which makes facies identification difficult. Mata and Bottjer (2011) interpreted this portion as deposits of the offshore transition zone. However, the top of the sec-



Table 1. Body fossils found in the Spathian, Lower Triassic Virgin Formation during this study and their ecological classification. Mode of life: n, nektonic; mi, mobile infaunal; ssi, stationary semi infaunal; se, stationary epifaunal; me, mobile epifaunal. Trophic groups: sf, suspension feeder; df, deposit feeder; c, carnivore; g, grazer; psc, primary or secondary consumer. Echinodermata and ichnia were not included in the cluster analysis.

	Species	Trophic guild
Bivalvia	Astartidae spp.	mi, sf
	<i>Bakevellia costata</i> (Schlotheim, 1820)	ssi sf
	<i>Bakevellia exporrecta</i> (Lepsius, 1878)	ssi sf
	<i>Eumorphotis</i> cf. <i>venetiana</i> (Hauer, 1850)	se sf
	<i>Eumorphotis</i> cf. <i>multiformis</i> (Bittner, 1899)	se sf
	<i>Eumorphotis ericius</i> Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	<i>Eumorphotis virginensis</i> Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	<i>Leptochondria curtocardinalis</i> (Hall and Whitfield, 1877)	se sf
	<i>Leptochondria nuetzeli</i> Hautmann, Smith, McGowan, and Bucher, 2013	se sf
	<i>Myalinella</i> sp. A	me, sf
	<i>Neoschizodus laevigatus</i> (Zieten, 1830)	mi, sf
	<i>Pernopecten</i> sp. A	me, sf
	<i>Promyalina putiatinensis</i> (Kiparisova, 1938)	se sf
	<i>Promyalina spathi</i> (Newell and Kummel, 1942)	se sf
	<i>Protopsis</i> sp.	se sf
	<i>Sementiconcha recuperator</i> Hautmann, Smith, McGowan, and Bucher, 2013	mi, sf
	<i>Trigonodus</i> cf. <i>sandbergeri</i> Alberti, 1864	mi, sf
	<i>Trigonodus</i> cf. <i>orientalis</i> Alberti, 1864	mi, sf
	<i>Unionites</i> cf. <i>canalensis</i> (Catullo, 1846)	mi, sf
	<i>Unionites</i> cf. <i>fassaensis</i> (Wissmann in Münster, 1841)	mi, sf
Gastropoda	<i>Natiria</i> cf. <i>costata</i> Münster, 1841	me, g
	Gastropod ind. A	me, g
Ammonoida	<i>Tirolites</i> sp. A	n, psc
	Ammonite ind. A	n, psc
	Ammonite ind. B	n, psc
Brachiopoda	<i>Piarorhynchella triassica</i> (Girty in Mansfield, 1927)	se, sf
	<i>Protogusarella smithi</i> Perry and Chatterton, 1979	se, sf
Porifera	<i>Cypellospongia</i> sp. A	se, sf
Echinodermata	<i>Holocrinus smithi</i> (Clark in Clark and Twitchell, 1915)	se, sf
	<i>Miocidaris utahensis</i> (Kier, 1968)	me, g
Ichnia	<i>Conichnus</i> isp.	se, sf
	<i>Cruziana problematica</i> (Schindewolf, 1928)	me, df/c
	<i>Diplichnites</i> isp.	me, df/c
	<i>Diplocraterion</i> isp.	mi, sf
	<i>Gyrochorte</i> cf. <i>comosa</i> Heer, 1865	mi, df
	<i>Lockeia siliquaria</i> James, 1879	mi, sf
	<i>Ophiomorpha</i> isp.	mi, df
	<i>Palaeophycus tubularis</i> Hall, 1847	mi, sf/c
	<i>Planolites montanus</i> Richter, 1837	mi, df
	<i>Rhizocorallium</i> isp.	mi, sf
	<i>Spongiomorpha</i> isp.	mi, df
	<i>Skolithos</i> isp.	mi, sf
	<i>Thalassinoides</i> cf. <i>suevicus</i> (Rieth, 1932)	mi, df
	Arthropod trackway	mi,df/c

tion HC-D, which is likely to represent a lateral equivalent, is herein suggested as representing lagoonal deposits (see section HC-D). The following grainstone beds, which are mainly composed of crinoidal debris, are similarly difficult to interpret because trough cross bedded crinoidal limestone occur in various settings ranging from shallow to deep ma-

rine as discussed in Mata and Bottjer (2011). However, the finding of a comparatively large articulated columnal segment of *Holocrinus smithi* (Fig. 9E) suggests that these beds record conditions very close to the living site of the crinoids, which were bound to shallow water conditions during Palaeozoic and Mesozoic times. We therefore suggest that

Table 2. Data matrix showing absolute abundances of species in the samples. Occurrences of *Holocrinus smithi* and *Miocidaris utahensis* are estimated and were not included in the cluster analysis. Abbreviations: a, abundant; c, common; r, rare; vr, very rare.

Species	Samples													
	BD-A-4	BD-A-6	HC-A-1	VR-1	BD-A-7	BD-A-5	BD-B-1	BD-B-0	VR-2	BD-A-3	HC-B-1	HC-C-1	HC-B-4	HC-D-7
<i>Astartidae</i> sp. A	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Bakevella costata</i>	0	0	1	1	8	1	0	7	0	8	0	0	5	37
<i>Bakevella exorrepta</i>	103	25	12	7	0	0	7	19	0	34	0	2	0	0
<i>Eumorphotis</i> cf. <i>venetiana</i>	1	0	0	0	4	1	0	11	0	0	0	0	6	0
<i>Eumorphotis</i> cf. <i>multiformis</i>	5	0	0	6	5	0	0	3	3	0	0	3	0	1
<i>Eumorphotis ericius</i>	3	0	0	12	36	9	21	9	35	31	0	1	0	0
<i>Eumorphotis virginensis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Leptochondria curtocardinalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Leptochondria nuetzeli</i>	41	40	0	5	4	0	0	0	0	14	0	0	0	0
<i>Myalinella</i> sp. A	0	0	0	0	6	0	0	0	0	1	0	0	0	0
<i>Neoschizodus laevigatus</i>	0	0	0	5	0	0	0	0	3	0	0	0	0	0
<i>Pernopecten</i> sp. A	0	0	0	0	5	1	0	0	1	0	0	0	0	0
<i>Promyalina putiatinensis</i>	3	0	11	9	10	2	40	7	39	5	0	0	1	0
<i>Promyalina spathi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	15
<i>Protopis</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Sementiconcha recuperator</i>	89	0	0	0	0	0	0	3	1	19	0	0	0	0
<i>Trigonodus</i> cf. <i>sandbergi</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Trigonodus</i> cf. <i>orientalis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Unionites canalensis</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Unionites fassaensis</i>	2	0	0	0	1	0	0	3	2	4	0	0	0	0
<i>Natiria</i> cf. <i>costata</i>	0	0	0	0	0	0	0	2	0	2	0	0	0	0
Gastropod ind. A	0	0	1	0	1	0	0	6	0	1	0	1	0	0
<i>Piarorhynchella triassicus</i>	4	0	0	0	4	1	100	24	31	2	20	97	0	0
<i>Protogusarella smithi</i>	0	0	0	0	12	0	400	50	48	59	5	2	0	0
Ammonite ind. A	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tirolites</i> sp. A	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Ammonite ind. B	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Cypellospongia</i> sp. A	0	0	0	0	7	2	0	0	0	0	0	0	0	0
<i>Holocrinus smithi</i>	0	0	0	c	c	c	0	r	c	0	r	0	c	0
<i>Miocidaris utahensis</i>	0	0	0	r	a	c	r	vr	c	0	c	r	0	0

the upper part of the section HC-A represents shallow subtidal bars alternating with quiet water conditions of protected marginal marine embayments.

**HC-B** (Fig. 7B).—This ca. 8 m thick interval largely corresponds with the lower series of limestone beds of section HC-A. The first five meters are readily comparable, although, the thicknesses of the silty limestone beds are variable in comparison to HC-A. These beds are interpreted as deposits of the shoreface zone as well. The base of the shaly interval from section HC-A is here marked by an interval of siltstones containing patches of fine-grained ripple cross-laminated sandstone capped by a 30-cm-thick bed of fine-grained hummocky cross stratified sandstone (Fig. 8D). This supports the interpretation of this interval as deposits of the

lowermost shoreface and upper offshore transition (Cheel and Leckie 1993).

**HC-C** (Fig. 7C).—The first 9 m of this section are entirely composed of large-scale through cross-bedded bioclastic grainstone beds. Individual beds are variable in thickness, ranging from 3 cm to 20 cm and are occasionally separated by mud drapes. This interval varies laterally on outcrop scale, pinching out within less than 200 meters towards the north. These beds grade upsection into a 2.5 m thick interval of sandy, planar-bedded grainstone.

The next 8 m of this section comprise rhythmic interbeddings of 3–5 cm thick marlstone and 1–4 cm thick limestone beds (Fig. 8B). Internal sedimentary structures are not observed. This interval shows a thickening upward cycle



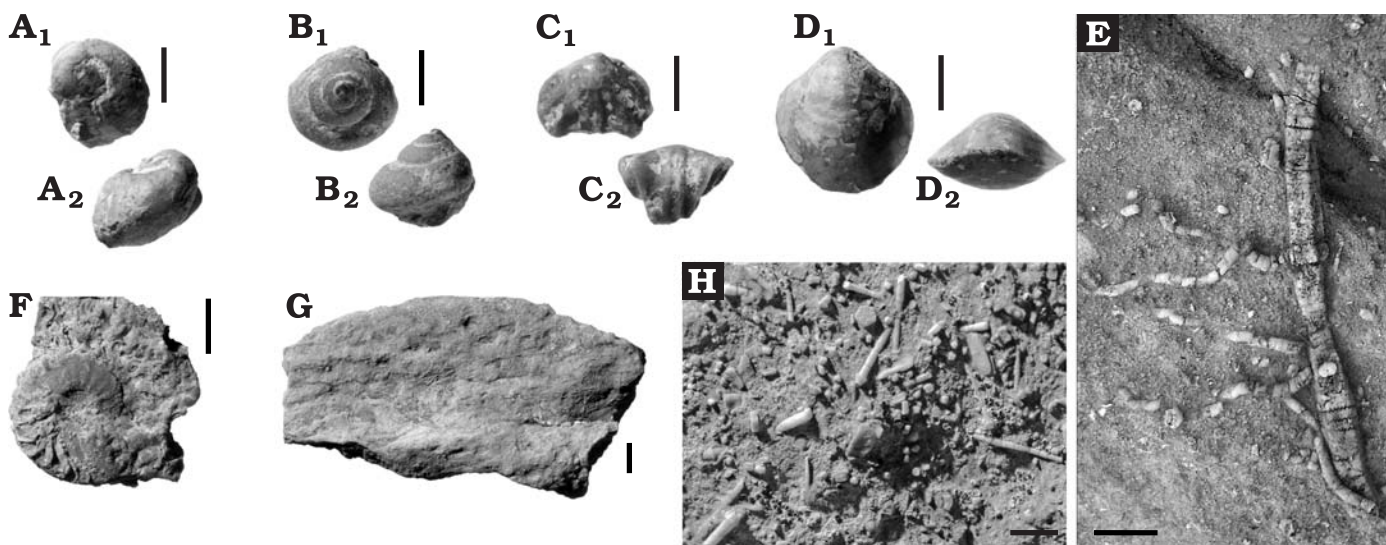


Fig. 9. Fossils of the Spathian (Lower Triassic) Virgin Formation, Utah, USA. A. *Natiria* cf. *costata*, PIMUZ29595. B. Gastropod ind. A, PIMUZ29594. C. *Piarorhynchella triassica*, PIMUZ29589. D. *Protogusarella smithi*, PIMUZ29612. E. Field photograph of *Holocrinus smithi*, specimen not collected. Topmost limestone of Section HC-A. F. *Tirolites* sp. A, PIMUZ29591. G. *Cypellospongia* sp. A, PIMUZ29598. H. Spines of *Miocidaris utahensis*, PIMUZ29611. Scale bars 5 mm.

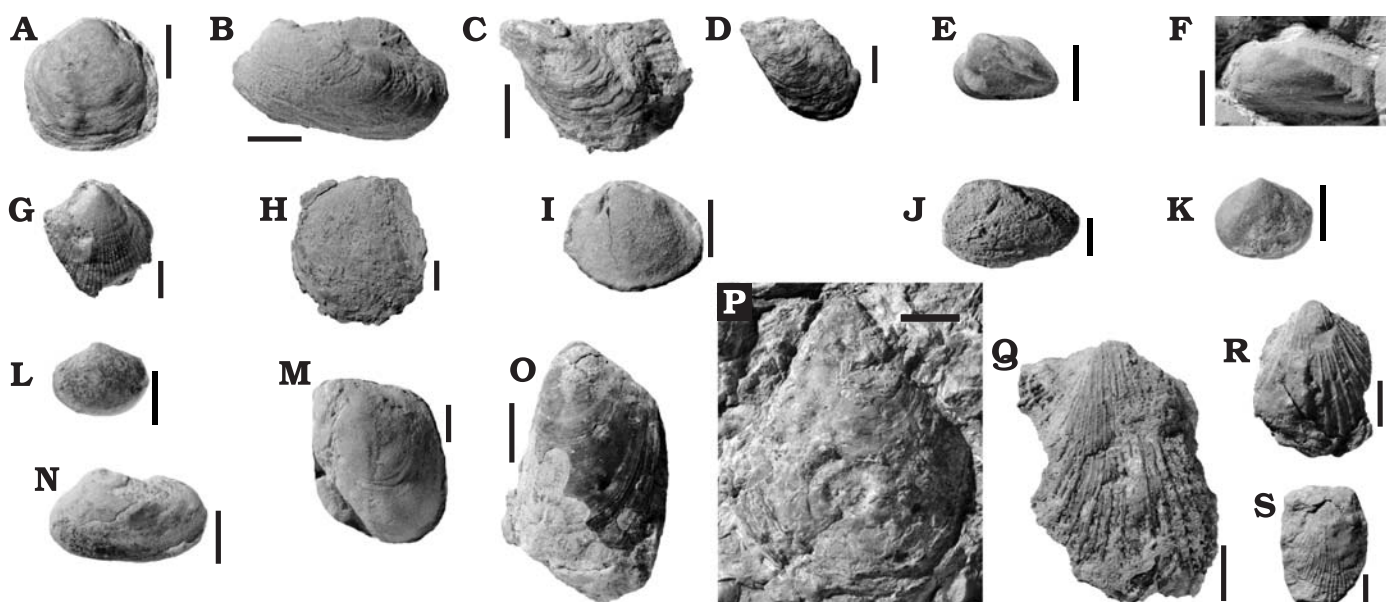


Fig. 10. Fossil bivalves from the Spathian (Lower Triassic) Virgin Formation, Utah, USA. A. *Astartidae* sp. A, PIMUZ29588. B. *Bakevellia exporrecta*, PIMUZ29592. C. *Bakevellia costata*, PIMUZ29614. D. *Myalinella* sp. A, PIMUZ29597. E. *Sementiconcha recuperator*, PIMUZ29600. F. *Protopsis* sp. A, PIMUZ29609. G. *Leptochondria nuetzeli*, PIMUZ29615. H. *Eumorphotis virginensis*, PIMUZ29616. I. *Neoschizodus laevigatus*, PIMUZ29599. J. *Trigonodus* cf. *sandbergeri*, PIMUZ29603. K. *Trigonodus* cf. *orientalis*, PIMUZ29604. L. *Unionites* cf. *fassaensis*, PIMUZ2960. M. *Promyalina spathi*, PIMUZ296102. N. *Unionites* cf. *canalensis*, PIMUZ29596. O. *Promyalina putiatinensis*, PIMUZ29601. P. *Pernopecten* sp. A., PIMUZ29590. Q. *Eumorphotis ericius*, PIMUZ29587. R. *Eumorphotis* cf. *multiformis*, PIMUZ29613. S. *Eumorphotis* cf. *venetiana*, PIMUZ29593. Scale bars 5 mm; except O, P, Q 10 mm.

with decreasing thickness of the marlstone beds. The unit is capped by a 2 m thick interval of planar bedded sandy limestone (Fig. 8F). The top of the section is made up of 1.5 m of slightly calcareous, fine-grained sandstone. This whole succession is interpreted as a large tidal inlet complex with a subsequent channel fill.

**HC-D** (Fig. 7D).—This 19 m thick succession is composed

of an alternation of fine-grained, shale-dominated intervals with some prominent limestone ledges. The lowermost 2 m comprise trough cross-bedded, highly sandy grainstone and silty, indistinctly planar bedded packstone, and grainstone. Mud drapes are frequently observed along individual cross sets. This lower unit is interpreted as shallow subtidal to lower intertidal deposits. The following 9 m thick interval (Fig. 8G) is composed of slightly calcareous siltstone beds,

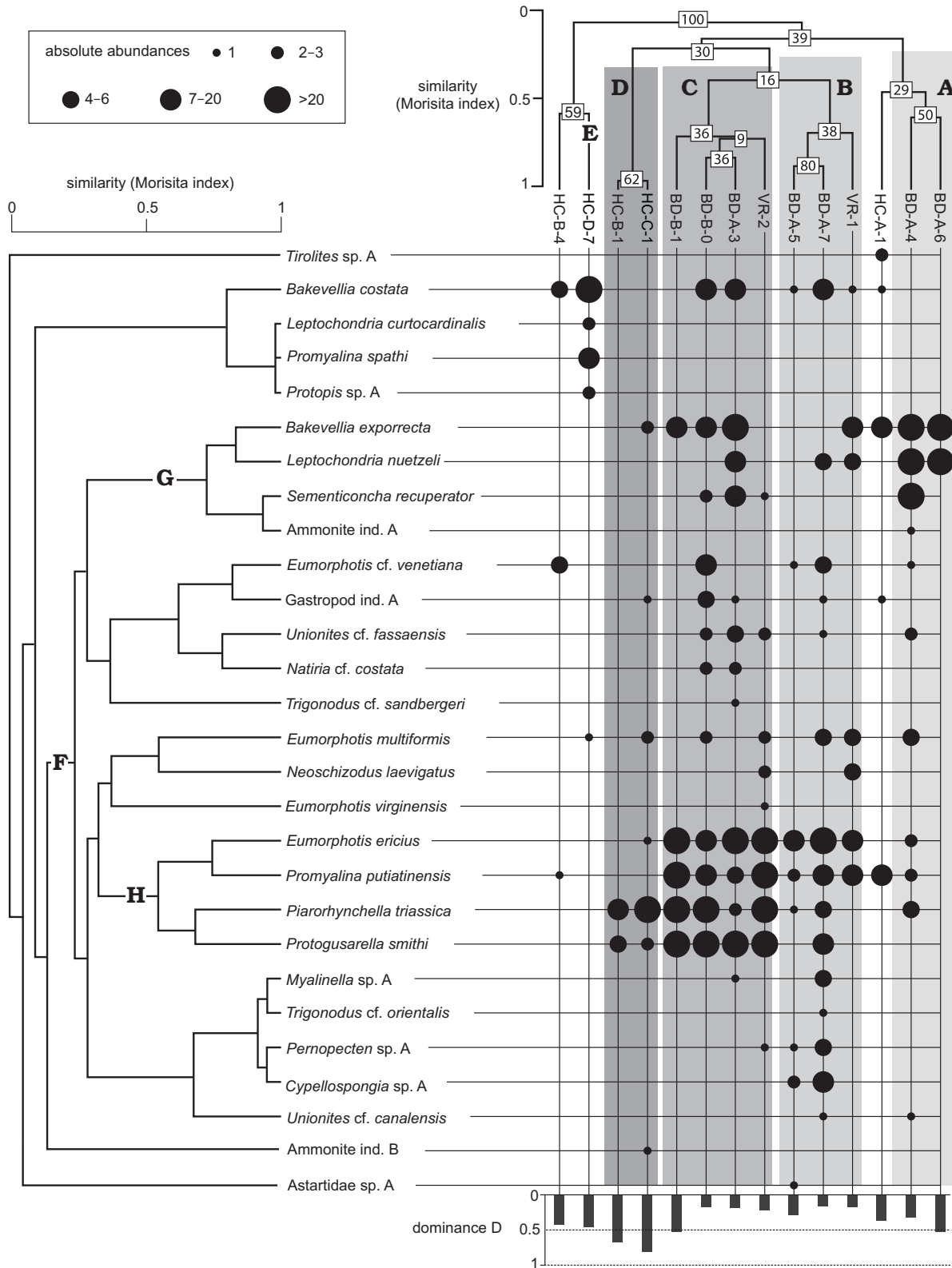


Fig. 11. Q (samples) and R-mode (species) cluster analysis using the unweighted paired group algorithm and Morisita index of similarity. Classes of abundances (circle size) represent the quintiles of absolute-abundance frequencies. Bootstrap values are shown in the white boxes within the Q-mode cluster. Dominance is given as  $D = 1 - \text{Simpson index}$ . **A.** *Bakevella exporrecta* Association. **B.** *Eumorphotis ericius* Association. **C.** *Protogusarella smithi* Association. **D.** *Piarorhynchella triassica* Association. **E.** *Bakevella costata* Assemblage. **F.** Main R-mode cluster incorporating the nuclei of several associations. **G.** Subcluster reflecting the nucleus of the *Bakevella exporrecta* Association and it probably incorporates those species, which are adapted to low energy, softground conditions. **H.** Subcluster reflecting the nuclei of the *Eumorphotis ericius* Association and *Protogusarella smithi* Association, and it incorporates species adapted to high energy, near shore conditions.



which are intercalated with thin, fine-grained, combined flow ripple cross-laminated sandstone beds that yield comparably well preserved trace fossils (see chapter Biological sedimentary structures) and wrinkle marks. This shale interval predominantly records quiet water conditions. Some characteristics such as the lack of marine body fossils, and the presence of discrete rippled sandstone beds points to deposition within a protected embayment or lagoon. A 1 m thick bed of trough cross-bedded grainstone is developed above. The next 5 m are composed of shale similar to those described above. However, the uppermost 1.5 m are maroon in colour, and rippled sandstone is absent. The section is capped by 2 m of planar bedded sandy and silty limestone, which grade upwards into thin, indistinctly planar bedded siltstone. This upper part is interpreted as deposits of a marginal marine embayment.

## Palaeoecology of the Virgin Formation

**The Virgin fauna.**—In terms of abundance and diversity, the main constituents of the Virgin fauna are bivalves with 20 species reported herein. Locally, numerical dominant elements are brachiopods (two species). More rarely recorded are gastropods (two species) and sponges (one species). Echinoids and crinoids are represented by one species each. Nekton is represented by rare finds of ammonites (three species), which are presented in open nomenclature due to their poor state of preservation. In general, our study confirms the taxonomic composition and overall diversity of recent analyses of the Virgin Formation (McGowan et al. 2009; Hautmann et al. 2012). The whole faunal content is shown in Table 1. All body fossils mentioned in this study are illustrated in Figs. 9 and 10.

**Results of the Q-mode cluster analysis (faunal associations and assemblages).**—In the Q-mode cluster analysis, samples are grouped into clusters that are similar with respect to presence and abundance of taxa. The result of the cluster analysis is shown in Fig. 11. Absolute abundance data for each sample are given in Table 2. There are four associations (recurrent assemblages) and one assemblage recognised in the data set, which in the first place reflect varying abundances rather than a different content of taxa. Owing to the homogenous composition of the Virgin fauna, groupings of samples are not very robust. Bootstrap values (Fig. 11) indicate that most branches show low reproducibilities.

**Bakevella exporrecta Association.**—This association (Fig. 12) is represented by the samples BD-A-4 and BD-A-6. The trophic nucleus comprises semi-infaunal (*Bakevella exporrecta*) and epifaunal bivalves (*Leptochondria nuetzeli*). In BD-A-4, the shallow infaunal (*Sementiconcha recuperator*) is extremely abundant, and a few other, mostly epifaunal bivalves are recorded in very small numbers (e.g., *Eumorphotis*

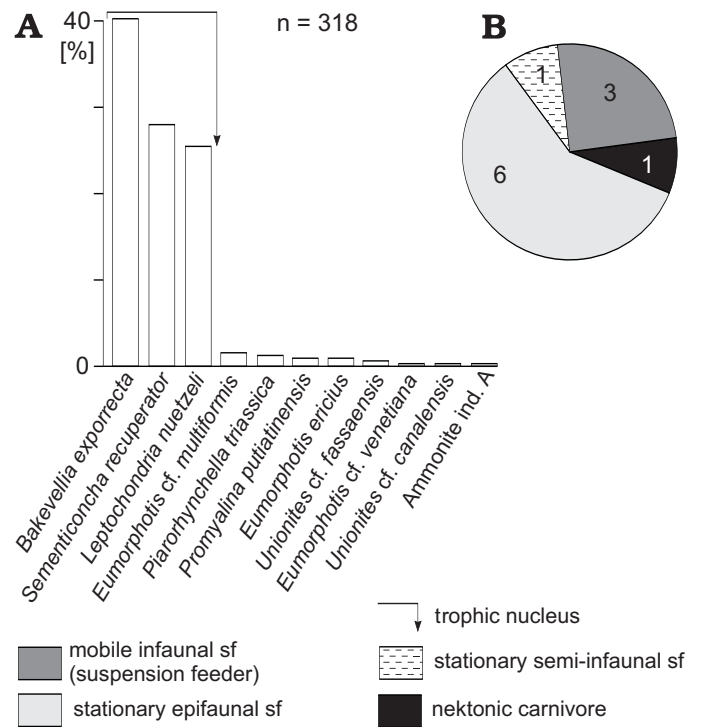


Fig. 12. Characteristics of the *Bakevella exporrecta* Association showing frequency distribution and trophic nucleus (A) and ecological structure (B). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

*ericus*, *Promyalina putiatinensis*). Species richness ranges from 2 to 11 (mean average = 6.5) and dominance D is relatively high, ranging from 0.32 to 0.53 (mean average = 0.42). The higher diversity in BD-A-4, which reflects rare occurrences of taxa that typically occur in other faunas, suggests that there might be some time averaging involved (Fürsich and Aberhan 1990). Since the trophic nucleus of both samples is very similar, it can be assumed that the habitats were not fundamentally different. However, the higher portion of epibyssate bivalves in the sample BD-A-4 may result from more firm substrate conditions provided by the limestone bed in which the fossils were observed. In contrast, BD-A-6 is exclusively derived from a shaly interval, which originally provided poorly consolidated substrate conditions. This interpretation is supported by the high numerical abundance of semi-infaunal (*B. exporrecta*) and infaunal (*Sementiconcha recuperator*) bivalves in the trophic nucleus of this sample.

**Eumorphotis ericius Association.**—This association (Fig. 13) is recorded by the samples BD-A-5, BD-A-7, and VR-1 and comprises the most diverse faunas. The trophic nucleus is represented by epifaunal bivalves (*Eumorphotis ericius*, *Eumorphotis cf. multiformis*, *Promyalina putiatinensis*, and *Leptochondria nuetzeli*), epifaunal brachiopods (*Protogusarella smithi*), semi-infaunal bivalves (*Bakevella exporrecta* and *Bakevella costata*) and sponges (*Cypellospongia* sp. A). In all samples of this assemblage, echinoderms are very common (*Holocrinus smithi* and *Miocidaris utahensis*). Species

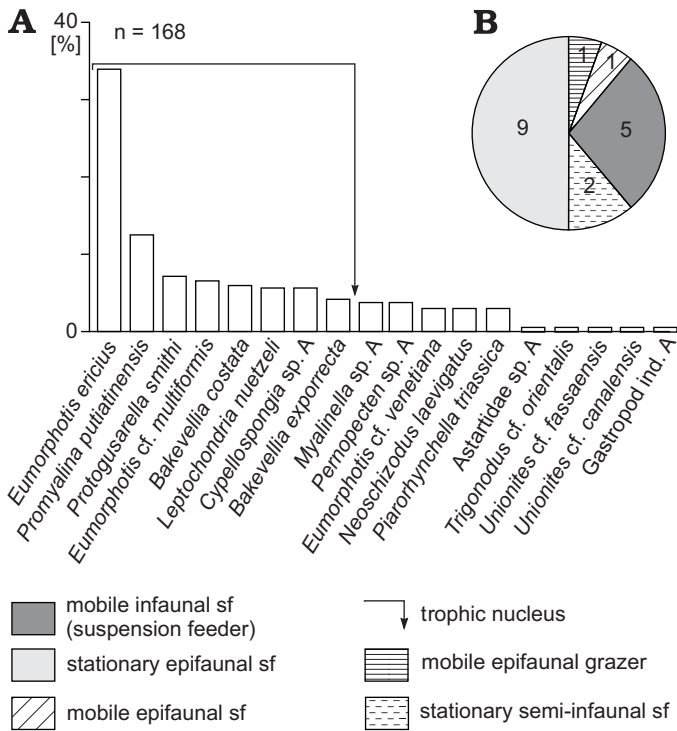


Fig. 13. Characteristics of the *Eumorphotis ericius* Association showing frequency distribution, trophic nucleus (A) and ecological structure (B). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

richness ranges from 7 to 15 (mean average = 10). The dominance is low and ranges from 0.16 to 0.29 (mean average = 0.21). This association is exclusively recorded in thin to medium bedded limestone of the lower shoreface to proximal offshore transition zone. Specimen size of the shelly fauna is, in general, highly variable, which suggests that the samples are unaffected by size sorting or alteration by waves or currents. Bivalve shells are usually separated, but very little fragmentation and the lack of graded bedding points to negligible reworking by storms. These taphonomic characteristics and the relatively high species-overlap among individual samples suggest that this association records an autochthonous to para-autochthonous community. The beds recording this assemblage are composed of slightly siliclastic limestone, which was deposited in the inner and proximal outer shelf zone. Ecologically, this fauna is dominated by stationary, attached epifaunal and infaunal suspension feeders, which points to a soft but consolidated substrate. Although represented by few species with a rather low abundance, most other trophic groups of the Virgin fauna are recorded within this association, indicating unstressed ecological conditions. The high diversity and the presence of stenohaline organisms (echinoderms and sponges) suggest normal, fully marine conditions.

**Protogusarella smithi Association.**—A high diversity association (Fig. 14) is recorded by the samples BD-A-3, BD-B-1, BD-B-0, and VR-2, which is characterised by high abun-

dances of epifaunal brachiopods (*Protogusarella smithi*, *Piarorhynchella triassica*) and epifaunal bivalves (*Eumorphotis ericius* and *Promyalina putiatinensis*). A semi-infaunal bivalve species (*Bakevellia exporrecta*) is locally abundant. The faunal composition of this association is quite heterogeneous, and many of the bivalve and gastropod species recorded in the Virgin Formation are spread within these samples. Debris of echinoderms is very frequent. Species richness ranges from 5 to 13 (mean average 10). This association shows comparably low dominance values (0.18–0.53, mean average 0.28). Similar to the *Eumorphotis ericius* Association, this fauna shows little evidence for reworking and, thus, is herein considered to record a palaeocommunity. The ecological structure is also very similar to the *Eumorphotis ericius* Association, but the dominance of epifaunal suspension feeders is much higher due to the high abundance of the brachiopods *Protogusarella smithi* and *Piarorhynchella triassica* in the sample BD-B-1. The sedimentological framework of this fauna is comparable to that of the previous association, but the somewhat higher thicknesses and the position within the sections indicate that the beds containing this fauna were deposited in slightly shallower waters with more persistent high current velocities.

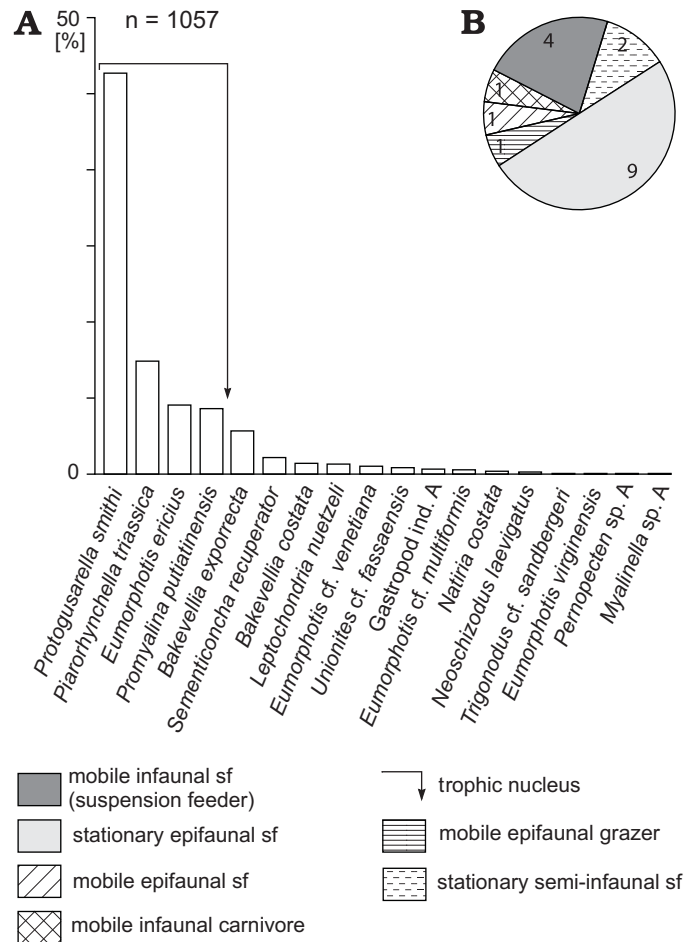


Fig. 14. Characteristics of the *Protogusarella smithi* Association showing frequency distribution, trophic nucleus (A) and ecological structure (B). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

Abundant echinoderm fragments point to normal marine conditions.

***Piarorhynchella triassica* Association.**—This association (Fig. 15A, B) is represented by the samples HC-C-1 and HC-B-1 and yields epifaunal brachiopods (*Piarorhynchella triassica* and *Protogusarella smithi*) as the most dominant elements. In only one sample, some epifaunal bivalves are recorded in low numbers. Species richness is between 2 and 7 (mean 3.5). Dominance is highest in these samples (0.68–0.82, mean 0.75). *P. triassica* is frequently observed in life position, indicating that this element of the community is largely autochthonous. Other faunal elements are relatively rare, but the prevalence of complete shells suggests that they were transported over short distances or lived near this habitat. This association is exclusively recorded in calcareous foreshore and tidal inlet deposits. The high dominance most likely reflects the high abiotic stress which is provided by persisting currents in very shallow waters.

***Bakevellia costata* Assemblage.**—This assemblage (Fig. 15C, D), dominated by a semi-ifaunal bivalve (*Bakevellia costata*), is represented by one sample only, with a quite unique composition comprising epifaunal bivalves (*Promyalina spathi*, *Protopis* sp., and *Leptochondria curtocardinalis*) observed in this bed only. Richness is low (5 species) and dominance is moderate ( $D = 0.46$ ). The ecological structure of this community is very simple, with two trophic guilds present. Echinoderms were not observed. This fauna is recorded in marlstone beds with densely packed specimens, and the sedimentary facies is difficult to interpret. Adjacent strata (upper part of section HC-D) point to a marginal marine environment (see depositional environment HC-D on p. 163). The shells are not oriented, and sizes are variable, which suggests that the fauna is not highly reworked or sorted by currents. However, since this assemblage is represented by a single sample, it contributes only little data, and its low diversity should not be overemphasised.

**Results of the R-mode cluster analysis (grouping of species).**—The grouping of species roughly indicates which taxa have similar occurrence patterns in a set of samples. Although this information is of lesser significance for community analysis than the Q-mode algorithm (Gahr 2002), it can help to refine the interpretation of sample associations (e.g., Ludvigsen and Westrop 1983; Brinkman et al. 2004). As presented in Fig. 11, some groups can be recognised. Branches that comprise only one taxon but are well separated yield almost no information, because this just reflects the very rare occurrence of this species. A group of two or more taxa largely delineates joint occurrences with similar abundances. An apparent pattern which can be deduced from Fig. 11 is that two sets of taxa seem to be readily distinguishable. The first contains *Bakevellia exporrecta*, *Leptochondria nuetzeli*, and *Sementiconcha recuperator* (Fig. 11G) and the second *Eumorphotis ericius*, *Protogusarella smithi*, *Piarorhynchella triassica*, and *Promyalina putiatinensis* (Fig. 11H). The latter is, in particular,

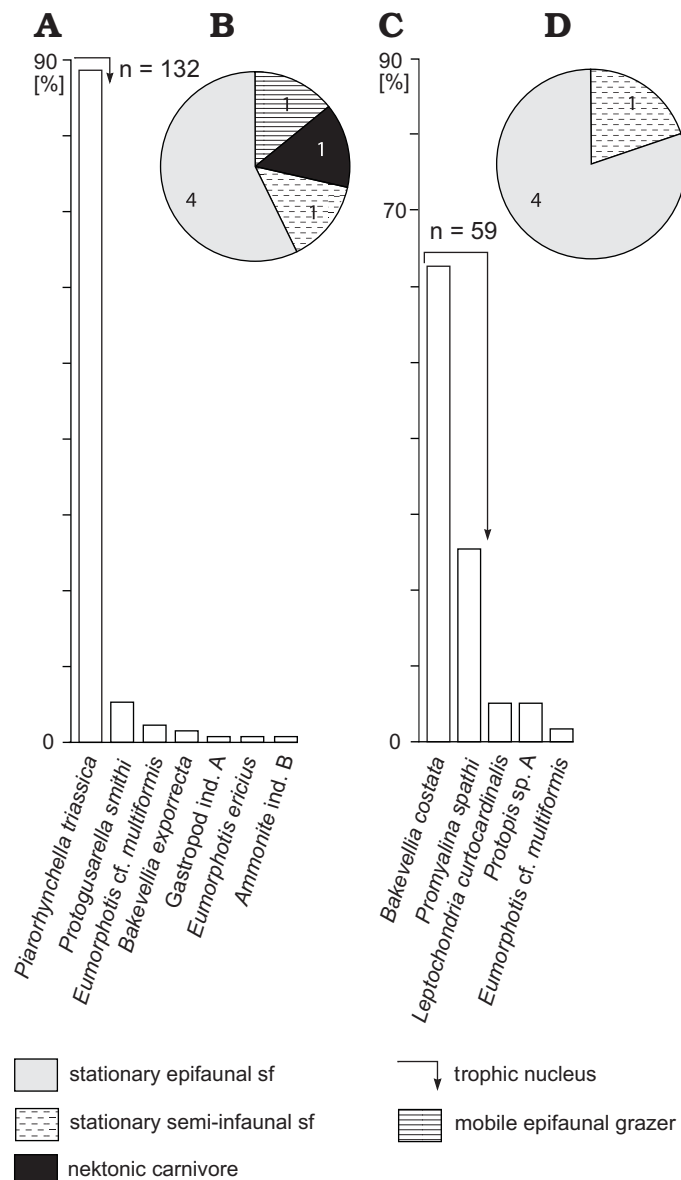


Fig. 15. A, B. Characteristics of the *Piarorhynchella triassica* Association showing frequency distribution, trophic nucleus (A) and ecological structure (B). C, D. Characteristics of the *Bakevellia costata* Assemblage showing frequency distribution and trophic nucleus (C) and ecological structure (D). The numbers in the pie-chart sections correspond with the species pertaining to each guild.

recorded by those associations which were found in high-energy, near-shore deposits (Fig. 11B–D). Accordingly, this cluster unites suspension feeding taxa that are adapted to high water turbulence. In contrast, the cluster dominated by *Bakevellia exporrecta* primarily constitutes the *Bakevellia exporrecta* Association, which is found in environments recording quiet water conditions. It is therefore not surprising that most clusters more or less reproduce the trophic nuclei of associations (Fig. 11G–H). However, the clusters subsumed under Fig. 11F are not well resolved, with rather short stems and high similarities within these clusters. This suggests that these taxa are relatively unspecialised, which, by approximation, is



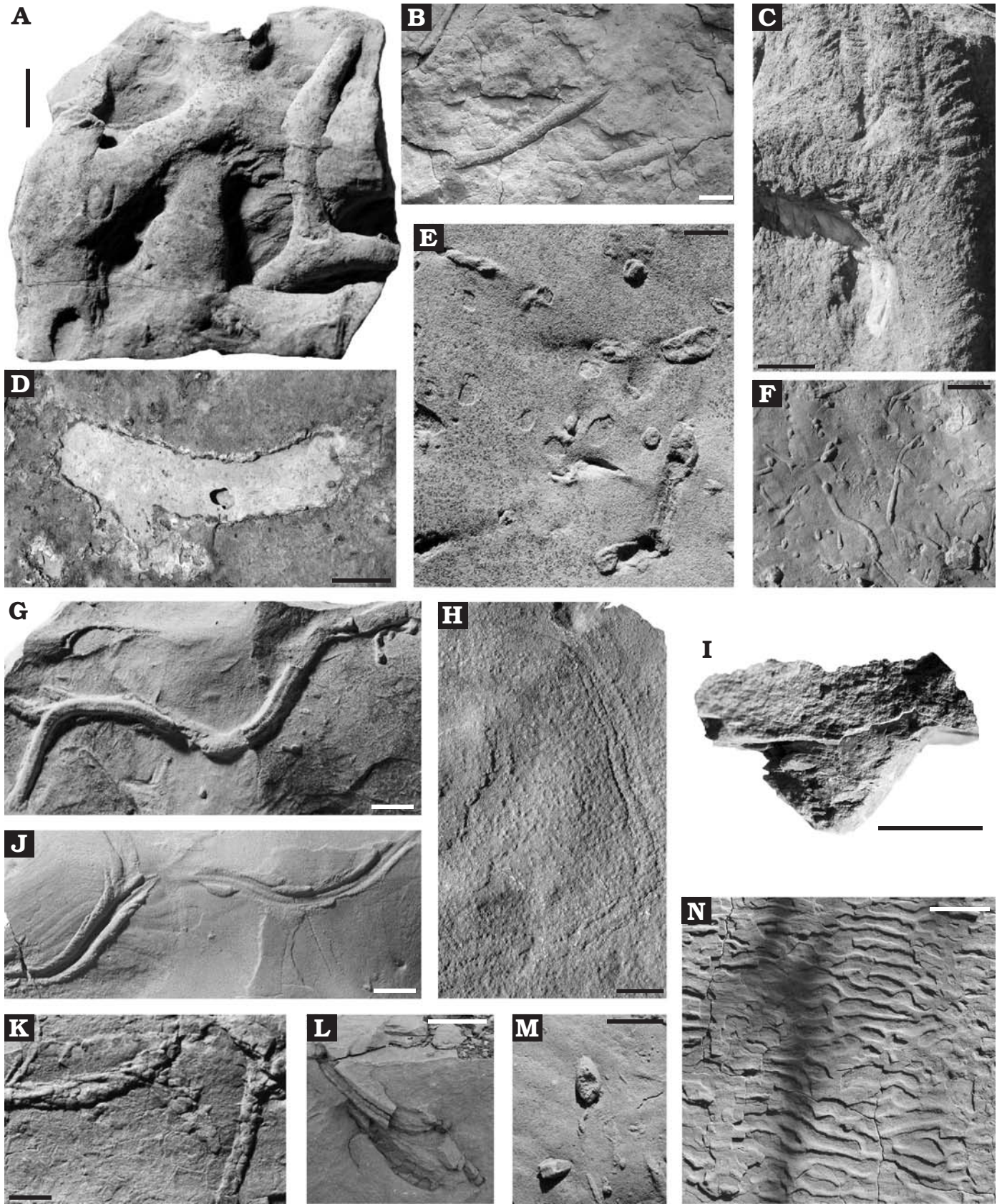


Fig. 16. Trace fossils of the Spathian, Lower Triassic Virgin Formation. A. *Thalassinoides* cf. *suevicus* Rieth, 1932 in lower bedding plane view found at the base of beds containing sample BD-A-7, PIMUZ29586. B. *Palaeophycus montanus* Hall, 1847 in upper bedding plane view observed the lower calcareous unit of section HC-A. C. *Spongiomorpha* isp. found at the base of grainstone which represents a lateral equivalent of BD-A-7 in the section BD-C. →

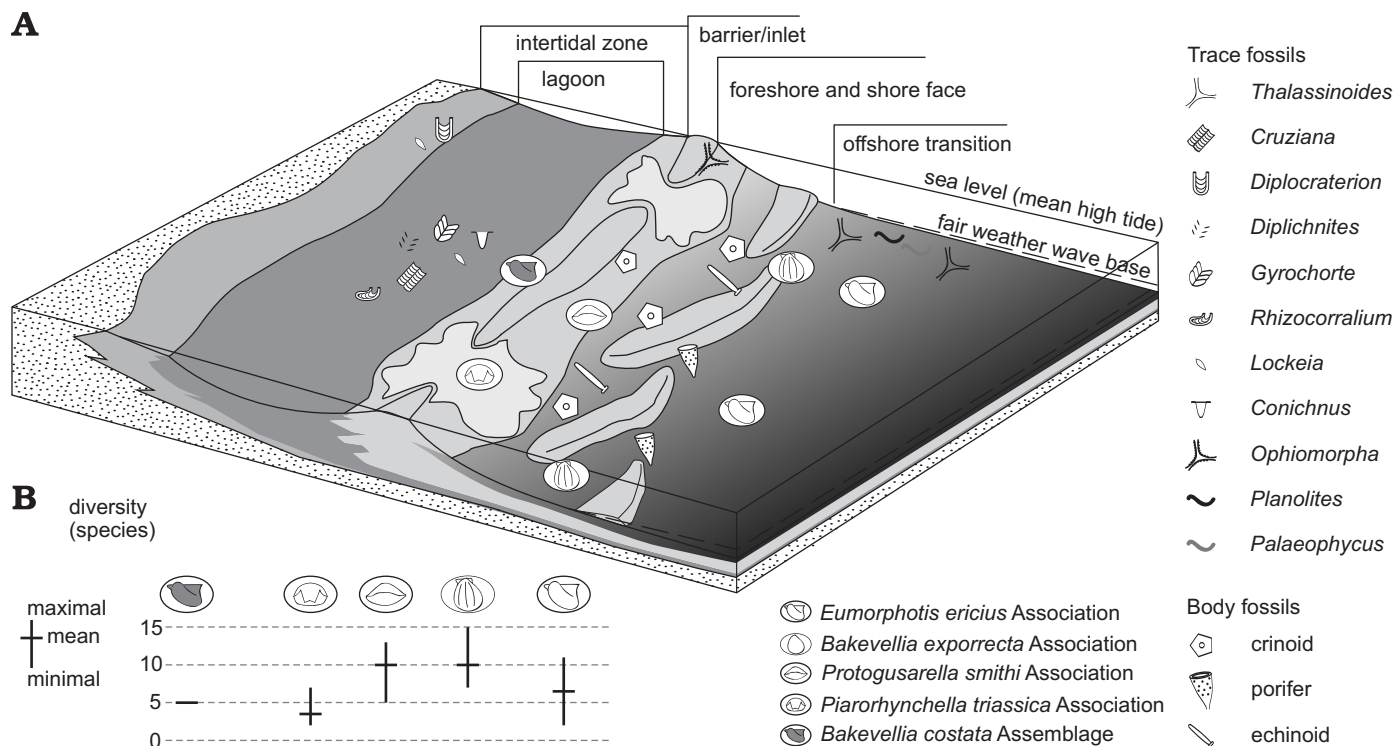


Fig. 17. Comprehensive model of the Spathian (Lower Triassic) Virgin Formation as recorded in south-western Utah. **A.** Distribution of sedimentary facies and faunal assemblages. **B.** Diversity gradient along the general environmental gradient.

expressed in the groupings of samples obtained by the Q-mode cluster analysis. Another possibility is that shared Q-mode occurrences of distant R-mode clusters represent time averaging and community palimpsesting, respectively. The sample BD-A-3 could represent such a case, where the core of two communities is recorded in one bed, because both clusters seem to dominate this sample to a similar extent. The combined analysis of Q- and R-mode clustering thus potentially enables to detect time averaging and community mixing, which is otherwise difficult to deduce unequivocally from sedimentologic and taphonomical criteria alone (Fürsich and Aberhan 1990).

**Biological sedimentary structures.**—A comprehensive review of the trace fossils is beyond the scope of this study, but they are mentioned because some forms were not reported in earlier studies (e.g., Pruss and Bottjer 2004; Mata and Bottjer 2011) and they are useful for testing sedimentologic and ecological interpretations. Most trace fossils are recorded in siliclastic intervals. All ichnofossils encountered in the field are listed in the Table 1 and are illustrated in Fig. 16. Their

stratigraphic occurrences are shown Figs. 4 and 7. Their principal facies occurrences are included in the Fig. 17A and briefly reviewed in the following as loosely defined ichno-assemblages (sensu Bromley 1996).

**Open marine ichnoassemblage.**—This assemblage is observed in intervals that record shoreface and shallow subtidal environments and largely corresponds with the environmental range of the *Eumorphotis ericius* and the *Protogusarella smithi* Association. *Thalassinoides* cf. *suevicus* (Fig. 16A), *Palaeophycus tubularis* (Fig. 16B), *Spongiomorpha* isp. (Fig. 16C), and *Planolites montanus* are predominantly recorded in more distal deposits of the lower shoreface and upper offshore transition zone. Although exhibiting a relatively simple structure and comparably low diversity, the dominance of infaunal deposit feeding structures in this assemblage roughly corresponds with the characteristics of a depauperate *Cruziana* ichnofacies (McIlroy 2004), which supports the sedimentologic interpretation. In the near shore high energy facies, *Ophiomorpha* (Fig. 16D) is occasionally observed, which agrees well with sedimentologic interpreta-

This specimen shows a cruzianid scratchpattern similar to that observed in *Cruziana seilacheri* Zonneveld, Pemberton, Saunders, and Pickerill, 2002). **D.** *Ophiomorpha* isp. from uppermost calcareous beds of section HC-A. **E.** *Diplocraterion* isp. in upper bedding plane view. Upper siliclastic interval of BD-B. **F.** *Lockeia siliquaria* James, 1879 showing intergradation with very indistinct locomotion tracks of the same tracemaker. Intertidal interval of section BD-A. **G.** *Cruziana problematica* Schindewolf, 1928 from the lagoonal siltstone interval of section HC-D, PIMUZ29606. **H.** *Diplichnites* isp. from the lagoonal siltstone interval of section HC-D. **I.** *Conichnus* isp. from the lagoonal siltstone interval of section HC-A, PIMUZ29607. **J.** Arthropod trackway (cf. *Diplopodichnus* intergrading with *Diplichnites*) from the lagoonal siltstone interval of section HC-D, PIMUZ29605. **K.** *Gyrochorte* cf. *comosa* Heer, 1865 from the lagoonal siltstone interval of section HC-A, PIMUZ29608. **L.** *Rhizocorallium* isp. from the lagoonal siltstone interval of section HC-A. **M.** *Lockeia siliquaria* James, 1879 from the lagoonal siltstone interval of section HC-D. **N.** Wrinkle marks from the lagoonal siltstone interval of section HC-D. Specimens B-F, H, L, M, N not collected. Scale bars 10 mm; except C, H, N, 20 mm; F, 30 mm.



tion and delineates a low diverse *Skolithos* ichnofacies (McIlroy 2004). These open marine assemblages suggest that an environmental gradient is faintly mirrored in the ichnotaxonomic composition, making the ichnofacies concept (Seilacher 1967) applicable in the Virgin Formation.

**Intertidal ichnoassemblage.**—This assemblage is observed in the tidal flat facies recorded in the upper part of the Beaver Dam sections (BD-A, BD-B, and VR; Fig. 4). It contains the trace fossils *Diplocraterion* isp. (Fig. 16E) and *Lockeia siliquaria* (Fig. 16F). The low diversity of this assemblage possibly reflects the high rate of abiotic stress to which biota are subjected in such environments. However, the paucity of ichnotaxa could also result from very limited exposures of this facies in the Virgin Formation.

**Lagoonal ichnoassemblage.**—This assemblage is observed in the lagoonal intervals identified in the section HC-A and HC-D and includes the trace fossils *Lockeia siliquaria* (Fig. 16M), *Cruziana problematica* (Fig. 16G), *Gyrochorte* cf. *comosa* (Fig. 16K), *Conichnus* isp. (Fig. 16J), *Diplichnites* isp. (Fig. 16H), *Rhizocorallium* isp. (Fig. 16L), *Diplocraterion* isp. and an arthropod trackway which could be referred to an intergradational form of *Diplopodichnus* and *Diplichnites* (Fig. 16I). Furthermore, wrinkle structures (Fig. 16N) are recorded in some of beds of this facies. This is the most diverse trace fossil assemblage, which most likely reflects the high content of siliclastic material, alternating grain sizes, and modest sedimentation rates. These characteristics provide a high preservation potential for trace fossils. In protected marginal marine embayments, the rate of bioturbation is highly variable (Mángano and Buatois 2004), which is seen in our data as well. The generally low rate of biogenic mixing could result from local stress factors in marginal marine settings such as high water temperatures, salinity fluctuations and poor mixing of the water body. These shale beds are devoid of marine body fossils, which are recorded in otherwise similar deposits of the offshore transition (e.g., BD-A-6).

**Controls on the distribution and ecological structure of the Virgin Fauna.**—Based on the sedimentological data and palaeoecological analysis outlined above, a model of the palaeoecological conditions recorded by the Virgin Formation can be inferred (Fig. 17A). All assemblages record marine conditions in a shallow water environment with relative water depths not ranging below the storm wave base. Main trends in diversity, dominance and trophic complexity are chiefly controlled by substrate conditions and hydrodynamic regime.

The *Bakevella exporrecta* Association is present in the most distal marine facies recorded in the study area. As already noted, its rather low diversity and modest dominance probably reflects soft substrate conditions, which are unfavourable for attached, epifaunal bivalves that otherwise represent the major faunal elements in the Virgin Formation and generally, in Early Triassic benthic ecosystems. The carbonate-dominated units of the inner shelf environment (or shore-

face zone) of the Virgin Formation contain the most diverse and ecologically most heterogeneous associations. Their distribution seems to roughly follow an environmental gradient that is largely controlled by hydrodynamic regime. The *Eumorphotis ericius* Association is present in the most distal parts of the shoreface zone and probably the proximal offshore transition. This is the only facies where sponges are abundant. The *Piarorhynchella triassica* Association probably represents somewhat shallower water depths, which can be inferred from the sedimentological context of these samples, including medium-to-thick-bedded as well as cross-bedded grainstone units. The highest energy deposits of very shallow subtidal and probably intertidal conditions, which are represented by tidal inlet and tidal channel deposits, host the *Piarorhynchella triassica* Association, which is chiefly dominated by this rhynchonellid brachiopod. All of these associations contain abundant crinoid fragments indicating normal marine, well oxygenated, current agitated waters with low siliclastic input. The sedimentological context (see last paragraph on the sedimentary environment of HC-D on p. 163) of the *Bakevella costata* Assemblage suggests a very marginal setting.

Although epifaunal suspension feeders are the main constituents of the Virgin Fauna, the general trophic structure with guilds represented by body fossils and three additionally inferred from trace fossils (Table 1) indicate that the ecological diversity is comparably advanced and not fundamentally different from later Mesozoic shallow marine habitats (see Aberhan 1994).

## Discussion

**A delayed recovery?**—Our study confirms the comparably high bulk diversity of benthic taxa in the Virgin Formation (McGowan et al. 2009; Hautmann et al. 2012), to which it adds one more genus (*Myalinella*), the presence of the family Astartidae, and one more species (*Promyalina spathi*), resulting in the highest bivalve diversity (30 species, 18 genera) of any formation from the Early Triassic reported so far and considerably exceeding the ten bivalve genera identified in earlier studies (e.g., Schubert and Bottjer 1995). Although the individual sample diversity observed by Schubert and Bottjer (1995) is similar on the generic level, these authors noted that the Spathian communities still show a simple ecological structure containing mainly generalistic taxa, which led to the conclusion that the recovery was significantly delayed throughout the Early Triassic. However, the bivalve diversity of the Virgin Formation is not so different from that of similar settings from the Middle Triassic post-extinction radiation interval of bivalves in different areas, for instance in Vietnam (28 species and 19 genera for the Anisian and Ladinian; Komatsu et al. 2010) and the Dolomites (15 genera for the early Anisian, 32 genera for the late Anisian; Posenato 2008). Bivalve diversity was higher in the middle Anisian Jena Formation (lower Muschelkalk) of the Germanic



Basin (57 species and 30 genera; Schmidt 1928, 1938), but McGowan et al. (2009) suggested that this may partly reflect its longer study history, the longer duration of the time interval recorded and the larger outcrop area. This view is supported herein by finds of additional bivalve taxa (*Myalinella* sp., Astartidae sp., *Promyalina spathi*) that were not identified by McGowan et al. (2009) and Hautmann et al. (2012) in the same area, although the overall richness as reported in these studies was not achieved herein. This suggests that, at least to some extent, the lower bulk diversity of the Virgin Formation in comparison with well studied Middle Triassic faunas reflects lower sampling effort.

Summarized, bivalve diversity of the Virgin Formation is more similar to faunas from comparable settings of Anisian age than to pre-Spathian faunas of the Early Triassic, suggesting that significant recovery has already taken place. This does not imply that recovery was already completed by that time, as shown by the extraordinary diverse bivalve fauna from the Late Anisian Leidapo Member in China (103 species, 49 genera; Stiller 2001). However, the relatively high diversity, the appearance of other typical Mesozoic benthic organisms such as articulated brachiopods, porifers, echinoderms, and the presence of certain ichnotaxa that indicate advanced recovery stages (Twitchett and Wignall 1996; Hofmann et al. 2011) suggest that recovery was already underway in the Early Spathian, contrary to earlier studies on the Virgin Formation (e.g., Schubert and Bottjer 1995; Boyer et al. 2004; Pruss and Bottjer 2004; Mata and Bottjer 2011).

**Harsh environmental conditions?**—The benthic associations of the Virgin Formation in the investigated area reflect normal marine conditions. Deleterious environmental conditions, caused, for example, by the upwelling of anoxic and alkaline waters (Mata and Bottjer 2011), are not confirmed because the taxonomic composition does not change between different stratigraphic levels and thus indicates the absence of faunal turnovers, which would one expect in case of discrete environmental perturbations. The reduced diversity and high dominance of the faunas recorded by the *Bakevella exporrecta* Association and the *Piarorhynchella triassica* Association are most likely related to substrate properties and hydrodynamic conditions as well as taphonomic bias possibly introduced by sorting (*Piarorhynchella triassica* Association). Alternatively, this pattern could be interpreted by the “habitable zone” concept of Beatty et al. (2008). In this model, onshore habitats remain oxygenated by wave action and thus may have served as refuges for benthic biota to escape from oxygen deficiency in open oceanic settings. However, all observed genera that occur in the most distal deposits within the study area (*Bakevella exporrecta* Association) are not diagnostic for oxygen restricted habitats. *Bakevella* has frequently been documented from oxygenated, shallow marine habitats (e.g., Aberhan 1992; Muster 1995; Fürsich et al. 1995; Aberhan and Muster 1997). *Leptochondria*, ranging from the late Permian to the Norian, is also known occur in well oxygenated deposits such as the Middle Triassic Muschelkalk (Schmidt 1928). The

presence of infaunal bivalves (*Sementiconcha recuperator*) additionally argues against a notably impact of anoxic or hypoxic ocean waters. Furthermore, the presence of *Thalassinoides*, *Ophiomorpha*, and *Spongeliomorpha* points to well oxygenated conditions (Savrda and Bottjer 1986) throughout all environmental settings recorded by the Virgin Formation in the investigated area.

**Comparison with other Spathian benthic faunas.**—Very few studies on Spathian faunas from other palaeogeographic regions are available for comparison. 30 benthic species (19 genera) are reported from the uppermost Werfen Formation (Cencenighe and San Lucano members) of the Dolomites (Neri and Posenato 1985). Broglia-Loriga et al. (1990) observed 23 benthic species (17 genera) in the Spathian part of the Werfen Formation, and 19 species (16 genera) in the palaeogeographically closely related Transdanubian Mountains (Hungary). Both studies document a similar taxonomic composition to the Virgin fauna, at least with respect to the mollusc genera. Furthermore, it has been suggested that the Olenekian part of the Werfen Formation marks the initial recovery phase succeeding a surviving phase in the Induan (Posenato et al. 2008). In fact, Werfen faunas reached their highest diversity in the Spathian (Broglia-Loriga et al. 1990; Posenato 2008; personal observation RH and MH). Similarly, Twitchett and Wignall (1996) noted that the ichnofaunas of the Werfen Formation show the highest stage of recovery in the Spathian. All these data suggest that the recovery signal observed in the western USA is of interregional significance. Faunal differences between the western USA and the Alps include the local dominance of articulated brachiopods and the presence of porifers in the Virgin Formation, which are not observed in the Werfen Formation. However, sponge build-ups were reported in the western Tethys realm (Szulc 2007), which adds further evidence for similar recovery patterns on either coast of Pangaea (Brayard et al. 2011b).

Data from other palaeogeographic regions are scarce, and comparable palaeoecological surveys were not presented, yet. Bivalve faunas from a southern Tethyan succession (Pakistan) yield 14 Spathian species (11 genera) (Wasmer et al. 2012) with a somewhat different taxonomic composition, possibly indicating increasing faunal provincialism. Future studies are necessary to further clarify the picture of benthic recovery and possible migration patterns of benthic species.

**Habitat differentiation and a new ecological recovery model.**—In spite of the relatively high bulk diversity observed in the Virgin Formation, the taxonomical differentiation between adjoining habitats and along environmental gradients is surprisingly low (Figs. 11, 17). In fact, the benthic associations identified as clusters (Fig. 11) largely reflect the variable dominance of certain taxa, whereas differences in the taxonomic composition are of minor importance. Those taxa that are unique to associations are recorded in very small numbers, which probably indicates sampling bias rather than notable taxonomic differences. Low bootstrap values (Fig. 11) addi-

tionally suggest that the groupings obtained in the Q-mode clustering reflect only minor differences between associations, chiefly caused by variable abundances of taxa. If confirmed by future studies in other regions, this pattern would indicate a time lag between increasing habitat diversity (alpha diversity) and increasing taxonomical differentiation between habitats (beta diversity), contrary to the expectations of Whittaker (1975). We hypothesise that competition, roughly expressed as the average number of species in a set of habitats, needs to exceed a certain threshold before taxonomical differentiation between habitats starts, and that this threshold was not yet reached in the Early Spathian of the investigated area. Accordingly, a significant increase in beta diversity could be used to divide recovery intervals into two major phases, the first ending with reaching a habitat saturation threshold and the second ending with the completion of ecosystem differentiation, indicated by the end of an increase in beta diversity.

The herein proposed model (Fig. 18) is in accordance with the niche overlap theory of Pianka (1974), which predicts decreasing niche overlap with increasing number of competing species and a corresponding increase of diffuse competition sensu MacArthur (1972). The existence of a competition threshold before significant taxonomic differentiation along an environmental gradient starts is not part of the theory of Pianka (1974), but it is compatible with standard models of interspecific competition with a prevalence

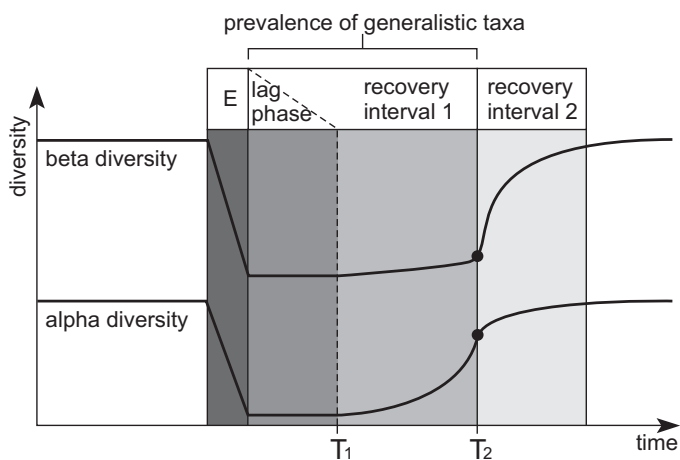


Fig. 18. Generalised model illustrating the role of habitat saturation in recovery processes. Following the extinction (E), a lag phase marks a time interval in which no significant radiation and increase in alpha diversity is observed (Erwin 2001). The duration of this lag phase may be variable or it could even be absent (Hautmann et al. 2008) but it is commonly postulated for the end-Permian mass extinction (e.g., Erwin 2001). After initiation of diversification ( $T_1$ , start of recovery interval 1), competition within habitats increases following recovering alpha diversity. Beta diversity remains low throughout this interval because adding new species does not yet result in significant competition for resources. Eventually, alpha diversity reaches a threshold value where a critical number of species competes for same, limited resources. The time when this habitat saturation is reached is herein referred to as  $T_2$ . From this time onward (recovery interval 2), habitat restriction increases because of competitive exclusion of species from neighbouring habitats. Recovery interval 2 ends when all curves level off. Logistic growth of alpha diversity adopted from Erwin (2001).

of diffuse competition. In this situation, an increase of the number of competing species  $i$  in a given habitat will lead to exclusion of a species  $j$  from this habitat when the sum of  $\alpha_{ij}N_i$  ( $\alpha$ , competition coefficient;  $N$ , equilibrium abundance) has exceeded the threshold where  $N_j < 0$  for the equilibrium condition of the multi-species Lotka-Volterra equation (e.g., Pianka 1974: equation 2).

Our findings somewhat contradict the interpretation of ANOSIM (analysis of similarity) analyses presented by McGowan et al. (2009), who suggested that the Virgin Fauna is comparatively heterogeneous. A detailed comparison of the different methods (cluster analysis versus ANOSIM) is beyond the scope of this paper, but when running cluster analyses with the dataset of McGowan et al. (2009) we obtained similar results as in our study. In particular, well separated clusters of samples (associations) identified in the dataset of McGowan et al. (2009) contain few or no taxa that are truly unique to these associations, similar to the results of our study. The difference in the interpretation may simply result from different views of what should be called "heterogeneous", but we note that the R-values presented by McGowan et al. (2009: table 4) are all close to zero, with subtle differences that indicate a low heterogeneity with respect to facies gradients and stratigraphic levels.

Our interpretation is an alternative to the hypothesis that the prevalence of generalistic taxa in the Early Triassic reflects protracted environmental stress, which has been advocated in recent studies on the Virgin Formation (e.g., Pruss and Bottjer 2004; Boyer et al. 2004; Mata and Bottjer 2011). Our results rather support the view of Schubert and Bottjer (1995: 28) that the generalistic character of Spathian faunas of the western USA largely reflects intrinsic controls, which we identified as relatively low levels of competition among species within most habitats. Future studies on Early Triassic and Middle Triassic benthic communities of different environments are necessary to test the proposed model.

## Conclusions

The quantitative palaeoecological analysis of the Virgin Formation in south-western Utah yields the following main conclusions:

- The Virgin Formation contains the taxonomically and ecologically most diverse benthic fauna in the Early Triassic aftermath of the end-Permian mass extinction.
- Relatively small differences in the taxonomic composition and abundances data led to the recognition of four associations and one assemblage, delineating an environmental gradient ranging from intertidal to subtidal habitats.
- Comparably low diversities in some associations were chiefly caused by hydrodynamic conditions and substrate properties.
- Unusual environmental conditions were not found to have had any significant impact on benthic ecosystems recorded by the Virgin faunas. This suggests that oceano-

graphic conditions during the Early Spathian enabled ecosystems to re-diversify without major abiotic limitations in the western USA.

- The similarity in the taxonomical composition of individual habitats indicates that the high bulk diversity of the Virgin Fauna was mainly achieved by the pan-environmental establishment of species. This generalistic nature of biota probably reflects low levels of competition rather than stressful environmental conditions.
- The onset of increasing taxonomical differentiation between habitats is a potential indicator of the relative state of ecosystem recovery after mass extinction events.

## Acknowledgements

We are indebted to Andrew Smith (Natural History Museum, London, UK), who provided us with detailed locality information, and Andrew Milner (Dinosaur Discovery Site, St. George, Utah, USA) for his advice on finding the most appropriate outcrops. Claude Monnet (Université de Lille, France) is thanked for his support in the data analysis. We thank Arnaud Brayard (Université de Bourgogne, Dijon, France) and an anonymous reviewer for their valuable comments, which helped to significantly improve the manuscript. This study was supported by the Swiss National Science Foundation project 546 200021\_121774 granted to MH. A travel grant provided by the Swiss Academy of Sciences was awarded to MW.

## References

- Aberhan, M. 1992. Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile. *Beringeria* 5: 3–174.
- Aberhan, M. 1994. Guild-structure and evolution of Mesozoic benthic shelf communities. *Palaos* 9: 516–545.
- Aberhan, M. and Muster, H. 1997. Palaeobiology of Lower Jurassic bivalve-like bivalves from western Canada. *Palaeontology* 40: 799–815.
- Alberti, F. von 1864. *Überblick über die Trias, mit Berücksichtigung ihres Vorkommens in den Alpen*. 353 pp. J.G. Cotta'sche Buchhandlung, Stuttgart.
- Beatty, T.W., Zonneveld, J.P., and Henderson, C.M. 2008. Anomalously diverse Early Triassic ichnofossil assemblages in Northwest Pangea: a case for a shallow-marine habitable zone. *Geology* 36: 771–774.
- Bissell, H.J. 1973. Permian–Triassic boundary in the eastern Great Basin area. In: A. Logan, and L.V. Hills (eds.), *Permian and Triassic Systems and Their Mutual Boundary*. *Canadian Society of Petroleum Geologists Memoirs* 2: 318–344.
- Bambach, R.K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3: 152–167.
- Bittner, A. 1899. Trias–Ablagerungen des Süd-Ussuri-Gebietes in der ostibirischen Küstenprovinz. *Mémoires du Comité Géologique* 7: 1–35.
- Blakey, R.C. 2011. Colorado Plateau Stratigraphy and Geology and Global and Regional Palaeogeography. <http://www2.nau.edu/rcb7/index.html>. (Accessed February 2011).
- Boyer, D.L., Bottjer, D.J., and Droser, M.L. 2004. Ecological Signature of Lower Triassic Shell Beds of the Western United States. *Palaos* 19: 372–380.
- Bray, J.R. and Curtis, J.T. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., and Guex, J. 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* 325: 1118–1121.
- Brayard, A., Nützel, A., Stephen, D.A., Bylund, K.G., Jenks, J., and Bucher, H. 2010. Gastropod evidence against the Early Triassic Lilliput effect. *Geology* 38: 147–150.
- Brayard, A., Nützel, A., Kaim, A., Escarguel, G., Hautmann, M., Stephen, D.A., Bylund, K.G., Jenks, J., and Bucher, H. 2011a. Gastropod evidence against the Early Triassic Lilliput effect: REPLY. *Geology* 39: e233.
- Brayard, A., Vennin, E., Olivier, N., Escarguel, G., Bylund, K.G., Jenks, J., Stephen, D.A., Hofmann, R., Goudemand, N. and Bucher, H. 2011b. Transient metazoan reefs in the aftermath of the end-Permian mass extinction. *Nature Geoscience* 4: 693–697.
- Brinkman, D.B., Russell, A.P., Eberth, D.A., and Peng, J. 2004. Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213: 295–313.
- Broglio-Loriga, C., Góczán, F., Haas, J., Lenner, K., Neri, C., Oravec-Scheffer, A., Posenato, R., Szaboacute, I., and Tóth Makk, A. 1990. The Lower Triassic sequence of the Dolomites (Italy) and Transdanubian Mid-Mountains (Hungary) and their correlation. *Memorie di Scienze Geologiche, Padova* 42: 41–103.
- Bromley R.G. 1996. *Trace fossils. Biology, taphonomy and applications*. 361 pp. Chapman and Hall, London.
- Catullo, T.A. 1846. Memoria geognostico-paleozoica sulle Alpi Venete. *Memorie della Società Italiana delle scienze residente in Modena* 24: 1–158.
- Cheel, R.J. and Leckie, D.A. 1993. Hummocky cross-stratification. *Sedimentology Reviews* 1: 103–121.
- Clark, W.B. and Twitchell, M.W. 1915. The Mesozoic and Cenozoic Echinodermata of the United States. *Monographs of the United States Geological Survey* 54: 1–341.
- Erwin, D.H. 1993. *The Great Paleozoic Crisis: Life and Death in the Permian*. 327 pp. Columbia University Press, New York.
- Erwin, D.H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. *Proceedings of National Academy of Science* 98: 5399–5403.
- Fürsich, F.T. and Aberhan, M. 1990. Significance of time-averaging for palaeocommunity analysis. *Lethaia* 23: 143–152.
- Fürsich, F.T., Freytag, S., Röhl, J., and Schmid, A. 1995. Palaeoecology of benthic associations in salinity-controlled marginal marine environments: Examples from the Lower Bathonian (Jurassic) of the Causses (southern France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 113: 135–172.
- Fraiser, M.L. and Bottjer, D.J. 2005. Fossil preservation during the aftermath of the end-Permian mass extinction: Taphonomic processes and palaeoecological signals. In: D.J. Over, J. Morrow, and P.B. Wignall (eds.), *Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards an Integrated Approach*. *Developments in Palaeontology and Stratigraphy* 20: 299–311.
- Gahr, M.E. 2002. Palökologie des Makrobenthos im Unter-Toarc SW-Europas. *Beringeria* 31: 3–204.
- Galfetti, T., Bucher, H., Brayard, A., Hochuli, P.A., Weissert, H., Guodun, K., Atudorei, V., and Guex, J. 2007. Late Early Triassic climate change: Insights from carbonate carbon isotopes, sedimentary evolution and ammonoid paleobiogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 394–411.
- Goodspeed, T.H. and Lucas, S.G. 2007. Stratigraphy, sedimentology, and sequence stratigraphy of the Lower Triassic Sinbad Formation, San Rafael Swell, Utah. In: S.G. Lucas and J.A. Spielmann (eds.), *Triassic of the American West*. *New Mexico Museum of Natural History and Science Bulletin* 40: 91–102.
- Guex, J., Hungerbühler, A., Jenks, J.F., O'Dogherty, L., Atudorei, V., Taylor, D.G., Bucher, H., and Bartolini, A. 2010. Spathian (Lower Triassic) ammonoids from western USA (Idaho, California, Utah and Nevada). *Mémoires de Géologie Lausanne* 49: 82.
- Hall, J. 1847. *Palaeontology of New York, Vol. I. Natural History of New York, I*. 338 pp. Van Benthuysen, Albany.



- Hall, J. and Whitfield, R.P. 1877. Part II. Palaeontology. In: C. King (ed.), *Annual Report to the Secretary of War on the U.S. Geological Exploration of the Fortieth Parallel 4*, 198–302. Government Printing Office, Washington.
- Hallam, A. 1991. Why was there a delayed radiation after the end-Palaeozoic extinctions? *Historical Biology: An International Journal of Paleobiology* 5: 257–262.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1): 9 p. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)
- Hammer, Ø. and Harper, D.A.T. 2006. *Paleontological data analysis*. 351 pp. Blackwell, Malden.
- Hauer, F. von 1850. Ueber die von Herrn Bergrath W. Fuchs in den Venetianer Alpen gesammelten Fossilien. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 2*: 109–126.
- Hautmann, M. and Nützel, A. 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic: Palaeoecological significance and implications for the 'Lazarus problem'. *Palaeontology* 48: 1131–1138.
- Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A., and Nützel, A. 2011. An unusually diverse mollusk fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. *Geobios* 44: 71–85.
- Hautmann, M., McGowan, A.J., Smith, A.B., and Bucher, H. 2012. Bivalves from the Spathian (Early Triassic) of southwestern Utah: Systematics and evolutionary significance. *Journal of Systematic Palaeontology* (published online).
- Hautmann, M., Stiller, F., Cai, H., and Sha, J. 2008. Extinction-recovery pattern of level-bottom faunas across the Triassic–Jurassic boundary in Tibet: implications for potential killing mechanisms. *Palaïos* 23: 711–718.
- Heer, O. 1865. *Die Urwelt der Schweiz*. 622 pp. Friedrich Schultheß, Zürich.
- Heydari, E., Arzani, N., and Hassanzadeh, J. 2008. Mantle plume: The invisible serial killer—Application to the Permian–Triassic boundary mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 264: 147–162.
- Hofmann, R., Goudemand, N., Wasmer, M., Bucher, H., and Hautmann, M. 2011. New trace fossil evidence for an early recovery signal in the aftermath of the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 216–226.
- Kier, P.M. 1968. The Triassic echinoids of North America. *Journal of Paleontology* 42: 1000–1006.
- Kiparisova, L.D. 1938. Lower Triassic bivalves of the Ussuri region [in Russian]. *Trudy Geologičeskogo Instituta* 7: 197–311.
- Klein, G.D. 1971. A sedimentary model for determining paleotidal range. *Geological Society of America Bulletin* 82: 2585–2592.
- Komatsu, T., Huyen, D.T., and Huu, N.D. 2010. Radiation of Middle Triassic bivalve: Bivalve assemblages characterized by infaunal and semi-infaunal burrowers in a storm- and wave-dominated shelf, An Chau Basin, North Vietnam. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 190–204.
- Kreisa, R.D. and Moiola, R.J. 1986. Sigmoidal tidal bundles and other tide-generated sedimentary structures of the Curtis Formation, Utah. *Geological Society of America Bulletin* 97: 381–387.
- James, U.P. 1879. Descriptions of new species of fossils and remarks on others from the lower and upper Silurian rocks of Ohio. *The Paleontologist* 1 (3): 17–24.
- Lepsius, R. 1878. *Das westliche Südtirol*. 375 pp. Verlag Wilhelm Hertz, Berlin.
- Lucas, S.G., Krainer, K., and Milner, A.R.C. 2007. The Type section and age of the Timpoweap Member and the stratigraphic nomenclature of the Triassic Moenkopi Group in Southwestern Utah. In: S.G. Lucas and J.A. Spielmann (eds.), *Triassic of the American West*. *New Mexico Museum of Natural History and Science Bulletin* 40: 109–118.
- Ludvigsen, R. and Westrop, S.R. 1983. Trilobite biofacies of the Cambrian–Ordovician boundary interval in northern North-America. *Alcheringa* 7: 301–319.
- MacArthur R.H. 1972. *Geographical Ecology*. 269 pp. Harper and Row, New York.
- Mángano, M.G. and Buatois, L.A. 2004. Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent. *Geological Society, London, Special Publications* 228: 157–178.
- Mansfield, G.R. 1927. Geography, geology, and mineral resources of part of southeastern Idaho. *U.S. Geological Survey Professional Papers* 152: 1–453.
- Mata, S.A. and Bottjer, D.J. 2011. Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions: Ichnology, applied stratigraphy, and the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 300: 158–178.
- McGowan, A.J., Smith, A.B., and Taylor, P.D. 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA. *Australian Journal of Earth Sciences: An International Geoscience Journal of the Geological Society of Australia* 56: 859–872.
- McIlroy, D. 2004. Some ichnological concepts, methodologies, applications and frontiers. *Geological Society, London, Special Publications* 228: 3–27.
- Morisita, M. 1959: Measuring of interspecific association and similarity between communities. *Memoires of the Faculty of Science, Kyushu University, Series E. Biology* 3: 65–80.
- Mundil, R., Ludwig, K.R., Metcalfe, I., and Renne, P.R. 2004. Age and Timing of the Permian Mass Extinctions: U/Pb Dating of Closed-System Zircons. *Science* 305: 1760–1763.
- Münster, G. Graf zu 1841. *Beiträge zur Petrefacten-Kunde. IV. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen*. 152 pp. Buchner'sche Buchhandlung, Bayreuth.
- Muster, H. 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). *Beringeria* 14: 1–161.
- Myrow, P.M. 1992. Pot and gutter casts from the Chapel Island Formation, Southeast Newfoundland. *Journal of Sedimentary Research* 62: 992–1007.
- NACSN (North American Commission on Stratigraphic Nomenclature). 2005. North American stratigraphic code. *AAPG Bulletin* 89: 1547–1591.
- Neri, C. and Posenato, F. 1985. New biostratigraphical data on uppermost Werfen Formation of western Dolomites (Trento, Italy). *Geologisch-Paläontologische Mitteilungen Innsbruck* 14: 83–107.
- Newell, N.D. and Kummel, B. 1942. Lower Eo-Triassic stratigraphy, western Wyoming and southeast Idaho. *GSA Bulletin* 53: 937–995.
- Neyman, A.A. 1967. Limits to the application of the 'trophic group' concept in benthic studies. *Oceanology, Academy of Sciences of the USSR* 7: 49–155.
- Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A., and Guex, J. 2007. 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.
- Perry, D.G. and Chatterton, B.D.E. 1979. Late Early Triassic brachiopod and conodont fauna, Thaynes Formation, southeastern Idaho. *Journal of Paleontology* 53:307–319.
- Pianka E.R. 1974. Niche Overlap and Diffuse Competition. *Proceedings of National Academy of Science* 71: 2141–2145.
- Poborski, S.J. 1954. Virgin Formation (Triassic) of the St. George, Utah, Area. *Geological Society of America Bulletin* 65: 971–1006.
- Posenato, R. 2008. Patterns of bivalve biodiversity from Early to Middle Triassic in the Southern Alps (Italy): Regional vs. global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 261: 145–159.
- Pruss, S.B., Corsetti, F.A., and Bottjer, D.J. 2005. The unusual sedimentary rock record of the Early Triassic: A case study from the southwestern United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 222: 33–52.
- Pruss, S.B. and Bottjer, D.J. 2004. Early Triassic trace fossils of the western

- United States and their implications for prolonged environmental stress from the end-Permian mass extinction. *Palaios* 19: 551–564.
- Pruss, S.B. and Payne, J.L. 2009. Early Triassic microbial spheroids in the Virgin Limestone Member of the Moenkopi Formation, Nevada, USA. *Palaios* 24: 131–136.
- Pruss, S.B., Payne, J.L., and Bottjer, D.J. 2007. *Placunopsis* bioherms: The first metazoan buildups following the end-Permian mass extinction. *Palaios* 22: 17–23.
- Reese, J.B. and Bassler, H. 1922. Stratigraphic sections in southwestern Utah and northwestern Arizona. *U.S. Geological Survey Professional Paper* 129-D: 53–77.
- Reif, D.M. and Slatt, R.M. 1979. Red bed members of the Lower Triassic Moenkopi Formation, southern Nevada; sedimentology and paleogeography of a muddy tidal flat deposit. *Journal of Sedimentary Research* 49: 869–889.
- Richter, R. 1937. Marken und Spuren aus allen Zeiten. I–II. *Senckenbergiana* 19: 150–163.
- Rieth, A. 1932. Neue Funde spongeliomorpher Fucoiden aus den Jura Schwabens. *Geologische und Paläontologische Abhandlungen* 19: 257–294.
- Savrda, C.E. and Bottjer, D.J. 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology* 14: 3–6.
- Schlotheim, E.F. von 1820. *Die Petrefactenkunde auf ihrem jetzigem Standpunkte durch die Beschreibung seiner Sammlung versteinerner und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. Erste Abtheilung. Das Thierreich*. 437 pp. Beckersche Buchhandlung, Gotha.
- Schindewolf, O.H. 1928: Studien aus dem Marburger Buntsandstein III–VI, *Senckenbergiana* 10: 16–54.
- Schmidt, M. 1928. *Die Lebewelt unserer Trias*. 461 pp. Rau, Öhringen.
- Schmidt, M. 1938. *Die Lebewelt unserer Trias; Nachtrag*. 144 pp. Rau, Öhringen.
- Schubert, J.K. and Bottjer, D.J. 1995. Aftermath of the Permian–Triassic mass extinction event: Paleocology of Lower Triassic carbonates in the western USA. *Palaogeography, Palaeoclimatology, Palaeoecology* 116: 1–39.
- Seilacher, A. 1967. Bathymetry of trace fossils. *Marine Geology* 5: 413–428.
- Sepkoski, J.J. Jr. 1988. Alpha, beta or gamma: Where did all the diversity go. *Paleobiology* 14: 221–234.
- Sokal, R. and Michener, C. 1958. A statistical method for evaluating systematic relationships. *University of Kansas Science Bulletin* 38: 1409–1438.
- Stiller, F. 2001. Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im Oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupou, Provinz Guizhou, Südwestchina. *Münstersche Forschungen zur Geologie und Paläontologie* 92: 1–523.
- Szulc, J. 2007. Sponge-microbial stromatolites and coral-sponge reef recovery in the Triassic of the western Tethys domain. In: S.G. Lucas and J.A. Spielmann (eds.), *The Global Triassic*. *New Mexico Museum of Natural History and Science Bulletin* 41: 402.
- Twitchett, R.J. and Wignall, P.B. 1996. Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaogeography, Palaeoclimatology, Palaeoecology* 124: 137–151.
- Wasmer, M., Hautmann, M., Hermann, E., Ware, D., Roohi, G., Rehman, K., Yassen, A., and Bucher, H. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. *Palaentology* 55: 1043–1073.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.
- Whittaker, R.H. 1975. *Communities and ecosystems*. 385 pp. Macmillan; Collier Macmillan, New York.
- Wignall, P.B. and Hallam, A. 1992. Anoxia as a cause of the Permian/Triassic mass extinction: facies evidence from northern Italy and the western United States. *Palaogeography, Palaeoclimatology, Palaeoecology* 93: 21–46.
- Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296–302.
- Zieten, C.H. von 1830. *Die Versteinerungen Württembergs*. 102 pp. Verlag & Lithographie des Werkes Unsere Zeit, Stuttgart.
- Zonneveld, J.-P., Pemberton, S.G., Saunders, T.D.A., and Pickerill, R.K. 2002. Large, robust *Cruziana* from the Middle Triassic of northeastern British Columbia: Ethologic, biostratigraphic, and paleobiologic significance. *Palaios* 17: 435–448.