

Alexander Nützel · Christian Schulbert

Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction

Received: 11 January 2005 / Accepted: 23 March 2005 / Published online: 26 May 2005
© Springer-Verlag 2005

Abstract Two important lagerstätten of Early Triassic gastropods, the Sinbad Limestone (Utah, USA) and the Gastropod Oolite (North Italy) yield about 40% of all described Early Triassic species. This great contribution to the global diversity and the exceptional good preservation render high information content, which characterizes fossil lagerstätten. The Smithian Sinbad Limestone contains the most diverse Early Triassic gastropod fauna. At the type locality, it occurs in single, probably storm-induced shell bed within a series of high energy deposits underlain by intertidal microbial mats and subtidal oolite/peloid shoals. The main shell bed contains about 40 invertebrate taxa. Gastropods, scaphopods, and bivalves are most abundant and form an assemblage, which is dominated by small neritaemorphs, the opisthobranch *Cylindrobullina convexa* and the scaphopod *Plagioglypta* (annulated tubes). This assemblage lived on shallow, subtidal soft-bottoms based on sedimentological and ecological characteristics. The Dienerian (to Smithian?) Gastropod Oolite Member (North Italy) has extremely abundant, probably salinity-controlled gastropod faunas with low species richness. Almost monospecific assemblages of *Pseudomurchisonia kokeni* as well as assemblages with about four species are present in the Gastropod Oolite. Modern hydrobiid mudsnail faunas which are adapted to strongly fluctuating salinity in intertidal to shallow subtidal coastal areas form probably a suitable model for the Gastropod Oolite biota. Gastropods from the Werfen- and Moenkopi-Formation lagerstätten are well preserved compared to other Early Triassic deposits. The high contribution to the global diversity of just two sites suggests very incomplete sampling and preservational bias. However, the low richness of the major faunas reflects depauperate Early Triassic faunas and slow recovery from the Permian/Triassic crisis.

Keywords Gastropoda · USA · Italy · Early Triassic · Recovery · Permian/Triassic mass extinction

Introduction

Fossil lagerstätten are rock bodies with exceptional high paleontological information content (Seilacher et al. 1985). For four reasons, the Sinbad Limestone Member (Utah, USA) and the Gastropod Oolite Member (North Italy) represent outstanding Early Triassic fossil lagerstätten:

1. They contain beds with extremely abundant gastropods and other molluscs (concentration lagerstätten).
2. They were deposited in a particularly critical time-interval: the aftermath of the end-Permian biotic crisis.
3. They contribute a great portion to the global Early Triassic species richness, as is indicated by our own species-level database (as much as 40% of nominate species).
4. They are exceptionally well preserved (especially gastropods from the Sinbad Limestone).

This paper describes and interprets microfacies, sedimentology, fossil preservation, and faunal content of shell beds from both members. Generally, shell beds form an important source of paleontological, paleoecological, and taphonomic information (e.g., Kidwell 1991a, b; Fürsich and Oschmann 1993; Boyer et al. 2004). The concentration of shells in distinct beds was produced by storms (tempestites) or they represent lag deposits (e.g., Kidwell 1991a, b).

The shell beds studied here represent benthic mollusc coquinas. We use this term in order to separate such shell beds from cephalopod coquinas (e.g., the Jurassic Ammonitico Rosso Facies, or the Paleozoic *Orthoceras* Limestones), which represent another distinct type of mollusc concentrations and depositional environment. Benthic mollusc coquinas are more common in the post-Paleozoic reflecting the rise of modern bivalve- and gastropod-dominated faunas (Sepkoski et al. 1991; Kidwell and Brenchley 1994). The increase of this facies was accentuated by the end-Permian mass extinction event, which removed or diminished typical Paleozoic faunal elements, e.g., articulate

A. Nützel (✉) · C. Schulbert
Institute of Palaeontology, University Erlangen-Nürnberg,
Loewenichstrasse 28,
D-91054 Erlangen, Germany
e-mail: nuetzel@pal.uni-erlangen.de
Tel.: +49-(0)9131-8524849
Fax: +49-(0)9131-8522690

brachiopods. The analysis of Early Triassic shell beds helps to understand the evolutionary history of the gastropods at the Paleozoic/Mesozoic transition and the recovery from the end-Permian mass extinction. It is particularly interesting which factors potentially limited the diversity during the aftermath of the end-Permian catastrophe. This aftermath is considered to be extremely long lasting and was obviously connected with major high-frequency perturbations of the carbon cycle (Payne et al. 2004). Among other possible reasons, anoxia was discussed as limiting factor, especially for biota during the earliest Triassic (Griesbachian; Wignall and Twitchett 2002). However, the proximate limiting conditions during the whole length of the recovery interval are still poorly understood. An important step to unravel these factors is the analysis of the facies and depositional environments of the main fossil lagerstätten of the Early Triassic. Gastropods play an important role in any recovery analysis because they form one of the most diverse invertebrate groups in the Early Triassic. This study is about the facies and depositional environments of two important Early Triassic gastropod occurrences: the Sinbad Limestone locality where the collection of Batten and Stokes (1986) comes from (American Museum of Natural History (AMNH) Locality #3026; Fig. 1) and one of Wittenburg's (1908a, b) collecting sites (Gastropod Oolite Member, Valsugana, near Trento; Fig. 2). The Sinbad Limestone Member is of Smithian (Olenekian) age and the Gastropod Oolite is of Dienerian age (maybe ranging into the Smithian; Fig. 3). Previous microfacies, sedimentological and paleoecological studies exist for both members (Sinbad: Blakey 1974; Dean 1981; Schubert and Bottjer 1995; Fraiser and Bottjer 2004; Gastropod Oolite: e.g., Broglio Loriga et al. 1983; Boeckelmann 1988; Wignall and Twitchett 1999). However, no detailed analysis was made specifically for the

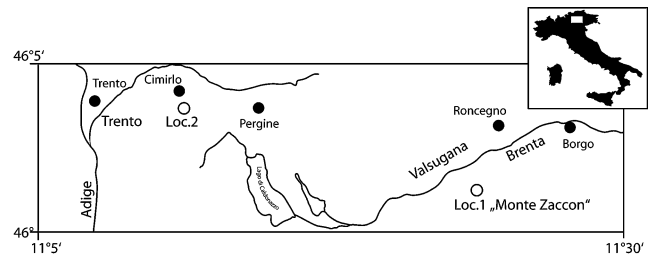


Fig. 2 Location of the studied sites of the Early Triassic Gastropod Oolite Member (Valsugana, N Italy)

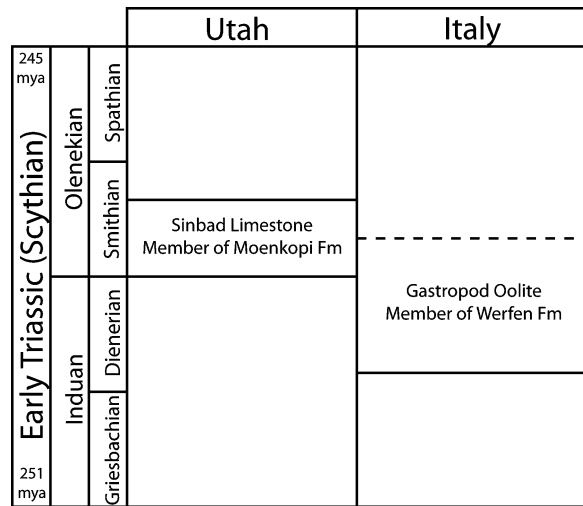


Fig. 3 Approximate stratigraphic position of the Sinbad Limestone Member (Smithian) and the Gastropod Oolite Member (Dienerian and probably Smithian) in the Early Triassic

main fossil bearing units and previous studies were not primarily concentrated on the gastropod occurrence but generally stood in a wider frame or dealt with particular phenomena, such as small size of the shells (e.g., Fraiser and Bottjer 2004).

To date, only 74 described gastropod species are known from Early Triassic rocks around the world as is indicated by our own species-level database (see also Nützel 2005, in press). This number accounts for the reported actual occurrences of nominate species and does not consider Lazarus taxa and species in open nomenclature. Diversity seems to be extremely low in the immediate aftermath of the end-Permian mass extinction event. Lowermost Triassic (Induan, Griesbachian) gastropod faunas usually comprise only a few species and reports of single species occurrences are common. The state of preservation of Early Triassic gastropods (especially those from the Griesbachian) is generally poor. The only relatively diverse Griesbachian fauna is from the Wadi Wasit Block in Oman (Twitchett et al. 2004; Wheeley and Twitchett in press). This fauna comprises about 10 species and genera and is considered to represent the only Griesbachian fauna from a well-oxygenated environment (Twitchett et al. 2004). These Oman gastropods are coarsely silicified so that taxonomic assignments are tentative. The number of reported species rises considerably in the Olenekian. Most Olenekian gastropod occurrences

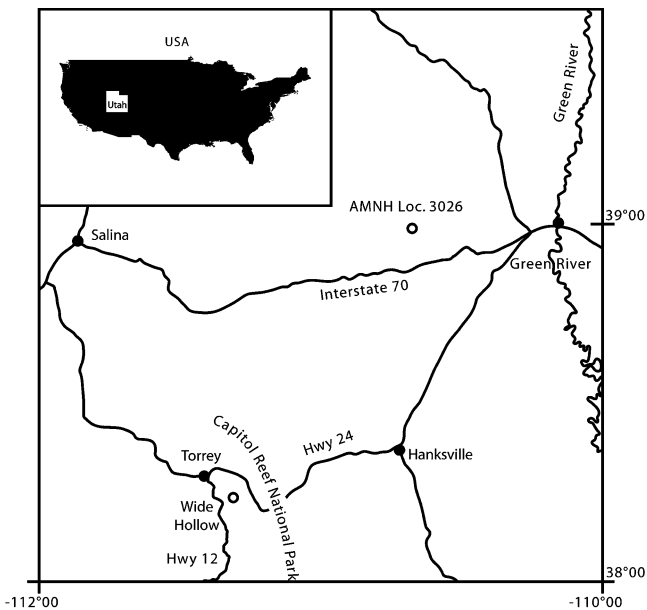


Fig. 1 Location of the studied sites of the Early Triassic Sinbad Limestone (Utah, San Rafael Swell and Capitol Reef, near Torrey)

were reported from the Werfen Formation (Alps) and the Sinbad Limestone (Moenkopi Formation, Utah). Together, the Sinbad Limestone Member of the Moenkopi Formation and the entire Werfen Formation contribute about 50% to the global number of described nominate gastropod species from the Early Triassic. The Olenekian (Smithian) fauna from the Sinbad Limestone (Moenkopi Formation) comprises 26 described gastropod species. Faunas with more than 100 gastropod species have not been reported prior to the Late Anisian (Stiller 2001a). Early Triassic gastropod faunas, including those from the Werfen and Moenkopi Formations, have been interpreted as disaster faunas, which were dominated by small, commonly abundant, r-selected species and are characterized by a relatively low species richness (Batten 1973; Schubert and Bottjer 1995; Fraiser and Bottjer 2004). The impact of the Permian/Triassic mass extinction event on the evolution of the Gastropoda was substantial (Erwin 1990; Nützel 2005, *in press*). For instance, the Sinbad Limestone Member contains abundant heterostrophic opisthobranchs, small neritae-morphs, and several Mesozoic caenogastropod genera (see below) which represents an assemblage not found in the Paleozoic (Nützel 2005, *in press*). Typical Late Paleozoic elements are absent or uncommon, e.g., bellerophonitids, pleurotomarioids, euomphalids, and pseudozygopleurids. There are some Paleozoic holdovers present in the Sinbad Limestone Member, but they do not form the dominant elements. Similarly, there are no typical Paleozoic gastropod genera present in the Gastropod Oolite Member and in the Upper Werfen Formation of the European Alps. With all caution and considering the insufficient preservation of most Early Triassic gastropods, this suggests that the end-Permian mass extinction and the subsequent recovery period caused major shifts within the Gastropoda (Nützel 2005, *in press*).

Methods

Shell beds were disaggregated with the hammer and cracked out fossils were collected in the field (Sinbad Limestone April 2003; Werfen Formation June 2004). The remaining rock debris and powder (about 50 kg disaggregated of rock samples) were wet sieved at 0.5 mm mesh size. The residues were picked under a stereomicroscope and obtained invertebrate fossils were studied with a Scanning Electron Microscope. About 50 thin-sections and polished slabs were studied from representative facies types which were recognized in the field. Most of the thin-sections were made from oriented samples of measured sections. The intensity of this study is uneven for both the sites. At the Sinbad Limestone locality, a well-exposed section was studied in detail and the vertical facies succession is documented here. However, the Gastropod Oolite from Valsugana is not as well exposed and only the fossil bearing shell beds could be studied regarding microfacies and fossil preservation.

Geological setting

Geological setting of the Sinbad Limestone Member (Moenkopi Formation)

The studied section belongs to the Sinbad Limestone Member and is exposed in the San Rafael Swell, south Utah. The Sinbad Limestone Member is a 15–30 m thick carbonate unit within the predominantly siliciclastic, terrestrial Moenkopi Formation (e.g., Blakey 1974; Dean 1981). It is Smithian (Olenekian) in age. The Moenkopi Formation unconformably overlies Late Paleozoic deposits of the Colorado Plateau. The Sinbad Limestone Member represents a marine episode (transgression) in the Moenkopi siliciclastic beds and contains fossiliferous limestones, dolostones, and calcareous siltstones. The Sinbad Limestone was deposited in an epicontinental sea with free access to the Paleo-Pacific Ocean Panthalassa to the west. Blakey (1974) provided a comprehensive overview of the Moenkopi Formation in southeastern Utah. Dean (1981) studied the Sinbad Limestone Member in the Teasdale Uplift area (near Torrey; Fig. 1). Blakey (1974) and Dean (1981) reported all major facies types of the Sinbad Limestone which are also present in the section studied here, e.g., skeletal calcarenites and oolitic grainstones, all formed in a shallow, epicontinental sea. Storm deposition seems to be common in the Sinbad Limestone (e.g., Blakey 1974). However, Blakey's (1974) and Dean's (1981) study were not primarily focused on the fossil occurrences. Subsequently, a rich Early Triassic gastropod fauna was described from the Sinbad Limestone, comprising 26 species representing 16 genera (Batten and Stokes 1986).

Stromatolites were repeatedly reported from the Sinbad Limestone (Blakey 1974; Dean 1981; Schubert and Bottjer 1992). Generally, the presence of stromatolites in normal subtidal, marine environments was interpreted as a disaster phenomenon (Schubert and Bottjer 1992). Stromatolites and oolites in the marine limestones of the Moenkopi Formation indicate warm, shallow-marine conditions. Stromatolites are absent at the gastropod type locality of Batten and Stokes (1986) which is reported here in detail (see below). However, stromatolites were studied by us at the Miners Mountain section near Torrey (Capitol Reef, Teasdale Uplift; Figs. 1 and 4). These stromatolites show a variety of growth forms: laminar (Fig. 4A), wavy (Fig. 4B), columnar (Fig. 4C, right), and microstromatolitic (Fig. 4C, left). They commonly occur together with gastropods and even grew on gastropods (Fig. 4C).

Geological setting of the Gastropod Oolite Member (Werfen Formation)

The Early Triassic Werfen Formation crops out in a vast area of the South Alps (Italian Dolomites) and North Alps (Germany, Austria) and overlies the Late Permian (Wuchiapingian to Changhsingian) Bellerophon Formation, which yields a rich, typical Late Paleozoic marine

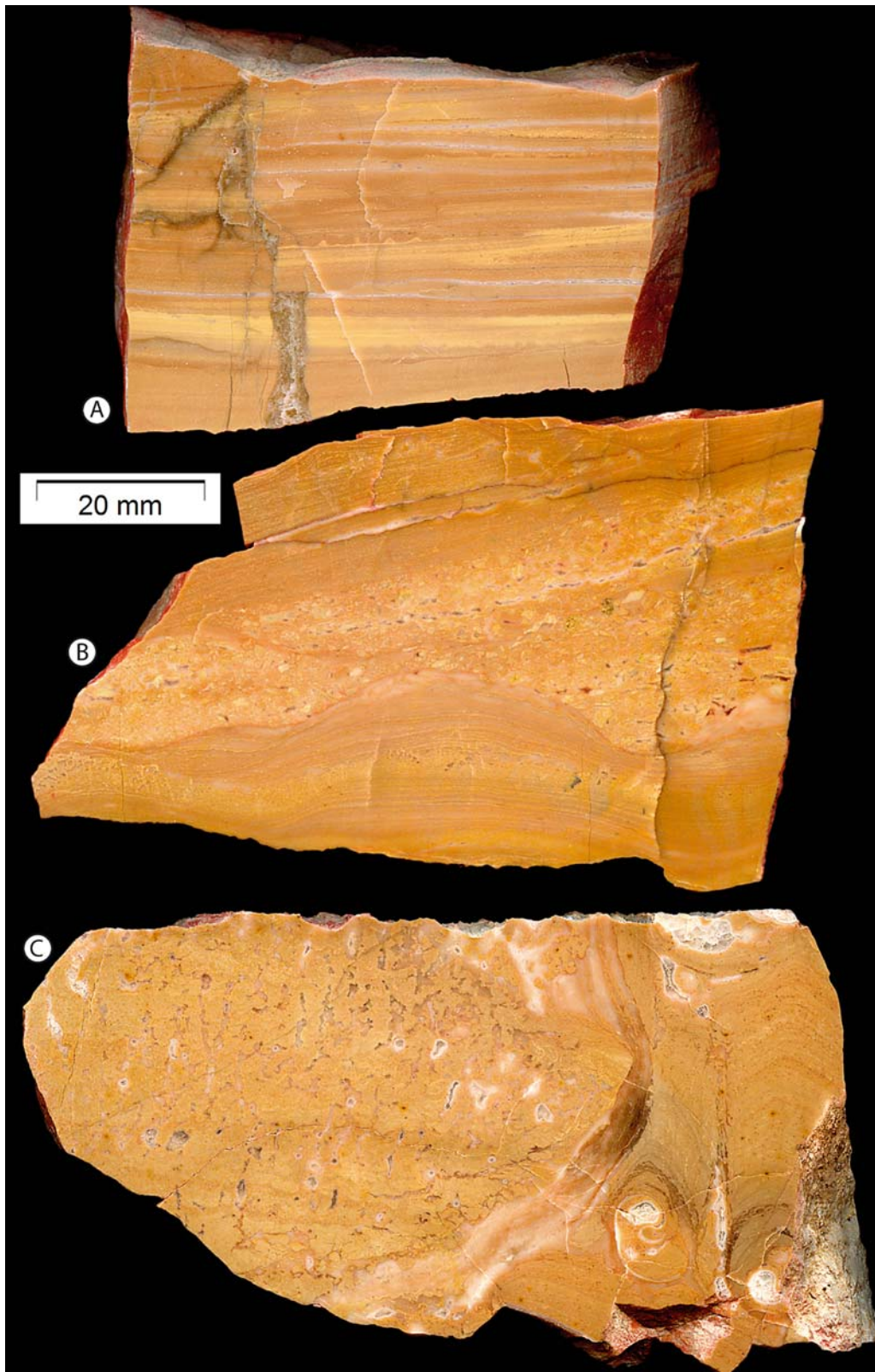


Fig. 4 Polished slabs showing stromatolites (bindstones) from Sinbad Limestone near Torrey (Miners Mountain, Wide Hollow, 2315 m, 38°13'40.0"N, 111°18'38.6"W); in contrast to the section at the gastropod collection site of Batten and Stokes (1986), stromatolites are abundant in the Torrey area. **A** Stromatolitic bindstone

with plane lamination. **B** Wavy stromatolites at base covered by a bioclastic layer and laminated bindstone on top. **C** On right side two columnar stromatolites growing on gastropod shells; left: microstromatolites with sparitic cavities (no birdseyes)

fauna with brachiopods and bellerophonitids in its upper part. The Werfen Formation is up to several hundred metres thick and comprises the entire Early Triassic. Its abundant fauna is dominated by bivalves and gastropods. Microgastropods are very abundant and rock-forming in a facies which is called 'Gastropod Oolite'. This term is also used in a lithostratigraphic sense for a member between the Seis and Campil Members. However, this facies-type seems to recur throughout the Werfen Formation (e.g., Boeckelmann 1988) and is also present in the Servino Formation (e.g., Assereto and Rizzini 1975). The Gastropod Oolite Member has probably a Dienerian age as is indicated by conodonts (Twitchett 1999; Wignall and Twitchett 1999) and is therefore somewhat older than the Smithian Sinbad Limestone. However, the Gastropod Oolite-facies is also contemporaneous and inter-fingering with the Seis (Siusi) Member and could be Smithian in its upper part. It is also heterogeneous and comprises a variety of different facies types (e.g., Broglio Loriga et al. 1983; Boeckelmann 1988). The Gastropod Oolite Member consists of oolites in which gastropods and other bioclasts form the cores of the ooids or they occur as iron oxide encrusted bioclasts of wackestones and grainstones. This facies is also widely distributed in Early Triassic platform carbonates and is known from the Alpine-Mediterranean region to Iran and China (e.g., Assereto and Rizzini 1975; Flügel 2004). Transported ferroan dolomites were reported from the Gastropod Oolite equivalent in the Servino Formation (Assereto and Rizzini 1975). Wignall and Twitchett (1999) reported gastropod grainstones with erosive base, intraclasts (flat pebbles), multidirectional tool marks, and graded bedding for the Gastropod Oolite and discussed a tempestitic deposition of such beds.

Here, the Gastropod Oolite was studied at two localities from the Valsugana and Trento area in Northern Italy at the southern border of the Dolomites. One locality lies 4.6 km SW Borgo Valsugana (GPS (WGS 84): 46°01'32.5"N, 11°24'39.6"E; Fig. 2). Relatively well-preserved gastropods were reported from this site by Wittenburg (1908a, b). A second location was studied and sampled 750 m south of Cimirlo (near the road from Cimirlo to Busa del Vent, where road crosses creek in a narrow curve; GPS (WGS 84): 46°03'50.5"N, 11°10'58.0"E; Fig. 2). At this location, well-preserved gastropods occur in rocks of the same facies as were found near Borgo Valsugana.

Results and discussion

Facies of the Sinbad Limestone at the gastropod type locality

Description and interpretation of the section

The section at the gastropod collection locality of Batten and Stokes (1986) (Sinbad Limestone, AMNH Locality #3026 GPS (WGS 84): 38°59'51.0"N, 110°40'53.2"W; Fig. 1) was studied and measured (Table 1). The section comprises about 12 m of essentially calcareous beds with considerable siliciclastic input in its uppermost beds.

Thirteen units (Bed I–XIII; Figs. 5–13D; Table 1) with distinct facies are recognized. Bed VIII is the main fossil-bearing unit where the described Sinbad Limestone gastropod fauna originates from. The lateral extension of the present beds was only followed for some 10–100 m because sampling was primarily focused on the fossil occurrence at Batten and Stokes's (1986) collecting locality. The studied section represents probably a part of a single transgressive–regressive cycle and comprises a wide range of different microfacies-types and different faunal compositions. This heterogeneity is probably a result of the shallow-water conditions and sea-level changes combined with several storm- or other high-energy events. The lower part of the section from Bed I to Bed IV/V is characterized by intertidal microbial mats (laminated bindstones) and oolitic/peloidal shoals. Peloids in Beds I and II represent micritized ooids as is indicated by micritic grains which show relicts of concentric striation (see also Blakey 1974). Current ripples and abrupt grain-size changes in the oolitic/peloidal shoals suggest that the material was transported. Gastropods are common but not abundant in these beds. Bed III represents intertidal algal mats, which were moderately reworked in a semi-consolidated state and finally cemented with sparry calcite. The lower units (Beds I–IV/V) are not very fossiliferous and lack benthic mollusc coquinas. The few fossils are generally not well preserved.

Bed V represents an intraclast/peloid/ooid shoal with incised channels. The breccia-like channel fill represents a high-energy event and could be a proximal tempestite (or tsunami deposit) as is indicated by poor sorting and the large size of the clasts which are commonly suspended in a fine-grained matrix. Similar deposits were reported from the Sinbad Limestone of the Torrey area (Dean 1981). Deposition in tidal channels during transgression is also possible (see Flügel 2004 for comparable deposits). The relatively large clasts of the channel fills represent probably a mixture of marine intertidal to shallow subtidal and eventually supratidal mudstones. The channel fill seems to belong to the so-called flat pebble conglomerates, which have been interpreted as anachronistic, non-actualistic facies. Accordingly, such conglomerates were common during the Cambro–Ordovician and in the aftermath of the end-Permian extinction mainly due to low bioturbation which allowed preservation of thin beds and rapid lithification (e.g., Sepkoski et al. 1991; Wignall and Twitchett 1999).

Bed V marks a change in sedimentation: above it, several shell beds and other fossiliferous units occur (Bed VI–XII). Of these, Bed VI, VIII, and XII are probably tempestites based on sharp erosive base, graded bedding and a faunal content which differs strongly from that of the under- or overlying beds. Thus, from Bed V onward, storm sedimentation repeatedly re-deposited marine, subtidal biota. Storm sedimentation was previously reported for the Sinbad Limestone (Blakey 1974; Schubert and Bottjer 1995; Boyer et al. 2004). It is remarkable that the main shell beds (Beds VI, VIII, XII) differ strongly from each other in faunal content and microfacies. Bed VI contains two distinct units: a rather coarse biosparite in the lower

Table 1 Descriptions and interpretations of microfacies and sedimentary fabrics of the studied Simbad Limestone section

Bed	Figure	Thickness (cm)	Facies type	Dominant clasts	Sedimentary fabric and other features	Interpretation
XIII	13D	300	Sandstone with micritic matrix	Angular quartz, fine sand to silt size; few bivalve steinkerns	Plane bed lamination and asymmetric cross-bedding	Strong siliciclastic input; end of sedimentation
XII	13B and C	60	Rudstone	Thin-shelled pteriomorph bivalves; strongly deformed and compacted; few gastropods; small round objects with micritic rims	Erosional base; with several (about 7) horizontal partitioning planes	Probably tempestite (faunal content very different from that of upper and lower beds)
XI	-	35	Mudstone, silty	No larger clasts, unfossiliferous	Homogeneous, nodular weathering	Probably low energy; resembles Bed IX
X	12H and 13A	35	Floatstone with packstone matrix	Thin-shelled bivalves, disarticulated, convex up; rare gastropods; matrix with small unidentifiable bioclasts and quartz in fine sand to silt size	Sheltered porosity filled with sparitic cement under bivalves; plane bed lamination; several horizontal partitioning planes	Deposition under moderate current conditions with some siliciclastic input
IX	-	50	Mudstone	No larger clasts	Homogeneous	Probably low energy
VIII	8D, 9F and G, 10, 11 and 12A-G	40	Rud-, grain- and packstones	Abundant molluscs (gastropods, scaphopods, bivalves), commonly with micritic envelopes; echinoderm ossicles (ophiuroids, echinoids); intraclasts; small peloids	Base sharp; graded bedding common; molluscs commonly filled with micrite even if sparite between bioclasts; clast-supported fabric; bivalves commonly with articulated valves	Tempestite (sharp, erosional base, graded bedding; intraclasts); faunal content differs from that of upper and lower beds; Main fossil bearing unit (= lagerstätten)
VII	8D and 9E	30	Wacke- packstone	Rare echinoderms; quartz in silt and fine sand size	Chip-like weathering	Probably distal tempestite with terrigenous quartz
VI	8C, D and 9A-D	30-40	Grain- and rudstones	Lower part: mostly bivalves, completely micritized; upper part: peloids and ooids	Sharp, erosional base and eroded top; large sparitic spots with sparite, commonly as syntaxial cement of echinoderm ossicles	Lowermost shell bed in the section; lower part probably eroded tempestite
Vb	7F-H and 8B and C		Rudstone; conglomerates, mostly matrix supported	Large intraclasts (several cm to dm), commonly flat and rounded	Laterally-linked channels; upper and lower erosional contact	Flat pebble conglomerate; proximal tempestites or fill of tidal channels; high energy (maybe tsunami deposit)
Va	7D-E	75	Grain- and packstones	Ooids, peloids, oncoids, bioclasts with micritic rims	Cross-bedding (field observation)	Shallow, subtidal oolite shoal
IV	-	40	Mudstone	No larger clasts, unfossiliferous	Homogeneous	Probably low energy
III	7A-C and 8A	120m	Reworked bindstones	Bindstone-slabs; peloids; rare, poorly preserved gastropods	Sparitic cement between large bindstone slabs	Moderately reworked, parautochthonous, intertidal algal mats
II	6C-H	100	Grain- and packstones	Ooids and peloids; well-rounded intraclasts; rare gastropods (poorly preserved)	Massive, hard, edge-forming; current ripples observed in the field; abrupt grain-size changes	Shallow, subtidal; transported
I	6A and B	260	Pack- and grainstones, laminated bindstones	Ooids and micritized ooids (peloids); bioclasts rare to absent	Thin-bedded, thickening upward; mud-cracks in bindstones	Subtidal peloid/oolite shoal and intertidal microbial mats

This section is exposed at the type locality of the gastropod fauna studied by Batten and Stokes (1986) (AMNH locality 3026; Fig. 1)

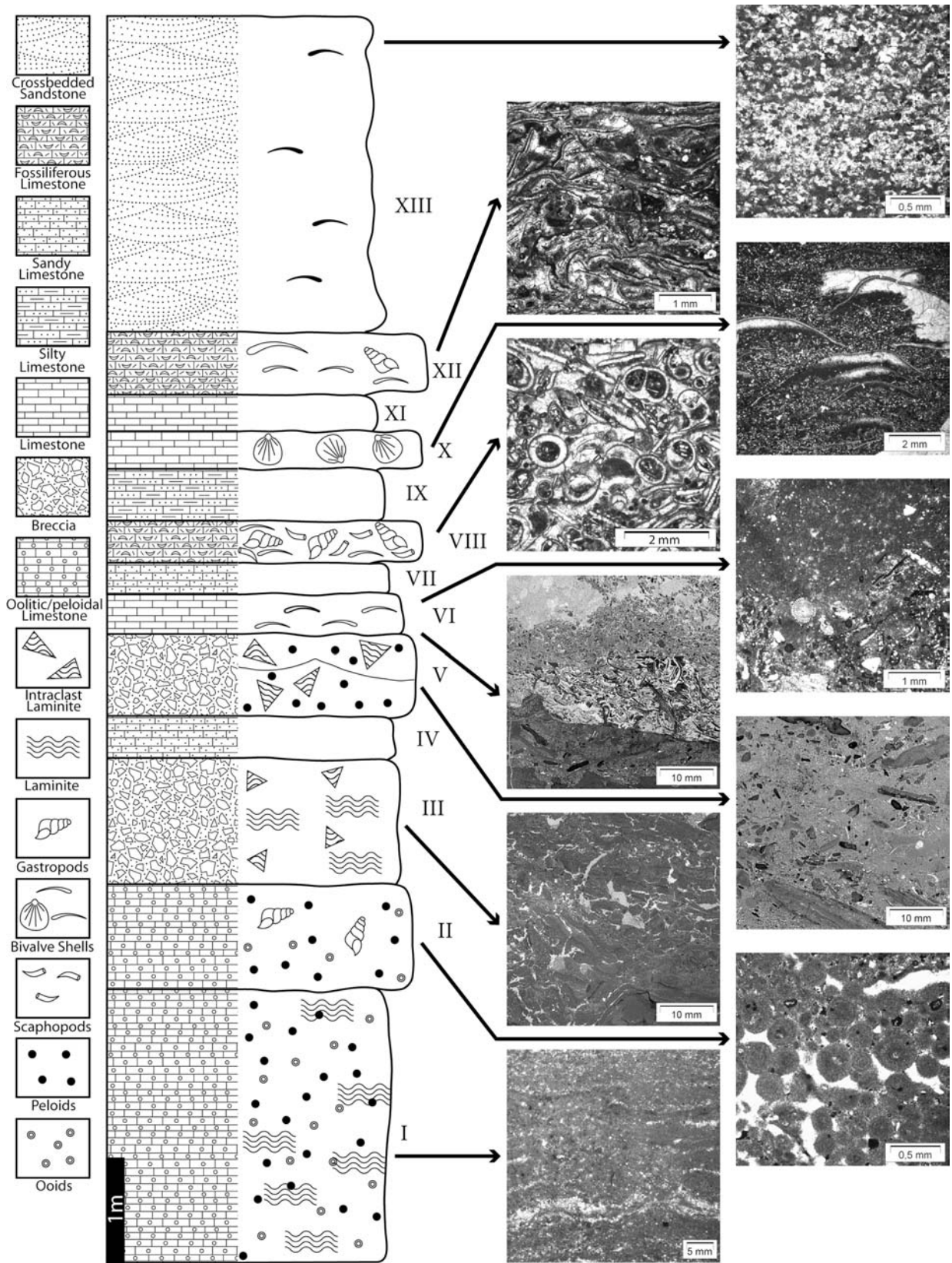
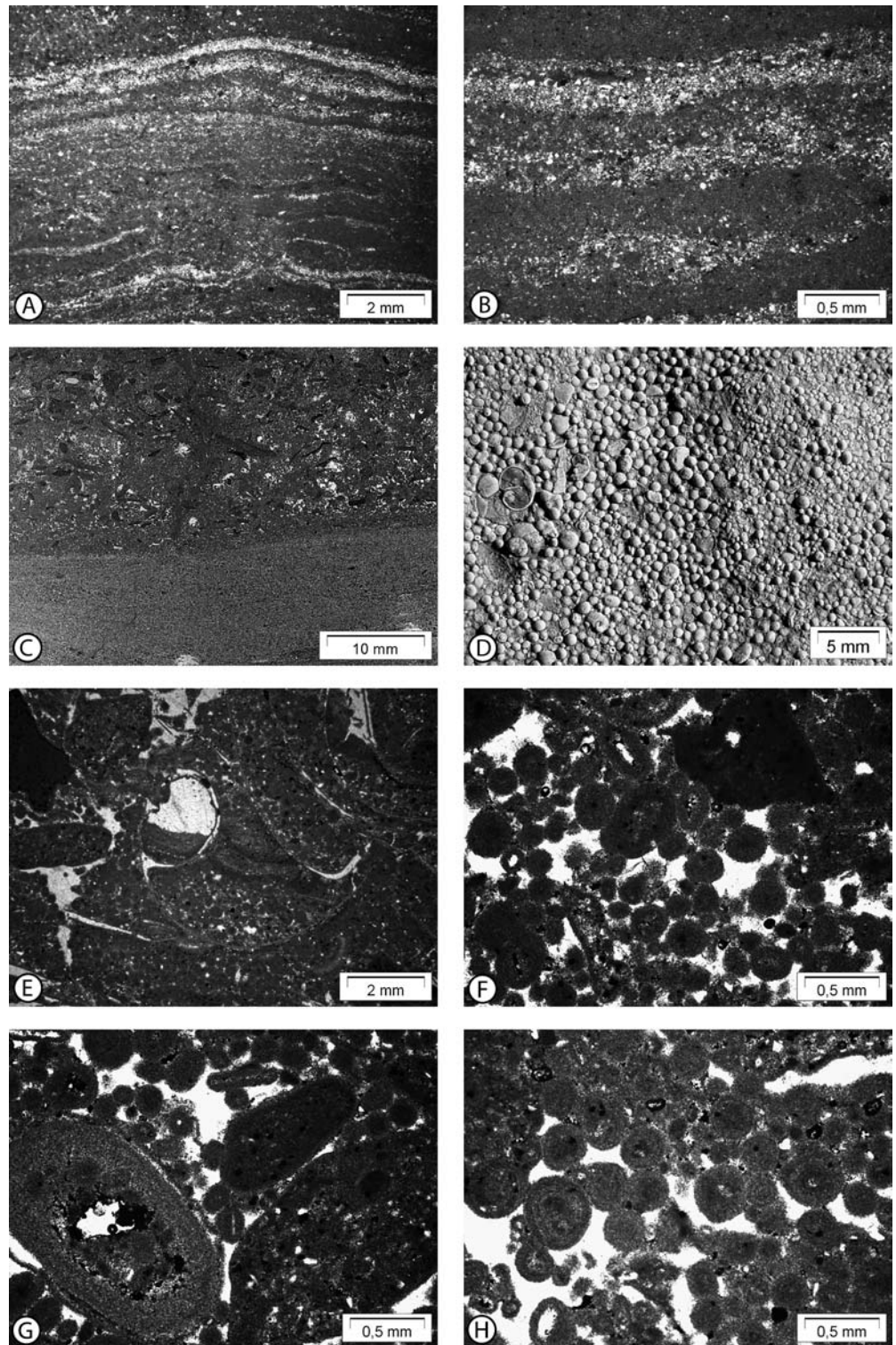


Fig. 5 Section of Sinbad Limestone at gastropod collection locality of Batten and Stokes (1986), American Museum of Natural History (AMNH) locality 3026, with 13 distinct beds (I–XIII). The lower beds (I–V) are dominated by laminated intertidal bindstones and oolitic/peloidal shoals. The upper part of Bed V is a coarse channel

fill. From this bed onward, several tempestitic shell beds occur; one of these beds (Bed VIII) is the main fossil bearing unit (lagerstätte) which yields an abundant, well-preserved gastropod fauna as well as abundant bivalves and scaphopods. Bed XIII is essentially siliciclastic and indicates an increasing terrestrial input

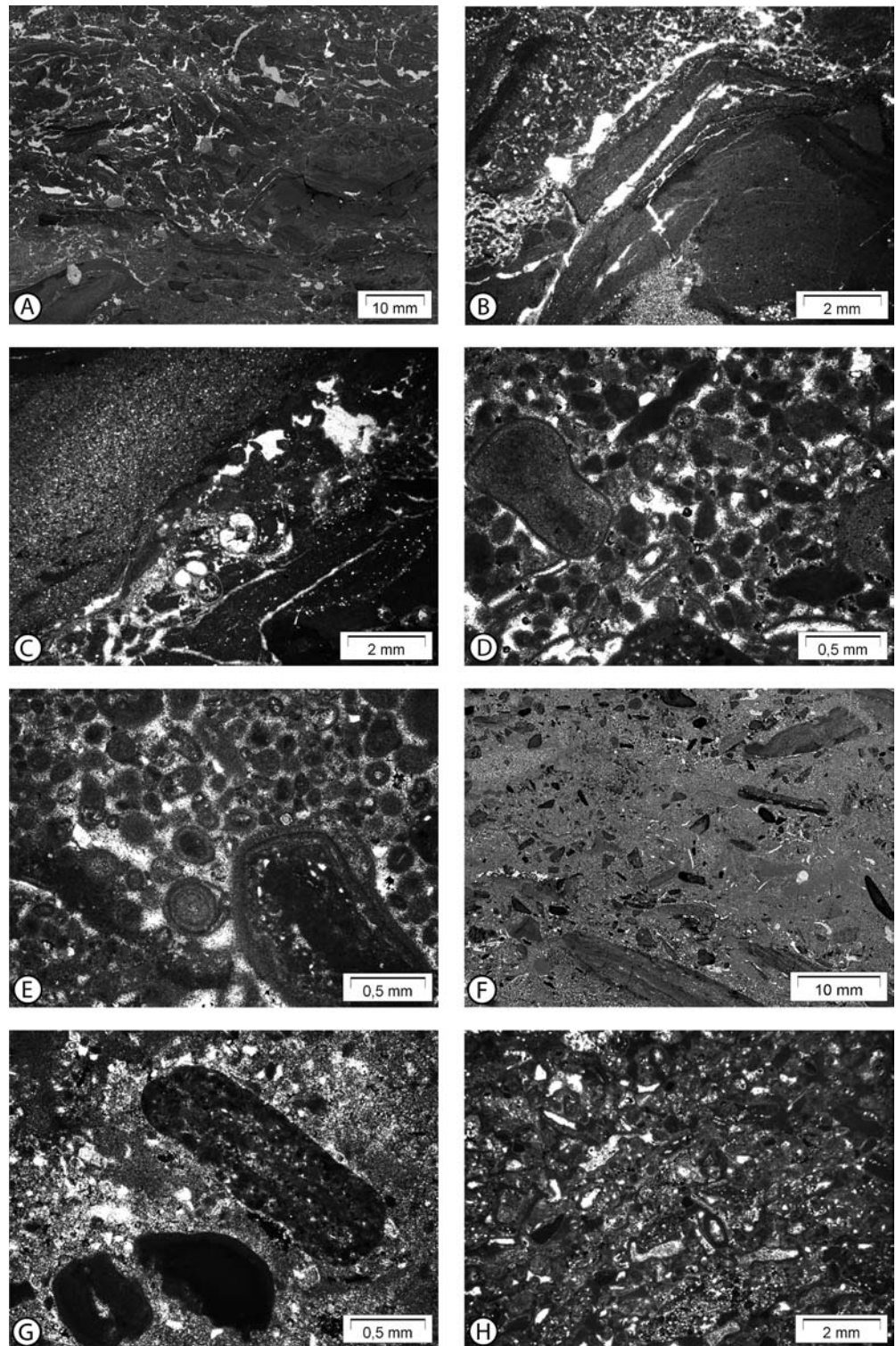
Fig. 6 Microfacies of Bed I and II of the Sinbad Limestone at AMNH locality 3026. **A–B** Bed I, laminated bindstone (intertidal algal mats). **A** Overview of laminated bindstone with an alternation of dark and light layers; interruption of layers in lower portion could suggest bioturbation or presence of mud cracks. **B** Close-up of laminated bindstone with dark, micritic layers and light, somewhat coarser grained layers. **C–H** Bed II, oolitic/peloidal/intraclast grainstones. **C** Abrupt change in grain size within Bed II indicating transport; fine grained peloids and ooids in lower part; coarser peloids/ooids and intraclasts in upper part. **D** Weathered surface of oolitic/peloidal bed with several poorly preserved gastropods. **E** Peloids, intraclasts, shells with geopetal fabric and sparry cementation. **F** Peloidal grainstone. **G** Intraclast/peloidal grainstone. **H** Peloidal/oolitic grainstone; ooids/peloids with relics of concentric striation, indicating that peloids are mainly micritized ooids



portion with micritized mollusc shells (mainly bivalves) and an upper portion with more fine-grained material and large sparitic areas which contain echinoderm ossicles with syntaxial cements. The micritized shell coquina probably represents a partly eroded tempestite which overlies the channel fill. Bed VI represents the lowermost shell bed in this section. It is also the first appearance of

common echinoderm ossicles. This suggests that the biota came from a fairly normal marine, subtidal environment. Due to micritization, the bed does not yield well-preserved fossils. Gastropods are rare to absent. Bed VIII is the main fossil-bearing unit and essentially the fossil lagerstätte which yields the well-preserved gastropod, bivalve and scaphopod material (Figs. 10 and 11). The marked

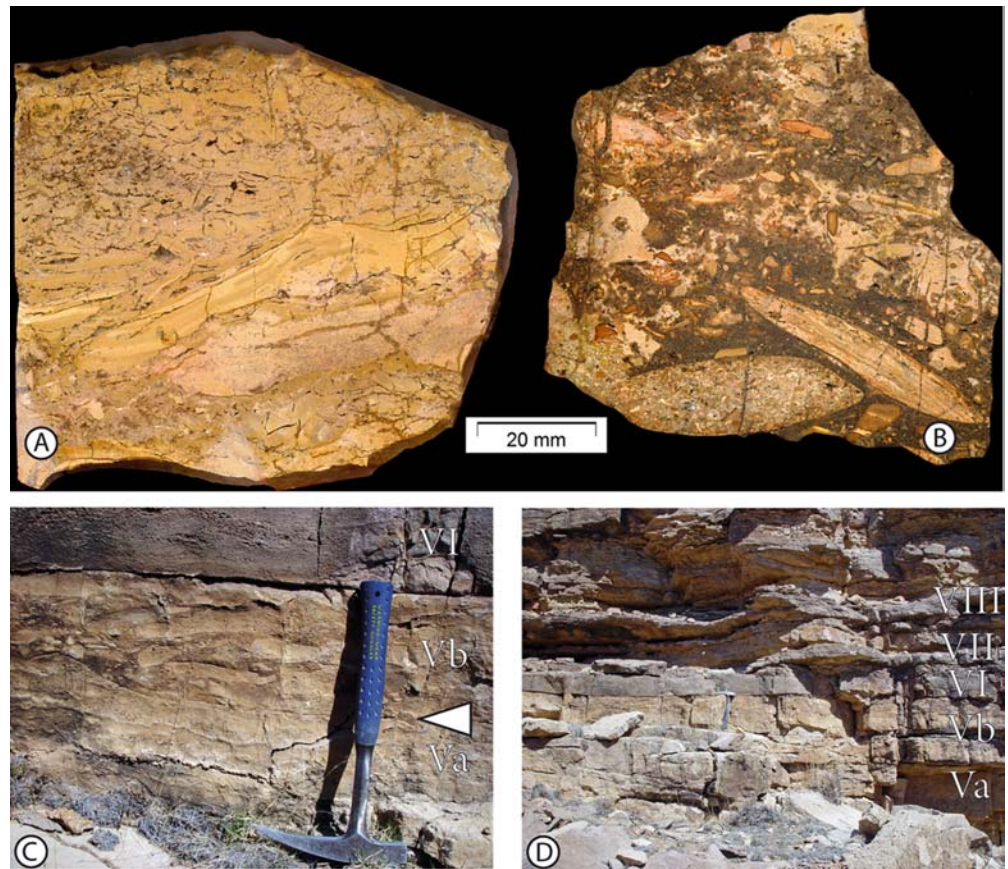
Fig. 7 Microfacies of Beds III and V of the Sinbad Limestone at AMNH locality 3026. **A–C** Bed III, slightly reworked, parautochthonous bindstones formed by intertidal algal mats, cemented with sparite; contains rare gastropods (see also Fig. 8A). **A** Overview showing fabric of deformed mudstones. **B** Laminated, deformed mudstone (bindstone) slab and peloidal grainstone. **C** Peloidal grainstone layer with gastropods between mudstone (bindstone) slabs. **D–E** Lower portion of Bed V (i.e., Bed Va), oolite/peloidal/intraclast grainstones; in this unit, laterally linked channels are incised (Bed Vb). **D** Grainstone with peloids, intraclasts and biolasts with micritic rims. **E** Grainstone with ooids, peloids (commonly micritized ooids) and oncoids. **F–H** Bed Vb, channel fill within Bed V with large clasts, “flat pebble conglomerate” (see also Figs. 8B and C). **F** Predominantly matrix-supported intraclast floatstone to rudstone. **G** Detail with several rounded clasts. **H** Detail of large clast (thin-section from lowermost large clast in Fig. 8B) showing probably microbial tubes (bacteria)



lithological and faunal differences to the underlying and overlying beds, graded bedding, and presence of intraclasts indicate that this bed is a tempestite. Such beds correspond to the “skeletal calcarenite facies”, which was previously reported for the Sinbad Limestone Member (Blakey 1974). The paleoecology and preservation of Bed VIII is discussed below. Bed XII is very rich in thin-shelled, densely

packed bivalves. The bivalves cannot be isolated from the rock because cementation and packing is too intense. Apart from the main fossil bearing unit (Bed VIII), this bed (XII) has the highest fossil concentration. The strong dominance of thin-shelled, probably pteriomorph bivalves and the rarity of gastropods shows that the assemblage of Bed XII differs strongly from that of Bed VIII.

Fig. 8 **A** Polished slab of Bed III, slightly reworked, parautochthonous bindstones formed by intertidal algal mats, cemented with sparite (see also Figs. 7A–C). **B** Polished slab of channel fill within Bed V (Bed Vb); with large, flat clasts; see also Figs. 7F–H, 8C, 9A; thin-section of large, lowermost clast in Fig. 7H. **C** Bed V, oolite/peloidal/intraclast grainstones (Bed Va) with incised channel fill with large clasts (Bed Vb; triangle marks base of channel fill) and sharp contact to overlying shell bed (Bed VI). **D** Outcrop photograph of Beds V–VIII



Biota, preservation and paleoecology of the Sinbad Limestone gastropod lagerstätte

The diverse and well-preserved gastropod fauna of the Sinbad Limestone occurs largely in a single, probably tempestitic bed of the studied section (Bed VIII). This shell bed represents a benthic mollusc coquina of 20–40 cm thickness. It consists of rudstones, packstones and grainstones with common graded bedding. The fabric is generally clast-supported with sparry cement or is poorly washed with portions with micritic matrix.

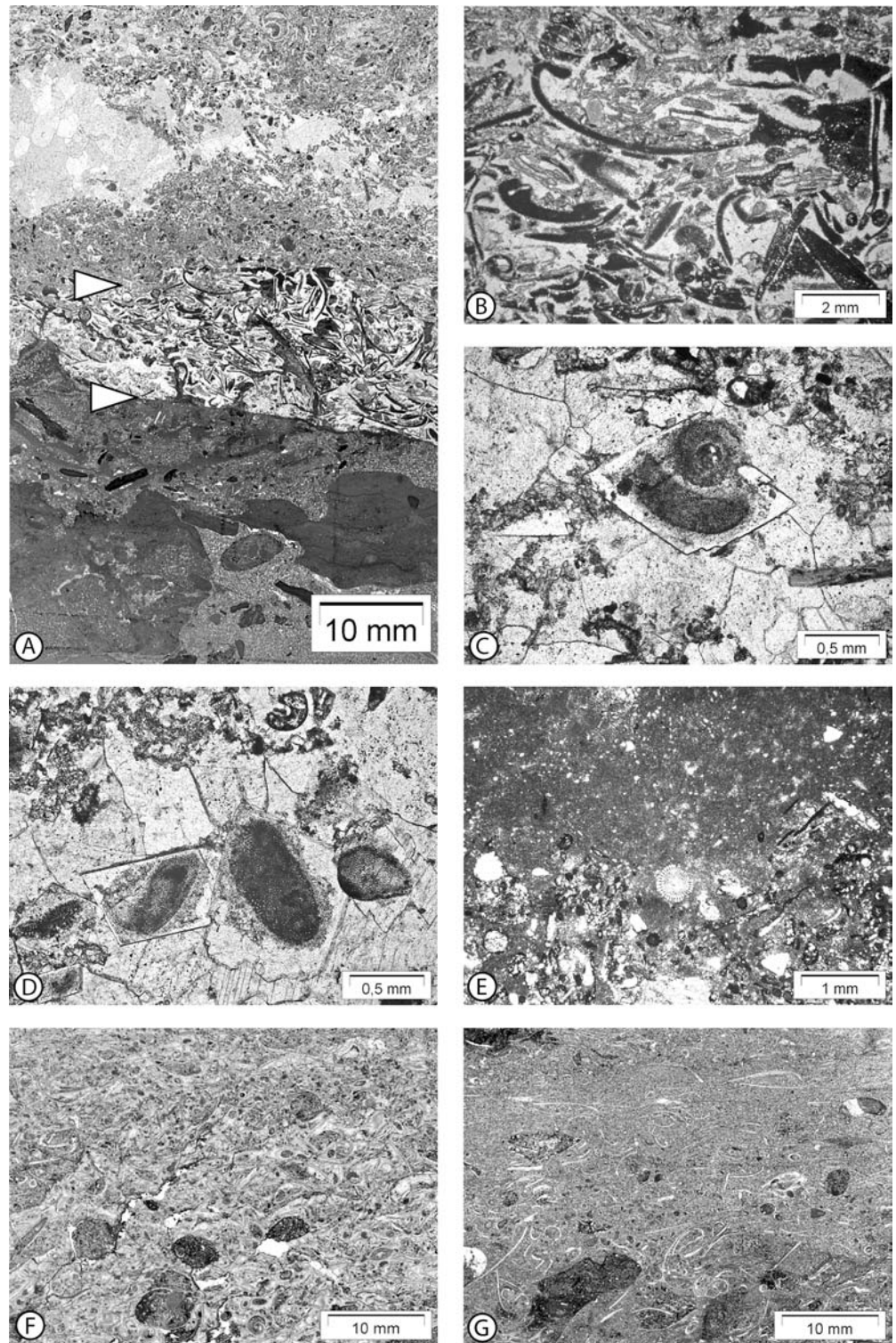
Biota

Bed VIII contains 26 gastropod species (Batten and Stokes 1986), about 10 bivalve species (unstudied according to their taxonomy), and one scaphopod species. Moreover one serpulid species, an echinoid species and ophiurid ossicles are present although not as common. A few ammonoids were found, amongst them *Anawasatchites* sp. confirming a Smithian age of this fauna. Thus, Bed VIII contains about 40 invertebrate species. Small gastropods (<10 mm) contribute most to species richness and some of these species are extremely abundant (see also Batten and Stokes 1986; Fraiser and Bottjer 2004). Small neritaemorphs and the opisthobranch *Cylindrobullina convexa* are most abundant. Some examples for well-preserved gastropods from Bed VIII are illustrated in Fig. 11.

Annulated tubes (supposed scaphopods of the genus *Plagioglypta*) are abundant in the main fossil bearing unit (Bed VIII) and are here illustrated for the first time (Figs. 100–S). Their great abundance even becomes obvious in thin-sections (Figs. 12B–D and G), where they appear circular in transverse section, elliptical in oblique section, and tube-like in longitudinal section. The presence of scaphopods in the Sinbad Limestone was previously noted (Stewart et al. 1972; Blakey 1974; Fraiser and Bottjer 2004) but they were not considered in paleoecological studies. *Plagioglypta* has its type species in the Late Triassic Cassian Formation and was reported from the Anisian of South West China (Stiller 2001b). *Plagioglypta* has also a rich Late Paleozoic record but the mollusc affinity of these species is questionable (Yochelson and Nützel, own observation). The great abundance of *Plagioglypta* in the Sinbad limestone as seen in some of the thin-sections represents a remarkable phenomenon unknown from other Early Triassic sites.

Serpulids are relatively common in Bed VIII and are documented here for the first time from the Sinbad Limestone (Figs. 10A–F). They are mostly detached from their substratum but are sometimes found attached to bivalve shells (Fig. 10C). The serpulids from the Sinbad Limestone are similar to *Spirorbis valvata* Berger 1859, a widespread species in the Anisian/Ladinian Muschelkalk of Central Europe. Similar serpulids are also present in the Werfen Formation (e.g., Boeckelmann 1988), where they are assigned to *Spirorbis valvata* and *Spirorbis phlyctaena*

Fig. 9 Microfacies of Beds V–VIII of the Sinbad Limestone at AMNH locality 3026. **A** Transition of Bed V (lower dark portion with intraclasts) to Bed VI (upper light portion); lower triangle marks sharp contact between channel fill at base and biosparite (rudstone) with completely micritized mollusc shells (between both triangles); upper triangle marks erosional surface; above it, oolitic/peloidal grainstone with large sparitic areas with syntaxial echinoderm cements (see **C**, **D** for details). **B** Bed VI, detail from **A** (between triangles), biosparite (rudstone) with completely micritized mollusc shells. **C**, **D** Bed VI, detail from **A**, echinoderm ossicles with syntaxial cement forming idiomorphic crystals. **E** Bed VII, packstone/wackestone with echinoid spine. **F–G** Bed VIII main fossil-bearing unit, grain-, rud- and wackestones with abundant mollusc shells; graded bedding. **F** Poorly washed grain- to rudstone with graded bedding. **G** Pack- to floatstone with large dark intraclast in lower portion, with graded bedding

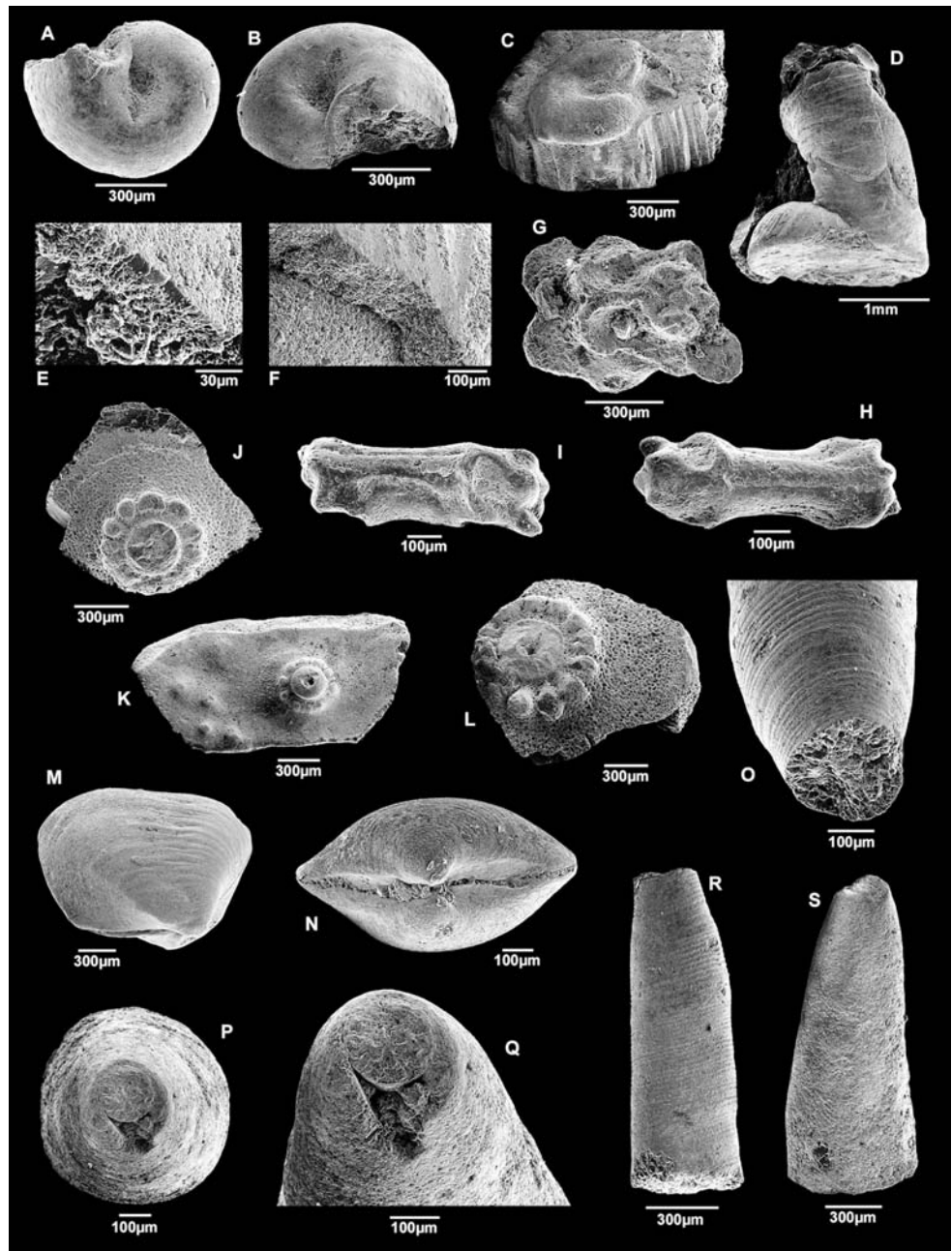


(Brönnimann and Zaninetti 1972) (e.g., Broglio Loriga et al. 1986; Boeckelmann 1988). The genus *Spirorbis* itself seems to represent a dustbin taxon for coiled sessile worm tubes.

Echinoderms occur always as isolated ossicles. They occur from Bed VI to XII and are also present in the main fossil bearing unit (Bed VIII). Ossicles are common but not

very abundant. They represent ophiurioids (Figs. 10G–I) and cidaroid sea urchins (Figs. 10J–L). These ossicles probably indicate normal marine salinity. Echinoid ossicles were studied from the main fossil bearing unit (Bed VIII). They represent interambulacral plates of *Lenticularis utahensis* Kier, 1968 (Hans Hagdorn, written communication 2004). This species was originally described from the

Fig. 10 Fossils other than gastropods from the Sinbad Limestone, Bed VIII, main fossil bearing unit. **A–F** Polychaete “*Spirorbis*” cf. *valvata*. **A** Upper view. **B** Oblique side view. **C** Attached to bivalve shell with prismatic structure. **D** Rare specimen with intact erect tube, side view. **E** Detail of microgranular shell structure. **F** Detail of microgranular shell structure. **G–I** Ophiuroid ossicles. **J–L** Echinoid (cidaroid) plates. **M–N** Examples for small bivalves representing two species; such bivalves commonly have attached valves. **O–S** Annulated tubes of the *Plagioglypta* type (supposed scaphopods) are extremely abundant in Bed VIII



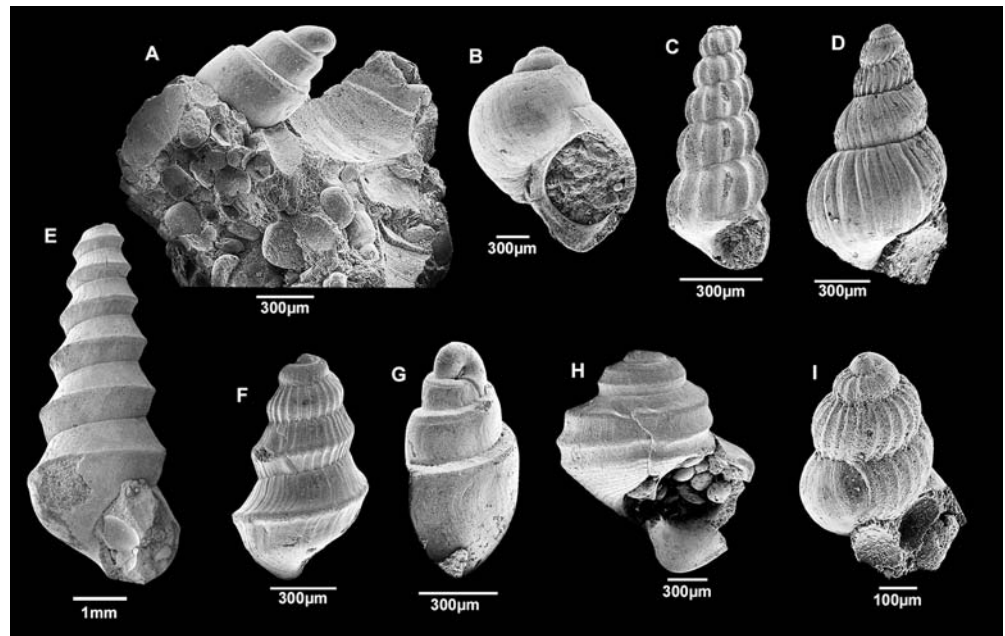
Virgin Limestone, which is slightly younger (Spathian) than the Sinbad Limestone. *Lenticularis* was considered to represent a synonym of *Miocidaris* (Schubert and Bottjer 1995). However, this synonymization is probably not justified (Hans Hagdorn, written communication 2004). No crinoid ossicles have been recovered from the section studied here although they are abundant in the slightly younger (Spathian) Virgin and Thaynes Limestones (Schubert and Bottjer 1995).

Fossil preservation in the Sinbad Limestone lagerstätte

The gastropods (and other molluscs) from Bed VIII are uniquely well preserved (Figs. 10M–S and 11) when com-

pared with gastropods from other Early Triassic localities. Most of the molluscs were originally aragonitic and are replaced by a sparry calcite. Shells commonly have dark micritic rims which suggests bioerosion by microborers prior to deposition (e.g., Flügel 2004). In thin-section, these rims are mostly uninterrupted around the bioclasts. This indicates that breakage during storm transport was not important and fragmentation happened prior to deposition. Bivalves with articulated valves are common. An isopachous rim cement covers the bioclasts where no micritic matrix is present (e.g., Figs. 12E and F). Micritic rims and the presence of micritic matrix in poorly washed parts of the shell beds cause discontinuities with the pore-filling cement and facilitate the good fossil preservation. Together with

Fig. 11 Examples for exceptionally well-preserved Early Triassic gastropods from the Sinbad Limestone, Bed VIII, main fossil bearing unit; this good preservation is unique for the Early Triassic. **A** *Cylindrobullina convexa* in peloidal limestone. **B** *Neritaria* sp. **C** “*Kittliconcha*” *sciaphostera*. **D, I** *Ampezzopleura rugosa* with well-preserved planktotrophic larval shell with axial ribs. **E, F** *Battenizyga eotriassica*. **F** Juvenile specimen of *Battenizyga eotriassica* with well-preserved protoconch. **G** *Cylindrobullina convexa*, with well-preserved heterostrophic, transaxial larval shell. **H** *Worthenia windowblindensis* with shell repair



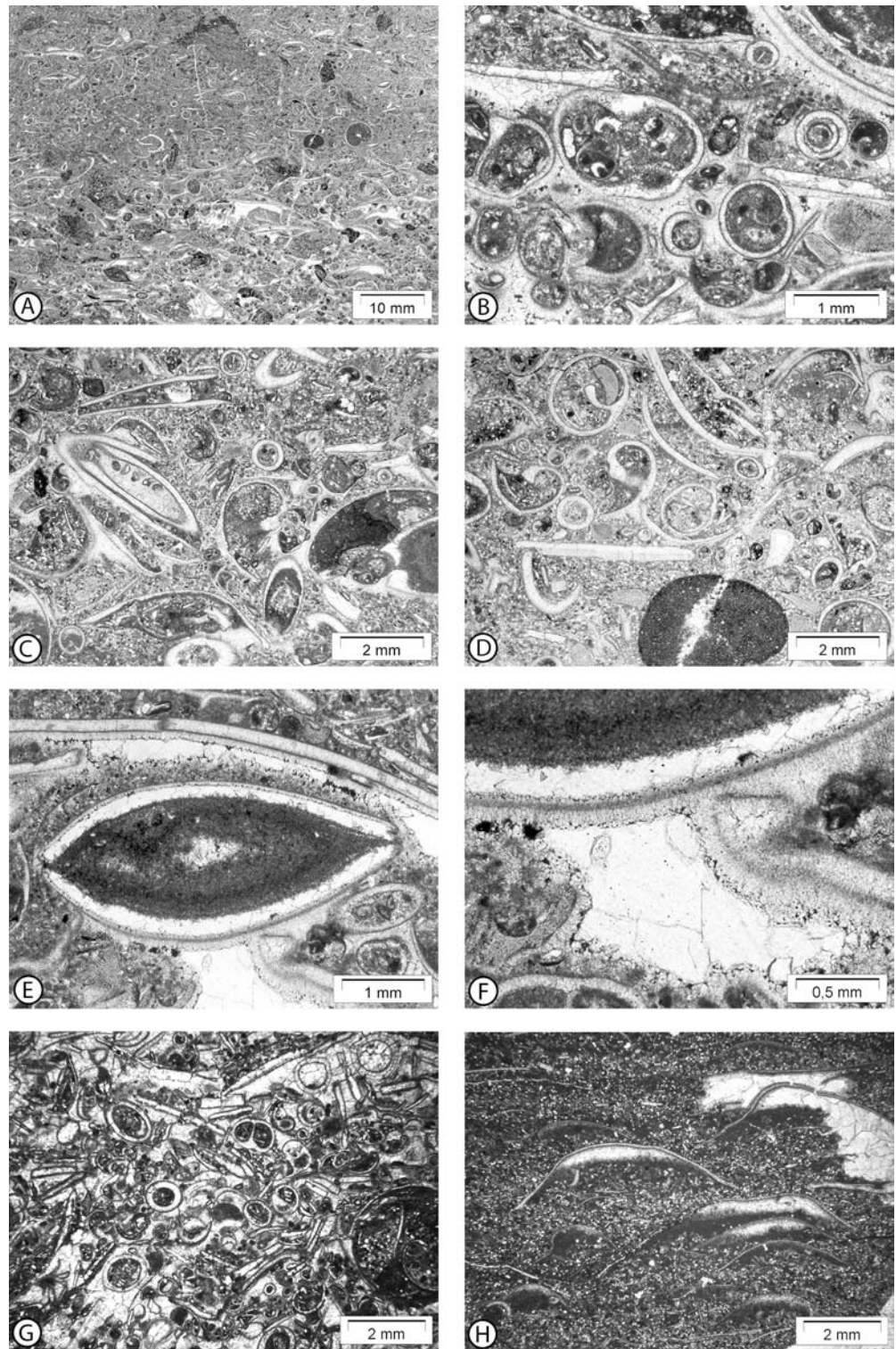
certain state of weathering, these factors allow mechanical isolation of the fossils from the rock (crack-out). Bivalves, scaphopods, and gastropods are commonly filled with mud (micrite; see also Blakey 1974). The Sinbad Limestone is the only Triassic formation with well-preserved gastropod protoconchs (Figs. 11A, D, F, G and I) except for the Late Triassic (Early Carnian) Cassian Formation in the Italian Alps. Protoconch morphology is crucial for a correct taxonomy, phylogeny, systematics, and recognition of larval strategies of gastropods. The excellent fossil preservation is a main reason for the high information content of the Sinbad lagerstätte.

Discussion of the Sinbad Limestone lagerstätte

It is striking that about one-third of the reported global gastropod diversity can be found in a single shell bed (tempestite) of 20–40 cm thickness (Bed VIII). Several of the gastropod genera originally reported by Batten and Stokes (1986) were also found in other Early Triassic strata of the western United States (e.g., in the slightly younger Virgin and Thaynes Limestones), but these occurrences are not as rich and diverse (Schubert and Bottjer 1995; Fraiser and Bottjer 2004). However, the other locations were not studied with a primarily taxonomic purpose and these studies commonly lack species-level identifications. Instead, generic identifications and open nomenclature were used. Moreover, there are no reports of the Sinbad gastropod species outside the western United States. Given the paleogeographic position as an epicontinental sea with free access to Panthalassa, it is very unlikely that the Sinbad gastropod fauna was really endemic in this area. This pseudo-endemism is probably produced by preservational or sampling bias.

The micritic infillings of gastropods, scaphopods and articulated bivalves suggest that the original habitat of the molluscs was a fine-grained, muddy subtidal soft bottom. The scaphopods, some of the bivalves, and the gastropod *Cylindrobullina convexa* were probably infaunal while the other species were epifaunal. Most of the small gastropods (except *Cylindrobullina convexa*) were either living directly on the muddy sea bottom, or on non-calcifying algae. Recent small-sized neritaemorphs commonly live in tropical seagrass environments (seagrass, an angiosperm, is only known from the Late Cretaceous onward). The great abundance of small neritaemorphs in the Sinbad limestone could indicate that an analogous habitat existed (e.g., thickets of non calcifying algae). A rigorous census and statistical analysis has not been undertaken here, but it is obvious that small neritaemorph gastropods and the opisthobranch *Cylindrobullina* as well as scaphopods (*Plagioglypta*) form the most abundant fossils in this assemblage. This *Plagioglypta-Cylindrobullina*-small neritaemorph assemblage is newly recognized in this study. However, it is likely that size-sorting by storm transport biased the original composition of the fauna in the source area to an unknown degree. Such bias was shown for Miocene tempestites from Austria (Zuschin et al. 2005). In these tempestitic beds, size-sorting (measured as standard deviation from mean shell size) is a significant predictor of diversity, i.e., diversity increases with decreasing sorting (Zuschin et al. 2005: 147). But transport-related size-sorting is not the only factor which controls diversity in shell beds. The other important factor is the availability of shells and diversity of the primary communities in the source area prior to transport. The good preservation of the molluscs in Bed VIII of the Sinbad Limestone (even with preserved larval shells) and the fact that bivalves are commonly articulated suggests that the storm took up a living assemblage or that

Fig. 12 Microfacies of Beds VIII and X of the Sinbad Limestone at AMNH locality 3026. **A–G** Bed VIII; main fossil-bearing unit; grain-, rud- and wackestones with abundant mollusc shells. **A** Rud-packstone with distinct graded bedding. **B** Gastropods and scaphopods (circular in section) filled with micrite and having dark micritic rims (bioerosion); matrix sparry to micritic. **C** Mollusc packstone with several scaphopods (*Plagioglypta*) in longitudinal section. **D** Mollusc packstone with dark, well-rounded clast in lower part. **E** Bivalve with articulated valves and micritic infilling; note that no rim cement is present on the upper side of shell because micritic matrix is present. In contrast, the lower shell (where micritic matrix is absent) is partly covered with a rim cement and subsequent sparry cement. **F** Detail of **E**, upper part with dark micritic infilling, below sparitic shell replacement; original shell surface as micritic rim; this rim is covered on inner and outer side by a fibrous rim cement (narrow on inner side wide on outer side). **G** Poorly washed mollusc grain- to packstone with abundant scaphopods (*Plagioglypta*) and gastropods, commonly with micritic infillings and micritic rims. **H** Bed X, bivalve floatstone; thin-shelled disarticulated pteriomorphs with convex side up, indicating currents during deposition; note geopetal fabric with sheltered porosity, filled with sparry cement

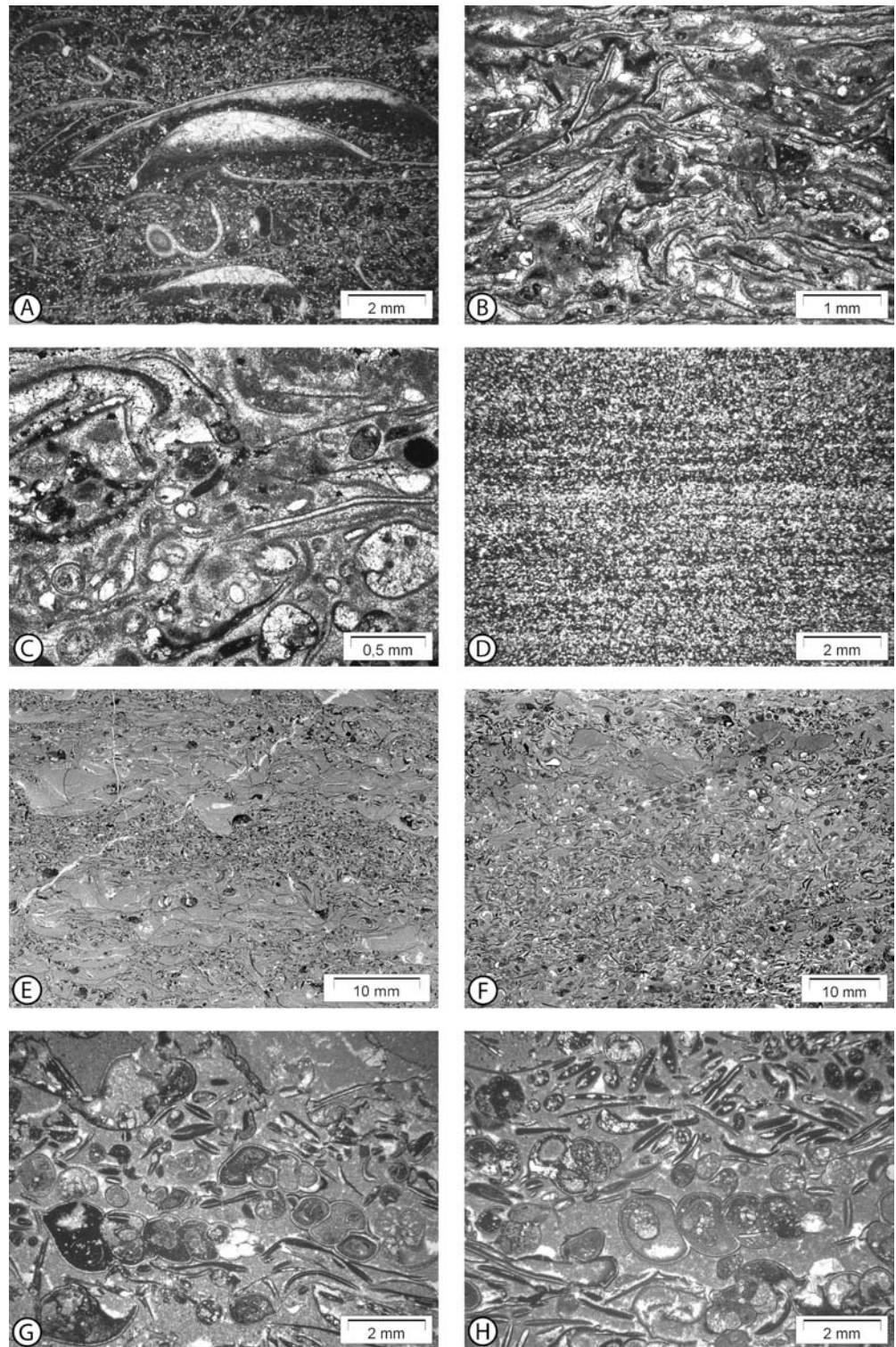


the bioclasts were not strongly reworked and time averaged before storm deposition. Therefore, this assemblage probably reflects the gone living assemblage to a relatively high degree. The species richness and diversity of the Sinbad gastropod fauna is not extraordinarily low for a non-reefal Early Mesozoic environment. However, rarefaction analyses of the most diverse Late Triassic gastropod faunas

have shown that the Sinbad fauna (i.e., the most diverse Early Triassic gastropod fauna) is clearly less diverse than the most diverse Late Triassic faunas (Nützel and Erwin 2004).

Most of the Moenkopi snails have an adult size smaller than 10 mm (Batten and Stokes 1986; Fraiser and Bottjer 2004; own observation). The dominance of

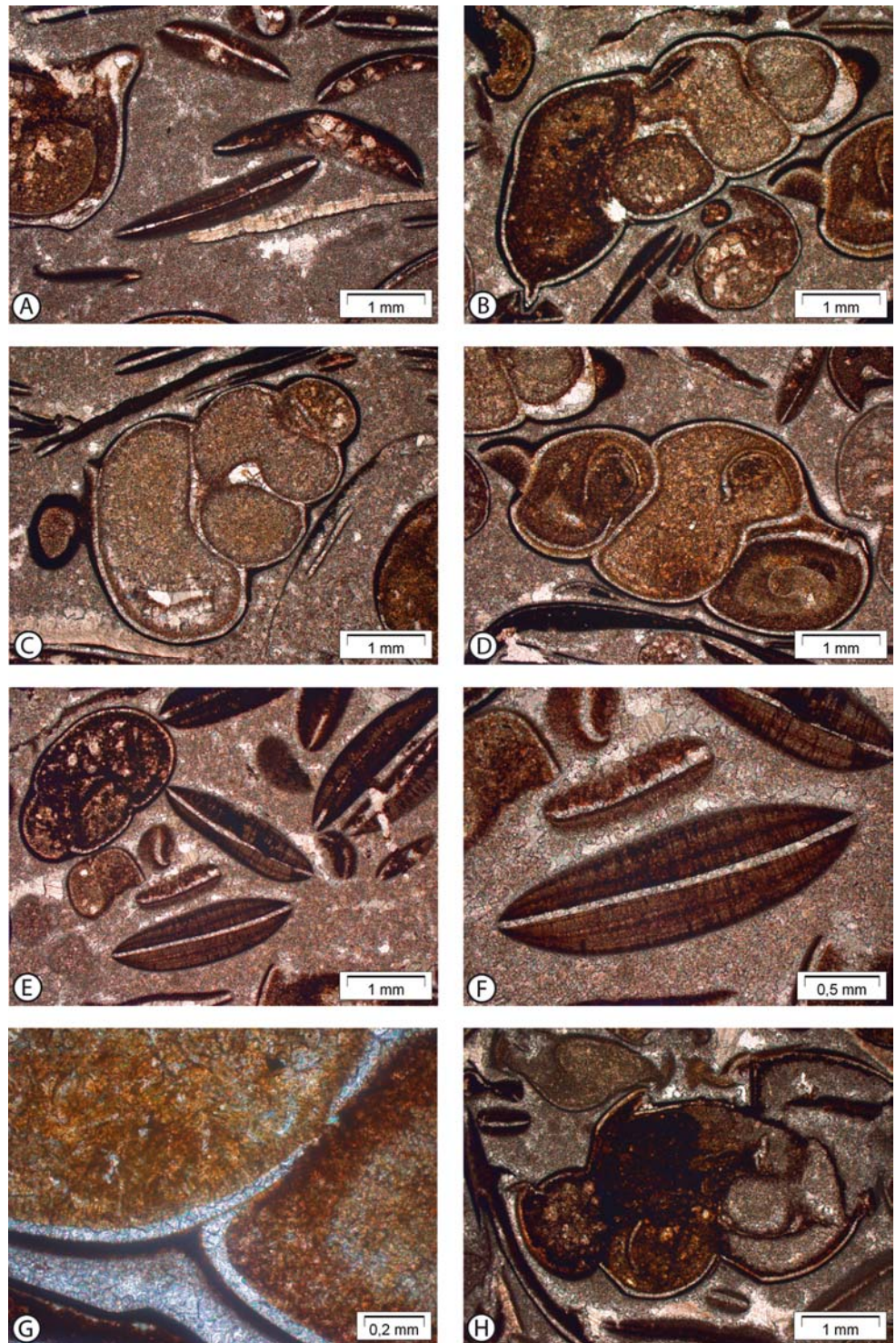
Fig. 13 A–D Microfacies of Beds X, XII, and XIII of the Sinbad Limestone at AMNH locality 3026. **A** Bed X, bivalve floatstone (as in Fig. 12H); thin-shelled disarticulated pteriomorphs with convex side up, geopetal fabric with sheltered porosity, filled with sparry cement; packstone matrix with small, dark peloids; gastropod fragment. **B** Bed XII; coquina of densely packed, thin-shelled bivalves, deformed and fractured by compaction. **C** Detail of Bed XII showing small, round objects with micritic rims. **D** Bed XIII (uppermost bed of section) parallel-laminated siltstone and fine sandstone, unfossiliferous. **E–H** Gastropod Oolite Member of North Italy. **E** From Cimirlo near Trento; gastropod/bivalve wacke- and floatstone; alternating layers with small and large bioclasts have stylolitic contact, therefore layering does not represent a primary sedimentary fabric. **F–H** From Valsugana near Borgo (“Monte Zaccon” locality); all represent gastropod/bivalve wacke- and floatstones with oolitic, iron oxide coated bivalve and gastropods shells; at least four gastropod species can be recognized in thin-sections (see Fig. 14 for details). **F** Overview, no apparent graded bedding. **G** Largest gastropod represents the problematic taxon “*Polygyrina gracilior*”; other gastropods enlarged in Figs. 14B and D. **H** Largest gastropod represents the problematic taxon “*Polygyrina gracilior*”



microgastropods and the lack of large gastropods in the Early Triassic seem to be global phenomena (Fraiser and Bottjer 2004) and small body size was interpreted as result of a productivity decline (Twitchett 2001). However, even most Recent gastropods are small (e.g., Bouchet et al. 2002) and there are also larger gastropods in the Early Triassic: the abundant gastropod “*Werfenella*” *rectecostata*

and *Natiria costata* from the Upper Werfen Formation are as large as 20–35 mm and therefore no microgastropods (<10 mm) (Nützel and Erwin 2002; Nützel 2005). The relatively small size of the Sinbad gastropods could also reflect size-sorting during storm transport to some degree. As outlined above, the effect of size sorting was demonstrated for other tempestitic shell beds (Zuschin et al. 2005).

Fig. 14 Gastropod/bivalve wacke- and floatstones with microsparitic matrix from the Gastropod Oolite Member from near Borgo, Valsugana (“Monte Zaccon” locality); bivalve and gastropod shells very thin, present as calcite replacements of original aragonite; gastropods are covered with thin brown to reddish sheets of iron oxide; bivalve fragments commonly with thick, layered coatings. **A** Several thin bivalve fragments as ellipsoidal ooids; due to flat ooid cores (bivalve shells), they did not grow to a spherical shape. **B** High-spired gastropod representing the problematic dustbin taxon “*Polygyrina gracilior*”; as in the other gastropods and in contrast to the bivalve fragments, the iron oxide coating has a relatively constant thickness. **C** *Pseudomurchisonia kokeni*, preservation as in **B**. **D** Minutely phaneromphalous gastropod (*Coelostylinia werfensis*?), preservation as in **B**. **E** Several thin bivalve fragments as ellipsoidal, spindle-shaped ooids (as in Fig. 14A); ooids show distinct layering; in contrast, gastropod on upper left has relatively thin coating of constant thickness. **F** Bivalve fragment as ellipsoidal ooid (as in Figs. 14A and E); ooid shows distinct layering and faint radial structures. **G** Detail of **E** showing thin gastropod shell, calcite replacement of aragonite and outer iron oxide coating. **H** *Pseudomurchisonia kokeni* fractured by compaction due to point contacts between shells (compare Zuschin et al. 2003)



The Gastropod Oolite Member of the Werfen Formation

Microfacies of the Gastropod Oolite near Borgo, Valsugana (Monte Zaccon) (Figs. 13E–H and 14)

Vividly reddish-brown blocks of mollusc coquinas occur near a forest road near Borgo Valsugana (Wittenburg’s

(1908a, b) “Monte Zaccon” locality). They represent wackestones, packstones, and floatstones with bivalves and gastropods in a fine-grained, microsparitic, calcitic matrix (staining with Alizarin Red). Blocky calcitic cement as well as idiomorphic dolomite crystals may also be developed. The size of the bioclasts is usually less than 2–4 mm and does not exceed 10 mm. Graded bedding was not observed. Gastropods are commonly fractured by compaction



Fig. 15 Crack surface of Gastropod Oolite, near Borgo, Valsugana (“Monte Zaccon” locality of Wittenburg 1908b); gastropods (*Pseudomurchisonia kokeni* and “*Polygrina gracilior*”) as well as other clasts covered with iron oxide; Wittenburg’s (1908a, b) material, collection of University of Tübingen

due to point contacts between shells (compare Zuschin et al. 2003). Geopetal fabrics are common, e.g., sparry calcite within gastropod shells restricted to the upper part and microsparite in the lower part. All shells are coated with brown-reddish crusts (probably iron oxide, hematite). The crusts are relatively thin with a constant thickness around the gastropod shells. On bivalve fragments, the coatings are relatively thick in the centre of the fragment and thin to absent at its edge (forming flattened ellipsoidal chips; Figs. 14A, E and F). Some of the crusts show a distinct layering and faint radial striation. Spherical ooids are absent. The rock breaks along the red crusts on the bioclasts so that the breakage surfaces are vividly red (Fig. 15). However, the matrix is light grey to white or only slightly reddish. The shells of the bivalves and gastropods are very thin and present as calcite replacements of aragonite below the crusts. The thickness of these shell remains is usually 40–60 μm . There are probably not more than three or four gastropod species. A high-spired gastropod (“*Polygrina gracilior*”) and more low-spired forms which represent the genus *Pseudomurchisonia* are abundant. The bivalves were not determined but seem to be of low species diversity. They were never found with articulated valves.

Microfacies of the Gastropod Oolite near Cimirlo (Fig. 13E)

A limestone bed of about 40 cm thickness crops out above the road from Cimirlo to Busa del Vent. Its facies is basically identical to that of the previously described facies from Borgo Valsugana. However, the gastropod assemblage seems to be almost monospecific with *Pseudomurchisonia kokeni* Wittenburg 1908a, b (isolated specimens are illustrated in Fig. 16). The bivalves represent a low-diversity assemblage of Entoliidae and *Neoschizodus*(?) (Michael Hautmann, written communication 2004). The bed experienced considerable pressure solution and stylolites are abundant throughout. Layers displaying different micro-

facies are separated by stylolites. Layers with few, relatively large shells and dominant microsparite alternate with layers of smaller bioclasts and grain-supported fabric. The stylolites suggest that the abrupt changes between these layers do not represent an original depositional fabric.

Interpretation of the facies and paleoecology of the Gastropod Oolite samples

The investigated thin-sections of the Gastropod Oolite show a characteristic facies that reflects a depositional environment which differs strongly from that of the Sinbad Limestone Member. Thin-sections of the Gastropod Oolite studied here, resemble gastropod wackestones from the Werfen Formation from Austria (Gartnerkofel; Flügel 2004: pl. 89.1) and oolitic gastropod-bivalve grainstones from the Precaucasian fordeep (Russia; Flügel 2004: fig. 10.43).

The oolitic, reddish coatings (iron oxides) were probably formed in shallow water and the iron was probably transported from nearby land areas with intensive weathering. The chemical regime leading to this kind of oolitic iron oxide precipitation is not clear but it seems to be likely that microbial activity played a role in this process as is suggested by the layered oolitic coatings. There is no clear evidence for oxygen depletion during deposition. Iron oxide coatings on the gastropods are of continuous thickness and relatively thin when compared to the crusts on the bivalves or bivalve fragments. This reflects the round, conical shape of the gastropods which allowed a more or less constant rolling even under low water energy conditions. The constant movement of the gastropod shells could also explain why the coatings are thinner than on the bivalves. Due to the flat shape of the bivalves and bivalve fragments, the iron ooids are not spherical but flat and spindle-shaped in transverse section. The uneven thickness of the crusts suggests that the bivalve shells were turned more rarely than the round gastropod shells. Otherwise, these clasts seem to represent typical ooids with distinct layering and radial structures.

Shell beds of the Gastropod Oolite were interpreted as tempestites (e.g., Broglio Loriga et al. 1983; Boeckelmann 1988; Wignall and Twitchett 1999). Broglio Loriga et al. (1986) mentioned that the Gastropod Oolite in the Adige Valley (Trento) and the Valsugana area consists of tidal-controlled oolitic bars alternating with muddy siltstones. The currently studied samples of the Gastropod Oolite show no clear indication for storm deposition (e.g., no graded bedding and intraclasts). Abundant geopetal and clast-supported fabric could point to storm deposition. In other areas, storm deposition seems to be more obvious. Wignall and Twitchett (1999) reported intraclasts (flat pebbles) in the Gastropod Oolite at the l’Uomo section of the central Dolomites.

Gastropods are highly abundant at both studied sites of the southern Dolomites. The samples from the Monte Zaccon locality near Borgo Valsugana contain only a few (probably three to five) species all of which are abundant.

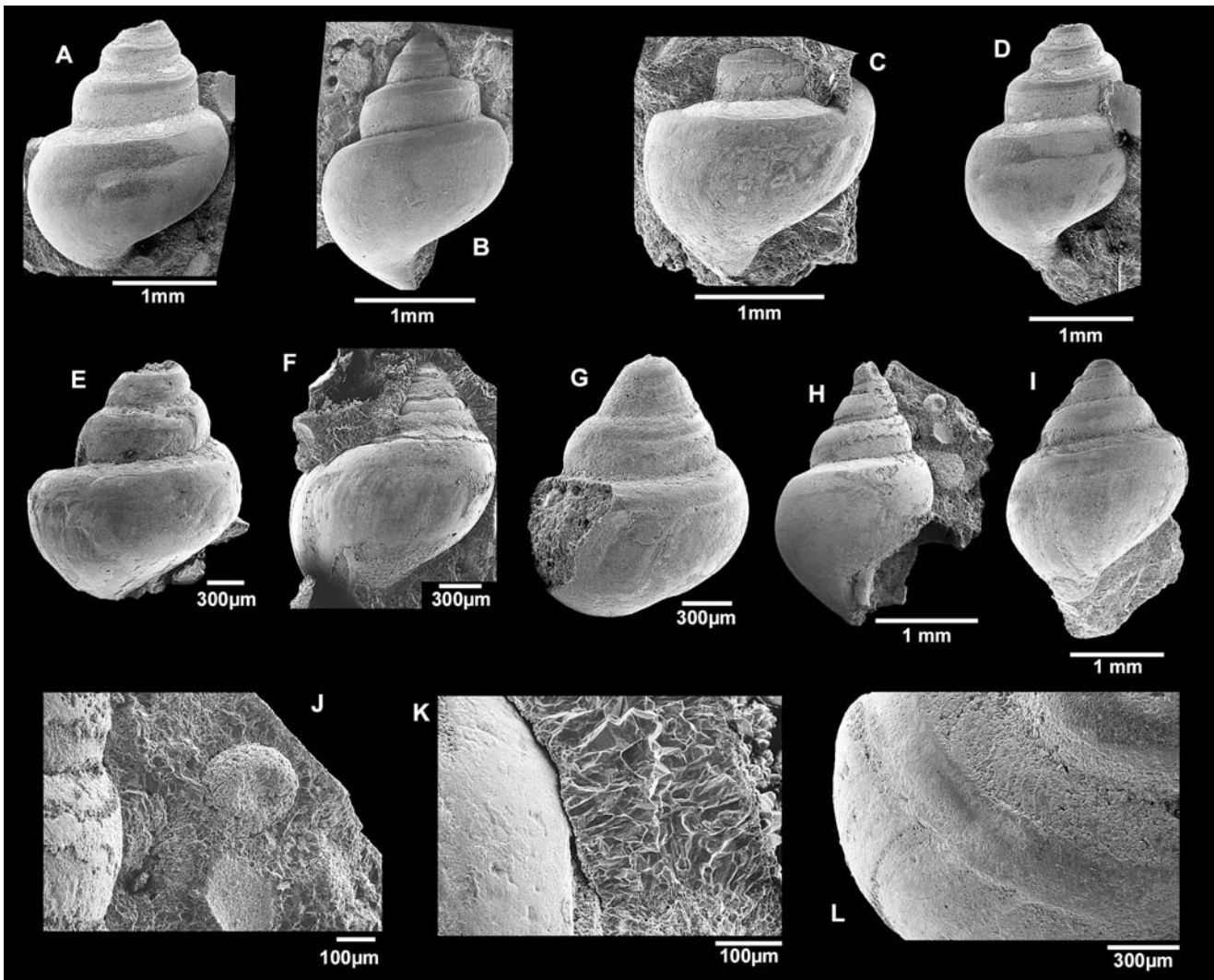


Fig. 16 A–I, L Examples for well-preserved Early Triassic gastropods the Gastropod Oolite (Werfen Formation) *Pseudomurchisonia kokeni* forms an almost monospecific gastropod assemblage in beds of the Gastropod Oolite near Cimirlo (Werfen Formation); the

species has a characteristic shape and a slit-like structure at the shoulder (well visible in L); it displays a considerable intraspecific variability. J Microsparitic matrix with ooid. K Microsparitic matrix

In contrast, *Pseudomurchisonia kokeni* (Figs. 14C, H and 16) forms an almost monospecific assemblage near Cimirlo. Wittenburg (1908a, b) described *P. kokeni* based on a single specimen (holotype) from the Col di Rodella (North Italy, South Tyrol, near the Sella Group, about 46°30'N, 11°45'E). The holotype (collection of the University of Tübingen) was studied by the senior author. As the specimens from Cimirlo, it is coated with iron oxides and therefore probably comes from the same lithofacies.

Apart from the mentioned taxa, no other gastropods could be found in the present samples, neither as body fossils nor in thin-sections. For instance, neritaemorphs are absent although this group is abundant in other Early Triassic rocks (e.g., the Sinbad Limestone Member) and have a characteristic low-spined shape. Only microgastropods (<10 mm) are known from the Gastropod Oolite and relatively few species have been reported, amongst them *Polygyrina gracilior*, *Coelostylina werfensis*, “*Nat-*

ica” *gregaria*, and *Pseudomurchisonia kokeni*. Generic assignments and species identity of these taxa are generally questionable due to poor preservation. However, it is obvious that more or less high-spined, smooth, *Hydrobia*-resembling snails were extremely abundant during the deposition Gastropod Oolite and that these gastropods formed assemblages of low species richness and high abundance. A possible analogy of the Gastropod Oolite snails with modern hydrobiids was casually mentioned by Zapfe (1958: 163) and Wignall and Twitchett (1999: 314). Some Recent hydrobiid mudsnail species occur in great densities (>300,000 individuals per m²) in the marine and estuarine intertidal zones (Barnes 1999). As in the Gastropod Oolite, they form monospecific or paucispecific assemblages of small, high-spined gastropods. Due to their ability to swim at the air/water-interface, they are able to populate areas quickly. They are euryhaline, e.g., *Hydrobia ulvae* tolerates a salinity range of 10–33‰. Hydrobiid

mudsnails can also live in the subtidal zone and are able to burrow. Thus, Recent mudsnails are well adapted to tidally influenced ephemeric habitats with a brackish or strongly fluctuating salinity and they may serve as a model for small high-spined gastropods from the Gastropod Oolite. The high abundance and low species richness of the gastropods and bivalves from the Gastropod Oolite indicate a stressed, not normal marine environment. Invertebrates other than bivalves and gastropods are absent in the present samples. There are no unequivocal indicators for normal marine conditions, such as echinoderms.

In summary, facies and faunal content suggest the following conclusions about biota from the Gastropod Oolite: The biota probably came from a shallow subtidal to intertidal source area with fine-grained bottoms. Salinity was not euhaline but probably decreased or strongly fluctuating. A community of a few gastropod and bivalve species was adapted to this environment. This community was characterized by low diversity and extreme abundance. Modern hydrobiid mudsnail communities may serve as a model for the Gastropod Oolite snails. Iron coating and ooids were formed in shallow water above fair-weather wave base. Shells were then probably concentrated and deposited under storm conditions.

Conclusion and discussion

Two major lagerstätten of Early Triassic gastropods, the Sinbad Limestone (Utah, USA) and the Gastropod Oolite from Valsugana (North Italy) were studied regarding facies, paleoecology, fossil preservation, and depositional environment. About 30 nominate gastropod species were reported from these localities which represents about 40% of the global Early Triassic gastropod species richness (and more than 50% the gastropod species, if the entire Werfen Formation is considered). The studied samples from the Sinbad Limestone and the Gastropod Oolite represent benthic mollusc coquinas. These shell beds are composed of bivalves, gastropods, and of scaphopods (Sinbad Limestone). Shells were probably concentrated and transported by storms (tempestites) as is indicated by clast-supported fabric, presence of graded bedding, common geopetal fabrics and the presence of intraclasts.

Gastropods are very abundant in the Smithian (Olenekian) Sinbad Limestone Member at the collecting locality of Batten and Stokes (1986). They occur in a single bed of grain- and packstones while they are rare in the over- and underlying beds. This bed was probably deposited under storm influence. It yields a relatively diverse invertebrate fauna of about 40 taxa. Gastropods, scaphopods (*Plagioglypta*), and bivalves are most abundant. Serpulids ("*Spirorbis*" cf. *valvata*) and echinoderm ossicles (echinoids and ophiurids) are present but not as abundant as molluscs. The biota lived in a shallow subtidal, soft bottom environment prior to transport as is indicated by micrite fillings in gastropods, scaphopods, and articulated bivalves as well as by the fact that some of these organisms were probably infaunal and burrowing. The gastropods of the Sinbad

Limestone of the San Rafael Swell are exceptionally well preserved as calcite replacement of the originally aragonitic shells. Teleoconch details and even larval shells are commonly preserved. Protoconch preservation is almost unique for the Early Triassic and the only other Triassic fauna with well-preserved protoconchs is the Late Triassic (Early Carnian) Cassian Formation. The good preservation and the relatively high diversity of the gastropods from the studied shell bed of the Sinbad Limestone make it the most important Early Triassic gastropod lagerstätte.

About 15 nominate gastropod species were reported from the Werfen Formation (e.g., Wittenburg 1908a, b; Leonardi 1935) and a maximum of about five species occur in each of its members. The gastropod faunas are characterized by high abundance but low species richness. The abundance of gastropods in several beds of the Werfen Formation shows that this group formed a considerable part of the benthic fauna in the Early Triassic of the Western Tethys. The studied samples of the Gastropod Oolite Member near Borgo Valsugana and Trento (North Italy) are characterized by extremely abundant gastropods and bivalves. They represent mostly oolitic gastropod/bivalve packstones, wackestones, and floatstones. At Cimirlo (near Trento), an almost monospecific gastropod fauna of *Pseudomurchisonia kokeni* occurs. The fauna near Borgo Valsugana is more diverse comprising at least four species. Thin-sections show that these molluscs were thin-shelled and coated with iron oxides. Clearly, the studied Gastropod Oolite faunas lack the diversity and complexity of the Sinbad Limestone fauna. Similar to modern gastropod faunas with high abundance and low species richness (e.g., modern hydrobiid mudsnail assemblages), gastropod assemblages of the Gastropod Oolite were possibly controlled by a strongly fluctuating salinity in a tidal-influenced environment. The shells were subsequently concentrated and transported. Other parts of the Gastropod Oolite facies were probably deposited under normal marine conditions as is indicated by the presence of conodonts and echinoderms.

Although similar at a first glance, beds with small, extremely abundant gastropods from the Sinbad Limestone and the Gastropod Oolite differ strongly from each other, regarding species richness and taxonomic inventory. Species richness is much higher in the Sinbad fauna (26 species) than in the Gastropod Oolite (probably not more than five species). No species and probably also no genus is shared between both occurrences. This suggests that gastropods were not cosmopolitan during the Dienerian/Smithian. The fauna of the Sinbad Limestone is marine with a normal salinity as is indicated by the presence of planktonic larval shells (access to the ocean), echinoderm ossicles, the abundance of scaphopods, and the relatively high diversity. In contrast, biota of the Gastropod Oolite were probably salinity-controlled and not formed under normal marine conditions.

The fact that a couple of shell beds from two areas of the world contain as many as 40% of the global Early Triassic gastropod richness corroborates earlier suggestions that the Early Triassic fossil record is exceptionally poor. For instance, any two samples of even the richest Recent shell

accumulations, could not possibly produce 1% of the extant global species richness. However, the fact that the richest known Early Triassic gastropod fauna contains less than 30 species, preserves probably an original signal of a strongly reduced global species richness during the Early Triassic.

Acknowledgements We dedicate this work to the late Erik Flügel, an excellent scientist and inspiring teacher. We would like to thank Roger L. Batten (Phoenix) for help in the field and stimulating discussions, Hans Hagdorn (Ingelfingen) for the identification of the echinoid ossicles, Mrs Barbara Seuß and Mrs Birgit Leipner-Mata (both Erlangen) for making the thin-sections and polished slabs. We thank Martin Zuschin (Vienna) and Oliver Weidlich (London) for the reviews which improved this paper. The Deutsche Forschungsgemeinschaft is acknowledged for financial support (Grant NU 96/6-1, 6-2).

References

- Assereto RL, Rizzini A (1975) Reworked ferroan dolomite grains in the Triassic "Oolite a Gasteropodi" of Camoniche Alps (Italy) as indicators of early diagenesis. *N Jb Geol Paläontol Abh* 2:215–232
- Barnes RSK (1999) What determines the distribution of coastal hydrobiid mudsnails within north-western Europe. *Mar Ecol* 20:97–110
- Batten RL (1973) The vicissitudes of the gastropods during the interval of the Guadalupian-Ladinian time. In: Logan A, Hills A (eds) *The Permian and Triassic systems and their mutual boundaries*. *Can Soc Petrol Geol Mem* 2:596–607
- Batten RL, Stokes WL (1986) Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *Amer Mus Novitates* 2864:1–33
- Berger HAC (1859) Die Versteinerungen des Röt von Hildburghausen. *N Jb Min Geol Paläontol Abh* 1859:68–171
- Blakey RC (1974) Stratigraphic depositional analysis of the Moenkopi Formation, Southeastern Utah. *Utah Geol Min Surv Bull* 104:1–81
- Boeckelmann K (1988) Die Werfener Schichten in den Karnischen Alpen und westlichen Karawanken (Österreich und Italien). Unpublished PhD thesis, Rheinisch-Westfälische Tech Hochsch Aachen, 213 pp
- Bouchet P, Lozouet P, Maestrati P, Heros V (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biol J Linn Soc* 75:421–436
- Boyer DL, Bottjer DJ, Droser M (2004) Ecological signature of Lower Triassic shell beds of the western United States. *Palaios* 19:372–380
- Brönnimann P, Zaninetti L (1972) On the occurrence of the Serpulid *Spirorbis* Daudin, 1800 (Annelida, Polychaetia, Sedentaria) in thin sections of Triassic Rocks of Europe and Iran. *Riv Ital Paleontol* 78:67–90
- Broglio Loriga C, Masetti D, Neri C (1983) La formazione di Werfen (Scitico) delle Dolomiti occidentali: sedimentologia e biostratigrafia. *Riv Ital Paleontol Stratigr* 88:501–598
- Broglio Loriga C, Neri C, Posenato R (1986) Excursion B: the Werfen Formation (Lower Triassic) in the Costabla Mt., Uomo section. In: Italian IGCP 203 Group Members (eds) *Excursion Guidebook, Field Conference on Permian and Permian-Triassic boundary in the south-alpine segment of the Western Tethys* (July 4–12, 1986), pp 116–133
- Dean JS (1981) Carbonate petrology and depositional environment of the Sinbad Limestone Member of the Moenkopi Formation in the Teasdale Dome area, Wayne and Garfield Counties, Utah. *Brigham Young Univ Geol Ser* 28:19–51
- Erwin DH (1990) Carboniferous-Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Paleobiology* 16:187–203
- Flügel E (2004) *Microfacies of carbonate rocks*. Springer, Berlin Heidelberg New York
- Fraiser ML, Bottjer DJ (2004) The non-actualistic Early Triassic gastropod fauna: a case study of the Lower Triassic Sinbad Limestone Member. *Palaios* 19:259–275
- Fürsich FT, Oschmann W (1993) Shell beds as tool in facies analysis: the Jurassic of Kachchh, western India. *J Geol Soc Lond* 150:169–185
- Kidwell SM (1991a) Taphonomic feedback (live/dead interactions) in the genesis of bioclastic beds: keys to reconstructing sedimentary dynamics. In: Einsele G, Ricken W, Seilacher A (eds) *Cycles and events in stratigraphy*. Springer, Berlin Heidelberg New York, pp 268–282
- Kidwell SM (1991b) The stratigraphy of shell concentrations. In: Allison D, Briggs DE (eds) *Taphonomy: releasing the data locked in the fossil record*. Plenum, New York, pp 211–290
- Kidwell SM, Brenchley PJ (1994) Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction? *Geology* 22:1139–1143
- Kier PM (1968) The Triassic echinoids of North America. *J Paleontol* 42:1000–1006
- Leonardi P (1935) Il Trias inferiore delle Venezie. *Mem Inst Geol Min Univ Padova* 11:1–136
- Nützel A (2005) A new gastropod genus from the Early Triassic Werfen Formation and its meaning for the recovery of gastropods from the Permian/Triassic mass extinction event. *Acta Palaeontol Pol* 50:19–24
- Nützel A (in press) Recovery of gastropods in the Early Triassic. *CR Palevol* 4
- Nützel A, Erwin DH (2002) *Battenizyga*, a new early Triassic gastropod genus with a discussion on the gastropod evolution at the Permian/Triassic boundary. *Paläontol Z* 76:21–27
- Nützel A, Erwin DH (2004) Late Triassic (Late Norian) gastropods from the Wallowa terrane (Idaho, USA). *Paläontol Z* 78:361–416
- Payne JL, Lehrmann DJ, Wie J, Orchard MJ, Schrag DP, Knoll AH (2004) Large perturbations of the carbon cycle during recovery from the end-Permian mass extinction. *Science* 305:506–509
- Schubert JK, Bottjer DJ (1992) Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* 20:883–886
- Schubert JK, Bottjer DJ (1995) Aftermath of the Permian-Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 116:1–39
- Seilacher A, Reif W-E, Westphal F (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Phil Trans R Soc Lond B* 311:5–23
- Sepkoski JJr, Bambach RK, Droser ML (1991) Secular changes in Phanerozoic event bedding and biological overprint. In: Einsele G, Ricken W, Seilacher A (eds) *Cycles and events in stratigraphy*. Springer, Berlin Heidelberg New York, pp 298–312
- Stewart JH, Poole FB, Wilson RF (1972) Stratigraphy and origin of the Triassic Moenkopi Formation and related strata in the Colorado Plateau region. *US Geol Surv Prof Pap* 961:1–195
- Stiller F (2001a) Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupou, Provinz Guizhou, Südwestchina. *Münstersche Forsch Geol Paläontol* 92:1–523
- Stiller F (2001b) Scaphopods from the Upper Anisium (Middle Triassic) of Qingyan, south-western China. *N Jb Geol Paläontol Mh* 10:617–632
- Twitchett RJ (1999) A high resolution biostratigraphy for the Lower Triassic of northern Italy. *Palaeontol Newsl* 43:19–22
- Twitchett RJ (2001) Incompleteness of the Permian-Triassic fossil record: a consequence of productivity decline? *Geol J* 36:341–353
- Twitchett RJ, Krystyn L, Baud A, Wheeley JR, Richo S (2004) Rapid marine recovery after the end-Permian mass extinction event in the absence of marine anoxia. *Geology* 32:805–808
- Wheeley J, Twitchett RJ (in press) Palaeoecological significance of a new Early Triassic gastropod assemblage from Oman. *Lethaia*

- Wignall PB, Twitchett RJ (1999) Unusual intraclastic limestones in Lower Triassic carbonates and their bearing on the aftermath of the end-Permian mass extinction. *Sedimentology* 46:303–316
- Wignall PB, Twitchett RJ (2002) Extent, duration, and nature of the Permian-Triassic superanoxic event. *Geol Soc Amer Spec Pap* 356:395–413
- Wittenburg P (1908a) Einige neue Fossilien aus den Werfener Schichten Südtirols. *N Jb Geol Palaeontol Abh* 1:16–21
- Wittenburg P (1908b) Beiträge zur Kenntnis der Werfener Schichten Südtirols. *Geol Palaeontol Abh* 8:251–289
- Zapfe H (1958) Die Fauna der Werfener Schichten vom Ulrichsberg bei Klagenfurt in Kärnten. *Verh Geol Bundesanst* 2:155–164
- Zuschin M, Stachowitsch M, Stanton RJ Jr (2003) Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth Sci Rev* 63:33–82
- Zuschin M, Harzhauser M, Mandic O (2005) Influence of size-sorting on diversity estimates from tempestitic shell beds in the Middle Miocene of Austria. *Palaios* 20:142–158