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SHELL BEDS OF DICERATID RUDISTS AHEAD OF A LOW-ENERGY GRAVELLY BEACH (TITHONIAN, NORTHERN CALCAREOUS ALPS, AUSTRIA): PALAEOECOLOGY AND TAPHONOMY.

Diethard SANDERS¹⁾, Michaela LUKESCH¹⁾, Michael RASSER²⁾ & Peter SKELTON³⁾

¹⁾ Institute of Geology and Palaeontology, University of Innsbruck, 6020 Innsbruck, Austria.

²⁾ Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany.

³⁾ Department of Earth Sciences, The Open University, Milton Keynes MK7 6AA, United Kingdom.

⁷⁾ Corresponding author, diethard.g.sanders@uibk.ac.at

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ABSTRACT

In the Tithonian Lofer unit (Northern Calcareous Alps, Austria), *Heterodicerias* shell beds accumulated ahead of a low-energy gravelly beach. This is the first detailed description of diceratid shell beds from the Northern Calcareous Alps.

In the Eastern Alps, during Late Jurassic tectonic deformation, parts of structurally highest preserved thrust nappes became islands. During the following latest Jurassic transgression over vegetated land, a variegated succession of shore zone to shallow neritic lithologies accumulated. Near the village Lofer, the transgressive succession records a low-energy gravelly beach ahead of a shallow subtidal, protected bay or lagoon with a bottom of organic-rich, argillaceous lime mud. The proximal area of the bay/lagoon received abundant phytoclasts and clay from land. On organic-rich lime-muddy substrata that may have supported fleshy algal meadows, the larger textulariine foraminifer *Anchispirocyclus* thrived. Seaward, level-bottoms dominated by the rudist *Heterodicerias* or by milleporidian hydrozoans were present. The milleporidian banks interfingered with storm spillover lobes shed from oolite dunes farther offshore.

The *Heterodicerias* beds consist of floatstones to rudstones of toppled, disoriented shells in highly different taphonomic states, as a result of episodic toppling and reworking by high-energy events, burrowing, bioerosion, and in-situ shell disintegration. The matrix of lime mudstone to bioclastic wackestone is characterized by terebratulacean brachiopods and microgastropods. While the brachiopods thrived as suspension feeders attached on toppled shells of dead rudists, the microgastropods perhaps scavenged on microbial biofilms and/or on fine-grained dead particulate organic matter. A few of the diceratid shells are variably overgrown by sessile textulariine foraminifera, by microbialites, by milleporidians, and by the microproblematica *Lithocodium* and *Bacinella*. The majority of the diceratids had been largely to completely stripped of their thin calcitic outer shell layer. Spalling of the calcitic layer took place early, when the shells were exposed on the sea floor, and during shallow burial within soft sediment. Effective spalling probably was associated with decomposition of organics embedded between the aragonitic, inner shell layer and the calcitic, outer layer.

In der Lofer Einheit (Tithonium) der Nördlichen Kalkalpen (Österreich) wurden *Heterodicerias*-Schillbänke gefunden, die sich seewärts von einer niedrigenergetischen Kiesküste bildeten. Dies ist die erste eingehende Beschreibung von Diceratiden-Schillbänken aus den Nördlichen Kalkalpen.

Während der spätjurassischen Tektonik im Bereich der Ostalpen wurden Teile höherer struktureller Einheiten als Inseln über den Meeresspiegel gehoben. Im Verlaufe einer noch im Späten Jura wiederum erfolgenden marinen Transgression über bewachsenes Festland gelangte eine vielfältige Abfolge von Sedimentgesteinen küstennaher bis flachneritischer Bereiche zum Absatz. Die transgressive Folge nahe der Gemeinde Lofer zeigt eine niedrigenergetische Kiesküste entlang einer flachsubtidalen geschützten Bucht oder Lagune auf, in welcher organika-reicher tonmineralhaltiger Kalkschlamm zur Ablagerung kam. Der landnahe Teil der Bucht/Lagune stand unter reichlicher Zufuhr von Phytoklasten und Tonmineralen vom Festland her. Organika-reiche Kalkschlamm-Böden, die vielleicht auch von Weichalgen besiedelt waren, waren das Habitat der textulariinen Grossforaminifere *Anchispirocyclus*. Weiter seewärts traten fleckenhafte, dichtbesiedelte Bodengemeinschaften auf, die vom diceratiden Rudisten *Heterodicerias* oder von Hydrozoen (*Milleporidium*) gebildet wurden. Die Milleporidien-Bänke verzahnten örtlich mit Spülloben, die während Stürmen von weiter seewärts gelegenen Ooid-Sandbarren geschüttet wurden.

Die *Heterodicerias*-Schillbänke bestehen aus Floatstones bis Rudstones von umgelagerten Schalen in sehr unterschiedlichem Erhaltungszustand. Die verschiedene Erhaltung der Rudisten ergab sich durch Umkippen und Aufarbeitung der Schalen während Hochenergie-Ereignissen sowie durch Sedimentdurchwühlung, Bioerosion und Zerlegung in situ. Die Grundmasse der Schillbänke ist ein Lime Mudstone bis bioklastischer Wackestone mit häufigen Brachiopoden (Terebrateln) und zahlreichen (sub)mikroskopisch kleinen Schneckengehäusen. Die Brachiopoden lebten als Suspensionsfresser festsitzend auf den Schalen toter Rudisten. Die Mikro-Schnecken dagegen lebten vom Abgrasen von Mikrobenfilmen und/oder von feinstkörniger toter partikulärer organischer Substanz. Einige Diceratidenschalen wurden verschiedentlich von festsitzenden textulariinen Foraminiferen, von Mikrobialiten, von Milleporidien sowie von den Mikroproblematica *Lithocodium* und *Bacinella* überwachsen. An den meisten Diceratiden lässt sich ein weitgehender

oder völliger Verlust der dünnen, kalzitischen Aussenlage der Schale feststellen. Die Ablösung der kalzitischen Aussenlage erfolgte noch während die Rudistenschalen frei am Meeresboden lagen, aber auch noch im weichen, durchwühlten Sediment unterhalb. Die rasche Ablösung erfolgte wahrscheinlich durch Zersetzung einer sehr dünnen Lamina aus organischer Substanz, die zwischen der äusseren kalzitischen und der inneren, ursprünglich aragonitischen Schalenlage eingeschaltet war.

1. INTRODUCTION

Understanding the placement and taphonomy of fossil assemblages in their sedimentary environment is crucial to palaeoecological interpretation. Bivalve shells and shell beds provide information on aut- and synecology, time-averaging and taphonomy (Fürsich & Aberhan, 1990; Kidwell, 1991; 2002). The shells of bivalves are well-defined with respect to shape, physical construction and mineralogy, hence taphonomic modification of these parameters is readily seen. Analysis of taphonomic loss in shelly fossil assemblages revealed that syndepositional CaCO_3 -dissolution takes place also within shallow-water sediments below tropical sea waters supersaturated for calcium carbonate (Sanders, 1999, 2001, 2003; Sanders & Krainer, 2005; Wright et al., 2003). For the Northern Calcareous Alps (NCA) of Austria, the presence of rudist shell beds of Late Cretaceous age is well-documented (Sanders & Pons, 1999; Sanders & Höfling, 2000).

Up to now, the presence of shell beds of diceratid rudists in Upper Jurassic neritic successions of the NCA was not described. This is perplexing in view of the fact that shell beds tend to be a distinctive carbonate facies already in the field. The diceratid bivalves appeared during the Oxfordian from megalodontoid ancestors and, in turn, were the ancestors to all subsequent clades of the Hippuritoidea, or rudists (Skelton, 1979; Skelton & Smith, 2000). By contrast to their megalodontoid ancestors, which had aragonitic shells only, the rudists had an outer shell layer of fibrillar prismatic low-magnesian calcite. In the present paper the sedimentary facies, ecology and taphonomy of shell beds of diceratid rudists discovered near the village Lofer (federal state Salzburg, Austria), and their placement in a transgressive succession are described and interpreted.

2. GEOLOGICAL SETTING

The investigated succession is situated in the Northern Calcareous Alps (Fig. 1) which comprise part of the Austroalpine tectonic unit. The NCA consist of stacked cover thrust nappes dominated by Triassic shallow-water carbonates, whereas Triassic to Jurassic deep-water lithologies (limestones, radiolarites) and younger deposits comprise a subordinate proportion (Tollmann, 1976). Nappe stacking started during the Middle to Late Jurassic, and propagated from the southern margin of the Austroalpine towards the west and north (Frisch, 1979; Mandl, 1999). During Jurassic convergence, while the structurally highest nappes became subject to subaerial exposure, deep-water deposition continued on tectonic units in a more external position. Herein, we follow the tectonic subdivision of Tollmann (1985) and Frank & Schlager (2006, their figs. 2, 3) and consider the stratigraphic rock substrate of the investigated succession as pertaining to the Lower Juvavic (Hallstatt)

nappe (Fig. 1) (see also Rantitsch & Russegger, 2005). In the considered central sector of the NCA, the Juvavic nappe stack comprises the structurally highest preserved unit. During the Late Jurassic, over parts of its presently preserved extent, the Juvavic unit became subject to tectonically-induced shoaling of water depth and subaerial exposure while

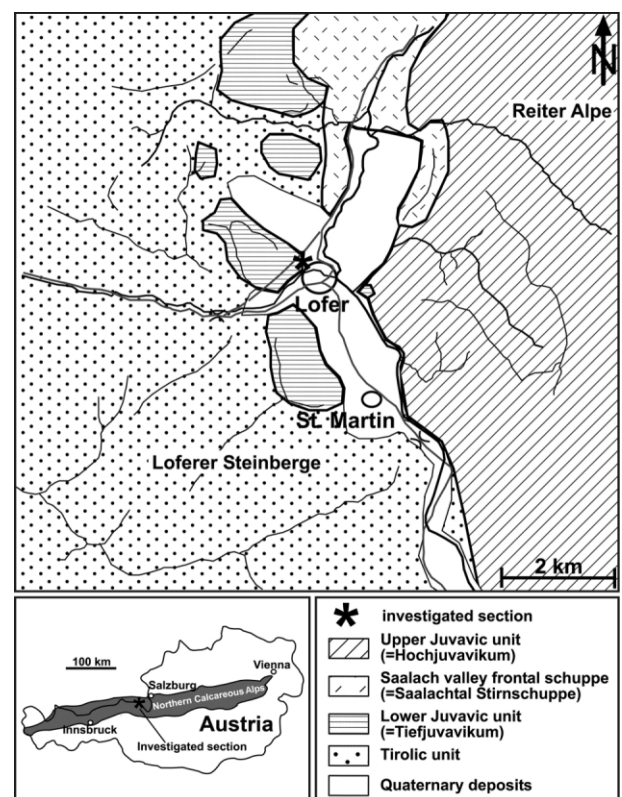


FIGURE 1: Position of investigated succession in Austria (inset), and geological map of environs of Lofer (simplified from Lukesch, 2003).

deep-water deposition persisted in syntectonic basins (Gawlick & Schlagintweit, 2006). During the latest Jurassic, the exposed areas became again transgressed by the sea, and carbonate platforms established. The corresponding successions of shallow-water limestones are termed Plassen Limestone, after its type location Mount Plassen some 60 km to the east of the section near Lofer (Fenninger, 1967). At its type location, the Plassen Limestone is of early Kimmeridgian to early Berriasian age (Gawlick & Schlagintweit, 2006). The Plassen Limestone platform, in turn, drowned during the late Berriasian and became buried by deep-water marls with synorogenic terrigenous clastics (Schrambach Formation) (Gawlick & Schlagintweit, 2006).

At Lofer, the uppermost Jurassic succession is subdivided into two informal units, these are, the Lofer unit and the overlying Lärchkogel limestone unit (Fig. 2). At Lofer, the Lofer unit is between about 20-35 m in thickness, and is a mixed siliciclastic-carbonate succession that accumulated during transgression and overstep of the older rock substrate (Fig. 3). At the base of the overlying Lärchkogel unit, an interval about 10 meters thick mainly of oolitic limestones is present (Ferneck, 1962; Dya, 1992; Lukesch, 2003). The Lärchkogel unit is up to about 250 m in preserved thickness, and represents a succession of more-or-less pure shallow-water lime-

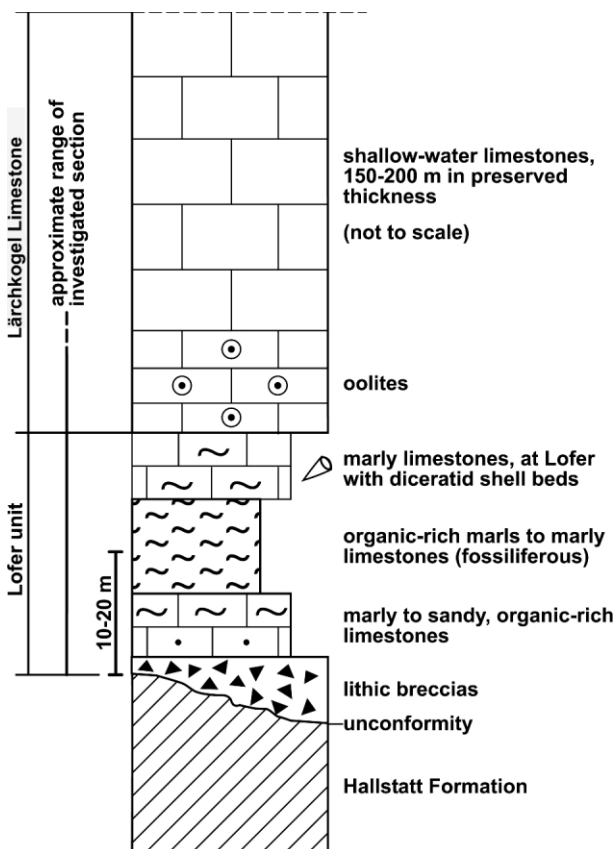


FIGURE 2: Schematic generalized section of Lofer unit and its lateral correlatives in the environs of Lofer, and overlying Lärchkogel limestone, respectively (modified from Ferneck, 1962, and Lukesch, 2003).

stones (Ferneck, 1962). Both the Lofer and Lärchkogel unit, respectively, are characterized by a diversified biotic assemblage of both smaller and larger complex Textulariina, Miliolina, calcareous green algae, nerineacean gastropods, demosponges (*Cladocoropsis*, *Burgundia*), chaetetids and corals; in addition, cyanoids (*Rivularia*), *Bacinella*, and oncoids are common. No genuine reefs were recognized, but level-bottoms of skeletal sponges, chaetetids and/or milleporidians are locally present (Dya, 1992). The depositional environment of the Lärchkogel unit probably was that of a shallow subtidal platform of overall moderately high to low water energy. For the Lärchkogel unit at Dietrichshorn, based on benthic for-

minifera and calcareous algae, Darga & Schlagintweit (1991, p. 216) concluded that, there, a Tithonian to Berriasian age for parts of the unit is highly probable, whereas the termination of Lärchkogel deposition still is poorly constrained. Clasts of Lärchkogel limestone are present in the Lackbach unit (Berriasian to Barremian) a few kilometers farther towards thenorth (Darga & Weidich, 1986; Lukesch, 2003). The Lackbach unit is a succession of deep-water marls with intercalated turbidite beds. The lithoclasts in the Lackbach unit thus record erosion of Lärchkogel limestone during Early Cretaceous time (Darga & Weidich, 1986). Because there is no evidence that deposition of Lärchkogel limestone persisted high up into the Cretaceous, it seems probable that the "Lärchkogel platform" drowned during the same time or perhaps slightly later than the Plassen Limestone platform at Mount Plassen farther towards present ESE (cf. Gawlick & Schlagintweit, 2006, their Fig. 7).

The basal part of the Lofer unit consists of an interval 1-5 m thick of carbonate-lithic breccias to conglomerates (Figs. 2, 3) composed of clasts derived from the local rock substrate (Triassic deep-water carbonates in sections on the lower Juvavic unit; Upper Triassic shallow-water limestones in section on the upper Juvavic unit) (Dya, 1992). In most cases, the matrix of the basal rudstones is a limestone, but matrices of marl also are present (Dya, 1992). At most locations, a few or most of the clasts are of low degree of rounding, bored, and/or encrusted oncooidally. In addition, the basal transgressive rudstones typically are overlain by marls and/or by bioclastic wackestones to packstones (Ferneck, 1962; Dya, 1992). For the Lofer unit at Dietrichshorn, potential presence of intermittently brackish conditions is suggested by the characean fragment *Clavator reidi* together with the dasyclad *Zergabriella embergeri* (Darga & Schlagintweit, 1991, p. 208). Higher up in the Lofer unit, marly limestones and a progressive tendency towards pure limestones with a diversified assemblage of fossils such as larger benthic foraminifera, diceratid rudists and hydrozoans records prevalence or persistence of normal saline shallow-marine conditions, under progressive dwindling of terrigenous input. For closer investigation, we chose the section exposed immediately north of the village of Lofer. The geological environs of Lofer have been described and mapped in the field on a scale of 1/10 000 (Lukesch, 2003). For the present paper, aside of polished slabs, a total of 65 thin sections has been investigated. In the investigated section, a truncated succession of dolomitized limestones of the Hallstatt Limestone Formation (Lower Juvavic unit) provided the substrate for the latest Jurassic transgression. Down to a few meters below the truncation surface, the Hallstatt Limestone Formation is riddled by veins and small dykes with complex infillings (Fig. 4A). The walls are highly irregular in outline, and may locally be fringed by micritic cements, overlain by fringes of calcite spar. The top of the Hallstatt Limestone is represented by a vertical transition, over a few centimeters, into an interval of carbonate-lithic stylobreccia at the base of the Lofer unit (Fig. 3). The veins and dykes within the Hallstatt Limestone probably formed upon subaerial exposure during Late

Jurassic uplift of the succession.

3. AGE OF LOFER UNIT

The age range of the Lofer unit is not precisely known. Index fossils and fossil assemblages indicate that both the Lofer unit and the overlying Lärchkogel unit must have accumulated during the latest Jurassic to earliest Cretaceous, but more precise age assignments are difficult. Biostratigraphic dating was based mainly on interval zones of larger benthic foraminifera plus calcareous algae (Darga & Schlagintweit, 1991; Dya, 1992). North of Lofer, we found the larger benthic foraminifer *Anchispirocyclus lusitanica* about a meter above the base of the Lofer unit (see also Ferneck, 1962; Dya, 1992). The presence of *A. lusitanica* (the index fossil of the *lusitanica* taxon-range zone) up from closely above base (sample 8/5 of Dya, 1992, p. 24f.) of the Lofer unit merely indicates that this part of the section accumulated somewhere during Kimmeridgian to earliest Valanginian time (largest taxon range known for *A. lusitanica*; Darga & Schlagintweit, 1991, their tab. 3). As mentioned, the characteristics of the lower part of the Lofer unit indicate intermittent freshwater input, such that contemporaneous other taxa (e. g. calcareous green algae) may have been absent because of adverse ecological conditions. Higher up, in marly limestones of the Lofer unit closely below the Lärchkogel unit, among other forms, in her sample 7/10, Dya (1992) determined *A. lusitanica* and the calcareous green alga *Clypeina jurassica*. This co-presence probably indicates a latest Tithonian to late early Berriasian age range (see Dya, 1992, p. 22-25, 121). The shell beds of *Heterodicerias* described herein provide an additional constraint on chronostratigraphy. Because *Heterodicerias* is confined to the Tithonian, this indicates that for the upper part of the section at Lofer, a latest Tithonian age seems well-established by the co-presence of *A. lusitanica*, *C. jurassica* and *Heterodicerias*.

4. LOFER UNIT (LOFER SECTION): FACIES AND SUCCESSION

4.1 DESCRIPTION

4.1.1 LOWER PART:

In the investigated section, we distinguished seven sedimentary facies (Tab. 1). These are described and interpreted according to their relative position in vertical succession. Directly above the Hallstatt Limestone Formation, the interval of carbonate-lithic stylobreccia (Fig. 4B) about 60-100 cm in thickness is present. Within this interval, aside of a few imbricated clast fabrics formed by a few platy clasts, the [a,b]-planes of clasts are arranged subparallel to bedding (bedding: 234/55, mean of three measurements) (terminology of clast axes and clast fabrics according Collinson & Thompson, 1989). The stylobreccia consists mainly of poorly sorted, fine to coarse-gravel sized, subangular to subrounded clasts derived from the Hallstatt Limestone Formation. In addition, clasts of micritic limestones, and clasts of onco-floatstones to rud-

stones riddled by numerous narrow calcite-cemented cracks of highly irregular distribution are common. In thin section, the oncoids of the onco-limestones appear of yellow to brown tints, consist of micrite to micrite with a 'cloudy' texture, and are riddled by numerous small cracks filled by calcite. In addition, the oncoids may be coated by fringes of micritic cement and/or of pendant calcite cement (Fig. 4C). The matrix of the stylobreccia is a very poorly sorted, lithic stylo-arenite (origi-

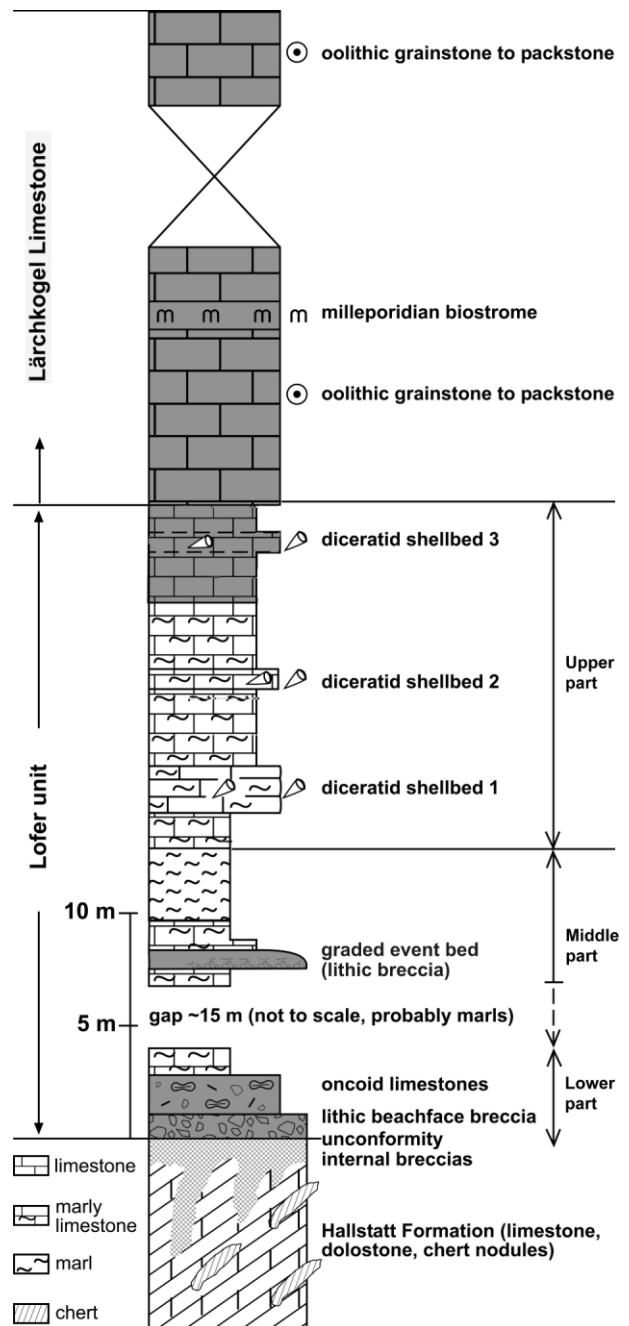


FIGURE 3: Section of Lofer unit immediately north of village Lofer. The approximate position of the 'graded event bed (breccia)' as described in the text has been laterally projected over a distance of about 15 m into the section. Higher above, diceratid rudists are abundant in three distinct shell beds. The subdivision of the Lofer unit into a lower, middle and upper part, respectively, refers to the description of the section in the text.

nally winnowed carbonate-lithic sand) of apparently similar composition than the larger clast fraction. In the matrix, isolated bioclasts are very rare. Only a single, very poorly preserved hyaline benthic foraminifer and another poorly preserved, hyaline ?foraminiferal test were seen. At the top of this interval, a few oncoids are admixed to the carbonate-lithic gravelly sediment. These oncoids are of identical composition than those of the immediately overlying interval.

Above the stylobreccia, an interval of limestones composed mainly of piso- and macro-oncoids is present (Figs. 3, 4D). The oncoid cortices show stromatolithically-laminated lime mudstone, bundles of micritic filament tubules of *Cayeuxia/Rivularia*-type, and *Lithocodium*. In addition, sessile textulariine foraminifera are common elements of oncoid cortices. The nuclei, in turn, were provided by brown-stained clasts of Hallstatt Limestone, by micritic oncoids as described above for the stylobreccia, or by bioclasts (e. g. echinoid fragments, brachiopod shells, small diceratids) (Fig. 4E). In the limestone matrix, disarticulated and articulated shells of terebratulace-

ans are common. In addition, abraded and more-or-less micritized fragments of diceratids are present. At their top, the oncoid limestones vertically grade into an interval of at least 55 cm in thickness of dark grey, mixed bioclastic/carbonate-lithic packstones with a matrix of argillaceous-sandy lime mudstone. The marly packstones contain a few oncoids, *Anchispirocyclina lusitanica*, *Amijiella amiji* and other textulariines, and are rich in peloids. Many of the components are blackened, or are more-or-less replaced by pyrite. Above, dark brown organic-rich, marly to sandy limestones are present that emit a 'bituminous' odour upon fracture. The limestones are argillaceous to silty bioturbated wackestones and micropeloidal packstones, and contain a few small carbonate lithoclasts. Typical bioclasts are small high-spined gastropods (probably cerithiaceans), disarticulated shells of small non-rudist bivalves, wood fragments, fine-grained coalified plant fragments, and a few smaller textulariine foraminifera. Lithoclasts are up to coarse sand size, and include more-or-less silicified radiolarian wackestones to lime mudstones, filament wackestones, and

Facies type number, Designation	Description	Characteristic fossils	Position in section, vertical facies association	Interpretation
1 Carbonate-lithic stylobreccia with caliche nodules	Lithic rudstones of angular to subrounded Hallstatt dolostone clasts and caliche nodules. Matrix: carbonate-lithic stylobreccia	(none)	basal position, overlain by facies 2	low-energy gravelly beachface, formed during transgression over soil-covered substratum
2 Oncoid limestones	Floatstones to rudstones of piso- to macro-oncoids. Matrix: very poorly sorted bioclastic wackestone to floatstone	Micritic oncoids, and porostromate oncoids with <i>Lithocodium</i> , <i>Bacinella</i> , <i>Girvanella</i> and sessile Textulariina in their cortex Matrix: terebratulaceans, echinoid fragments, small diceratids, <i>Anchispirocyclina lusitanica</i> , <i>Rivularia</i>	lower part of section, associated with facies 4 and 6	substrata of low to moderate energy, of lime-muddy bioclastic sand with oncoids, hit by episodic high-energy events
3 Organic-rich marly limestones to fine-sandy to silty wackestones with matrix of marly lime mudstone	Dark brown, bioturbated bioclastic wackestones to micropeloidal packstones, with wood fragments and pyritized wood fragments	Small high-spined gastropods (cerithiaceans), small non-rudist bivalves, textulariines, cyanoids, few <i>A. lusitanica</i>	lower part of section, associated with facies 2 below and 5, 6 above	restricted (?schizohaline) bay/lagoon with dysanaerobic, lime-muddy substrate rich in organics
4 Milleporidian floatstones to boundstones	Milleporidian floatstones to rudstones. Boundstones with milleporidians as frame component	<i>Milleporidium remesi</i> , <i>Tubiphytes</i> , bryozoans, sessile Textulariina, <i>Anchispirocyclina</i> , terebratulaceans	middle to upper part of section, associated with facies 6 and 7	level-bottoms with milleporidians and bryozoans
5 (Micro)bioclastic limestones	Microbioclastic packstones, bioclastic wackestones	Few: smaller benthic foraminifera (mainly textulariines), few to common <i>Anchispirocyclina</i> , <i>Amijiella</i> , <i>Pseudocyclamina</i> , few oncoids (locally)	middle and upper part of section, associated with facies 7	low-energy substrata of microbioclastic material (silt to mud)
6 Diceratid floatstones to rudstones (shell beds)	Floatstones to rudstones of disoriented (toppled) and taphonomically more-or-less altered diceratids	<i>Heterodicerias</i> , microgastropods, terebratulaceans, <i>Anchispirocyclina</i> , <i>Milleporidium remesi</i>	middle part of section, associated with facies 5	level-bottoms mainly of diceratids, reworked during episodic high-energy events
7 Oolitic limestones	Bioturbated, oolitic to oobioclastic grainstones to packstones to wackestones	Bioclasts of benthic foraminifera, molluscs, milleporidians	upper part of section, associated with facies 5 and 6	spillover lobes from ooid bars formed more seaward; spillover during episodic high-energy events

TABLE 1: Sedimentary facies of Lofer unit (section at Lofer).

fragments of calcite orthosparite. Some of both the larger bioclasts and the lithoclasts are coated by oncoidal crusts and/or bear a micrite rim. Wood fragments and other plant debris may be more-or-less pyritized. The heavy mineral fraction (determined by K. Krainer, Innsbruck) is dominated by both framboidal and idiomorphic pyrite, whereas zircon, rutile, apatite and ?amphibole are rare.

4.1.2 MIDDLE PART:

Above, an interval about 16 m thick is present that is very poorly exposed (Fig. 3). Excavations suggest that it consists mainly or entirely of backweathering, organic-rich, dark grey to brown marls to marly limestones. Samples from the basal part of this interval are dark brown, marly, bioturbated fine-grained peloidal packstones to wackestones with burrows filled by peloidal packstone to grainstone. A few carbonate rock fragments up to fine gravel size and bioclasts may float in the matrix. At least most rock fragments can be assigned to the Hallstatt Limestone Formation, and typically show an irregular, embayed outline. Both bio- and lithoclasts may bear micrite rims, and/or are encrusted by thin oncoid cortices. Typical bioclasts include small high-spined gastropods, small non-rudist bivalves, a few *Anchispirocyclus* and a few smaller textulariine foraminifera, fine-grained plant debris and wood fragments. In addition, a few ooids and grains with a thin oolitic coating ('surficial ooids') may be present.

Within the poorly exposed part of the section, a normally-graded bed of lithic rudstone overlain by milleporidian limestone crops out (Fig. 3). In its lower part, the graded bed consists of clasts of dolomitized Hallstatt Limestone in a matrix of carbonate-lithic arenite. In the matrix, bioclasts are scarce, and include mollusc shell fragments and abraded *Anchispirocyclus*. The middle part of the bed is a well-sorted, fine-gravelly rudstone to floatstone of clasts of dolomitized Hallstatt Limestone and of silicified Hallstatt Limestone. Chert clasts are angular, dolostone clasts are subrounded to well-rounded. Many of the rounded clasts are coated by a thin fringe of micrite and/or show a brown-stained fringe. The matrix is a lithic packstone with *Anchispirocyclus*, and a few fragments of *Milleporidium*, diceratids, plants, wood, and *Tubiphytes*. The topmost part of the bed is a fine-gravelly lithic floatstone with large nerineid fragments, common *Anchispirocyclus*, a few micro-oncoids, and a bioclast spectrum similar to the middle part.

4.1.3 UPPER PART:

In its upper part, the Lofer unit consists mainly of (a) bioclastic limestones, and (b) diceratid shell beds.

4.1.4 BIOCLASTIC LIMESTONES:

These include slightly marly, bioturbated, fine-grained bioclastic packstones to wackestones that are dark grey to brown in fracture. Aside of peloids, the bioclastic fraction is characterized by unidentifiable biodetritus, smaller benthic foraminifera, a few *Anchispirocyclus* and mollusc fragments.

4.1.5 DICERATID BEDS:

The shell beds tend to weather out, and consist mainly of floatstones to rudstones of shells of diceratid rudists. These are described in more detail farther below. In the topmost part of the Lofer unit, the bioclastic limestones become practically pure (Fig. 3). Because a diceratid shell bed is intercalated into these limestones, this package is ascribed to the Lofer unit. The base of the overlying Lärchkogel Limestone is placed at the first appearance of oolites of pure limestone composition (Figs. 2, 3). In the profile, as far as investigated up-section, the Lärchkogel Limestone is characterized by (a) oolitic limestones, and (b) by a bed of milleporidian limestone.

4.1.6 OOLITHIC LIMESTONES:

These are mainly represented by oolitic to oobioclastic grainstones to packstones. In the grainstones, no cross-stratification and cross-lamination has been observed; the texture seems to be bioturbated throughout. The oolitic limestones are vertically associated with bioturbated oobioclastic to bioclastic packstones to wackestones.

4.1.7 MILLEPORIDIAN LIMESTONE:

Limestones rich in milleporidian hydrozoans are floatstones and, less commonly, rudstones and floatstones with small patches of boundstone texture (Fig. 4F). The milleporidians may be more-or-less densely encrusted by bryozoans, *Tubiphytes morronensis*, and by sessile textulariine foraminifera. Aside of milleporidians, the larger textulariine foraminifer *Anchispirocyclus lusitanica* and shells of terebratulacean brachiopods are present to common in these limestones.

4.2 INTERPRETATION

At the base of the Lofer unit, the stylobreccia composed mainly of subangular to subrounded clasts of Hallstatt Limestone Formation is interpreted as deposit of a very low-energy gravelly beachface. In the stylobreccia, the clasts of micritic limestones to oncoid-bearing micritic limestones riddled by numerous narrow calcite-cemented cracks of highly irregular distribution are typical of carbonate nodules (caliche) formed within soil profiles. The oncoids in these clasts represent vadoids. These clasts thus record transgressive reworking of a soil profile. A marginal-marine setting of the interpreted beachface breccia is suggested by its gradual transition into overlying oncoid limestones rich in marine fossils. The beachface was subject to quite limited clast transport and sorting as well as to a low degree of abrasion, as indicated by the preferred orientation of [a,b]-planes of clasts subparallel to bedding, and by the subangular to subrounded shape of most clasts. The content of the breccia in the comparatively soft, easily abradable clasts of caliche underscores the overall very low intensity of abrasion. 'High-energy' beach intervals described from other locations show thicknesses of up to more than 10 meters, and mainly consist of well- to very-well rounded lithoclasts of sand- to cobble size (Sanders, 1997, 1998). Conversely, the thickness of the beachface interval, described herein,

of only about 1 meter, and the prevalent subangular to sub-rounded shape of clasts as well as the common clasts of calciche indicate that the transgressive fringe of the Lofer unit overall was of very low energy. Above, the limestones rich in pisolite and macro-oncoids accumulated seaward ahead of the gravelly beachface, on substrata of sandy lime mud to lime-muddy, mixed lithic-bioclastic carbonate sand. Because of input of nutrients for instance by rivers, by transgressive reworking of soil and, perhaps, by near-shore emergence of nutrient-rich, alkaline groundwaters (Johannes, 1980), the setting was favourable to growth and calcification of cyanobacteria, resulting in well-developed oncolite cortices. Whereas most of the larger bioclasts such as the shells of brachiopods and diceratids may have been swept in during high-energy events, intermittently, a few of these stenohaline forms may also have thrived in this area.

The poorly exposed interval of dark brown, argillaceous to silty organic-rich limestones accumulated in an overall low-energy, shallow subtidal environment with copious input of plant fragments. The low-diverse fossil assemblage mainly of small, high-spined gastropods, small non-rudist bivalves and a low content of smaller benthic foraminifera suggest that the environment was stressful to most shallow-marine organisms. In shallow, quiet bay/lagoonal settings in a humid tropical climate, several stress factors are possible, such as episodic salinity lowering by rainfall or groundwater seepage, and/or by marked temperature fluctuations. Moreover, high input of land-derived particulate organic matter may have exerted stress by nutrification, shading, and by inducing (intermittent) development of organic-rich soupground substrate. Organic-rich soupgrounds are common in very low-energy settings, such as sheltered bays and lagoons, and are hardly available for benthic colonization (Bromley, 1996). The presence of the backweathering interval of organic-rich marly limestones closely above the basal beachface rudstones and oncolite limestones underscores the low-energy character of transgression. Furthermore, the abundance of fine-grained coalified plant fragments and wood debris indicates that the transgressed area was vegetated. The described, normally-graded bed of lithic rudstone intercalated into the backweathering succession of marly limestones (Fig. 3) accumulated during waning of a flow that was of exceptional intensity relative to the prevalent energy level of the depositional setting. If fluid flows set up by normal storms would have had the effect to re-deposit lithoclasts into sheets across the bay/lagoonal setting, these should be much more common. This bed thus may have accumulated during a storm of very rare impact, or during backflow of a tsunami.

Higher up-section, in the 'upper part' of the Lofer unit as described, the packages of marly to pure limestones bioclastic limestones and the diceratid shell beds accumulated farther offshore in an open, normal-marine, shallow subtidal environment. For the shell beds, we assume that these accumulated from level-bottoms at or very close to the locations the mollusks thrived at, but the development of cluster reef fabrics

(see Riding, 2002, for terminology of reef fabrics) was prevented by reworking and toppling during episodic high-energy events. As mentioned, the base of the Lärchkogel Limestone overlying the Lofer unit is placed at the appearance of pure oolitic to oobioclastic limestones. The oolitic limestones accumulated mainly upon landward spillover, during high-energy events, from more seaward actively-forming ooid bars. This is suggested by their bioturbated fabrics with textures in many cases variable on the scale of cut slabs, by the absence of cross-stratification and cross-lamination, and by their wide variations in both texture and composition. After spillover, the oolite sand became churned by burrowing into a local substrate of lime-muddy bioclastic sand to lime mud. The milleporidial limestones were deposited from level-bottoms repeatedly destroyed or disturbed during high-energy events. The milleporidians had provided hard substrata suited for terebratulacean brachiopods to settle. Biostromes of milleporidial hydrozoans (*Milleporidium remesi*) also are present in the Lärchkogel limestone at Dietrichshorn (Darga & Schlagintweit, 1991). The characteristics of the major facies belts during deposition of the Lofer unit are summarized in table 2.

The reconstruction of facies belts in the Lofer section overall fits with the reconstructed transgressive depositional environments as proposed for the Lofer unit at Dietrichshorn by Darga & Schlagintweit (1991, their fig. 2), that is, a low-energy transgressive fringe ahead of a vegetated emergent area with low micro- to meso-scale relief, and with freshwater runoff. Similar environments today are present along the western, sheltered shore of the Florida panhandle, where swampy freshwater environments seaward grade into a low-energy trans-

FIGURE 4: Rock substrate and facies of Lofer unit.

A: Hallstatt Formation about 1 m below base of Lofer unit. Lime mud-to wackestones with radiolarians, ammonite fragments and brachiopod shells, riddled by irregular veins (V) filled by lime mudstone, cement fringes, and patches of internal breccias (b). Width of view 17 mm.

B: Stylofitted rudstone mainly of clasts of Hallstatt Limestone Formation, and of lime mudstones and micro-oncolite bearing wackestones. Slab 14 cm in length.

C: Stylobreccia immediately above Hallstatt Limestone Formation. Clasts of Hallstatt Limestone (H) and clast of micro-oncolite wackestone (W) that is riddled by calcite-cemented cracks of irregular geometry. Note 'pendant fringes' of cement (C) on the oncolite-wackestone clast. Width of view 10.5 mm.

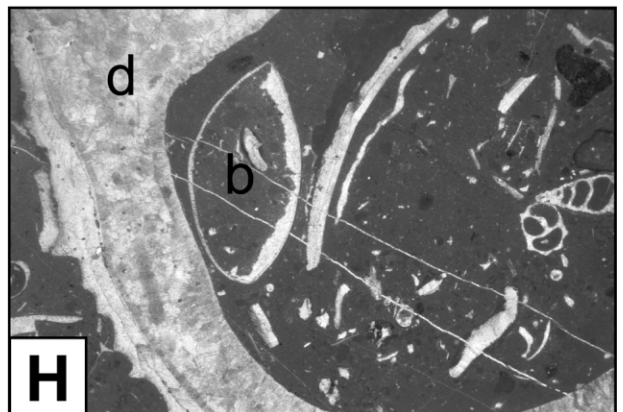
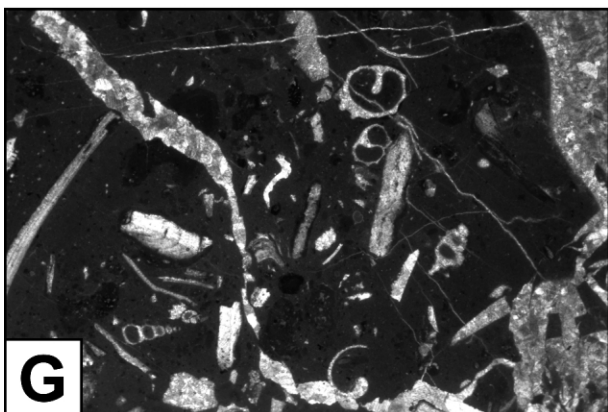
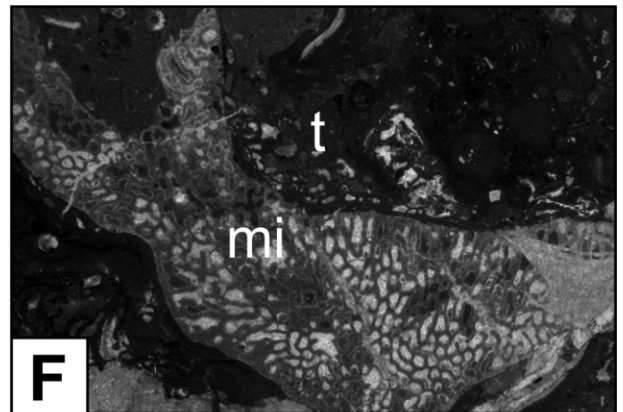
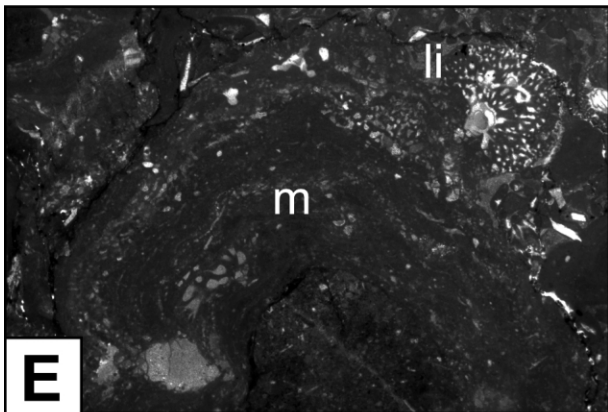
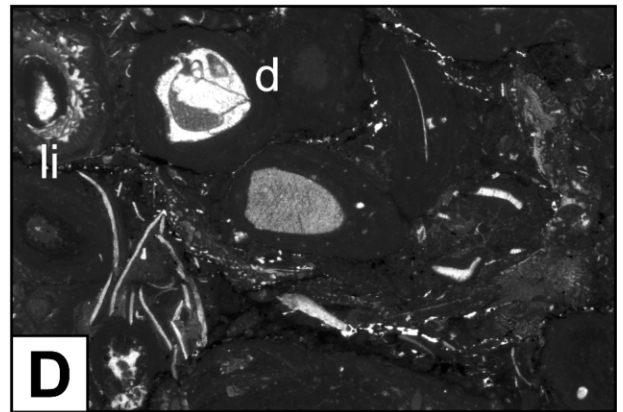
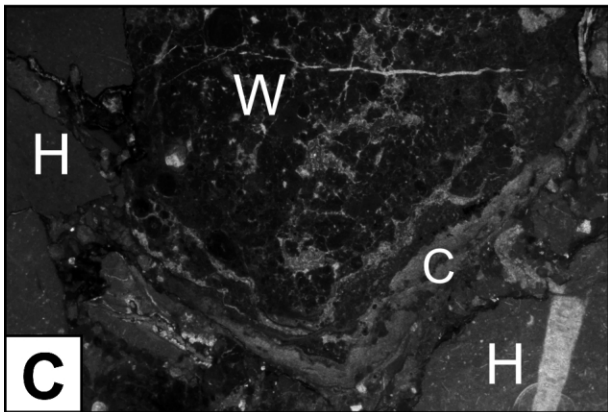
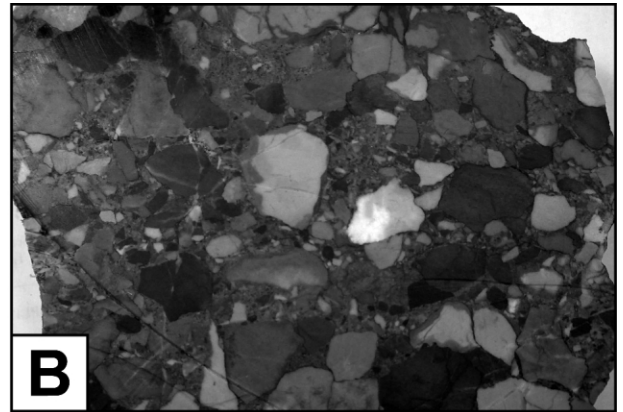
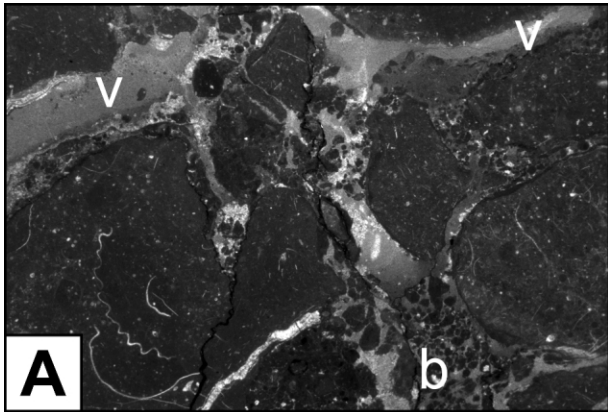
D: Rudstone of pisolite to macro-oncoids. Note small diceratid (white shell labelled d) as nucleus of an oncolite. Width of view 17 mm.

E: Cortex of a macro-oncolite. The cortex is dominated by 'wrinkly'-laminated lime mudstone (m) of probable microbialite origin, and by the sessile microproblematicum *Lithocodium* (li). Width of view 12 mm.

F: Detail of bed of milleporidial limestone with small patches of milleporidial-sessile foraminiferal boundstone. Note milleporidial colony (mi) overgrown by sessile textulariine foraminifer (t). Width of view 17 mm.

G: Matrix of diceratid shell beds. Bioturbated lime mudstone to bioclastic wackestone rich in small high-spined gastropods, terebratulacean brachiopods, and in platy fragments of the outer, calcitic shell layer of diceratids. Width of view 17 mm.

H: Diceratid shell bed. Large shell is a diceratid (d) with preserved outer (calcitic) shell layer. In the matrix, note high-spined gastropods, terebratulacean brachiopod (b), and a fragment of the outer calcitic shell layer of diceratids. Width of view 10 mm.



gressive shoreface (Hine et al., 1988). A gentle morphological relief of transgressed areas may explain the general low-energy character also of other sections of the Lofer unit not described herein (see brief characterizations in Dya, 1992), combined with absence of terrigenous input during deposition of the Lärchkogel limestone. To date, the origin of the siliciclastic minerals in the Lofer unit is not clear. The silt- to sand-sized grains of zircon, rutile and apatite indicates that volcanic rocks (cf. Frisch & Gawlick, 2003; Gawlick & Schlagintweit, 2006) and/or basement rocks (cf. Frank & Schlager, 2006) were exposed to erosion. More data on silicic minerals in the Lofer unit are needed to arrive at a more conclusive interpretation with respect to their palaeogeographic significance. In the context of the "Lofer-Lärchkogel transgression", it may suggest that wider afar, areas with higher morphological relief may have persisted during Lärchkogel deposition.

5. DICERATID SHELL BEDS

5.1 FACIES

Along section, three diceratid shell beds are present (Fig. 3). The shell beds consist of floatstones to rudstones of toppled and disoriented shells of diceratids. Within several large, multiply slabbed samples of the beds, all determined shells are of the genus *Heterodicerias* (Skelton et al., 2004). This suggests a monogeneric diceratid community. The matrix of the shell beds is a brown to dark grey, slightly argillaceous lime mudstone to wackestone with diceratid bioclasts; most of these bioclasts are flaky fragments of the calcitic outer shell

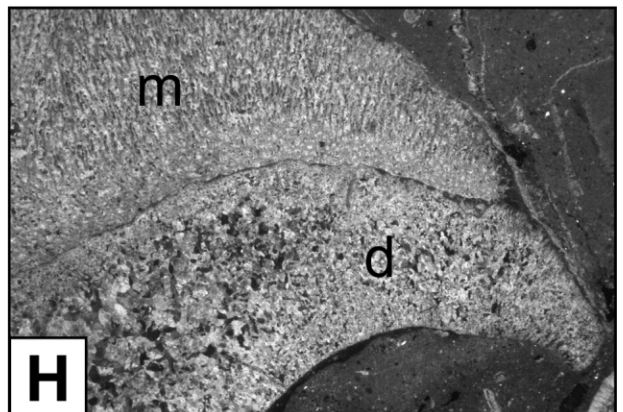
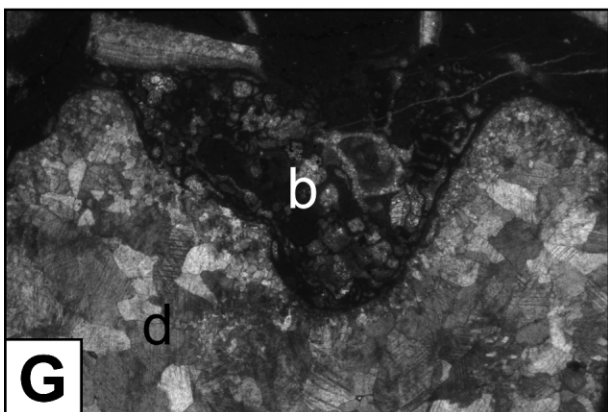
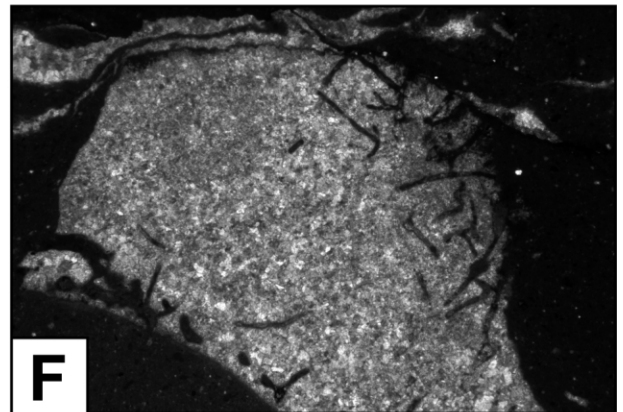
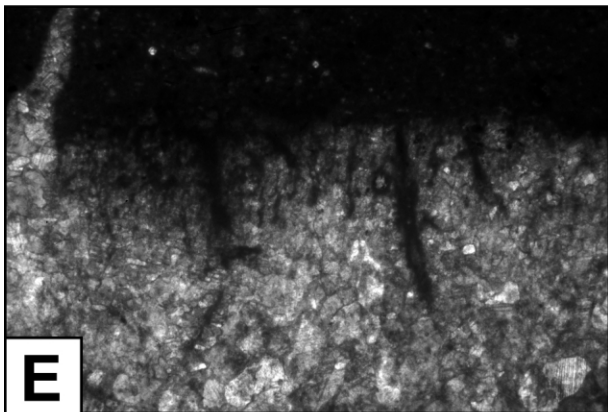
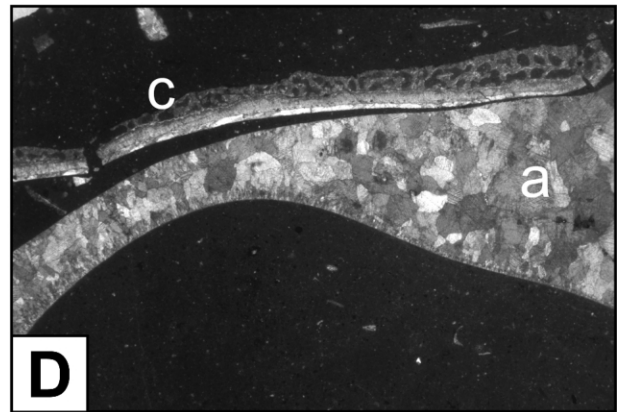
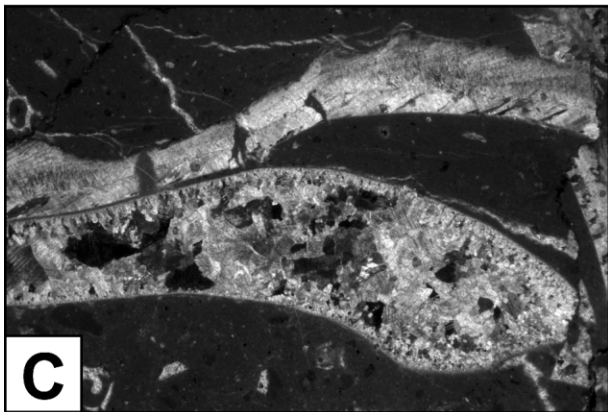
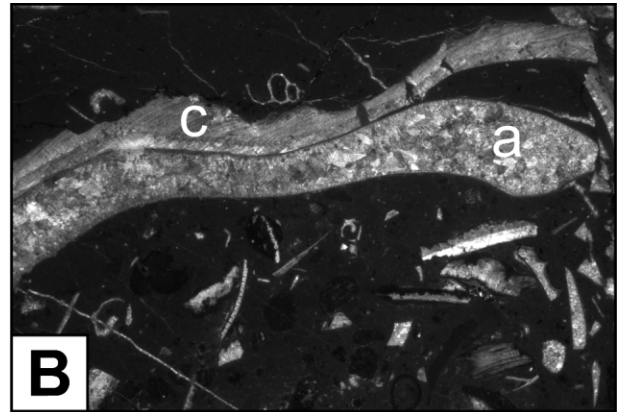
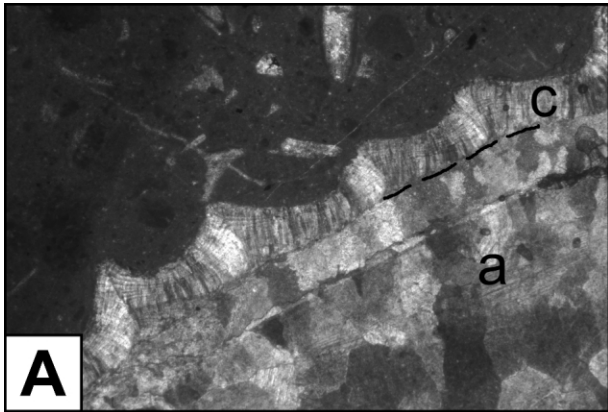
layer that preferentially spalled off (Fig. 4G; see also farther below). A few diceratid fragments and other larger bioclasts may be encrusted by dark-grey, thrombolitic microbialite, or

FIGURE 5: Taphonomy of diceratid shell beds.

- A: Detail of Fig. 4H. Diceratid shell with outer, calcitic layer (c, delimited by dashed black line) with preserved shell ornamentation. Note faint growth lamination in the calcitic shell layer. Underneath the calcitic layer the thicker, inner shell layer of former aragonite (a) is present. The aragonitic shell layer became preserved as blocky calcite spar. Partly crossed nicols. Width of view 4 mm.
- B: Disintegration of diceratid shell. 'Peel-off' spalling of the outer calcitic shell layer (c) from the inner aragonitic layer (a). Width of view 17 mm.
- C: Detail of preceding image, showing 'peel-off' of the calcitic shell layer. Crossed nicols. Width of view 8.5 mm.
- D: Diceratid shell with partly abraded and bored calcitic shell layer (c), spalled off the underlying, formerly aragonitic shell layer (a, now preserved as blocky calcite spar). Partly crossed nicols. Width of view 14 mm.
- E: Detail of formerly aragonitic layer of diceratid shell. The formerly aragonitic layer is preserved as blocky calcite spar. The numerous narrow, dark grey tubes within the formerly aragonitic layer are interpreted as microborings. Width of view 3.2 mm.
- F: Aragonitic shell layer (preserved as blocky calcite spar) of diceratid, riddled by relatively straight, branched tunnels. In the Lofer diceratid shell beds, borings of this type are rare. Width of view 12 mm.
- G: Microproblematicum *Bacinella* (b), located in a crevice on the outer side of a diceratid shell (d). The calcitic shell layer had been removed before settlement of *Bacinella*, such that the diceratid shell became preserved only by its formerly aragonitic portion (now blocky calcite spar). Width of view 7 mm.
- H: Diceratid shell (d), preserved only in its aragonitic shell part (now blocky calcite spar), overgrown by milleporidian (m) colony about 5 cm in size (only basal part of colony visible). Crossed nicols. Width of view 17 mm.

PROXIMAL (LANDWARD)		DISTAL (SEAWARD)	
FACIES BELT 1	FACIES BELT 2	FACIES BELT 3	FACIES BELT 4
narrow, low-energy gravelly beachface, with a fringe of lime-muddy "oncoïd grounds" seaward ahead	low-energy, intermittently restricted shallow subtidal area with substrate of organic-rich, sand/silt-bearing argillaceous lime mud Environment perhaps intermittently suited for colonization by <i>Anchispirocyclina</i> Episodic high-energy events	medium-energy to episodically high-energy open subtidal area with bottoms of argillaceous lime mud to lime-muddy skeletal sand Diceratid level-bottoms <i>Anchispirocyclina</i> environment Episodic high-energy events	moderate-energy open subtidal area characterized by: (a) Milleporidian biostromes, (b) ooid dunes, (c) bottoms of lime-muddy oobioclastic sand
SEDIMENTARY FACIES			
Gravelly beachface: poorly to moderately sorted, carbonate-lithic stylobreccias with scarce matrix of carbonate-lithic stylo-arenite "Oncoïd grounds": floatstones to rudstones of micro- to macrooncoïds	(a) ± marly, organic-rich, mixed shallow-water bioclastic/lithic wackestones to packstones, (b) marls Event bed (?tsunami, ?storm): bed graded from lithic breccia at base to lithic/shallow-water bioclastic grainstones to packstones at top	Level-bottoms: marly to pure shallow-water bioclastic packstones to wackestones Diceratid shell beds: preserved as rudstones to floatstones of toppled diceratid shells	(a) Boundstones to floatstones with milleporidians (b) Oolitic grainstones to packstones (c) Oobioclastic to bioclastic-peloidal packstones to wackestones
FOSSIL ASSEMBLAGE			
Beachface breccias: no indigenous fossils preserved "Oncoïd grounds": Oncoïd cortices composed of microbialites, sessile <i>Textulariina</i> , porostromate algae.	Very poor to low-diverse assemblage of benthic foraminifera (small <i>Textulariina</i> , small ? <i>Miliolina</i>), small cerithiacean gastropods, <i>Anchispirocyclina</i> locally common, dasycladalean algae	<i>Anchispirocyclina</i> , smaller <i>Textulariina</i> , few stromatoporoids, <i>Heterodicerias</i> (few outside of shell beds), nerineid gastropods, dasycladalean algae, <i>Bacinella</i> <i>Heterodicerias</i> in shell beds (see table 3 for assemblage of shell beds)	(a) <i>Milleporidium</i> , <i>Burgundia</i> , encrusted by sessile <i>Textulariina</i> , <i>Tubiphytes</i> , <i>Lithocodium</i> (b) (no indigenous fossils) (c) Bottoms of lime- muddy oobioclastic sand with molluscs, dasycladalean algae, <i>Textulariina</i> ,

TABLE 2: Schematic reconstruction of major facies belts, Lofer unit (Tithonian) at Lofer. A broadly similar reconstruction was provided by Darga & Schlagintweit (1991) for the Lofer unit at Dietrichshorn, but without diceratid shell beds.



may comprise the nucleus to stoutly branched piso- to macro-encrustations, but overall, encrustation is scarce. Other typical bioclasts of the matrix include small terebratulacean brachiopods and high-spired microgastropods up to a few millimeters in length (Fig. 4H). In some samples, these microgastropods are the most abundant non-diceratid fossils. Based on shell ornamentation, the microgastropods may pertain at least to two taxa, because one group is devoid of shell ornamentation and another shows, in thin section, ornamentation by transverse ribs or knots. Subordinately, a few *Anchispirocyclus*, and fragments of *Milleporidium*, *Bacinella*, branched corals, microgastropods, porostromate algae, small non-punctate brachiopods, peloids, wood fragments, a few smaller textulariines, and a few ostracods and *Tubiphytes* fragments are present. The ma-

are preserved only or largely by their thick, formerly aragonitic layer. Preserved intermediate stages of spalling indicate that large, thin flakes of the calcitic layer detached at once, or 'curled off' the aragonitic shell layer (Fig. 5C). In diceratids with a partly preserved calcitic layer, a dark 'hair line' between the originally aragonitic and the calcitic layer, respectively, is present (Fig. 5D). In the matrix of the diceratid beds, the flaky calcitic shell fragments are common. On by far most of the shells, the outer calcitic layer shows a highly irregular, pitted and microbored outline. Remnants of shell ornamentation (ribs) of the calcitic layer are rarely preserved. In most cases, the diceratid shells became completely stripped of their calcitic layer. In the exposed aragonitic layer, microborings are common (Fig. 5E), and may lead to a thin fringe of 'destructive' micrite chiefly along the outer surface of the aragonitic shell remnants. Conversely, evidence for macroboring is rare (Fig. 5F). Notwithstanding presence and preservation of the calcitic shell layer, many shells are encrusted by sessile epibionts, such as textulariacean foraminifera, *Lithocodium*, *Bacinella* and milleporidians (Figs. 5G, 5H), or by stromatolitic microbialites up to a few millimeters thick. In addition, large flakes of calcitic shell layer set apart of the adjacent aragonitic layer by an interval up to only a few millimeters in thickness of lime mudstone are fairly common. Also the aragonitic shell layer, including the thick portions near the hinge of the lower valve, may be disintegrated into angular fragments, with fitted margins separated by a lamina of lime mudstone matrix. The preservation of the aragonitic shell layer and fragments thereof is highly variable, also on the scale of single rock samples, and ranges from very good, without features of abrasion, dissolution or bioerosion, to bored, abraded and corroded.

Skeletal frame component of shell beds

Heterodicerias

Epibenthic settlers on diceratid shells

Sessile textulariine foraminifera

Terebratulacean brachiopods

Milleporidium

Bacinella

Lithocodium

Porostromates ('porostromate algae')

Serpulids

Stromatolites (=cryptmicrobially laminated lime mudstone)

Grazers or scavengers

Microgastropods

Uncommon to rare bioclasts swept in from adjacent environments

Fragment of branched corals

Tubiphytes

Anchispirocyclus, *Amijiella*

TABLE 3: Benthic assemblage of *Heterodicerias* shell beds (Lofer unit at Lofer).

trix of the diceratid floatstones to rudstones is locally riddled by larger softground burrows, evident by patches of slightly different texture and composition, and by a 'swirly' disorientation of components. In burrow mottles, the texture of the matrix ranges from fine-grained bioclastic/peloidal wackestone to packstone.

5.2 TAPHONOMY

In the diceratid limestones, shell preservation is highly variable even on the scale of rock samples (20-40 cm), and ranges from more-or-less taphonomically altered to, rarely, well-preserved without features of abrasion, bioerosion and dissolution (Figs. 4H, 5A). In the shell beds, a feature observed for practically all shells is partial to complete spalling of the thin calcitic outer shell layer (Fig. 5B). Thus, by far most shells

5.3 INTERPRETATION AND DISCUSSION

A summary of the benthic assemblage of the diceratid shell beds is given in table 3. For the shell beds, their texture of floatstone to rudstone composed of toppled, disoriented shells in various states of taphonomic alteration indicates that the diceratids thrived at or near to site of preservation, but were subject to toppling and short-distance transport mainly during episodic high-energy events. Additional toppling and disorientation of shells may have occurred upon burrowing. The microgastropods common over most of the section may have thrived within the rudist level-bottoms and/or adjacent thereof, where they scavenged the sea floor for microbial films and/or for fine-grained particulate organic matter. The terebratulacean brachiopods, in turn, probably thrived attached to rudist shells. Brachiopods are common elements of hard-substrate fossil assemblages also in Cretaceous and Cenozoic transgressive successions of the Eastern Alps (Sanders, 1997, 1998; Sanders & Baron-Szabo, 2007). The rudist shells also provided settlement substrate to milleporidians and other sessile organisms (*Lithocodium*, *Bacinella*, porostromates). The overall composition of the shell beds, however, indicates that the rudist banks were not a setting favourable to persistent

milleporidian colonization. As mentioned, although shells overgrown by sessile foraminifera, milleporidians, bryozoans, serpulids and by patches of microstromatolithic microbialites are present, overall, such shells and thicker encrustations are uncommon. This may suggest that the shells were frequently turned over and/or buried by sediment after reworking events, so that only a small portion of total dead shell surface was available to colonization. We interpret the prevalent 'life appearance' of the diceratid banks as a mix of shells of both dead and living rudists sticking upright constrictally in the substrate. The substrate of the rudist banks seems to have been hostile to benthic foraminifera, as suggested by their low abundance and diversity in the matrix.

The described different taphonomic states of diceratids also within single rock samples underscores repeated reworking and, probably, mixing of shells of different age. For the calcitic shell layer, the overall rare preservation of shell ornamentation and the highly irregular, pitted and microbored surface suggest infestation and dissolution by microborers. The widespread spalling of the thin calcitic shell layer from the aragonitic layer may be related to rapid, early decomposition of an organic lamina between the two shell layers. This is suggested by a thin, dark 'hair line' visible in some samples between the aragonitic and calcitic shell layer, and by the described spalling of large, but very thin and delicate flakes of calcitic shell. Toppling and short-distance transport during high-energy events, as well as churning of shelly lime mud upon burrowing aided in removal of the calcitic layer. That removal of the calcitic layer took place quite early is indicated by numerous shells stripped partly or completely thereof, followed by growth of sessile epibionts on the exposed aragonitic shell layer. Furthermore, the calcitic layer probably could spall off even when the shell was buried in soft sediment, as indicated by fitted margins between large calcitic flakes set apart by a lamina of matrix from the adjacent aragonitic layer. The 'curled' ends of some calcitic layers that, in part, are still attached to the underlying shell may even suggest that, upon decomposition or racemization of shell organics, the layer was subject to tensile stress favouring removal. The observation that the thick aragonitic layer locally is disintegrated to angular fragments with fitted margins indicates shell fracture during mechanical compaction. In the investigated shell beds, we found no clear-cut evidence for widespread syndepositional, 'chemical' dissolution of calcitic and aragonitic bioclasts. Because in rocks, however, dissolution can only be recognized by criteria of texture or of shell fabrics/structures, and because the compact structure of the diceratid shells allows only for dissolution of outer bioclast surfaces, this does not necessarily imply that no dissolution occurred (Sanders, 2004). Selective disintegration into aragonitic and calcitic shell layers was observed also in the major Cretaceous rudist family Radiolitidae, whereas the other major family Hippuritidae (Turonian to Maastrichtian) overall records a much lower inclination for this style of taphonomy (Sanders, 1999). On a qualitative observational basis, it seems that the tendency for diceratids to

rapidly lose their calcitic shell layer was higher than in the radiolitids. The inclination to spalling of the calcitic layer perhaps was also related to the spirogyrate growth geometry of diceratid shells, in contrast to the erect, non-spirogyrate growth of the Radiolitidae (see Skelton, 1979, for growth styles of rudist shells).

6. CONCLUSIONS

1. In the section at Lofer, the Lofer unit records transgression of a very low-energy gravelly beach that overstepped a soil-covered vegetated land surface. The beach fringed a protected bay or lagoon that received copious terrigenous input (clay, silt, phytoclasts). Farther off shore, level-bottoms dominated, either, by *Heterodicerias* or by milleporidian hydrozoans were present that interfingered with storm spillover lobes shed from oolite dunes situated farther seaward.
2. The *Heterodicerias* shell beds are floatstones to rudstones of disoriented rudists. These beds accumulated from (par) autochthonous rudist level-bottoms hit by episodic high-energy events. The shell beds provided settlement substrate to terebratulacean brachiopods, as well as to sessile foraminifera, *Lithocodium*, *Bacinnella* and milleporidians, and were habitat to microgastropods.
3. Most of the diceratids became partly or completely stripped of their calcitic (outer) shell layer. Spalling of the calcitic layer started early and proceeded until shallow burial within soft sediment. This disintegration of the diceratid shells may be related to decomposition or racemization of organic substances within the shell.

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Diethard SANDERS^{1*)}, Michaela LUKESCH¹⁾, Michael RASSER²⁾ & Peter SKELTON³⁾

¹⁾ Institute of Geology and Palaeontology, University of Innsbruck, 6020 Innsbruck, Austria.

²⁾ Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany.

³⁾ Department of Earth Sciences, The Open University, Milton Keynes MK7 6AA, United Kingdom.

^{*)} Corresponding author, diethard.g.sanders@uibk.ac.at