

# Revision of thelodonts, acanthodians, conodonts, and the depositional environments in the Burgen outlier (Ludlow, Silurian) of Gotland, Sweden

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## Abstract

Ludfordian strata exposed in the Burgen outlier in eastern Gotland record a time of initial faunal recovery after a global environmental perturbation manifested in the Ludfordian Carbon Isotope Excursion (LCIE). Vertebrate microfossils in the collection of the late Lennart Jeppsson, hosted at the Swedish Museum of Natural History, hold the key to reconstruct the dynamics of faunal immigration and diversification during the decline of the LCIE, but the stratigraphic relationships of the strata have been debated. Historically, they had been

placed in the Burgsvik Formation, which included the Burgsvik Sandstone and the Burgsvik Oolite members. We revise the fauna in the Jeppsson collection and characterize key outcrops of Burgen and Kapellet. The former Burgsvik Oolite Member is here revised as the Burgen Oolite Formation. In the Burgen outlier, back-shoal facies of this formation are represented and their position in the *Ozarkodina snajdri* Biozone is supported. The shallow-marine position compared to the coeval strata in southern Gotland is reflected in the higher  $\delta^{13}\text{C}_{\text{carb}}$  values, reaching +9.2‰. The back-shoal succession includes high-diversity metazoan reefs, which indicate a complete recovery of the carbonate producers as the LCIE declined. The impoverishment of conodonts associated with the LCIE in southern Gotland might be a product of facies preferences, as the diverse environments in the outlier yielded all 21 species known from the formation. Fish diversity also returned to normal levels as the LCIE declined, with a minimum of nine species. In line with previous reports, thelodont scales appear to dominate samples from the Burgen outlier.

## Keywords

acanthodians, biostratigraphy, Burgsvik Formation, Ludlow, thelodonts, Lau event, carbon isotope excursion, extinction, recovery, palynology

## 1. Introduction

The Ludlow-aged strata placed in the Burgsvik Formation (Fig. 1) in Gotland, Sweden, represents an important archive of the evolution of early vertebrates (Fredholm, 1989, 1990; Märss, 1992; Bremer & Blom, 2015; Bremer et al., 2020) and plants (see Mehlqvist et al., 2015 and references therein), and of global sea-level and palaeoclimate perturbations (Samtleben et al., 2000; Calner, 2005; Eriksson & Calner, 2008; Kozłowski & Munnecke, 2010; Jeppsson et al., 2012). The formation follows the onset of the Lau Event (Jeppsson et al., 2006; Eriksson & Calner, 2008; Jarochovska et al., 2020a), which is one of several episodes to be coupled with major faunal turnovers and extinctions (Jeppsson, 1987; Koren, 1987; Kaljo & Märss, 1991; Eriksson et al., 2009) and changes in eustatic sea level (Loydell, 2007; Eriksson & Calner, 2008; Kozłowski & Munnecke, 2010). The same event was identified based on fossil fish by Märss (1992), and is subsequently also known as the *A. hedei* Event. It was later found that these episodes coincided with the most pronounced carbon isotope excursion in the Phanerozoic (Samtleben et al., 1996; Wenzel & Joachimski, 1996; Bickert et al., 1997; Kaljo et al., 1997; Märss et al., 1998; Wigforss-Lange, 1999; Samtleben et al., 2000; Calner et al., 2008; Jarochovska et al., 2020a; Younes et al., 2017), also recognized on a global scale (see

Munnecke et al., 2010 and references therein). This Ludfordian Carbon Isotope Excursion (LCIE), also known as the Late Ludfordian CIE (LLCIE) or Middle Ludfordian CIE (MLCIE), reached maximum  $\delta^{13}\text{C}_{\text{carb}}$  values of +11‰ (Wigforss-Lange, 1999) and permitted high-resolution global correlations (Jeppsson et al., 2012). The stratigraphy of the strata placed in the Burgsvik Formation (Fig. 2) holds the key for understanding the sequence of biotic and sea-level changes during this time, but its complex and fragmentary exposures and great lateral variability have hindered comprehensive correlations.

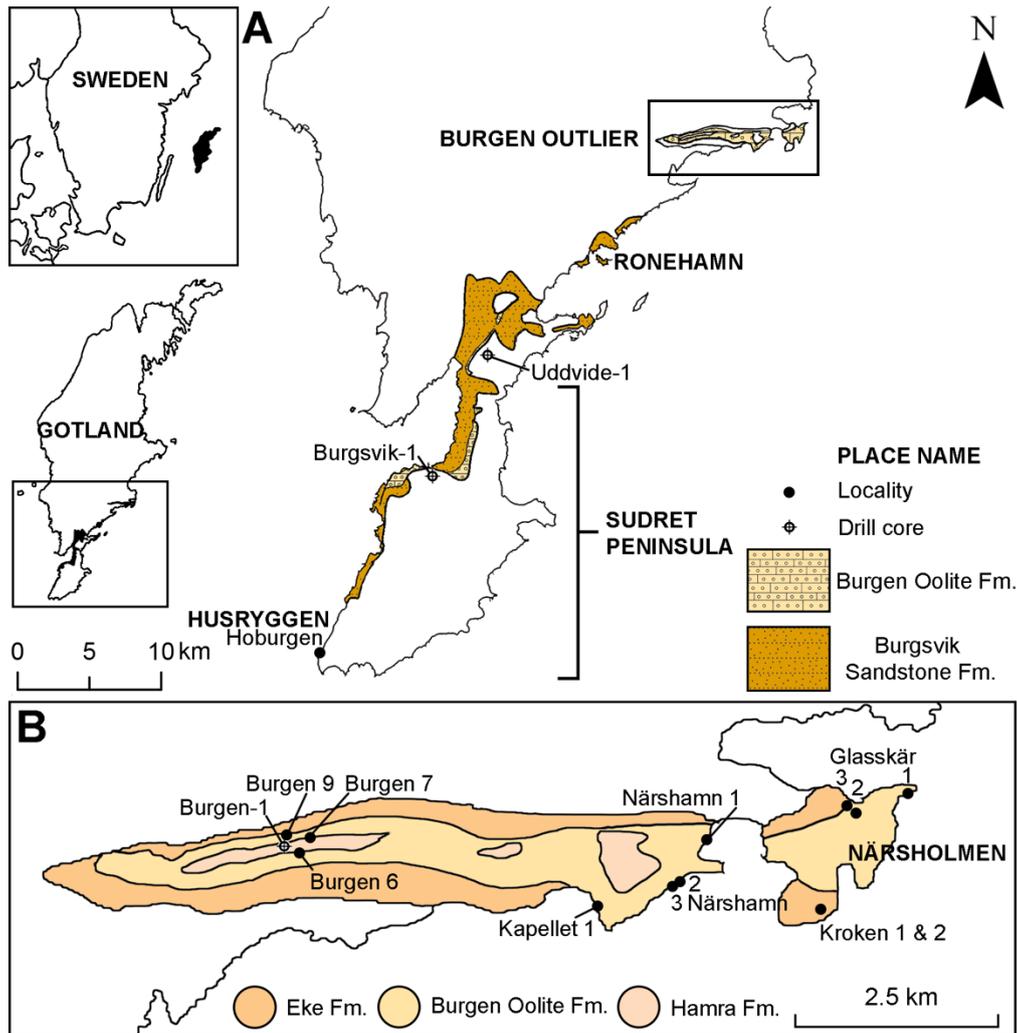


Figure 1. Map of the southern part of Gotland with the Burgsvik Sandstone and Burgsvik Oolite formations in yellow (A) and a detailed map of the Burgen outlier (B) with Eke Formation in orange, Burgsvik Formation in yellow, and Hamra Formation in light pink. Geographical areas (capital letters), localities, and positions of drillcores that are discussed in the text are also indicated. The geographical extent of the formation and its lithologies are based on Eriksson and Calner (2005) and data from the Geological Survey of Sweden (SGU).

The Burgsvik Formation is exposed along a narrow SW-NE-trending strip in the south of Gotland (Fig. 1): a semi-continuous stretch of outcrops in the western coast of Sudret peninsula and in three small areas in the eastern coast of the island: (1) near Ronehamn, (2) in the Burgen outlier, and (3) in the nearby Närsholmen peninsula (Fig. 1A-B). The strata in

eastern Gotland represent shoreward facies compared to the westward-lying exposures. On one hand, shallow marine environments may provide diverse fauna and more evidence for sea-level changes in the form of e.g. erosional surfaces, but on the other hand, fauna and carbon isotope values are affected by the facies shifts, making correlations more difficult. This difficulty is particularly relevant to the strata in the Burgen outlier, which have yielded important collections of vertebrate and conodont faunas which could contribute to the understanding of the diversity dynamics during this pivotal time, but which could not be placed biostratigraphically with confidence.

The aim of this study is to document and revise vertebrate and conodont faunas from existing collections housed in the palaeozoological collections of the Swedish Museum of Natural History, Stockholm, and in the Palaeontological collections, Museum of Evolution, Uppsala University. For several samples and localities, the stratigraphic position was not resolved with sufficient precision with respect to recent high-resolution Silurian stratigraphy (Märss & Männik, 2013; Kaljo et al., 2015; Melchin et al., 2020). In these cases, we revisited outcrops in the Burgen outlier area, identified the depositional environments and re-evaluated the age of the Burgsvik Formation in this area with the rest of the formation in Gotland, based on  $\delta^{13}\text{C}_{\text{carb}}$  chemostratigraphy and biostratigraphy.

## **1.1. Lithostratigraphy of the Burgsvik Formation**

The Burgsvik Formation has a maximum thickness of roughly 47 m in the Burgsvik-1 drillcore (Hede, 1919) and has historically been sub-divided into two units respectively composed of mainly sandstone and oolite (Hede, 1921; Munthe, 1921; Stel & de Coo, 1977; Long, 1993). These were formally described as the Burgsvik Sandstone Member and Burgsvik Oolite Member by Eriksson and Calner (2008), and are included in the Burgsvik Formation despite being lithologically and genetically distinct and separated by a sequence boundary (Eriksson & Calner, 2008; Younes et al., 2017). This lithological and genetic difference is addressed here and the two members are elevated to the rank of formations as the Burgsvik Sandstone Formation and the Burgen Oolite Formation. When referring to previous literature reports not differentiating between the two members, we use the 'Burgsvik Formation'. To characterise the Burgen Oolite Formation, we describe the strata exposed in the Burgen outlier and the adjacent Närsholmen peninsula (Fig. 1B). We examine here the depositional position and correlation of these strata with previously described exposures of the Burgen Oolite Formation using the composite section compiled from the

Uddvide-1 core, Husryggen 4, and Hoburgen in the Sudret peninsula (Fig. 1; Younes et al., 2017).

The Burgen Oolite Formation (formerly: Burgsvik Oolite Member, Fig. 2) is exposed for 15 km between Hoburgen and Burgsvik along the western coast of Sudret peninsula, unconformably overlying the Burgsvik Sandstone Formation (formerly: Burgsvik Sandstone Member; Eriksson and Calner, 2008). It varies in thickness from several metres to only a few decimetres (Munthe, 1921) and Eriksson and Calner (2008) suspected it to underlie the entire Sudret peninsula based on its occurrence in drillcores. The ooids show great diversity in size and form and are generally sorted into layers according to size (Manten, 1971). On the whole, the member is very heterogeneous and contains shell-lags, sandstones, and locally thin layers of lenticular-bedded mudstones, in addition to the ooid grainstones (Eriksson & Calner, 2008). The reader is referred to Manten (1971), Calner and Eriksson (2006), and Eriksson and Calner (2008) for detailed lithological descriptions of both formations (as the 'Burgsvik Formation').

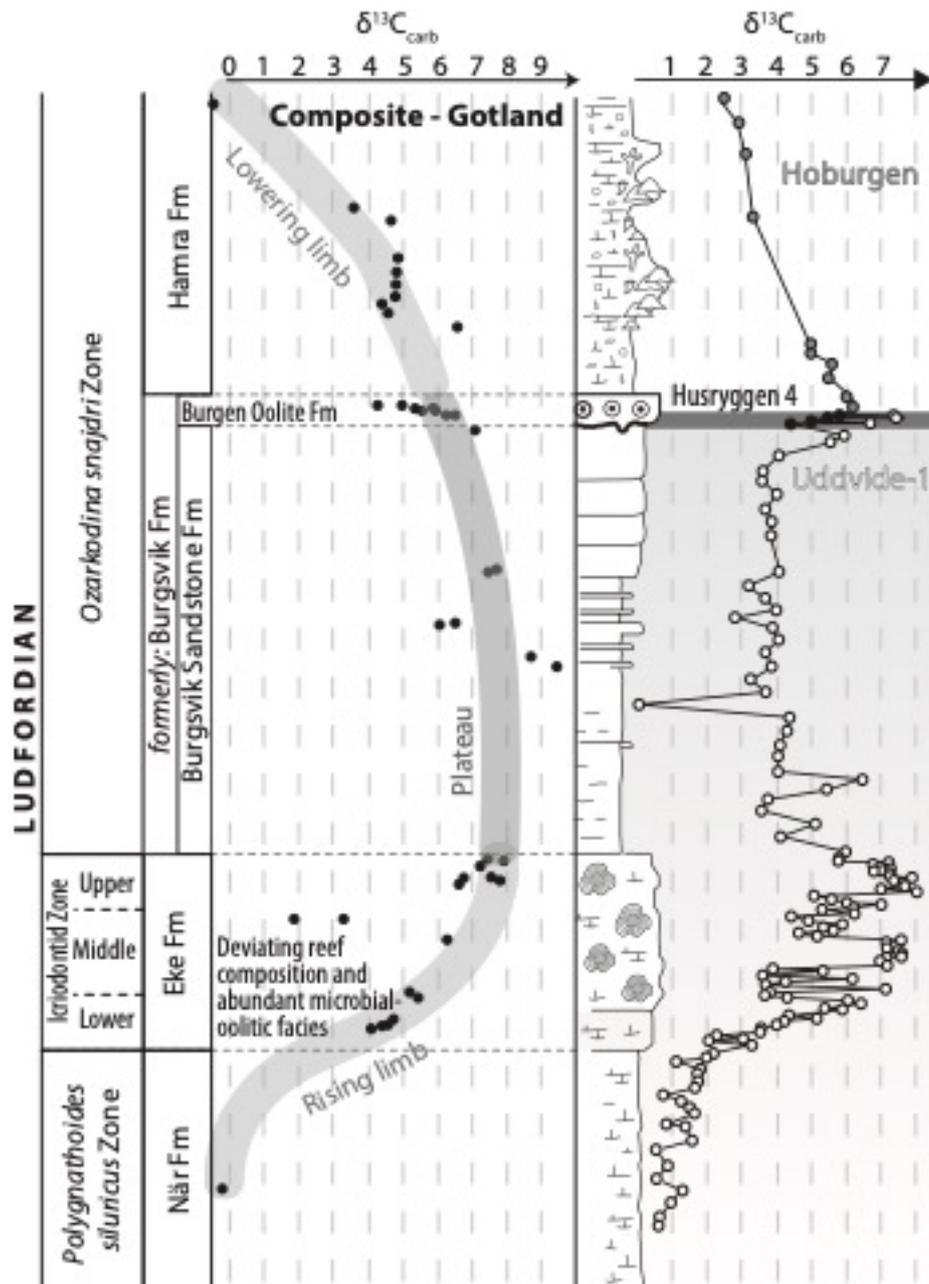


Figure 2. Stratigraphic chart across the LCIE development in Gotland correlated with the composite record of the Uddvide core. The composite  $\delta^{13}\text{C}_{\text{carb}}$  curve (left) is compiled from Jeppsson et al. (2007) and Samtleben et al. (1996, 2000). Conodont biostratigraphy follows Jeppsson (2005) and Jeppsson et al. (2006). The composite profile on the right is from Younes et al. (2017) and was compiled from the Uddvide-1 core (white dots), Husryggen 4 (black dots) and Hoburgen (grey dots).

Traditionally, the 'Burgsvik Formation' was also reported further to the northeast in the Burgen outlier (Munthe et al., 1924, 1925; Manten, 1971), including the Närsholmen peninsula (Fig. 1B; Munthe et al., 1925). These occurrences correspond to the Burgen Oolite Formation, represented by oolites, but there are also local occurrences of marly, time-equivalent reefal limestones according to the studies by Munthe et al. (1924, 1925), which are herein included in the formation. These are mainly built up by crinoids, bryozoans, stromatoporoids, and corals (Munthe et al., 1925; Manten, 1971; Larsson, 1975; Stel & de

Coo, 1977). Inter-reef deposits are present in both the Burgen and Närsholmen areas and are composed of marly, ruggedly stratified limestones rich in reef-debris such as fragments of crinoids, bryozoans, corals and stromatoporoids (see Manten, 1971). There is a clear difference in the reef and the inter-reef limestones between the Burgen and Närsholmen areas, where the latter seem to have formed in slightly deeper water according to Manten (1971). He described the Närsholmen reefs as forming entirely during 'Burgsvik time', whereas the Burgen reefs continued growing during the deposition of the overlying Hamra Formation.

The wording of Manten (1971) reflects the history of research about Gotland stratigraphy and the basic works by Johan Ernhold Hede during the 1920s to 1940s (summarized in Hede, 1960) that established 13 topostratigraphical units referred to as 'beds' on Gotland. This division heavily influenced later studies (see also Erlström et al., 2009), which is evident in the biostratigraphical subdivision presented in Jeppsson et al. (2006). This has led to some discrepancies regarding the nomenclature of sedimentary units, thus the stratigraphic position of strata in the Burgen and Närsholmen areas has varied between studies. Calner and Eriksson (2006) identified typical lithologies corresponding to the Eke Formation, the Burgen Oolite Formation, and the Hamra Formation in the Burgen-1 drillcore. However, in terms of carbon isotope composition, the 'Burgsvik Formation' in the Burgen-1 drillcore records a steady increase of  $\delta^{13}\text{C}_{\text{carb}}$  values (Calner & Eriksson, 2006), a trend that is elsewhere on Gotland observed within the Eke Formation (Samtleben et al., 2000; Jeppsson et al., 2007; Younes et al., 2017). A revised stratigraphy was proposed by Eriksson and Calner (2008), who correlated the entire upper part of the Burgen outlier with the Eke Formation and excluded the 'Burgsvik' and Hamra formations from it entirely. Samtleben et al. (2000) had reached a similar conclusion and excluded the Hamra Formation from the Burgen area. Eriksson and Calner (2008) correlated the clastic-rich interval in the Burgen-1 core with the lower part of Eke Formation in other areas. However, Kozłowski and Munnecke (2010) interpreted the same interval to be coeval with the middle part of the Eke Formation based on the similar increase in isotope values. A recent, continuous  $\delta^{13}\text{C}_{\text{carb}}$  curve across the LCIE in the Uddvide-1 core (Younes, 2012), Husryggen 4 and Hoburgen (Younes et al., 2017) confirmed elevated values throughout the Burgsvik Sandstone and Burgen Oolite formations and a decline first in the lower part of the Hamra Formation. The difficulties in correlating the Burgen-1 core with the southern part of the island exemplify the lateral variability of the 'Burgsvik Formation'. In the Burgen-1 core, the clastic-rich interval corresponding to the Burgsvik Sandstone Formation is unusually thin (compare

with fig. 5 in Eriksson & Calner, 2008) and carbonate-rich. It also shows higher  $\delta^{13}\text{C}_{\text{carb}}$  values than the typical sandstone facies. Based on correlation with the new composite section in Uddvide-1, Younes et al. (2017) attributed this difference to slight diagenetic overprint in the sandstone facies.

## 1.2. Previous biostratigraphic constraints on the age of strata exposed in the Burgen outlier

The age of the strata in the Burgen and Närsholmen areas has been constrained by conodont biostratigraphy (Jeppsson, 1983, 2005). In fact, the majority of conodonts used to place the Burgen Oolite Formation within the biostratigraphy come from this area (Jeppsson, 2005). The formation is placed in the *Ozarkodina snajdri* Zone (Jeppsson, 2005; Jeppsson et al., 2006) based on the appearance of the zonal species in the lower part of the unit. *Oz. snajdri* belongs to a morphologically variable group of *Oz. bohémica* and has been reported from strata as old as Wenlock (Jeppsson, 1983; Jarochowska et al., 2016), suggesting that it may not be a very sensitive index species (see also Märss & Männik, 2013). In addition to *Oz. snajdri*, Jeppsson and Aldridge (2000) reported the following taxa from the 'Ozarkodina steinhornensis' group in what they referred to as the Burgsvik Beds: *Oz. scanica* in its older part and '*Oz. remscheidensis* n. ss. b' in the younger one. These taxa have been the subject of intensive taxonomic and stratigraphic revisions since 2000 (Murphy et al., 2004; Carls et al., 2007; Corradini & Corrigan, 2012), so that the original identifications by Jeppsson and Aldridge (2000), which lack illustrations, cannot be compared with currently employed diagnoses and, therefore, zonations. A later revision of the Gotland zonation by Jeppsson et al. (2006) suggested the occurrence of '*Oz. remscheidensis*' in the upper part of the Hamra Formation only. Additionally, according to Jeppsson (2005), other taxa appearing first in this formation include *Oulodus* n. sp. aff. *elegans*, *Ou. elegans*, and *Ctenognathodus confluens* Jeppsson, 1972.

## 1.3. Previous reports on the vertebrate fauna in the Burgen outlier

Spjeldnaes (1950); Fredholm (1989); Märss (1992, 2001); Blom et al. (2002) and Eriksson et al. (2009) only gave infrequent reports of fossil agnathans and gnathostomes from the 'Burgsvik Formation'. Most of these reports correspond to the Burgen Oolite Formation, which displays one of the highest diversity of dermal vertebrate remains in the Gotland sequence, as summarized in Bremer and Blom (2015). Fredholm (1989) dissolved large quantities of rock material from the Burgen Oolite Formation of the Burgen outlier (Fig. 1B). Two samples from localities Burgen 6 and 7 collectively contained a few *Thelodus* sp. and *Loganellia* sp.

scales. Samples from the Glasskär 1 locality were particularly rich in remains that were dominated by thelodonts *Thelodus parvidens* Agassiz 1839, *Th. sculptilis* Gross, 1967, '*Loganellia cuneata*' Gross, 1947, *Paralogania ludlowiensis* Gross, 1967, and *Lanarkia?* sp. Traquair, 1898, but also contained a subordinate number of acanthodians that she identified as *Gomphonchus sandelensis* Pander, 1856, *Nostolepis striata* Pander, 1856, and *Poracanthodes porosus* Brotzen, 1934 (Fredholm, 1989). A sample from the nearby locality Glasskär 3 contained two *Th. parvidens* scales, a trilobatiform thelodont scale, one *G. sandelensis* scale, and some unidentifiable fish remains. Another sample from the Burgen outlier (Kroken 1) showed a similar acanthodian composition as Glasskär 1, but lacked thelodonts *Th. parvidens*, *Th. sculptilis*, and *Lanarkia?* sp., while a sample from Kroken 2 only contained one *Loganellia* sp. scale. Samples from localities Närshamn 1-3 mainly contained thelodonts referred to as *Log. cuneata?*, *Loganellia* sp., and *Th. parvidens*, a few acanthodian scales identified as *N. striata* and *G. sandelensis*, as well as a single fragment of an unidentified osteostracan (Fredholm, 1989). Fredholm (1989) also described one sample from Kapelludden 1 (=Kapellet 1) that produced scales of *Th. parvidens*, *Log. cuneata*, and *N. striata*.

Three samples from the Burgen Oolite Formation were treated in Nilsson (2005) and the results were later summarized in Eriksson et al. (2009). Two of them came from the Burgen area, namely Burgen 7 and 9, and collectively contained remains of *Th. parvidens*, *Thelodus* sp., *P. ludlowiensis*, *Paralogania?* sp., *N. striata*, *G. sandelensis*, and *Por. porosus*. The previous reports of *Log. cuneata* from Burgen outlier localities Glasskär 1, Kapellet 1, Kroken 1, and Närshamn 1 by Fredholm (1989) were revised as *Paralogania?* sp. (see Nilsson, 2005 for discussion). We would argue that the scales found and figured as *Paralogania?* sp. by Nilsson (2005, fig. 13g-i), although eroded, fit within the scale-set presented for *P. ludlowiensis* (compare Miller and Märss, 1999, plate 2: figs. 16, 21, plate 3: fig. 25). However, Nilsson (2005) also included forms lacking lateral thornlets in this revision, and the previous exclusion of *Log. cuneata* from the Burgen outlier is further complicated by findings of typical *Log. cuneata* scales in the Burgen 9 sample presented in this work.

*Institutional abbreviations* – NRM-PZ, Naturhistoriska riksmuseet, PalaeoZoological Collections, Stockholm, Sweden; PMU, Palaeontological collections, Museum of Evolution, Uppsala University, Uppsala, Sweden.

## 2. Material and Methods

### 2.1. Field sampling and new material

To place previous collections from the Burgen outlier in a palaeoenvironmental and stratigraphic context, we produced lithological sections of the outcrops Burgen 7 (N 57° 13' 47.4", E 18° 34' 52.6") and Burgen 9 (N 57° 13' 48.4", E 18° 34' 36.6") in September 2017 (Figs 1, 3-4). Samples representative of lithologies in both outcrops were used to make thin sections: three from Burgen 7 (Fig. 5) and four from Burgen 9 (Fig. 6). High-resolution scans of thin sections are provided as supplementary data in Jarochovska et al. (2020b).

The Kapellet 1 locality near the bay Närshamn (RT90 6347452, 1671319; N 57° 13' 15.7", E 18° 38' 29.7", Fig. 1) has been examined and sampled. No lithological log was produced as the exposure includes a few square metres of nearly horizontal bedding planes, but the bedding planes were cleaned up and are documented here (Fig. 7A). A slide for micro-facies analysis was prepared from a small lithological sample (PMU 23104, Fig. 7C) corresponding to the microfossil sample G14-26-OB, which was also analysed for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values. All thin sections were photographed using Zeiss Axio Zoom V16 binocular microscope with an Axiocam 506 camera and are stored at PMU.

### 2.2. Isotope analyses

For carbon isotope analysis 25 samples were taken in Burgen 9 (Fig. 4) and one at Kapellet 1, directly from sample G14-26-OB (Fig. 7C). Freshly cut surfaces were powdered using a hand drill. Carbonate powders were processed at GeoZentrum Nordbayern by reacting with 100% phosphoric acid at 70°C using a Gasbench II connected to a ThermoFisher Delta V Plus mass spectrometer. All values are reported in per mil relative to V-PDB. Reproducibility and accuracy was monitored by replicate analysis of laboratory standards calibrated by assigning  $\delta^{13}\text{C}$  values of +1.95‰ to NBS19 and -47.3‰ to IAEA-CO9 and  $\delta^{18}\text{O}$  values of -2.20‰ to NBS19 and -23.2‰ to NBS18. Reproducibility for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  was  $\pm 0.02$  and  $\pm 0.03$ , respectively. Values are presented in Tab. S2 in Jarochovska et al. (2020b).

### 2.3. Fish data

Numerous samples with undescribed fish remains were found in Jeppsson's (1940-2015) Gotland collection housed at NRM. Three of these derive from Burgen outlier localities, namely Burgen 9 (G94-30 LJ and G94-31 LJ) and Närshamn 2 (G82-12LJ), and they are described here for the first time. Another sample (G14-26-OB) was collected at Kapellet 1 in

September 2014 and weighted 9.3 kilograms. The sample was dissolved at the Department of Geology, Lund University using techniques described by Jeppsson and Anehus (1995) and Jeppsson (2005). The residues were then separated using the heavy liquid separation technique described by Schiøler (1989). Scanning electron microscopy (SEM) of microremains coated in a gold-palladium alloy was performed at the Evolutionary Biology Centre, Uppsala University with a Zeiss Supra 35VP. Selected specimens are shown in Fig. 8.

## 2.4. Conodont data

Lennart Jeppsson's Gotland conodont collection housed at NRM has been catalogued using his original identifications (where provided) and revised taxonomic names proposed here. The sample position information is assembled from published articles, his handwritten notes hosted at NRM, and his unpublished locality catalogue. All this information has been deposited in the Paleobiology Database ([www.paleodb.org](http://www.paleodb.org)). Selected specimens were photographed using a Zeiss Axio Zoom V16 with an Axiocam 506 camera. Examples of relevant taxa are shown in Fig. 9. The figured specimens of both conodonts and fish remains are stored at the NRM (samples starting with Co and C) and PMU.

## 3. Results

### 3.1. Facies and depositional environments

#### 3.1.1. Burgen 7

The Burgen 7 locality is a face of a disused quarry exposing ca. 1.7 m of the Burgen Oolite Formation (Figs 3, 5). The base consists of a 0.4 m thick bed of grainstone with centimetre-scale undulating bedding. The grainstone consists of moderately sorted ooids and an admixture of oncoids (sample AY 2, Fig. 5E-F). The ooid nuclei are represented by a range of fossils, including crinoid ossicles, bryozoans, brachiopods, ostracods, fragments of tabulate corals and thelodont scales. Most ooids occur in initial stages, with only two-three layers present (Fig. 5F). The ooid grainstone is followed by 1.2 m of similarly bedded oncoidal rudstone (sample AY 7, Fig. 5B). The beds in the rudstone are between 4 and 8 cm thick and show trough (festoon) cross stratification. The beds in the topmost 15 cm of the rudstone are thinner (<4 cm) and contain single large components. A thin section taken from this topmost part revealed very poorly sorted initial oncoids (Fig. 5C) formed around crinoid ossicles, fragments of the tabulate coral *Coenites*, brachiopods, recrystallised mollusc shells, lithoclasts, or aggregations of calcareous microproblematica (Fig. 5D). Some ooid nuclei

appear to have undergone lithification, partial dissolution or mechanical destruction and filling with cement or intensive abrasion. The matrix is spotted, with areas formed by clotted peloidal micrite and areas filled with sparitic cement. The top of the outcrop is formed by grainstone transitioning to massive framestone. The thin section through the grainstone revealed bimodal sorting: the fine fraction consists of peloids and highly fragmented skeletal grains dominated by ostracod shells, the coarse fraction consists of complete, in some cases articulated, brachiopod shells and crinoid ossicles (sample AY 8, Fig. 5A).

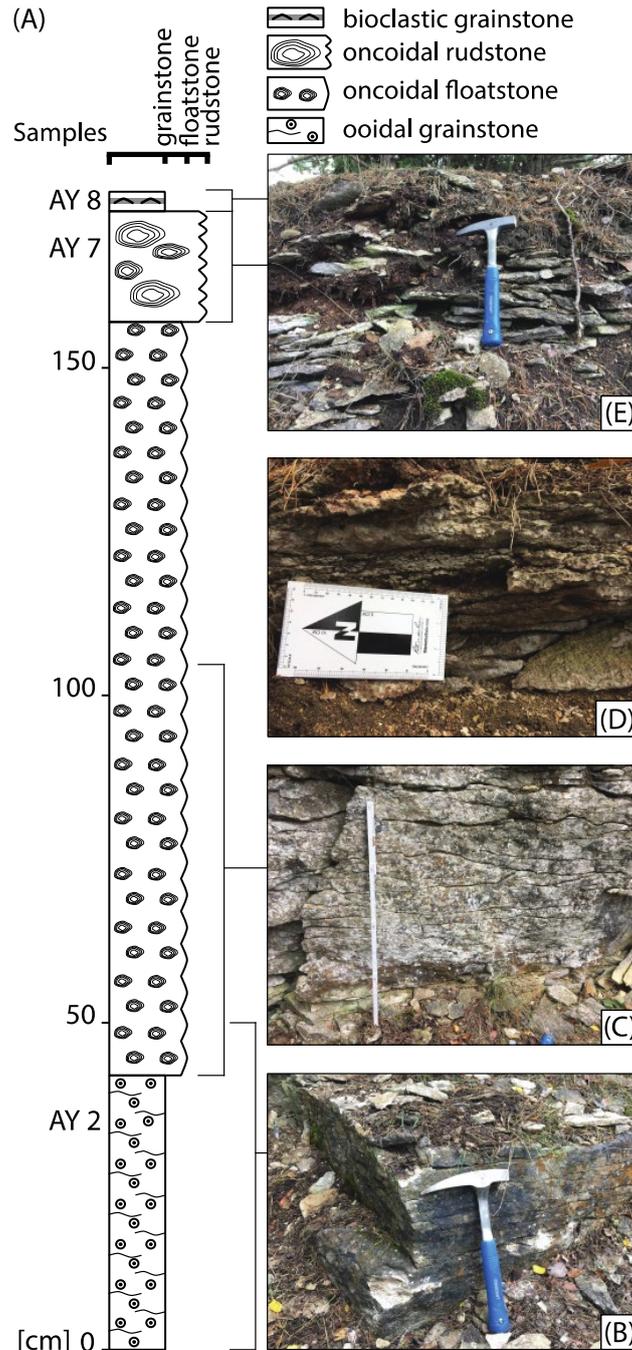


Figure 3. The Burgen 7 section across the Ludfordian Burgen Oolite Formation in the Burgen outlier in eastern Gotland. AY2, 7-8 refer to thin section samples (Fig. 5).

### 3.1.2. Burgen 9

This outcrop is a disused quarry, which has been extensively cleaned for the needs of this study (Fig. 4). The 23 m-long northern wall of the quarry has been logged along with the adjacent 6 m-long western corner. The strata show great lateral variability along this short distance. The floor consists of large, level bedding planes of well-sorted coarse crinoidal rudstone with decimetre-scale beds and low-angle cross stratification. The thickness from the lowest exposed level reaches up to 2 m, but the top of this unit is undulating. The transition from the coarse crinoidal rudstone to the more brittle and thinner bedded oolite, forming most of the quarry walls, is a layer of bioclastic-oidal grainstone-rudstone with bimodal sorting (sample AY 10, Fig. 6A). The larger size fraction in this transitional layer consists of crinoid ossicles, brachiopod and trilobite shells and initial oncoids, whereas the smaller fraction consists of ooids and ostracod shells. The proportion of microbial structures increases here and small patches of bindstones intercalate directly with the grainstone-rudstone beds (sample AY 11, Fig. 6B-C). The bindstone is formed by macroscopic patches of *Rothpletzella* with small stromatoporoids and spongiostromate oncoids (Fig. 6C). The intercalating fauna is poorly sorted and diverse, including crinoids, rhynchonellid and strophomenid brachiopods, ostracods, trilobites and rostroconchs (Fig. 6C). The overlying oolite is thin bedded, with normal grading in the eastern part of the quarry (sample AY 14, Fig. 6D-E) and small-scale trough (festoon) cross stratification in the central part. The ooids are radial and consist only of a few layers, with bioclasts in their cores recognizable as echinoderm ossicles, brachiopod and recrystallized shells or fragments of microbial structures. Centimetre-scale normal grading is formed by repeated influx of coarse crinoid ossicles and is enhanced by stylolites.

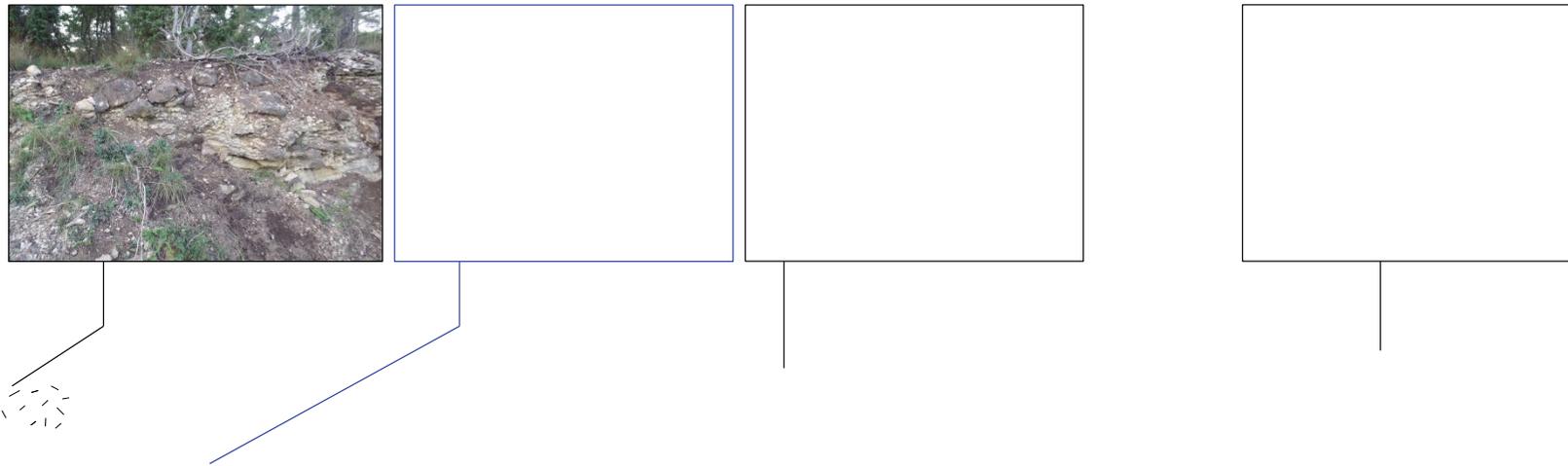


Figure 4. Lateral sketch of the Ludfordian Burgen Oolite Formation at Burgen 9 in the Burgen outlier in eastern Gotland. Red numbers along the vertical transect correspond to isotope samples in Fig. 10 and blue numbers correspond to thin section samples (Fig. 6). The section exposes lateral transition between metazoan reefs and oolites, overlying well-sorted crinoidal grainstones, which form the base of the former quarry (condition in 2017).

In the northern wall of the quarry, the crinoidal rudstone transitions laterally into metre-scale patch reefs (Fig. 4). The reefs have varying compositions, with bryozoans, stromatoporoids and rugose corals present in the westernmost part (only partly exposed) and a crinoid-microbial-bryozoan association exposed in the quarry corner (sample AY 17, Fig. 6F-I). The reefs have sharp margins and partly erosional boundaries (Fig. 6I). The cores are formed by crinoidal-microbial framestone-boundstone, with tabulate corals and serpulids intergrowing within crinoids and encrusting them. The frame-builders are coated with dense filamentous microbial carbonates formed by *Rothpletzella* and the matrix is mottled micritic with fenestral structures. The fabric surrounding the sharp margin of the patch reef is a poorly sorted bioclastic rudstone. The components are aligned with the edge of the reef, either by syndimentary processes or by compaction. The bioclasts include crinoids, diverse brachiopods, bryozoans and tabulate corals, trilobites, spongiostromate oncoids, recrystallized shells with initial porostromate oncoids forming on their surfaces, solenoporaceans, rostroconchs (Fig. 6G) and scattered microbial structures including *Ortonella* (Fig. 6H) and *Rothpletzella*. The matrix consists of nearly equal proportions of micrite and sparite.

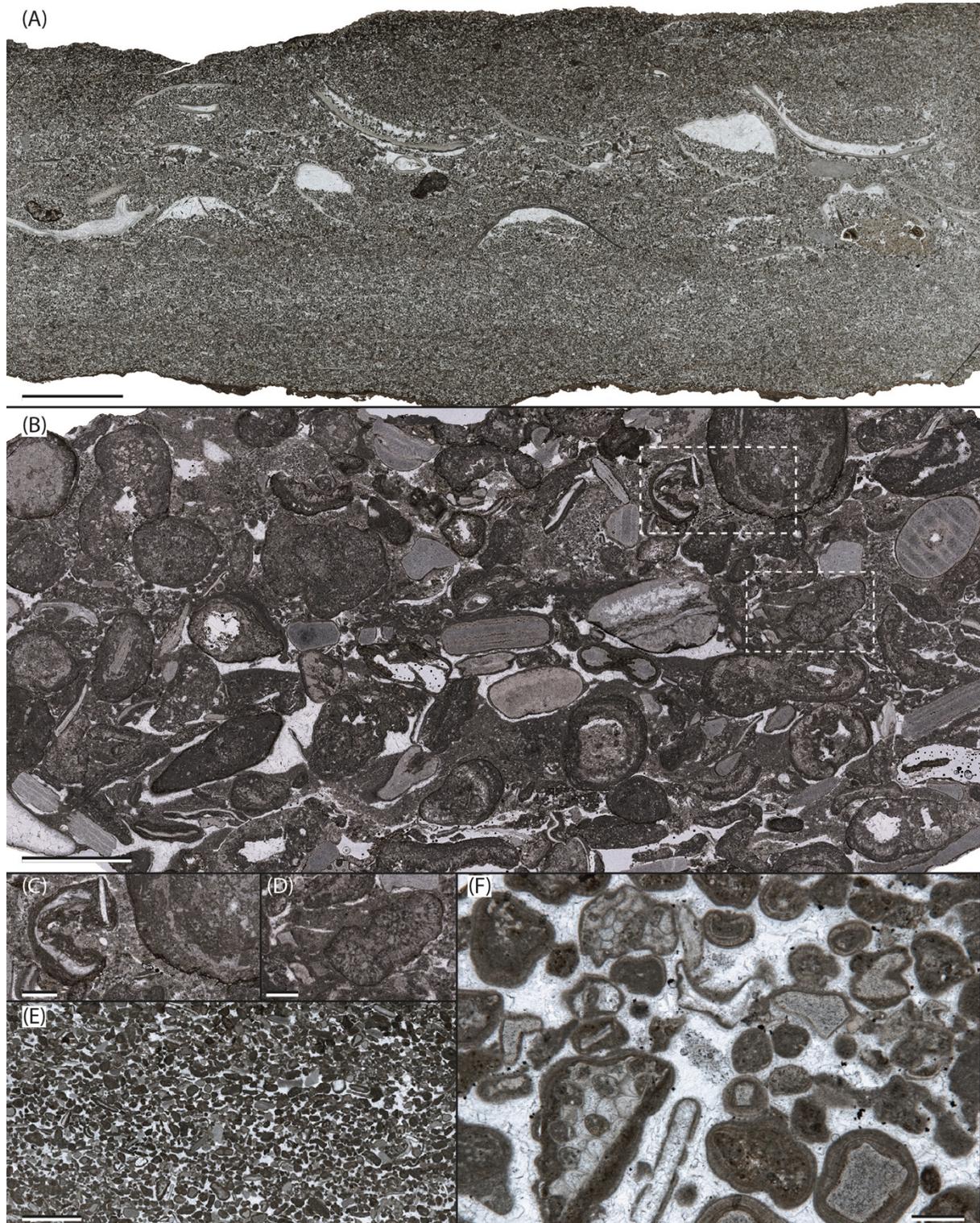


Figure 5. Microfacies at the Burgen 7 section. A. Sample AY 8: peloidal grainstone with a brachiopod shell layer. Scale bar 500  $\mu\text{m}$ . B-D. Sample AY 7: oncoidal rudstone. Scale bar 500  $\mu\text{m}$ . B. Scale bar 500  $\mu\text{m}$ . C-D. Scale bar 100  $\mu\text{m}$ . E-F. Sample AY 2: ooidal grainstone. E. Scale bar 500  $\mu\text{m}$ . F. Scale bar 100  $\mu\text{m}$ .

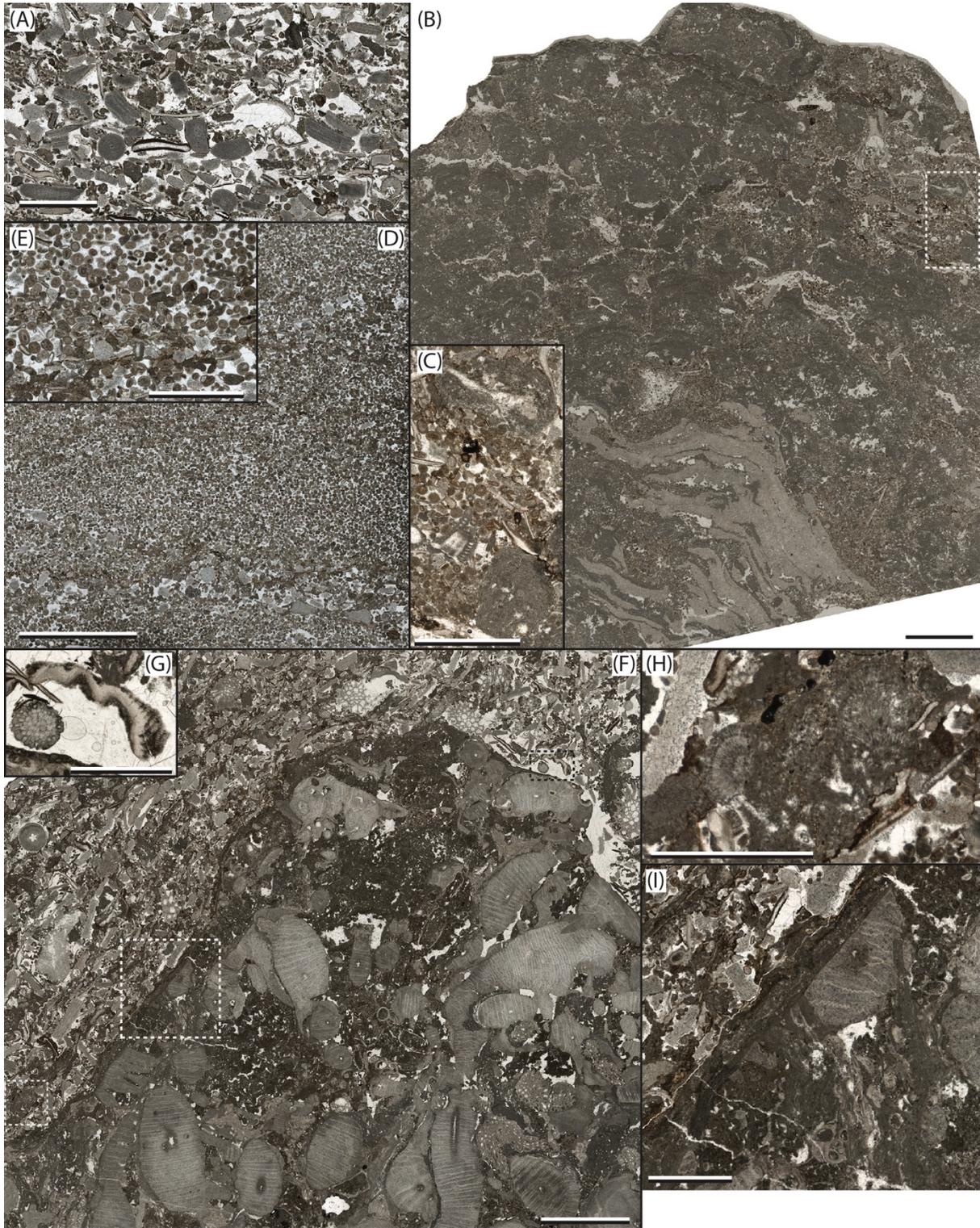


Figure 6. Microfacies at the Burgen 9 section. A. Sample AY 10: bioclastic rudstone with bimodal sorting. Scale bar 250  $\mu\text{m}$ . B-C. Sample AY 11: microbial bindstone intercalating with bioclastic-oidal grainstone. Scale bar 500  $\mu\text{m}$ . C. Close up of sample AY 11 showing a spongiostromate oncoid, a rostroconch fragment and a Rothpletzella colony. Scale bar 250  $\mu\text{m}$ . D-E. Sample AY 14: ooidal grainstone with normal grading. Scale bar 500  $\mu\text{m}$ . E. Detail of sample AY 14: fitted fabric partly dissolving echinoderm ossicles, ooids and fragments of microbial structures. Scale bar 250  $\mu\text{m}$ . F-I. Sample AY 17: contact between crinoidal-microbial boundstone and bioclastic rudstone. Scale bar 500  $\mu\text{m}$ . G. Probable rostroconch. Scale bar 250  $\mu\text{m}$ . H. Problematica resembling Ortonella. Scale bar 250  $\mu\text{m}$ . I. Erosional contact truncating crinoid roots intertwined with microbial structures. The contact surface is overgrown by another generation of microbial colonies dominated by Rothpletzella. Scale bar 250  $\mu\text{m}$ .

### 3.1.3. Kapellet 1

This is a coastal outcrop consisting of a strip of bedding planes gently dipping towards the West (Fig. 7A). It was placed in the 'Burgsvik Formation' based on conodont fauna, which was assigned by Jeppsson et al. (2006) to the lowermost part of the *Oz. snajdri* Biozone ("*Oz. scanica* without *Oz. (Wurmiella) excavata*"). Within the small Kapellet 1 outcrop a full transition from a slightly calcareous sandy siltstone to a bioclastic-oncoidal rudstone is exposed (Fig. 7B-C). The rudstone consists of very coarse, partly still articulated crinoid stems, large disarticulated trilobite, brachiopod and recrystallized bivalve shells, as well as colonies of bryozoans and tabulate and rugose corals, which are *ex situ* but not fragmented. Most grains are initial-stage oncoids, with spongiostromate fabrics dominating. The matrix consists of similar proportions of sparite forming fenestral structures and clotted, peloidal micrite (Fig. 7C). Below this layer, large (2-3 cm) mature spongiostromate oncoids are the dominant components, with a bioclastic packstone-rudstone as a matrix. The sandy, calcareous siltstone is thin-bedded and intercalates between the components of the rudstone. Scattered bioclasts can be found on its bedding planes. At the scale of the outcrop, the siltstone appears to be overlying the rudstone or filling shallow troughs in its uneven surface, but outcrop size and conditions did not allow establishing larger-scale relationships between these two units.



Figure 7. The Burgen Oolite Formation at the Kapellet 1 section. A. Outcrop overview in 2017. B. Intercalation of carbonate-rich sandy siltstone with crinoidal-rudstone corresponding to the boundary between the Burgsvik Sandstone and Burgen Oolite formations. C. Microfacies slide (PMU 23104) showing oncoids forming around partly articulated crinoids, bryozoans, trilobites, and brachiopods in a micritic matrix with fenestral structures.

### 3.2. Dermal vertebrate remains of the Burgen Oolite Formation in the Burgen outlier

The sample from the Närshamn 2 locality (G82-12LJ) contains 28 *P. ludlowiensis* scales of several different morphologies, many of which preserve parts of the extremely fine lateral extensions (Fig. 8A) and some, as in Figure 8B, display fin scale morphologies (compare Miller & Märss, 1999: pl. 2, fig. 25). There are also eight thelodont scales of unclear affinity that have three-pointed crowns and small anterior spurs (Fig. 8C). One additional scale has a *Th. traquairi*-like morphology (Fig. 8D), but is quite large and laterally compressed with an oval, low base that hosts a relatively large pulp opening. The crown is vertically steep and high, and it has a number of ridges that converge and end in a single central point. This probably represents a special scale in the squamation of a thelodont, potentially *Th.*

*parvidens*. Peculiarly, there are no other scales of *Th. parvidens* in this sample, which is odd because this taxon is found in both older and younger strata on Gotland (and all other samples presented here), and occurs in a wide range of depositional environments (see Kaljo et al., 2015). A single *Thelodus trilobatus* Hoppe, 1931 scale (Fig. 8E) has been identified in the sample and only one acanthodian scale was found, but it was too poorly preserved for identification.

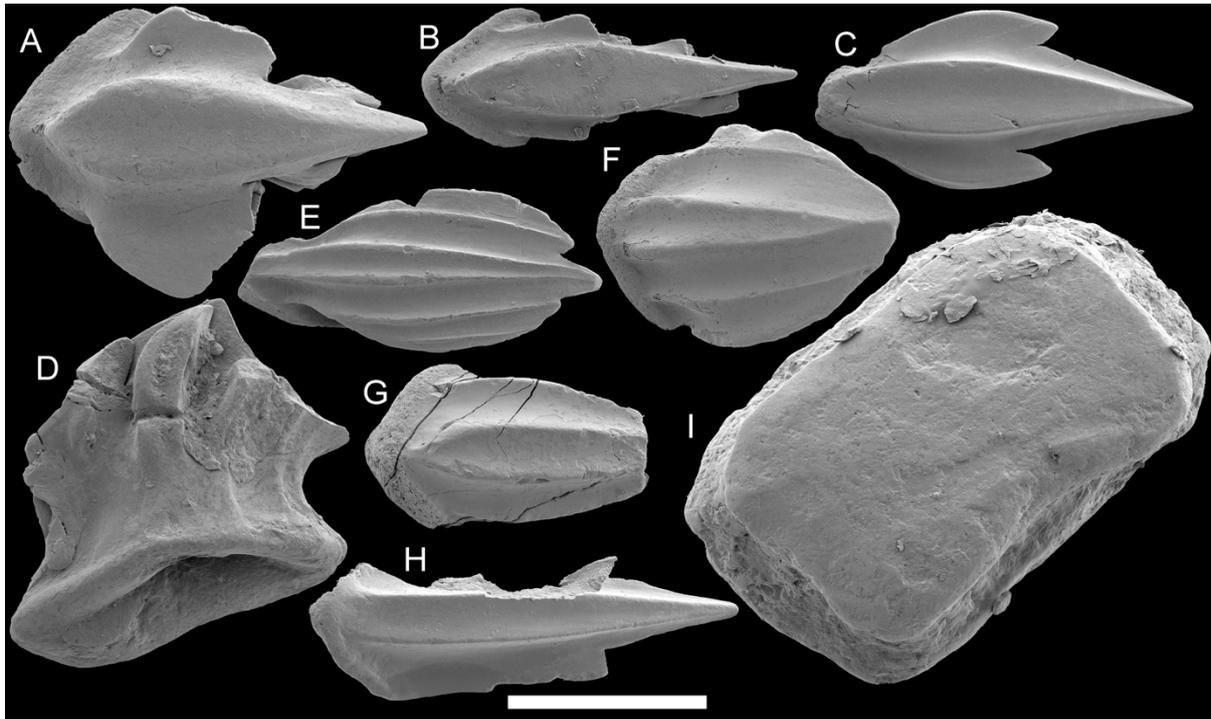


Figure 8. *Thelodont* and *acanthodian* scales from Burgen outlier. *Paralogania ludlowiensis* (A-B, NRM-PZ C6011-6012), three-pointed thelodont scale (C, NRM-PZ C6013), traquiriform scale (D, NRM-PZ C6014), and *Thelodus trilobatus* (E, NRM-PZ C6015) from Närshamn 2 (G82-12LJ). *Loganellia cuneata* (F-G, NRM-PZ C6009-6010) from Burgen 9 (G94-30LJ). Three-pointed thelodont scale (H, PMU 24034) and *Gomphonchus* sp. (I, PMU 24035) from Kapellet 1 (G14-26OB). Scale bar represents 200  $\mu$ m.

The two samples G94-30 LJ and G94-31 LJ from the Burgen 9 locality from L. Jeppsson's collection contain 20 scales of typical *Th. parvidens* morphologies similar to those presented by Eriksson et al. (2009: fig. 4D), 25 *P. ludlowiensis* scales, five scales with affinities to *N. striata*, and a couple of acanthodian tesseræ collectively. G94-30 LJ also contains two leaf-like scales (Fig. 8F) resembling the transitional? scales presented for *Log. cuneata* in Märss and Miller (2004: fig. 6c), as well as a few typical *Log. cuneata* trunk scales (Fig. 8G). The faunas in these samples are similar to those described by Nilsson (2005) from Burgen 9, but lack the poracanthodid scales (described as *Por. porosus*), and in addition have climatiid scales and scales identified as *Log. cuneata*.

The new sample from the Kapellet 1 locality (G14-26OB) only produced a few remains and the fauna is similar to that presented in Fredholm (1989) from the same locality.

The sample contains five *Th. parvidens* trunk scales and two three-pointed thelodont scales with a small anterior spur on the base (Fig 8H) similar to those found in the G82-12LJ sample described above. The sample also contained three small scales of *N. striata* and three *G. sandelensis* scales. Another scale has a rhomboidal outline, flat crown and deep base (Fig 8I) and is interpreted as a special 'gomphonchid' scale and referred to *Gomphonchus* sp.

### 3.3. Conodonts of the Burgen Oolite Formation in the Burgen outlier

Jeppsson's unpublished catalogue of localities on Gotland lists over seventy localities and three drillcores where the 'Burgsvik Formation' is accessible. However, only a fraction of these localities expose the Burgen Oolite Formation and a subset of those is represented in the conodont collection (Table 1, Fig. 9). The conodont fauna from the Burgen Oolite Formation in the Burgen outlier is more diverse than that reported from the Sudret peninsula. Young, not fully developed ozarkodinins in samples from 1994 (G94-29 LJ from Burgen 7 and G94-30 LJ from Burgen 9) were assigned by Jeppsson to '*Oz. remscheidensis*' Ziegler, 1960, as indicated by labels on the microslides. Later articles by Jeppsson did not mention this taxon in this area, reporting the presence of *Oz. scanica* instead (Jeppsson, 2005; Jeppsson et al., 2006). These specimens are here revised as '*Oz.*' *eosteinhornensis* '*scanica*', but a thorough revision of the morphological variability across ontogeny would be warranted to support this revision (see Discussion). Sample G83-21LJ from Burgen 7 was reported by Jeppsson (2005) to contain *Aldridgeodus minimus*? Jeppsson in Calner et al. (2008), a species otherwise known from strata no younger than the *Polygnathoides siluricus* Biozone (on Gotland corresponding to the uppermost Hemse Group), and *Panderodus serratus* Rexroad, 1968, which occurs in the Eke and Hamra formations, but has otherwise not been known from the Burgsvik Sandstone or the Burgen Oolite formations. Resampling of the same level did not confirm the presence of these taxa, therefore Jeppsson (2005) suggested treating these findings as erroneous. *Panderodus greenlandensis* Armstrong, 1990 was found in a single sample G94-32 LJ from Burgen 9, at the stratigraphically youngest position ever reported. A specimen from Glasskär 2 (G72-19LJ) labeled by Jeppsson as *Ozarkodina wimani* (Jeppsson, 1974) is herein identified as *Zieglerodina inordinata* (Viira, 2000) based on the wide gaps between the cusp and adjacent denticles (Fig. 8L). This species was described from the Pridolí of Estonia and Latvia by Viira (2000) as *Oz. inordinata*, but the generic assignment has been queried by Murphy et al. (2004). Subsequent works placed the species in *Zieglerodina* based on the morphology of the P<sub>1</sub> element and the similarity to *Z. ivochlupaci* (Peavey, 2013; Spiridonov et al., 2020b).

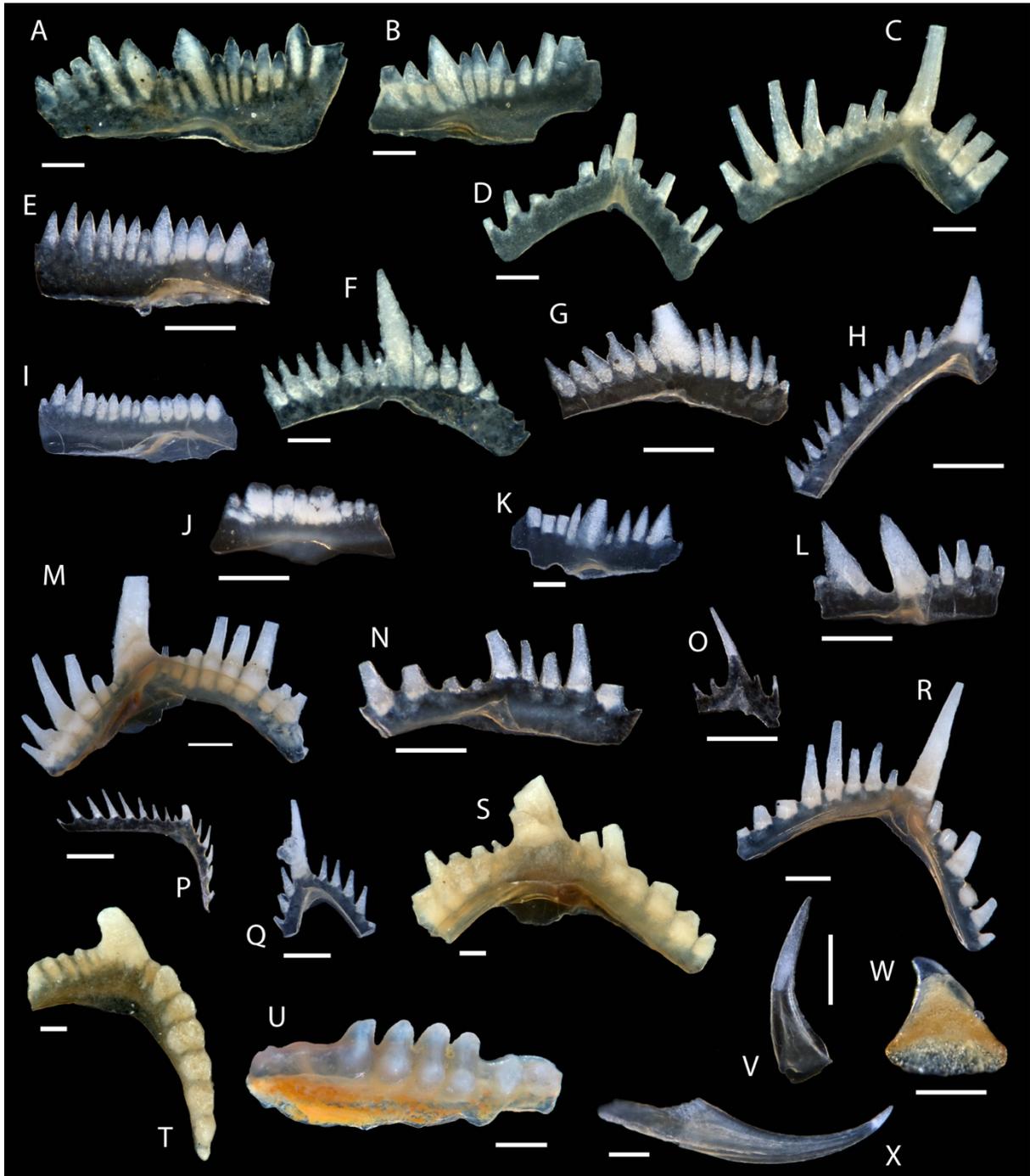


Figure 9. Conodonts from the Burgen Oolite Formation in the Burgen outlier and Närsholmen peninsula. L. Jeppsson's collection and newly collected from Kapellet 1. *Ozarkodina confluens* Branson and Mehl, 1933 from Kapellet 1 (A-B, PMU 23109-23110, C, Co210, D, PMU 23107). 'Oz.' *eosteinhornensis scanica* (Oz. *scanica* in the original identification) Jeppsson, 1974 from Närshamn 1 (G83-11LJ; E, Co66, H, Co67) and Närshamn 2 (G83-12LJ; G, Co69). 'Oz.' *eosteinhornensis?* (F, PMU 23108) from Kapellet 1 (G14-26OB). *Ozarkodina snajdri* Walliser, 1964 from Närshamn 2 (I, Co68, G83-12LJ) and Glasskär 2 (J, Co63, G72-19LJ). *Oz. wimani* Jeppsson, 1974 from Glasskär 2 (G72-19LJ; K, Co64). *Zieglerodina inordinata* (Viira, 2000) from Glasskär 2 (G72-19LJ, L, Co65). *Ou. novoexcavatus* Jeppsson, 1972 (M, Co0000075, N, Co76, O, Co74, P, Co77, Q, Co73) from Närshamn 1 (G83-11LJ) and from Närshamn 2 (R, Co71, G83-12LJ). *Ou. excavatus* Branson and Mehl, 1933 from Kapellet 1 (S-T, PMU 23105-23106). *Icriodus* sp. (U, Co174) from Burgen 9 (G94-31LJ). *Decoriconus fragilis* Branson and Mehl, 1933 (V, Co78) from Närshamn 1 (G83-11LJ). *Pseudooneotodus beckmanni* Bischoff and Sannemann, 1958 (W, Co79) from Närshamn 1 (G83-11LJ). *Panderodus equicostatus* Rhodes, 1953 (X, Co72) from Närshamn 2 (G83-12LJ). All scale bars equal 100  $\mu$ m.

Table 1 also lists conodonts identified at Glasskär, Kroken and Närshamn, most of them were probably collected in the Burgen Oolite Formation. '*Oz.*' *eosteinhornensis* was represented by both forms referred to by L. Jeppsson as '*scanica*' (Fig. 9E, H, G) and '*non scanica*'.

The Kapellet 1 locality, recorded in the collection under the name Kapelludden 1, has been included by L. Jeppsson in the 'Burgsvik Formation' based on the presence of *Oz. wimani* (Table 1), although the exposed strata differ from the typical lithology and the conodonts he collected there were not diagnostic. The newly collected sample from Kapellet 1 (G14-26-OB) contained a possible P<sub>2</sub> element of '*Oz.*' *eosteinhornensis* (Fig. 9F).

### 3.4. Isotope chemostratigraphy

Carbon isotope values at Burgen show steady values ranging between +8.8‰ and +9.2‰ <sup>13</sup>C<sub>carb</sub> in spite of lithological variations (Fig. 10). The oxygen isotopes range between -5.9‰ and -7.1‰ δ<sup>18</sup>O<sub>carb</sub>, which does not indicate any extreme diagenetic alteration. The lithological sample from Kapellet 1 shows isotope values of +7.5‰ δ<sup>13</sup>C<sub>carb</sub> and -6.9‰ δ<sup>18</sup>O<sub>carb</sub>. The relationship between δ<sup>13</sup>C and δ<sup>18</sup>O was weak (R<sup>2</sup> = 0.27) but significantly different from no relationship (p = 0.0049, n = 25), suggesting a possible diagenetic overprint (Fig. S1 in Jarochowska et al., 2020b).

## 4. Discussion

### 4.1. Interpretation of depositional environment

The Burgen 7 and 9 outcrops record a transition from a very high-energy, fully marine shoal setting represented by the well-sorted coarse crinoidal rudstone, exposed in the quarry floor at Burgen 9, to a more patchy, topographically complex environment with intercalation of patch reefs, ooid shoals and oncolites. Oncolites have been associated with restricted conditions, e.g. in the Eke Formation, but high faunal diversity indicates fully marine conditions and oolitic shoals and metazoan reefs point to an environment above the wave base. The interval exposed at Burgen 7 likely corresponds to the facies exposed in the eastern part of the quarry, where the isotope transect had been sampled (Fig. 4). In both outcrops, oncoids differ from the 'cauliflower' type known from the Eke Formation (Eriksson & Calner, 2008) and corresponding to type C oncoids of Ratcliffe (1988). Such ooids are commonly interpreted to have grown *in situ* and are found in low-energy settings with restricted fauna, where their development is attributed to reduced grazing by herbivores

(Calner, 2005). This is clearly not the case here, as oncoids co-occur with gastropods and a diverse fauna. They also represent type A of Ratcliffe (1988), typical of high-energy settings, and bear traces of transport and abrasion.

## 4.2. Conodont biostratigraphy and diversity

Minimum conodont species richness in the Burgen outlier was estimated at 21 (with four species in open nomenclature and one uncertain identification, Tab. 1). The generic richness reaches 11, although the position of species assigned to *Ozarkodina* is debated (see 4.6 and 4.7). The high diversity in the outlier might reflect high spatial diversity and patchiness of the back-shoal settings compared with the high-energy open shoal environment of the oolite in the Sudret peninsula (Jarochovska et al., 2017).

The Burgsvik Sandstone and Burgen Oolite formations have been placed in the *Oz. snajdri* Interval Biozone (Jeppsson et al., 2006). In its original definition by Walliser (1964), the lower limit of this biozone is defined by the Last Appearance Datum (LAD) of *Pedavis latialata*, a species not reported from Gotland and rejected by Jeppsson (2005) as a useful index taxon. A broader definition of the *Oz. snajdri* Biozone uses the LAD of *Po. siluricus* (Aldridge & Schönlaub, 1989; Corradini & Serpagli, 1999). Elsewhere a broader definition of the *Oz. snajdri* Biozone has been adopted (Corradini et al., 2015). The *latialata* Biozone was proposed by Jeppsson (2005) to be defined on Gotland by the 'extinction' of *Polygnathoides* and *Kockelella* and the appearance of more than one species of *Icriodus* spp. This biozone is termed 'icriodontid' and is, according to Jeppsson et al. (2006), represented on Gotland by the Eke Formation, but the zonal genus *Icriodus* has been found in only three samples in the entire collection of L. Jeppsson stored at NRM. It is also more widespread in the uppermost Silurian and Lower Devonian (not represented on Gotland), and is therefore a poor choice for an index taxon for the Ludfordian Stage.

The *Oz. snajdri* Biozone has been redefined on Gotland by Jeppsson (2005) as the interval with high abundance of *Oz. snajdri*, which he related to the 'extinction' of several other species. *Ozarkodina snajdri* is common in samples from the Burgen outlier, but it is absent in the Burgen Oolite Formation in the Sudret Peninsula and at Uddvide (Table 1). It is therefore difficult to establish the base of this biozone on Gotland, as the Eke Formation is overall extremely poor in conodonts and effectively lacks distinctive taxa. Moreover, *Oz. snajdri* morphologies are found as early as in the *Oz. bohémica* Biozone on Gotland (Jeppsson, 1983, 2005).

The upper limit of the *Oz. snajdri* Interval Biozone is defined by the first occurrence of *Oz. crispa*. However, *Oz. crispa* has also been found in sample G72-17CB from Glasskär 1 (probably Burgen Oolite Formation). This species is also known from earlier occurrences in the Baltic area (Viira & Aldridge, 1998; Bremer et al., 2020), although Märss and Männik (2013) suggested that these may represent specific morphologies of *Oz. snajdri* and considered them *Oz. snajdri sensu lato*. Jeppsson et al. (2006) assigned only the Sundre Formation to the *Oz. crispa* Biozone, although the taxon has been identified by L. Jeppsson in samples from the Hamra Formation (Bremer et al., 2020). The Hamra Formation was placed by Jeppsson et al. (2006) in the *Oz. snajdri* Interval Biozone, which was then subdivided based on the occurrences of '*Oz. scanica*' and '*Oz. remscheidensis*'. Both these taxa underwent multiple revisions of their taxonomic ranks and diagnoses, resulting in their distribution being difficult to reconstruct from previous reports, unless exhaustive descriptions are provided (see chapter 4.6 below). In any case, the presence of '*Oz.*' *eosteinhornensis* '*scanica*', *Oz. crispa* and *Oz. snajdri* at Glasskär 1, and of '*Oz.*' *eosteinhornensis* '*scanica*' and *Oz. snajdri* at both Burgen 7 and 9 are the basis for assigning the Burgen Oolite Formation in the Burgen outlier to the *Oz. snajdri* Biozone *sensu* Jeppsson et al. (2006) and exclude an older age, which will be further discussed in 4.5. The diagnostic taxa could not be identified at Kapellet 1, except for a P<sub>2</sub> element of '*Oz.*' *eosteinhornensis* '*non scanica*'.

The finding of *Zi. inordinata* at Glasskär 2 extends downwards the range based on rare reports from the Pridolí of Estonia and Latvia by Viira (2000), of Lithuania by Spiridonov et al. (2020) and of Oklahoma by Peavey (2013). However, as noted by Spiridonov et al. (2020b), the scarcity of reports might reflect a strong affinity of this taxon to very shallow water environments, which saw a diversification in the late Silurian (Einasto & Viira, 2003; Jarochowska et al., 2017). Accordingly, it has not been found in samples from the more open-marine facies of the Burgen Oolite Formation in the Sudret peninsula.

### 4.3. Vertebrate biostratigraphy and diversity

*Thelodus parvidens* and its possible scale-variant *Th. trilobatus* have long stratigraphic ranges and occur in a wide range of lithologies (Kaljo et al., 2015). *Paralogania ludlowiensis* has also been suggested as having a fairly long temporal range, but has been shown to mainly occur in high-energy, shallow-marine environments often with a clastic input (Kaljo et al., 2015; Bremer et al., 2018; 2020). However, the previous reports of *Th. sculptilis* (Fredholm, 1989) and poracanthodid acanthodians (Fredholm, 1989; Eriksson et al., 2009) from Burgen outlier indicate a late-, rather than mid-Ludlow age of these samples (see Märss and Männik, 2013).

Indeed, these taxa are more readily found in younger strata on Gotland (Bremer et al., 2020). Furthermore, the samples from Burgen outlier lack the thelodonts *Thelodus carinatus* Pander, 1856 and *Phlebolepis elegans* Pander, 1856 that are typical for faunas found in older strata on Gotland (e.g., Fredholm, 1989; Eriksson et al. 2009). In fact, the latter is an index taxon for the *Phlebolepis elegans* Vertebrate Zone Märss, 1982 and has a partial range into the mid-Ludlow *Andreolepis hedei* VZ Märss, 1982 (Märss & Männik, 2013).

The whereabouts of Doris Fredholm's samples are at the time of writing unknown, so a review of her material has not been possible. For this reason, it remains unclear how the previous revision of all reports of *Log. cuneata* in the Burgen outlier to *Paralogania? sp.* by Nilsson (2005) compares to the findings of typical *Log. cuneata* scales in the samples presented here, especially because Nilsson (2005) included forms both with and without lateral thornlets in her preliminary designation.

Eriksson et al. (2009) described a step-wise disappearance of vertebrate taxa during the Lau Event, starting at the top of the När Formation (Hemse Group) and continuing throughout the Eke Formation on Gotland. They recorded a shift from an acanthodian-dominated fauna before the event to a thelodont-dominated fauna in the Burgen Oolite Formation during the initial recovery, which was also noted by Fredholm (1989). The fishes display a post-Lau Event recovery after their overall scarcity in the preceding Eke Formation (Fredholm, 1988a, b; Eriksson et al., 2009; Bremer & Blom, 2015) with the return or first appearance of several taxa (Märss, 1992, 2001; Eriksson et al., 2009). The samples investigated here similarly show a relatively diverse fauna with a higher abundance of thelodont scales compared to acanthodian remains, but the sampling size is too small to discuss any further implications.

#### **4.4. Comparison with palynozones**

The Silurian was a significant interval for land plant evolution, a period under which the plants became well-established on most continents, markedly increasing in abundance, and with new and more derived forms appearing (Gray et al., 1974; Richardson & McGregor, 1986; Wellman et al., 2013; Mehlqvist et al., 2015). This is clearly reflected in the spore assemblages with more ornamented spores appearing in the upper Silurian sedimentary record (Richardson & McGregor, 1986; Mehlqvist et al., 2015). Combining terrestrial palynology with marine micropalaeontological data provides information on stratigraphy and paleoenvironments, such as distance from shore and level of anoxia (Mehlqvist et al., 2012, 2014b; Badawy et al., 2014).

The knowledge on the terrestrialization of Baltica is scarce and patchy, with the oldest known records of embryophyte (land plant) spores from the *Eoplacognathus lindstroemi* conodont subzone of the Furudal Limestone (mid-Ordovician: Darriwillian) of central Sweden (Rubinstein & Vajda, 2019). Definite trilete spores, produced by tracheophytes, occur in the Sandbian Dalby Limestone within the *Baltonidus gerdae* conodont sub-zone (Rubinstein & Vajda, 2019). Non-marine palynological data from Gotland is sparse and results have so far only been published from the nearshore deltaic successions of the Burgsvik Formation, southern Gotland (Gray et al. 1974, Sherwood-Pike & Gray 1985, Hagström, 1997; Hagström & Mehlqvist, 2012). The palynomorph assemblages of the Burgsvik Formation are typified by cryptospores, such as *Laveolancis* spp. *Tetraedraletes medinensis* and *Acontotetras gotlandica*, together with granulate trilete spores, such as *Apiculiretusispora burgsvikensis* and the tetrad *Pachytetras rugosa* (Hagström 1997; VV. unpublished data).

The record of upper Silurian palynological successions is better known from Skåne, mainly through the detailed studies of Mehlqvist et al. (2012, 2014a, 2014b, 2015). The Burgsvik Sandstone and Burgen Oolite are coeval with the successions belonging to the Klinta Formation in Skåne. The *Oz. snajdri* Biozone and the succeeding *Oz. crispa* Biozone correspond to the *Synerisporites inframurinata* (spore) sub-zone by Burgess & Richardson (1995). This spore zone is typified by an early land plant flora of both cryptospores-producing liverworts and trilete spore-producing tracheophytes (e.g. *Cooksonia*), both in Skåne and on southern Gotland, Burgsvik Sandstone. Within this zone, the spore assemblages are dominated by the long-ranging cryptospores attributable to *Dyadospora* and *Laevolancis*, together with trilete spores of *Ambitisporites*. Stratigraphically significant spore taxa in the *Oz. snajdri* interval in both Skåne and on southern Gotland, include *Synorisporites* cf. *libycus*, *Hispanaediscus verrucatus* and *H. major*, all typical of a Ludlow age. No palynological analyses have yet been carried out on the strata exposed in the Burgen outlier but there is no reason to suspect that the palynological successions differ from those of the succession at Burgsvik.

#### 4.5. Integration of bio- and chemostratigraphy

Very high  $\delta^{13}\text{C}_{\text{carb}}$  values and the abundance of oncoids at Burgen 9 and Kapellet 1 are suggestive of a stratigraphic position similar to the Upper Eke Formation (Fig. 10, arrow B), as this interval has been previously assumed to record the highest  $\delta^{13}\text{C}_{\text{carb}}$  values of the LCIE in Gotland (Samtleben et al., 2000; Eriksson & Calner, 2008). But, as noted in the

introduction, chemostratigraphic correlation across the LCIE is complicated by diachronous development of  $\delta^{13}\text{C}_{\text{carb}}$  trends across the onshore-offshore gradient, as observed also for other isotope excursions (LaPorte et al., 2009; Jarochovska & Munnecke, 2015; Danise et al., 2020; Ray et al., 2020). Considering how rapidly the excursion developed globally (Melchin et al., 2020; Sproson, 2020), it is possible that the  $\delta^{13}\text{C}_{\text{carb}}$  of dissolved inorganic carbon in the seawater changed at a higher pace than the lateral migration of facies and the associated migration of conodont taxa attached to specific environments (Jarochovska et al., 2017). Therefore an integration of new sedimentological evidence, chemo- and biostratigraphy is presented here, pointing to the correlation of the described strata in the Burgen outlier with the Burgen Oolite Formation and the locally occurring second peak of the LCIE (Fig. 10, arrow A):

1. Previous  $\delta^{13}\text{C}_{\text{carb}}$  data indicated  $\delta^{13}\text{C}_{\text{carb}}$  values in the Burgen Oolite Formation reaching around +7‰ (Samtleben et al., 2000; Eriksson & Calner, 2008), although additional samples listed by Samtleben et al. (2000) show values up to 8.7‰ at Närshamn 4, i.e. comparable with those obtained here at Burgen 9.
2. The occurrences of '*Oz.* *eosteinhornensis* *scanica*' and *Oz. snajdri* at Burgen 7, 9 and at Glasskkär 1 exclude the possibility that the strata correlate with the Upper Eke Formation, although they are very similar in terms of facies and  $\delta^{13}\text{C}_{\text{carb}}$  values. The younger age is supported by the co-occurrence of '*Oz.* *eosteinhornensis* *scanica*' in the lowering limb of the LCIE in the eastern part of the Baltic Basin (Spiridonov et al., 2017, 2020a).
3. Carbon isotope values correspond to either the Burgen Oolite Formation in the Uddvide-1 core (Fig. 10, arrow A) at the base of the lowering limb of the LCIE or to the rising limb in the Eke Formation in the Burgen core (the interval between -10 and -12 m; Calner & Eriksson, 2006; Eriksson & Calner, 2008) and the Uddvide-1 core (around -35 m; Younes et al., 2017, Fig. 10, arrow B). Based on conodont fauna (see chapter 4.2 above), variant A (younger) is here held as better supported.
4. The similarity suggested by the presence of oncoids is misleading, as the base of the Burgen Oolite Formation at Kapellet 1 represents a different depositional environment than the Upper Eke Formation throughout Gotland. The oncoids are formed in a fully-marine high-energy environment with diverse fauna, in the proximity of reefs. A similar facies is present in the base of the member in the Uddvide 1 core (Younes, 2012, Fig. 8E).

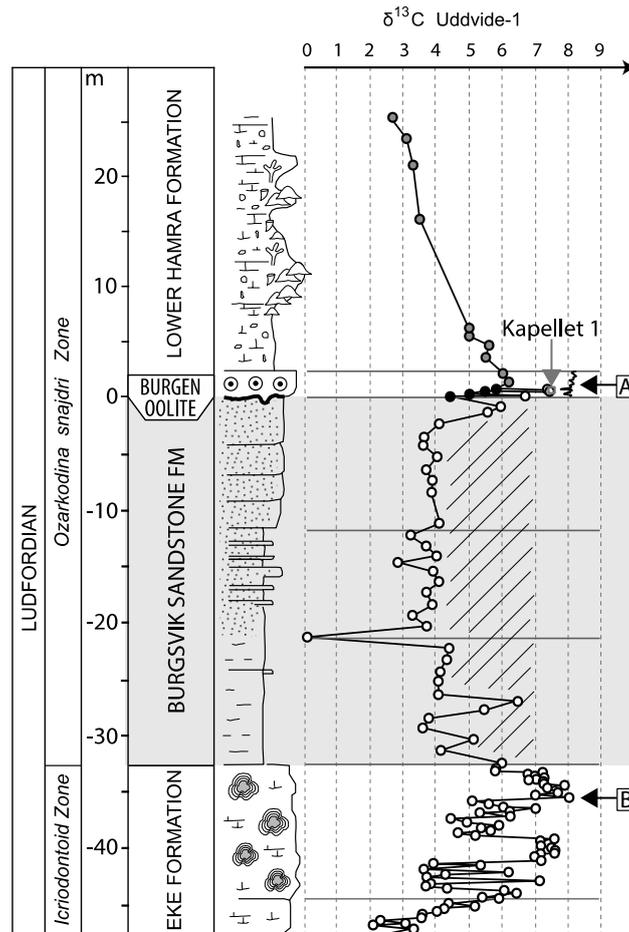


Figure 10. Correlation of Burgen 9 and Kapellet 1 sections with facies and  $\delta^{13}\text{C}$  stratigraphy in the composite profile from Younes et al. (2017), which was compiled from Uddvide-1 core (white dots), Husryggen 4 (black dots) and Hoburgen (grey dots). The arrow marked A indicates the proposed correlation of the Burgen 9 section, with B being the alternative discussed in the text. The gray square is the proposed correlation of the Kapellet 1 section (based on isotope values from sample PMU 23104, Fig. 7C).

The depositional environment of the Burgen Oolite Formation in the Burgen outlier was slightly more protected and heterogeneous than the well-sorted oolitic shoal exposed in the Sudret peninsula. This might explain a higher diversity of conodonts in this area. It is also in line with the observed spatial gradient of  $\delta^{13}\text{C}_{\text{carb}}$  values, which are often highest in platform-top settings. Nonetheless, faunal diversity and proliferation of reefs are not compatible with the interpretation of microbial carbonates forming reefs and contributing to reef formation as ‘disaster forms’. Similar observations have been made by Vennin et al. (2015) in the Lower Triassic, which is commonly interpreted as dominated by ‘anachronistic’ microbial carbonates owing to reduced grazing, but can also be important contributors to a ‘healthy’ carbonate factory. Reefs described in Burgen 9 form small structures in outcrops, but seismic profiles east of Gotland indicate that much larger barrier reefs developed at that time (Bjerkéus & Eriksson, 2001), suggesting that already at this time a diverse reef-building

fauna recolonized the carbonate platform, leading up to the proliferation of reefs in the overlying Hamra Formation.

#### 4.6. '*Oz. scanica*' and the *steinhornensis-remscheidensis* conundrum

'*Oz. scanica*' was originally introduced by Jeppsson (1974) as '*Oz. steinhornensis scanica*'. The original species *Spathognathodus steinhornensis* Ziegler, 1956 and *Sp. remscheidensis* Ziegler, 1960 are form taxa based on P<sub>1</sub> elements. The latter form species has subsequently been placed in the rank of subspecies of the former by Walliser (1964), who considered both of them to form a succession of subspecies, which he arbitrarily separated based on their occurrence before and after the first appearance of *Icriodus woschmidti*. Walliser (1964) also postulated that distinguishing the two forms required large collections and was often impossible for individual specimens. Klapper and Murphy (1974) assigned both subspecies to the multielement genus *Ozarkodina* but excluded the *steinhornensis* species from this genus based on the presence of a 'diplododellan' (possessing a denticulate posterior, i.e. caudal, process) S<sub>0</sub> element, which they proposed to be diagnostic for *Pandorinella* and absent in *Ozarkodina*. However, Murphy et al. (2004) noted that this character appeared independently in multiple lineages and could not be used as a sole basis for assignment to either *Pandorinellina* or *Ozarkodina*. Based on the shape of the denticulation and the basal cavity, they referred the *steinhornensis* material of Ziegler (1956) and a *steinhornensis* bedding plane assemblage (Mashkova, 1972) to the genus *Criteriognathus* Walliser, 1972.

Following the exclusion of the *steinhornensis* species from *Ozarkodina*, Klapper and Murphy (1974) assigned former subspecies of *Sp. steinhornensis* to *Oz. remscheidensis* (as the second available name with priority) and formulated a differential diagnosis that distinguished *Oz. remscheidensis eosteinhornensis* based on a nearly uniform height of denticles in its P<sub>1</sub> element from *Oz. remscheidensis remscheidensis* with irregular denticle heights. According to this revision, *Oz. steinhornensis scanica* should be referred to as *Oz. remscheidensis scanica*, because in Jeppsson's (1974) reconstruction it does not have a caudal process. Instead, in his later articles Jeppsson used '*Oz. scanica*', i.e. in the rank of species distinct from *Oz. remscheidensis* (Jeppsson, 2005; Jeppsson et al., 2006), but provided no taxonomic discussion of this decision. This is further complicated by the subsequent revision of *Oz. remscheidensis* placing it in a new genus *Zieglerodina*. Based on the type material, Murphy et al. (2004) excluded the *remscheidensis* species as described by Ziegler (1960) from *Ozarkodina* based on 'a more posterior position and shape and, generally, the larger size of the basal platform lobes, the alternation of denticle sizes, undulation of the processes of the

transition-series elements, and less deep distribution of white matter in all elements' in P<sub>1</sub> elements and alternating large and small denticles in S<sub>1</sub> through S<sub>4</sub> denticles. They excluded the *eosteinhornensis* subspecies from *Zieglerodina* and proposed that it might be placed in a separate genus, provisionally distinguished as 'W'. Until this genus is documented, current practice puts the *eosteinhornensis* form in the rank of species within *Ozarkodina* (Corradini & Corrigan, 2012), although it is also expressed as '*Ozarkodina*' to highlight the uncertainty and this approach is adopted here.

A cladistic analysis by Donoghue et al. (2008) taking into account four published reconstructions of the apparatus resolved '*Oz.* *remscheidensis* in one clade with *Nicollidina brevis* (Bischoff & Ziegler, 1957) and *Oz. confluens* (the type species of the genus) as a sister taxon to this clade. *Nicollidina* Dzik, 2002 would have priority over *Zieglerodina* Murphy et al., 2004, but a comparative analysis is lacking and it remains unresolved whether *brevis* and *remscheidensis* belong to the same genus (in this case it would have to be *Nicollidina*) or if their morphological disparity warrants assignment to two genera. The analysis did not include other species relevant to establishing the relationships between *Zi. remscheidensis*, *Cr. steinhornensis* and the *eosteinhornensis* species as the latter two lack complete reconstructions.

It remains to be clarified where the *scanica* form belongs in these taxa. Further subspecies of *Oz. remscheidensis* have been introduced by Miller and Aldridge (1997) based on British material, but reports of *Oz. remscheidensis scanica* or *Oz. scanica* have been minimal. Viira (1982) reported '*Oz. steinhornensis steinhornensis* aff. *Oz. st. scanica*' from the Ludlow of East Baltic and Helfrich (1978) reported '*Oz. steinhornensis scanica*' from the Silurian-Devonian transition in Virginia. The latter identification requires revision, since the specimens illustrated by Helfrich (1978) have clearly falling distal ends of both processes in the P<sub>1</sub> element, whereas the type *scanica* collection is characterized by aboral margins of P<sub>1</sub> elements forming a nearly straight line. Other diagnostic features are unfortunately unrecognizable in Helfrich's (1978) illustrations and no description is provided. Apart from these two reports, '*Oz. scanica*' is only known in L. Jeppsson's collections from Scania and Gotland. Based on the type collection, its assignment to *Zieglerodina* can be excluded as it lacks alternating denticles in the S element series and irregularly distributed lengths of denticles in the P<sub>1</sub> elements. The type collection of '*Oz. scanica*' comes from Scania and has not been examined in this study, therefore a conclusive revision was not possible. This form is here provisionally referred to as '*Oz. eosteinhornensis scanica*'. Other forms, identified by Jeppsson as '*Oz. steinhornensis*', and referable to *Oz. steinhornensis* ssp. 1 and ssp. 2 from the Přídolí of Scania (Jeppsson, 1974) were also found in the Ludfordian Eke, Burgen and

Hamra formations, and are here referred to as '*Oz.*' *eosteinhornensis* (*non scanica*) until the type material can be revised.

#### 4.7. The subspecies problem

A number of conodont taxa in this study have been moved between the ranks of species and subspecies, e.g. *Oulodus excavatus excavatus*, *Oulodus excavatus novoexcavatus*, '*Ozarkodina*' *eosteinhornensis scanica*, or *Zieglerodina remscheidensis*. In Jeppsson's articles the rank changes took place implicitly, without discussing the species concept and criteria (e.g. Jeppsson, 1972, 2005). This is a widespread practice in conodont taxonomy and a large part of the Silurian zonation on Gotland and elsewhere relies on subspecies (e.g. Jeppsson et al., 2006; Märss & Männik, 2013; Corradini et al., 2015). The use of subspecies (particularly with such a volatile status) is a hindrance in diversity and evolutionary analyses, or, as put by Mayr (1982), 'the entering of a wedge of destruction of a purely essentialistically defined species'. The popularity of subspecies in conodont taxonomy may reflect the fact that it relies on organs in which the morphology is strongly bound to the food-processing function and therefore to the biotic environment and the food base. Morphological variability of conodonts can be expected to vary along clines in these parameters, reflecting ecological and microevolutionary processes that the trinomials cannot capture.

The following approach is adopted here: the description of regional populations representing a constrained proportion of the intraspecific variation can be achieved through specifying the locality and age (e.g. '*Oz.*' *steinhornensis* from the Burgen Oolite Formation in the Ludfordian of Gotland) without producing a redundancy of Latin names. A morphologically distinct population in this sense may exist only fleetingly and will not be identical with any other population, making a trinomial dedicated to this population obsolete. Thus, following the reasoning of Wilson and Brown (1953), we adopt here the convention that morphologies showing the same unique combination of traits supraregionally can be validated as the same species, whereas endemic morphologies may represent either populations within existing taxa or new species, but not subspecies.

With respect to the conodont fauna in the Burgen Oolite Formation, two taxa originally described in the rank of subspecies, *Oulodus excavatus excavatus* and *Ou. ex. novoexcavatus*, are reported exclusively from Gotland, where they co-occur in the same samples starting from the upper Eke Formation. Silurian collections in Estonia (Männik, 2010) and our (Jarochowska et al., 2018) observations from the Silurian of England indicate that '*Ou. ex. excavatus*' occurs outside Gotland. Based on a comparison of its apparatus with

*Ou. cristagalli* Ziegler, 1960, Wickström (2005) proposed that the latter should be regarded as a synonym of *Ou. excavatus*, which would extend its occurrence to the upper Silurian and Lower Devonian of North America. The consistent co-occurrence of *Ou. excavatus* and *Ou. novoexcavatus* and the lack of transitional forms between them (*novoexcavatus* is easily distinguishable by a twisted tip of the basal cavity) and their disparate although overlapping stratigraphic ranges warrant their distinction as separate species. The lack of recognition of *Ou. novoexcavatus* outside Gotland may be related to the paucity of published illustrations and descriptions of this species (exclusively in Jeppsson, 1972) and to the fact that the diagnostic character is not recognizable under SEM.

## Conclusions

1. Revision of conodont faunas in Lennart Jeppsson's collection documented the occurrence of '*Oz.* *eosteinhornensis* *'scanica*', *Oz. crispera* and *Oz. snajdri* in the Burgen outlier. These occurrences support placing the Burgen Oolite Formation in this area in the *Ozarkodina snajdri* Biozone *sensu* Jeppsson et al. (2006).
2. Conodont species richness in this area is estimated at a minimum of 21 species. This includes '*Ozarkodina* *eosteinhornensis*, which occurs as the *'scanica*' form as well as the *'non scanica*' form corresponding to the original description of Walliser (1964). Previously reported *Aldridgeodus minimus*? and *Panderodus serratus* could not be confirmed in re-examined samples, but a specimen of *Ozarkodina wimani* is herein revised as the shallow-water species *Zieglerodina inordinata* (Viira, 2000) previously only known from the Přídolí of the eastern Baltic basin and Oklahoma.
3. The fish fauna from the Burgen outlier comprise an estimated nine species, chiefly represented by thelodonts that indicate a late- rather than mid-Ludlow age.
4. The facies in the Burgen outlier correspond to a more protected and heterogeneous environment compared with the Burgen Oolite Formation in the Sudret peninsula. The Burgen succession includes crinoidal, ooidal and bioclastic-oncoidal shoals and patch reefs formed by a diverse, fully marine fauna with a microbial contribution. The deposition took place above the wave base, in a fully marine, well oxygenated water. The high diversity of metazoan carbonate producers indicates a recovery from the impoverishment in the microbially-dominated underlying Eke Formation.
5. The  $\delta^{13}\text{C}_{\text{carb}}$  values reach +9.2‰ at Burgen 9 and are correlated here with the Burgen Oolite Formation in the Uddvide-1 core. The higher values in the Burgen outlier may reflect an onshore-offshore gradient across the carbonate platform.

6. A boundary between the Burgsvik Sandstone Formation and the Burgen Oolite Formation has been identified at Kapellet 1, with  $\delta^{13}\text{C}_{\text{carb}}$  values of +7.5‰.
7. Our data indicates a restoration of diverse conodont, benthic, and fish faunas as the LCIE was starting to wane. The NE-SW gradient in conodont diversity and  $\delta^{13}\text{C}_{\text{carb}}$  values across the Burgen Oolite Formation points to a facies contribution to previously recorded changes associated with the LCIE.

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## Data availability statement

The data that support the findings of this study are openly available in the Open Science Framework repository at DOI 10.17605/OSF.IO/GTMA7

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