

Calcareous nannofossils of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain) — biostratigraphy and palaeoecology

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Abstract: We obtained material from the Puerto Escaño section (southern Spain) to study the Jurassic/Cretaceous (J/K) boundary interval. The same samples had already been processed for magnetostratigraphic studies and biostratigraphic zonation based on calpionellids and ammonites (Pruner et al. 2010), but not for calcareous nannofossils. The aim of this study was to process the samples using micropalaeontological analysis and to compare and calibrate results for calcareous nannofossils with existing magnetostratigraphic and other biostratigraphic data. The calcareous nannofossil assemblage was dominated by the genera *Watznaueria*, *Cyclagelosphaera*, *Nannoconus*, *Conusphaera* and *Polycostella*. Several nannofossil bioevents were recorded on the basis of the distribution of stratigraphically important taxa, including zonal and subzonal markers. Based on the lowest occurrences (LO) of *M. chiastius*, *N. globulus minor*, *N. wintereri*, *N. steinmannii minor*, *N. steinmannii steinmannii*, *N. kamptneri minor* and *N. kamptneri kamptneri*, two nannofossil subzones (NJT 15b, NJT 17a) and two nannofossil zones (NJT 16, NK-1) were recognized. The paper introduces new palaeoecological data based on geochemical analysis and macrofauna occurrences.

Key words: Jurassic/Cretaceous boundary, southern Spain, Tethys, biostratigraphy, calcareous nannofossils, palaeoecology.

Introduction

The existence of two different temperate Realms in the Northern hemisphere (the Tethyan and the Boreal) during the J/K boundary interval was associated with the occurrence of different biotic elements in the two Realms due to their specific climatic and palaeoceanographic conditions (Zakharov et al. 2014). Also from this point of view, the J/K boundary is the last System boundary remaining to be defined. For the clarification and precise determination of the J/K boundary strata, several markers have been suggested as keys for the correlation — namely calpionellids, calcareous nannofossils, magnetostratigraphy (base M18r, M19.1n, M19n.1r), ammonites, palynomorphs, geochemistry (Wimbledon et al. 2011). One of the possible markers of the J/K boundary interval is based on the *Calpionella alpina* ‘acme zone’. This marker was identified in the Puerto Escaño section approximately in the middle part of the M19n magnetozone (Pruner et al. 2010) and it is partly re-interpreted here. The Jurassic/Cretaceous (J/K) boundary interval is currently one of the most studied, because no appropriate stratotype for the base of the Cretaceous has yet been defined despite an extensive research effort (e.g., Hoedemaeker et al. 1998; Houša et al. 1999, 2004; Lakova et al. 1999; Oszczytko et al. 2004; Michalík et al. 2009; Reháková et al. 2009; Channell et al. 2010; Grabowski et al. 2010; Lukeneder et al. 2010; Michalík & Reháková 2011; Wimbledon et al. 2011, 2013; Wimbledon 2014).

Globally, plankton assemblages with rock-forming potential developed during this time interval. The remarkable radiation of the some groups, especially nannoconids and calpionellids, significantly increases their biostratigraphical value. Moreover, the richness of different fossil groups (ammonites, calcareous nannofossils, calpionellids) offers the opportunity to compare and calibrate different biozonations and bioevents, improving the knowledge of Jurassic and Cretaceous biochronology (Marino et al. 2004). This study is focused on calcareous nannofossil biostratigraphy, an essential component of standard multidisciplinary J/K boundary research.

According to Pruner et al. (2010), the lithological succession of the Puerto Escaño section in southern Spain shows relatively continuous sedimentation with minor incidence of hiatuses, conditions favourable for study of palaeomagnetic polarity. They also reported rich fossil assemblages of calpionellids and ammonites; calpionellids, in particular, were very well preserved, highly diversified, and with a full record of their evolution.

The ammonite fauna of this section has been evaluated by Olóriz (1978); Olóriz & Tavera (1989, 1990); Tavera et al. (1994); Olóriz et al. (1995, 2004). Lithology, development and associated ichnofabric assemblages were investigated by Caracuel (1996); Caracuel et al. (2000). The first relevant geochemical data (stable isotopes) from this section, calibrated by bio- and magnetostratigraphy were given by Žák et al. (2011).

The aim of this paper is to describe the Late Jurassic–Early Cretaceous calcareous nannofossil assemblage from Puerto Escaño, and to discuss its biostratigraphy and possible palaeoecological affinities. We compare these calcareous nannofossil results with the magnetostratigraphic and biostratigraphic (ammonites, calpionellids) data of Pruner et al. (2010) to define the J/K boundary interval.

Geological setting

The section at Puerto Escaño, in the province of Córdoba, south-eastern Spain (Fig. 1) is located in the External Subbetic, which was positioned during the Late Jurassic and Early Cretaceous in a more distal, rather epiocenic environment, located in the S-E Iberian subplate palaeomargin (Coimbra et al. 2014a). Generally, the Subbetic Zone is a complex tectonostratigraphic unit which, palaeogeographically, was part of the pelagic domain of the southern passive margin of the Iberian Plate. Palaeoenvironmental characteris-

tics, based on geochemistry of carbonates, were recently provided by Coimbra et al. (2014a,b) and Coimbra et al. (2015).

According to Pruner et al. (2010), the Upper Jurassic to lowermost Cretaceous deposits in the studied section (specifically GA-7, UTM 30SUG44859) consist of upper Ammonitico Rosso and related facies, ranging from well-bedded limestones to clayey nodular limestone horizons reflecting deposition on a distal, epiocenic swell. The section studied is dominated by wackestone showing microfacies with variable contents of radiolarians, calcareous dinoflagellates, planktonic crinoids, planktonic and benthic foraminifers, calpionellids, ostracods, cephalopods, echinoderms (plates and spines), sponge spicules and pelagic bivalves, among others. Macroscopic fossil remains are mostly ammonites, and less abundant components are belemnites, brachiopods and echinoids. Their occurrence is concentrated into several limited horizons (beds — see below). Tavera et al. (1994) also reported relatively abundant calcareous nannofossils from this section.

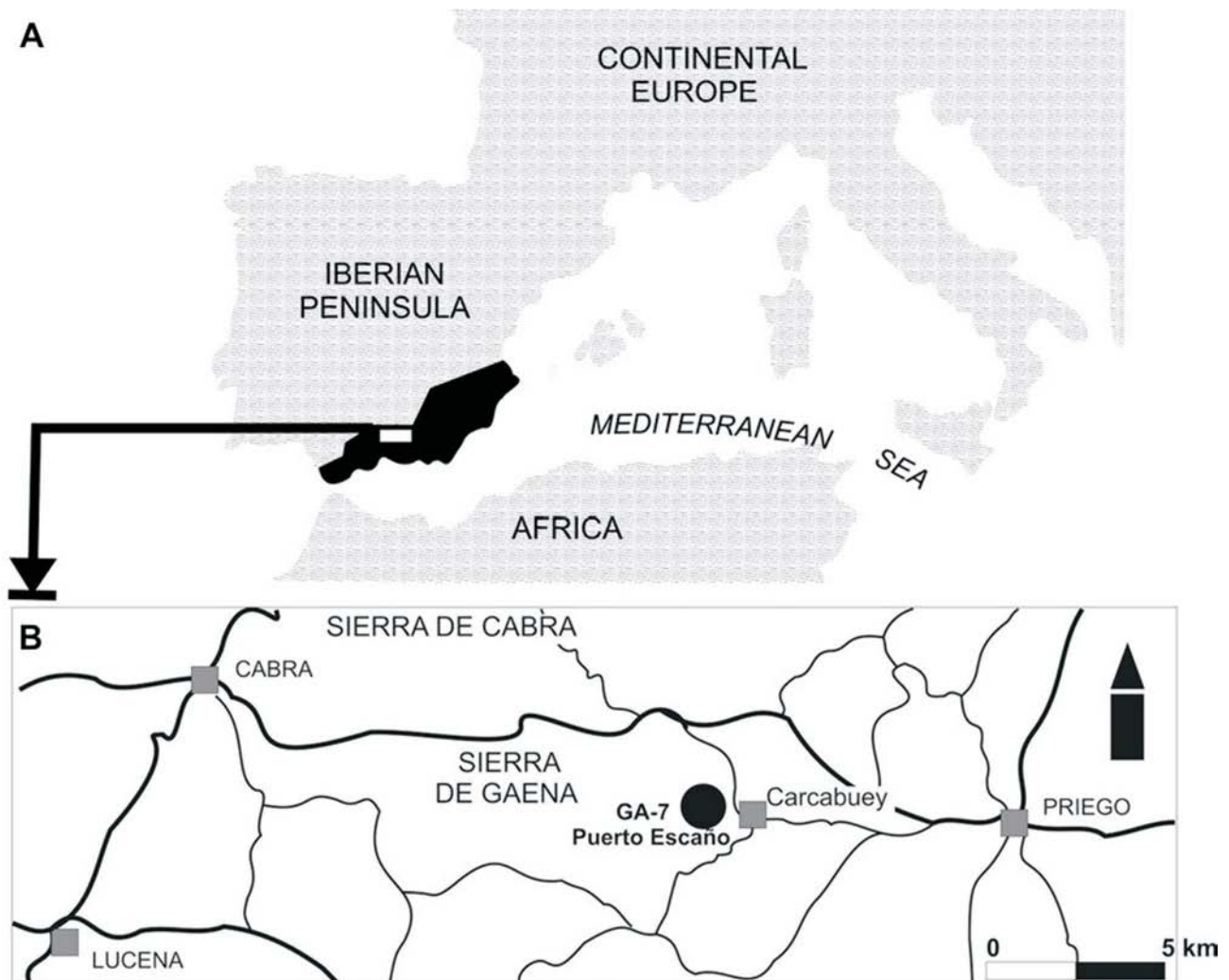


Fig. 1. Location of the studied section (A). The position of section GA-7 at Puerto Escaño with roads in the surroundings (B). Black area represents the Betic Cordillera. Maps modified from Pruner et al. 2010.

Material and methods

Calcareous nannofossils

We used the same rock material as in the previous study by Pruner et al. (2010) for calcareous nannofossil analysis. These were unused, very small fragments from samples in the same stratigraphic interval (an 8.1m-thick part of the section straddling the upper Tithonian and lower Berriasian), and numbering. These remnants provided enough material for detailed micropalaeontological analysis of the nannofossils. Samples numbered from No. 5 to No. 42 (Fig. 2) were chosen from throughout the profile (Fig. 2).

Calcareous nannofossils were analysed in 51 smear slides prepared using the standard techniques described by Švábenická (2001), under an Olympus BX51 light microscope using an immersion objective with a magnification of 100×. Digital images of nannofossil specimens were taken with an Olympus DP70 digital camera. At least 200 specimens were counted on each slide, to obtain relative abundances and semi-quantitative information about nannofossil species diversity. Each slide was then scanned for identification of scarce, but biostratigraphically important, species.

The set of smear slides is stored at the Institute of Geology and Palaeontology (Chlupáč's museum of Earth history), Faculty of Sciences, Charles University in Prague as item (IGP/2015/PE001).

Preservation of calcareous nannofossils was characterized using the abbreviations described by Bown (1992):

VP (very poor)=extreme etching

P (poor)=etching and overgrowth; obscured, damaged, or destroyed central area structures

M (moderate)=moderate etching or overgrowth.

The scale for the estimate of nannofossil total abundance was modified after Casellato (2010):

A (abundant): >11 specimens per field of view

C (common): 1–10 specimens per field of view

F (few): 1 specimen every 1–5 fields of view

R (rare): 1 specimen every 6 or more fields of view.

The individual abundances for each species per sample were counted according to the classification proposed by Bown (1992):

R (rare)=1–2 specimens

F (few)=3–10 specimens

C (common)=11–100 specimens

A (abundant)=more than 100 specimens (out of 200 specimens).

A full list of the calcareous nannofossil taxa found in this study is given in alphabetical order in Appendix A. The listed calcareous nannofossils are indexed according to Perch-Nielsen (1985) and Bown & Cooper (1998). Biostratigraphic data were interpreted with reference to the nannofossil zonation of Casellato (2010), commonly used for the Upper Jurassic and the Lower Cretaceous in the Tethyan/Mediterranean area.

Macrofossil record and geochemistry

The abundance of the macrofossils, also including the benthic assemblage is based on a simple quantitative analy-

sis, calculating the number of specimens recorded in a 1m-wide unit of the bed. An abundance exceeding 5–10 specimens or fragments per unit is considered herein to be significantly high (in relation to other beds within the profile, where almost no benthic fauna has been recorded). Higher belemnite abundance (≥ 3 –4 per unit) should be considered as a bio-event and it is reported in the “Palaeoecology” chapter.

Stable isotope curves have been published by Žák et al. (2011) and they are reduced herein into a single column ($\delta^{18}\text{O}$ — Fig. 3) as $\delta^{13}\text{C}$ values (varying from 1.14 to 1.53 ‰ V-PDB); they show no significant expressions suitable for palaeoecological interpretations (see below).

We have used additional AAS geochemical methods as a tool for recognizing possible terrigenous (siliciclastic SiO_2 and Al_2O_3) input within the Puerto Escaño section. All analysis (concentrated to oxide and element detections) was carried out using a VARIAN (type SpectrAA 280 FS) instrument at the Faculty of Science, Charles University in Prague (Laboratories of the Geological Institutes).

Results

In the samples studied, calcareous nannofossils were rare to abundant and very poorly to moderately well preserved. In total, 35 calcareous nannofossil taxa were identified (Fig. 2). The most common component of the assemblage is the genus *Watznaueria*, forming nearly 58 % of the nannofossils, including *W. barnesiae* (Fig. 4/1), *W. manivitiae* (Fig. 4/2), *W. communis* (Fig. 4/3), *W. fossacineta* (Fig. 4/4) and *W. britannica* (Fig. 4/5). *W. barnesiae* was present in all samples and ranged from 38 % to 59 % of the total assemblage. The highest abundance of this species was recorded in bed 19.

The percentages of *W. manivitiae* ranged from 3 % to 17 % of the total assemblage and the highest abundances were recorded from beds 11 to 22. *W. britannica* formed approximately 2 % of the total assemblage, while *W. fossacineta* and *W. communis* occurred only sporadically, representing ~0.5 % of the genus *Watznaueria*.

The second most common genus is *Cyclagelosphaera* spp. (~27 % of all identified nannofossils), particularly *C. margerelii* (Fig. 4/6), *C. deflandrei* (Fig. 4/7) and *C. argoensis* (Fig. 4/8). Other abundant genera are: *Conusphaera* spp. (~7 % represented by *C. mexicana mexicana* (Fig. 4/19, 20) and *C. mexicana minor*, *Nannoconus* spp. (~4 % represented by *Nannoconus* sp. (Fig. 5/1), *N. infans*, *N. erbae* (Fig. 5/2, 3), *N. puer* (Fig. 5/4, 5), *N. globulus minor* (Fig. 5/6–9), *N. globulus globulus* (Fig. 5/10–13), *N. wintereri* (Fig. 5/14–17), *N. steinmannii minor*, *N. steinmannii steinmannii* (Fig. 5/18–21), *N. kamptneri minor*, and *N. kamptneri kamptneri* (Fig. 5/22, 23), and finally *Polycostella beckmannii* (Fig. 4/22, 23), representing more than 2 % of the total nannofossil assemblage. Three nannoliths - *Conusphaera* spp., *Nannoconus* spp. and *Polycostella* sp. showed the most significant fluctuations in the nannofossil assemblage, as shown in previous studies (e.g., Tremolada et al. 2006a). The percentage representation and peaks in abundance of these most abundant genera across the studied profile are presented in Fig. 6.

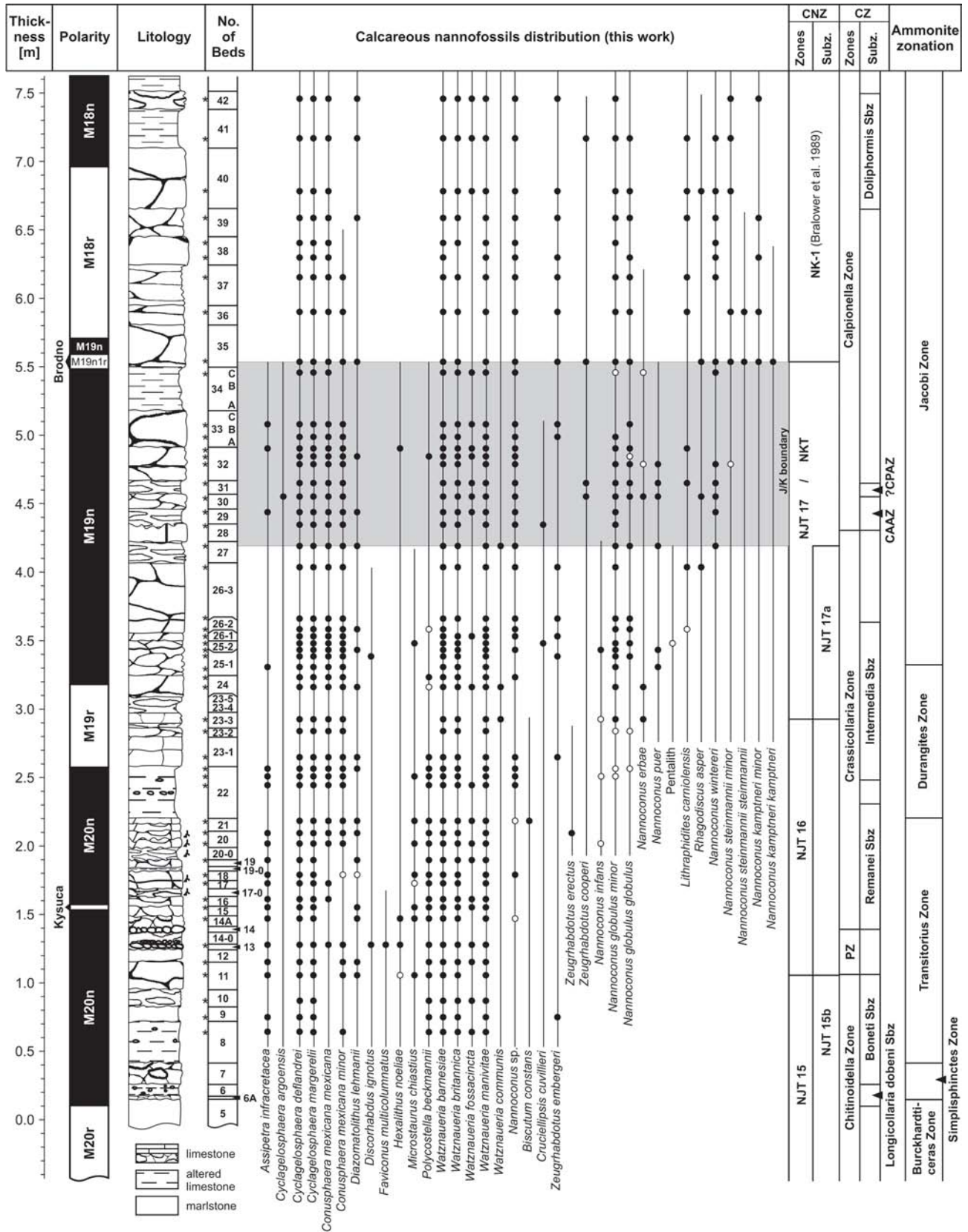


Fig. 2. Lithology, magnetostratigraphy, biostratigraphy (calpionellid, ammonite and calcareous nannofossil zonation) and vertical distribution of nannofossil species of the Puerto Escaño section. Open circles indicate uncertain species identification. Biozonal (ammonite, calpionellid) and magnetostratigraphic data after Pruner et al. 2010 (modified). Nannofossil zones follow Casellato (2010). The expected J/K boundary interval is marked in grey. CNZ — calcareous nannofossil zonation; CZ — calpionellid zonation; CAAZ — *Calpionella alpina* “acme zone”; ?CPAZ — *Crassicollaria parvula* “acme zone”; PZ — *Praetintinnopsella* Zone; * — beds studied for calcareous nannofossils (this work).

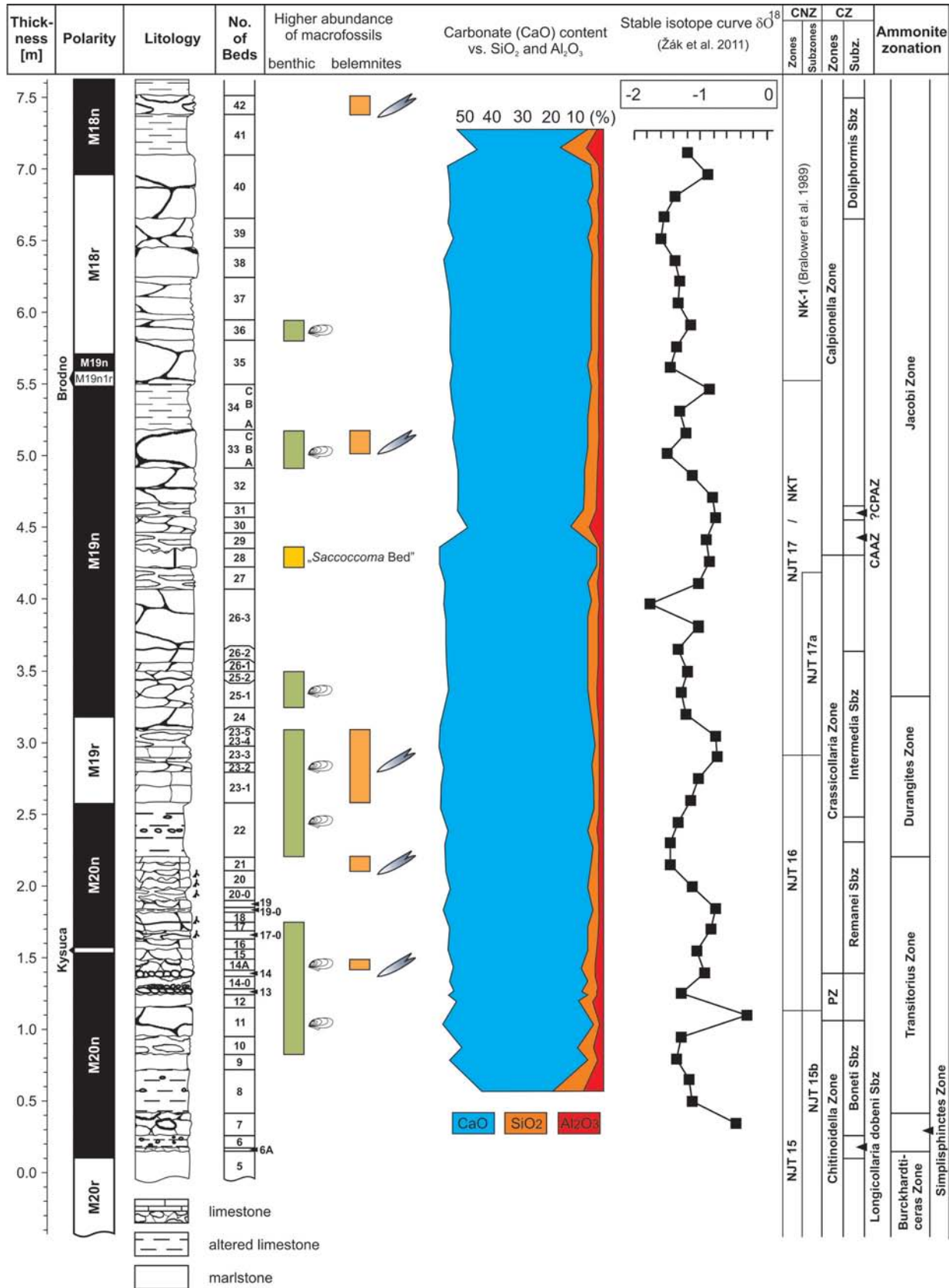


Fig. 3. Puerto Escaño section (after Pruner et al. 2010) — magnetostratigraphy, lithology, benthic organisms occurrence, belemnite relatively abundant horizons, geochemical analysis of the bulk rock samples (ratio of oxides CaO, SiO₂ and Al₂O₃) and the stable isotope signals of the δO¹⁸ curve (after Žák et al. 2011) in relation to the calcareous nannofossil (this paper), calpionellid and ammonite Zones (Pruner et al. 2010). CNZ — calcareous nannofossil zonation; CZ — calpionellid zonation.

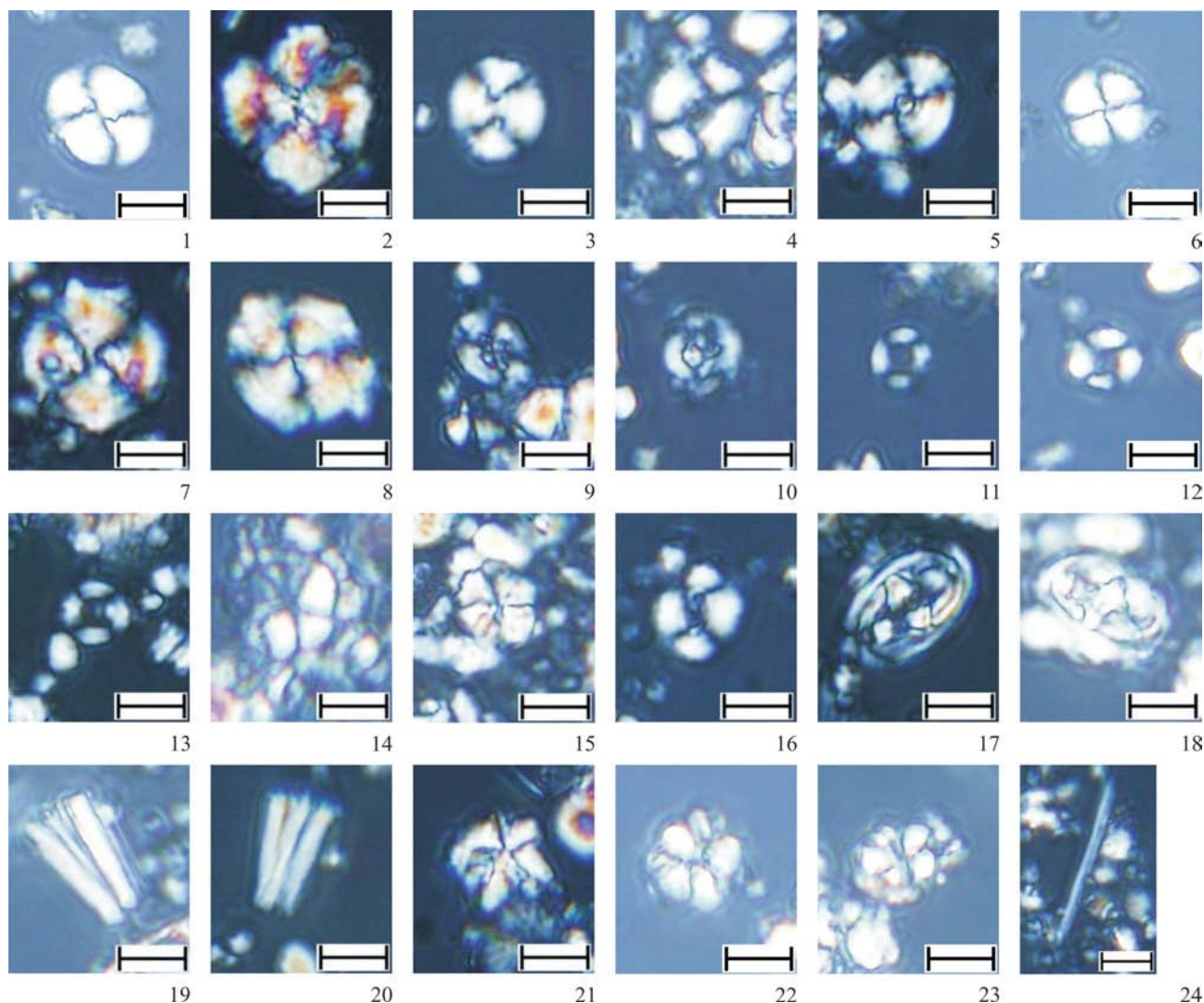


Fig. 4. Calcareous nannofossils from the Puerto Escaño section. Cross polarized light; scale bar represents 5 µm. **1** — *Watznaueria barnesia*; sample 25-1 t. **2** — *W. manivittiae*; sample 25-2 b. **3** — *Watznaueria communis*; sample 23-3. **4** — *W. fossacincta*; sample 41. **5** — *W. britannica*; sample 24 b. **6** — *Cyclagelosphaera margerelii*; sample 25-1 t. **7** — *C. deflandrei*; sample 24 b. **8** — *C. argoensis*; sample 30. **9, 10** — *Cruciellipsis cuvillieri*; **9** — sample 25-2 t, **10** — sample 28. **11–13** — *Diazomatolithus lehmanii*; **11** — sample 26-2, **12** — sample 41, **13** — sample 39. **14, 15** — *Hexalithus noeliae*; sample 13. **16** — *Microstaurus chiastius*; sample 25-2 t. **17** — *Zeugrhabdotus embergeri*; sample 40. **18** — *Z. cooperi*; sample 41. **19, 20** — *Conusphaera mexicana mexicana*; **19** — sample 22 b, **20** — sample 26-3 b. **21** — Pentalith; sample 25-2 t. **22, 23** — *Polycostella beckmannii*; sample 11. **24** — *Lithraphidites carniolensis*; sample 26-3 t.

Other nannoliths represented by *Faviconus multicolumnatus*, *Assipetra infracretacea*, *Hexalithus noeliae* (Fig. 4/14, 15), *Lithraphidites carniolensis* (Fig. 4/24) and an unidentified pentalith (one specimen, Fig. 4/21) occurred less frequently, as did other members of the coccolithophorids such as *Zeugrhabdotus embergeri* (Fig. 4/17), *Z. cooperi* (Fig. 4/18), *Z. erectus*, *Rhagodiscus asper*, *Diazomatolithus lehmanii* (Fig. 4/11–13), *Cruciellipsis cuvillieri* (Fig. 4/9, 10), *Discorhabdus ignotus*, *Microstaurus chiastius* (Fig. 4/16) and *Biscutum constans*. The preservation and total abundance of calcareous nannofossils and the individual abundances for each species are summarized in Fig. 7.

Discussion

Biostratigraphy

Generally, calcareous nannoflora represent an important source of biostratigraphic data for the Mesozoic and Cenozoic ages. Indeed, in some multiproxy studies, the most significant stratigraphic data were obtained by the analysis of calcareous nannofossils (e.g. Halássová et al. 2012).

Despite the relatively poor preservation of the calcareous nannofossils in our material, several biostratigraphic events have been defined. The lowest occurrence (LO) of *M. chias-*

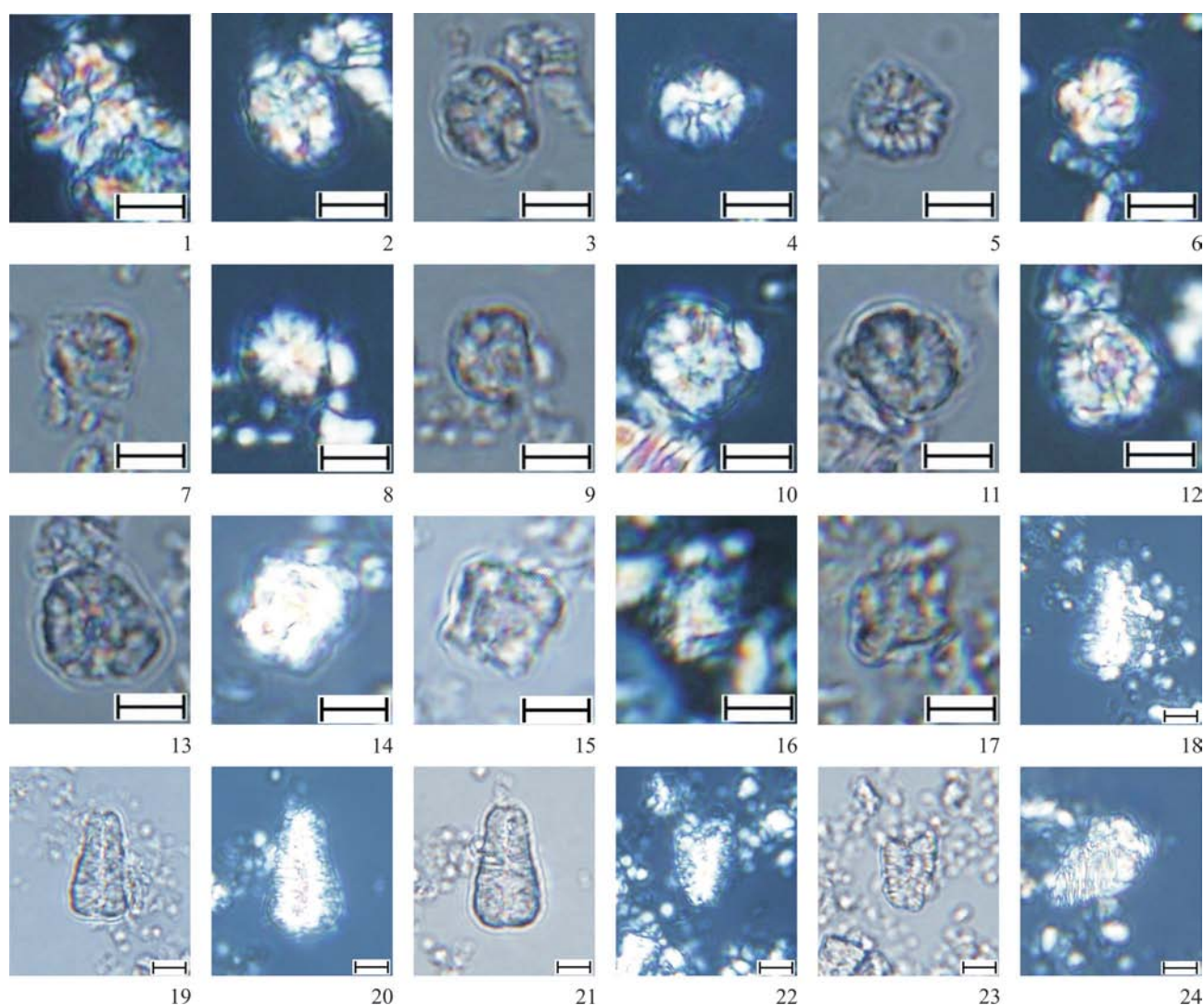


Fig. 5. Calcareous nannofossils from the Puerto Escaño section. **XPL** — cross polarized light, **PPL** — plane polarized light. Scale bar represents 5 μm . **1** — *Nannoconus* sp., cross section; sample 25-2 b, XPL. **2, 3** — *N. erbae*; 2 — sample 23-3, XPL; 3 — sample 23-3, PPL (the same specimen). **4, 5** — *N. puer*; 4 — sample 25-2 b, XPL; 5 — sample 25-2 b, PPL (the same specimen). **6–9** — *N. globulus minor*; 6 — sample 25-1 b, XPL; 7 — sample 25-1 b, PPL (the same specimen); 8 — sample 25-1 t, XPL; 9 — sample 25-1 t, PPL (the same specimen); **10–13** — *N. globulus globulus*; 10 — sample 25-1 t, XPL; 11 — sample 25-1 t, PPL (the same specimen); 12 — sample 30, XPL; 13 — sample 30, PPL (the same specimen). **14–17** — *N. wintereri*; 14 — sample 35, XPL; 15 — sample 35, PPL (the same specimen); 16 — sample 40, XPL; 17 — sample 40, PPL (the same specimen). **18–21** — *N. steinmannii steinmannii*; 18 — sample 35, XPL; 19 — sample 35, PPL (the same specimen); 20 — sample 35, XPL; 21 — sample 35, PPL (the same specimen). **22, 23** — *Nannoconus kamptneri kamptneri*; 22 — sample 35, XPL; 23 — sample 35, PPL (the same specimen). **24** — *Faviconus multicolumnatus*; sample 13.

tius indicating the beginning of the NJT 16 Zone sensu Casellato (2010) was recorded in the middle part of the M20n magnetozone, at the end of the *Chitinoidella* Zone and in the middle part of the *Transitorius* Zone (Tavera et al. 1994). The LO of *N. globulus minor* is found in the middle part of the M19r magnetozone and indicates the beginning of the NJT 17 Zone sensu Casellato (2010). The LOs of *N. globulus globulus* and *C. cuvillieri* were recorded in the lower part of the M19n magnetozone, in the middle part of the *Crassicolaria* Zone and at the beginning of the *Jacobi* Zone. In the upper part of the *Crassicolaria* Zone, the LO of *N. wintereri* was observed. This indicates the beginning of

the NJT 17b Subzone, that continues to the LO of *N. steinmannii minor* sensu Casellato (2010). Unfortunately, this bioevent has not been identified in the studied section and the LO of *N. steinmannii minor* has been observed in the middle parts of the *Calpionella* Zone and the *Jacobi* Zone and corresponds to the LOs of *N. steinmannii steinmannii*, *N. kamptneri minor* and *N. kamptneri kamptneri* (Figs. 6, 7), that indicates the beginning of the NK-1 Zone (sensu Bralower et al. 1989). In the interval between the LO of *N. wintereri* and the LOs of *N. steinmannii minor*, *N. steinmannii steinmannii*, *N. kamptneri minor* and *N. kamptneri kamptneri*, the *Calpionella alpina* 'acme zone' and the beginning

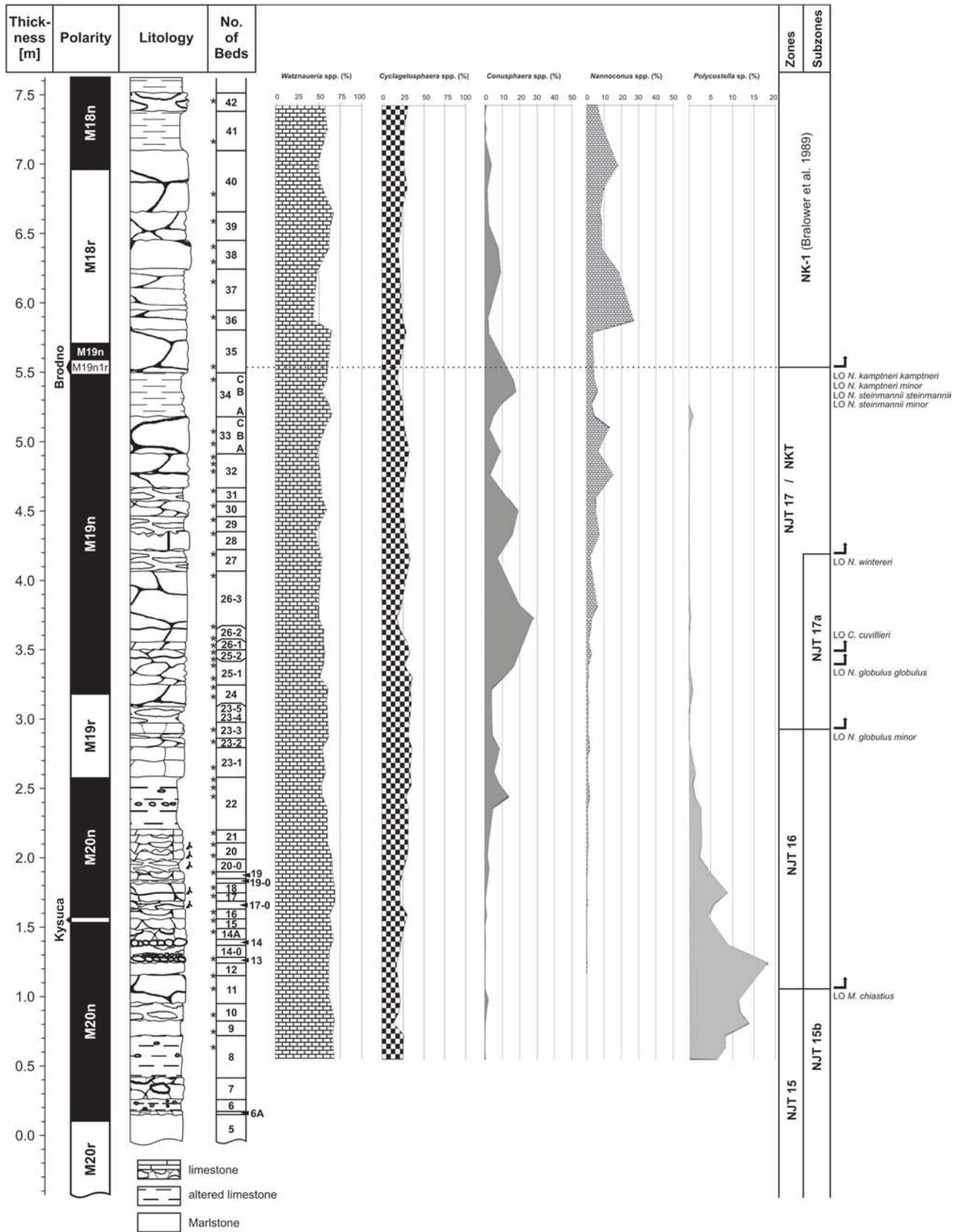


Fig. 6. Lithology, magnetostratigraphy and biostratigraphy (calcareous nannofossil zonation). Includes representation of selected nannofossil genera in the Puerto Escaño section as a percentage and the main recorded bioevents. Lithology and magnetostratigraphic data after Pruner et al. 2010 (modified). Nannofossil zones follow Casellato (2010). * — beds studied for calcareous nannofossils (this work); LO — lowest occurrence.

of the *Calpionella* Zone were observed (Pruner et al. 2010). It should be noted, that the LO of *N. kamptneri minor* usually appears a little above the LO of *N. steinmannii minor*, but in this paper it occurs together with the LOs of *N. steinmannii steinmannii* and *N. kamptneri kamptneri* in bed 35. This anomaly can be explained by the very poor preservation and extreme etching of calcareous nannofossils between beds 32 and 34 (Fig. 7). Moreover, the appearance of these four species together suggests the presence of a hiatus.

In the previous study by Tavera et al. (1994), the zonal scheme proposed by Bralower et al. (1989) was used. However, the zonation of Bralower et al. (1989) and specifically the definition of subzones NJK-A, NJK-B and NJK-C is based on the lowest occurrences of species with relatively delicate structures (*Umbria granulosa granulosa* and *Rotalapillus laffittei*) which may disappear from the association as a result of preservational effects (Tavera et al. 1994). The material studied in Tavera et al. (1994) was also not well preserved and *U. granulosa* and *R. laffittei* taxa have not been recorded. Indeed, only the NJK-D subzone based on the LO of *N. steinmannii minor* was determined. This subzone is correlated with the lowermost Berrisian (Tavera et al. 1994), corresponding to the NKT Zone *sensu* Casellato (2010). In comparison, two additional nannofossil subzones (NJT 15b, NJT 17a) and two nannofossil zones (NJT 16, NK-1) were recognized in this study. Moreover, the time interval of the NJT 17 and NKT Zones *sensu* Casellato (2010) has been observed.

Correlation of the main bioevents with magnetostratigraphic data (Pruner et al. 2010) is given in Fig. 8, where the comparison with other studied sections of the J/K boundary is shown. The LO of *N. wintereri* has been recorded in the M19n magnetozone in Puerto Escaño, as well as in Le Chouet, Brodno, Foza and Torre de' Bussi sections. In Fiume Bosso, this bioevent has been observed in M18r and in Barlya section in M17r magnetozone. Similarly, the LO of *N. steinmannii minor* within the M19n magnetozone has been recorded in Puerto Escaño, as well as in Le Chouet, Lokut and Torre de' Bussi sections. This bioevent has been recorded in M17n zone in Foza and Fiume Bosso and in M18r in Barlya section. The LO of *N. steinmannii steinmannii* in M19n magnetozone was observed only in Puerto Escaño section, then in M17r zone in Foza and Fiume Bosso sections.

Palaeoecological interpretations

This chapter is divided into four major parts: the calcareous nannofossils palaeoecology, macrofossil record, new additional geochemical data and remarks on the key Bed 28 (J/K boundary *sensu* Pruner et al. 2010).

Remarks on selected Late Jurassic calcareous nannofossils

In some cases, calcareous nannofossils provide only sporadic information about the palaeoecological conditions of a depositional area. But there is also evidence reported from the literature that calcareous nannoplankton may give important information regarding the trophic levels of the superfi-

cial oceanic water, about the water temperature or salinity (e.g., Erba 1992; Tremolada et al. 2006b; Aguado et al. 2008; Mattioli et al. 2008). Some palaeoecological aspects can also be presented from our study.

Generally, the most dominant genera in studied material are *Watznaueria*, *Cyclagelosphaera*, *Nannoconus*, *Conusphaera* and *Polycostella* (see chapter Results). This composition of calcareous nannofossil assemblages across J/K boundary interval is typical for "low latitudes" sections and has been already observed in previous studies (e.g. Tavera et al. 1994; Bornemann et al. 2003; Tremolada et al. 2006a; Michalik et al. 2009; Lukeneder et al. 2010).

The most common taxon recorded is *Watznaueria barnesiae*, representing 48 % of the entire taphocoenosis. This species is not susceptible to dissolution and is resistant to diagenetic alteration (Hill 1975; Thierstein 1980; Roth 1981; Roth & Bowdler 1981; Roth & Krumbach 1986). Roth & Krumbach (1986) described assemblages containing more than 40 % of *W. barnesiae* as heavily altered by diagenesis. However, the genus *Watznaueria* is generally considered to be the robust and most successful Mesozoic coccolithophore, in terms of abundance, across the widest range of environments. By some authors *Watznaueria* is considered to be an opportunistic, r-strategist taxa (e.g., Tremolada et al. 2006a; Lees et al. 2006; Tantawy et al. 2009; Colombié et al. 2014; Suchéras-Marx et al. 2015). It is ubiquitous and dominant through most of the Mesozoic, further illustrating its wide palaeoecological tolerance. In the fossil record, *W. barnesiae* displays a eurytopic, ecologically robust form, and was one of the first species to settle new habitats. In an ecological sense, it is similar to a recent species, *Emiliania huxleyi*. Together with *Cyclagelosphaera*, these two genera are stratigraphically long-ranging (Jurassic–earliest Palaeocene) and morphologically conservative, characteristics of generalist rather than specialist taxa (e.g., Mutterlose & Wise 1990; Street & Bown 2000; Melinte & Mutterlose 2001; Bown & Concheyro 2004; Lees et al. 2004). Both are considered to be cosmopolitan taxa and Lees et al. (2006) suggest, that *C. margerelii* lived in a higher trophic position than *W. barnesiae* and was more r-selected, possibly with more extreme nitrification affinities.

Species such as *Biscutum constans*, *Discorhabdus ignotus*, *Diazomatolithus lehmanii* and *Zeugrhabdotus erectus* occurred only sporadically in our samples. These species indicate eutrophic environments and preferred higher nutrient levels in the oceanic surface water (Roth 1981; Roth & Bowdler 1981; Roth & Krumbach 1986; Bornemann et al. 2003; Tremolada et al. 2006a,b). Dominance of *B. constans* and *Zeugrhabdotus* spp. is usually considered indicative of upwelling of cold water rich in nutrients (e.g., Mutterlose & Kessels 2000; Lees et al. 2005; Hardas & Mutterlose 2007; Lowery et al. 2014). Higher abundances of the taxa *B. constans* (~11 % of the total assemblage) and *Z. erectus* (~33 % of the total assemblage) have been associated with the occurrence of black shales and phosphorite deposition (Kessels et al. 2003). However, these species show very low abundances in our samples — only one specimen of each species (Fig. 7). It can be explained by high susceptibility to dissolution of these small coccoliths such as *Z. erectus*, *B. constans*

and *D. ignotus* (Hill 1975; Thierstein 1980; Roth 1981, 1983; Roth & Krumbach 1986), because a diagenetic overprint may imply a decrease in their relative abundance (Giraud 2009; Giraud et al. 2013).

Irregular occurrence of *Rhagodiscus asper* and *Lithraphidites carniolensis* began in bed 26, which corresponds to the NJT 17a nannofossil subzone, close below the J/K boundary interval. Erba (1987) and Erba et al. (1992) interpreted these species as thermophilous warm-water taxa indicating warm surface water that was poor in nutrients. In this context, there is also increased abundance of *Nannoconus* spp. in this part of the section (Fig. 6). Nannoconids have been characterized as typical Tethyan taxa of warm, low-latitude, carbonate-shelf environments. Similar to *Watznaueria* are considered to be r-selected taxa, moreover robust and not susceptible to dissolution (Street & Bown 2000; Melinte & Mutterlose 2001; Bown & Concheyro 2004; Tremolada et al. 2006b). These extinct 'incertae sedis' nannofossils are often interpreted as living in the lower photic zone (e.g., Erba 1994; Bornemann et al. 2003; Herrle 2003; Barbarin et al. 2012). The ecological affinities of other abundantly represented species, *Conusphaera* and *Polycostella*, are unknown, except considering *Conusphaera* to be a warm water taxon (e.g., Melinte & Mutterlose 2001; Mutterlose et al. 2005). However, Bornemann et al. (2003) proposed for them an ecological setting similar to that of *Nannoconus*, due to some similarities in the skeletons of these taxa.

Macrofossil abundance

The ammonite fauna has been studied in great details by numerous authors (Olóriz & Tavera 1989; Tavera et al. 1994; Pruner et al. 2010; etc.) and the belemnite record (stable isotopes) has partly been investigated by Žák et al. (2011). However, the presence and abundance of the macrofauna, predominantly benthic filter feeders and substrate feeders (i.e. brachiopods, echinoids, less abundant bivalves, echinoderms, sponges) is of great interest. Their presence/absence is shown in Fig. 3. The constant sedimentation rate (i.e. 1–5 mm/ky; 2.87 mm/ky with standard deviation 1.17 mm/ky for the whole section; Pruner et al. 2010) as well as palaeoecological conditions — namely a very low variation of geochemical content in carbonates (also supported by the stable isotope data; Žák et al. 2011, Fig. 3) within the limestone beds through the whole section do not suggest any rapid changes either in sedimentology (and bathymetry, not exceeding the CCD — supported by almost continuous ammonite record) or in taphonomy. Skeletons of all the above mentioned benthic groups as well as belemnites are composed predominantly by calcite. Thus, we assume very low fluctuations within the preservation potential of these fossils. So, the basic scheme for benthic assemblage distribution should be introduced based on simple fact — namely on relatively abundant/absent.

Both situations are probably connected with controlling factors, namely shallowing but rather the presence of higher nutrient flux. Shallowing should be excluded, maybe excepting that in Beds 10–17 (i.e. lower and middle part of the Transitorius ammonite Zone, Fig. 3), where siliciclastic and Al₂O₃ influx (with some signs of cyclicality) has been detected (Fig. 3), but this phenomenon could also be connected with periods with higher run-off. Probably, the sequences with abundant benthos represent the result of larger nutrient flux and subsequent biological productivity. In this context, the co-occurrence of *Biscutum constans*, *Discorhabdus ignotus*, *Diazomatolithus lehmanii* and *Zeughrabdodus erectus* with abundant benthic organisms (Fig. 3) — namely eutrophic communities, should indicate some correlation. This should also support the results of Bornemann et al. (2003) and Tremolada et al. (2006a,b), who suggested these nannofossil taxa were dependent on a eutrophic environment. However, we assume that more relevant data are needed. We could not confirm the hypothesis of Mutterlose & Kessels (2000), Lees et al. (2005), Hardas & Mutterlose (2007), Lowery et al. (2014) and others relative to the oxygen stable isotope curve, as no marked cooling (related to upwelling of cold waters) is recorded in the δ¹⁸O values (Fig. 3). Nevertheless, we agree with the conclusion that these taxa represent rather eutrophic organisms.

Benthic assemblages with skeleton remains occur in Bed complex 10–17 (in the middle part of the Transitorius Zone), 22–25 (corresponding approximately to the Durantiges ammonite Zone), 28 ("Saccocoma Bed", suggested J/K boundary), 33 (lower part of the standard Calpionella Zone) and 36 (i.e. the middle part of the Calpionella Zone) (Fig. 3).

Higher abundances of belemnites (active nektonic animals) have been recorded in beds 14A, 21, 23, 33B–C, and 42. Their occurrences partly correlate with the benthos presence — namely with more eutrophic conditions (see above). It has been suggested that higher belemnite abundances (predominantly hibolithids and pseudobelids) are dependent on the transgressive/regressive tracts (Mitchell 2005; Wiese et al. 2009), however, the sea-level oscillations in the epioceanic development of the Puerto Escaño sequence (Olóriz et al. 2004) seems to be under the analytical limits and further investigations are needed. In this respect, the winnowing effect, concentrating macrofossil records, cannot be excluded. On the other hand, the presence of these remains only in several horizons suggests that their original habitat, in terms of the environment, lithology and geochemical record in other beds, in which they are missing, is fully comparable.

Additional geochemical data

New geochemical data are based on the AAS silicate analysis (see above), which detects especially oxides and element

Fig. 7. Age, calcareous nannofossil zonation and calcareous nannofossil range chart of the Puerto Escaño section, including information on preservation, total abundance and relative abundance of each taxon. Question marks indicate uncertain species identification of heavily dissolved specimens or of nannofossils that occurred only as fragments. Uncertain occurrence was often associated with beds where preservation was very poor (marked by grey colour) (**b**=bottom, **m**=middle, **t**=top of the bed).

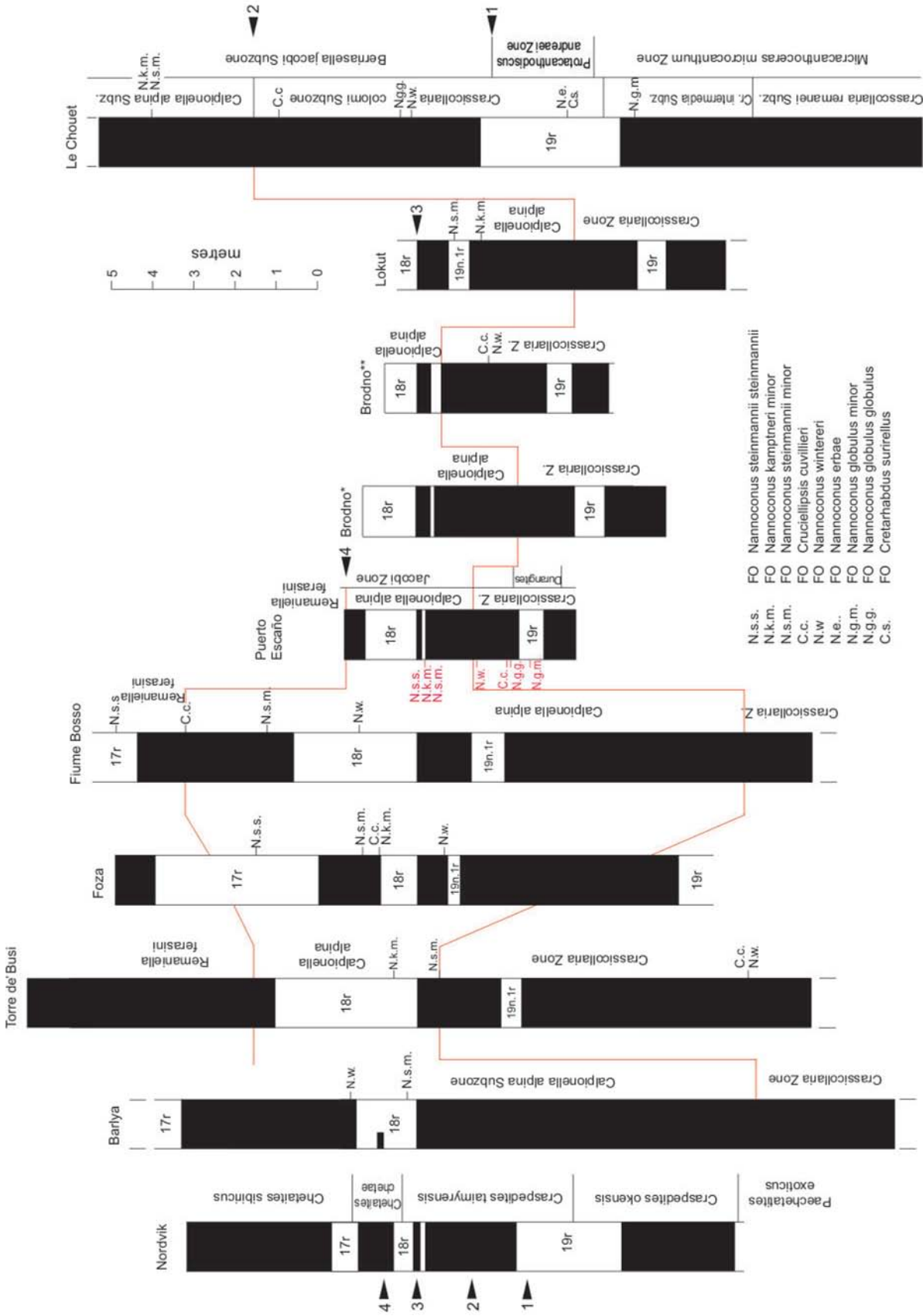


Fig. 8. Correlation of selected sequences showing the M20–M17 interval; Wimbledon et al. (2013), modified. Revised from Wimbledon et al. (2011). Brodno columns based on data in Housa et al. (2007)* and Michalik et al. (2009)**. Data 1–4 in Tethys (base of *B. jacobii* Subzone, base of Alpina Subzone, top of M19n.2n, and base of Ferasinii Subzone) and their approximate positions at Nordvik (column after Housa et al. 2007). The Barlya column is based on data provided by Platon Tchoumatchenco (unpublished magnetostratigraphy by B. Galbrun). Lokut after Grabowski et al. (2010). The lowest occurrences (LOs) of biostratigraphically significant calcareous nannofossils in the Puerto Escano section (this work) are indicated in red.

components of the sediment. Three major events representing marked inputs of terrigenous material were detected at the levels of the beds 8, 30-31 and 40-41 (Fig. 3). Positive curve excursions of oxides SiO_2 and Al_2O_3 are accompanied by marked increases (however, at the lower concentrations) of FeO , K_2O , TiO_2 and Na_2O , as well as marked increases of U^{238} , Th^{232} , Pb^{208} and other rare elements (unpublished data), clearly documenting a terrigenous input. A positive (however, not so straightforward) correlation between the increase of calcareous nannoplankton diversity and the terrigenous input is indicated in the beds 13, 29-31 and 40-41, but less marked in the in beds 22 and 35 levels. Higher terrigenous input should be evidence of weathering and/or the regression trend. In the studied profile, we should recognize three major sequences with higher terrigenous input — namely bed 8 (and overlying beds 9-14A), beds 29-31 and the upper part of bed 40 into the lower part of bed 41. The almost identical chemical composition of oxides and element content probably proves the same source area. However, its position within the Subbetic Basin margin is unknown.

The stable isotope data were precisely analysed by Žák et al. (2011). The $\delta^{18}\text{O}$ curve (Fig. 3), shows minor positive excursions in beds 8, 12, 23, 27-32, 34 and 40 levels, and the major negative peak has been recorded in bed 26-3 (Fig. 3). Only the peak in the Bed 12 corresponds to the higher abundance of *Polycostella* sp. (Fig. 6) and the positive excursion at level 34 corresponds to abundance increase of *Conusphaera* spp. In this respect, we cannot estimate any significant correlation between the calcareous nannofossil diversity development and the temperature changes, as only limited variations in the $\delta^{18}\text{O}$ curve have been recorded.

Remarks on the key Bed 28

Bed 28 (J/K boundary *sensu* Tavera et al. 1994; see also Pruner et al. 2010) contains a large accumulation of smaller globular (spherical) *Calpionella alpina* (Pruner et al. 2010). Bed 28 (“Saccocoma Bed” herein, Fig. 3) also contains extremely large, calcitic skeletal debris of *Saccocoma* skeletons, and thus, the reworking of smaller calpionellids cannot be excluded. However, there is no sign of siliciclastic input in this horizon, and the highest ratio between Ca-oxide and minimum SiO_2 and Al_2O_3 input is recorded in this bed (Fig. 3). The opposite trend is visible in the overlying beds, beds 29-31, where the marked decrease of Ca-oxide and increase of siliciclastics input (represented by SiO_2), as well as an increase of Al_2O_3 seems to prove a run-off increase due to an acceleration of weathering and/or rather a regressive sequence. The regression hypothesis should be supported by the presence of a marked increase in crassicollian abundance (*C. parvula* — parvula Acme zone, “CPAZ” *sensu* Pruner et al. 2010), suggested to have been reworked from older upper Tithonian limestones and incorporated into the micrite matrix of the Alpina Subzone (Wimbledon et al. 2013). We agree with this interpretation and we preliminarily suggest the section studied represents a regressive sequence (beds 29-31). A similar trend is recorded in the uppermost part of bed 40 and especially in the lower part of bed 41, where decrease of Ca-oxide and increase of SiO_2 and

Al_2O_3 (as a product of the laterite weathering) input have been detected (Fig. 3).

Conclusions

We have studied the calcareous nannofossils from the GA-7 section at Puerto Escaño. Consistent with the results of Tavera et al. (1994), the dominant genera in the calcareous nannofossil associations of the section are *Watznaueria* spp., *Cyclagelosphaera* spp., *Nannoconus* spp. and *Conusphaera* spp. and *Polycostella* sp.

We have applied the nannofossil zonation of Casellato (2010), and recognized several nannofossil LOs (Figs. 6, 7): *Microstaurus chiastius*, *N. globulus minor*, *N. globulus globulus* and *Cruciellopsis cuvillieri*, *N. wintereri* and finally *N. steinmannii minor*, *N. steinmannii steinmannii*, *N. kamptneri minor* and *N. kamptneri kamptneri*. Moreover, the composition of the nannofossil assemblage indicated a warm, carbonate-shelf environment with oligotrophic conditions.

The J/K boundary transition has been approximated with the LO of *N. wintereri* to the LOs of *N. steinmannii minor*, *N. steinmannii steinmannii*, *N. kamptneri minor* and *N. kamptneri kamptneri*. This interval is located between beds 27 and 35. Consistent with Pruner et al. (2010), the J/K boundary lies in approximately the upper middle part of the M19n magnetozone and includes the *Calpionella alpina* ‘acme zone’ (Fig. 2).

The co-occurrence of taxa *Biscutum constans*, *Discorhabdus ignotus*, *Diazomatolithus lehmanii* and *Zeughrabdodus erectus* with abundant benthic organisms should confirm their preferences for higher nutrient levels.

The diversity of calcareous nannofossils at higher levels partly corresponds to the levels with terrigenous input, well documented by geochemical methods.

Here we suggest that the increase in abundance of *Crassicolliaria parvula* (i.e. — Parvula Acme zone, “CPAZ” *sensu* Pruner et al. 2010) is the result of reworking from older upper Tithonian deposits, in relation to the regressive sequence between beds 29-31.

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Appendix A — Taxonomic index in alphabetical order

- Assipetra infracretacea* (Thierstein, 1973) Roth, 1973
- Biscutum constans* (Górka, 1957) Black, 1967
- Conusphaera mexicana* (Trejo, 1969) subsp. *mexicana* Bralower in Bralower et al., 1989
- Conusphaera mexicana* (Trejo, 1969) subsp. *minor* (Bown & Cooper, 1989) Bralower in Bralower et al., 1989
- Cruciellipsis cuvillieri* (Manivit, 1956) Thierstein, 1971
- Cyclagelosphaera argoensis* Bown, 1992
- Cyclagelosphaera deflandrei* (Manivit, 1966) Roth, 1973
- Cyclagelosphaera margerelii* Noël, 1965
- Diazomatolithus lehmanii* Noël, 1965
- Discorhabdus ignotus* (Górka, 1957) Perch-Nielsen, 1968
- Faviconus multicolumnatus* Bralower in Bralower et al., 1989
- Hexalithus noeliae* (Noël, 1956) Loeblich & Tappan, 1966
- Lithraphidites carniolensis* Deflandre, 1963
- Microstaurus chiastius* (Worsley, 1971) Bralower et al., 1989
- Nannoconus* sp. Kamptner, 1931
- Nannoconus erbae* Casellato, 2010
- Nannoconus globulus* (Brönnimann, 1955) subsp. *globulus* Bralower in Bralower et al. 1989
- Nannoconus globulus* (Brönnimann, 1955) subsp. *minor* Bralower in Bralower et al. 1989
- Nannoconus infans* Bralower in Bralower et al. 1989
- Nannoconus kamptneri* (Brönnimann, 1955) subsp. *kamptneri* Bralower in Bralower et al., 1989
- Nannoconus kamptneri* (Brönnimann, 1955) subsp. *minor* Bralower in Bralower et al. 1989
- Nannoconus puer* Casellato, 2010
- Nannoconus steinmannii* (Kamptner, 1931) subsp. *minor* Deres & Achéritéguy, 1980
- Nannoconus steinmannii* (Kamptner, 1931) subsp. *steinmannii* Deres & Achéritéguy, 1980
- Nannoconus wintereri* Bralower & Thierstein in Bralower et al., 1989
- Polycostella beckmannii* Thierstein, 1971
- Rhagodiscus asper* (Stradner, 1963) Reinhardt, 1967
- Watznaueria barnesiae* (Black in Black & Barnes, 1959) Perch-Nielsen, 1968
- Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964
- Watznaueria communis* Reinhardt, 1964
- Watznaueria fossacincta* (Black, 1971a) Bown in Bown & Cooper, 1989
- Watznaueria manivittiae* (Bukry, 1973) Moshkovitz & Ehrlich, 1987
- Zeugrhabdotus cooperi* Bown, 1992b
- Zeugrhabdotus embergeri* (Noël, 1958) Perch-Nielsen, 1984
- Zeugrhabdotus erectus* (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965