- Taxonomic revision of genus Carinolithus (Early Middle Jurassic) based on morphometric 1
- 2 analyses and diagenesis observations: implications for biostratigraphy and evolutionary trends.
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11 **Abstract**

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We applied morphometric analyses performed with a polarizing light microscope on a total of 100 12

specimens of Carinolithus superbus and C. magharensis to clarify the taxonomy based on

measurements of total height (TH), stem height (SH), stem width (SW), proximal shield width (PS),

distal shield width (DS) and thickness of the distal shield (TDS). Statistical analyses showed that

three of these parameters, namely the DS, TDS and SW, are diagnostic for taxa discrimination. New

taxa include C. superbus subsp. crassus subsp. nov. and C. magharensis subsp. minor subsp. nov.

Specimens of *C. cantaluppii* were qualitatively investigated to assess the potential role of secondary

modifications and our results revealed that, indeed, C. cantaluppii is a diagenetic artefact due to

different degrees of overgrowth on specimens of C. poulnabronei, C. superbus subsp. crassus, C.

superbus subsp. superbus, C. magharensis subsp. minor and C. magharensis subsp. magharensis.

This implies that C. cantaluppii is not a true taxon, and the overgrowth phase of Carinolithus

specimens is an effective proxy to assess the diagenetic degree. The morphometry-based revised

taxonomy of the genus Carinolithus was applied to improve the biostratigraphic resolution of the

Toarcian-Aalenian interval, with further implications for the reconstruction of evolutionary trends.

Keywords

Calcareous nannofossils; Early-Middle Jurassic; Carinolithus; Morphometry; Taxonomy; Diagenesis 28

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1. Introduction

The genus Carinolithus was initially established as Rhabdolithus by Deflandre in Deflandre & Fert 31 (1954) and, in the same work, the new species R. sceptrum, R. superbus and R. clavatus (Fig. 1) were 32 introduced. Later, Prins in Grün et al. (1974) established the genus Carinolithus and emended R. 33 superbus as C. superbus. Similarly, Medd (1979) emended R. sceptrum and R. clavatus as C. 34 sceptrum and C. clavatus, respectively. Bown (1987a) interpreted C. sceptrum as a variant of C. 35 36 superbus and considered C. clavatus to group incomplete specimens of C. superbus without the distal 37 shield. Consequently, the species *C. clavatus* and *C. sceptrum* were abandoned by subsequent authors. The species C. magharensis was initially established within the genus Hexalithus (Moshkovitz & 38 39 Ehrlich, 1976) and later Bown (1987a) moved it to genus Carinolithus based on scanning electron microscope investigations since the hexaliths are distal shields of carinolithids. According to Bown 40 (1987a), C. superbus and C. magharensis are easily discriminated if detected in distal view (DV) as 41 the number of wedge-shaped elements forming their distal shields is ten to twelve in C. superbus and 42 six in C. magharensis. Moreover, Bown (1987a) observed that the distal shield of C. magharensis 43 44 flares sharply (roughly at right angles) from the stem and has a rectangular shape in a transverse section whereas that of C. superbus flares more gradually. Taxonomic incongruity, however, emerges 45 when Carinolithus coccoliths are observed in side view (SV), because the shape is essentially the 46 47 same (T-shape structure). Two additional species were established: C. cantaluppii by Cobianchi (1990) and C. poulnabronei by Mattioli (1996). The latter possesses a peculiar V-shape structure in 48 SV and is, thus, easily distinguishable from *C. superbus* and *C. magharensis*. 49 A solid taxonomy is fundamental since the different species of this genus are used as events in 50 standard zonations of higher (Bown, 1987a; Bown et al., 1988; Bown & Cooper, 1998; Fraguas et al., 51 2015) and lower latitudes (Mattioli & Erba, 1999; Ferreira et al., 2019). In particular, the first 52

occurrence (FO) of C. superbus marks the inception of the NJT6 and NJ6 Zones in the Tethyan and 53 54 Boreal Realms, respectively, and is calibrated with the positive carbon isotope rebound preceding the negative carbon isotope excursion which is correlative to the Toarcian Oceanic Anoxic event (T-55 OAE) on a supraregional scale (Mattioli et al., 2004; 2013; Casellato & Erba, 2015; Ferreira et al., 56 2019). The FO of C. magharensis is used to define the base of the NJT8f Subzone (Ferreira et al., 57 2019), which corresponds to the basal Aalenian Opalinum Zone. Moreover, although not considered 58 zonal/subzonal events, the FOs of C. cantaluppii and C. poulnabronei are indicated as additional 59 biohorizons in the standard biozonations. 60 In this work morphometric analyses, performed on smear slides under a polarizing light microscope, 61 62 were applied to C. superbus and C. magharensis specimens in order to clarify the taxonomy. Moreover, a detailed study of C. cantaluppii was conducted to ascertain the potential role of 63

65 Fig. 1, about here, one column and half.

overgrowth on its morphology.

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2. Materials and Methods

A total of 100 specimens of the C. superbus and C. magharensis groups were investigated for morphometric analyses using photographs taken with polarizing light microscope. A total of 62 images were selected from published works (Appendix 1) complemented with 38 additional specimens from sections in the Lombardy Basin (Sogno Core in northern Italy and Breggia section in southern Switzerland). In Appendix 1, for each investigated specimen the following information (as reported in the original paper) is given: calcareous nannofossil Zones/Subzones, ammonite Zones/Subzones, stage/substage, core/section. Smear slides were prepared with the random settling technique (Geisen et al., 1999) for the Sogno Core and the standard smear slide technique (Bown & Young, 1998) for the Breggia section. Photographs were acquired using a Leitz Laborlux optical polarizing light microscope at 1250X magnification and a Q imaging Micropublisher 5.0. RTV digital camera. Images were analyzed using

a PC with Q-capture Pro suite software adapted for nannofossil analyses. Measurements were taken 79

80 using ImageJ software, with an error of measurements of ± 0.08 µm.

Six parameters were measured: the Total Height (TH); the Stem Height (SH); the Stem Width (SW); 81

the Proximal Shield diameter (PS); the Distal Shield diameter (DS) and the Thickness of the Distal

Shield (TDS) as illustrated in Fig. 2. In case of observations in side view or when specimens are

broken or heavily overgrown, a few parameters could not be measured. A total of 341 measurements

were obtained: 29 for the TH, 29 for the SH, 75 for the SW, 29 for the PS, 100 for the DS, 79 for the

TDS. 86

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Statistical parameters like mean, mode, median, standard deviation and 95% confidence level were 87

calculated using the Matlab and PAST softwares and reported in Tab. 1. Moreover, a mixture analysis

was run, using PAST software (Hammer et al., 2001), in order to find the overall mixing proportions

of specimens belonging to different taxa. This probabilistic model is a maximum-likelihood method

for estimating the parameters (mean, standard deviation and proportion) of two or more univariate

normal distributions, based on a pooled univariate sample (Hammer & Harper, 2006).

As far as C. cantaluppii is concerned, 50 specimens were qualitatively investigated taking four 93

pictures of each specimen, both with and without quartz lamina, both at 0° and 45° to the polarizers.

95 Fig. 2, about here, two columns.

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3. Results

Figure 2 synthesizes the results obtained for TH, SH, SW, PS, DS and TDS for *C. superbus* (blue) 98

and C. magharensis (red) specimens. Based on the DS and TDS two different-sized groups of

coccoliths are distinguished. As far as the DS is concerned, one group shows values ranging from 2.8

to $6.8 \mu m$ whereas the other is from 7.8 to $10.9 \mu m$. The bigger-sized group comprises only specimens

of the C. magharensis group whereas the smaller-sized coccoliths belong to both groups. We also

notice that no specimens have a DS in the range of 6.9 to 7.7 µm.

- The TDS separates a first group varying between 0.4 and 1.5 µm from a second one in the range of 104
- 1.8 2.9 μm. This latter bigger-sized group entirely consists of specimens of the C. magharensis 105
- group while the smaller-sized only comprises specimens of the C. superbus group. 106
- The parameters TH, SH, SW and PS do not discriminate between the C. superbus and C. magharensis 107
- 108 groups. Nevertheless, C. magharensis specimens generally show higher values of TH and SH. Mode,
- median, mean and standard deviation are provided in Tab. 1 for each parameter by considering a) all 109
- the investigated specimens; b) specimens of the C. magharensis group; c) specimens of the C. 110
- superbus group. Both DS and TDS have mode, median, mean and standard deviation much higher 111
- (almost double) in the *C. magharensis* group, thus showing systematic differences. 112
- 113 Tab. 1, about here, one column and half.
- The Pearson's correlation coefficient (Fig. 3) shows: a) positive values for TH/SH, TH/DS, TH/TDS, 114
- SH/PS, SH/DS, SH/TDS, SW/PS, SW/DS, PS/DS, DS/TDS and b) negative coefficients for TH/SW, 115
- TH/PS, SH/SW, SW/TDS, PS/TDS. In particular, a strong positive correlation exists for TH/SH (r = 116
- 0.97), DS/TH (r = 0.69), TDS/TH (r = 0.66), DS/SH (r = 0.62), TDS/SH (r = 0.51), TDS/DS (r = 117
- 0.64). 118
- The Pearson's correlation coefficient was also calculated separately for the C. magharensis and C. 119
- superbus specimens: a clear distinction between the two groups is indicated only for the TH/TDS, 120
- 121 SH/TDS, SW/TDS, PS/TDS, and DS/TDS ratios, as evidenced by the red and blue clouds in Fig. 3.
- Fig. 3, about here, two columns. 122

4. Discussion 124

- 4.1. Taxonomic revision of C. superbus and C. magharensis 125
- Morphometric analyses turned out to be an excellent tool to separate *C. magharensis* and *C. superbus* 126
- specimens. In particular, the DS (Fig. 4a) discriminates 23 specimens with sizes of 7.8 10.9 µm 127
- from a group of 77 specimens with a DS ranging between 2.8 and 6.8 µm. The former group 128
- comprises exclusively large C. magharensis specimens, whereas the second group includes C. 129

- superbus coccoliths and small specimens of C. magharensis. Within this latter group, the TDS 130
- separates two clusters (Fig. 4b): one cluster includes 56 specimens characterized by a TDS ranging 131
- from 0.4 to 1.5 µm and a second one, grouping 18 specimens, with a TDS varying from 1.8 to 2.9 132
- um. The latter group consists exclusively of C. magharensis with a thicker distal shield relative to C. 133
- 134 superbus specimens.
- A further subdivision was obtained using the SW of C. superbus specimens (Fig. 4c): a group includes 135
- 30 specimens characterized by a SW spanning from 0.5 to 1.0 µm and another cluster of 26 coccoliths 136
- with a SW varying from 1.3 to 2.5 µm. Therefore, within C. superbus, the SW separates thin from 137
- thick morphotypes. 138
- 139 Fig. 4, about here, two columns.
- Our morphometric analyses allowed the identification of four separate groups: large C. magharensis 140
- (DS \geq 7.8 µm), small C. magharensis (DS \leq 6.8 µm and TDS \geq 1.8 µm), thin C. superbus (SW \leq 1 141
- 142 μ m, TDS < 1.5 μ m and DS < 6.8 μ m) and thick C. superbus (SW \geq 1.3 μ m, TDS \leq 1.5 μ m and DS
- $< 6.8 \mu m$). 143
- The large C. magharensis specimens (DS \geq 7.8 µm) are characterized by DS fully consistent with the 144
- holotype of H. magharensis possessing a DS of 8 µm, whereas the small C. magharensis specimens 145
- (DS \leq 6.8 µm) evidently do not fall within the original definition of this taxon. Therefore, the two 146
- 147 morphogroups can be distinguished as C. magharensis subsp. magharensis (large specimens) and C.
- magharensis subsp. minor subsp. nov. (small specimens; see taxonomic remarks later on). 148
- Within the C. superbus group, the thin specimens (SW $\leq 1.0 \mu m$) are consistent with the original 149
- 150 description of this species. In fact, the holotype of R. superbus (Deflandre in Deflandre & Fert, 1954;
- figs. 24, 25) has a SW of 0.7 μ m. The specimens with SW \geq 1.3 μ m, instead, are distinctly thicker. 151
- Accordingly, the two morphogroups can be distinguished as C. superbus subsp. superbus (thin 152
- specimens) and C. superbus subsp. crassus subsp. nov. (thick specimens; see taxonomic remarks later 153
- on). 154

Recently, Ferreira et al. (2019) documented C. superbus specimens characterized by a thinner and longer stem which they named "C. superbus thin and long"; also, they made a distinction between C. magharensis and "C. magharensis large". The qualitative taxonomic subdivision of Ferreira et al. (2019) is consistent with our morphometric results and, specifically, their C. superbus corresponds to C. superbus subsp. crassus, C. superbus "thin and long" to C. superbus subsp. superbus, C. magharensis to C. magharensis subsp. minor, and C. magharensis "large" to C. magharensis subsp. magharensis. Figure 5 summarizes the morphometric data of the holotypes and specimens analyzed in this work for C. superbus subsp. crassus, C. superbus subsp. superbus, C. magharensis subsp. minor and C. magharensis subsp. magharensis. Polarizing light microscope photos are presented in Fig. 6. Based on morphometric investigations, we established size-dependent new taxa.

- 165 *Fig. 5, about here, one columns and half.*
- In the following section, the systematics of C. superbus subsp. crassus, C. superbus subsp. superbus, 166
- C. magharensis subsp. minor and C. magharensis subsp. magharensis are detailed. Diagnosis, 167
- description, remarks and differentiation are provided for each taxon. 168

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- Genus Carinolithus Prins in Grün et al. (1974) 170
- Carinolithus superbus subsp. crassus Visentin & Erba subsp. nov. 171
- 172 Fig. 6, a-f; Fig. 8, c1-c7, d1-d6.
- **Etymology:** the name derives from the diagnostic thick stem. 173
- **Diagnosis:** a subspecies of *Carinolithus superbus* with a thick stem (width $> 1 \mu m$). 174
- 175 **Description:** this new subspecies is characterized morphometrically by possessing a stem width > 1
- μm and a relatively narrow but still open axial canal. 176
- **Remarks:** on the basis of available data the total height varies between 6.3 12.1 µm; stem width: 177
- $1.3 2.5 \mu m$; proximal shield diameter: $2.1 3.9 \mu m$; distal shield diameter: $3.0 5.6 \mu m$; thickness 178
- of distal shield: $0.4 1.5 \mu m$. 179

- Stratigraphic range: FO in the Lower Toarcian, Polymorphum or Tenuicostatum ammonite Zone, 180
- correlative with the positive carbon isotope rebound preceding the negative carbon isotope excursion 181
- which is correlative to the Toarcian Oceanic Anoxic event (T-OAE). The FO of this subspecies 182
- substitutes the FO of *C. superbus* as a marker for the base of the NJT6 and NJ6 Zones. 183
- 184 **Differentation:** Carinolithus superbus subsp. crassus differs from C. superbus subsp. superbus by
- its thicker stem (width $> 1 \mu m$) and by its wider and well distinguishable axial canal, from C. 185
- poulnabronei by its T- shape, from C. magharensis subsp. minor by its thinner distal shield (\le 1.5) 186
- µm) and from C. magharensis subsp. magharensis by its thinner ($\leq 1.5 \, \mu m$) and smaller ($< 6 \, \mu m$) 187
- distal shield. The T-shape of C. superbus subsp. crassus is unambiguously different for the V-shape 188
- 189 of C. poulnabronei.
- Holotype: Fig. 8, c1-c4. Holotype total height: 8.8 μm; stem width: 1.7 μm; proximal shield diameter 190
- 3.1 µm; distal shield diameter: 4.6 µm; thickness of the distal shield: 1.3 µm. 191
- **Type locality:** Colle di Sogno (Italy). 192
- Type level: Jurassic, Toarcian. 193
- **Depository:** Department of Earth Sciences "Ardito Desio" of Milan (Reference MPUM 1870). 194
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- Carinolithus superbus (Deflandre in Deflandre & Fert, 1954) Prins in Grün et al. (1974) 196
- 197 subsp. superbus emend. Visentin & Erba
- Fig. 6, g-l; Fig. 8, e1-e8, f1-f6. 198
- Basionym: 199
- 200 1954 Rhabdolithus superbus Deflandre in Deflandre & Fert, p. 160; pl. 15; figs. 24-25; text-fig. 93.
- Reference: 201
- 1974 Carinolithus superbus Deflandre; Prins in Grün et al., p. 313; pl. 15; figs. 1-3; text-fig. 13. 202
- **Description:** the original description of *Carinolithus superbus* by Deflandre *in* Deflandre & Fert 203
- (1954) is maintained for Carinolithus superbus subsp. superbus. This subspecies is further 204
- characterized morphometrically by possessing a stem width $\leq 1 \mu m$. 205

- **Remarks:** on the basis of available data the total height varies between $5.8 15.9 \mu m$; stem width: 206
- $0.5 1.0 \mu m$; proximal shield diameter: $1.4 3.9 \mu m$; distal shield diameter: $3.0 5.6 \mu m$; thickness 207
- of distal shield: $0.4 1.5 \mu m$. 208
- Stratigraphic range: FO between the uppermost part of the Levisoni Zone and the base of the 209
- Bifrons Zone (Ferreira et al., 2019; Lower/Middle Toarcian boundary), in the lowermost part of the 210
- NJT7 and NJ7 Zones. 211
- **Differentation:** Carinolithus superbus subsp. superbus differs from C. superbus subsp. crassus by 212
- its thinner stem ($\leq 1 \mu m$), from C. poulnabronei by its T- shape, from C. magharensis subsp. minor 213
- by its thinner distal shield ($\leq 1.5 \,\mu m$) and from C. magharensis subsp. magharensis by its thinner (\leq 214
- 215 1.5 μ m) and smaller (< 6 μ m) distal shield.
- Holotype: Deflandre in Deflandre & Fert (1954; figs. 24-25). Holotype total height: 10.3 µm; stem 216
- width: 0.7 μm; proximal shield diameter: 2.7 μm; distal shield diameter: 4.3 μm; thickness of the 217
- distal shield: 1.0 µm. 218
- **Type locality:** Villers-sur-Mer, Calvados (Spain) (Deflandre & Fert, 1954). 219
- **Type level:** Jurassic, Oxfordian (Deflandre & Fert, 1954). 220
- Depository: Collection du Laboratoire de Micropaléontologie de l'Ecole pratique des Hautes Etudes, 221
- Paris (Deflandre & Fert, 1954). 222
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- Carinolithus magharensis subsp. minor Visentin & Erba subsp. nov. 224
- Fig. 6, m-r; Fig. 8, g1-g7, h1-h4. 225
- **Etymology:** the name derives from the diagnostic small diameter of the distal shield relative to C. 226
- magharensis subsp. magharensis. 227
- **Diagnosis:** a subspecies of C. magharensis with a thick (> 1.5 μ m) and small (< 7 μ m) distal shield. 228
- The distal shield is constituted by 6 elements. 229
- **Description:** this new subspecies is characterized morphometrically by possessing a thickness of the 230
- distal shield $> 1.5 \mu m$ and a distal shield diameter $< 7 \mu m$ which is constituted by 6 elements. 231

- **Remarks:** on the basis of available data the total height varies between $11.1 16.6 \mu m$; stem width: 232
- $0.6-1.1 \mu m$; proximal shield diameter: $1.7-3.0 \mu m$; distal shield diameter: $4.1-6.8 \mu m$; thickness 233
- of distal shield: $1.8 2.9 \mu m$. Morphometric analyses separate specimens with distal shield $\leq 6.8 \mu m$ 234
- from specimens $\geq 7.8 \, \mu \text{m}$ (C. magharensis subsp. magharensis) and no intermediate sizes have been 235
- found. According to the morphometric diagnosis of C. magharensis subsp. minor, specimens 236
- attributed to C. magharensis by Bown (1987a; page 59) show features (distal shield diameter varying 237
- between 4.5 and 5.9 µm) consistent with C. magharensis subsp. minor. 238
- Stratigraphic range: Hexalithus magharensis was reported from the late Opalinum Zone (Early 239
- Aalenian) in the Tethyan Realm occurring shortly after Watznaueria contracta (Mattioli & Erba, 240
- 241 1999). Recent data from the well-dated Cabo Mondego section (Portugal) show an earlier occurrence
- 242 of C. magharensis, close to the base of the Opalinum ammonite Zone still shortly following the FO
- of W. contracta reported from the basal Aalensis ammonite Zone of latest Toarcian age (Ferreira et 243
- al., 2019). Because of its distinctive morphological characters, the FO of C. magharensis was 244
- proposed to define the base of the NJT8f Subzone (Ferreira et al., 2019). The separation of the two 245
- subspecies C. magharensis subsp. minor and C. magharensis subsp. magharensis implies that future 246
- investigations will clarify their FOs. 247
- **Differentation:** Carinolithus magharensis subsp. minor differs from C. magharensis subsp. 248
- 249 magharensis for its smaller distal shield (< 7 µm), from C. superbus subsp. crassus and C. superbus
- subsp. superbus for its thicker distal shield (> 1.5 µm). 250
- Holotype: Fig. 8, g1-g4. Holotype distal shield diameter: 5.6 µm; thickness of the distal shield: 2.3 251
- 252 μm.

- Type locality: Breggia (Switzerland). 253
- Type level: Jurassic, Aalenian. 254
- **Depository:** Department of Earth Sciences "Ardito Desio" of Milan (Reference MPUM 1869). 255

- Carinolithus magharensis (Moshkovitz & Ehrlich, 1976) Bown (1987a) subsp. magharensis emend. 257
- 258 Visentin & Erba
- Fig. 6, s-x; Fig. 8, i1-i6. 259
- Basionym: 260
- 1976 Hexalithus magharensis Moshkovitz & Ehrlich, p. 16, pl. 8; figs. 12-15. 261
- Reference: 262
- 1987a Carinolithus magharensis Moshkovitz & Ehrlich; Bown, pp. 58-59; pl. 8; figs. 4-6; pl. 14; 263
- figs. 17-20. 264
- **Description:** the original description of Moshkovitz & Ehrlich (1976) is maintained for specimens 265
- 266 observed in top view. This subspecies is further characterized by a thick (> 1.5 μ m) and large (≥ 8
- μm) distal shield constituted by 6 elements. The original description of Hexalithus magharensis 267
- applies to hexaliths more or less hexagonal in shape composed of 6 distinct triangular elements; 268
- 269 towards the margin, the corners of these triangles are obliquely truncated. In light microscope each
- element has its own optical orientation. Hexalithus magharensis comprises specimens of 8-9 µm in 270
- diameter. Bown (1987a) emended H. magharensis by transferring the species into the genus 271
- Carinolithus. However, the illustrated specimens possess a distal shield diameter varying between 272
- 273 4.5 and 5.9 μm, thus definitively smaller than the holotype and species variability of *H. magharensis*.
- 274 Our morphometric analyses confirm the separation of two groups, and we attribute to C. magharensis
- subsp. magharensis only specimens with a distal shield larger than 8 µm. 275
- Remarks: the original description of Moshkovitz & Ehrlich (1976) is confirmed for specimens 276
- observed in top views. On the basis of available data, the stem width varies between $1.2 1.7 \mu m$; 277
- distal shield diameter: $7.8 10.9 \mu m$; thickness of distal shield: $2.0 2.9 \mu m$. 278
- **Stratigraphic range:** Although *C. magharensis* subsp. *minor* and *C. magharensis* subsp. 279
- magharensis are very rare after their first occurrence (i.e., 1-2 specimens in 250 fields of view at 1250 280
- X magnification), a re-analysis of the Cabo Mondego section shows the presence of both subspecies 281

- from the Early Aalenian (base Opalinum Zone). However, C. magharensis subsp. magharensis
- becomes more common from the Bajocian upwards.
- Differentation: Carinolithus magharensis subsp. magharensis differs from C. magharensis subsp.
- *minor* for its larger distal shield ($> 8 \mu m$) and more sharply truncated triangular elements.
- Holotype: Moshkovitz & Ehrlich (1976, figs. 14-15). Holotype distal shield diameter: 8 μm.
- 287 Type locality: Israel. This species occurs in the Gebel Maghara outcrop, in the Lower Sherif and
- Upper Daya Formations (Moshkovitz & Ehrlich, 1976).
- **Type level:** Jurassic, Bajocian-Bathonian (Moshkovitz & Ehrlich, 1976).
- **Depository:** Geological Survey of Israel (Moshkovitz & Ehrlich, 1976).
- 291 Fig. 6, about, here, two columns.

4.2. Effects of diagenesis on the genus Carinolithus

The taxon *C. cantaluppii* was established by Cobianchi (1990; fig. 4, h) as a species of *Carinolithus* with a small proximal shield and a large distal spine that typically broadens at about ¼ (from the base) maintaining the size (width) up to the distal shield. Under crossed nicols *C. cantaluppii* shows high birefringence colors (from white to orange) and a clear extinction line in the middle of the spine. The proximal shield diameter is 2.3-2.8 μm, the distal shield diameter is 3.0-4.0 μm, and the height is 8.0-10 μm. Cobianchi (1990) used the term "spine" as the equivalent of "stem" and, therefore, the "broadening of the spine" corresponds to the broadening of the stem. Based on the original description, *C. cantaluppii*, similarly to other *Carinolithus* species, should have a symmetric shape including the broadening of the stem. However, the only specimen (presumably the holotype) illustrated by Cobianchi (1990) is clearly asymmetric as the two sides of the stem broaden at different points and with different widths. The right side of the stem (Fig. 1e) broadens at about ¼ from the base (as provided by the author's description) whereas the left side of the stem slightly broadens (less wide and with a different shape) at about ½ from the base. The drawing of *C. cantaluppii* in Mattioli (1996; fig. 3) shows a symmetric stem broadening at about ¾ from the base. In the literature, several

photos of C. cantaluppii specimens show an extremely asymmetric shape (e.g. Cobianchi 1990, fig. 308 4, h; Cobianchi 1992, fig. 20, g; Perilli & Duarte, 2006, pl. 1, fig. 5; Ferreira et al., 2015, pl. 1, fig. 309 12) whereas other specimens appear broadly symmetric (e.g. Gardin & Manivit, 1994, pl. 3, fig. 11; 310 Perilli & Duarte, 2006, pl. 1, fig. 9; Sandoval et al. 2012, fig. 10, n. 8-10). In both cases, the stem 311 312 broadens at a different height from the base. We underline that C. cantaluppii is often not documented or is reported with a sparse occurrence and, 313 consequently, its biostratigraphic value remains highly questionable. In order to clarify the diagnostic 314 features of this taxon, a detailed characterization was conducted in smear slides using four different 315 configurations under the polarizing light microscope: with and without quartz lamina, both at 0° and 316 45° to the polarizers (Fig. 7). Pictures at 0° to the polarizers show that specimens are rarely symmetric 317 318 due to extremely variable broadening of the stem and the extremely high birefringence colors concur in suggesting that the stem broadening is due to overgrowth. Differences in asymmetry, height of 319 320 stem broadening and its extension advocate variable degrees of diagenetic modifications. Indeed, pictures at 45° to the polarizers – both with and without the quartz lamina - document the overgrowth 321 of the stem while showing the original distal shield and stem, thus allowing recognition of the original 322 323 taxon.

324 Fig. 7, about here, one column

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Figure 8 includes pictures of moderately and poorly (overgrown) preserved specimens of C. poulnabronei, C. superbus subsp. crassus, C. superbus subsp. superbus, C. magharensis subsp. minor and C. magharensis subsp. magharensis. The light blue bands (Fig. 8 specimens b, d, f, h) evidence overgrown specimens referable to C. cantaluppii of Cobianchi (1990). Specimens characterized by moderate preservation show an intermediate diagenetic phase (Fig. 8 specimens a, c, e, g, i). The use of the quartz lamina at 45° to the polarizer appears to be the best way to recognize those specimens which underwent the diagenetic modification, as in the case of photos a and b = C. poulnabronei, c and c superbus subsp. crassus, c and c superbus subsp. superbus, c and c superbus subsp. magharensis.

Fig. 8, about here, two columns

Three diagenetic phases are separated based on the extent of overgrowth (O) starting from the base of the distal shield downwards and eventually reaching the proximal shield (Fig. 9). Phase 1 characterizes specimens with negligible diagenetic modification (O = 0). In phase 2 diagenesis affects the uppermost part of the stem without reaching the middle point of the stem (0 < O < SH/2) (Fig. 8 specimens a, c, e, g, i). In phase 3 overgrowth is more pervasive and exceeds the middle point of the stem (O > SH/2) (Fig. 8 specimens b, d, f, h). Diagenetic modifications are generally prevalent on one side of the stem as a result of differential overgrowth producing asymmetry as in the case of the holotype of *C. cantaluppii* (Cobianchi, 1990; fig. 4, h). The species *C. cantaluppii* is, therefore, an artefact due to advanced diagenesis and not a separate taxon. In addition to taxonomic clarification, the recognition of the diagenetic phase in *Carinolithus* specimens is an effective proxy to assess the impact of overgrowth and the diagenetic degree in the studied material. In Appendix 1 we present the characterization of the diagenetic phase for all the investigated specimens illustrated in the literature.

4.3. Implications for the Lower and Middle Jurassic biostratigraphy

T-OAE. Consistent results are reported by Ferreira et al. (2019).

Fig. 9, about here, one column and half

The taxonomic revision of *Carinolithus* species has shown that the subsequent first occurrences (FOs) of C. superbus subsp. crassus and C. superbus subsp. superbus, have the potential to significantly increase the biostratigraphic resolution (Fig. 10). The FO of C. superbus subsp. crassus has been recently identified just before the C isotopic negative anomaly associated with the T-OAE in the Sogno Core (Visentin & Erba, unpublished data; Visentin, 2020). Pictures of C. superbus subsp. crassus are documented in several works (see Appendix 1) and the oldest ones (Mattioli et al., 2013; Menini et al., 2018; Da Rocha et al., 2016) derive from samples concomitant with the C isotopic positive rebound preceding the negative anomaly associated with the

The oldest photographic documentation of C. superbus subsp. superbus (see Appendix 1) indicates a 359 FO in the Serpentinus ammonite Zone (Baldanza & Mattioli, 1992). Ferreira et al. (2019) placed the 360 FO of C. superbus "thin and long" at the Lower/Middle Toarcian boundary, in the lowermost part of 361 the NJT7 Zone. Ongoing investigations (Visentin, 2020) confirm the FO of C. superbus subsp. 362 superbus in the lowermost part of the NT7 Zone in the Schandelah Core from the Boreal Realm 363 (Visentin, 2020). 364 The FO of C. superbus subsp. crassus is, therefore, older than that of C. superbus subsp. superbus 365 and corresponds to the FO of C. superbus in the biozonations of Mattioli & Erba (1999) and Bown 366 & Cooper (1998) used to define the base of the NJT6 and NJ6 Zones, respectively. Based on our 367 368 taxonomic revision, the FO of C. superbus subsp. crassus should be considered the marker for the 369 base of the NJT6 and NJ6 Zones. As far as the FOs of C. magharensis subsp. minor and C. magharensis subsp. magharensis are 370 371 concerned, these two taxa have been grouped together until now, so future investigations are needed to discriminate their respective first appearance level. However, C. magharensis subsp. minor and C. 372 magharensis subsp. magharensis, although very rare after their first occurrence, co-occur in samples 373 from the Lower Aalenian (base Opalinum Zone) of the Cabo Mondego section. However, C. 374 magharensis subsp. magharensis became more common from the Bajocian upwards in Portugal. 375

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4.4. Evolution of the genus Carinolithus

Fig. 10, about here, one column

During the Late Pliensbachian – Early Toarcian time interval, calcareous nannoplankton underwent an intense phase of diversification evidenced by the appearance of several species and genera (Mattioli & Erba, 1999; Bown et al., 2004; Erba, 2004; 2006; Menini et al., 2018). As previously discussed by Crux (1987), Bown (1987b) and Mattioli (1996), the genus *Calyculus* gave rise to the genus *Carinolithus*. Mattioli (1996; fig. 3) illustrated the transition between *Calyculus* spp. and *C. poulnabronei* characterized by the gradual closing of the axial canal and the development of a vertical

stem showing progressive thinning along with thickening of the distal shield. The hypothesis that C. cantaluppii descended from C. poulnabronei is here rejected since the former species, as aforementioned, represents a diagenetic artefact due to overgrowth. Therefore, C. poulnabronei passes to C. superbus subsp. crassus through a decrease of both shield width and thinning of the stem. Thus, in the Early Toarcian the V-shape of both the stem and the axial canal of C. poulnabronei coexisted with the typical T-shape of C. superbus. subsp. crassus. A further decrease of the stem width characterizes C. superbus subsp. superbus, that is generally represented by taller specimens (Fig. 5). The transition between the C. superbus group and the C. magharensis group seems related to variations in thickness and ultrastructure of the distal shield. In fact, morphometry evidenced a progressive thickening of the distal shield (TDS) correlated to TH and DS (r = 0.66 and 0.64, respectively) passing from C. superbus subsp. superbus to C. magharensis subsp. minor. A further increase of the DS diameter characterizes the transition from C. magharensis subsp. minor to C. magharensis subsp. magharensis directly correlated to an increase of PS and SW (r = 0.80 and 0.87, respectively).

5. Conclusions

Morphometric investigations of the genus *Carinolithus* resulted in a revision of its taxonomy. Statistical treatment of the measurements validated the significance of the proposed coccolith parameters to separate taxa between and within the *C. superbus* and *C. magharensis* groups. Specifically, based on the stem width, as well as thickness and width of the distal shield two new subspecies, *C. superbus* subsp. *crassus* and *C. magharensis* subsp. *minor*, were established. The qualitative characterization of overgrowth affecting *Carinolithus* coccoliths revealed that *C. cantaluppii* represents a diagenetic artefact. The use of the lamina at 45° to the polarizers turned out to be an excellent tool to recognize the real species which underwent the diagenetic modification, and three diagenetic phases were distinguished. Overgrowth generally starts in the uppermost part of the

coccoliths at the base of the distal shield. Identification of the diagenetic phases can be used to 410 evaluate nannofossil/sediment preservation and degree of secondary modifications. 411 The application of the revised taxonomy implies a revised evolution of the genus Carinolithus and a 412 higher resolution of calcareous nannofossil biostratigraphy in the Toarcian and Lower Aalenian 413 interval. In particular, the FO of C. superbus subsp. superbus, which approximates the Lower/Middle 414 Toarcian boundary, has been recently used as an additional event in zonal schemes. 415 416 Acknowledgements 417 The authors are grateful to the Editor Richard Jordan and two anonymous Reviewers, whose 418 419 comments improved the quality of the manuscript. The research was conducted within the PRIN 420 2017RX9XXXY awarded to EE. 421 422 References Aguado, R., O'Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the 423 Aalenian (mid-Jurassic) of the Western Tethys as revealed by calcareous nannofossils and 424 carbon-cycle perturbations. Marine Micropaleontology. 68, 268-285. 425 Aguado, R., O'Dogherty, L., Sandoval, J., 2017. Calcareous nannofossil assemblage turnover in 426 427 response to the Early Bajocian (Middle Jurassic) palaeoenviromental changes in the Subbetic Basin. Palaeogeography, Palaeoclimatology, Palaeoecology. 472, 128-145. 428 Baldanza, A., Mattioli, E., 1992. Biostratigraphical synthesis of nannofossils in the Early Middle 429 430 Jurassic of southern Tethys. Knihovnička ZPN. 14a (1), 111-141. Bodin, S., Mattioli, E., Fröhlich, S., Marshall, J.D., Boutib, L., Lahsini, S., Redfern, J., 2010. Toarcian 431 carbone isotope shifts and nutrient changes from the Northern margin of Gondwana (High 432 Atlas. Jurassic): Palaeoenviromental implications. Palaeogeography, 433 Morocco. Palaeoclimatology, Palaeoecology. 297, 377-390. 434

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537 CAPTIONS

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Fig. 1. Holotypes of *R. superbus* (Deflandre *in* Deflandre & Fert, 1954) (a), *R. sceptrum* (Deflandre in Deflandre & Fert, 1954) (b), *R. clavatus* (Deflandre in Deflandre & Fert, 1954) (c), *H. magharensis* (Moshkovitz & Ehrlich, 1976) (d), *C. cantaluppii* (Cobianchi, 1990) (e) and *C. poulnabronei* (Mattioli, 1996) (f).

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Fig. 2. Synthesis of the morphometric analyses performed on the *C. superbus* (in blue) and *C. magharensis* (in red) groups. Total height, stem height, stem width, proximal shield diameter, distal shield diameter and thickness of distal shield are indicated. The number of specimens measured (N) for each parameter is indicated.

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Fig. 3. Correlation plots of the measured parameters. Every parameter is compared with each other.

For each scatter plot, the Pearson's correlation coefficients (r), the linear regression line, the number of measured specimens (N) are given. Note that for TDS/SW, TDS/SH, TDS/PS, TDS/TH and TDS/DS the two groups are confined to clearly separated and distinct sets that do not overlap.

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Fig. 4. Distribution histograms for a) the distal shield diameter (histogram class sizes 0.5 μm), b) thickness of the distal shield (histogram class sizes 0.2 μm) and c) stem width (histogram class sizes 0.2 μm). Histograms provide the number of data for each size bin, highlighting differences in morphology.

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Fig. 5. Summary of sizes of investigated parameters in the holotypes and the variability quantified for the measured specimens for individual *Carinolithus* taxa. Number of specimens measured (N) are provided for each parameter.

Fig. 6. Photographs documenting the revised taxonomy. A = C. superbus subsp. crassus (a-f); B = C. superbus subsp. superbus (g-1), C = C. magharensis subsp. minor (m-r), D = C. magharensis subsp. magharensis (s-x). Specimens a, b, g, h, i, j, k, l, m, n, o, p, s, t are from this work: (a, b) Sogno Core; (g, h, i, j, k, l, m, n, o, p, s, t) Breggia section. Specimens c, d, e, f, q, r, u, v, w, x are from literature: (c) Bown & Cooper (1998; pl. 4.13, fig. 11); (d) Bown (1987a; pl. 14, fig. 15); (e) Menini et al. (2018; pl. 1, fig. 33); (f) Van de Schootbrugge et al. (2018; pl. 6, fig. 11); (q) Bown (1987a; pl. 14, fig. 17); (r) Bown & Cooper (1998; pl. 4.13, fig. 8); (u) Aguado et al. (2017; fig. 8, y); (v) Aguado et al. (2008; fig. 5, n. 19); (w) Bown & Cooper (1998; pl. 4.13, fig. 6); (x) Bown & Cooper (1998; pl. 4.13, fig. 7).

Fig. 7. Specimens of *C. cantaluppii* photographed in four different combinations both with and without quartz lamina, at 0° and 45° to the polarizers. Illustrated specimens are from the Breggia section.

Fig. 8. Photographs of *Carinolithus* specimens investigated in this study and taken from the literature. Specimens investigated in this study are illustrated with and without quartz lamina, at 0° and 45° relative to the polarizers. Based on the description proposed by Cobianchi (1990) specimens highlighted with light blue rectangles were assigned to *C. cantaluppii* before the current taxonomic revision. The new taxonomic identification of *Carinolithus* specimens allows to distinguish the true taxon which underwent diagenetic modifications. (a1-a4, b1-b4, c1-c4, d1-d4) Sogno Core; (e1-e4, f1-f4, g1-g4, h1-h4, i1-i4) Breggia section; (a5, a6) Sandoval et al. (2012; fig. 10, n. 16, 17); (b5, b6, b7) Mattioli (1996; pl. 2, figs. 9,11,12); (c5) Menini et al. (2018; pl. 1, fig. 33); (c6) Casellato & Erba (2015; pl. 1, fig. 16); (c7) Van de Schootbrugge et al. (2018; pl. 6, fig. 11); (d5) Reolid et al. (2014; fig. 6, CE30); (d6) Bodin et al. (2010; fig. 5, i); (e5) Sandoval et al. (2012; fig. 10, n. 20); (e6) Sandoval et al. (2012; fig. 10, n. 12); (e7) Aguado et al. (2008; fig. 5, n. 18); (e8) Molina et al. (2018; fig. 8, LL6); (f5) Ferreira et al. (2015; pl. 1, fig. 12); (f6) Cobianchi (1990; fig. 4, h); (g5) Sandoval et al.

589 (2012; fig. 10, n. 19); (g6) Bown & Cooper (1998; pl. 4.13, fig. 8); (g7) Bown (1987a; pl. 14, fig.

17); (i5) Aguado et al. (2008; fig. 5, n. 19); (i6) Bown & Cooper (1998; pl. 4.13, fig. 6).

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Fig. 9. Schematic representation of increasing diagenetic phases of *Carinolithus* specimens: SH =

stem height; SH/2 = half the stem height; O = overgrowth. Phase 1: no or negligible diagenetic

overprint (O = 0); **Phase 2**: overgrowth affects the uppermost part of the stem, starting from the base

of the distal shield downwards without reaching the stem middle point (0 < O < SH/2); Phase 3:

diagenesis becomes more pervasive and exceeds the middle point of the stem (O > SH/2). Overgrowth

may affect one or both sides of the stem and with different degrees.

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- Fig. 10. Stratigraphic distribution of C. poulnabronei, C. superbus subsp. crassus and C. superbus
- 600 subsp. *superbus*.

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- Tab. 1. Number of specimens, mean, median, mode and standard deviation of measured taxonomic
- characters (TH, SH, SW, PS, DS, TDS): a) all specimens; b) C. magharensis group; c) C. superbus
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- **Appendix 1** Data set of *Carinolithus* specimens from literature used for morphometric analyses.
- Data are organized following the publication date and for each specimen the following information
- 608 is given: investigated core/section; nomenclature adopted in the original paper; revised nomenclature
- following the revised taxonomy (this study); stage/substage; ammonite and calcareous nannofossil
- Zones and Subzones. Specimens selected for morphometric analyses are characterized with an X. The
- other specimens were used to characterize the diagenetic overprint. Carinolithus * is reported for
- specimens not attributable to a species due to high overgrowth.

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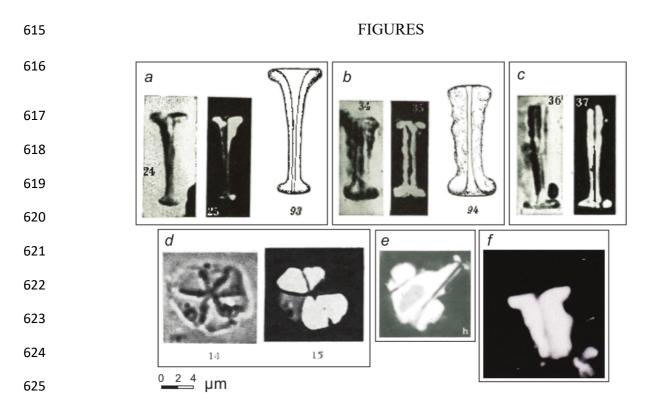


FIG. 1.PDF (one column and half) NOT COLOURS

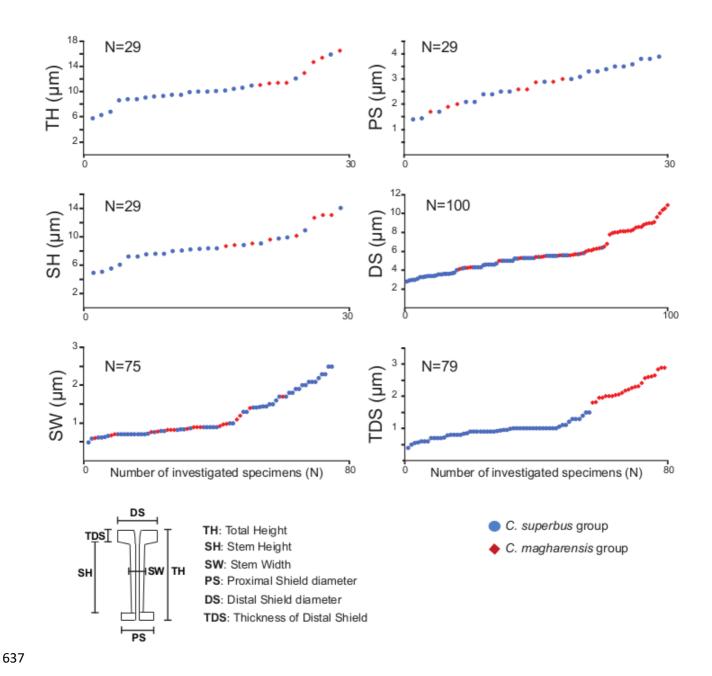


FIG. 2.PDF (two columns) COLOURS

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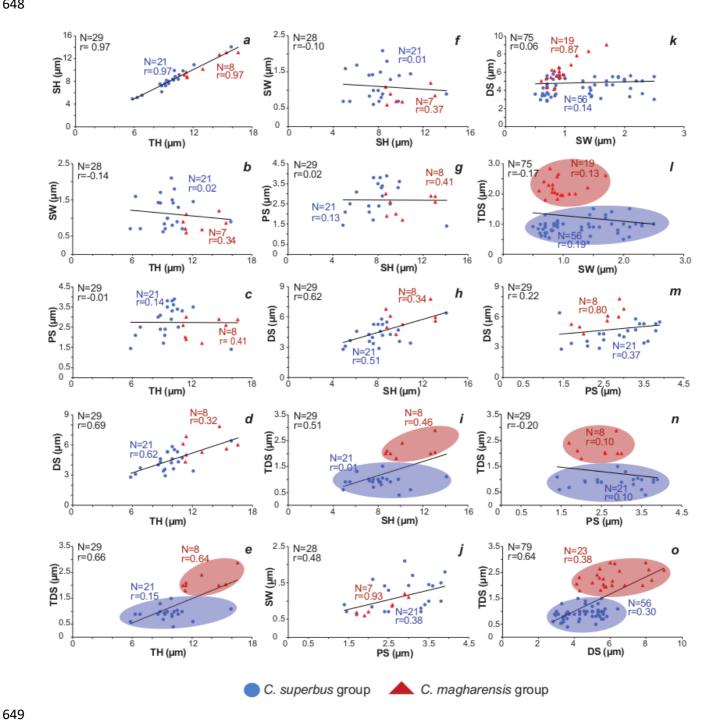


FIG. 3.PDF (two columns) COLOURS

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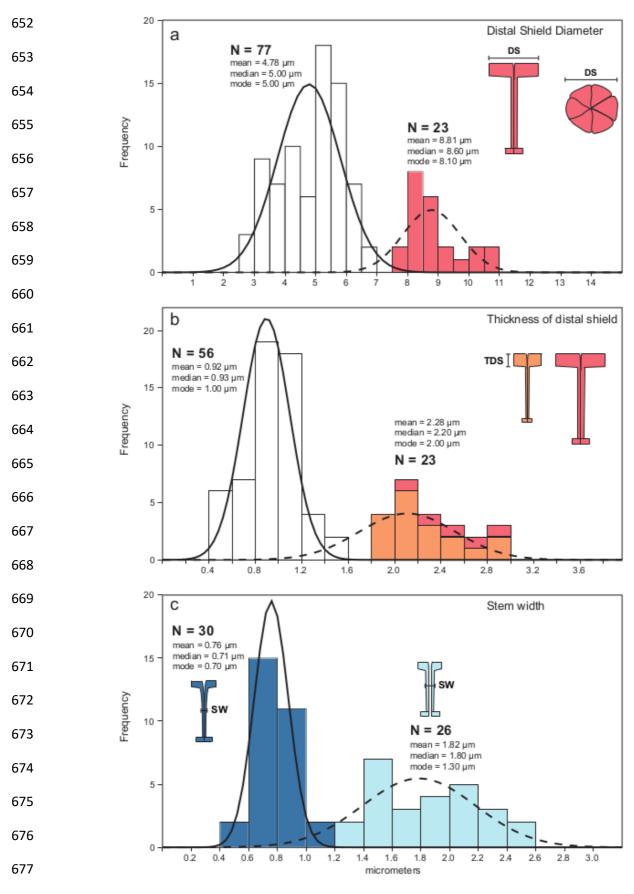


FIG. 4.PDF (two columns) COLOURS

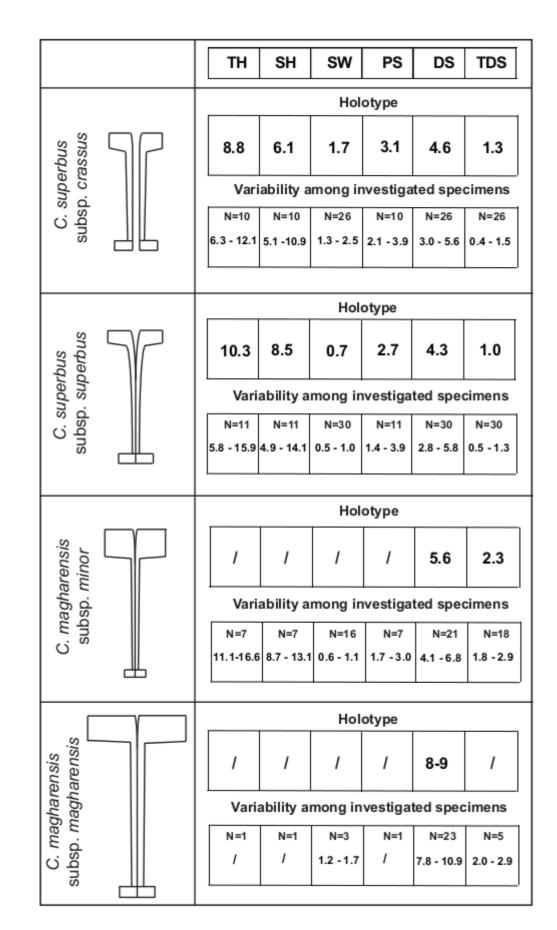


FIG. 5.PDF (one column and half) NOT COLOURS

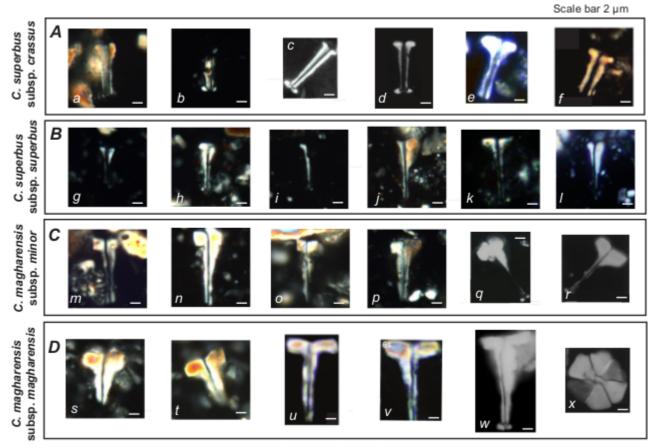


FIG. 6.PDF (two columns) COLOURS

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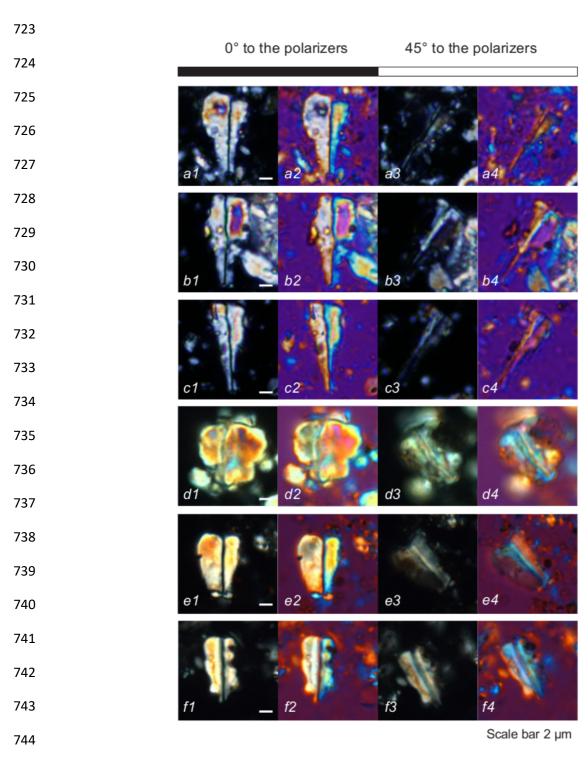


FIG. 7.PDF (one column) COLOURS

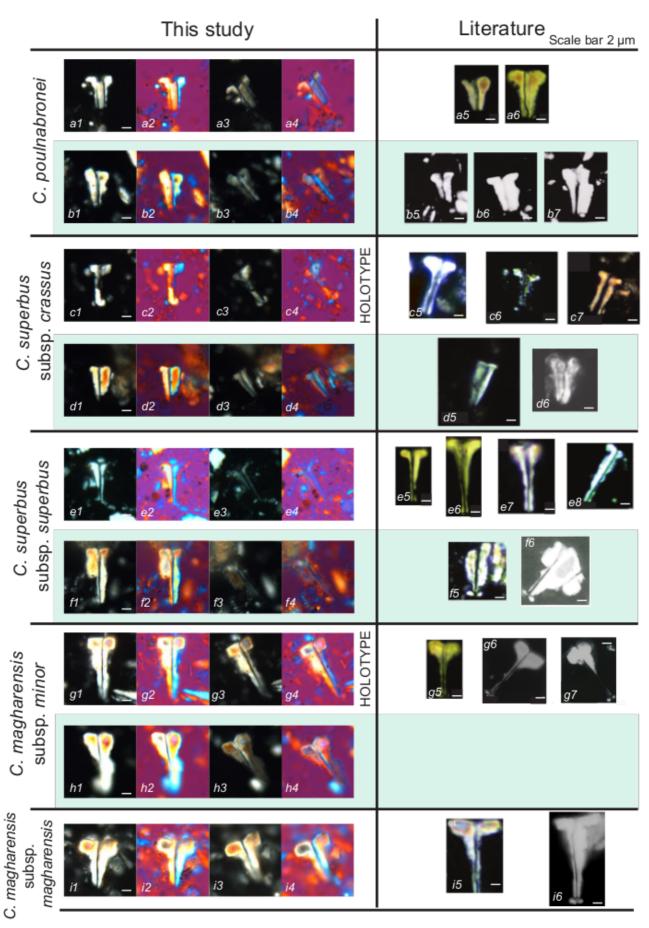


FIG. 8.PDF (two columns) COLOURS

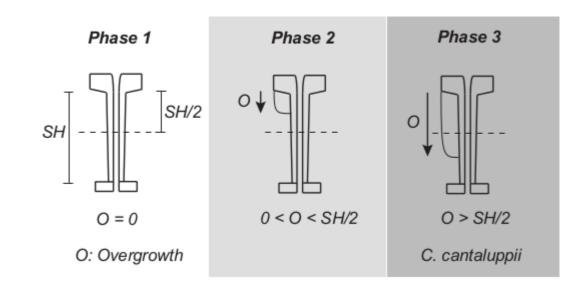


FIG. 9.PDF (one column and half) NOT COLOURS

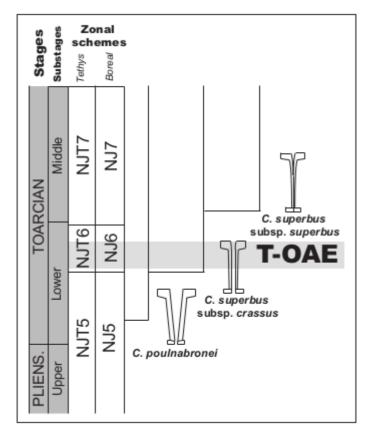


FIG10.PDF (one column) NOT COLOURS

TABLE 1. (one column and half)

	TH	SH	SW	PS	DS	TDS	
a. Total specimens							
Number of specimens	29	29	75	29	100	79	
Mode	8.80	8.40	0.70	1.70	5.00	1.00	
Median	10.20	8.40	0.90	2.87	5.40	1.00	
Mean	10.59	8.82	1.17	2.73	5.71	1.32	
Standard deviation	2.60	2.29	0.55	0.73	1.97	0.67	
b. Carinolithus magharensis group							
Number of specimens	8	8	19	8	44	23	
Mode	11.40	/	0.90	/	8.10	2.00	
Median	12.19	9.81	0.90	2.59	7.88	2.20	
Mean	13.11	10.63	0.94	2.44	7.28	2.28	
Standard deviation	2.16	1.97	0.26	0.51	1.81	0.34	
c. Carinolithus superbus group							
Number of specimens	21	21	56	21	56	56	
Mode	8.80	8.40	0.70	2.40	5.00	1.00	
Median	9.50	8.10	0.95	3.00	4.60	0.93	
Mean	9.63	8.12	1.25	2.84	4.47	0.92	
Standard deviation	2.08	2.04	0.59	0.78	0.95	0.23	