Substrate type and palaeodepth do not affect the Middle Jurassic taxonomic diversity of crinoids

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Crinoids are largely considered as good indicators for determining environmental conditions. They are robust proxies for inferring changes in salinity and sedimentation rate and for inferring substrate type. Some crinoid groups (e.g., certain comatulids, cyrtocrinids, millericrinids) have a depth preference, thus, making them useful for paleodepth estimation. The hypotheses that crinoid distribution is substrate-dependent (rock type) or palaeodepth-dependent is tested here based on (a) archival Bathonian-Callovian (Middle Jurassic) crinoid occurrences from Poland and (b) newer finds from five boreholes from eastern Poland. Qualitative data suggests that isocrinids and cyclocrinids occur in both carbonate and siliciclastic rocks. The cyrtocrinids and roveacrinids occur within carbonate rocks, whereas the comatulids are exclusive to siliciclastics. In terms of palaeodepth, most crinoid groups dominate in shallow environments with the sole exception of cyrtocrinids, that are ubiquitous and occur in both shallow (near shore and shallow marine) and slightly deeper (deeper sublittoral to open shelf) settings. The occurrences of the cosmopolitan taxa, Chariocrinus andreae and Balanocrinus subteres (isocrinids), is independent of both substrate type and paleodepth. Quantitative analyses (Analysis Of Variance; ANOVA) based on substrate type, i.e., substrate-dependency (claystones, sandstones and limestones), and palaeodepth i.e., palaeodepth-dependency (near shore, shallow-marine, mid-ramp and off shore), corroborate qualitative results. Statistical analysis suggest that the distribution of crinoids shows a strong substrate-dependency but not for palaeodepth, although very weak significance (low p value) is noted for near shore and shallow marine settings and crinoid distribution.

1 **Does substrate type and palaeodepth affect the Middle Jurassic taxonomic diversity of**

2 **crinoids?**

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18 **Abstract**

19 **Crinoids are largely considered as good indicators for determining environmental**

20 **conditions. They are robust proxies for inferring changes in salinity and sedimentation rate**

21 **and for inferring substrate type. Some crinoid groups (e.g., certain comatulids,**

22 **cyrtocrinids, millericrinids) have a depth preference, thus, making them useful for**

23 **paleodepth estimation. The hypotheses that crinoid distribution is substrate-dependent**

24 **(rock type) or palaeodepth-dependent is tested here based on (a) archival Bathonian-**

25 **Callovian (Middle Jurassic) crinoid occurrences from Poland and (b) newer finds from five**

26 **boreholes from eastern Poland. Qualitative data suggests that isocrinids and cyclocrinids**

27 **occur in both carbonate and siliciclastic rocks. The cyrtocrinids and roveacrinids occur**

28 **within carbonate rocks, whereas the comatulids are exclusive to siliciclastics. In terms of**

29   **palaeodepth, most crinoid groups dominate in shallow environments with the sole**

30   **exception of cyrtocrinids, that are ubiquitous and occur in both shallow (near shore and**

31   **shallow marine) and slightly deeper (deeper sublittoral to open shelf) settings. The**

32   **occurrences of the cosmopolitan taxa, *Chariocrinus andreae* and *Balanocrinus subteres***

33   **(isocrinids), is independent of both substrate type and paleodepth. Quantitative analyses**

34   **(Analysis Of Variance; ANOVA) based on substrate type, i.e., substrate-dependency**

35   **(claystones, sandstones and limestones), and palaeodepth i.e., palaeodepth-dependency**

36   **(near shore, shallow-marine, mid-ramp and off shore), corroborate qualitative results.**

37   **Statistical analysis suggest that the distribution of crinoids shows a strong substrate-**

38   **dependency but not for palaeodepth, although very weak significance (low p value) is noted**

39   **for near shore and shallow marine settings and crinoid distribution.**

41   **Key words: echinoderms, crinoids, Jurassic, Bathonian, Callovian, Poland, boreholes.**

43   **Introduction**

45   The Middle Jurassic (especially Bajocian and Callovian) strata of the epicratonic Poland (Central

46   European province = Submediterranean province) are well-known for their excellently preserved

47   and strongly diversified fossil fauna and flora (e.g., Kopik, 1974, 1976, 1979a, b, 1998, 2006;

48   Zatoń et al., 2006a, b). These occur within clays and carbonate concretions and are represented

49   by ammonites, gastropods, scaphopods, bivalves, belemnites, brachiopods, bryozoans, echinoids,

50   asteroids, ophiuroids, wood fragments, and many others (for details see Matyja & Wierzbowski,

51   2000, 2003; Gedl et al., 2003; Kaim, 2004; Zatoń & Marynowski, 2004, 2006; Zatoń et al.,

52   2006a, b; Zatoń, 2010a, b). Crinoids, the group under study, are also diverse and abundant (more

53   so in the boreholes of eastern Poland), and often form encrinites (a grain-supported bioclastic

54   sedimentary rock) in which all or most of the grains are crinoid ossicles (e.g., Salamon &

55   Feldman-Olszewska, 2018). Despite such rich diversity and abundance, the crinoid data from the

56   Middle Jurassic of Poland has largely been relegated to either brief mentions of species

57   occurrences or of citing crinoid-yielding localities (see Salamon & Feldman-Olszewska, 2018

58   and literature cited therein).

59 The present Middle Jurassic study, based on new data from five eastern Poland boreholes

60 (see Fig. 1 and Table 1) and previously published crinoid records has twin objectives: (a) to

61 standardize crinoid taxonomic disparity with added remarks on systematic issues and previous

62 collections, and, (b) to test two hypotheses using this standardized dataset. These include: (1) Do

63 crinoids occur equally and frequently in both terrigenous and carbonate facies (test for substrate-

64 dependency)? and, (2) Do crinoids occur equally and frequently in both deep and shallow water

65 environments (test for palaeodepth-dependency)? Besides, qualitative analysis, the Analysis Of

66 Variance (ANOVA) is used to quantitatively test these two hypotheses.

67 During the Bathonian-Callovian duration, the Polish Basin was part of the epicratonic

68 Central European Basin that separated the Fennoscandian plains on the north from the Western

69 Tethys to the south. Only the extreme southern part of Poland (Tatra Mountains and Pieniny

70 Klippen Belt) was part of the Tethyan realm (see Fig. 1). These two realms display distinct

71 provincial characteristics (as evident from the distribution of ammonites; see Hallam, 1975;

72 Brand, 1986), but this provincialism is not noted for crinoids. Hence, this study, also analyses

73 crinoid taxonomic diversity trends between these two palaeobiogeographic provinces, i.e.,

74 Tethyan and Central European.

75

76 **Figure 1 around here**

77

78 **Previous records**

79

80 The Middle Jurassic (Callovian) crinoids of the epicratonic basins of Poland have been recorded

81 from the Polish Jura Chain ('A' on Fig. 1) and the Mesozoic margin of the Holy Cross

82 Mountains ('B' on Fig. 1). Early records only mentioned crinoid localities (e.g., Wójcik, 1910;

83 Makowski, 1952; Różycki, 1953). Later, Dayczak-Calikowska (1980) listed several taxa but did

84 not mention the exact locations from where the crinoid specimens were collected or where they

85 were kept (sample repository). Furthermore, neither description, nor illustration, or even basic

86 taxonomic group assignment was provided; most, however, belong to balanocrinids. Radwańska

87 & Radwański (2003) from northern Poland recorded Callovian columnals of *Cyclocrinus*

88 *macrocephalus* and Oxfordian cyclocrinid of *Cyclocrinus couiavianus*. Salamon & Zatoń (2006)

89 from the Callovian marly limestones of the Zalas Quarry in southern Poland ('A' in Fig. 1; see

90   also Table 2) erected a new species of balanocrinid (*Balanocrinus hessi*); this was later

91   synonymized with *B. pentagonalis* by Krajewski et al. (2019). Salamon & Gorzelak (2007), from

92   the same locality (Zalas Quarry in southern Poland; 'A' in Fig. 1) described few isolated remains

93   of indeterminable cyrtocrinids associated with the cyrtocrinid cup of *Dolichocrinus* cf. *aberrans*

94   (see Table 2). Salamon & Zatoń (2007) from a collection of ~1500 remains of columnals,

95   pluricolumnals, brachials and cups, illustrated 11 crinoid taxa, including some isocrinids,

96   comatulids, millecrinids and cyclocrinids (see Table 2). These specimens came from three

97   Bajocian, four Bathonian and two Callovian localities of the southern part of the Polish Jura

98   Chain and the Mesozoic margin of the Holy Cross Mountains (see Salamon & Zatoń, 2007).

99   Current re-examination of this material led to the assignment of the columnals described as

100   *Millericrinina* to the cyrtocrinids, Cyrtocrinida indet. (see Salamon & Feldman-Olszewska,

101   2018) (Table 2). Salamon (2008a, b) from two Callovian localities (Polish Jura Chain, 'A' in

102   Fig. 1 and the "glacial drift" of Łuków in eastern Poland: 'C' in Fig. 1) recorded several crinoid

103   taxa. The "glacial drift" assemblage of Łuków ('C' in Fig. 1) is dominated by isocrinids with

104   associated comatulids. The carbonate rocks of the Polish Jura Chain yielded a rich assemblage of

105   cyrtocrinids with dozens of complete individuals and a few isolated isocrinid remains. Salamon

106   & Feldman-Olszewska (2018) from the Callovian crinoidal limestones of the Żebrak IG 1

107   borehole (eastern Poland; 'D' in Fig. 1) described a-collection of five isocrinid taxa with some

108   unidentifiable cyrtocrinids (see also Table 2). This collection contained a relatively small number

109   of complete or nearly complete individuals, as a side-effect of the maceration process. Before the

110   maceration process, the samples formed a typical encrinite and consisted largely of crinoids, as is

111   also the case in the present study, yielding only fragmentary crinoids (see Table 2). Additionally,

112   the Middle Jurassic (Bathonian-Callovian carbonates) exposures in southern Poland (Tethyan

113   province, 'E' and 'F' in Fig. 1) have also yielded isocrinids, cyrtocrinids, roveacrinids, and

114   cyclocrinids (see Głuchowski, 1987; see Table 2).

115

116   **Material and methods**

117

118   The archival cores (72 core samples) drilled in eastern Poland (G1-G5 on Figs. 1 and 2) were

119   investigated for crinoids. These cores are stored in the Polish Geological Institute National

120   Research Institute, Warsaw (Poland). The samples selected for the maceration process were

121   selected from the following boreholes at respective depths: 1) Kock IG 2 (core depth: 859.0 m;

122   age: Callovian?); 2) Maciejowice IG 1 (core depth: 1,431.5 m; age: late Bathonian?); 3)

123   Magnuszew IG 1 (core depths: 1,505.7 m, 1,507.3 m, 1,508.65 m, and 1,522.4 m; age: middle

124   and late Callovian respectively); 4) Siedliska IG 1 (core depths: 824.65 m, 828.25 m, 828.77 m,

125   830.8 m, and 837.65 m; age: late Bathonian?-early Callovian); 5) Tłuszcz IG 1 (core depth:

126   1,047.7 m and 1,049.95 m; age: late Callovian?-early Oxfordian); 6) Żyrzyn IG 1 (core depths:

127   1,134.95 m, 1,137.7 m, 1,147.9 m, and 1,155.4 m; age: late Bathonian-Callovian) (for a

128   summary see Table 2).

129   The present paper also includes a large collection of Callovian crinoids from Poland

130   collected by Mariusz Salamon and Bartosz Płachno (2006-present) and others, mentioned in the

131   *Acknowledgements* section.

132   The first step for the current analysis consisted of examining the drill cores under a

133   binocular microscope for crinoids. Thereafter, the carbonate samples were soaked with Glauber's

134   salt. Based on sample cohesion, these were then successively boiled and frozen. The residue

135   was then washed under running tap water and sieved (mesh sizes: Ø1.0, 0.315 and 0.1 mm,

136   respectively). The final step consisted of drying the screened residue at 170-180˚C (following the

137   methodology outlined by Krajewski et al., 2019).

138   Both the sandstone sample Maciejowice IG 1 (core depth: 1,431.5 m; age: late

139   Bathonian?) and the carbonate sample Magnuszew IG 1 (core depth: 1,505.7 m; age: late

140   Callovian) were naturally macerated and left outside for 30 days (from January 22nd to February

141   21st, 2021). As a result of this natural maceration, the samples were partially disintegrated. In

142   addition to this, several thin sections (TS) and polished slabs (PS) were also made. All crinoids

143   were hand-picked from the maceration residue and photographed using a Canon Eos 350D

144   digital camera, LeicaWildM10 coupled with a NikCamPro1 microscope and a Scanning Electron

145   Microscope Philips XL-20. All specimens are housed in the Institute of Earth Sciences of the

146   University of Silesia in Katowice, Poland, and catalogued under registration number GIUS 8-

147   3734. Other Middle Jurassic specimens used in the current study are also housed at the Institute

148   of Earth Sciences of the University of Silesia in Katowice, Poland, and catalogued under: GIUS

149   8-2510, 8-2569, 8-2571, 8-3460Cr, 8-3466, 8-3678/1-6, 8-3734.

150

151 *Statistical methods*

152

153 The taxonomically standardized dataset was subjected to Analysis Of Variance (ANOVA). To

154 check for substrate-dependency (Hypothesis 1), the dataset was categorized under claystones,

155 sandstones and limestones (the former two represent siliciclastics, whereas the latter,

156 carbonates). For palaeodepth-dependency (Hypothesis 2), the dataset was categorized under near

157 shore, shallow-marine, mid-ramp and off shore categories. For pairwise comparisons, the

158 Tukey's HSD (honestly significant difference) test was applied.

159

160 **Table 1 around here**

161

162 *Taxonomic standardisation*

163

164 The cyrtocrinids are identified at the specific level based on their cups. In some cases, when the

165 cups are fragmentary or some typical features are not visible, the samples were assigned to the

166 generic level, only. Most of the disarticulated remains of cyrtocrinids (holdfasts, columnals,

167 radials, basals, brachials, etc.) are assigned under Cyrtocrinida indet.

168   As for comatulid centrodorsals, where cups with basals and radials were not available for

169 additional information, they were also classified at the generic level. The brachial with muscular

170 articulation on the proximal side and syzygial one on the distal side are classified as

171 Paracomatulidae sp. et gen. indet.

172   The isolated remains of isocrinids, consisting of columnals, pluricolumnals, cirrals, cup

173 plates, and brachials, are classified at the specific level. If they were found in different levels,

174 they are described as Isocrinida indet.

175   A complete individual of cyclocrinid has not been found so far. Despite this, the

176 uniqueness of their remains (e.g., large cylindrical columnals with peculiar tuberculate facets)

177 allows us to identify them at the specific level (see detailed discussion in Radwańska &

178 Radwański, 2003). Głuchowski (1987) assigned some remains from the Pieniny Klippen Belt to

179 *Cyclocrinus* sp. due to the incompleteness of columnals. Głuchowski (1987) classified all

180 roveacrinids (saccocomids) as *Saccocoma* sp.; these were recorded either as isolated cup remains

181 or observed in thin sections (TS).

182   Thus, the dataset used in the present study is taxonomically standardised. The crinoids

183 classified in the present study are given in Tables 1-4. A summary of all data with their

184 respective inferred palaeodepth and species diversity (number of taxa) is given in Table 3 (see

185 also Fig. 3).

186

187 **Tables 2, 3 around here**

188

189 **Results**

190

191 The present study identified several crinoid remains of cups, columnals, cirrals and brachials

192 from the 5 boreholes drilled in eastern Poland (Fig. 1). Only two pluricolumnals were recorded.

193 The first one consists of three or four columnals observable on the surface of a rock fragment

194 from the Magnuszew IG 1 core (depth: 1,505.7 m). The second one consists of two columnals

195 and comes from the sample of Siedliska IG 1 (depth: 828.77 m). The other echinoderms

196 observed on slab surfaces include numerous partly preserved cidaroid spines, cidaroid

197 interambulacral plates and asteroid marginal plates. The echinoderm remains were also observed

198 in thin sections and on the surface of polished slabs. In addition to these echinoderm remains,

199 bivalves, gastropods and ostracods were observed both on the slab surfaces and in the macerated

200 residues. In the late Bathonian sample Maciejowice IG 1, the remains of carbonized plant

201 remains were also observed (for a summary of the above data see Table 4). In general, the

202 Bathonian and Callovian crinoid assemblages are almost identical (see also Table 1). The other

203 investigated Middle Jurassic crinoids were represented by numerous cups, cup remains,

204 brachials, columnals, pluricolumnals, cirri, cirrals, and holdfasts (for details see Głuchowski,

205 1987; Salamon & Gorzelak, 2007; Salamon & Zatoń, 2007; Salamon, 2008a-c; Salamon &

206 Feldman-Olszewska, 2018).

207

208 **Table 4 around here**

209

210 *State of preservation*

211

212   The preservation of crinoids was examined only on the non-macerated surfaces of fresh core

213   fragments. These were screened for signs of abrasion, bioerosion traces, chemical alteration of

214   ossicle structure, evidence of epibionts and predation traces. Most of the crinoids display a high

215   degree of disarticulation (almost 100%). However, they are all well preserved and do not show

216   any traces of lateral surface abrasion. Excellent preservation and lack of abrasion are also noticed

217   for columnal articular surfaces; the crenulae, petal floors, perilumens and lumens are complete.

218   The two pluricolumnals also show no signs of abrasion. Additionally, the studied crinoid remains

219   are very rarely bioeroded (bioerosion was only noticed in case of three columnals in the form of

220   small and rounded holes). These may be ascribed to acrothoracican cirripedes, algae, fungi,

221   polychaetes, sipunculans, or to sponge activities (for more details see Salamon & Zatoń, 2006;

222   Zatoń et al., 2007; Salamon & Gorzelak, 2010).

223   Donovan (1991) suggested that under normal oxygenated conditions, complete crinoid

224   disarticulation takes place within two weeks. However, Brett et al. (1997) argued that under

225   certain circumstances, complete disarticulation may occur even after a year. In living comatulids,

226   disarticulation starts just after death and by the end of the first week, only isolated calyx and a

227   few arm fragments remain articulated (Ausich, 2001). Under high water temperatures and with

228   increased physical disturbance, the disarticulation process significantly speeds up (see Ausich,

229   2001; Hess, 2006). Baumiller & Ausich (1992) noted that after 19 days, the isocrinid stem

230   disarticulates into noditaxes and after 22 days, the column segments get disarticulated into

231   isolated columnals. Gorzelak & Salamon (2013) noted that under high-energy conditions

232   (constant transportation), and at room temperature, disarticulation of the crinoid skeleton is

233   nearly complete after 17 days, where only a few articulated arms and cirral ossicles remain

234   intact.

235   In the present study, the crinoid remains are preserved as cups, isolated columnals,

236   brachials, and cups. Therefore, these remains can confidently be classified as taphonomic types 2

237   and 3 *sensu* Brett et al. (1997). Type 2 includes isocrinids with some remains of cyrtocrinid that

238   undergo rapid postmortem disarticulation, on account of weak sutures. Type 3 comprises of

239   cyrtocrinid cups in which major portions of the skeleton are resistant to disarticulation.

240   Thus, for the present study, all the data suggest that the recorded crinoids are

241   autochthonous with negligible or no post-mortem transportation. Possibly, after death, they

242   remained for some time on the sea bottom, but were not subjected to significant transportation or

243 reworking before burial, or they were shortly covered by sediment, as suggested by the lack of

244 abrasion surfaces. Bearing this in mind we assume little time-averaging that might alter the

245 palaeoecological and palaeodepth information. Additionally, no trace of chemical alteration,

246 predation traces and epibionts were noticed, suggesting that the inferred palaeoecological and

247 palaeodepth signals are primary.

248

249 *Statistical analyses*

250

251 Substrate dependency (Hypothesis 1)

252 The ANOVA test (Table 5a) yielded a statistically significant differences among the fauna of the

253 different substrate types (claystones, sandstones and limestones) at $p < .001$. For pairwise

254 comparisons, the Tukey's HSD (honestly significant difference) test was applied (Table 5b). This

255 yielded a significant difference between both claystones-sandstones and limestones but no

256 significance difference between claystones and sandstones (both being siliciclastics; Table 5b).

257

258 Palaeodepth-dependency (Hypothesis 2)

259 The comparison between paleodepth parameters (near shore, shallow-marine, mid-ramp and off

260 shore) did not yield any statistically significant results (Table 5c). The pairwise comparisons,

261 Tukey's HSD test (Table 5d) retained a statistically significant difference only between the first

262 two variables (Near shore and Shallow marine); although, the p value is very low ($p > 0.01$).

263

264 Table 5 around here

265

266 **Discussion**

267

268 *Depositional environment of the eastern part of the epicontinental Polish Basin*

269

270 Upper Bathonian and Callovian of the eastern part of Polish Basin are represented by

271 organodetritic, mostly crinoidal limestones with abundant limonite. There are grainstones and

272 packstones which are dominated by echinoderm plates, less frequently appear echinoid spines,

273 bryozoans, bivalves and brachiopods, occasionally gastropods, foraminifera, ammonites and

274 belemnites are present. Quartz grains are frequently an admixture. In places also ferruginous

275 ooids are present. Sedimentary environment is interpreted as a mid-ramp located between normal

276 and storm wave base (Feldman-Olszewska, 2018).

277

278 *Depositional environment of the Łuków glacial draft*

279

280 The Łuków glacial drift exposed in eastern Poland ('C' in Fig. 1), is a 30 m-thick Callovian unit

281 containing black clays with carbonate concretions (see also Mizerski & Szamałek, 1985),

282 deposited in an offshore setting (e.g., Olempska & Błaszczyk, 2001; Kaim, 2004). However,

283 recently, based on the presence of a high diversity asteroid assemblage, a varied environment

284 (ranging from coastal to deep-shelf) was proposed (Villier, 2008). This unusually high crinoid

285 diversity is likely a reflection of ossicles being transported by currents from shallow- to deep-

286 water offshore environments (Villier, 2008). However, according to Salamon (2008a), based on

287 the ecology of crinoids, the Łuków clays was deposited in a relatively shallow environment and

288 contrary to asteroids, they were not transported. Based on the presence of macro- and micro-

289 remains of land flora, a nearshore environment was also inferred (see also Brand, 1986;

290 Marynowski et al., 2008). Similarly Gedl (2008) using dinoflagellate cysts concluded that these

291 originated presumably from shallow marine environments. Sedimentological investigations of

292 the Aalenian-Bathonian (Middle Jurassic) claystones and shales from central Poland indicate that

293 their sedimentation took place in offshore (below storm wave base) and transition (between

294 normal and storm wave base) zones of the epeiric sea (see Feldman-Olszewska, 2007, 2008,

295 2012a, b; Pieńkowski et al., 2008). Water depth corresponds to the *Cruziana* ichnofacies but

296 shallower than the *Zoophycus* ichnofacies (see Knaust & Bromley, 2012). The same depositional

297 environment is expected for the Callovian clays from Łuków.

298

299 *Problems with isolated isocrinid classification*

300

301 The isocrinids are a dominant crinoid group in the Middle Jurassic sediments of Poland.

302 However, their correct classification into families and genera is very complicated. The ideal

303 situation is when complete crinoid findings are available (e.g., Simms, 1989; Hess, 1999c, d;

304 Hess & Messing, 2011), but these are rare due to the unique structure of their skeletons (see *State*

305   *of preservation*). There are of course also isocrinids that have a unique structure of columnals

306   and it is easier to identify them from others. A classic example is that of *Balanocrinus subteres*

307   or *B. pentagonalis* (see Klikushin, 1992; Hess, 2014a, b; Krajewski et al., 2016, 2019, 2020).

308   Hess (2014a, b) stated that the columnals of *B. subteres* could be associated with its isolated

309   calyx elements. Likewise, with remains of *Pentacrinites dargniesi* or *Isocrinus nicoleti* display a

310   unique shape and ornamentation of their articular facets, as also *P. dargniesi* with its

311   characteristic, ellipsoidal cirrals.

312   However, there is an issue with non-balanocrinid isocrinids, that have columnals of a

313   similar morphology, and were erected on the basis of isolated skeletal remains. There are many

314   such forms in the Middle and Upper Jurassic strata of Poland. According to de Loriol (1887), the

315   most similar taxon to *Isocrinus amblyscalaris* is *I. munieri*. But there are some noticeable

316   differences between them, also i.e., the height of columnals and the ornamentation of the latera.

317   Hess (2014a) added that *Pentacrinus pellati* with low columnals alternating with higher ones,

318   and ridges occurring on its latera, is also a very similar form. He concluded that both species are

319   of middle Oxfordian age and therefore may be conspecific. In turn, Bather (1898) suggested that

320   *I. amblyscalaris* collected from the Oxfordian and Kimmeridgian of Poland is a synonym of

321   *I. pendulus*. Hess (1975) added that both these species originated from the same middle

322   Oxfordian strata (Bärschwil Fm, NW Switzerland). On the other hand, Klikushin (1992) stated

323   that there is a series of morphological differences between these two species that supersedes

324   Bather's (1898) opinion. The latter author, elsewhere in his monograph, however, proposed to

325   consider *I. pendulus*, Oxfordian *I. amblyscalaris*, and Callovian-Oxfordian *I. oxyscalaris* as

326   junior synonyms of the Oxfordian *I. desori*. Krajewski et al. (2019) differed from this view and

327   emphasized that there are some differences in the facet morphology of the mentioned taxa. Apart

328   from the differences in the articular facets (i.e., the presence of deep furrows between petal

329   floors), the shape of columnals may also be different (compare Hess, 1975, p. 55, text-fig. 8,

330   pl. 19, fig. 4; Klikushin, 1992, pl. 11, fig. 1-7 vs. pl. 13, fig. 8-10; Radwańska, 2005, fig. 8/4;

331   Salamon, 2009a, fig. 2H).

332   Taking into account all of the above, it is difficult to say unequivocally whether there are

333   one or more biological species within the Middle/Upper Jurassic strata of Poland. Therefore,

334   such forms, whose taxonomic affiliation raises serious doubts (*Balanocrinus berchteni, Isocrinus*

335   *bajocensis, I. bathonicus*, and *I. pendulus*), must be evaluated with great caution in any analysis.

336

337 *Taxonomic status of cyclocrinids*

338

339 The Cyclocrinids (Cyclocrinidae) were classified by Biese (1935-1937) as millericrinids

340 (Millericrinida, Apiocrinitidae). Sieverts-Doreck (1953, in Ubaghs) and later Hess (1975) placed

341 the cyclocrinids within cyrtocrinids (Cyrtocrinida). According to Radwańska & Radwański

342 (2003) cyclocrinid columnals are elements of radical cirrals and therefore belong to

343 bourgueticrinids (Bourgueticrinida). Following Hess (2008), the ordinal position of *Cyclocrinus*

344 and of the family Cyclocrinidae is left in the open nomenclature though the form has some

345 resemblance to the Early Jurassic millericrinid genus *Amaltheocrinus*. Hess & Messing (2011)

346 placed *Cyclocrinus* within uncertain order pending proper classification of its cup plates that still

347 remain unknown.

348   One of the previously investigated Callovian sections (the abandoned Wysoka Quarry

349 placed within the Polish Jura Chain; 'A' in Fig. 1), exposes sandy limestones where numerous

350 cyclocrinid columnals were collected from a narrow level. Remains of other crinoids were not

351 found there. Along with these columnals, several "millericrinid"-like brachial (see Fig. 3) plates

352 were found, which probably belong to the same crinoid as the columnals. Brachials display a

353 proximal synostosis and a muscular distal side, sometimes with a pinnule socket. Both facets are

354 parallel. This seems to confirm Hess's (2008) idea of linking cyclocrinids to millericrinids. On

355 the other hand, the "bourgueticrinid"-like, strongly abraded cup was found by us in the

356 Czerwieniec locality. This cup is very similar in shape and size to bourgueticrinid cup that may

357 suggest that cyclocrinids really belong to bourgueticrinids as suggested by Radwańska &

358 Radwański (2003).

359

360 **Figure 3 around here**

361

362 *Cyclocrinids from Poland*

363

364 Wójcik (1910) first listed the occurrence of *Cyclocrinus macrocephalus* in Poland and the

365 occurrence of columnals in the sands of Filipowice, Polish Jura Chain ('A' in Fig. 1).

366 Głuchowski (1987) noted the occurrence of *Cyclocrinus rugosus* and *Cyclocrinus* sp. within the

367   Bathonian and/or Callovian crinoidal limestones of the Tatra Mountains and the Pieniny Klippen

368   Belt ('E' and 'F' in Fig. 1). Radwańska & Radwański (2003) questioned this assignment,

369   claiming that the sketches and photographs are not of sufficient quality, specimens are poorly

370   preserved, and that the 'cyclocrind' were small-sized. Re-examinations of Głuchowski

371   specimens (1987, fig. 13/1, 13/4 and pl. 1, fig. 1-6), stored at the Institute of Earth Sciences of

372   the University of Silesia in Katowice, Poland, prove that they are significantly smaller than the

373   columnals collected from other areas. Additionally, they are cylindrical, low and with a slightly

374   convex latera, suggesting that they may well belong to cyclocrinids. Therefore, the original

375   designations of Głuchowski (1987) are currently upheld. Moreover, Radwańska & Radwański

376   (2003) recognized four cyclocrinid species within the Middle and Upper Jurassic strata of

377   Poland, namely: *Cyclocrinus rugosus* from the Bajocian, *C. macrocephalus* from the Callovian,

378   *C. areolatus* from the Oxfordian, and *C. couiavianus* from the upper Oxfordian. They stated that

379   all mentioned taxa (with the exception of *C. couiavianus*) lie within the variability of *C. rugosus*

380   (Radwańska & Radwański, 2003). Though describing columnals with articular surfaces covered

381   by numerous and irregular tubercles, Salamon & Zatoń (2007) included these remains under

382   *C. macrocephalus*. Re-observation of columnals coming from the same Callovian levels of the

383   Polish Jura Chain, both ornamented by and devoid of tubercles, confirm the suggestion of

384   Radwańska & Radwański (2003) that all these cyclocrinids actually belong to a single species,

385   *Cyclocrinus rugosus*.

386

387   *Distribution of crinoids within particular facies. Does it really work?*

388

389   Hans Hess in several of his papers pointed out that the occurrence of certain species of crinoids

390   may be closely related to or strictly defined by substrate (sediment type) and palaeodepth. He

391   claimed that *Chariocrinus andreae* inhabited muddy bottoms and its dense colonies occurred in

392   somewhat deeper waters, below fair-weather wave base, i.e., at depths around 10-15 m (Hess,

393   1972, 1999a). In this study, *Chariocrinus andreae* occurs in large amount in both carbonate and

394   siliciclastic rocks. *Balanocrinus subteres* is one of the most cosmopolitan crinoid ever recorded

395   in the Mesozoic and is known from both shallow and deeper environments (compare Table 3 and

396   Fig. 2). Hess (1999a) claimed that another very common Middle Jurassic crinoid taxon, *Isocrinus*

397   *nicoleti*, frequently occurring in Poland, may also occur within both ooid shoals of the carbonate

398 shelf and in slightly deeper environments (intercalating marls and bioclastic limestones). Tang et

399 al. (2000) recorded *I. nicoleti* from the shallow-water tidal facies of the Middle Jurassic Carmel

400 Formation in Mount Carmel Junction and also from the open shallow subtidal (carbonate) facies

401 of the Gypsum Spring and Twin Creek Formations of Wyoming (USA). Hunter & Underwood

402 (2009) further noticed that *I. nicoleti* from the Bathonian of England and France, occurred only

403 in shallow-water sediments, represented by low-energy, inner muddy shelf and outer lagoon,

404 oolitic high-energy shoal system, carbonate/muddy low-energy, marine lagoon complex and in

405 the shallow subtidal zone. All these are actually consistent with our own observations that

406 indicates *I. nicoleti* (Tables 2 and 3) occurred in both carbonate and siliciclastic rocks, although

407 it preferred shallow-water carbonates. Hunter & Underwood (2009) concluded that the

408 distribution of crinoids corresponds quite nicely to particular facies (but see also the comment on

409 this paper by Salamon et al., 2010). This substrate-dependence is also corroborated by the

410 ANOVA test (although at the generic-level) that the crinoid distribution is highly sensitive for

411 carbonates (limestones) as opposed to siliciclastics (Table 5a-b).

412   Of interest is the observation on *Pentacrinites dargniesi*. Hunter & Underwood (2009)

413 also collected *P.* cf. *dargniesi* from shallow, muddy and carbonate habitats. *P. dargniesi*, despite

414 being predominantly found in carbonates, also occurs in offshore claystones of Poland (see Table

415 2 and 3). Contextually, it must be keep in mind that *P. dargniesi* was a pseudo-planktonic crinoid

416 that transported on the lower surfaces of driftwood fragments, and hence, is likely to occur in

417 varied facies (see Simms, 1999; Hess, 1999a).

418   The most numerous isocrinids within the Middle Jurassic of Poland are balanocrinids

419 (*Balanocrinus subteres* and *B. pentagonalis*). Hess (2014a, b) argued that balanocrinids settled

420 mostly on hardgrounds but they are also be found these in mudstone-dominated settings, possibly

421 on swells of the fine-grained bottom. The largest species of the slender crinoid genus (viz., *B.*

422 *subteres*) was reported from below storm wave-base (Hess & Spichiger, 2001), where it thrived

423 due to ample nutrient availability and well-oxygenated bottom waters (Hess, 2014a, b).

424 Klikushin's (1992) noted, as also in the present study, that *Balanocrrinus subteres* is another

425 most cosmopolitan Mesozoic crinoid species. It occurs in both carbonate and siliciclastic facies

426 and in environments of varying depth, from near shore (close to a beach) to the open shelf, but

427 usually below normal wave base (Table 3 and Fig. 2). This lack of palaeodepth-dependency

428 (although at the generic-level) is also reflected in the ANOVA test that suggests that paleodepth

429 played no or minor role in the distribution of crinoids (Table 5c-d), although very weak (low p

430 value) significance is noted for near shore and shallow marine settings, as discussed above, also

431 (see Figs. 2 and Table 5).

432   On the other hand, Hunter & Underwood (2009) concluded that the occurrences of

433 balanocrinids (*Balanocrinus* cf. *subteres*) were restricted to neritic mudstone facies and

434 brachiopod-rich limestones (i.e., within the offshore, low-energy shelf setting). Hunter &

435 Underwood (2009) also noted that the comatulids show a wide range of distribution from

436 offshore, low-energy shelf up to oolitic high-energy shoal system. In the present study,

437 corroborating previous observations (e.g., Hunter & Underwood, 2009) (see also Table 5c-d), the

438 comatulids are restricted to siliciclastic rocks of near shore, below wave-base settings (Table 3

439 and Fig. 2).

440   The cyrtocrinids are considered as suggestive of relatively deep-sea depths and with

441 carbonate facies association (e.g., Arendt, 1974; Hess, 1975; Žítt, 1973, 1974, 1975, 1978a-d,

442 1979a, b, 1982, 1983). According to Ausich et al. (1999 and references cited therein), the

443 cyrtocrinids prefer depths exceeding 100 m. Recent cyrtocrinids such as *Cyathidium foresti* live

444 at depths ranging from 380 to 900 m, and *C. plantei* lives at a depth of 200 m (Hess, 1999b).

445 Nevertheless, rare single reports also indicate their presence in shallow (and extremely shallow)

446 environments (e.g., Salamon & Gorzelak, 2007; Salamon, 2019; Krajewski et al., 2020). From

447 the Jurassic Yátova Formation of Spain, Zamora et al. (2018) illustrated the spongiolithic facies

448 as having been deposited in relatively shallow and open platform areas with depths not

449 exceeding 60 m, containing the following cyrtocrinid cups: *Eugeniacrinites* sp., *Pilocrinus* sp.,

450 *Gammarocrinites* sp.; and a basal circlet of Tetracrinidae indet. that actually belongs to

451 *Tetracrinus moniliformis* (see fig. 9e in Zamora et al., 2018). In the current study,

452 *Gammarocrinites* sp., *Pilocrinus moussoni* and *Tetracrinus moniliformis* occur in carbonates of

453 near shore and shallow marine, to deeper sublittoral under storm influence to open shelf

454 environments.

455   The roveacrinids represented by the genus *Saccocoma* are exclusive to the shallow

456 marine Bathonian and/or Callovian carbonates of the Tatra Mountains and the Pieniny Klippen

457 Belt (Tethyan province). Kowal-Kasprzyk et al. (2020) mentioned saccocomids from the

458 Oxfordian-Kimmeridgian exotic clasts of the Outer Carpathians in southern Poland.

459 Matyszkiewicz (1996, 1997) mentioned *Saccocoma*-calciturbidites resting on the slope beds of

460   Oxfordian cyanobacterial-sponge carbonate buildups formed in the Polish epicontinental basin

461   (for summary see Fig. 2).

462   The cyclocrinids are not considered in the present study due to their controversial

463   taxonomic assignment (e.g., Hess, 2008).

464   Thus, qualitatively (see Fig. 2) isocrinids and cyclocrinids occur in both carbonate and

465   siliciclastic rocks. The cyrtocrinids and roveacrinids occur within carbonate rocks, whereas the

466   comatulids are exclusive to siliciclastics. In terms of palaeodepth, most crinoid groups dominate

467   in shallow environments with the sole exception of cyrtocrinids, that are ubiquitous and occur in

468   both shallow (near shore and shallow marine) and slightly deeper (deeper sublittoral to open

469   shelf) settings. The occurrences of the cosmopolitan taxa, *Chariocrinus andreae* and

470   *Balanocrinus subteres* (isocrinids), is independent of both substrate type and paleodepth. This

471   qualitative inference (Fig. 2) is largely mirrored quantitatively, also (Table 5).

472   The quantitative analysis (Fig. 2 and Table 5) suggests that the distribution of crinoids

473   show a strong substrate-dependency (Hypothesis 1) (see Fig. 2 and Table 5) corroborating results

474   by Simms (1988) and Hunter & Underwood (2009). The palaeodepth-dependency (Hypothesis 2)

475   did not yield significant results, although very weak (low p value) significance is noted for near

476   shore and shallow marine settings (Table 5), as also reflected in qualitative analysis (see Figs. 2).

477   Although it must be accepted that the quantitative analysis (Table 5) is genus-based.

478   Nevertheless, and until more species-based datasets are available, present quantitative analysis

479   (Table 5) should prove useful in better understanding crinoid diversity trends. These results have

480   important bearing on crinoid diversity studies and underline the importance of incorporating

481   substrate details (facies analysis) while inferring distribution patterns of crinoid species diversity

482   and paleobiogeography. A more rigorous and quantitative species-based analysis may enable to

483   better understand their varied distribution patterns.

484

485   **Conclusion**

486

487   Almost all Bathonian and Callovian crinoids recorded from Poland dominate in relatively

488   shallow environments. The only exception are cyrtocrinids, that are equally common in both

489   shallow and deeper settings. The most commonly recorded Isocrinids, occur frequently in both

490   carbonate and siliciclastic rocks. Cyrtocrinids also occur likewise, but dominate in carbonates.

491 Roveacrinids are exclusive to carbonates, whereas cyclocrinids occur in both carbonates and
492 siliciclastics. The comatulids occur exclusively in siliciclastics. The most cosmopolitan crinoids
493 are the isocrinids, *Chariocrinus andreae* and *Balanocrinus subtrees*, that occur both in carbonate
494 and siliciclastic rocks, and in shallow and open-shelf environments. Statistical analyses
495 (ANOVA) corroborate these qualitative inferences, and suggests that the distribution of crinoids
496 show strong substrate-dependency (Hypothesis 1) but not palaeodepth-dependency (Hypothesis
497 2), although statistical significance (albeit very weak; low p value) is noted for near shore and
498 shallow marine settings. A more exhaustive species-based analysis may enable to better
499 understand their varied distribution patterns.

500

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502

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504

505 **Competing interests**

506

507 We declare we have no competing interests.

508

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523

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786

787   **Figure captions:**

788

789   **Figure 1. A.** Palaeogeographic map of central Europe during the Middle Jurassic (modified after

790   Šimkevičius et al., 2003). A– Bathonian and Callovian exposures of the southern part of the

791   Polish Jura; B – Bathonian and Callovian exposures of the southern margin of the Holy Cross

792   Mountains; C – Callovian exposure of the glacial drift in Łuków; G1-G6 – location of the

793   Bathonian-Callovian boreholes described in this constribution [Tłuszcz IG 1 (G1), Siedliska IG 1

794   (G2), Kock IG 2 (G3), Żyrzyn IG 1 (G4), Maciejowice IG 1 (G5), Magnuszew IG1 (G6)], D

795   location of borehole Żebrak IG 1 (details in Salamon & Feldman-Olszewska, 2018); A–D –

796   Central European province; E – Bathonian and Callovian exposures of the Tatra Mountains; F –

797   Bathonian and Callovian exposures of the Pieniny Klippen Belt; E, F – Tethyan province **B.** Map

798   of Callovian lithofacies noted in Poland (modified after Dayczak-Calikowska & Moryc, 1988).

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800   **Figure 2.** Model showing distribution of selected Callovian crinoids.

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802   **Figure 3.** Cyclocrinid remains from southern Poland. A. Columnal, articular facet. B. Brachial

803   plate. Scale bar equals 1 mm. Blue arrows mark granules covering the articular facet of

804   columnal.

805

806   **Table captions:**

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808   **Table 1.** Bathonian-Callovian crinoids collected in particular boreholes in eastern Poland.

809   **Table 2.** Bathonian and Callovian crinoid list recorded in different areas of Poland.

810   **Table 3.** Distribution of Bathonian-Callovian crinoids recorded in Poland within different facies

811   and settings.

812   **Table 4.** Number of collected crinoid remains during observation of respective cores and

813   maceration process.

814   **Table 5.** Analysis Of Variance (ANOVA). a. ANOVA test between different substrate types

815   (Claystones, Sandstones and Limestones). b. Tukey's HSD (honestly significant difference) test

816   for pairwise comparisons. c. ANOVA test between different paleodepth parameters (Near shore,

817   Shallow-marine, Mid-ramp and Off shore). d. Tukey's HSD (honestly significant difference) test

818   for pairwise comparisons.

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Bathonian-Callovian crinoids collected in particular boreholes in eastern Poland.

Borehole	Depth (in m)	Age	Lithology	determinable crinoid taxa
Kock IG 2	859.0	Callovian?	Yellowish grey, crinoidal limestone, packstone composed of echinoderm plates, bivalve shells, rare bryozoa fragments with ferruginous impregnations, ferruginous ooids, rounded quartz grains and sparite cement.	Isocrinida indet. *Balanocrinus subteres*
Maciejowice IG 1	1,431.5	late Bathonian	Dark grey, medium-size sandstone	none
Magnuszew IG 1	1,505.7	late Callovian	Yellowish grey, crinoidal limestone, grainstone composed of echinoderm plates, echinoid spines, rounded quartz grains, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Balanocrinus subteres* *Pentacrinites dargniesi*
	1,507.3	late Callovian	Yellowish grey, crinoidal limestone with amonite and belemnite, grainstone composed of echinoderm plates, echinoid spines, bivalve shells, rounded quartz grains, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Pentacrinites dargniesi*
	1,508.65	late Callovian	Grey crinoidal limestone, grainstone composed of echinoderm plates, echinoid spines, bivalve shells, bryozoa fragments, rare gastropoda, rounded quartz grains and sparite cement	Isocrinida indet. *Balanocrinus subteres* *Pentacrinites dargniesi*
	1,522.4	middle-late Callovian	Yellow-brown, dolomitic crinoidal limestone with foraminifera, quartz grains and iron oxides/hydroxides	Isocrinida indet. *Isocrinus nicoleti* *Balanocrinus subteres* *Balanocrinus pentagonalis* *Pentacrinites dargniesi*
Siedliska IG 1	824.65	early Callovian	Beige-grey, crinoidal limestone, grainstone composed of echinoderm plates, echinoid spines and bryozoa fragments frequently with ferruginous impregnations, crushed bivalve and bryozoa shells, gastropods, lithoclasts with iron hydroxides, rare ferruginous ooids, quartz grains, sparite or sparite-micrite cement and iron oxides/hydroxides	Isocrinida indet. *Pentacrinites dargniesi*
	828.25	early Callovian	Beige-grey, crinoidal limestonegrainstone composed of echinoderm plates, echinoid spines and bryozoa fragments frequently with ferruginous impregnations, crushed bivalve and bryozoa shells, gastropods, lithoclasts with iron hydroxides, rare ferruginous ooids, quartz grains, sparite or sparite-micrite cement and iron oxides/hydroxides	Isocrinida indet. *Balanocrinus subteres* *Pentacrinites dargniesi*
	828.77	early Callovian	Beige-grey, crinoidal limestone	Isocrinida indet.

	Depth	Age	Lithology	Fauna
			grainstone composed of echinoderm plates, echinoid spines and bryozoa fragments frequently with ferruginous impregnations, crushed bivalve and bryozoa shells, gastropods, lithoclasts with iron hydroxides, rare ferruginous ooids, quartz grains, sparite or sparite-micrite cement and iron oxides/hydroxides	*Isocrinus nicoleti* *Balanocrinus subteres* *Pentacrinites dargniesi* Cyrtocrinida indet.
	830.8	late Bathonian?	Yellow-brown, crinoidal limestone with abundant iron hydroxides, lithoclasts and bivalve shells.	none
	837.65	late Bathonian?	Yellow crinoidal limestone, grainstone composed of echinoderm plates, echinoid spines and bryozoa fragments frequently with ferruginous impregnations, crushed bivalve and bryozoa shells, gastropods, lithoclasts with iron hydroxides, rare ferruginous ooids, quartz grains, sparite or sparite-micrite cement and iron oxides/hydroxides	Isocrinida indet. *Chariocrinus andreae* *Balanocrinus subteres* *Balanocrinus pentagonalis* *Pentacrinites dargniesi*
Tłuszcz IG 1	1,047.7	late Callovian?-early Oxfordian	Beige-grey, crinoidal limestone	none
	1,049.95	late Callovian	Cream crinoidal limestone, grainstone composed of echinoderm plates, echinoid spines and bryozoa fragments, bivalve shells, very rare foraminifera, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Balanocrinus pentagonalis* *Pentacrinites dargniesi* *Phyllocrinus* sp.
Żyrzyn IG 1	1,134.95	Callovian	Yellowish grey, crinoidal limestone, grainstone composed of echinoderm plates, bryozoa fragments, bivalve shells, quartz grains, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Chariocrinus andreae* *Pentacrinites dargniesi* Cyrtocrinida indet.
	1,137.7	late Bathonian?	Beige-grey, crinoidal limestone with cement and iron hydroxides	none
	1,147.9	late Bathonian	Beige-grey, crinoidal limestone grainstone composed of echinoderm plates, echinoid spines, bryozoa fragments, bivalve and brachiopods shells, quartz grains, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Isocrinus nicoleti* *Chariocrinus andreae* *Balanocrinus subteres* *Pentacrinites dargniesi* Cyrtocrinida indet.
	1,155.4	late Bathonian	Yellow-brown, crinoidal limestone, grainstone composed of echinoderm plates, bryozoa fragments, bivalve and brachiopods shells, sparite cement and iron oxides/hydroxides	Isocrinida indet. *Isocrinus nicoleti* *Balanocrinus pentagonalis* *Pentacrinites dargniesi*

Bathonian and Callovian crinoid list recorded in different areas of Poland.

Location area (see also details in Fig. 1 and its caption)	Age	Number of crinoid taxa	List of crinoids
A – glacial drift in Łuków; Central European province	Callovian	10, including: 8 isocrinids and 2 comatulids	**Isocrinids:** *Chariocrinus andreae* *Balanocrinus berchteni* *Balanocrinus pentagonalis* *Balanocrinus subteres* *Isocrinus* sp. *Isocrinus nicoleti* *Isocrinus pendulus* *Pentacrinites* cf. *dargniesi* **Comatulids:** Paracomatulidae sp. et gen. indet. *Palaeocomaster* sp.
B – boreholes in eastern Poland (Kock IG 2, Maciejowice IG 1, Magnuszew IG 1, Siedliska IG 1, Tłuszcz IG 1, Żyrzyn IG 1); Central European province	latest Bathonian-Callovian	8, including: 6 isocrinids and 2 cyrtocrinids	**isocrinids:** Isocrinida indet. *Chariocrinus andreae* *Balanocrinus subteres* *Balanocrinus pentagonalis* *Isocrinus nicoleti* *Pentacrinites dargniesi* **Cyrtocrinids:** Cyrtocrinida indet. *Phyllocrinus* sp.
B – Żebrak IG 1; Central European province	Callovian	6, including: 5 isocrinids and 1 cyrtocrinid	**isocrinids:** *Chariocrinus andreae* *Balanocrinus* cf. *subteres* *Isocrinus* sp. *Isocrinus* cf. *nicoleti* *Pentacrinites* sp. **Cyrtocrinids:** Cyrtocrinida indet.
C – southern margin of the Holy Cross Mountains; Central European province	Bathonian	3, including: 2 isocrinids and 1 comatulid	**Isocrinids:** *Chariocrinus andreae* *Balanocrinus berchteni* **Comatulids:** *Paracomatula helvetica*
C – southern margin of the Holy Cross Mountains; Central European province	Callovian	2, including: 1 isocrinid and 1 cyclocrinid	**Isocrinids:** *Chariocrinus andreae* **Cyclocrinids** (order uncertain according to Hess & Messing, 2011): *Cyclocrinus macrocephalus*
D – southern part of the Polish Jura; Central European province	Bathonian	6, including: 3 isocrinids, 2 comatulids and 1 cyrtocrinid	**Isocrinids:** *Chariocrinus andreae* *Balanocrinus berchteni* *Isocrinus bajociensis* **Comatulids:** *Paracomatula helvetica* *Palaeocomaster* sp. **Cyrtocrinids:** Cyrtocrinida indet. (=Millericrinina in Salamon & Zatoń, 2007)

D – southern part of the Polish Jura; Central European province	Callovian	15, including: 3 isocrinids, 11 cyrtocrinids and 1 cyclocrinid	**Isocrinids:** *Chariocrinus andreae* *Balanocrinus subteres* *Balanocrinus pentagonalis* (=*Balanocrinus hessi* in Salamon & Zatoń, 2006) **Cyrtocrinids:** Cyrtocrinida indet. (=Millericrinina in Salamon & Zatoń, 2007) *Phyllocrinus* sp. *Phyllocrinus stellaris* *Phyllocrinus belbekensis* *Tetracrinus moniliformis* *Sclerocrinus* sp. *Cyrtocrinus* sp. *Pilocrinus moussoni* *Dolichocrinus aberrans* *Fischericrinus ausichi* *Lonchocrinus dumortieri* **Cyclocrinids**: *Cyclocrinus macrocephalus*
E – Tatra Mountains; Tethyan province	Bathonian	8, including: 6 isocrinids, 1 cyrtocrinid and 1 cyclocrinid	**Isocrinids:** *Isocrinus* sp. *Isocrinus bathonicus* *Isocrinus nicoleti* *Isocrinus pendulus* *Balanocrinus* sp. *Pentacrinites dargniesi* **Cyrtocrinids:** Cyrtocrinida indet. **Cyclocrinids:** *Cyclocrinus rugosus*
E – Tatra Mountains; Tethyan province	Callovian	3, including: 1 isocrinid, 1 cyrtocrinid and 1 roveacrinid	**Isocrinids:** *Isocrinus* sp. **Cyrtocrinids:** Cyrtocrinida indet. **Roveacrinids:** *Saccocoma* sp.
F – Pieniny Klippen Belt; Tethyan province	Bathonian	16, including: 10 isocrinids, 5 cyrtocrinids and 1 roveacrinid	**Isocrinids:** *Chariocrinus andreae* *Isocrinus* sp. *Isocrinus bathonicus* *Isocrinus nicoleti* *Isocrinus pendulus* *Balanocrinus* sp. *Balanocrinus berchteni* *Balanocrinus pentagonalis* *Balanocrinus subteres* *Pentacrinites dargniesi* **Cyrtocrinids:** Cyrtocrinida indet. *Plicatocrinus tetragonus* *Lonchocrinus dumortieri* *Remisovicrinus* sp. *Dolichocrinus* sp. *aberrans* **Roveacrinids:** *Saccocoma* sp.

| F – Pieniny Klippen Belt; Tethyan province | Callovian | 14, including: 2 isocrinids, 9 cyrtocrinids, 1 roveacrinid, and 2 cyclocrinids | **Isocrinids:** *Balanocrinus subteres* *Balanocrinus pentagonalis* **Cyrtocrinids:** Cyrtocrinida indet. *Lonchocrinus dumortieri* *Remisovicrinus* sp. *Dolichocrinus* cf. *aberrans* *Eudesicrinus* sp. *Pilocrinus moussoni* *Gammarocrinites* sp. *Sclerocrinus compressus* *Phyllocrinus* sp. **Roveacrinids:** *Saccocoma* sp. **Cyclocrinids:** *Cyclocrinus* sp. *Cyclocrinus rugosus* |

Number of collected crinoid remains during observation of respective cores and maceration process.

Species	Details
Isocrinida indet.	Plenty of more or less complete columnals, brachials, and cirrals
Isocrinus nicoleti (Desor, 1845)	Plenty of more or less complete, isolated columnals
Chariocrinus andreae (Desor, 1845)	Plenty of more or less complete, isolated columnals
Balanocrinus subteres (Münster in Goldfuss, 1826)	Plenty of more or less complete, isolated columnals
Balanocrinus pentagonalis (Goldfuss, 1826-1844)	21 almost complete columnals
Pentacrinites dargniesi Terquem & Jourdy, 1869	Plenty of cirrals, 14 almost complete columnals
Cyrtocrinida indet.	Plenty of cup remains and partly preserved columnals and 27 nearly complete columnals
Phyllocrinus sp.	Two cups

Analysis Of Variance (ANOVA)

(A) ANOVA test between different substrate types (Claystones, Sandstones and Limestones). (B) Tukey's HSD (honestly significant difference) test for pairwise comparisons. (C) ANOVA test between different paleodepth parameters (Near shore, Shallow-marine, Mid-ramp and Off shore). (D) Tukey's HSD (honestly significant difference) test for pairwise comparisons.

a

Source	SS	df	MS	
Between-treatments	96	2	48	$F = 8.57872$
Within-treatments	335.7143	60	5.5952	
Total	431.7143	62		

b

Pairwise comparisons		$HSD_{.05} = 1.7543$	$Q_{.05} = 3.3987$
		$HSD_{.01} = 2.2104$	$Q_{.01} = 4.2822$
Claystones: Sandstones	M1 = 0.90 M2 = 0.33	0.57	$Q = 1.11$ ($p = .71491$)
Claystones: Limestones	M1 = 0.90 M3 = 3.19	2.29	**$Q = 4.43$ ($p = .00748$)**
Sandstones: Limestones	M2 = 0.33 M3 = 3.19	2.86	**$Q = 5.54$ ($p = .00068$)**

c

Source of variation	SS	df	MS	
Between-treatments	28.9	3	9.6333	$F = 3.32335$
Within-treatments	220.3	76	2.8987	
Total	249.2	79		

d

Pairwise Comparisons		$HSD_{.05} = 1.4143$	$Q_{.05} = 3.7149$ $Q_{.01} = 4.5530$
		$HSD_{.01} = 1.7333$	
$T_1:T_2$	$M_1 = 0.35$ $M_2 = 2.00$	1.65	**$Q = 4.33$ ($p = .01563$)**
$T_1:T_3$	$M_1 = 0.35$ $M_3 = 0.85$	0.5	$Q = 1.31$ ($p = .78958$)
$T_1:T_4$	$M_1 = 0.35$ $M_4 = 1.20$	0.85	$Q = 2.23$ ($p = .39675$)
$T_2:T_3$	$M_2 = 2.00$ $M_3 = 0.85$	1.15	$Q = 3.02$ ($p = .15112$)
$T_2:T_4$	$M_2 = 2.00$ $M_4 = 1.20$	0.8	$Q = 2.10$ ($p = .45097$)

T_3:T_4	$M_3 = 0.85$	0.35	$Q = 0.92$ ($p = .91521$)
	$M_4 = 1.20$		

Figure 1

Location maps

(A) Palaeogeographic map of central Europe during the Middle Jurassic (modified after Šimkevičius et al., 2003). A– Bathonian and Callovian exposures of the southern part of the Polish Jura; B – Bathonian and Callovian exposures of the southern margin of the Holy Cross Mountains; C – Callovian exposure of the glacial drift in Łuków; G1-G6 – location of the Bathonian-Callovian boreholes described in this constribution [Tłuszcz IG1 (G1), Siedliska IG1 (G2), Kock IG2 (G3), Żyrzyn IG 1 (G4), Maciejowice IG1 (G5), Magnuszew IG1 (G6)], D location of borehole Żebrak IG1 (details in Salamon & Feldman-Olszewska, 2018); A–D – Central European province; E – Bathonian and Callovian exposures of the Tatra Mountains; F – Bathonian and Callovian exposures of the Pieniny Klippen Belt; E, F – Tethyan province. (B) Map of Callovian lithofacies noted in Poland (modified after Dayczak-Calikowska & Moryc, 1988).
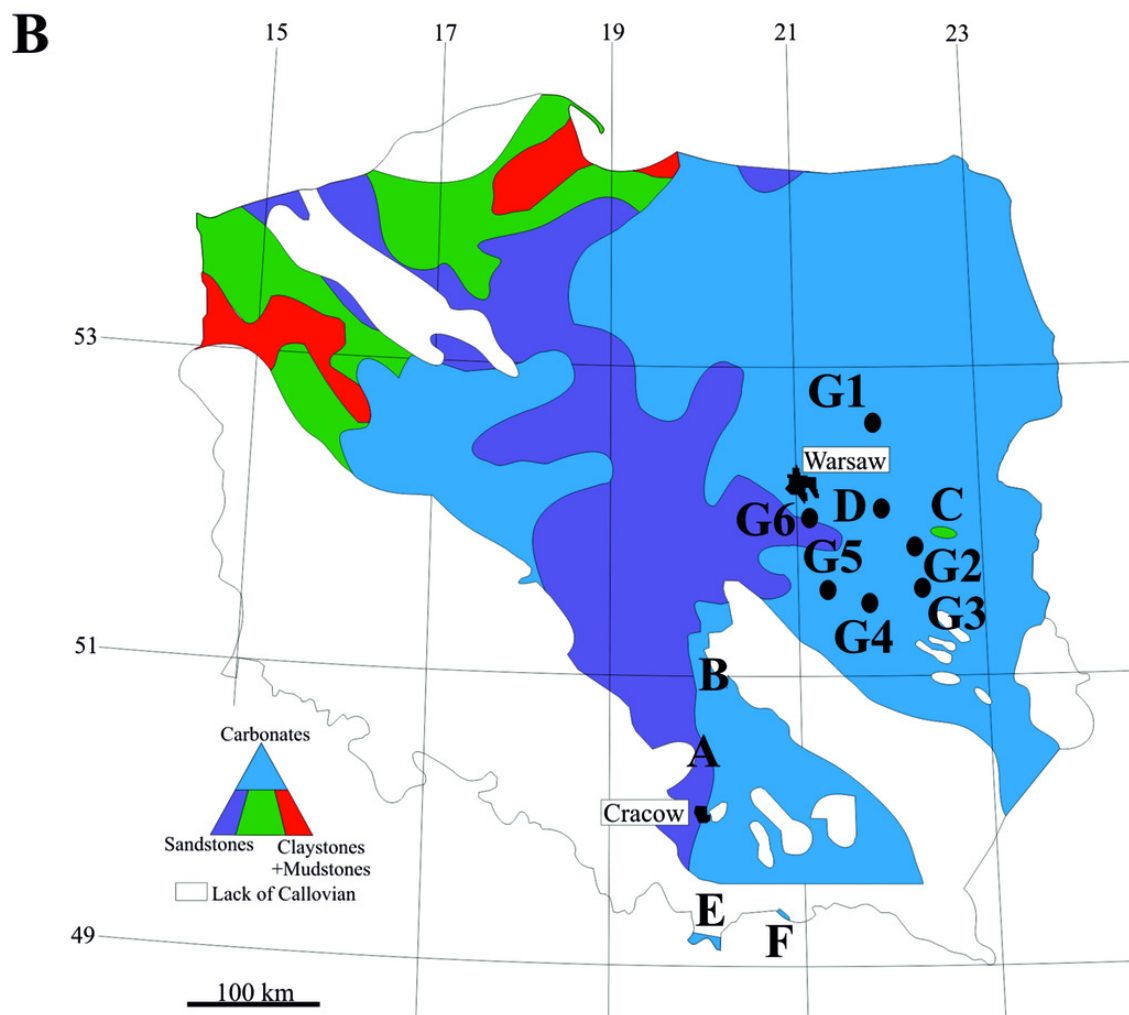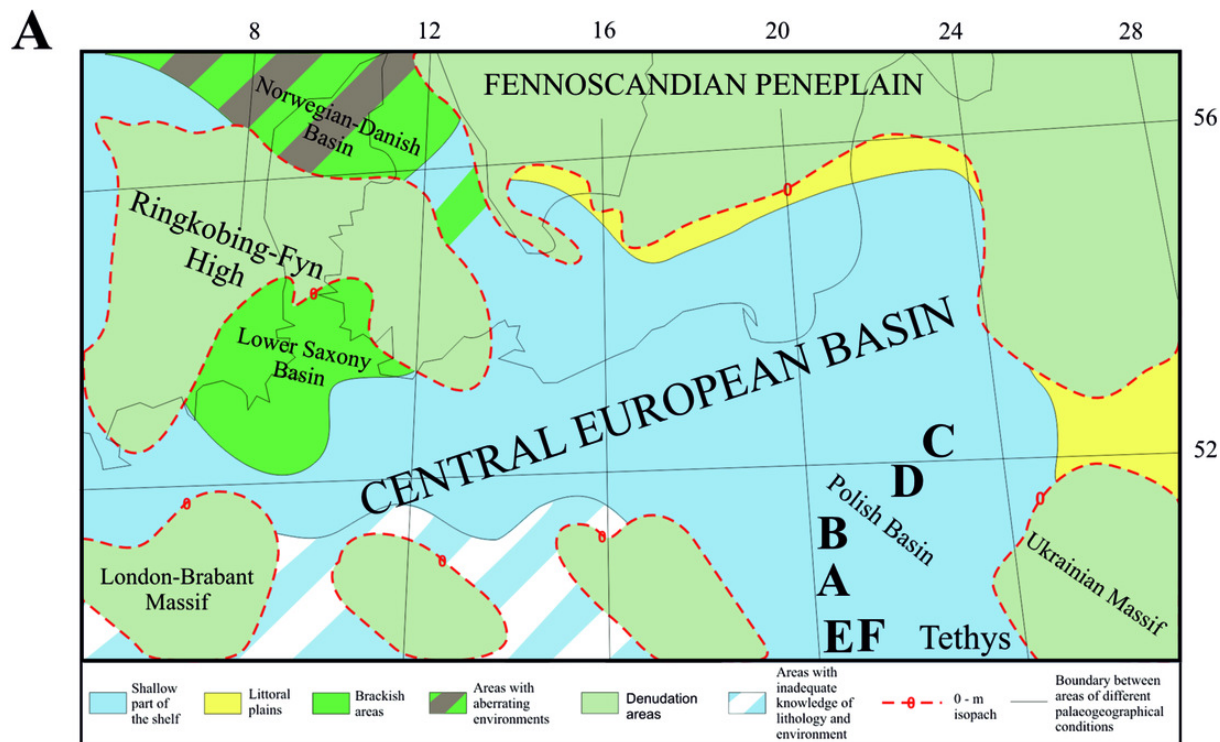
Figure 2

Model showing distribution of selected Callovian crinoids.
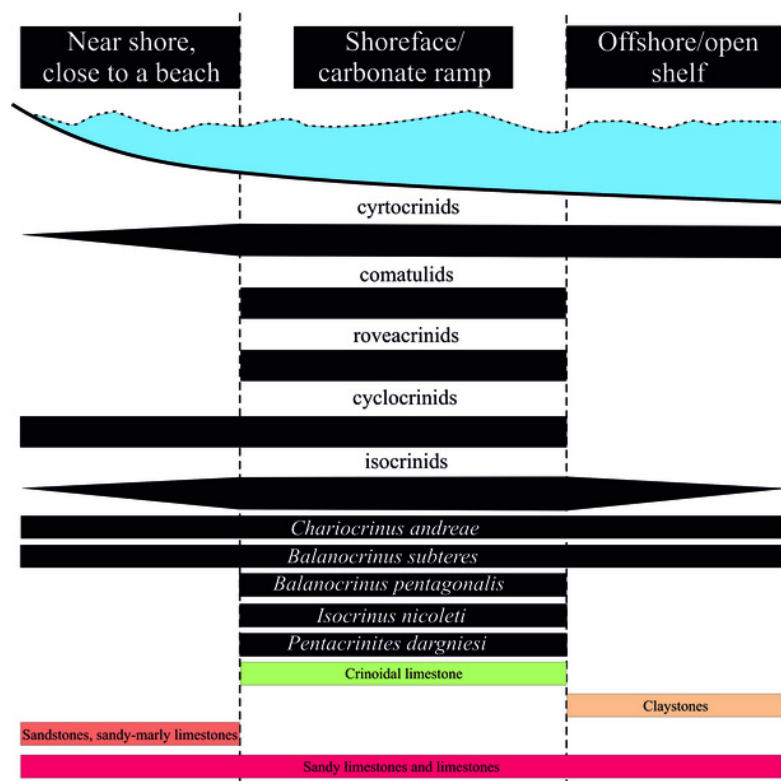
Figure 3

Cyclocrinid remains from southern Poland.

(A) Columnal, articular facet. (B) Brachial plate. Scale bar equals 1 mm. Blue arrows mark granules covering the articular facet of columnal.