

1 **Mass extinction or Extirpation: Permian biotic turnovers in the northwestern margin of**  
2 **Pangea**

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16 The Capitanian (Middle Permian) mass extinction event, prior to and separated from the  
17 end-Permian mass extinction, has been suggested as a severe biotic crisis comparable to the  
18 big five mass extinctions of the Phanerozoic. However, there is still controversy about its  
19 global significance. In particular, this purportedly disastrous event in the Capitanian has been  
20 mostly recognized from the eastern Tethys (especially South China) whereas its extent in  
21 higher latitudinal regions remains unclear. A few recent studies have reported the  
22 biostratigraphic and chemostratigraphic evidence for the Capitanian extinction at the  
23 northwestern marginal shelf of Pangea including the Kapp Starostin Formation in  
24 Spitsbergen. However, we here report a contrasting result to these previous studies, based on  
25 a study of abundant brachiopod fossils collected from eight geological sections representing  
26 the same formation in western and central Spitsbergen. Our biostratigraphic investigation  
27 recognizes a total of five brachiopod assemblages from the type section of the Kapp Starostin  
28 Formation at Festningen. The most striking biotic change in species composition is observed  
29 at the interval between the lowermost Vøringen Member (late Artinskian) and its overlying  
30 member (Kungurian) of the Kapp Starostin Formation in Spitsbergen, thus much earlier than  
31 the Capitanian. A similar faunal shift at the same stratigraphic interval is also observed from  
32 bryozoan-based biostratigraphic data. This faunal turnover could be linked to a significant  
33 climatic shift (cooling) along the northwestern margin of Pangea during the  
34 Artinskian–Kungurian. Specifically, it is inferred that a climatic perturbation (cooling) likely  
35 had driven the extirpation (emigration) of marine faunas out of Spitsbergen and dispersal  
36 eastward into some lower latitudinal and climatically more ameliorated areas. Our result  
37 indicates that the Capitanian interval in Spitsbergen does not record a catastrophic event  
38 corresponding to the Capitanian mass extinction in Tethyan regions, rather it is more  
39 characterized by gradual faunal transitions throughout the Middle to Late Permian. This  
40 faunal transition was accompanied with some major changes in lithology, suggesting a degree  
41 of local environmental control, especially in the changes of substrate and water depth, on the  
42 composition of the benthic faunas. The Wegener Halvø and Schuchert Dal formations  
43 (Lopingian) in central East Greenland contain a diverse brachiopod fauna comparable to that  
44 from post-Vøringen Member in Spitsbergen. This implies that the brachiopods in the  
45 northwestern marginal shelf of Pangea did not suffer a severe mass extinction in the  
46 Capitanian; instead, many of them migrated southward with the development of the Zechstein  
47 seaway.

## 50 INTRODUCTION

51 Mass extinctions are one of the most significant mechanisms shaping the history of life  
52 on Earth. Most of the well-known mass extinctions during the Phanerozoic have resulted in  
53 large changes of ecological structures, bringing about the advent of new ecosystems. On the  
54 other hand, some mass extinction events have been inferred through regional-scale  
55 investigations and their global extent has not been clearly identified.

56 The notion of a possible global Capitanian (or end-Guadalupian) mass extinction first  
57 came to the literature through the work of Jin (1993), Jin et al. (1994) and Stanley and Yang  
58 (1994). Since then, numerous studies have been published on this topic, generally in support  
59 of the idea that a major biotic event of regional to global scale had occurred at or near the end  
60 of the Middle Permian (Guadalupian), which preceded and was separated from the end-  
61 Permian mass extinction. Among the previous studies, a few (e.g., Bambach, 2006; Bond et  
62 al., 2010; Rampino and Shen, 2019) have suggested that the Capitanian extinction was a  
63 global crisis, comparable to the big five mass extinctions of the Phanerozoic. However, there  
64 are still ongoing controversies, particularly about the intensity and extent of the event. Some  
65 studies (e.g., Clapham et al., 2009; Grove and Wang, 2013) have regarded the Capitanian  
66 event just as a protraction of a long-term gradual diversity loss trend throughout the  
67 Guadalupian. Further, it has been viewed as a minor species-diversity fluctuation either by  
68 sea-level change or volcanism in more recent publications (Fan et al., 2020; Shen et al.,  
69 2020). In terms of the geographical spread, to date the Capitanian extinction event has been  
70 detected mostly from the eastern Tethys, particularly in South China (Shen and Shi, 1996,  
71 2009; Shi and Shen, 2000; Wang and Sugiyama, 2000; Isozaki et al., 2004; Wignall et al.,  
72 2009; Bond et al., 2010) and Japan (Isozaki and Ota, 2001; Isozaki et al., 2007). Another  
73 ongoing debate concerning the Capitanian extinction is in regard to its causes, with two  
74 leading scenarios: one linking the event to the eruption of the Emeishan large igneous  
75 province in southwest China and Vietnam (Wignall, 2001; Zou et al. 2002; Wignall et al.,  
76 2009; Bond et al., 2010; Huang et al., 2019), and the other relating the event to a major global  
77 cooling episode, the Kimura event (e.g., Isozaki et al., 2007; Isozaki, 2009).

78 To date, evidence in support of the purported Capitanian mass extinction from higher  
79 latitudinal regions (including the Boreal Realm and Gondwana Realm) has been scanty, with  
80 the exception of Bond et al. (2015, 2020). The first of these two papers documented  
81 significant changes in biostratigraphy and chemostratigraphy through the upper part of the  
82 Kapp Starostin Formation at Festningen (type locality of the formation) in Spitsbergen, which  
83 the authors interpreted as evidence for a Capitanian mass extinction. According to their fossil  
84 occurrence range chart (Bond et al., 2015, fig. 7), the diversity of brachiopod species suffered  
85 a severe setback 40 m below the Kapp Starostin-Vardebukta formational boundary, marked  
86 by the loss of 87% of the species. Stratigraphically, the position of the biotic event coincided  
87 with a level of significant elemental enrichment of some trace metals (molybdenum, uranium  
88 and vanadium) as well as a reduction in the mean size of pyrite framboids. Consequently,  
89 Bond et al. (2015) attributed oxygen depletion, as well as ocean acidification, as the main  
90 cause of the Capitanian extinction in Spitsbergen. In search for evidence for a similar event in  
91 other parts of the Boreal region, Bond et al. (2015) compared the Capitanian extinction and  
92 subsequent biotic recovery pattern in Spitsbergen with the Permian fossil records in the  
93 Wegener Halvø Formation and the overlying Schuchert Dal Formation of central East  
94 Greenland. The comparison led them to conclude that a contemporaneous Capitanian  
95 extinction also occurred in central East Greenland. More recently, Bond et al. (2020) also  
96 reported on a similar extinction event from the Permian of Arctic Canada then located on the  
97 northwestern marginal shelf of Pangea.

98 The two studies reviewed above are, potentially, of utmost importance as far as the  
99 Capitanian mass extinction is concerned. This is because that until the publication of these  
100 two papers, the Capitanian marine mass extinction as a concept had only been recognized in  
101 palaeoequatorial (Tethys) regions and even there, evidence in support of this mass extinction  
102 event has been equivocal. Furthermore, it is notable that the sudden Capitanian mass  
103 extinction in Spitsbergen, postulated by Bond et al. (2015), had never been identified in any  
104 earlier detailed biostratigraphic studies of the same area including studies based on identical  
105 sections (e.g., Stepanov, 1957; Gobbett, 1964; Ustritskii, 1979; Nakamura et al., 1987;  
106 Nakamura et al., 1992; Nakrem et al., 1992). This considerable discrepancy raises the  
107 question of sampling, taxonomy, and biostratigraphic dating and resolution. In addition,  
108 faunal comparison and age correlation between key regions of the present Arctic is critical for  
109 ascertaining the timing and causes of regional biotic turnover events for Permian marine  
110 benthos, as some significant temporal changeovers may represent regional extirpation  
111 (emigration) events rather than signaling global mass extinctions.

112 The primary objective of the present study is to test the scenario proposed by Bond et al.  
113 (2015) that there was a severe and sudden Capitanian biotic crisis in Spitsbergen, by using  
114 our own biostratigraphic data obtained from eight sections, all representing the Kapp  
115 Starostin Formation including the Festningen section, the type section of the formation.  
116 Together with examining the Boreal extension of the Capitanian catastrophic event, we also  
117 investigate how marine benthos (mainly brachiopods) reacted to the dynamic evolution and  
118 configuration of the northwestern marginal shelf of Pangea during the Permian.

## 121 **GEOLOGICAL SETTINGS**

122 The northwestern marginal shelf of the supercontinent Pangea was composed of the  
123 current Arctic region during the late Palaeozoic. The region includes, from west to east,  
124 Canadian Arctic Islands (Sverdrup Basin), North Greenland, Svalbard, Barents Shelf, Novaya  
125 Zemlya, Kanin Peninsula, and the Timan-Pechora Basin (Fig. 1; Ziegler, 1988; Golonka and  
126 Ford, 2000; Stemmerik and Worsley, 2005; Angiolini et al., 2013). The west-east oriented  
127 shelf was positioned at around 20°N palaeolatitude in the Mississippian and reached to 45°N  
128 palaeolatitude by the latest Permian through the continuous northward drift of Pangea  
129 (Golonka and Ford, 2000; Stemmerik and Worsley, 2005). The Ural seaway connecting the  
130 northwestern marginal shelf of Pangea to the Palaeo-Tethys was closed off by the collision  
131 between Baltica and Kazakhstan in the Cisuralian (Ziegler, 1988; Shi et al., 1995; Puchkov,  
132 1997; Fokin et al., 2001). With the closure of the Ural seaway, the proto-Atlantic seaway  
133 connecting Svalbard and the Barents Shelf with East Greenland and northwest Europe started  
134 to develop. As a result, the Zechstein Basin was formed with the development of a large  
135 epeiric sea extending southward into northern and central Europe covering parts of Britain,  
136 Germany and Poland in the Middle to Late Permian (Heeremans et al., 2004).

137 Upper Palaeozoic successions are widely distributed in Spitsbergen, the largest island of  
138 Svalbard (Fig. 2; Dallmann, 1999). The deposition of these successions was mainly  
139 controlled by the major structural elements (Steel and Worsley, 1984). Throughout the  
140 Carboniferous, narrow troughs and adjacent highs were mostly developed along currently  
141 NNE-SSW oriented fault lines by extensional tectonism, which led to differential  
142 sedimentation between the troughs. However, since the cessation of tectonic movement in the  
143 Late Carboniferous, stable marine shelf conditions developed (except for southern  
144 Spitsbergen), and continued until the Late Permian with continuous subsidence (Dallmann,  
145 1999; Stemmerik and Worsley, 2005).

146 The Permian strata in Spitsbergen are composed of three groups: the Gipsdalen,  
147 Tempelfjorden and Sassendalen groups in ascending order (Fig. 1; Dallmann, 1999). The  
148 Gipsdalen Group, lasting from the Serpukhovian (Late Carboniferous) to early Artinskian,  
149 consists of diverse lithostratigraphic units, which together represent a gradual transition from  
150 terrestrial clastic deposition to marine carbonate deposition through progressive transgression  
151 and basin deepening (Johannessen and Steel, 1992; Hüneke et al., 2001). Thus, the upper part  
152 of the Gipsdalen Group is characterized by widely distributed carbonates and evaporates  
153 developed under warm and arid conditions, represented by the Wordiekammen and  
154 Gipshuken formations (Fig. 1).

155 The Tempelfjorden Group disconformably overlies the Gipsdalen Group in Spitsbergen  
156 (Fig. 1), consisting of a mixed carbonate and siliciclastic succession deposited in relatively  
157 stable marine shelf environments. The Tempelfjorden Group is characterized by the Kapp  
158 Starostin Formation (late Artinskian to Lopingian?) in most areas of Spitsbergen (Figs. 1 and  
159 2). The mixed siliciclastics and carbonates dominated in the formation suggest that the  
160 deposition occurred under open-marine, cooler and deeper conditions (Dallmann, 1999;  
161 Stemmerik and Worsley, 2005; Blomeier et al., 2013). The whole formation reaches to  
162 several hundred meters in thickness (385 m thick in the type section).

163 The Vøringen Member (late Artinskian to early Kungurian), defined as the basal part of  
164 the Kapp Starostin Formation (Fig. 1), is mainly composed of bioclastic limestones with  
165 abundant brachiopods, bryozoans, crinoids and other marine fossils. This bioclastic limestone  
166 unit has been interpreted to be deposited in nearshore environments (Nakrem, 1994; Blomeier  
167 et al., 2011). The lithological contrast with the underlying upper part of the Gipshuken  
168 Formation dominated by dolomites indicates a widespread marine transgression during the  
169 Artinskian (Steel and Worsley, 1984; Ezaki et al., 1994; Blomeier et al., 2011). The  
170 Svenskeegga member or other equivalent units which overlies the Vøringen Member  
171 represents the middle part of the Kapp Starostin Formation and is composed of cherts and  
172 siliceous shales with intercalated bioclastic limestones; these rocks have been interpreted as  
173 relatively deep marine deposits (Ezaki et al., 1994; Dallmann, 1999; Blomeier et al., 2013).  
174 The upper part of the Kapp Starostin Formation mainly consists of silicified shales,  
175 glauconitic sandstones and sandy limestones; together, they suggest sedimentation in  
176 shoreface to deeper shelf environments (Ezaki et al., 1994; Ehrenberg et al., 2001; Hüneke et  
177 al., 2001; Blomeier et al., 2013). Several local units, including the Hovtinden and  
178 Stensiöfjellet members, have been suggested for the upper part of the formation (Dallmann,  
179 1999). However, the overall lithostratigraphic correlation of the formation across Spitsbergen  
180 (and other adjacent islands) has not been clearly understood yet, and all the member  
181 subdivisions except for the Vøringen Member are still informally used.

182 The Tempelfjorden Group is overlain by the Sassendalen Group (latest Permian to  
183 Middle Triassic). The Vardebukta Formation, representing the basal part of the Sassendalen  
184 Group in Spitsbergen (Fig. 1), is mainly composed of non-siliceous dark shales and siltstones,  
185 suggesting the demise of biogenic silica production during the latest Permian to Early  
186 Triassic times (Ehrenberg et al., 2001; Worsley, 2008). To date, whether or not the distinct  
187 lithological change across the Tempelfjorden and Sassendalen group boundary represents a  
188 hiatus remains a matter of debate (Mørk et al., 1989; Stemmerik and Worsley, 2005; Nakrem  
189 et al., 2008a; Blomeier et al., 2011), and is beyond the scope of the present study.

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### 191 **Previous biostratigraphic records from the Kapp Starostin Formation and age** 192 **assignments**

193 There has been debate over the stratigraphy and age range of the Kapp Starostin  
194 Formation for several decades, mainly due to the scarcity of biostratigraphically important

195 microfossils (e.g., conodonts, foraminiferans and palynomorphs). A few studies (Szaniawski  
196 and Małkowski, 1979; Nakrem et al., 1992; Igo, 1995; Buggish et al., 2001) have reported  
197 rare conodont fossils, including *Neostreptognathodus pequopensis*, a characteristic late  
198 Artinskian species (Henderson, 2018; Henderson and Shen, 2020), from the basal Vøringen  
199 Member. Based on the conodont occurrences, the deposition of the Vøringen Member can be  
200 reasonably considered to have, at least, commenced in the late Artinskian. By comparison,  
201 the biostratigraphy and age determination for the upper units of the Kapp Starostin Formation  
202 are far less certain and remain a matter of continuous debate (see Shen et al., 2005, fig. 3),  
203 primarily due to the extreme scarcity and poor preservation of conodonts throughout the  
204 succession.

205 There have been several different views with respect to the ages of the brachiopod  
206 assemblages in the Kapp Starostin Formation. Stepanov (1957; see also Gobbett, 1964)  
207 regarded all the brachiopod assemblages of this formation as a single fauna characterizing a  
208 crucial stage of the Permian timescale in the Arctic (Svalbardian Stage). On the other hand,  
209 following detailed field collecting and stratigraphic analysis, Nakamura et al. (1987, 1992)  
210 proposed a succession of five brachiopod biozones spanning the Kapp Starostin Formation  
211 from Kungurian to early Lopingian. This biostratigraphic scheme was subsequently criticized  
212 by Stemmerik (1988), who concluded that the four upper brachiopod biozones actually  
213 represent local ecological communities with strong local environmental control rather than a  
214 succession of broad basin-wide biostratigraphic horizons. However, despite the suggested  
215 invalidity of the brachiopod biozones, Stemmerik (1988) agreed on the stratigraphic  
216 correlation of Nakamura et al. (1987) that the lowermost and mid to upper parts of the Kapp  
217 Starostin Formation would be comparable with the Mallemuk Mountain Group in  
218 northeastern Greenland and the Foldvik Creek Group in central East Greenland, respectively,  
219 therefore implying the age range of the Kapp Starostin Formation to be Kungurian to  
220 Lopingian.

221 More recently, Shen (2018) elevated the ages of the two uppermost biozones of  
222 Nakamura et al. (1987, 1992) into the Lopingian, based on a comparison with the brachiopod  
223 fauna from central East Greenland originally described by Dunbar (1955). Bond et al. (2015),  
224 on the other hand, recognized an extinction event at the boundary of these two uppermost  
225 brachiopod biozones which they equated to the Capitanian mass extinction of the low-latitude  
226 Tethyan regions.

227 Up until now, the age for the upper boundary of the Kapp Starostin Formation remains  
228 uncertain, despite the fact that Permian–Triassic boundary is now well defined at the lower  
229 part of the overlying Vikinghøgda Formation (corresponding to the Vardebukta Formation) by  
230 the discovery of the conodont *Hindeodus parvus* from a drillcore section in central  
231 Spitsbergen (a level of 4 m above the base of the Vikinghøgda Formation) (Zuchuat et al.,  
232 2020). Based on the overall biostratigraphy and age range of the Kapp Starostin Formation,  
233 both Nakamura et al. (1992) and Nakrem et al. (1992) speculated that the uppermost part of  
234 this formation, a short stratigraphic interval characterized by condensed sedimentation and  
235 lacking well-preserved fossils, might extend into the Lopingian. This assertion has  
236 subsequently been corroborated by evidence from more recent chemostratigraphy-based  
237 studies, all in favor of a continuous succession between the Kapp Starostin Formation and the  
238 overlying Vardebukta Formation. Under this scenario, it would mean that, at least, the  
239 uppermost part of the Kapp Starostin Formation would represent the late Changhsingian.  
240 However, a recent sequence stratigraphic study for the Kapp Starostin Formation conducted  
241 by Bond et al. (2018) demonstrated that the formation's two youngest (Capitanian to  
242 Lopingian) sequences were detected only at the outcrops in western Spitsbergen, implying a  
243 possible cessation of sedimentation, at least, in central and eastern Spitsbergen during the

244 time interval, thus casting doubt on a continuous Permian-Triassic transition from the Kapp  
245 Starostin Formation to the Vardebukta Formation for the whole of Spitsbergen.

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## 248 **MATERIALS AND METHODS**

249 In order to obtain detailed biostratigraphic data from the Kapp Starostin Formation, the  
250 logging data and fossil samples from three intensive geologic expeditions over two decades  
251 have been re-investigated. The expeditions were conducted firstly by a Japanese party (led by  
252 Prof. K. Nakazawa) in 1986 (see Nakazawa et al., 1990), then followed by the Japanese  
253 Norwegian Research Group in 1989-1991 (see Nakamura, 1992), and most recently  
254 performed by the Korea Polar Research Institute in 2012-2016. In total, eight outcrop  
255 sections across Spitsbergen were logged in detail and several thousands of brachiopod  
256 samples were systematically collected from 59 fossil horizons through the expeditions. These  
257 sections are widely distributed across western and central Spitsbergen, including  
258 Scheteligfjellet and Trygghamna sections (Oscar II Land), Festningen section (in outer  
259 Isfjorden), Reinodden and Ahlstrandodden section (in Wedel Jarlsberg Land), and Idodalen as  
260 well as Skansbukta A and B sections (Dickson Land) (Fig. 2). Although the sections were  
261 investigated by three different expedition bodies, the modern lithostratigraphic scheme  
262 established by Cutbill and Challinor (1965) was consistently applied, and an identical  
263 sampling procedure was employed. Moreover, a few sections investigated by the earlier  
264 expeditions were revisited by the latest one for checking the consistency of data collection.

265 The brachiopod fossils were collected from various lithologies in the sections. These  
266 fossil specimens have supported previous publications (e.g., Nakamura et al., 1987, 1992;  
267 Shen et al., 2005; Lee et al., 2016, 2019), but the majority have not been taxonomically  
268 studied yet. We have re-assessed the brachiopod species through our own observation for the  
269 fossil materials as well as the re-evaluation from the publications. The biostratigraphic data of  
270 the brachiopod species have been established for each section and a correlation among the  
271 sections has been undertaken.

272 We have also included biostratigraphic data of bryozoans independently collected at the  
273 Festningen section by one of the authors (HAN), in order to examine the biostratigraphic  
274 pattern of another marine sessile fauna. In addition, the brachiopod range data from Bond et  
275 al. (2015, fig. 7) has been correlated on our columnar log of the Festningen section.

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277

## 278 **RESULTS**

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### 280 **Biostratigraphic data at the Festningen section**

281 Our brachiopod biostratigraphy from the Kapp Starostin Formation at its stratal type  
282 locality, the Festningen section, displays a gradual faunal change throughout the formation. In  
283 particular, the result is very well-matched with the biozones suggested by Nakamura et al.  
284 (1987, 1992). Nakamura et al. (1987) originally established five brachiopod biozones at the  
285 type section of the Kapp Starostin Formation, Festningen section, consisting of, in ascending  
286 order: *Horridonia timanica*, *Waagenoconcha* sp. A, *Megousia weyprechtii*, *Pterospirifer*  
287 *alatus*, and *Haydenella wilczeki* zones. Subsequently, the *Waagenoconcha* sp. A Zone was  
288 renamed as the *Paeckelmanella* sp. Zone in Nakamura et al. (1992). Numerous species have  
289 been taxonomically revised and reassigned to other genera or species and their stratigraphic  
290 ranges modified as a result of our taxonomic re-assessment. The newly reconstructed  
291 biostratigraphy at the Festningen section, however, still demonstrates the presence of five

292 brachiopod stratigraphic assemblages, which are nearly identical to the biozones proposed by  
293 Nakamura et al. (1987, 1992) (Fig. 3).

294 The “*Horridonia timanica*” Zone, corresponding to the basal Vøringen Member, exhibits  
295 a very distinctive brachiopod assemblage (Fig. 3). *Horridonia timanica* was originally  
296 thought by Nakamura et al. (1987) to be a diagnostic species for this biozone, but this species  
297 was later found to be a synonym of *Bruntonia maynci* in Angiolini and Long (2008).  
298 Consequently, the age range of the species is considerably longer than originally thought and  
299 extends, at least, into the younger “*Megousia*” *weyprechtii* Zone. However, aside from this  
300 species, most other species included in the “*Horridonia timanica*” Zone, including  
301 *Fasciculatia groenwalli*, *Arcullina polaris*, *Timaniella wilczeki*, *Chaoiella neoinflata*,  
302 *Yakovlevia mammata*, and *Bruntonia granulifera*, are restricted to the Vøringen Member at  
303 the type section. These species also occur exclusively from the basal part of the formation  
304 (Vøringen Member) at all other studied sections.

305 The *Paeckelmanella* sp. Zone is defined by *Linoproductus janischewskianus*, *Yakovlevia*  
306 *duplex*, and *Paeckelmanella* sp. in the lower part of the zone, and *Licharewia* cf. *L. grewingki*  
307 and *Stenosisma* sp. in the upper part (Fig. 3). In addition, several species with relatively long  
308 stratigraphic ranges, such as *Fasciculatia striatoparadoxa*, *Spiriferella loveni*, *Cleiothyridina*  
309 *pectinifera*, *Cleiothyridina kotlukovi*, and *Lissochonetes superba*, also appear for the first  
310 time in this zone. At the Festningen section, this zone occupies the upper part of Svenskeegga  
311 member as well as the lower part of the Hovtinden member.

312 The overlying “*Megousia*” *weyprechtii* Zone simply corresponds to the stratigraphic  
313 range of the species (re-assigned to *Kuvelousia weyprechtii* herein), occupying the middle part  
314 of the Hovtinden member at the Festningen section. This zone is also characterized by the  
315 occurrence of *Waagenoconcha payeri*, *Thamnusia crassauritus*, and ?*Larispirifer* sp. (Fig. 3).  
316 There are several other species also confined within this zone at the Festningen section, but  
317 they display variable stratigraphic ranges at the other sections.

318 The succeeding *Pterospirifer* “*alatus*” Zone at the Festningen section is characterized by  
319 the ranges of *Pseudohorridonia scoresbyensis*, spiriferellinid gen. sp. indet., and *Pterospirifer*  
320 *cordieri* (to which *Pterospirifer alatus* is re-assigned herein), but all these species are rare at  
321 many of the other studied sections. This zone is located in the upper part of the Hovtinden  
322 member together with the overlying *Haydenella wilczeki* Zone.

323 The *Haydenella wilczeki* Zone is the youngest biozone in the Festningen section, and is  
324 represented by an assemblage including *Haydenella wilczeki*, *Haydenella gefoensis*, and  
325 *Dielasma elongatum*, all of which only occur ~10 m below the top of formation at the  
326 Festningen section (Fig. 3). *Waagenoconcha irginaeformis* and *Megousia yakutica* are also  
327 present in this horizon, however, they appear in much lower horizons in other sections.

328 It is clear from the consecutive compositional changes of the brachiopod biozones at the  
329 Festningen section that the most striking brachiopod faunal change occurred between the two  
330 lowermost biozones divided by a ~100-m thick fossil gap (Fig. 3). Seventy-five percent of  
331 brachiopod species from the Vøringen Member failed to extend into the upper horizons  
332 (Table 1). In comparison, only 50% of brachiopod species disappeared within the interval of  
333 the Capitanian mass extinction suggested by Bond et al. (2015) (Fig. 3). Moreover, it is worth  
334 noting that the highest number of species (11) disappeared within the “*Megousia*” *weyprechtii*  
335 Zone (Fig. 3; Table 1).

336 The biostratigraphy of bryozoan species also provides a similar stepwise pattern of  
337 faunal changes throughout the formation, although their diversity is more strongly biased  
338 with the lithology type (most diverse in limestone beds) (Fig. 3; Table 1). Similar to the  
339 brachiopod data, 78.57% of bryozoan species from the Vøringen Member are confined to the  
340 member (also “*Horridonia timanica*” Zone), showing their striking faunal distinction from

341 the bryozoans of overlying horizons in the formation. The middle part of the formation with  
342 relatively thick limestone beds (particularly, Bed F5 in the *Paeckelmanella* sp. Zone and Bed  
343 F8 in the “*Megousia*” *weyprechtii* Zone) still contains diverse bryozoan species, whereas the  
344 upper part, corresponding to both the *Pterospirifer* “*alatus*” Zone and the *Haydenella wilczeki*  
345 Zone, is represented by a few species (4 and 5, respectively). Only one bryozoan species (out  
346 of four) became extinct at the Capitanian crisis interval of Bond et al. (2015) (Fig. 3). It is  
347 noteworthy that biostratigraphy of Permian bryozoans from the Sverdrup Basin, briefly  
348 discussed in Nakrem et al. (2008b), also presented similar gradual faunal turnovers during the  
349 Middle and Late Permian without any significant reduction in the Capitanian.

### 350 **Biostratigraphic data at other sections**

351 Although the succession of the five brachiopod biozones has been well established at the  
352 type section of the formation, the distinction and recognition of these biozones at other  
353 sections vary considerably. In general, the basal “*Horridonia timanica*” Zone has been traced  
354 in all studied sections from the Vøringen Member of the Kapp Starostin Formation (Fig. 4),  
355 with two common species: *Timaniella wilczeki* and *Arcullina polaris*, both of which are  
356 restricted to this biozone. Similarly, the *Paeckelmanella* sp. and “*Megousia*” *weyprechtii*  
357 zones are also commonly recognized in the middle part of the formation in the majority of  
358 these sections (Fig. 4).

359  
360 On the other hand, the *Pterospirifer* “*alatus*” Zone is known only from two sections  
361 (Festningen and Trygghamna sections), and the uppermost *Haydenella wilczeki* Zone is  
362 uniquely only present at the Festningen section. Furthermore, the presence of two lower  
363 biozones (*Paeckelmanella* sp. and “*Megousia*” *weyprechtii* zones) at the Reinodden and  
364 Ahlstrandodden sections is also uncertain, as the diagnostic species of the “*Megousia*”  
365 *weyprechtii* Zone co-occurs with or appear at lower horizons than the brachiopods indicative  
366 of the *Paeckelmanella* sp. Zone at these two sections, thus rendering the separation of these  
367 two zones impossible. With the exception of the Festningen section, all other sections have  
368 yielded fewer species, particularly from the middle and upper horizons of the Kapp Starostin  
369 Formation. It is, therefore, difficult to apply the biozonation scheme of Nakamura et al.  
370 (1992) as a regional standard for the biostratigraphic correlation of Spitsbergen brachiopod  
371 assemblages.

372 The brachiopod biostratigraphy in Spitsbergen appears to be more consistent between  
373 distant sections. In general, closely-located sections exhibit more similar biostratigraphic  
374 compositions than those widely separated. In addition, it is evident that the brachiopod fauna  
375 as a whole persisted much longer in western Spitsbergen (e.g., Festningen and Trygghamna  
376 sections) than they did in northwestern and central Spitsbergen (Fig. 4).

## 377 378 **DISCUSSION**

### 379 **Biostratigraphic correlation across Spitsbergen**

380  
381 In spite of the difficulty in applying the brachiopod biozonal scheme of Nakamura et al.  
382 (1987, 1992) across Spitsbergen, most sections display a stratigraphic division into three  
383 lower brachiopod assemblages, corresponding respectively to the “*Horridonia timanica*”,  
384 *Paeckelmanella* sp., and “*Megousia*” *weyprechtii* zones. This common division enables us to  
385 correlate among the different sections through the comparison of brachiopod assemblages  
386 (Fig. 4). Interestingly, this biostratigraphic subdivision and correlation among the sections  
387 bears a general similarity to the lithological divisions within the same sections. This  
388 coincidence would suggest, as has been noted by Malkowski and Hoffman (1979) and  
389



390 Stemmerik (1988), that the stratigraphic variation in brachiopod faunal composition among  
391 the studied sections might also be related to local environmental and/or ecological controls.  
392 In this sense, the brachiopod biozones proposed by Nakamura et al. (1987, 1992) may be best  
393 regarded as eco-stratigraphic assemblages, implying that they are of broad  
394 chronostratigraphic significance in regional scale (e.g., within Spitsbergen or Svalbard) but  
395 only limited potential for correlation with other basins.

396 In addition, it needs to be noted that the brachiopod fauna from the Vøringen Member in  
397 Skansen, central Spitsbergen reported by Angiolini and Long (2008), somewhat differs  
398 from our biostratigraphic results at our nearby Skansbukta A and B sections (Fig. 2). It is  
399 certain that the fauna from Angiolini and Long (2008) includes some genuine representatives  
400 of the Vøringen Member, such as *Fasciculatia groenwalli*, *Spiriferella keilhavii*,  
401 *Archboldevia impressa*, and *Bruntonia granulifera*. However, it also contains a few taxa  
402 which, as shown in our biostratigraphic chart (Fig. 3), occur only in the middle to upper parts  
403 of the Kapp Starostin Formation, such as *Kochiproductus plexicostatus* and *Kuvelousia*  
404 *weyprechtii*. Further, some species we have found abundantly in the Vøringen Member of the  
405 Skansbukta sections, including *Arcullina polaris* and *Timaniella wilczecki*, were absent in the  
406 fauna reported by Angiolini and Long (2008).

407 Also notable is the brachiopod assemblage reported by Gobbett (1964) from the  
408 Vøringen Member in various sections across Spitsbergen, which is neither matched with the  
409 fauna reported by Angiolini and Long (2008), nor with our assemblage from supposedly the  
410 same member. The differences could be explained by two scenarios: one is that the Vøringen  
411 Member was not deposited contemporaneously across the basin, hence explaining different  
412 age and composition for the faunas from the same rock unit (member). The other possibility  
413 is that this member might have been misconstrued by the different studies over time and may,  
414 in fact, represent different rock units. This is quite possible given each of the collections,  
415 respectively studied by Gobbett (1964), Angiolini and Long (2008) and the present study, was  
416 made by different field geologists with significant time apart. Unlike our collections, the  
417 fossil materials studied in Gobbett (1964) as well as Angiolini and Long (2008) had been  
418 collected much earlier (late 19th to early 20th centuries) than the establishment of the modern  
419 lithostratigraphic scheme in Spitsbergen (Cutbill and Challinor, 1965). At the time informal  
420 stratigraphic terms, such as 'Spirifer Limestone' and 'Productus Chert' (generally  
421 corresponding to the Vøringen Member and the remaining part of the Kapp Starostin  
422 Formation, respectively) were employed, and the use of these taxon-based terms might cause  
423 some confusion in recognition of the stratigraphic units (e.g., spiriferide brachiopod-  
424 dominant limestone beds are common not only in the basal member, but also in the middle  
425 and upper part of the formation). Our biostratigraphic results from the widely distributed  
426 sections (Fig. 4) strongly support that the Vøringen Member was deposited  
427 contemporaneously across Spitsbergen (see also Lee et al. 2019).

428 Contrary to the relatively well-correlated three lower assemblages, the lateral correlation  
429 of the two uppermost assemblages is more difficult, due to the absence of indicative  
430 brachiopod assemblages from most sections in Spitsbergen (see Fig. 4). However, the  
431 absence of these two assemblages in various places may be accounted for by the fact that  
432 sedimentation ceased at different times across Spitsbergen during the Late Permian, creating  
433 a spatially highly-varied diachronous upper boundary for the Kapp Starostin Formation in  
434 Spitsbergen. Bond et al. (2018) detected seven transgressive-regressive sequences from the  
435 Kapp Starostin Formation at a section located in western Spitsbergen, but two youngest of  
436 these seven sequences were missing in central and eastern Spitsbergen. This observation is  
437 well-matched with our biostratigraphic data in that the two uppermost brachiopod  
438 assemblages have been found missing at three sections in central Spitsbergen. This close

439 match between missing strata and missing faunal assemblages would suggest that the faunal  
440 absence may well have been caused by a regional cessation of sedimentation, in central and  
441 eastern Spitsbergen.

442 The spatial and temporal distribution of the *Paeckelmanella* sp. assemblage varies across  
443 Spitsbergen to some degree. It occurred earlier than and separated from the “*Megousia*”  
444 *weyprechtii* assemblage in the majority of the sections but is not clearly defined in two  
445 southwestern Spitsbergen sections (Reinodden and Ahlstrandodden sections) (Fig. 4). This  
446 spatio-temporal difference may be explained by the late arrival of the species of the  
447 *Paeckelmanella* sp. assemblage (e.g., *Paeckelmanella* sp. and *Licharewia* cf. *L. grewingki*) in  
448 these more southerly Spitsbergen sections (see also Lee, 2013, figs. 4.3 and 4.4). If so, why  
449 were the occurrences of these species in the southwestern Spitsbergen delayed? This might be  
450 explained by sedimentary facies difference, because the two southwestern Spitsbergen  
451 sections certainly contain more sandstone beds than other sections (Fig. 4); i.e. the relatively  
452 high influx of sands might be unfavorable for the taxa of *Paeckelmanella* sp. assemblage. Or  
453 perhaps it might be caused simply by randomness of sampling, considered that there is a fair  
454 amount of taxonomic overlap between the two brachiopod assemblages (see Fig. 3).  
455 However, the diachronous occurrences could be more related to the climatic preference of the  
456 taxa concerned. Since the taxa appeared lately in the southwestern Spitsbergen sections were  
457 all endemic to the high-latitude Boreal Realm and are thus considered to have been adapted  
458 to cold-water habitats, their delayed arrival in southwestern Spitsbergen would suggest that  
459 the region had become cold later than other areas of Spitsbergen (e.g., western and central  
460 Spitsbergen). According to the Permian palaeogeographic reconstruction of Spitsbergen and  
461 adjacent regions, Permian Spitsbergen was oriented differently from its current configuration:  
462 present-day southwestern Spitsbergen was positioned easterly from western and central  
463 Spitsbergen during the Permian (Fig. 1). As such, it might be supportive of eastward gradual  
464 cooling along the northwestern marginal shelf of Pangea during the Permian (Lee et al.  
465 2019), possibly affected also by transitional cooling from deep- to shallow-water  
466 environments (Blomeier et al., 2011). Further discussion about broader-scaled Permian  
467 climatic changes occurred on the entire northwestern margin of Pangea will be presented  
468 below.

469

### 470 **Is an intra-Capitanian mass extinction detectable in the Kapp Starostin Formation?**

471 In this study, we have carefully examined the evidence and interpretation of the  
472 Capitanian mass extinction recognized in Bond et al. (2015, 2020) and compared the  
473 stratigraphic ranges of brachiopod species they used with our own biostratigraphic results  
474 (Fig. 3). We found that some biostratigraphic and chemostratigraphic evidence presented by  
475 Bond et al. (2015, 2020) is likely either incomplete or misinterpreted and, consequently,  
476 cannot be viewed as strong evidence in support of their assertion for a Capitanian mass  
477 extinction in the Boreal region. We here address three major issues: (1) significant  
478 discrepancy in biostratigraphic records between their study and our data; (2) the uncertainty  
479 of the age suggested for the mass extinction interval; and (3) the inappropriate correlation of  
480 Permian strata between Spitsbergen and central East Greenland.

481 Our biostratigraphic data (Figs. 3 and 4), based on detailed and extensive field sampling  
482 by multiple expedition teams over two decades, then backed up by our own systematic  
483 palaeontological (taxonomic) investigations (Lee, 2013; Lee et al., 2016, 2019), demonstrates  
484 that the stratigraphic change of the brachiopod (and bryozoan) fauna throughout the Kapp  
485 Starostin Formation is gradual at all of our studied sections. This biostratigraphic pattern is in  
486 stark contrast with the sharp extinction recognized by Bond et al. (2015) at the boundary  
487 between the *Pterospirifer* “*alatus*” Zone and the uppermost *Haydenella wilczeki* Zone in the

488 Festningen section (Fig. 3). A close examination of the illustrated brachiopod specimens  
489 figured by Bond et al. (2015) may provide some clue as to why there are significant  
490 differences between the brachiopod faunal list and stratigraphic ranges given by Bond et al.  
491 and our own list derived from our own collections and systematic taxonomic investigations.  
492 In their paper, Bond et al. (2015) did not address the lower part of the Kapp Starostin  
493 Formation (their paper excluded the Vøringen Member and most of the Svenskeegga  
494 member), therefore it was not possible for them to assess and illustrate the lower ranges and  
495 first appearance datum (FAD) points of the brachiopod species they provided (see Fig. 3).  
496 Notwithstanding this fact, the continuous stratigraphic ranges of brachiopod species they  
497 provided for the upper part of the Kapp Starostin Formation is intriguing as they look  
498 remarkably different from our range charts, especially considering that both of the brachiopod  
499 species lists are based mostly on data from the same section (Festningen section, type section  
500 of Kapp Starostin Formation). Although we suspect that a significant part of the difference  
501 may be explained by different approaches to taxonomy, it is impossible to confirm this at the  
502 present time because, apart from one figure (Bond et al, 2015, fig. 5 which illustrated seven  
503 poorly preserved brachiopods), most of the brachiopods referred to by Bond et al. (2015)  
504 were only identified as indeterminate species, with no systematic descriptions. For example,  
505 several biostratigraphically-important taxa, found from considerably restricted stratigraphic  
506 intervals in our study (e.g., *Paeckelmanella* sp., *Licharewia* cf. *L. grewingki*, *Svalbardathyris*  
507 *kotlukovi*, *Kuvelousia weyprechtii* and *Pterospirifer cordieri*), were either totally missed or  
508 possibly misidentified in the range charts of Bond et al. (2015). Further, we suspect that many  
509 if not all of their spiriferellid species were also incorrectly identified. If our reasoning here  
510 can be seen as providing some benefit of a reasonable doubt, one would argue that the  
511 biostratigraphic range data provided by Bond et al. (2015) are open to questions and must be  
512 re-assessed against rigorous taxonomy before any claim of a mass extinction event in the  
513 upper part of the Kapp Starostin Formation.

514 Irrespective of a gradual change or a severe and sharp change in the stratigraphic  
515 distribution of brachiopod species richness through the upper part of the Kapp Starostin  
516 Formation, another aspect of the controversy is the age of the brachiopod faunas as a whole  
517 from this part of the formation and, by implication, the age of the debated extinction. Bond et  
518 al. (2015) estimated the age of the extinction interval as the mid-Capitanian, mainly based on  
519 two weakly developed lines of evidence: one from strontium isotope values of brachiopod  
520 shells and the other from biostratigraphic correlation with Mid-Late Permian faunas of central  
521 East Greenland. It has been widely accepted that the marine Permian strontium isotope  
522 ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) curve records the lowest point (below 0.7070) in the Capitanian (Korte et al.,  
523 2006; Kani et al., 2008). Bond et al. (2015, fig. 3) presented  $^{87}\text{Sr}/^{86}\text{Sr}$  values of the  
524 brachiopod shells from the upper part of the Kapp Starostin and correlated them with the  
525 global Permian strontium isotope curve, and concluded that the extinction interval would be  
526 matched with mid-Capitanian in age. However, two questions rose from their conclusion.  
527 First, they did not present any  $^{87}\text{Sr}/^{86}\text{Sr}$  values from their inferred extinction level. Second,  
528 the stratigraphic level from which they obtained the lowest  $^{87}\text{Sr}/^{86}\text{Sr}$  values at 0.7069 is  
529 located 90 m below the top of the Kapp Starostin Formation, 50 m lower than the inferred  
530 Capitanian mass extinction (which is 40 m below the top of the formation). Therefore, if the  
531 level where the lowest value of 0.7069 in  $^{87}\text{Sr}/^{86}\text{Sr}$  values was obtained is correlated to the  
532 middle and late Capitanian according to the global strontium isotope trend (Korte et al., 2006;  
533 Kani et al., 2008), the age of the extinction level inferred by Bond et al. would be younger  
534 than Capitanian. In addition to this reasoning, the validity of the strontium isotope values  
535 from the brachiopod shells has to be carefully considered, because brachiopod shells from the  
536 Permian strata of Svalbard have been revealed to commonly suffer significant diagenesis

537 (e.g., silicification) and, consequently, to be inappropriate for isotopic analysis (see Mii et al.,  
538 1997; Korte et al., 2006); this observation is also supported by our own observation of dozens  
539 of brachiopod specimens we have examined from the Kapp Starostin Formation during our  
540 previous studies (e.g., Lee et al., 2017, fig. 2.9–12). The strontium isotope values at the  
541 middle and upper part of stratigraphic column (0.7074–0.7080) in Bond et al. (2015, fig. 3)  
542 are substantially more radiogenic than global Guadalupian and Lopingian values (<0.7072),  
543 which could also indicate the diagenesis or local effects (e.g., basin restriction).

544 To support their proposition for an intra-Capitanian mass extinction at high northern  
545 latitudes, Bond et al. (2015, 2020) also referred to the faunas from the Wegener Halvø and  
546 Schuchert Dal formations of central East Greenland (see Fig. 1). They regarded the  
547 brachiopods from the (limestone-dominated) Wegener Halvø Formation as the pre-extinction  
548 fauna, and the brachiopods and bivalves from the (shale-dominated) Schuchert Dal Formation  
549 as a post-extinction fauna, thereby placing the Capitanian mass extinction event on the  
550 boundary between these two formations. However, contrary to their explanation, we do not  
551 see any testable evidence for the occurrence of a sudden extinction at the boundary between  
552 these two formations. According to the monograph of Dunbar (1955), the Schuchert Dal  
553 Formation (Changsingian) still yielded 25 genera and 38 species of brachiopods, which are  
554 insignificantly different from the brachiopods of the underlying Wegener Halvø Formation  
555 (25 genera and 40 species) both in faunal diversity and species composition (see Table 2 for  
556 more details). A minor faunal turnover between the two formations is more likely rather than  
557 a mass extinction, and this minor biotic turnover appears best explained by a change of local  
558 environments and ecological conditions as reflected by the lithological difference between the  
559 two formations. Stemmerik et al. (2001) suggested a climatic shift toward cooler climate near  
560 the formation boundary.

561 Additionally, Bond et al. (2015) also asserted that the age of the mass extinction event in  
562 central East Greenland was Capitanian, based on the reassessment of conodont species from  
563 the Ravnefjeld Formation (laterally equivalent to the Wegener Halvø Formation, see Fig. 1)  
564 by Legler and Schneider (2008). However, more recent study (Henderson, 2018, fig. 4)  
565 confined the age of the Ravnefjeld conodont species (e.g., *Mesogondoella rosenkrantzi* and  
566 *Merrillina divergens*) to Lopingian. The Ravnefjeld Formation also contains the ammonoid  
567 *Cyclolobus*, which is a typically Wuchiapingian genus and supports the conodont age  
568 (Bjerager et al., 2006).

569 In summary, the Capitanian mass extinction proposed by Bond et al. (2015, 2020) for the  
570 Boreal Realm appears to be poorly supported, at least by faunal and biostratigraphic  
571 evidence. As for the chemostratigraphic data and interpretations presented by Bond et al.  
572 (2015, 2020) in support of their claim for a Capitanian mass extinction, they warrant further  
573 study and discussions. One possibility is that the depositional environment and climatic  
574 conditions in Spitsbergen during the time of the Kapp Starostin Formation might have  
575 experienced substantial changes, forcing the local marine benthos to migrate elsewhere to  
576 track their optimal habitat conditions and thereby temporarily vacating their local habitats  
577 leaving a localized faunal break in the fossil record. The pyrite and trace metal data in Bond  
578 et al. (2015) suggest a shift to more oxygen-restricted conditions in the upper part of the  
579 Kapp Starostin Formation, which might be caused by extensive transgression during the  
580 Lopingian. The less-oxygenated environments could be formed locally within Spitsbergen  
581 (and other basins), especially in deeper places, possibly leading to the migration and local  
582 decline of brachiopods and other benthos. If this is the case, the local disappearance of taxa  
583 should be regarded as extirpations rather than true mass extinctions. As will be presented  
584 below, we argue that the brachiopod faunas of the Kapp Starostin Formation in Spitsbergen  
585 are more likely examples of extirpation rather than representing a consistent signal of a

586 sudden and widespread intra-Capitanian mass extinction in the Boreal realm as has been  
587 claimed by Bond et al. (2015, 2020).

588

### 589 **Permian brachiopod faunal changes and migrations along the northwestern marginal** 590 **shelf of Pangea**

591 The northwestern marginal shelf of Pangea is known to have experienced a progressive  
592 and sustained climatic cooling through the Permian (Beauchamp, 1994; Beauchamp and  
593 Desrochers, 1997; Stemmerik, 1997, 2000; Shi and Grunt, 2000; Shi and Waterhouse, 2010;  
594 Blomeier et al., 2011; Lee et al., 2019). In part, this sustained cooling trend was driven and  
595 enhanced by the continuous northward movement of Pangea, and in part by the closure of the  
596 Ural seaway (Shi et al., 1995; Beauchamp and Baud, 2002; Stemmerik and Worsley, 2005;  
597 Worsley, 2008). A strong link between this climatic change and biotic responses has been  
598 drawn and demonstrated by the pronounced change from a photozoan-dominated to  
599 heterozoan-dominated benthic faunas in the Artinskian across the northwestern marginal shelf  
600 of Pangea (Stemmerik, 1997; Ehrenberg et al., 2001; Hüneke et al., 2001; Beauchamp and  
601 Baud, 2002; Reid et al., 2007; Blomeier et al., 2011), roughly corresponding to the time of  
602 the closure of the Ural seaway at its southern end where the gateway connection to the Tethys  
603 had existed. Contrasted to the photozoan association containing warm-water benthos, such as  
604 colonial corals and fusulinids, the heterozoan-dominated fauna is characterized by cool- to  
605 cold-water elements of the Boreal Realm, with brachiopods, bryozoans and siliceous sponges  
606 as the predominant constituents. As a main component of the post-Artinskian heterozoan-  
607 dominated fauna, brachiopods from the Kapp Starostin Formation and other corresponding  
608 Permian strata at the northwestern shelf of Pangea demonstrate how marine benthos  
609 responded to the dynamics of climatic changes during this time.

610 In order to provide a more meaningful faunal correlation between different basins on the  
611 northwestern shelf of Pangea, we divided the brachiopods of the Kapp Starostin Formation  
612 simply into two spiriferellid-dominated assemblages: (1) a *Timaniella wilczeki* – *Arcullina*  
613 *polaris* assemblage from the Vøringen Member, and (2) a *Spiriferella loveni*-dominated  
614 assemblage from the overlying members of the formation, following the scheme of Lee et al.  
615 (2019) (see also Fig. 3). Although we have adopted the succession of five brachiopod  
616 biozones of Nakamura et al. (1987, 1992) for detailed biostratigraphic correlation among the  
617 sections within Spitsbergen, it is not practical to apply this biozonation scheme in its entirety  
618 to the faunal comparison between different basins across the northwestern margin of Pangea,  
619 due to significant faunal variability caused by local environmental factors. On the other hand,  
620 as demonstrated by Lee et al. (2019), the appearance/demise of some spiriferellid species was  
621 mostly influenced by climatic conditions (degree of cooling) and, as such, has a greater  
622 potential for demonstrating the spatial/temporal patterns and timing of climatic transition  
623 across the northwestern marginal shelf of Pangea.

624 Based on the examination of literature, the spatial distribution of these two spiriferellid-  
625 dominated assemblages on the northwestern marginal shelf of Pangea can be clearly  
626 delineated for three Permian time intervals: (1) Artinskian to early Kungurian, (2) late  
627 Kungurian to Capitanian, and (3) Lopingian. According to the distributional patterns (Fig. 5),  
628 the basins located in western and central parts of the northwestern margin of Pangea (from  
629 Yukon in western Canada to Svalbard) appear to have experienced comparable climatic  
630 conditions throughout the Permian. The Artinskian to early Kungurian strata in these basins  
631 are generally represented by the *Timaniella wilczeki* – *Arcullina polaris* assemblage  
632 characterizing a cool (or temperate) climatic regime. The younger *Spiriferella loveni*-  
633 dominated assemblage has commonly been reported from the outcrops of late Kungurian to  
634 Capitanian age, indicating the advent of colder climatic conditions in the same regions where

635 the *Timaniella wilczeki* – *Arcullina polaris* assemblage had prevailed during the earlier and  
636 relatively warmer Artinskian-early Kungurian times. On the other hand, some localities,  
637 positioned further east or south within the northwestern shelf of Pangea, record delayed  
638 appearances of these two brachiopod assemblages: the *Timaniella wilczeki* – *Arcullina polaris*  
639 assemblage reached the northern Urals in the late Kungurian, while the *Spiriferella loveni*-  
640 dominated assemblage flourished in central East Greenland during the Lopingian (Fig. 5).  
641 The temporal differences in the first appearances of these two assemblages in different  
642 locations might indicate that the cold ocean currents generated from the northern Panthalassa  
643 Ocean became warmer as they travelled southeastward (Fig. 5) and, consequently, that the  
644 strongly latitude-mediated temperature gradient likely had led to the differentiation of the  
645 northwestern marginal shelf of Pangea into a few different biotic provinces through the  
646 Permian (Fig. 5). Under this scenario, it is possible that the western to central regions of the  
647 shelf (from Yukon to Svalbard) consistently belonged to the same province throughout the  
648 Middle to Late Permian. The reason for a strong Permian Yukon-Svalbard biogeographic  
649 connection is that (1) both areas were situated in middle to high northern latitudes, thus  
650 conducive for the formation and prevalence of cold-water ocean currents, and (2) their  
651 Permian depositional settings were mainly composed of relative deep and narrow basins,  
652 facilitating the southeastward inflow of the cold-water currents into the more southerly  
653 located basins in central and northern Europe (i.e., Barents Shelf, the Uralian Basin and  
654 Zechstein Basin) (Fig. 5A–C). As these ocean currents traveled east or south, not only did  
655 they become warmer (but still cool-water), they also facilitated the invasion of the Early  
656 Permian brachiopod fauna of Spitsbergen into the Barents Shelf (Fig. 5A).

657 From late Early Permian through the Late Permian, the southeastward migration of the  
658 Early Permian brachiopod fauna of Spitsbergen seems to have taken place in two stages and  
659 in two separate pathways. First, during the late Kungurian–Capitanian (Fig. 5B), as Pangea  
660 continued to drift north, the *Timaniella wilczeki* – *Arcullina polaris* assemblage that had  
661 inhabited Spitsbergen was replaced by the *Spiriferella loveni*-dominated assemblage as the  
662 climate became colder there. At the same time, the northward drift of Pangea and the cooling  
663 in Spitsbergen forced, at least, some elements of the *Timaniella wilczeki* – *Arcullina polaris*  
664 assemblage to migrate southeast into the northern part of the Uralian Basin during the Early–  
665 Middle Permian transition (Fig. 5B, Migration I in Fig. 5D).

666 During the Late Permian, a second major southward faunal expansion is apparent from  
667 the fossil record but appears only limited to East Greenland and, presumably, further south  
668 into the Zechstein Basin in central and northern Europe (Fig. 5C). This southward migration  
669 event (Migration II in Fig. 5D) is clearly identified by the presence of the *Spiriferella loveni*-  
670 dominated assemblage in East Greenland (see Table 2), and can be linked to the opening of  
671 the Zechstein Basin during the Lopingian (Heeremans et al., 2004). A very similar southward  
672 migration pattern during the Lopingian was also reported in bryozoan fauna by Sørensen et  
673 al. (2007). The *Spiriferella loveni*-dominated assemblage was widely distributed across the  
674 northwestern shelf regions of Pangea, from western and Arctic Canada to northeastern  
675 Greenland and Spitsbergen during the Guadalupian (Fig. 5B), but thereafter it became mostly  
676 extirpated to East Greenland during the Lopingian (Fig. 5C). This extirpation was most likely  
677 driven by heightened cooling in the northern Pangea during the Lopingian as the  
678 supercontinent continued its drift toward northern high latitudes. Additionally, the oxygen-  
679 deficient conditions (Bond et al., 2015), most likely developed locally in deeper water  
680 environments might contribute to the extirpation pattern, restricting the habitats of benthos.

681 In summary, the inferred two temporally offset and spatially separate brachiopod  
682 migration pathways, as depicted in Figure 5D, suggest that the complex spatio-temporal  
683 distribution patterns of the Permian brachiopod assemblages on the northwestern shelf of

684 Pangea were mainly controlled by the interplay of two factors: progressive and sustained  
685 cooling through the Permian and changes in regional palaeogeographic configurations, with  
686 the cooling apparently linked to the continued northward drift of Pangea and significant  
687 palaeogeographic changes reflected by the gradual restriction of the Uralian Basin and, at the  
688 same time, the opening of a major seaway connecting the northwestern Pangean shelf with  
689 the Zechstein Basin in northern-central Europe via East Greenland (Fig. 5A–C).

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## 692 **CONCLUSIONS**

693 Our detailed biostratigraphic investigation recognizes five brachiopod assemblages from the  
694 Permian Kapp Starostin Formation in Spitsbergen. The most distinct faunal change is  
695 detected at the boundary between the lowermost Vøringen Member (late Artinskian) and its  
696 overlying member (Kungurian) of the Kapp Starostin Formation, consistently across  
697 Spitsbergen. This faunal turnover is interpreted to have coincided with and thus likely been  
698 driven by a significant climatic cooling along the northwestern margin of Pangea during the  
699 Artinskian–Kungurian transition. On the other hand, the mid-upper part of the Kapp Starostin  
700 Formation is characterized by gradual faunal transitions accompanied with some major  
701 changes in lithology, therefore negating a previous claim of a major and widespread  
702 Capitanian marine mass extinction (Bond et al., 2015, 2020). A similar gradual biotic  
703 turnover pattern is also demonstrated by our bryozoan-based biostratigraphic data from the  
704 Festningen section. All these results indicate that the marine faunas of the Kapp Starostin  
705 Formation in Spitsbergen are more likely examples of extirpation rather than representing a  
706 consistent signal of a sudden and widespread intra-Capitanian mass extinction in the Boreal  
707 realm. In addition, an analysis of the spatial/temporal distribution patterns of spiriferellid-  
708 dominated assemblages along the northwestern shelf of Pangea suggests that the marine  
709 basins in the northwestern Pangea experienced progressive and sustained cooling from  
710 middle Early Permian (Artinskian) to Late Permian in response to the closure of the southern  
711 end of the Uralian seaway and the continued northward drift of Pangea.

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715

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## 1030 **FIGURE CAPTIONS**

1031

1032 **Figure 1.** Permian palaeogeographic setting of the northwestern marginal shelf of Pangea,  
1033 with their lithostratigraphical correlation under the international chronostratigraphical scheme.  
1034 Palaeogeographic maps after Stemmerik and Worsley (2005). Source data for the Sverdrup  
1035 Basin from Beaucahmp et al. (2009); Greenland from Stemmerik and Worsley (2005) and  
1036 Sørensen et al. (2007); Svalbard from Dallmann (1999); and northern (Subpolar) Urals from  
1037 Chuvashov et al. (1993) and Enokian et al. (1993). The chronostratigraphical positions of  
1038 lithostratigraphical units from northern Urals were adjusted according to Lozovsky et al.  
1039 (2009).

1040

1041 **Figure 2.** Overview map of studied sections (1–8, closed circles) in this study and  
1042 distribution of late Palaeozoic and early Triassic strata in Spitsbergen and adjacent islands  
1043 (Base map from Dallman, 1999). **1**, Scheteligfjellet section; **2**, Trygghamna section; **3**,  
1044 Festningen section; **4**, Reinodden section; **5**, Ahlstrandodden section; **6**, Idodalen section; **7**,  
1045 Skansbukta A section; **8**, Skansbukta B section; **9**, Skansen fossil locality of Angiolini and  
1046 Long (2008) (open triangle).

1047

1048 **Figure 3.** Combined biostratigraphic (brachiopod and bryozoan) range chart from the  
1049 Festningen section (type section of the Kapp Starostin Formation). The formation in the  
1050 section is subdivided into 12 lithologic units (F1–F12) for convenience. For comparison,  
1051 brachiopod range chart of Bond et al. (2015, fig. 7) is also correlated here. It needs to be  
1052 noted that the data from Bond et al. (2015) did not extend to the lower part of the formation  
1053 (including the Vøringen Member and most of the Svenskeegga member). Brachiopod species  
1054 from the data of Bond et al. (2015) have asterisk and their range bars are questioned, either  
1055 because we suspect their taxonomic identification may be incorrect or because their  
1056 occurrence records as shown are considered dubious (see text for more discussion).

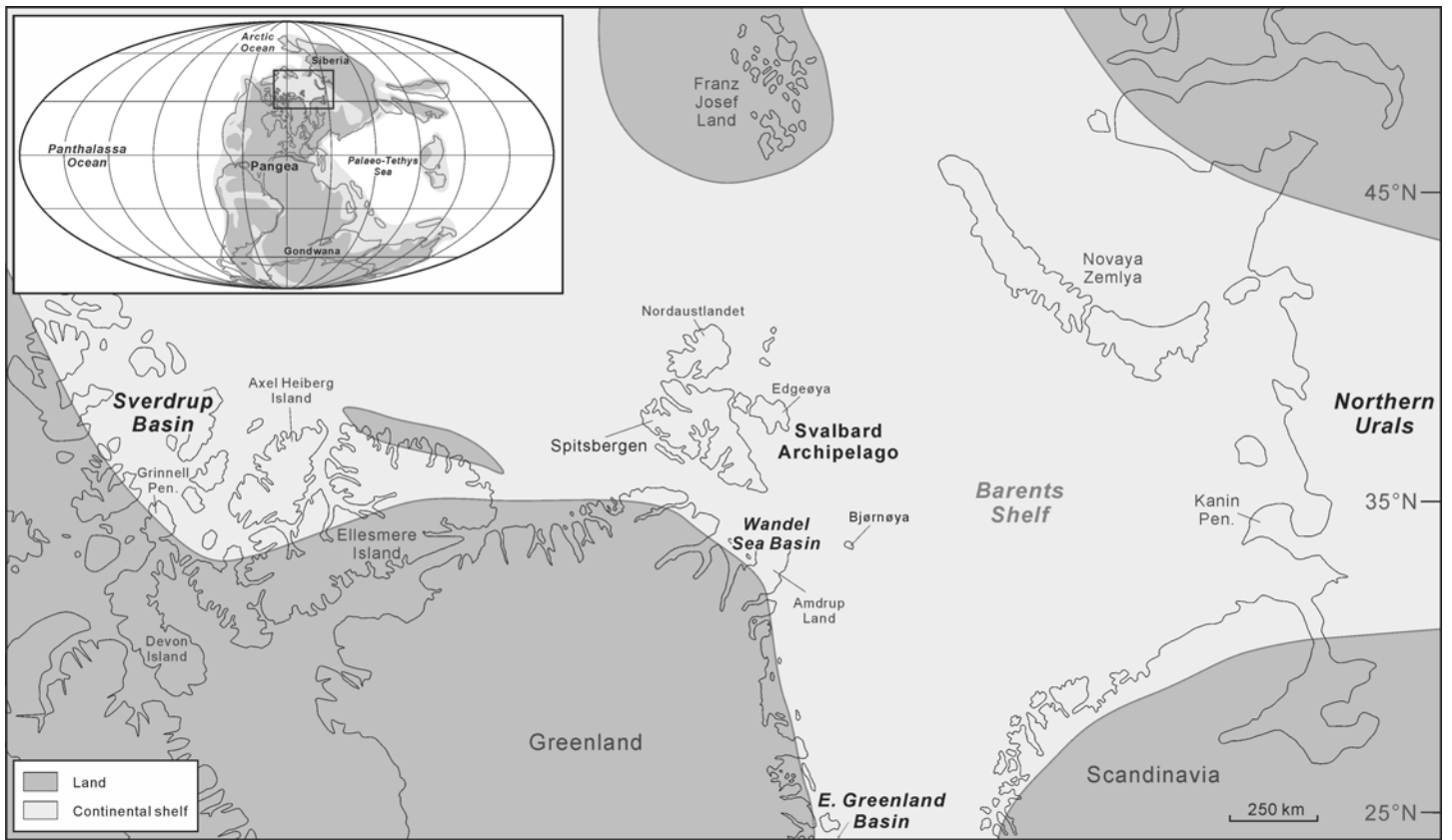
1057

1058 **Figure 4.** Biostratigraphic correlation among the studied sections of the Kapp Starostin  
1059 Formation across Spitsbergen. It is notable that all except the Festningen section contain  
1060 fewer brachiopod assemblages. In particular, the two uppermost assemblages (*Pterospirifer*  
1061 “*alatus*” assemblage and *Haydenella wilczeki* assemblage) are missing in the majority of the  
1062 sections. On the other hand, the basal Vøringen Member is commonly represented by the  
1063 “*Horridonia timanica*” assemblage in all of the sections. Reference maps for the section  
1064 localities are obtained from TopoSvalbard (<https://toposvalbard.npolar.no>)

1065

1066 **Figure 5.** Paleogeographic and paleoceanographic reconstructions of the northwestern  
1067 Pangea during the Permian (Artinskian to Lopingian), together with spatial/temporal  
1068 transitions of two brachiopod assemblages. **A–C**, Three different intervals; **A**, Artinskian to  
1069 early Kungurian; **B**, late Kungurian to Capitanian; **C**, Lopingian. Since the closure of the Ural

1070 seaway connecting the northwestern marginal shelf of Pangea to the Palaeo-Tethys in the late  
1071 Sakmarian, the northwestern marginal shelf of Pangea faced steady cooling until the latest  
1072 Permian as Pangea was gradually moving northward. The southeaster-directed cold ocean  
1073 currents from the Panthalassa Ocean became warmer as they moved to shallower basins in  
1074 the south and southeast (Uralian Basin and Zechstein Basin). Base map with evaporate and  
1075 photozoan carbonate occurrences modified from Reid et al. (2007). The occurrence data of  
1076 brachiopod assemblages for Yukon from Nelson and Johnson (1968) and Waterhouse and  
1077 Waddington (1982); for Arctic Canada from Tschernyschew and Stepanow (1916), Harker  
1078 and Thorsteinsson (1960), Waterhouse and Waddington (1982) and Reid et al. (2007); for  
1079 Greenland from Dunbar (1955, 1962); Svalbard from Wiman (1914) and Lee et al. (2019);  
1080 and for Urals from Barchatova (1968), Kalashnikov (1998) and Grunt et al. (1998). **D**,  
1081 Schematic diagram showing migration patterns of two brachiopod assemblages. The  
1082 *Timaniella wilczecki* – *Arcullina polaris* assemblage dominant in Svalbard during the late  
1083 Artinskian (a) migrated southeastward, flourishing in northern Urals in the late Kungurian  
1084 (a'). The *Spiriferella loveni*-dominated assemblage persisted in Spitsbergen probably from the  
1085 late Kungurian to Wuchiapingian (b) before it was extirpated southward to central East  
1086 Greenland where it prevailed during the whole Lopingian (b').



Time		Sverdrup Basin		North Greenland (Wandel Sea Basin)	Central East Greenland	Svalbard		Northern Urals	
Period	Epoch	Age	Basin margin	Basin centre		Spitsbergen	Bjørnøya		
TRIASSIC		INDUAN	Bjørne	Blind Fiord		Wordie Creek	Urda		
PERMIAN	GUADALUPIAN	CHANGHSINGIAN				Schuchert Dal	Urd		
		WUCHIAPINGIAN	Lindström	Black Stripe	Midnatsfjeld	Wegener Halvo	Ravnefjeld	Capitanian mass extinction purported by Bond et al. (2015)	
	GUADALUPIAN	CAPITANIAN	Trold Fiord Degerbøls	Van Hauen		Karstryggen			
		WORDIAN	Assistance			Huledal	Kapp Starostin		
		ROADIAN			Kim Fjelde		(Tempelfjorden Group)	Miseryfjellet	Intinskaya
	CISURALIAN	KUNGURIAN	Sabine Bay	Trappers Cove			Vøringen Mb		Kozhim Rudnik
		ARTINSKIAN	Great Bear Cape					Hambergfjellet	Chernorechenskaya
		SAKMARIAN	Raanes				Gipshuken		Kosinskaya
		ASSELIAN	Belcher Channel Tanquary Canyon	Hare Fiord			Wordiekammen	(Gipsdalen Group)	Losinoostrovskaya
	CARB.		GZHELIAN	Mount Bayley	Foldedal			Kapp Dunér	



Figure 1\_Correlation between northern Pangean regions\_180width



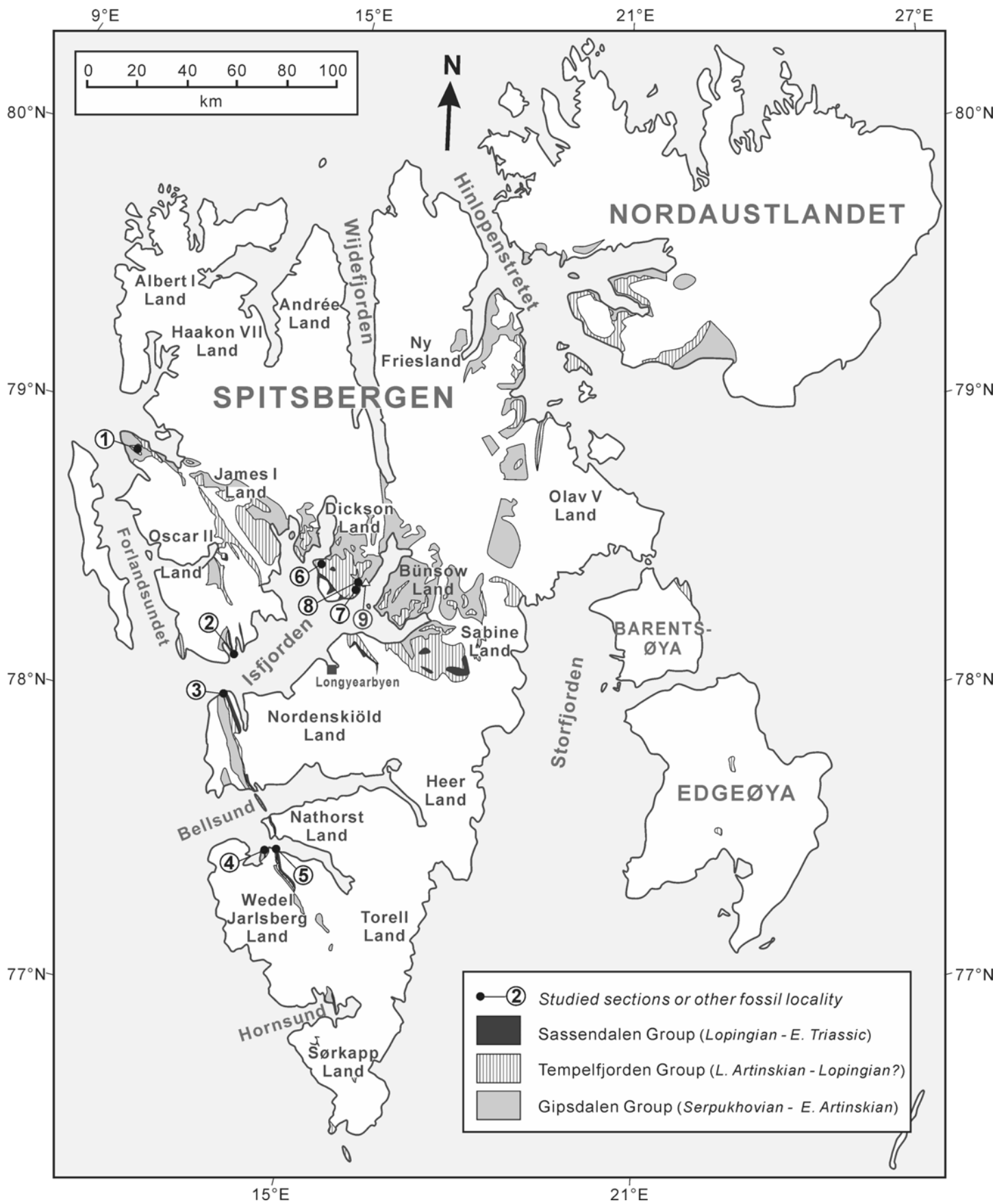


Figure 2\_ Studied sections in Spitsbergen\_190length

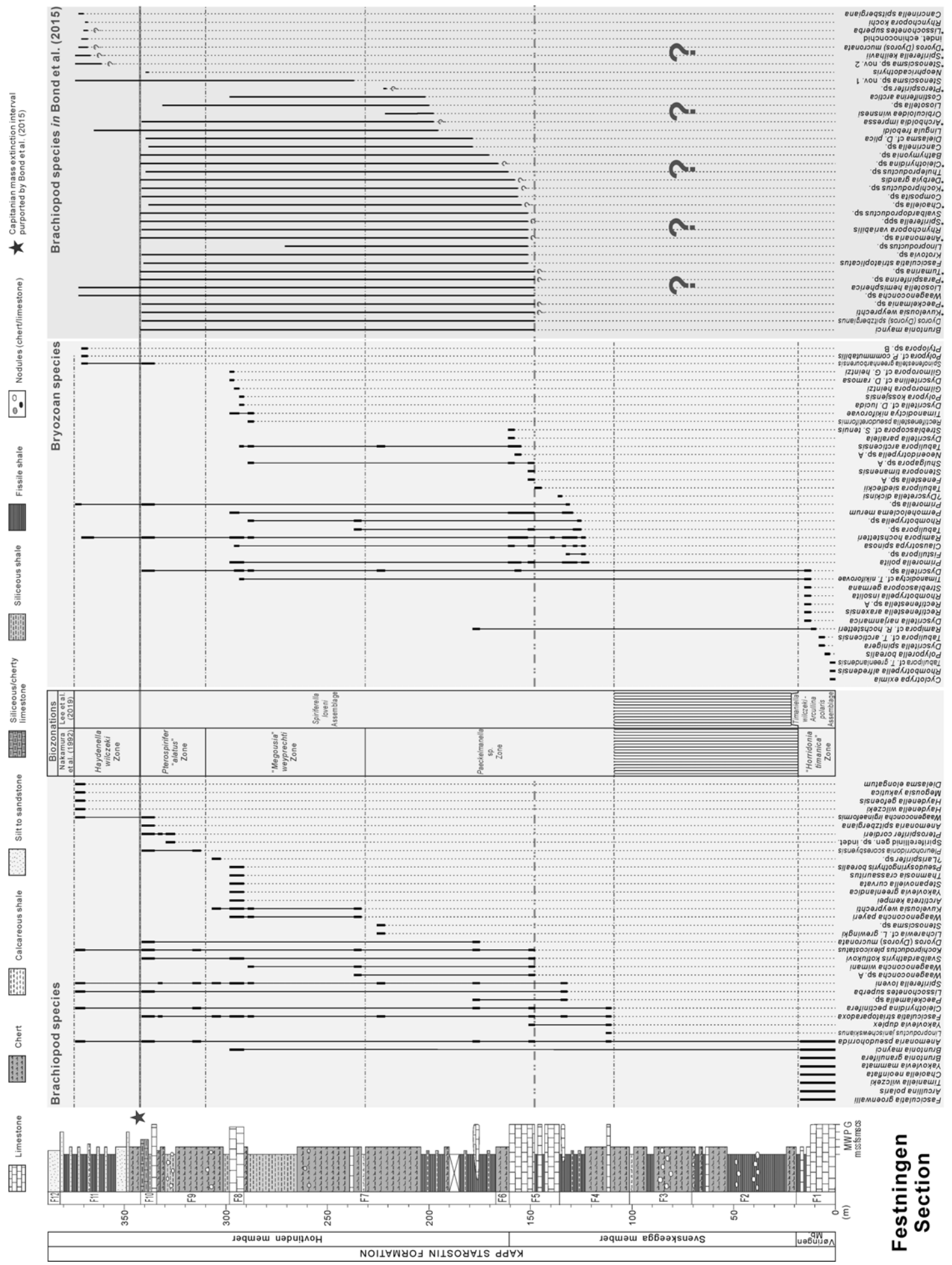


Figure 3\_Columnar section and biostratigraphy in Festningen\_225length

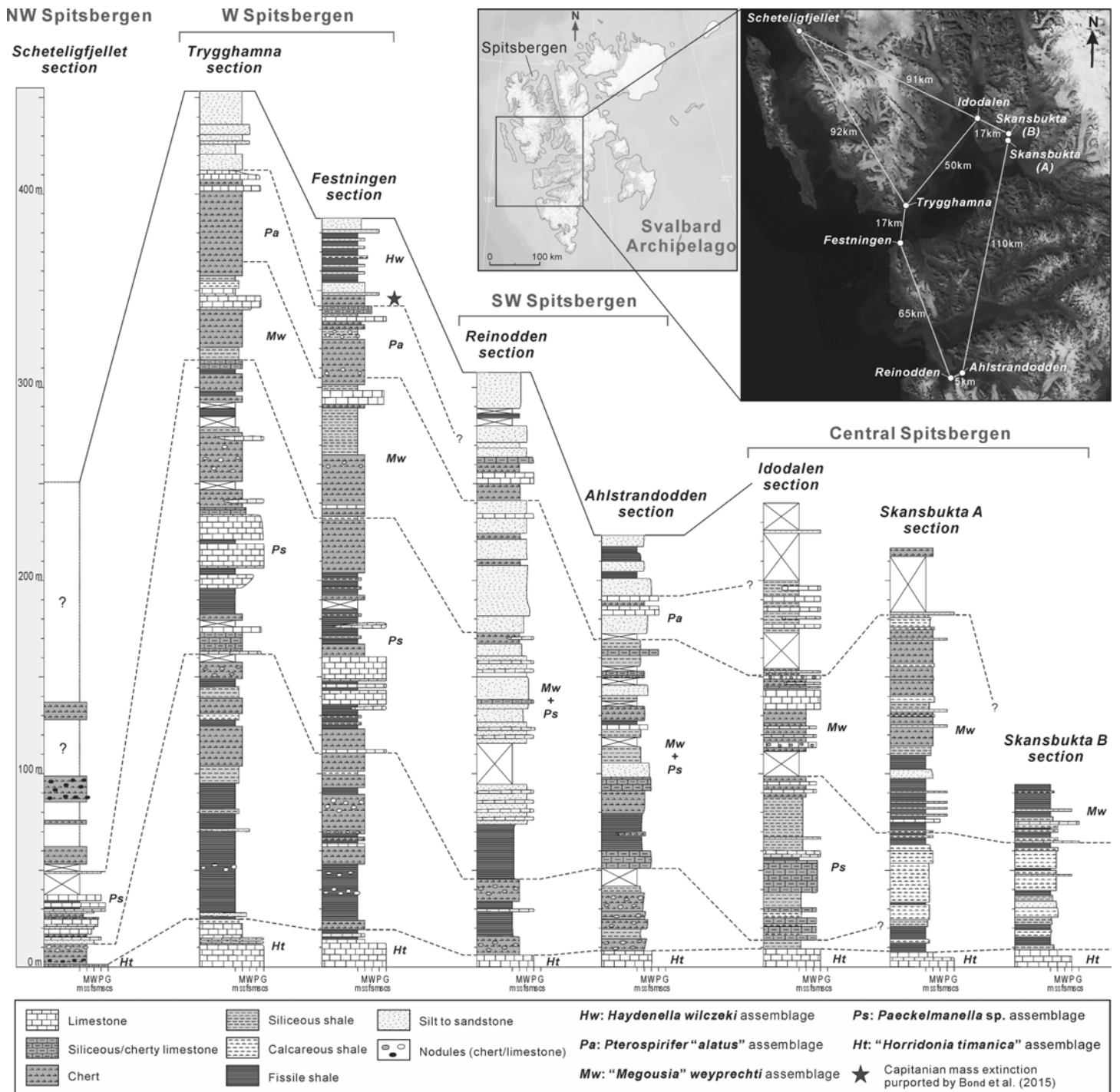


Figure 4\_Biozonation of Kapp Starostin Formation\_185width

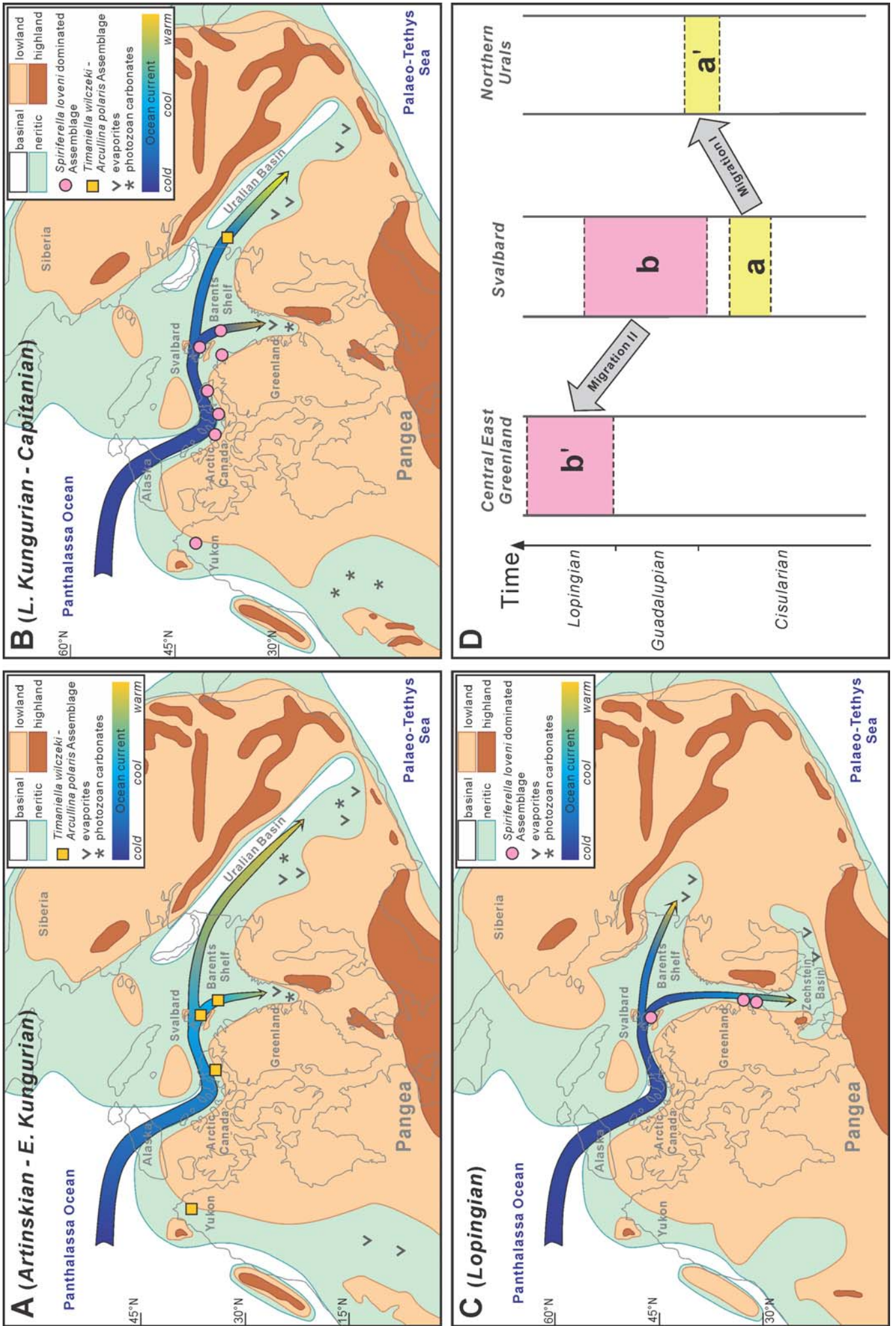


Figure 5\_Climatic changes in northern margin of Pangea\_revised\_170width