Global climate changes account for the main trends of conodont diversity but not for their final demise

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11

12   **Abstract**

13   Conodonts, one of the longest-lived early groups of vertebrates, have a very complete fossil record ranging from the late

14   Cambrian to the end of the Triassic and persisted through many global climatic and biotic events. In this paper, we

15   analyse a large dataset harvested from the Paleobiology Database to compute global diversity curves at the generic level

16   and explore patterns of conodont paleogeographic distribution. Our results partly confirm the most prominent findings

17   of earlier studies including the occurrence of an Ordovician acme, a Permian nadir and a short-lived Triassic recovery.

18   Major peaks of origination were found in the Early Ordovician and Early Triassic, while major extinctions occurred in

19   the Upper Ordovician and Pennsylvanian. Paleogeographical extent of conodonts was impacted by i) the position of

20   paleo-continents (notably impacting the latitudinal gradient of diversity), ii) the available continental shelf area and iii)

21   ice sheets expansion. Diversity trends were mostly impacted by transitions between hothouse and icehouse ages, with

22   major glaciations and associated marine regressions co-occurring with major extinctions. The influence of global sea

23   level was less marked than that of temperature. However, the final demise of conodonts at the end of the Triassic did

24   not coincide with either a major glaciation or marine regression. This supports the view that extinction of the group was

25   mostly due to biotic factors such as competition with 'Mesozoic' taxa.

26

27   **1. Introduction**

28   Biodiversity is impacted by numerous interconnected factors, and disentangling their effects is a challenge for

29   biologists and paleontologists alike. In this regard, the relative importance of biotic and abiotic factors in the variation

30   of global biodiversity through geological times remains an open debate, often referred to as the Red Queen vs. Court

31   Jester debate. Biotic factors encompass aspects intrinsic to the living organisms, as well as interactions between

32   organisms, such as competition; while abiotic factors include extrinsic aspects, often related to climatic or geological

33   changes (Benton 2009). At high taxonomic levels and broad timescales, abiotic factors may play a larger role (Benton

34   2009). Yet, it remains difficult to test biotic effects in the fossil record, where the interactions between taxa are hardly

35   accessible, and the true null hypothesis, namely that diversity follows a random walk through time is generally ignored.

36   Simulations and modeling, which are employed more and more frequently, are a way to remedy to this. For instance,

37   they allow to assess how trophic relationships in paleo-communities may affect the stability of the considered

38   ecosystem to perturbations, for instance whether the extinction of a few taxa or functional groups may lead to cascading

39   effects and eventually to the collapse of the ecosystem (Roopnarine et al. 2007); or to determine how and when within a

40 clade history biotic interactions are most likely to control the dynamics of speciation, extinction and diversity (Aguilée

41 et al. 2018, Hoffman et al. 2019).

42   Another currently outstanding challenge is to anticipate the evolution of biodiversity to the current

43 anthropogenic crisis, based on how biodiversity reacted in the past to global changes analogous to the ones Earth is

44 experiencing today (Payne and Clapham 2012). How are different parts of the biosphere differentially affected by

45 critical abiotic factors? Studies of the fossil record in correlation with major climatic and geological variables remain

46 the most direct way to address this challenge. Historically, marine biodiversity has been the focus of such studies,

47 essentially because the fossil record of marine organisms is more complete and better resolved than that of terrestrial

48 organisms (e.g. Sepkoski 1981).

49

50 *1.1. Conodont diversity through time*

51   Despite its long and global record, the clade of conodonts remains understudied in terms of macroevolution.

52 Conodonts form an early and diverse group of marine vertebrates, most probably associated to extant cyclostomes

53 (lampreys and hagfishes; Miyashita et al. 2019). Ecologically, conodonts are generally considered to have been small

54 active swimmers, mostly nektonic, primary consumers (Purnell 2001). This broad picture is however probably not true

55 for all conodont species, considering their high morphological disparity and the variety of sedimentological facies in

56 which their remains are found (Purnell and Jones 2012, Ginot and Goudemand 2019). Through their long fossil record

57 (over 300 My, from Cambrian to the end of the Triassic; Dong et al. 2004, Zhen et al. 2018, Tanner et al. 2004),

58 conodonts as a group have faced some of the most prominent events in the history of Earth, including four out of five

59 mass extinction crises (end Ordovician, Late Devonian, end Permian, and end Triassic), and they survived all, except

60 the last, eventually disappearing at the end of the Triassic. As such, they constitute a good model organism to study how

61 the diversity of small, nektonic organisms may be impacted by major environmental changes. The responses of

62 conodont diversity to environmental changes have been generally studied at the scale of individual events only, often

63 with the biostratigraphic objective of defining biozones (e.g. Orchard 2007), rather than as a whole. Conodont diversity

64 trends have not recently been tackled over large timeframes (Clark 1983, 1987, Sweet 1988) – although conodont data

65 was included in much broader studies (Friedman and Sallan 2012, Whalen and Briggs 2018) – which is now made

66 possible and more exhaustive by the advent of global fossil occurrence databases (i.e. the Paleobiology Database), and

67 more reliable thanks to new methods for the quantification of diversity, origination and extinction (e.g. Alroy et al.

68 2008, Alroy 2010b). Here, we aim not only at updating the previously published trends of conodonts diversity, but also

69 at statistically testing their potential control by some abiotic variables (temperature, sea-level, paleogeography) for

70 which we collected quantitative data from the literature. Other abiotic parameters, such as water pH, bathymetry or

71 paleo-currents, may also play a role but because of a lack of available, appropriate, quantitative data, those were not

72 included here.

73   The rise of the 'Paleozoic Fauna' identified by Sepkoski (1981) started in the Ordovician, forming what we

74 now call the Great Ordovician Biodiversification Event (GOBE). Although abiotic factors such as a cooling of sea

75 water temperatures have been proposed to be linked to the GOBE, there is still no consensus about the causes of this

76 event (Servais and Harper 2018). The 'plankton revolution' of the Early Ordovician, which represents the first major

77 biodiversity event of the GOBE, may be linked to increasing sea level, oceanographic changes and oxygenation. The

78 consequent increase in planktonic resources may have brought the diversification of other forms. Although the first

79 conodonts arose during the Cambrian (Dong et al. 2004), their radiation is mostly part of the GOBE, and may be related

80 to both biotic (plankton diversification) and abiotic factors. The Ordovician diversification was interrupted by the end
81 Ordovician extinction, the first of the 'Big Five' extinctions. This two-pulse extinction is generally attributed to a major
82 glaciation associated with a regression (first pulse), followed by a transgression associated with anoxia (second pulse).
83 Although short-spanned (~1Ma), it caused important habitat loss and impacted conodonts, among others, at both pulses
84 (Harper et al. 2014). However, the duration of this glaciation is debated, and may extend to 10Ma, which would have
85 put conodonts and the biosphere through an even greater challenge. The next major climatic episode may have been the
86 Middle Devonian 'super-greenhouse', although the nature of this event is now challenged (Joachimski et al. 2009): the
87 Early Devonian was already characterized by warm temperatures, and it now appears the Middle Devonian was in fact
88 characterized by a global cooling – without glaciation – followed by a global warming that led seawater temperatures to
89 reach two maxima around the Frasnian/ Fammenian boundary (Joachimski et al. 2009). The two Kellwasser
90 environmental events occurred before, and in-between those maxima and correspond to cooler and anoxic episodes.
91 These events are known to have affected both conodont diversity and morphology (Girard and Feist 1996, Balter et al.
92 2008). From the end of the Fammenian, and throughout the Carboniferous and Permian, a period known as the Late
93 Paleozoic Ice Age, the global climate was mostly cold and associated with glaciations and low sea levels, (Montanez
94 and Poulsen 2013). According to Buggish et al. (2008), the tipping point between the Devonian greenhouse and the Late
95 Paleozoic Ice Age was reached in the Mississippian. Two cycles of glaciation are recorded, the first peaking (coldest
96 temperatures) at the transition between the Mississippian and Pennsylvanian and the second around the Carboniferous /
97 Permian boundary (Buggish et al. 2008, Montanez and Poulsen 2013). These glacial events were accompanied by
98 important and rapid eustatic variations (e.g. Joachimski et al. 2006, Barrick et al. 2013, Montanez and Poulsen 2013,
99 Bahrami et al. 2014). During this ice age (Pennsylvanian), invertebrates showed low rates of origination and extinction
100 and diversity was low (Stanley and Powell 2003, Powell 2005, Alroy et al. 2008). Similar trends were reported by Clark
101 (1983) for conodonts, with a large drop in origination and extinction rates and in the number of genera between
102 Mississipian and Pennsylvanian.

103   There is evidence for episodic glacial deposits until the end of the Middle Permian, and deglaciation in the
104 upper Permian (~260Ma ; Montanez and Poulsen 2013). Global temperatures increased and peaked at the P/T boundary,
105 linked with the volcanic activity of the Siberian Traps, causing global greenhouse warming, ocean acidification,
106 associated with episodes of anoxia or euxinia (Sun et al. 2012, Romano et al. 2013, van de Schootbrugge and Wignall
107 2016) . Throughout the Permian only a handful of conodont genera remained, several of which crossed the P/T
108 boundary (Clark 1983, Orchard 2007), and thrived in the Early Triassic, in stark contrast with the majority of other
109 organisms at the time (e.g. Brayard et al. 2017, and references therein). The aftermath of the P/T crisis is marked by
110 generally unstable conditions, several cooling and warming episodes occurring in the Early Triassic (Goudemand et al.
111 2019). The transition between Early and Middle Triassic is marked by a global cooling and the appearance of
112 worldwide monsoon events, among which the Carnian Pluvial event was the largest (Preto et al. 2010, Sun et al. 2012).
113 These conditions were maintained through the Middle Triassic and Late Triassic, during which climate appears to have
114 been fairly stable (Preto et al. 2010). Conodont diversity apparently progressively declined throughout the Middle and
115 Late Triassic (e.g. De Renzi et al. 1996, Hallam 2002, Martinez-Perez et al. 2013, Van De Schootbrugge and Wignall
116 2016) and generally had high extinction rates during this interval, especially at the end of the Norian, which was
117 previously considered to correspond to their final extinction (Tanner et al. 2004). Indeed the Rhaetian conodonts are
118 represented by a handful of species only, the last ones eventually going extinct near the Triassic / Jurassic boundary.
119 The slow decline of conodont diversity throughout the Triassic may appear surprising considering the relatively stable

120 conditions of the Triassic, as well as the fact that the explanations for the P/T and T/J boundary crises are more or less
121 convergent (Lucas and Tanner 2004, Mazza et al. 2010), but would fit the null hypothesis of diversity following a
122 random walk.
123
124 *1.2. Previous studies and current problematics*
125   Considering their status of early vertebrates, their amazing resilience, and their fairly anti-climactic
126 disappearance, the global diversity of conodonts and its drivers have received surprisingly little attention since the end
127 of the eighties. Meanwhile, fossil occurrence and paleoenvironmental data have grown enormously. Clark (1983, 1987)
128 already recognized two diversity maxima in the Ordovician and Devonian, and a 'last hurrah' in the Triassic. He further
129 observed that origination and extinction peaked in the Ordovician, Mississippian and Triassic, with the latter two
130 intervals corresponding to higher extinction than origination rates. Clark, however, did not comment at length on the
131 possible drivers of conodont's diversity fluctuations. Sweet (1988) mostly agreed with the pattern Clark described,
132 although he split the Ordovician diversity peak into two 'long-term cycles'. Sweet went on to suggest that the final
133 extinction of conodonts was due to a sea level drop. On the contrary, De Renzi et al. (1996) showed that conodonts
134 declined progressively from the Middle through the Late Triassic, and therefore favored competition as the main player
135 in the disappearance of conodonts; an idea recently supported also by Martinez-Perez et al. (2013). In other words, the
136 Court Jester vs. Red Queen debate applies also to the extinction of conodonts. In our opinion, the abundant conodont
137 data at hand therefore constitute a unique opportunity to understand how abiotic factors – including large catastrophes –
138 may drive the diversity of nektonic animals, but also possibly how biotic interactions may be instrumental in explaining
139 the extinction of such a large taxonomic group.
140   In this study, we investigate whether the picture Clark (1987) and Sweet (1988) drew still holds today, using
141 updated dataset and methods. Using current knowledge on paleoenvironment, we will also aim at identifying the main
142 abiotic drivers of conodont diversity and associated paleogeographical patterns, and test whether those drivers may or
143 may not account for the final demise of conodonts.
144

2. Material and Methods

146
147 *2.1. Dataset*
148   The data used in this study was obtained from the Paleobiology Database. The occurrences were downloaded
149 from the Paleobiology Database (https://paleobiodb.org) on 26 June 2018, selecting by taxonomy, with group name =
150 'Conodonta'. The resulting dataset included 23520 occurrences, with associated generic or specific accepted names,
151 time intervals, localities and paleo-coordinates computed by the GPlates model implemented in the Paleobiology
152 Database (Wright et al. 2013). The references on which the dataset is based cumulate a total of 357 unique first authors
153 (secondary bibliography available as supplementary material), the main contributors (> 500 occurrences) being Zhang
154 (N=1236), Barrick (N=1167), Männik (N=964), Ji (N=904), Suttner (N=871), Farrell (N=832), Bultynck (N=743),
155 Klapper (N=714), Aboussalam (N=602), Gouwy (N=507). The main enterers (> 1000 occurrences) of the data into the
156 Paleobiology Database were M. Krause (N=5735), S. Gouwy (N=3547), E. Jarochowska (N=3010), P. Nätscher
157 (N=1363), J. Sessa (N=1169), M. Foote (N=1149), and P. Novack-Gottshall (N=1086). All subsequent data
158 manipulation and analyses were run in R (R Core Team 2018).
159

4

2.2. Diversity, origination and extinction

From this data, diversity was estimated for genera at the series level. First, the dataset was trimmed of single occurrences whose temporal resolution is not constrained to one series: their low stratigraphic resolution makes them useless and possibly would distort the results. Therefore the sample was reduced to N=19737 occurrences. The genus name was used even for occurrences identified at the specific level. A total of 265 unique genera were recorded in the dataset, after checking for duplicates due to spelling mistakes. From this subset was produced a generic presence / absence matrix. Generic diversity estimates were computed using Alroy's 'shareholder quorum sampling' (SQS; Alroy 2010a,b), running 1000 iterations while randomly resampling the presence / absence matrix with replacement. The final diversity estimate was the average across these iterations, and the associated standard deviations were also computed. SQS estimates for the Terreneuvian, Cambrian Series 2 and Lopingian could not be computed properly due to the very low generic diversity, and are therefore replaced by raw generic counts. A similar analysis was run for occurrences for which the resolution was at the stage level (N=15279). Because the resulting diversity curve was for a large part discontinuous, it is shown as supplementary material (SM1). Additionally, 'single-interval' diversity was computed (at the series level) as the number of genera present in only one series. From the same subset, extinction and origination rates were computed using the 'three-timer' formulas of Alroy (2010b). The use of SQS diversity estimates, and three-timer formulas aims at avoiding several biases present in most paleontological studies of diversity. These include the edge and Signor-Lipps effects by which the diversity artificially drops before and rises after boundaries (especially across mass extinctions), but not the Pull of the Recent effect, since conodonts do not have a fossil record in the Recent. The Lagerstatte effect, and unique taxa due to taxonomic identification difficulties in conodonts, are taken into account by calculating SQS and independently computing single-interval generic counts. Finally, poly-cohort contour graphs (Brayard et al. 2009) were produced, which allow a different representation of diversity, extinction and origination trends. The trends revealed by these graphs were similar to results from the SQS, origination and extinction curves, therefore they are only presented as supplementary material (SM2, SM3).

2.3. Conodont evolutionary faunas

To refine the analysis of conodont diversity, we investigated the existence of several 'evolutionary faunas' based on the temporal range of the various genera, excluding the 'single-interval' genera. First, a Multiple Correspondence Analysis (MCA) was run on the generic presence / absence matrix at the series level, using the 'MCA' function implemented in R package 'FactoMineR' (Lê et al. 2008). Hierarchical clustering (function 'HCPC' of 'FactoMineR') was then used on the produced multivariate space to form clusters and assign genera to them, to define 'evolutionary faunas'. Clusters were defined arbitrarily, based on two criterias: inertia gain and non-overlapping of the groups.

Patterns of diversity were assessed for each evolutionary fauna, without using SQS, but only raw generic counts, excluding single-interval taxa. Scotese's (2016) paleomaps were used to look at the paleobiogeographical patterns of the different evolutionary faunas, by displaying the presence / absence of each group as different colors in the cells (see below).

2.4. Generic counts and SQS diversity

Excluding single-interval taxa, which are biased by taxonomic difficulties and Lagerstatte effects, raw generic counts at the series level were computed. The relationship between the decimal logarithm of these counts and that of the

SQS values was tested by a linear regression. The Terreneuvian, Cambrian Series 2 and Lopingian were excluded of this model, since their SQS values could not be computed.

2.5. Paleobiogeographical patterns

To analyse paleobiogeographical patterns, we used the same approach as Kocsis et al. (2018). Scotese's 'PALEOMAPS PaleoAtlas' was downloaded and the paleomaps data for the Cambrian to Triassic period were imported in R (Scotese, 2016). For each map in the atlas, we defined an age range, corresponding to the stage represented by the map. Using R package 'icosa' (Kocsis, unpublished), a 2D penta-hexagonal grid was created, to be projected on the maps, with 'cells' (faces) of approximately equal surfaces and an average side ('edge') length of 740.74km. These cells were used as a coarse resolution unit for our paleogeographical investigations. Conodont occurrences whose range was entirely included within the age range of each map (N=12448) were automatically assigned to the corresponding cells, based on their paleolatitudes and paleolongitudes, using function 'locate' of package 'icosa'. The rest of the occurrences, which could not be restricted to the same resolution as the paleomaps, were excluded in this part, to avoid placing on the maps occurrences that may not have existed at the time represented by the paleomap.

The cells including areas of continental platforms and/or coast were manually counted for each stage as a proxy for the theoretically available area for conodonts. The number of cells was also computed for each stage, as a proxy of conodont geographical spread and occupation. The link between theoretically available area and occupied area was tested by a linear regression, out of which the residual variation was extracted to check for potential correspondence with other abiotic events. The maximal and minimal latitude occupied by conodonts were obtained as the latitudes of the center of the northernmost and southernmost occupied cells.

2.6. Abiotic variables trends

Sea surface temperature (SST) data were obtained from Song et al. (2019), and sea-level data were extracted from Hannisdal and Peters (2011) using the WebPlotDigitizer application (https://apps.automeris.io/wpd/). Data for the latter ultimately derived from Haq and Schutter (2008) and Haq et al. (1987). After extracting this data, we averaged it at the series level, to correlate it with our diversity, origination and extinction estimates. Those relationships were tested using linear models. The global mean annual temperature curve from Scotese (2015) was also extracted using WebPlotDigitizer and added for comparison with SST.

2.7. Latitudinal gradients

Finally, latitudinal gradients were investigated at the series level, by computing generic counts in bins of 10° latitude. No SQS was used here, the gradients represent raw generic counts. Latitudinal gradients of diversity were also computed for each evolutionary fauna as a whole (rather than by series), either as raw generic counts, or as proportion of their respective generic diversity. Bootstrapping of occurrence was used (10000 iterations) to test for significant differences between these gradients across the three evolutionary faunas. Finally, latitudinal gradients of extinctions (latest occurrence of a genus in the dataset) and originations (first occurrence in the dataset) were obtained and represented by kernel density plots (SM2).

3. Results

3.1. Conodont generic diversity, origination and extinction

Conodont SQS diversity (Fig. 1A) shows three conspicuous peaks: throughout Ordovician, in the Early

Devonian, and in the Early Triassic, matching with peaks of single-interval taxa diversity. Diversity is at its highest

throughout the Ordovician. Major decreases occur across the Ordovician – Silurian boundary, Early – Middle Devonian

boundary, and Carboniferous – Permian boundary. Peaks of conodont origination rates (Fig. 1B) are observed during

the Early Ordovician, Early Silurian (Llandovery), Late Carboniferous (Pennsylvanian) and Early Triassic. Extinction

peaks (Fig. 1B) are observed in the Late Ordovician, the Late Devonian (smaller peak) and Pennsylvanian (at which

time it overcomes the synchronous origination peak).

There is a significant negative linear relationship between average SST and extinction rate (adjusted R^2=0.265,

P=0.017, df=1, 16), and a positive relationship between average sea-level and SQS diversity (adjusted R^2=0.195,

P=0.029, df=1, 18) at the series level. Other relationships between SST or sea-level and diversity, extinction and

origination were non-significant (P > 0.05).

3.2. Evolutionary faunas

The multiple correspondence analysis, followed by hierarchical clustering, revealed three clusters, or

evolutionary faunas, based on temporal distribution of the genera (Fig. 2). The first (48 genera) is mostly restricted to

the Ordovician, the second (37 genera) also starts diversifying in the Early Ordovician, but reaches its acme during the

Silurian, and starts decaying progressively from the Early Devonian on (Fig. 3). The latest evolutionary fauna (48

genera) rises in the Early Devonian, reaches its acme in the Late Devonian, and then progressively goes down through

the Carboniferous, followed by a steeper decay during the Permian. This evolutionary fauna recovers and constitutes

most of the diversity of the Triassic period. Following the classification proposed by Donoghue et al. (2008), the stem

Prioniodontida, Balognathidae, stem Ozarkodinida, as well as several Prioniodinina are for the most part included in the

early evolutionary fauna (Fig. 3C). The intermediate evolutionary fauna contains stem Ozarkodinina, stem

Polygnathacea, as well as some Prioniodinina (*Oulodus*). The late evolutionary fauna contains some Prioniodinina, and

most derived Ozarkodinina (Polygnathacea and the unamed superfamily containing 'gondolellids').

3.3. SQS diversity estimates and generic counts

The SQS diversity estimates (Fig. 1A) and total of non-single-interval genera (Fig. 3A) are significantly

correlated at the series level, excluding the Terreneuvian, Series 2 and Lopingian (R^2 = 0.4, P < 0.01, df = 1, 17; Fig. 4).

Discrepancies between SQS and generic counts are frequent. For the Series 3, Furongian, Guadalupian, and Early

Triassic, generic counts are lower than expected. For the Middle Devonian, Late Devonian, Wenlock, Ludlow, and

Llandovery counts are higher than expected. The most notable discrepancies are the Middle and Late Devonian, and the

Guadalupian, during which SQS estimates and generic counts show opposite trends (Fig. 3A).

3.4. Paleogeographical patterns of conodont diversity

Geographically, the first occurrences of conodonts are rather spread out (Fig. 1E, 5A). The number of cells

occupied by conodonts sees an important rise in the Late Cambrian, which is sustained through the Ordovician despite a

short term drop at the Cambrian – Ordovician boundary (Fig. 1C-D). The Hirnantian glaciation clearly reduces the

geographical distribution of conodonts, both in its latitudinal extremes and number of occupied cells (Fig. 1C-E, 5C-D).

The extent of conodonts then increases again from the Wenlock into the Early Devonian (Lochkovian), but is restricted

280 during the rest of the Early Devonian (Fig. 1C-E, 5F-G). A short-lived spread is seen in the Eifelian (Middle Devonian),
281 followed by a continued decrease during the remaining of the Devonian and the Mississippian (Fig. 1C-E, 5H, 6A-B).
282 The geographical spread of conodonts remains fairly stable through the Mississippian and Pennsylvanian transition
283 (Fig. 1C, E), although the available space becomes more and more restricted (Fig. 1C, D), it decreases again at the end
284 of the Carboniferous, with conodonts being restricted to equatorial latitudes (Fig. 1E). An all-time low is reached during
285 the middle of the Cisuralian (Early Permian; Fig. 1C-E, Fig. 6D-E), associated with the near-total extinction of
286 conodonts (Fig. 1A), and despite ice sheets pulling back. A marked spread can be seen at the end of the Permian,
287 notably towards the extreme latitudes (Fig. 1C-E, Fig. 6F-G). The extent of conodonts remains high in the Early
288 Triassic, then goes back down for a short time in the Middle Triassic (Fig. 1C-E, Fig. 6H), before re-increasing in the
289 Late Triassic. The number of occupied cells is significantly correlated to the number of theoretically available cells (R^2
290 = 0.15, P < 0.01, df=1, 44), however with a large amount of residual variation (Fig. 1C-D), the latter being apparently
291 synchronous with the sea level curve until the Early Carboniferous (Fig. 1F).
292
293 *3.5. Latitudinal gradients*
294   Latitudinal gradients of generic diversity (LGGD) at the series level can be interpreted only from the Early
295 Ordovician on. In the Early Ordovician, the diversity is fairly spread out between -50 and 50°, with multiple modes, two
296 being found around 40° and -30°, and a third just north of the equator (Fig. 7). Two LGGD modes are also seen in the
297 Middle Ordovician, one just south of the equator, the other around 25°. During the Late Ordovician the LGGD flattens,
298 with conodont diversity spreading southward, only the northernmost latitudes being devoid of conodonts. Following the
299 Hirnantian, the southern occurrences disappear (Fig. 5D) and a fairly classical, mostly unimodal latitudinal gradient is
300 established, which is maintained until the Mississipian (Fig. 7). One particularity of this latitudinal gradient is that its
301 mode is not equatorial, but located in the Southern Tropics. The whole diversity of conodonts in this time frame seems
302 to concentrate in the Southern Hemisphere. In the Pennsylvanian, the distribution seems to shift slightly northward, but
303 conodont diversity is drastically reduced during the Permian (Fig. 6D-E). In the Early Triassic, a latitudinal gradient is
304 re-established but flatter than previously, with a small mode in the Northern Hemisphere. Diversity is again hit during
305 the Middle Triassic, before a more marked latitudinal gradient is established in the Late Triassic, with a mostly northern
306 diversity and a single mode in the Northern Tropics.
307
308 **4. Discussion**
309
310 *4.1. Factors impacting conodont diversity and geographical patterns*
311   The large conodont diversification after the Cambrian – Ordovician boundary occurs within a transgressive
312 cycle, peaking in the Middle Ordovician (Fig. 1F), combined with hot but decreasing temperatures. It constitutes a part
313 of the 'Great Ordovician Biodiversification Event' (GOBE, e.g. Harper et al. 2015), as conodonts may have been
314 among the first groups to colonize the water column. The increase in available shelf area may have enabled the
315 origination of many conodont taxa (Fig. 1B-C, Harper et al. 2015). However, it also appears that, at that time, some
316 conodonts colonized open sea environments (Fig. 5B), possibly via the increase in diversity and abundance of plankton,
317 and the likely establishment of open marine food chains (Harper et al. 2015, Servais et al. 2008). Either factors, or their
318 combination, may explain the dramatic increase in conodont diversity. The level of conodont diversity reached during
319 the Ordovician was not equaled at any later time (Fig. 1A).

320   The Hirnantian / end-Ordovician extinction brought an end to the acme of conodont diversity. It was
321   synchronous with a large drop in seawater temperature and sea level, and with ice sheets spreading (Fig. 5C-D, Harper
322   et al. 2014). The conodonts' geographical distribution was greatly reduced at that time, especially in southern localities
323   that became covered by ice (Fig. 1E, Fig. 5D). This extinction mainly affected the early evolutionary fauna (Fig. 3),
324   while the intermediate evolutionary fauna remained diverse across the boundary, and diversified in the Early Silurian.
325   The global diversity plummeted due to the loss of early fauna genera, but the intermediate fauna rose. At a finer
326   temporal resolution, the drop in conodont diversity appears as a two-step process, with one extinction event at the
327   Katian – Hirnantian boundary, and a second during the Hirnantian (Harper et al. 2014). It should be noted that the early
328   fauna taxa that disappeared shared their geographical and temperature distribution with the earliest intermediate fauna
329   taxa (Fig. 5C-E), suggesting that there was no fundamental difference in the temperature tolerance of the two groups.
330   Therefore the reason why some taxa survived and others not may instead be related to the presence of refugias, or to the
331   influence of temperature on the preys of the conodonts. The recovery fauna, which started to diversify at the end of the
332   Hirnantian may correspond to the early radiation of the intermediate evolutionary fauna. The turnover in conodont
333   diversity may therefore be explained roughly by the disappearance of early fauna taxa due to the drop in temperatures
334   and loss of available habitat (South Pole glaciation and sea level drop), leaving open ecological niches for intermediate
335   fauna taxa to diversify later on. Direct detrimental competition between the two faunas does not seem plausible, as both
336   were found in the same geographical areas earlier on (Fig. 5A-D). The Early Silurian peak of origination rate (Fig. 1B)
337   reflects the large increase in diversity of this intermediate fauna (Fig. 3A). Although it may have started in the
338   Hirnantian (Harper et al. 2014), most of the diversification coincides with a global increase of temperatures, associated
339   with ice sheets melting and a sea level rise (Fig. 1F).

340   In the Ordovician, conodonts constituted most of the nekton's diversity. The subsequent increase in nekton
341   diversity during the Silurian / Early Devonian (Whalen and Briggs 2018, Klug et al. 2010) may have played a role in the
342   limitation of the conodont's recovery via either predation pressures (the earliest known direct evidence of predation on
343   conodonts dates from the Late Devonian; see Zaton and Rakocinski 2014, Zaton et al. 2017), and/or competition for
344   ecological spaces. This scenario, if real, may converge with that of the final extinction of conodonts (see below).

345   The peak of conodont diversity in the Early Devonian occurred within a temperature decreasing trend (with
346   large variations) and coincided roughly with a lowstand (switch from a regressive to a transgressive trend) in the middle
347   Early Devonian (Fig. 1A, 1F). This series displayed stable standing diversity in the intermediate fauna taxa, while
348   several late fauna taxa appeared (Fig. 3A). Extinction and origination rates were almost equal, because several
349   intermediate fauna taxa disappeared by the end of the Early Devonian while the late evolutionary fauna was rising (Fig.
350   1B). Although there was an increase of occupied areas in the earliest Devonian, it was short lived (Fig. 1C-D), and was
351   not reflected in the latitudinal extremes of the distribution, which remained stable (Fig. 1E). This geographical pattern
352   may be explained by the position of the paleo-continents, which started to assemble. Areas occupied only by
353   intermediate fauna taxa were either emptied or became shared with late fauna taxa (Fig. 5F-H). This, combined with the
354   fact that intermediate evolutionary fauna taxa generally constitute groups that are basal to late fauna taxa along the tree
355   of Donoghue et al. (2008), could mean that some species of the intermediate fauna went through an episode of
356   speciation at that time and gave rise to the late fauna diversity, possibly linked with an increase in sea level (Fig. 3C).

357   The drop in diversity observed in the middle Devonian (Fig. 1A) is mostly explained by extinctions of
358   intermediate fauna and single-interval taxa (Fig. 1A, 3A), which are not compensated by originations of late fauna taxa.
359   This drop in global diversity happens despite the coeval sea-level high and may be related to the mid-Devonian

hothouse (Fig. 1F), which may have negatively impacted the intermediate fauna taxa, while favoring late fauna taxa. The loss of diversity is not reflected by a notable extinction peak (Fig. 1B), possibly because single-series genera are not taken into account in the computation of the extinction rate (Alroy 2010b). The small peak of extinction rate in the Late Devonian, despite an increase of SQS diversity (Fig. 1A-B), may also be due to the loss of single-interval taxa and intermediate fauna taxa. Both intermediate and late fauna generic diversity go down across the Devonian – Carboniferous boundary although not reflected by SQS diversity estimates.

Extinction rate culminates in the late Carboniferous, while some of the lowest temperatures and lowest sea level of the entire studied period are reached (Fig. 1B, 1F). Repeated or continuous glaciation(s) and regression(s) marked the Carboniferous (Fielding et al. 2008). Those clearly had a large impact on conodont diversity, as well as on their geographical extent, which was reduced to equatorial latitudes by the end of the Carboniferous (Fig. 1C-E, 6C-D). Following the large extinction peak of the Pennsylvanian, conodont diversity was reduced to only a handful of genera (Fig. 1A, 3A). Conodont diversity remained extremely low during the Early and Middle Permian, with conodonts being restricted to a few refugia (Fig. 6E). In the Late Permian (Lopingian) conodont diversity was still very low (Fig. 1A), but the geographical extent of conodonts started again to increase, possibly reflecting the increasing temperatures and the concurrent melting of the ice sheets (Fig. 1C-F, 6F).

Finally, diversity rose again after the P-T boundary, with a peak of origination and large numbers of single-interval taxa, mostly late fauna taxa (Fig. 1A-B, 3A-B). This occurred while the sea level was very low, and the temperatures very high (Fig. 1F). At a higher resolution, the widely fluctuating climate of the Early Triassic interval (e.g. Goudemand et al. 2019) may explain why so many taxa of this interval are single-interval only, and therefore produced a peak of origination. The fact that conodonts started to colonize new areas already in the Late Permian may have driven allopatric speciations following the extreme conditions of the P-T crisis.

It is clear from the paleomaps in Figs. 5 and 6 that conodonts were more abundant along coastlines and on continental shelves. Not surprisingly, the paleogeographical spread of conodonts is significantly correlated to the extent of continental shelves (Fig. 1C). Yet, conodonts were not restricted to these areas, as evidenced by the open sea locations during the Ordovician and Devonian (e.g. Fig. 5B, 5G-H). Residual variation in the geographical distribution of conodonts (Fig. 1D) corresponds with the sea level curve, and the ice ages of the end-Ordovician and Pennsylvanian clearly brought restrictions to the extension of conodonts, especially in their latitudinal extremes (Fig. 1E). Overall, our data suggest that conodonts were not ecologically restricted to coastlines or warm waters, but that they could not adapt to very cold / glacial waters. Extremely hot waters may also have been lethal to conodonts, but in general, increased temperatures seems to have favored conodont diversification.

It appears that the positions of paleo-continents had an influence on the evolution of the latitudinal gradient of conodont diversity (Fig. 7). Throughout the Ordovician, the LGGD is rather symmetrical between the Northern and Southern Hemispheres. Conodonts were then present in the northern extent of the Gondwanian continental shelf (Fig. 5B-C), around Laurentia and Baltica, and further North in the open ocean. From the Early Silurian (Llandovery) to the Carboniferous, the LGGD became restricted mostly to the Southern Hemisphere, and was generally unimodal. This is in accordance with the southern location of most coastlines and continental shelves from the Llandovery until the Early Carboniferous. Northern movements of Pangea during the Carboniferous, combined with the appearance of large South Pole ice sheets produced a northward shift of the conodonts, and the LGGD became almost centered on the equator (Fig. 6D, Fig. 7). When conodont diversity recovered in the Early Triassic, Pangea extended from North to South Pole,

400 with most continental shelves in the Northern Hemisphere (Fig. 6G-H). Consequently the LGGD moved to the
401 Northern Tropics, where it was maintained until the end of the Triassic (Fig. 7). This interpretation is in accordance
402 with studies of both past and present latitudinal diversity gradients that demonstrated a close link with the position of
403 continental shelves (e.g. Powell 2009, Chaudary et al. 2016).

404   Several of the major biases of the fossil record may affect our results. Notably, as we showed that most
405 conodonts occurrences are found in continental shelves environments, their diversity and paleogeographic patterns
406 might be related to the quantity of preserved sedimentary rock (Peters 2005). The correlation between SQS diversity
407 and sea-level, which is also known to impact the amount of sedimentary rock, may be an artifact of the preservation
408 bias, although we would favor a common-cause hypothesis (Peters 2005). Sampling effort bias is also probably playing
409 a role in the paleogeographic patterns observed, as conodont workers have mostly explored facies expected to yield
410 numerous fossils. Some paleo-environments (e.g. hypersaline) are undersampled, but can yield surprising diversity
411 (Jarochowska et al. 2017). Finally, although multi-element taxonomy has been adopted by conodont workers for several
412 decades now (Bergstrom and Sweet 1966), it is not always applicable, which may lead to taxonomic oversplitting and
413 overestimations of diversity. Notably, very few complete apparatuses are known for the oldest conodont genera and the
414 topological schemes used for establishing homologies between elements vary between earlier and later taxa (Donoghue
415 et al. 2008).

416

417   Keeping these caveats and biases in mind, it appears that, indeed, abiotic factors – temperature and sea-level,
418 as well as paleocontinent positions – influenced conodont diversity, as it is clear that the largest peaks of origination and
419 extinction and diversity are synchronous with peaks or lows in the global temperature and/or sea-level curve. When
420 testing these relationships, however, only a negative link between temperature and extinction and a positive link
421 between sea-level and diversity were significant. Furthermore, both correlations were driven by extreme points. It is
422 interesting to note that it was not a necessary condition to combine both sea-level and temperature to positively impact
423 conodont diversity. For example, the Ordovician radiation corresponded with a large transgression and high
424 temperatures, the Early Triassic origination and diversity peak was concomitant with a very low sea level and hot and
425 variable temperatures, while the Early Devonian diversity peak (which was more limited) was synchronous with
426 variable but not particularly extreme sea-level and temperatures (Fig. 1A, 1F). This shows that either factors can be self-
427 sufficient to have an influence. Additionally, our proxy of geographical areas available to conodonts (number of cells
428 including coast or continental shelf) was significantly related to occupied area (Fig. 1C), suggesting a partial
429 explanation of how sea level trends impacted the geographical spread of conodonts (Figs. 5-6). Conodont mobility may
430 have played a role in maintaining diversity in times of low sea level and glaciation. Our results suggest that the main
431 events in the history of conodont diversity were related to extreme abiotic conditions. Yet, much variation in diversity,
432 extinction and (in particular) origination remains unexplained, and could be due instead to biotic factors. Notably, the
433 first origination peak of the Early Ordovician, the Early Devonian peak of diversity and the final extinction of
434 conodonts require closer investigation, in particular regarding the interaction of conodonts with other marine groups.

435

436 *4.2. Comparison with previous studies and remarks on the final extinction of conodonts*
437   Our results regarding global conodont diversity trends are mostly in accordance with previously published
438 curves (Clark 1983, 1987, Sweet, 1988). Most of the major events of the group's history are recognized, in particular
439 the Ordovician acme, followed by a major drop in the Silurian. The Permian minimum, and the Early Triassic 'last

440 hurrah' of diversity are also corroborated. On the other hand, we note discrepancies for the Devonian and
441 Carboniferous. In particular, previous studies described diversity and origination as low in the Early Devonian and high
442 in the Late Devonian. Conversely, our results show a peak in diversity in the Early Devonian, followed by a drop in the
443 Middle Devonian and a very limited diversification in the Late Devonian (Fig. 1A). Likewise, previous studies
444 suggested important diversity drops during the Mississipian and Pennsylvanian, while our results suggest on the
445 contrary that diversity was fairly high and stable throughout the Carboniferous, with a major extinction between the
446 Pennsylvanian and the Permian (Fig. 1A). These discrepancies may be due to several factors: i) the geographical extent
447 of the dataset (e.g. Sweet, 1988 focused on North American data), ii) the taxonomic rank used (specific level in Sweet
448 1988, *versus* generic level in Clark 1983, 1987, and our study), iii) the sheer increase in size of the dataset, or iv)
449 methods to assess diversity and rates. Here, we chose to use advances notably promoted by Alroy (2010a,b) to limit the
450 impact of several biases: for example, Clark (1983) used a range-through counting method (although not defined as
451 such), which is subject to edge and Signor-Lipps effects (the Pull of the Recent having no impact on conodonts; Alroy
452 2010b) meaning that diversity estimates will tend to artefactually drop before and rise after boundaries, notably at mass
453 extinction events. Despite these biases, these older studies did manage to reveal the most prominent elements also
454 highlighted in the present work (Ordovician acme, Permian low and Triassic short-lived recovery), suggesting that these
455 trends are real, and robust to any kind of biases, as well as across taxonomic levels.

456

457   Clark (1983) suggested that the final extinction of conodonts may be linked to a drop in sea level, and was
458 followed in this interpretation by Sweet (1988). However, sea-level was low throughout the Triassic, and its variations
459 are not agreed upon. Furthermore, recent studies suggest that it may have been rising, rather than dropping, during the
460 Late Triassic (e.g. Van der Meer et al. 2017). Even if the regressive trend actually took place, its age was likely younger
461 than the start of conodonts' decline (Middle Triassic; Martinez-Perez et al. 2013). Furthermore our results suggest that
462 regressive trends do not necessarily correlate with major conodont extinctions. Global temperatures in the Late Triassic
463 were fairly similar to those in the Early and Middle Triassic, and the world was ice-free at that time, as was generally
464 the case in times when conodonts were thriving. Based on our results, considering the absence of glaciation and a late
465 drop in sea level and CAMP province influence, we may conclude that two of the most important abiotic factors
466 (temperature and sea-level) cannot be considered as sufficient to explain the extinction of conodonts. Other abiotic
467 factors, which are more difficult to assess, such as water salinity or pH may have played a role. Alternatively, and in
468 agreement with De Renzi et al. (1996) and Martinez-Perez et al. (2013), biotic factors such as predation by, or
469 competition with groups of the 'Modern Fauna' (Sepkoski 1981, Hu et al. 2011, Brayard et al. 2017), e.g. Neopterygian
470 fishes and Neoselachian sharks that started radiating in the Middle Triassic (Cuny and Benton 1999, Xu et al. 2013),
471 may have driven the last conodonts to extinction.

472

473 **5. Conclusion**

474   Our analysis confirms the influence of abiotic factors on conodont diversity at a large scale. Notably, despite
475 their mobility, these early vertebrates were strongly impacted by sea-level variations as well as major glaciations, which
476 restricted the extent of their favored coastal habitat and probably limited the possibility of allopatric speciation. Biases
477 of the fossil record should however be kept in mind as potentially confounding or correlated factors. These abiotic
478 factors do not however explain particular conodont events such as their Ordovician radiation or their final demise at the
479 end of the Triassic. Instead it is likely that biotic factors played a prominent role in the extinction of conodonts. Despite

480 the fact that biotic interactions arguably take place locally in time and space, the sum of their effects may ultimately

481 emerge as large-scale patterns, leading for example to the extinction of a highly successful group like conodonts, which

482 had thrived in oceans for more than 300 Ma.

483

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Figure 1. Synthetic view of diversity and paleobio-geographical patterns through the Phanerozoic. Alternating gray and white areas delimit the boundaries between series. **A)** Black line: average SQS generic diversity ± std. dev. over 1000 iterations (gray outline). Blue dashed line: count of single-series genera (i.e. genera which occur in only one series). **B)** Origination (red) and extinction (black) rates, computed using the 3-timer approach of Alroy (2014). **C)** Blue line and area: geographical area theoretically available to conodonts, as the number of cells of the paleomap including continental shelf or coast. Black line and area: geographical area where conodonts occur, computed as the number of cells including at least one occurrence of conodont (see Material and Methods). Available and occupied space are not at the same scale. **D)** Residual variation of a linear regression of number of cells occupied against number of cells available, i.e. variation in the occuped area after removing the effect of continental shelf / coastal area. **E)** Median northern (red) and median southern (blue) paleolatitudes of conodont occurrences, dashed lines are the maximal and minimal paleolatitudes occupied by conodonts, computed as the middle latitude of the northern-most and southern-most occupied cells. **F)** Phanerozoic global sea surface temperature curve, from Song et al. (2019; red curve and points, dashed red line is the series-averaged cruve), global mean temperature modified from Scotese et al. (2015; black line), and global sea level curve, modified from Haq and Schutter (2008; blue line and area).

Figure 2. First two axes of the Multiple Correspondance Analysis (MCA) run on the generic time series presence / absence matrix, excluding single-series taxa. Hierarchical clustering was used on this MCA, and three clusters were retained based on the inertia gain and non-overlap of the groups. Abbreviations represent the series in which genera were present. Csrl: Cisuralian, ErlD: Early Devonian, ErlO: Early Ordovician, ErlT: Early Triassic, Frng: Furongian, Gdlp: Guadalupian, Ldlw: Ludlow, Llandovery: Llnd, Lpng: Lopingian, LtDv: Late Devonian, LtOr: Late Ordovician, LtTr: Late Triassic, MddD: Middle Devonian, MddO: Middle Ordovician, Mddt: Middle Triassic, Msss: Mississippian, Pnns: Pennsylvanian, Prdl: Pridoli, Srs2: Series 2, Srs3: Series 3, Trrn: Terreneuvian, Wnlc: Wenlock. The first cluster (magenta triangles) forms the 'Early Evolutionary Fauna'. The second cluster (yellow circles) forms the 'Intermediate Evolutionary Fauna'. The third cluster (black squares) forms the 'Late Evolutionary Fauna'. See Fig. 3 for more details on these clusters.

Figure 3. Diversity trends of the three 'evolutionary faunas'. **A)** Raw generic count (excluding single-series taxa) by series for genera assigned to the different 'evolutionary faunas' (full lines), and the sum of these curves (dashed line). Gray outline shows the SQS diversity estimate std. dev. (see Fig. 1A) for comparison. **B)** Percentage represented by the faunas in the total diversity in each series. The 'Early Fauna' dominates through Cambrian and Ordovician, but is replaced by the 'Intermediate Fauna' at the start of the Silurian. Finally the 'Late fauna' becomes dominant in the Middle Devonian, although remnants of earlier faunas survive until the Triassic. **C)** Tree modified from Donoghue et al. (2008), with genera highlighted according to their evolutionary fauna. Genera not highlighted could not be included in the analysis (i.e. single-series taxa).

Figure 4. Plot of raw generic counts (excluding single-series taxa) against average SQS diversity estimate, by series. Black line shows the linear regression line (R² = 0.40, P < 0.01), dashed red lines represent 95% confidence intervals. Named points are those outside of the 95% C.I., i.e. series in which the raw counts do not follow the predicted relationship with the SQS estimates.
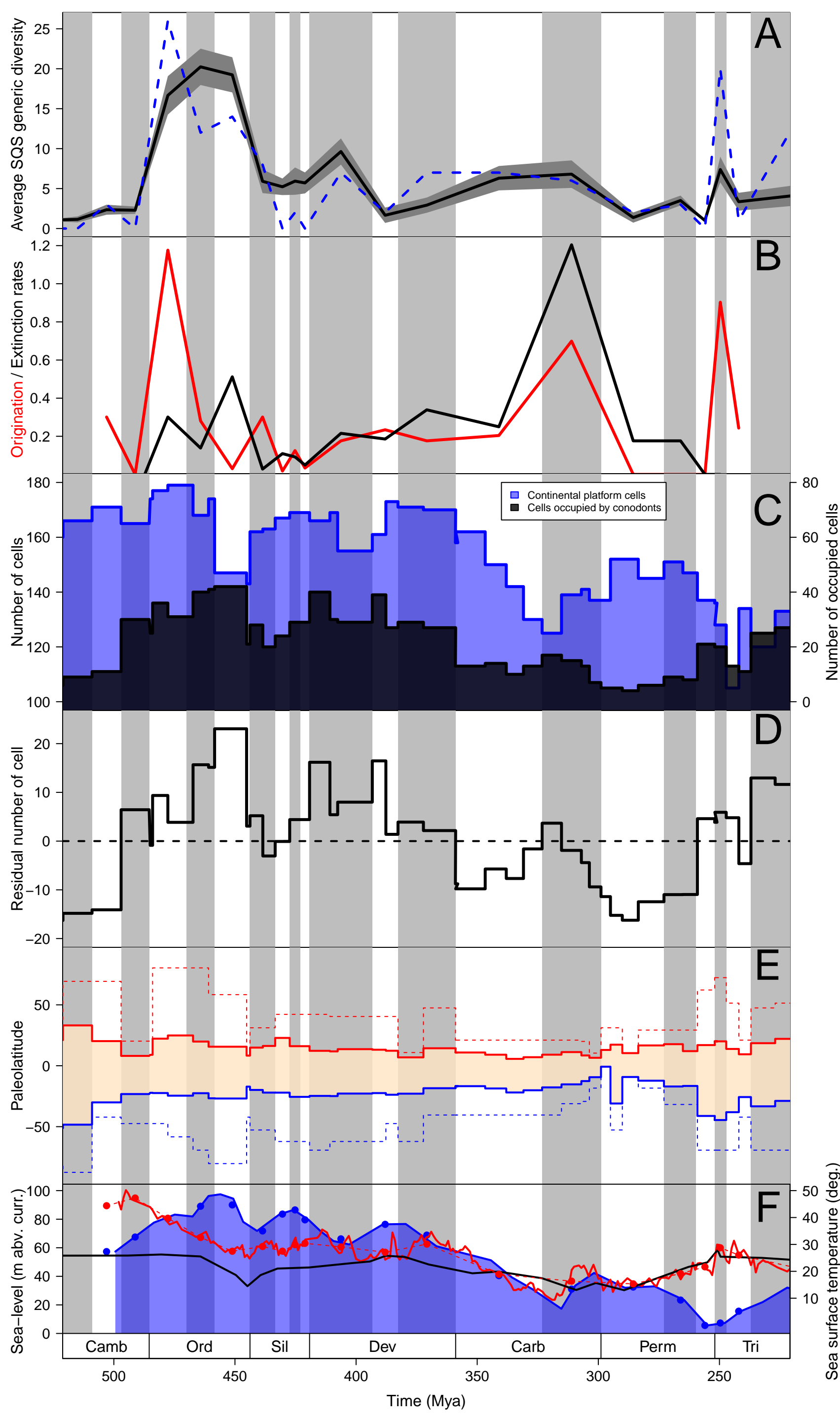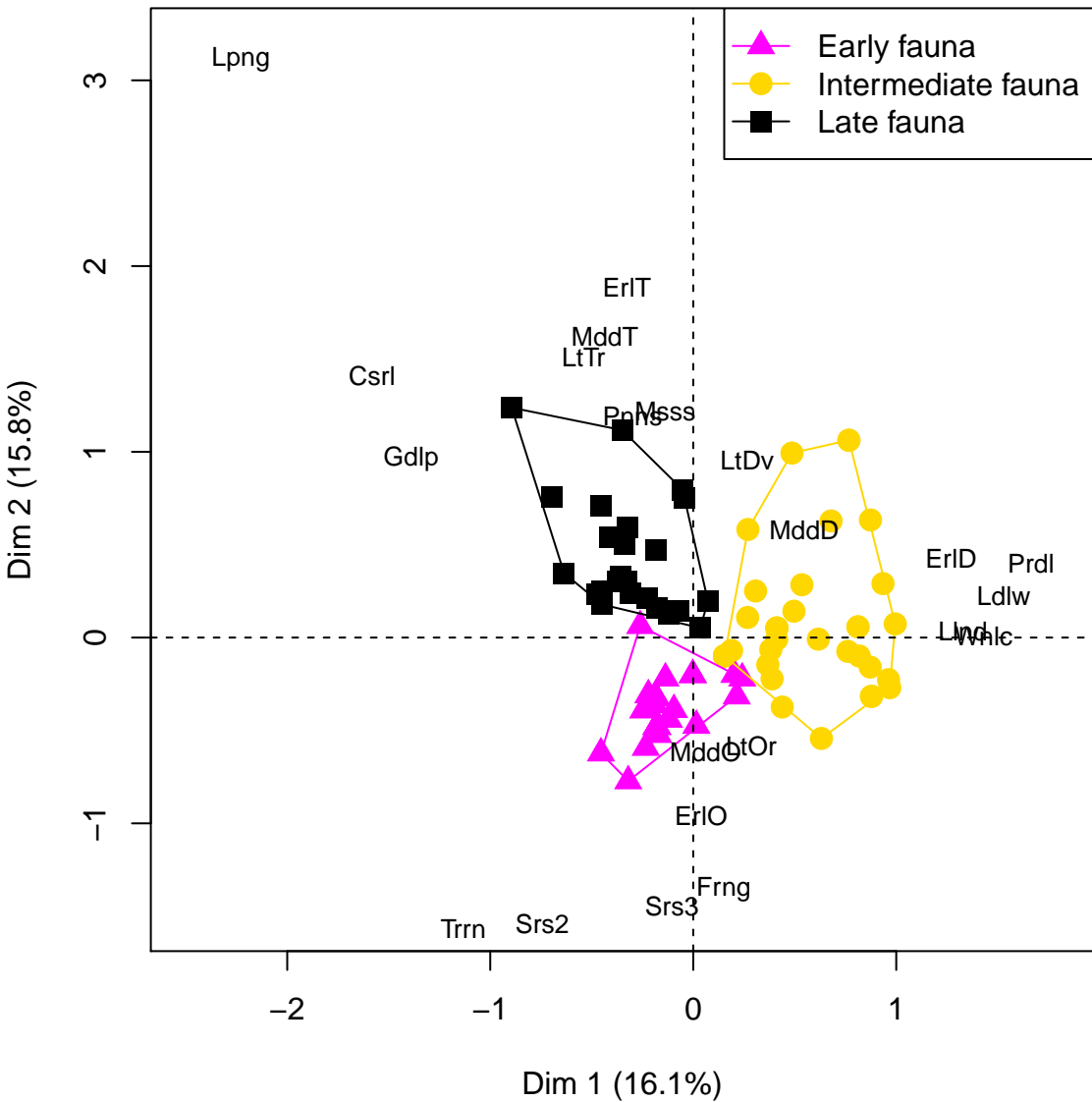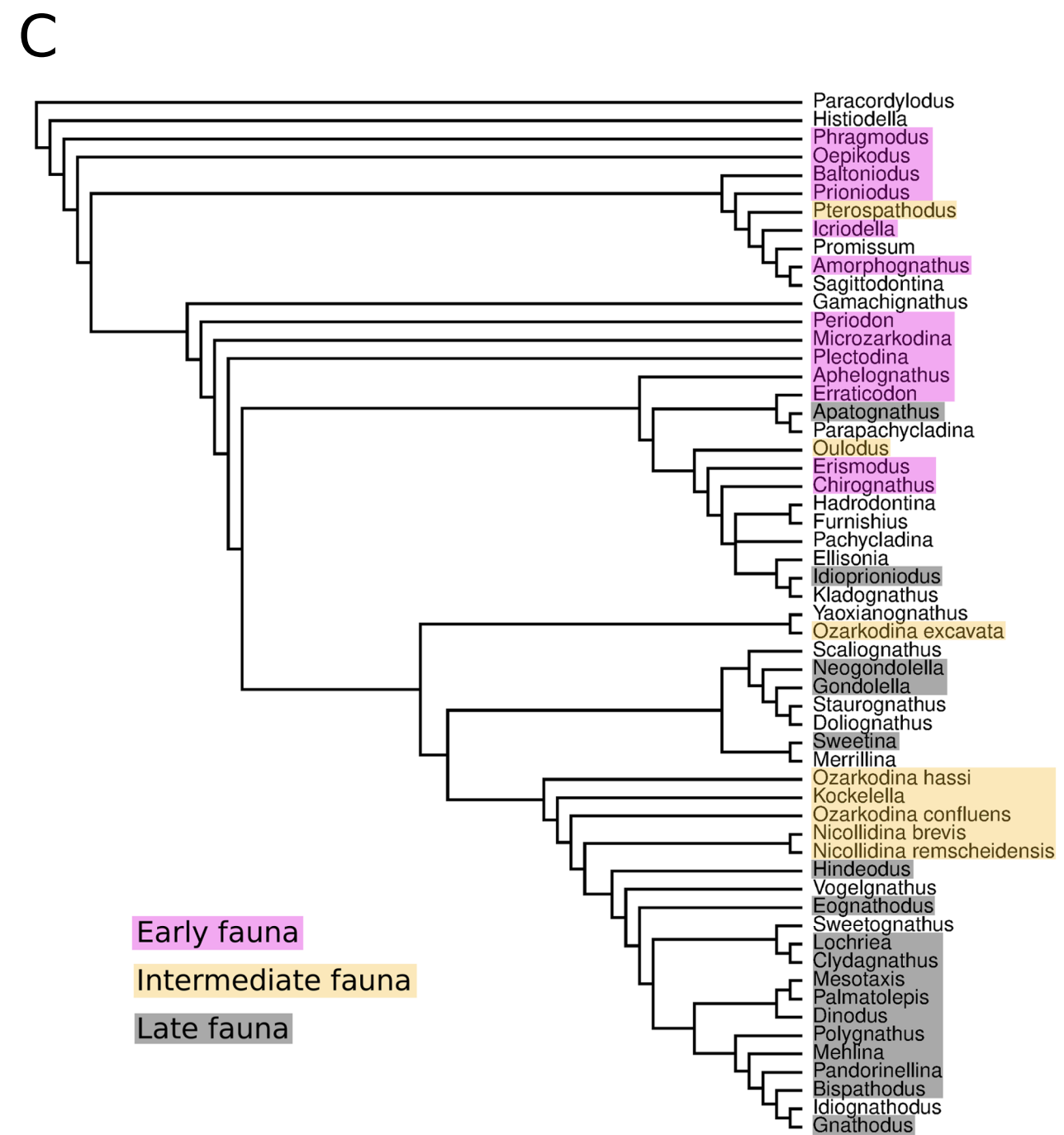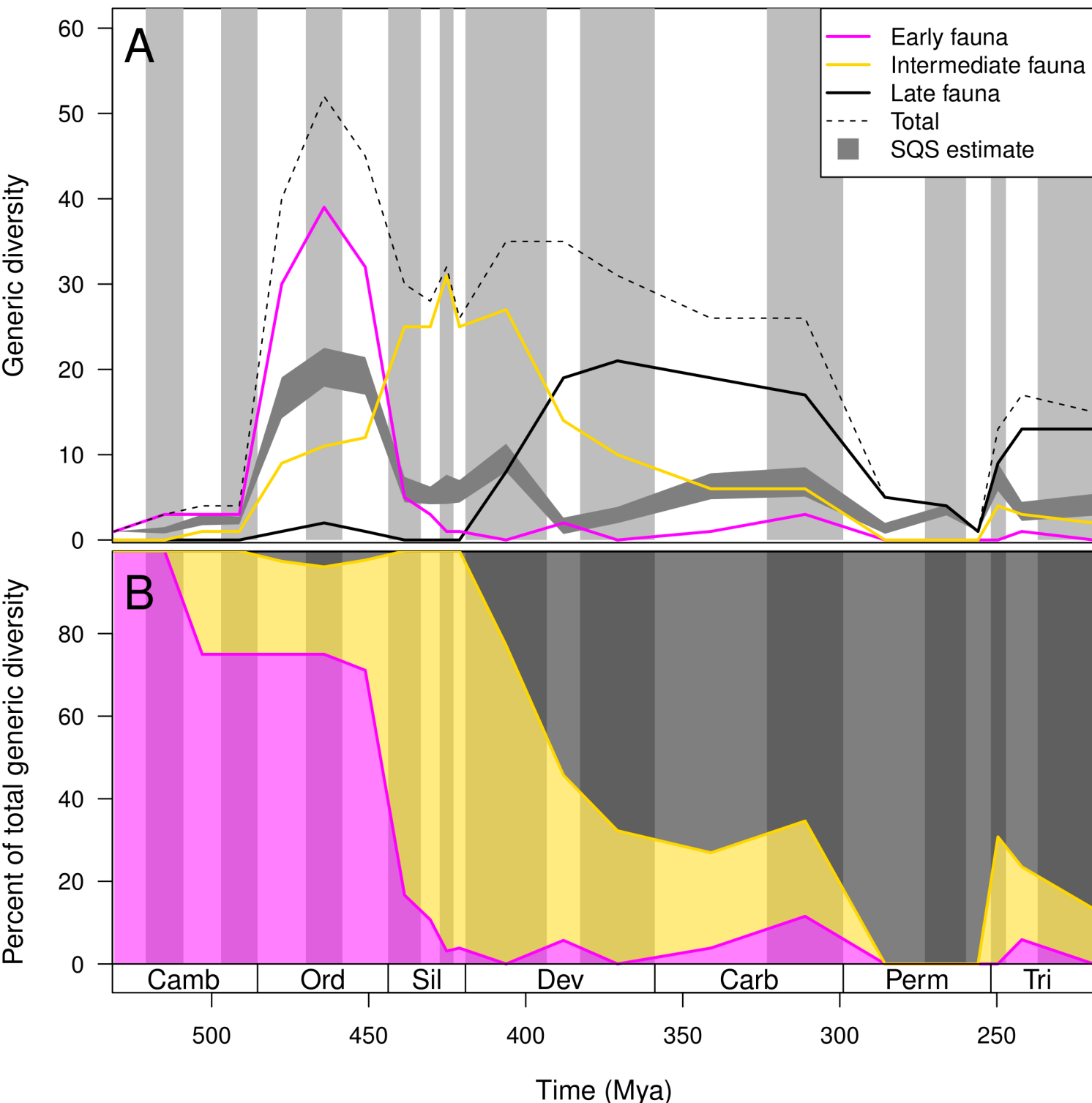
684

685 **Figure 5.** Paleobiogeographic evolution of conodont diversity from end-Cambrian to Late Devonian. Paleomaps from
686 Scotese et al. (2015) are divided into a grid of 362 pentagonal and hexagonal 'cells' (faces) with approximately equal
687 area and 'side' (edge) length. Average side length is 740.74 km. Conodont occurrences were automatically assigned to
688 the corresponding cells, based on their paleolatitudes and paleolongitudes from the Paleobiology Database. Each cell
689 occupied by a colored circle includes at least one occurrence. Multi-colored circles denote the presence of conodont
690 genera belonging to the different 'Evolutionary Faunas' described herein. Note that the proportions of each color are
691 entirely arbitrary and *do not* relate in any way to the proportions of local generic diversity. Circles were plotted at the
692 center of the cells and their position do not imply that the occurrences are actually found together at a finer scale (*i.e.*
693 within a cell).

694

695 **Figure 6.** Paleobiogeographic evolution of conodont diversity from Late Devonian to Middle Triassic. Paleomaps from
696 Scotese et al. (2015) are divided into a grid of 362 pentagonal and hexagonal 'cells' (faces) with approximately equal
697 area and 'side' (edge) length. Average side length is 740.74 km. Conodont occurrences were automatically assigned to
698 the corresponding cells, based on their paleolatitudes and paleolongitudes from the Paleobiology Database. Each cell
699 occupied by a colored circle includes at least one occurrence. Multi-colored circles denote the presence of conodont
700 genera belonging to the different 'Evolutionary Faunas' described herein. Note that the proportions of each color are
701 entirely arbitrary and *do not* relate in any way to the proportions of local generic diversity. Circles were plotted at the
702 center of the cells and their position do not imply that the occurrences are actually found together at a finer scale (*i.e.*
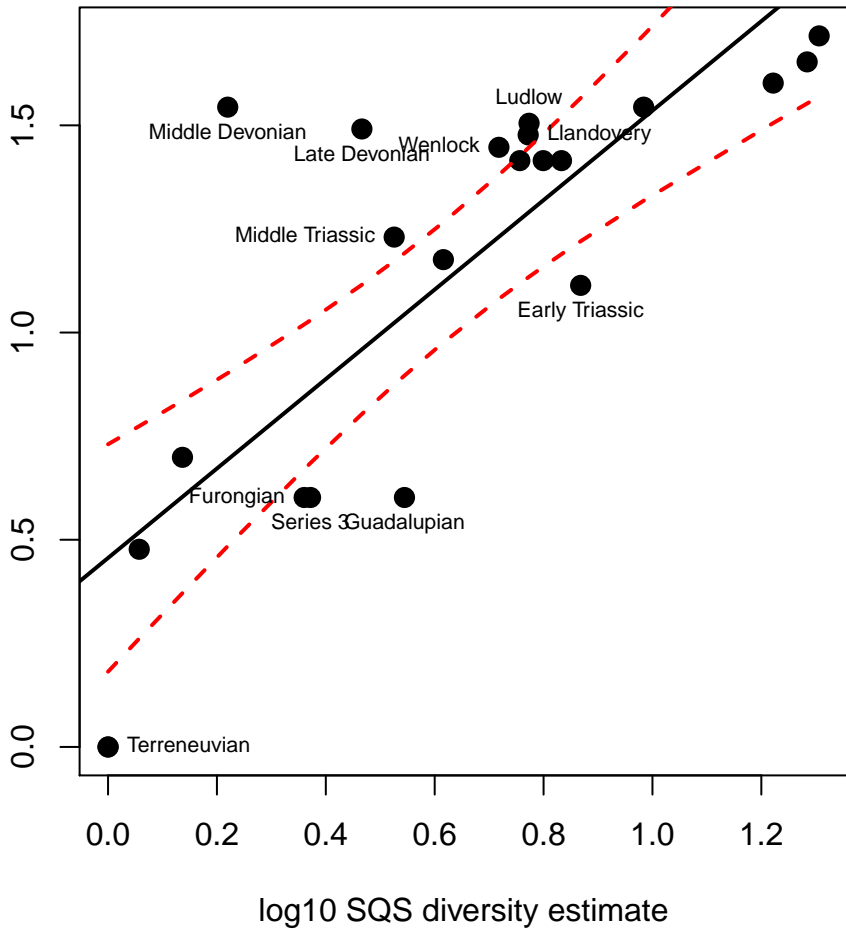703 within a cell)..

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705 **Figure 7.** Left panel. Paleolatitudinal gradients of conodont diversity through the Paleozoic, computed as raw generic
706 counts for each series, binned by 10° of latitude. Each generic diversity point is plotted against the corresponding mid-
707 bin value. The right panel shows the extent of epicontinental seas, computed as the total number of grid cells including
708 coastlines. The figure as a whole follows stratigraphic order in relative terms, but does not represent absolute ages.
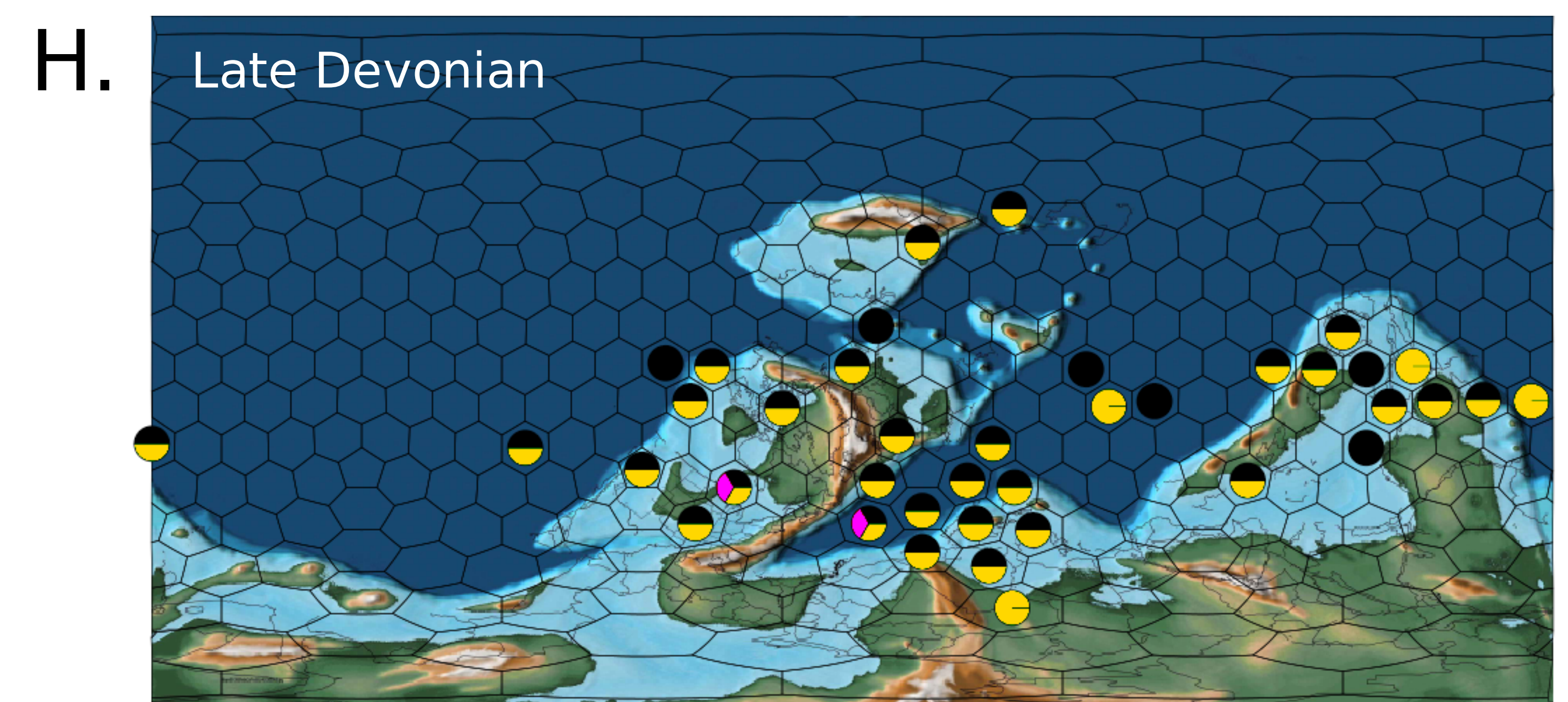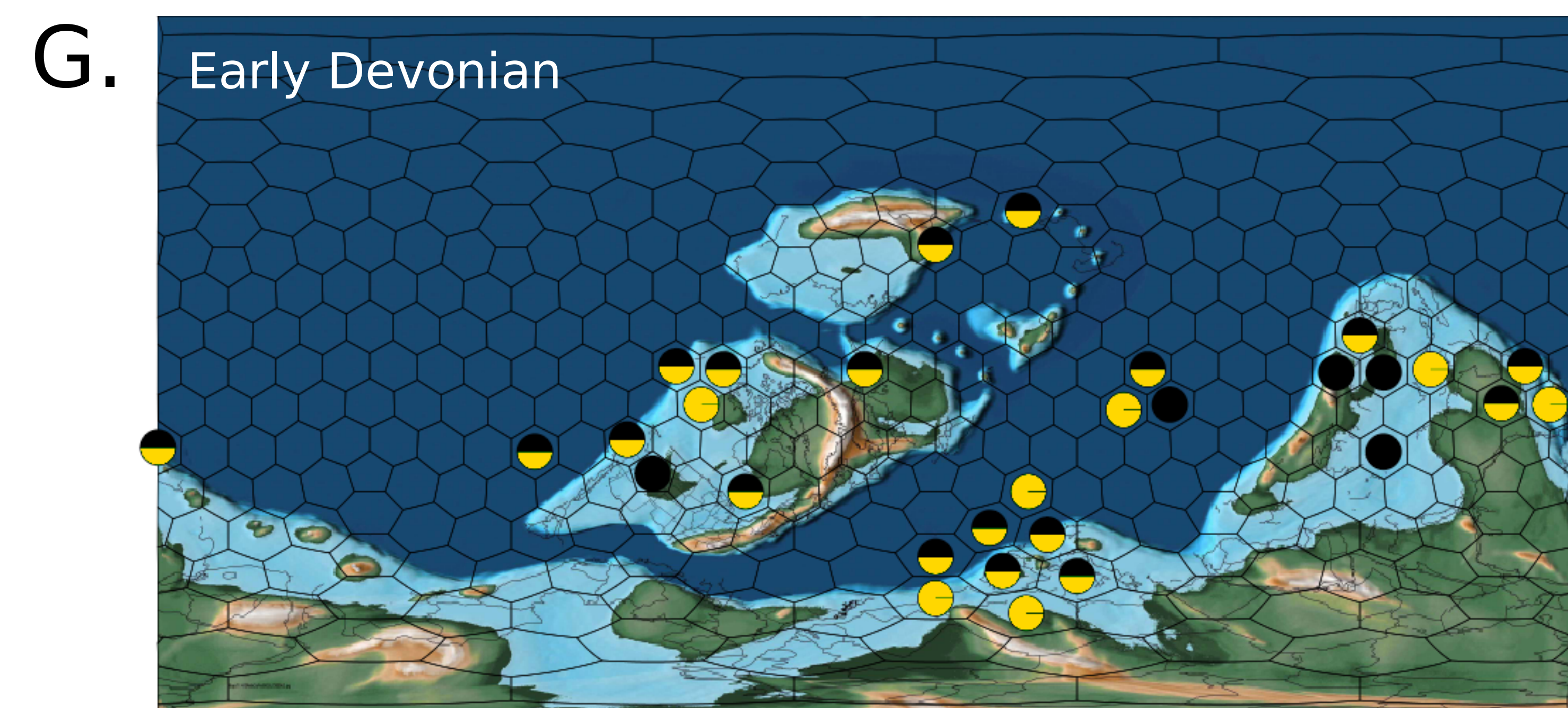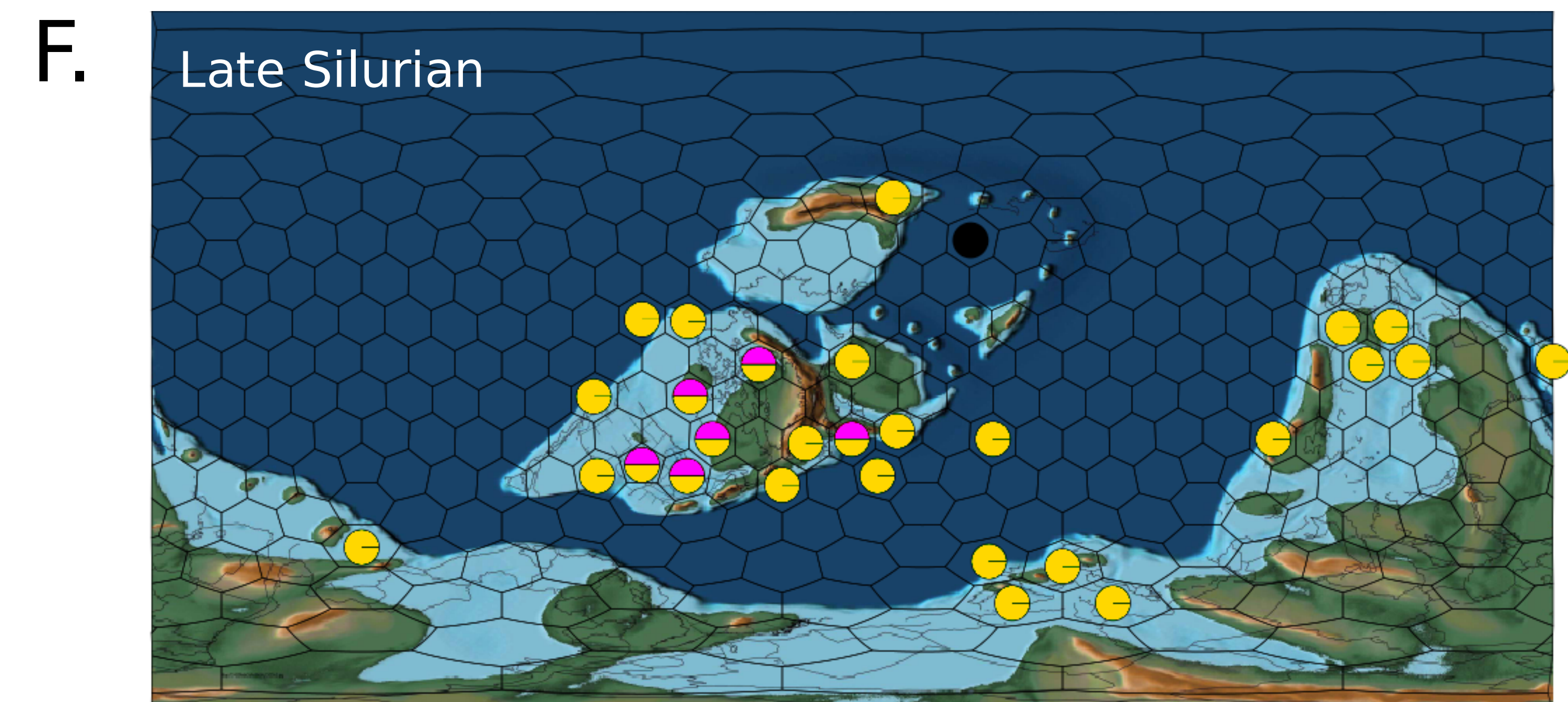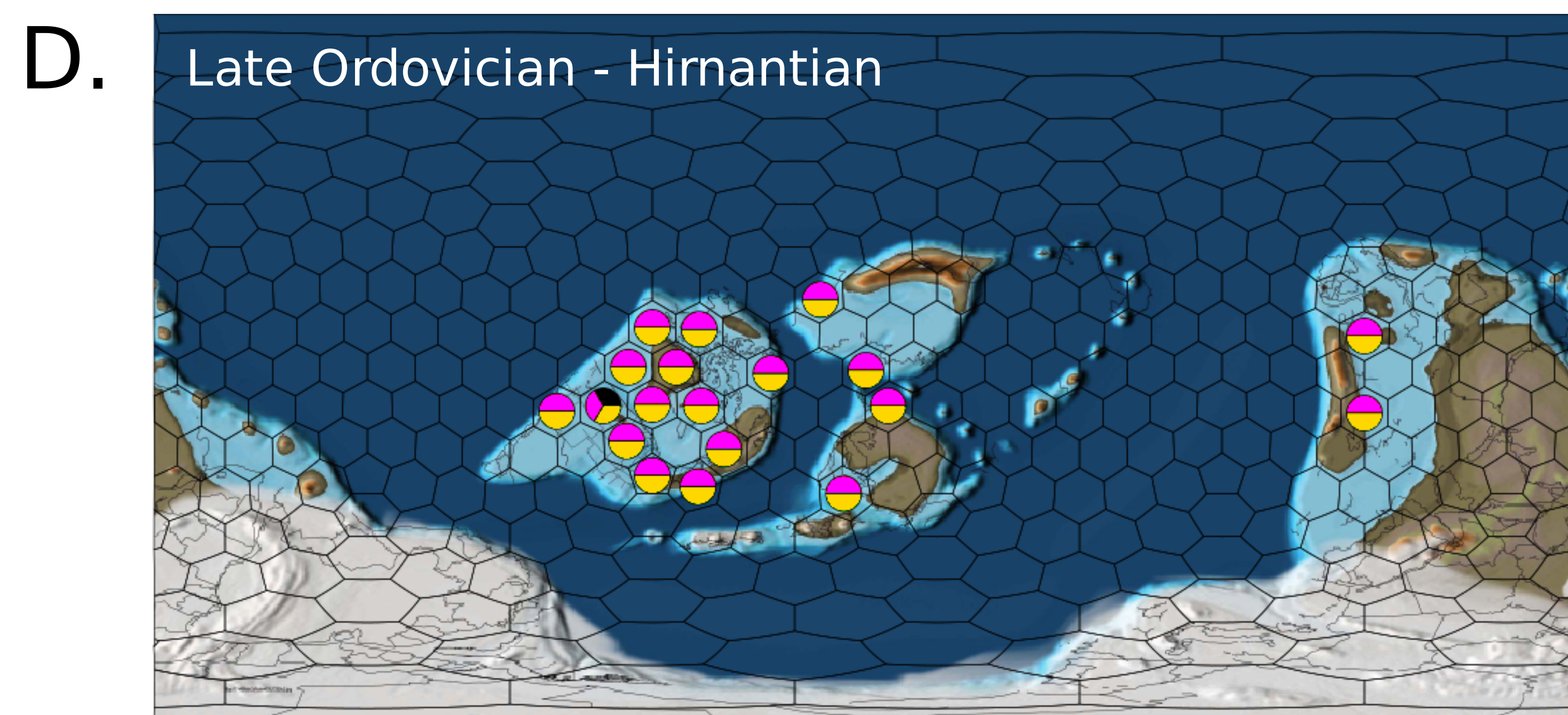
A — Generic diversity over time (Time, Mya) with Early fauna, Intermediate fauna, Late fauna, Total, and SQS estimate.

B — Percent of total generic diversity over time.

C — Phylogenetic tree with taxa labeled by fauna.

Legend:
- Early fauna
- Intermediate fauna
- Late fauna
- Total
- SQS estimate

Time periods: Camb, Ord, Sil, Dev, Carb, Perm, Tri

Taxa (C):
Paracordylodus
Histiodella
Phragmodus
Oepikodus
Baltoniodus
Prioniodus
Pterospathodus
Icriodella
Promissum
Amorphognathus
Sagittodontina
Gamachignathus
Periodon
Microzarkodina
Plectodina
Aphelognathus
Erraticodon
Apatognathus
Parapachycladina
Oulodus
Erismodus
Chirognathus
Hadrodontina
Furnishius
Pachycladina
Ellisonia
Idioprioniodus
Kladognathus
Yaoxianognathus
Ozarkodina excavata
Scaliognathus
Neogondolella
Gondolella
Staurognathus
Doliognathus
Sweetina
Merrillina
Ozarkodina hassi
Kockelella
Ozarkodina confluens
Nicollidina brevis
Nicollidina remscheidensis
Hindeodus
Vogelgnathus
Eognathodus
Sweetognathus
Lochriea
Clydagnathus
Mesotaxis
Palmatolepis
Dinodus
Polygnathus
Mehlina
Pandorinellina
Bispathodus
Idiognathodus
Gnathodus

Early fauna
Intermediate fauna
Late fauna

A. Cambro-Ordovician boundary

B. Early Ordovican

C. Late Ordovician - 'Caradoc'

D. Late Ordovician - Hirnantian

E. Early Silurian

F. Late Silurian

G. Early Devonian

H. Late Devonian
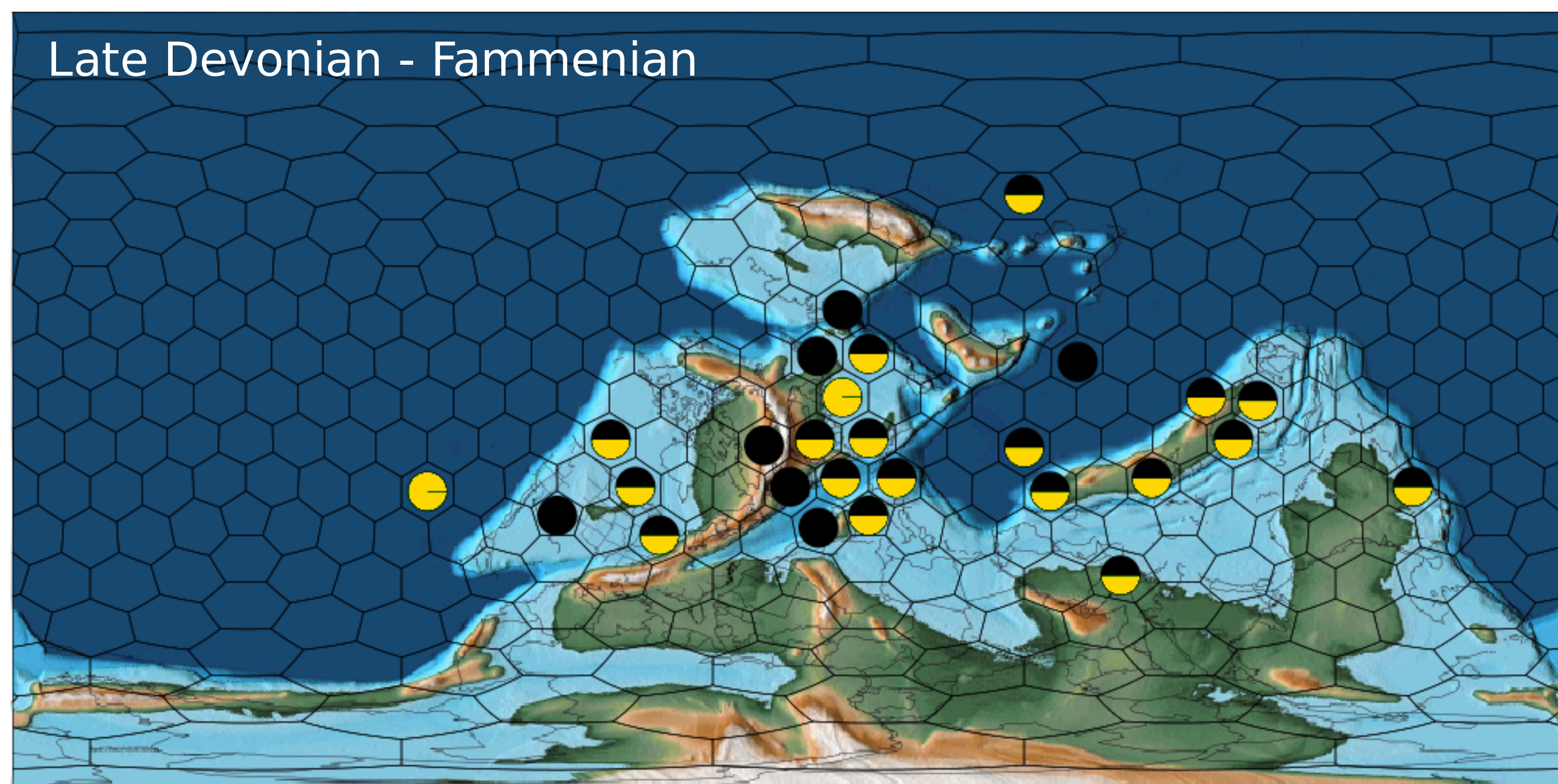
Early Fauna

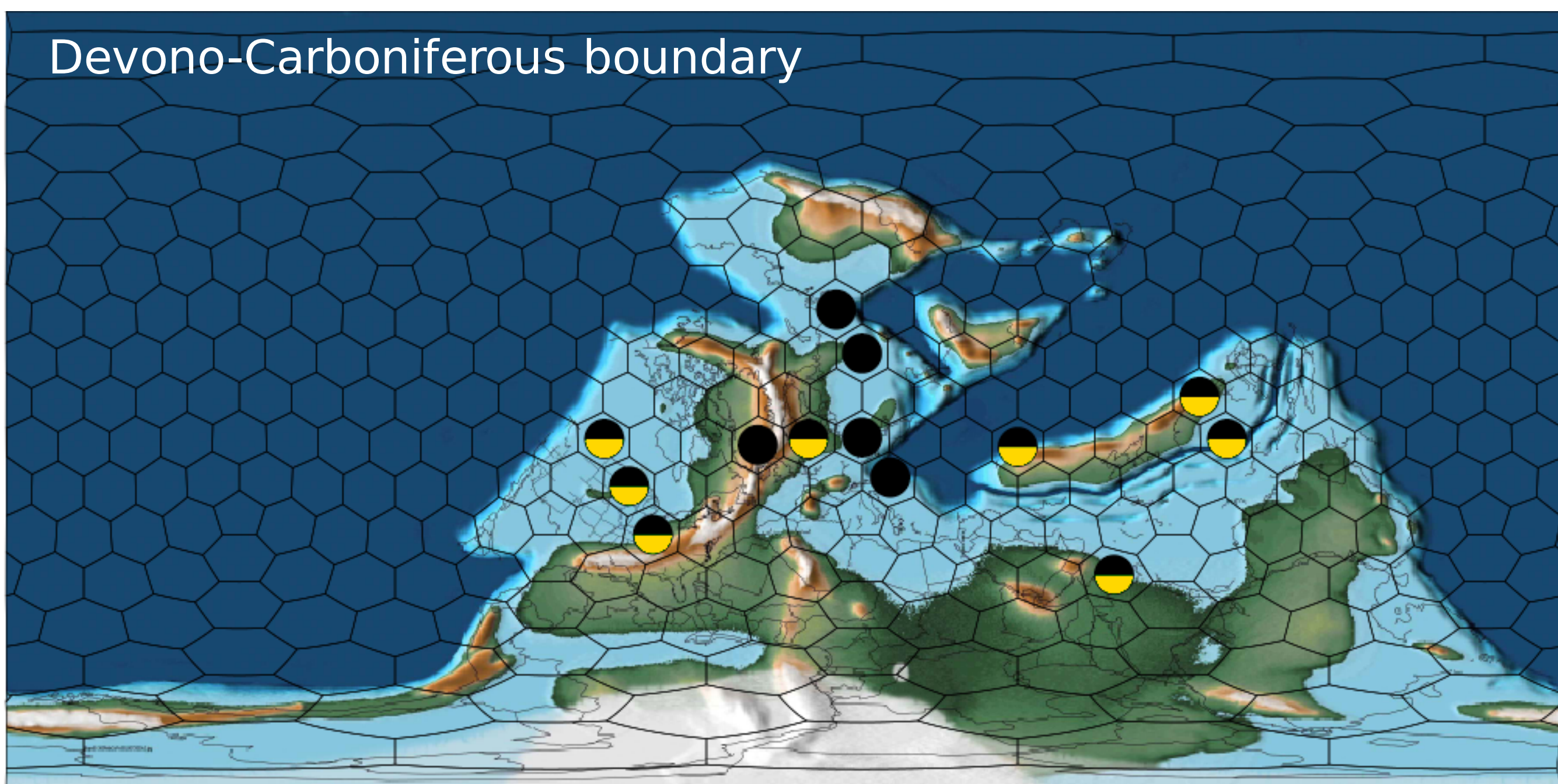Intermediate Fauna

Late Fauna
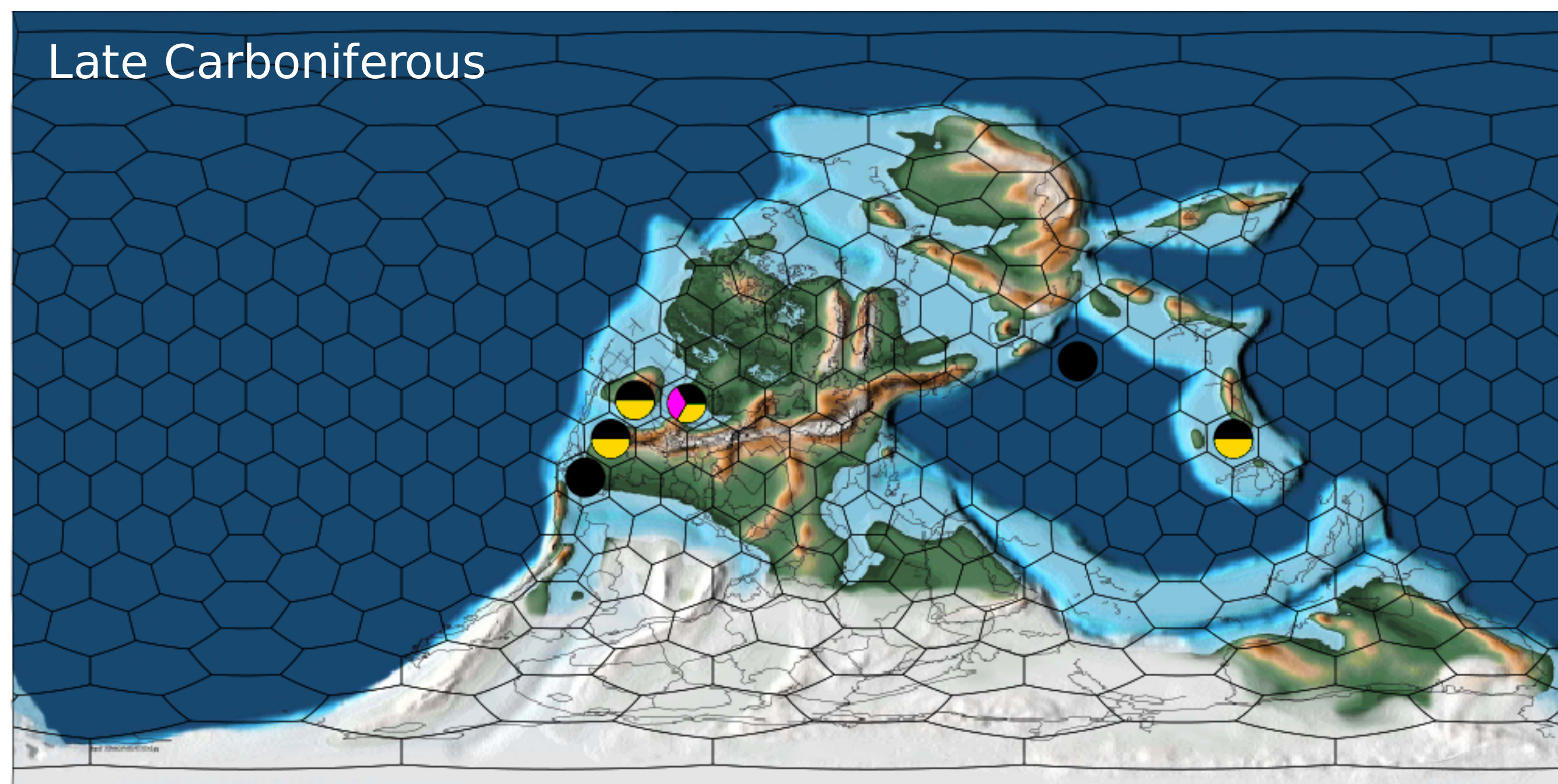
A. Late Devonian - Frasnian
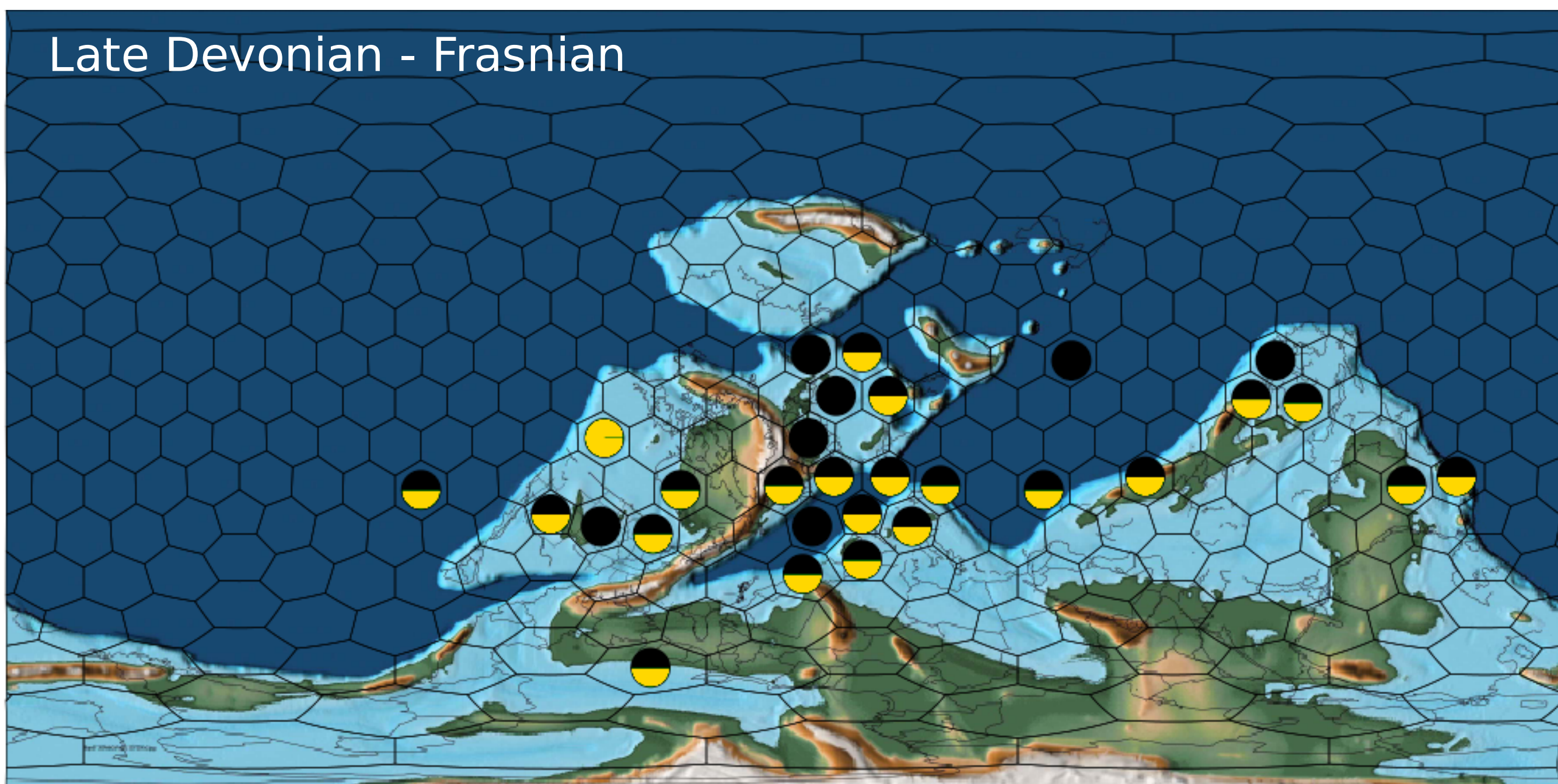
B. Late Devonian - Fammenian
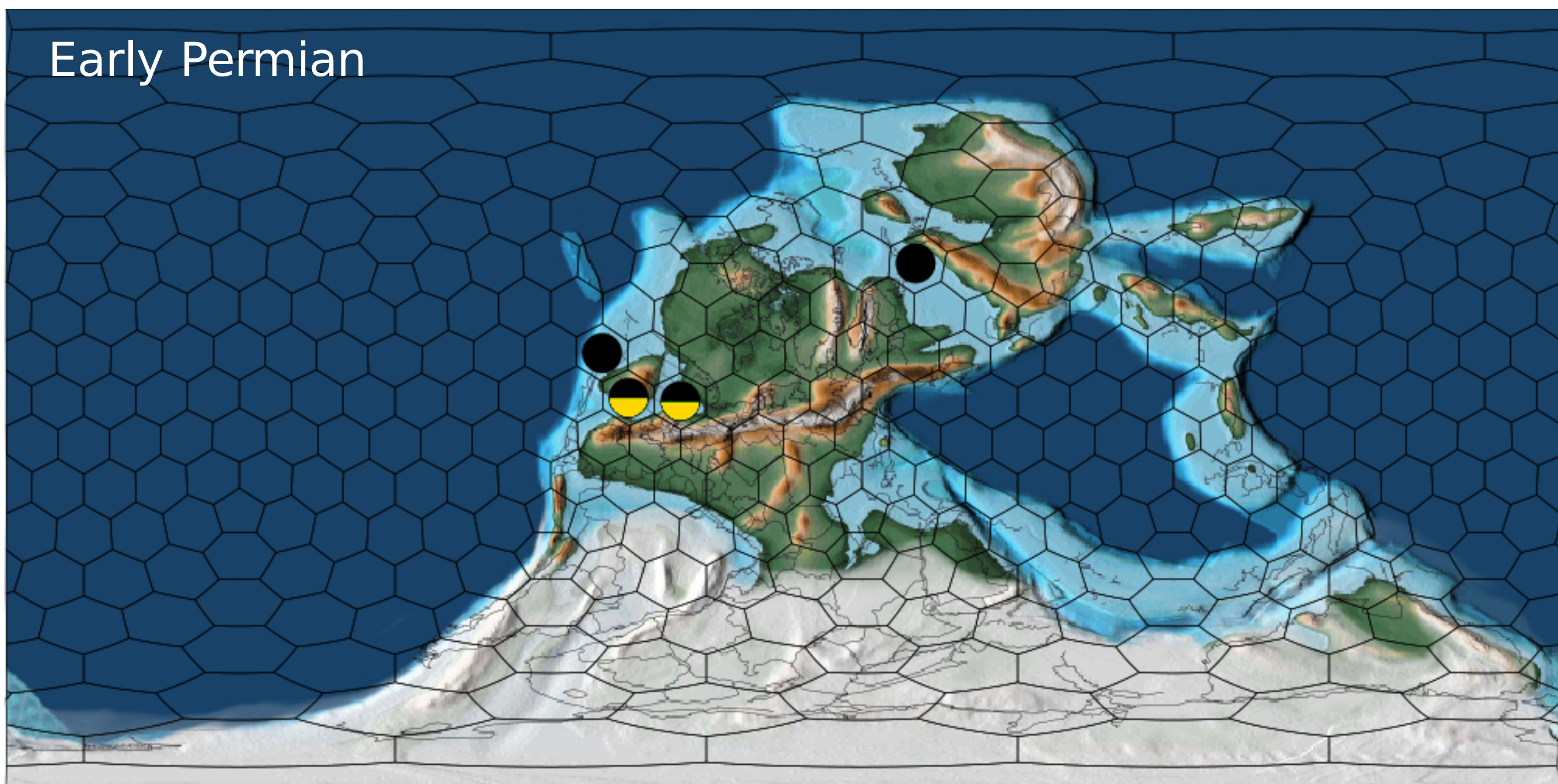
C. Devono-Carboniferous boundary
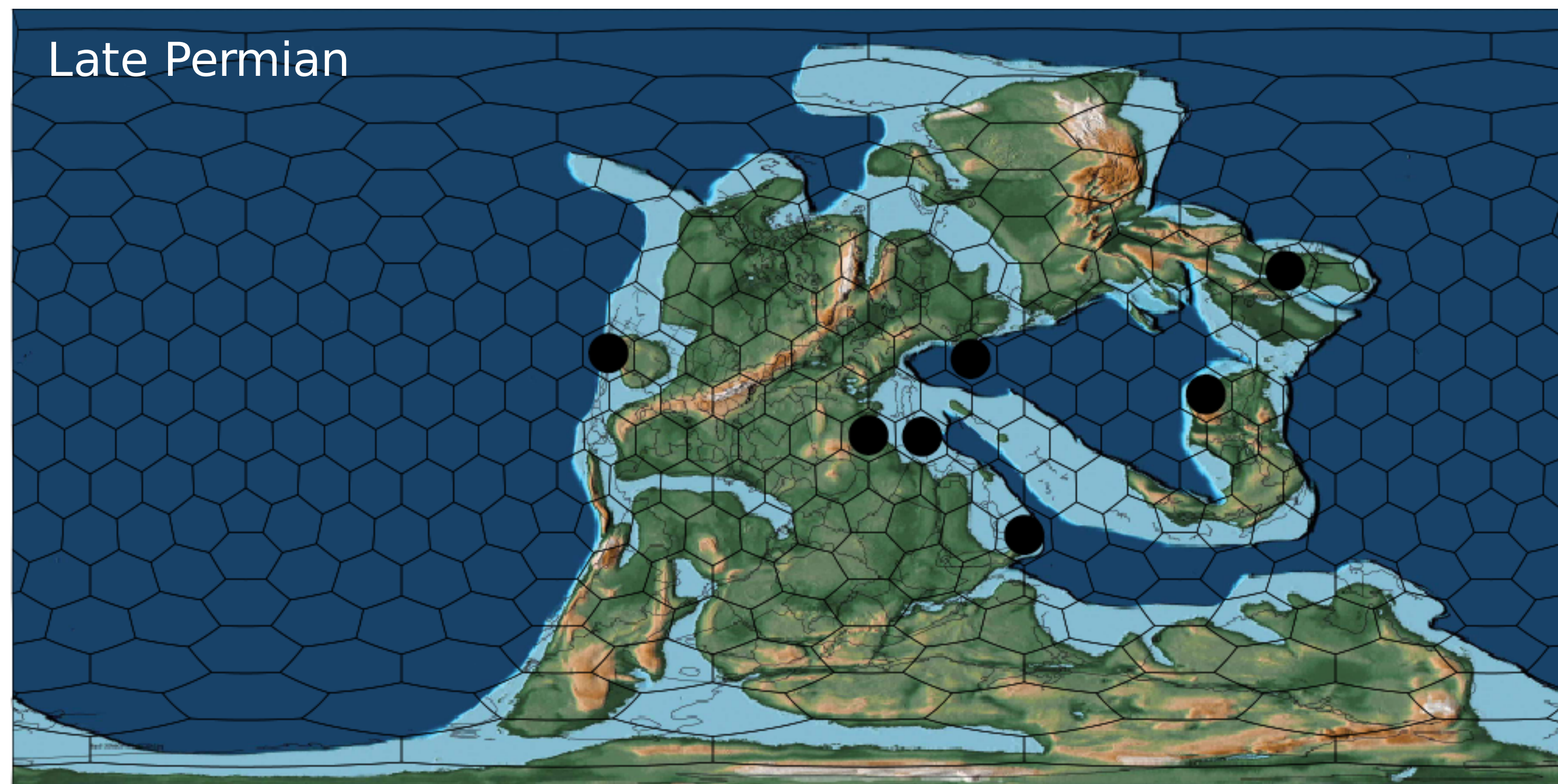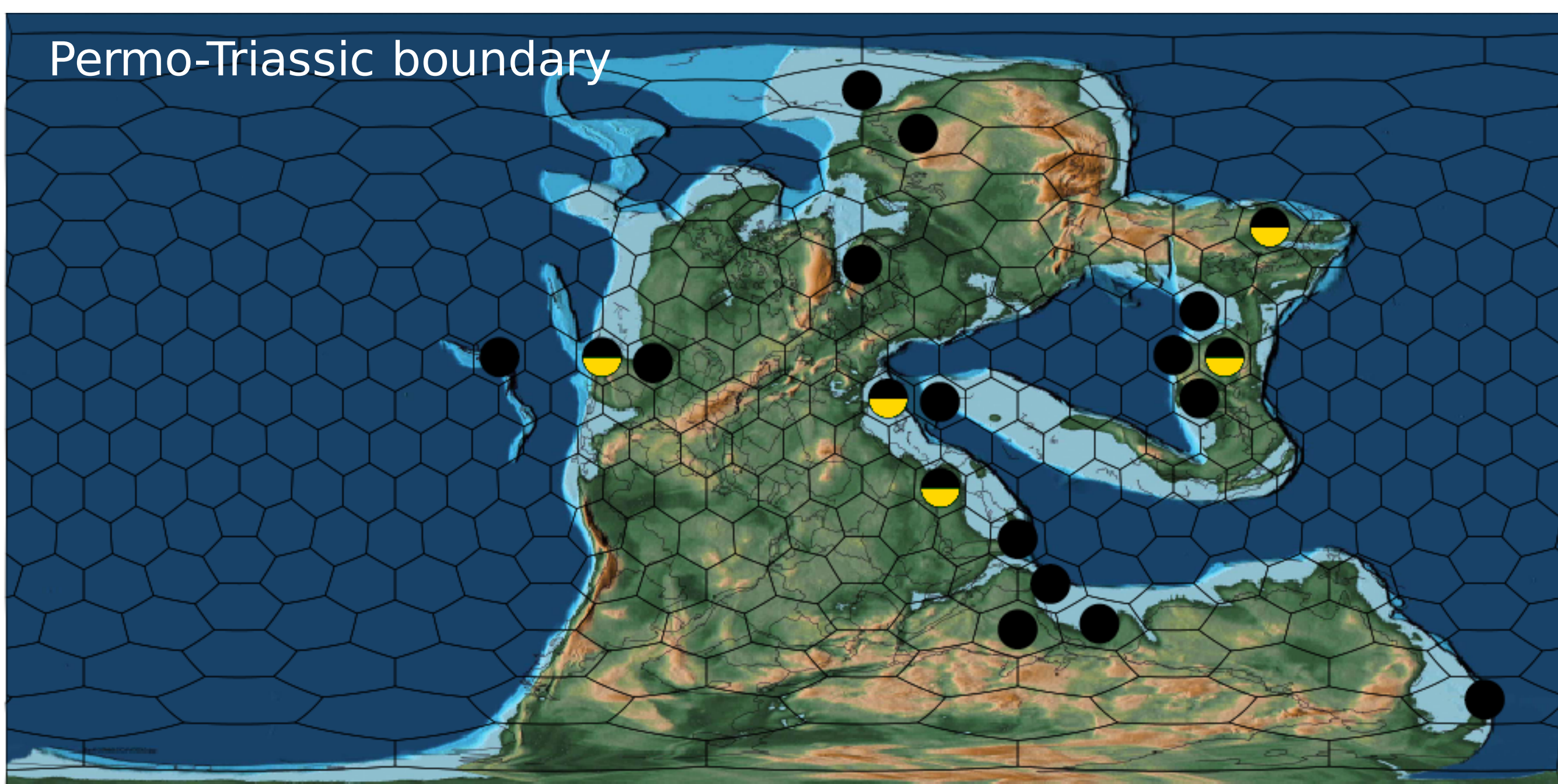
D. Late Carboniferous

E. Early Permian

F. Late Permian

G. Permo-Triassic boundary

H. Middle Triassic

Early Fauna

Intermediate Fauna

Late Fauna

Late Triassic

Middle Triassic

Early Triassic

Lopingian

Guadalupian

Cisuralian

Pennsylvanian

Mississippian

Late Devonian

Middle Devonian

Early Devonian

Pridoli

Ludlow

Wenlock

Llandovery

Late Ordovician

Middle Ordovician

Early Ordovician

Furongian

Series 3

Series 2

Terreneuvian

−50   0   50

Paleolatitude

100   140   180

N° coastal cells