

1                   ELETRONIC SUPPLEMENTARY DATA (ESM)

2  
3                   **Using ghost lineages to identify diversification events in the fossil**  
4                   **record**

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6                   Lionel Cavin<sup>1,2</sup> and Peter L. Forey<sup>1</sup>

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8                   <sup>1</sup> *Department of Palaeontology, The Natural History Museum, London SW7 5BD,*  
9 *England*

10                   <sup>2</sup> *Current address: Department of Geology and Palaeontology, Muséum d'histoire*  
11 *naturelle, CP 6434, 1211, Genève 6, Switzerland; [lionel.cavin@ville-ge.ch](mailto:lionel.cavin@ville-ge.ch). Corresponding*  
12 *author.*

13  
14                   MATERIAL AND METHODS

15  
16                   **Calculation of ghost lineage duration**

17                   Here we define rules to estimate ghost lineage duration across contemporaneous  
18 clades. We use genera here but the method only demands the use of equal ranked  
19 monophyletic clades as terminal taxa (species or families might be used). The ghost  
20 lineage of a clade is attributed to the basal-most member of that clade (taxon a in fig.  
21 ESM1A). When intra-relationships of a clade are not resolved, the ghost lineage is  
22 attributed to the oldest known member of that clade (taxon b in fig. ESM1B). Within a  
23 clade, the determination of ghost lineage ranges shows no difficulties when intra-  
24 relationships are resolved and when the genera have different stratigraphic ranges (fig.  
25 ESM1C). When intra-relationships within a clade are resolved, but the genera have  
26 similar stratigraphic ranges, the successive cladogenetic events do not increase the  
27 ghost extension duration (taxa b and c have no ghost lineage in fig. ESM1D). This is  
28 because a radiation event can be instantaneous at the geological time scale. When  
29 generic intra-relationships are not resolved within a clade but the genera have different  
30 ranges, the ghost lineage extends back to the beginning of the observed stratigraphic  
31 range of the next older taxon (fig. ESM1E). According to this rule, we always choose  
32 the shortest possible range extension among the available solutions. This is because an  
33 unresolved polychotomy is a summation of a number of possible fully resolved trees.

34 We therefore give the fossil record the ‘benefit of the doubt’ by choosing the solution  
35 that is in best accord with the known stratigraphic record.

36 The calculation of the average ghost lineage duration is exemplified in Figure ESM2.  
37 The stratigraphic range (fig. ESM2A) and the phylogenetic relationships (fig. ESM2B) of the  
38 observed genera within two clades are combined together according to the rules described  
39 above (fig. ESM2C). The ghost lineage durations are calculated for each taxon (fig. ESM2C,  
40 figures on the left of each occurrence), and the metrics are compiled for each time interval  
41 (fig. ESM2D).

42 The use of ghost lineages in the calculation of indices assessing the congruence  
43 between phylogeny and stratigraphy is common (Benton 1994; Hitchin and Benton  
44 1997, Wills 1999, Benton *et al.* 2000): but in those instances ghost lineages are used to  
45 assess the overall quality of phylogenetic trees and not to estimate the age of a cohort  
46 within a given time-slice as we do here.

47

## 48 **Case study: The Aptian-Maastrichtian marine actinopterygian diversity**

49

### 50 *Actinopterygian fossil record*

51 The database was built as a compilation from the primary taxonomic literature  
52 and literature related to the dating and palaeoecology of fish assemblages. The datings  
53 of fish occurrences are often coarse-grained, generally straddling a complete, a half or a  
54 third part of a geological stage. Fish diversity is here measured by using the genus as  
55 the standard unit, which we use as a proxy for real biodiversity where fossil species fail  
56 (Sepkoski 1998). This is especially true when we consider the numerous specific names  
57 coined for stratigraphic or geographic variants. We considered worldwide occurrences,  
58 although they are not evenly distributed geographically.

59

### 60 *Actinopterygian phylogeny*

61 We use inferred phylogenetic histories of actinopterygians in order to include  
62 ghost lineages in the computations of diversity and in the calculation of average ghost  
63 lineage duration. This is important in our attempt to distinguish between sampling bias  
64 and real evolutionary change. A phylogenetic tree including all genera occurring from  
65 the Late Jurassic to the Late Cretaceous was constructed. The phylogenetic tree used  
66 here is built up by anchoring available local phylogenies on a backbone phylogenetic  
67 tree of actinopterygians.

68 We are aware that other methods exist. For instance, supertree methods aim to  
69 combine rooted phylogenetic trees by using overlapping leaf sets (Bininda-Emonds &  
70 Bryant 1998). However, published phylogenies of Cretaceous actinopterygian sub-  
71 groups generally deal with taxonomically restricted clades, with little or no taxon  
72 overlap.

73 While the actinopterygian phylogenetic tree is far from resolved, the morphospace  
74 is not evenly occupied and clusters of low-rank monophyletic taxa are easily  
75 recognised. They are generally gathered within systematic ranks, such as orders (e.g.  
76 Pachycormiformes, Pycnodontiformes, Ichthyodectiformes, Tselfatiiformes) or families  
77 (e.g. Aspidorhynchidae, Dercetidae, Enchodontidae).

78 The backbone phylogenetic tree dealing with Late Jurassic – Late Cretaceous ray-  
79 finned clades is built up as follows:

80 The classification of Gardiner (1993) is used for basal actinopterygians,  
81 with the Semionotiformes *sensu* Cavin and Suteethorn (2006): (Cladistia  
82 (“Palaeonisciformes” (Acipenseriformes (Semionotiformes, Macrosemiidae  
83 (Pycnodontiformes, Halecomorpha (Teleostei ))))). The “palaeonisciforms” is an  
84 acknowledged paraphyletic or even polyphyletic assemblage, but its inclusion here  
85 has no influence in the calculation of ghost lineage durations since only a single  
86 representative genus (*Coccolepis*) occurs in the basal Cretaceous, i.e. before the time  
87 interval considered here (Aptian – Maastrichtian). Thus for our purposes *Coccolepis*  
88 = “paleonisciforms”.

89 The phylogeny of Patterson and Rosen (1977), with subsequent additions  
90 from Patterson (1993) is used for basal teleosts: (Pachycormiformes  
91 (Aspidorhynchiformes (Pleuropholidae, Ichthyokentemidae, Pholidophoridae,  
92 Siyuichthyidae, Archaeomaenidae (Ichthyodectiformes (Osteoglossomorpha  
93 (Crossognathidae (Elopomorpha, Euteleostei ))))))). The poor resolution within the  
94 five families constituting the “pholidophoriforms” has little impact on the  
95 computation of ghost lineage durations because only three genera (*Pleuropholis*,  
96 *Pholidophorus* and *Neopholidophorus*) are known in the Aptian. This branching  
97 pattern of lower teleosts is accepted by most authors, although Arratia and Lambert  
98 (1996) questioned the inclusion of pachycormiforms within the teleosts, Taverne  
99 (1989) placed the crossognathids with the pachyrhizodontids (as euteleosts), Filleul  
100 and Lavoué (2001) questioned the monophyly of Elopomorpha and Arratia (1997)  
101 found the relationships (Elopomorpha (Osteoglossomorpha, Euteleostei)). It is not the

102 place here to discuss these different hypotheses. However, it is worth mentioning, that  
103 elopomorphs, osteoglossomorphs and euteleosts occurred first in the Late Jurassic  
104 and their mutual branching pattern has little influence, if any, on the calculation of  
105 ghost lineage duration (see below for a test of this assumption) because, by the time  
106 we reach the Lower Cretaceous, it is the phylogenetic relationships *within* the clades  
107 that is of more concern than between the clades.

108 The phylogeny of Cavin (2001a) is accepted for stem euteleosts:  
109 (Tselfatiiformes (( Protobramoidei, Pachyrhizodontoidei) Clupeocephala)).

110 Lecointre (1995) and Arratia (1997) recognise the otocephala  
111 (Clupeomorpha, Ostariophysii) as basal Clupeocephala, a view with which we  
112 concur.

113 The phylogeny of Johnson and Patterson (1996) is used for basal  
114 euteleosts: ((Argentiniformes, Salmoniformes) (Esociformes, Neoteleostei)).

115 The phylogeny of Miya *et al.* (2003) is accepted for basal Neoteleostei:  
116 (Stomiiformes (Aulopiformes (Acanthomorpha))).

117 The phylogeny of Johnson and Patterson (1993) for Acanthomorpha:  
118 (Lampridiformes (Polymixiiformes (Paracanthopterygii (Stephanoberyciformes  
119 (Zeiformes (Beryciformes (Smegmamorpha, Perciformes)))))).

120 We are aware that alternative phylogenies have been proposed, especially for  
121 relationships within euteleosts. However, we emphasise that the calculation of ghost  
122 lineage duration rests mainly on the length *within* the clades listed above, and not on  
123 the length of ghost lineages *between* these clades. Accordingly, switches between the  
124 branching of the clades within the main framework have little effect on the computation  
125 of average ghost lineage durations through the time intervals considered here. This is  
126 especially true since most of these clades made their appearance contemporaneously -  
127 in the mid-Cretaceous. We acknowledge that, had we been interested in a different time  
128 period – say Late Jurassic to Early Cretaceous – then dispute about relationships  
129 between more inclusive clades may have been an issue.

130 Intra-relationships within the above mentioned clades are recognised by using 1)  
131 hierarchical classifications for the Macrosemiidae (Bartram 1977), extinct  
132 Aulopiformes (Goody 1969), 2) on ‘hand-made’ cladograms for the Tselfatiiformes  
133 (Taverne & Gayet 2005), extinct Siluriformes (Gayet & Meunier 2003), extinct  
134 Characiformes (Gayet *et al.* 2003) and on 3) computer-based cladograms for the  
135 Acipenseriformes (Grande *et al.* 2002), Pycnodontiformes (Poyato-Ariza & Wenz

136 (2002), Amiiformes (Grande & Bemis 1998), Aspidorhynchiformes (Brito 1997),  
137 Ichthyodectiformes (Cavin & Forey, submitted.), Osteoglossomorpha (Hilton 2003),  
138 Elopomorpha (Forey *et al.* 1996), fossil Clupeomorpha (Chang & Maisey 2003),  
139 Gonorynchiformes (Grande & Poyato-Ariza 1995) and Tetraodontiformes (Santini &  
140 Tyler 2003). Interrelationships among genera of some Cretaceous clades are still  
141 unresolved (e.g. Cladistia, Ionoscopiformes, extinct Salmoniformes, extinct  
142 Beryciformes) and are treated here as polytomies.

143 All of the phylogenies used above are based on morphological characters; some of  
144 them deal with modern representatives and also include molecular data. No  
145 stratocladistic-based results are used here, which is an important point as phylogenetic  
146 patterns are included into the calculation of the gaps in the fossil record. Thus, the  
147 inclusion of stratocladistic-based results would introduce circular reasoning in the  
148 method. The complete composite cladogram is shown in supplementary data from  
149 Cavin *et al.* (2006). In order to compare how a different phylogeny can affect the  
150 computation of the metrics, we used an alternative phylogeny. In this alternative  
151 phylogeny, we reversed the respective branching pattern of elopomorphs and  
152 osteoglossomorphs (Arratia 1997), regarded crossognathids and pachyrhizodontids as a  
153 monophyletic group of basal euteleosts (Taverne 1989), regarded otocephala (old view)  
154 and the elopomorpha (Filleul & Lavoué 2001) as paraphyletic groups and applied the  
155 intra-relationships of ichthyodectiforms from Taverne and Chanet (2002).

156

### 157 ***Analysis of fish diversity***

158 The stratigraphic ranges of fish genera and their phylogenetic relationships were  
159 documented in an Excel spreadsheet using “spelling” rules to distinguish the types of  
160 occurrences (marine or freshwater, observed, Lazarus or ghost, cladogenetic events).  
161 The calculations (standing diversity, average ghost lineage duration, rate of  
162 cladogenetic events) were computed with the Excel functions.

163 We plotted the marine fish diversity for 16 approximately equal absolute time  
164 intervals ranging from the Aptian to the Maastrichtian (early/late Aptian,  
165 early/middle/late Albian, early/late Cenomanian, Turonian, Coniacian, early/late  
166 Santonian, early/middle/late Campanian, early/late Maastrichtian) corresponding each  
167 to 3 Myrs in average duration. This duration is shorter than the average duration of the  
168 ghost lineages (see results below). We calculated four different diversity metrics. The  
169 first one is the standing diversity, which corresponds to the number of observed

170 occurrences of marine genera in each time interval. The second metric is the Lazarus  
171 diversity [a Lazarus taxon is without fossil record in a particular time interval but  
172 predicted to be present because its first and last occurrences straddle that time interval  
173 (Flessa & Jablonski 1983)]. The third metric is the Ghost lineages diversity as defined  
174 above. The fourth metric, called here the total diversity, is the sum of the standing  
175 diversity, Lazarus diversity and ghost lineage diversity. Computer simulations  
176 assessing the impact of ghost lineages in estimating paleodiversities showed that  
177 inclusion of ghost taxa in computations reflects better the palaeodiversity than taxic  
178 estimates (Lane *et al.* 2005), if some conditions are respected (namely the presence of  
179 extant representatives, absence of mass extinction, no ancestral species misdiagnosed as  
180 sister species). These conditions are applicable in the present case study, except  
181 possibly for the last part of the time interval under study that just precedes the  
182 Cretaceous – Tertiary boundary and that was marked by a selective extinction for ray-  
183 finned fishes (Cavin 2001b).

184 We also computed the number of cladogenetic events. A cladogenetic event is  
185 placed before the beginning of the observed range of the oldest occurrence of sister-pair  
186 clades (white circles in figs ESM1A, C, D) or just before the beginning of the observed  
187 stratigraphic range of the next older taxon within the clade when intra-relationships are  
188 not resolved (Figs ESM1B, E).

189

190

## 191 RESULTS

192

193 Figure ESM3 shows the variation of the total diversity, the number of  
194 cladogenetic events and the average ghost lineage duration based on the phylogeny  
195 used in Fig 2b and on the alternative composite phylogeny. Both phylogenies provide  
196 very similar curves: except minor changes in the total diversity and the number of  
197 cladogenetic events in the late Early Cretaceous, the only significant difference is  
198 observed in the average ghost lineage duration. But this difference does not affect the  
199 general shape of the curve; in particular the drop observed from the late Albian to the  
200 Cenomanian in association with the rise in marine fish diversity remains.

201

202

## 203 DISCUSSION

204

205 Today, the current status of the reconstruction Cretaceous actinopterygian  
206 phylogeny may be characterized by three features: 1) the recognition of clades is well  
207 established but 2) the intra-relationships within some of these clades and 3) the  
208 branching pattern between them is far from being resolved. We suspect that the main  
209 changes that could affect our computation in the near future will depend on better  
210 resolution of the intra-relationships of already-recognised clades, such as ionoscopids,  
211 pachycormiforms, “pholidophoriforms”, “salmoniforms”, aulopiforms and basal  
212 acanthopterygians.

213 One main weakness of the methodological tool introduced here rests on the way we  
214 constructed the composite phylogeny before calculating the various metrics. Because the  
215 cladogram is not based on a single data set, or on a reproducible method of supertree  
216 reconstruction, one can question the validity of its support. However, we mentioned above  
217 that an alternative phylogeny produced very similar curves (fig. ESM3). Although several  
218 parts of the actinopterygian phylogeny remain to be resolved, we suggest that the similarity  
219 between curves results from stability of the theories of relationships among members of the  
220 separate Cretaceous clades.

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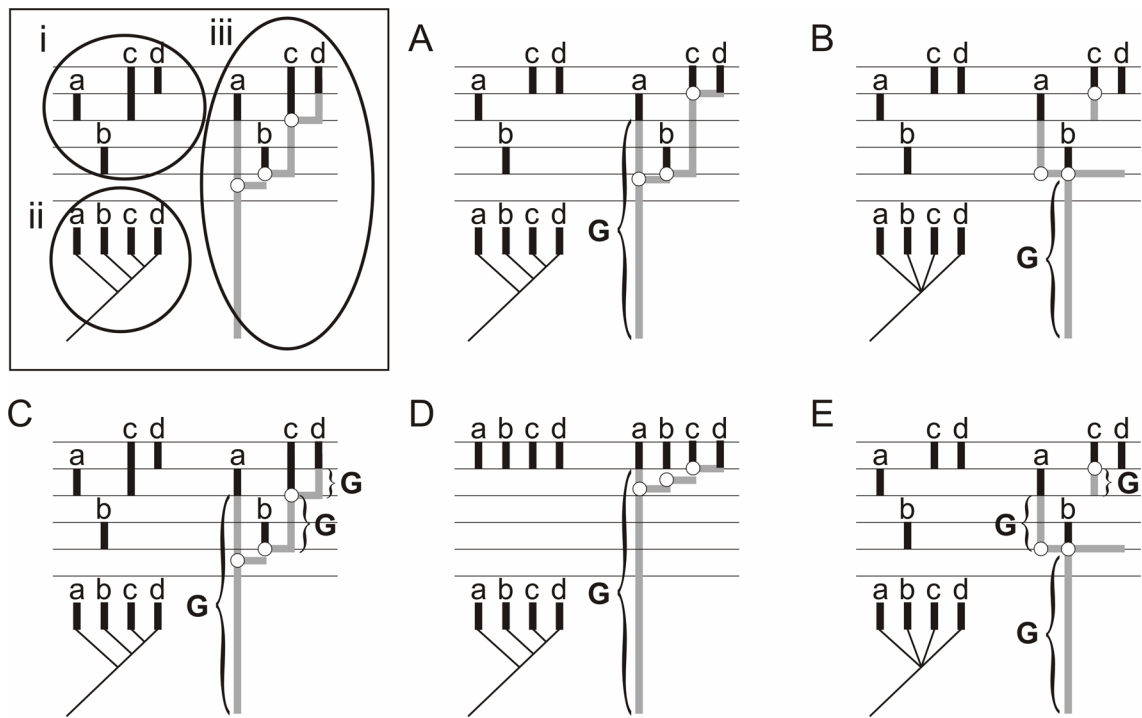
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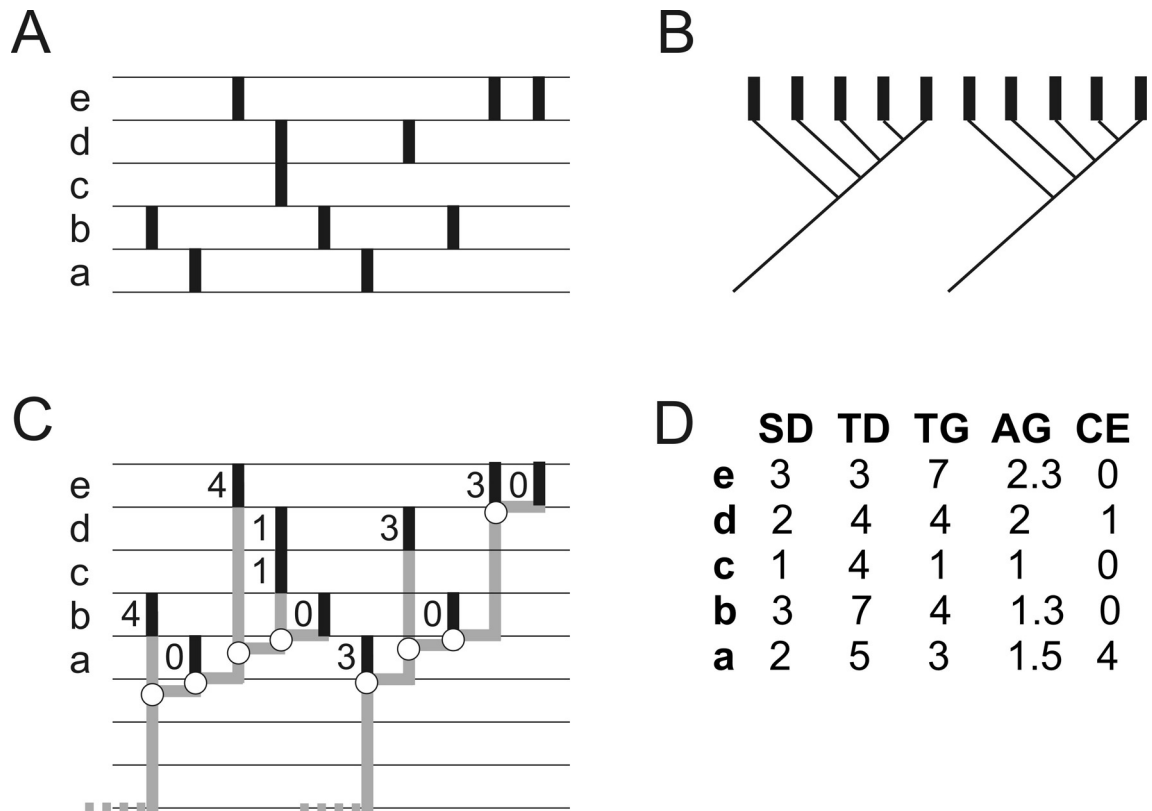
Figure ESM1

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Rules applied to the determination of ghost lineage duration. Framed chart indicates the content in the other charts (A-E) with: i, actual stratigraphical records of taxa a, b, c and d. ii, phylogenetic relationships of the taxa a, b, c and d. iii, determination of the ghost lineages (grey line) according to i and ii. White circles represent cladogenetic events. A, the ghost lineage of a clade is attributed the basal-most member of that clade. B, the ghost lineage of a clade is attributed to the oldest known member of a clade when the intra-relationships are not resolved. C, the ghost lineages within a clade when intra-relationships are resolved and the genera have different stratigraphic ranges. D, Same situation as in C, but all genera have a similar stratigraphic range. Here taxa b and c have no ghost lineage because a radiation event can be instantaneous at the geological time scale. E, the ghost lineages within a clade when intra-relationships are not resolved. Ghost lineage extends backwards to the beginning of the observed stratigraphic range of the next older taxon. The long ghost lineage shown at the base of each clade is calibrated on the basis of the sister clades and is the same for all situations here.

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349



350

351 Figure ESM2

352 Schematic example of the process used to calculate parameters discussed in this paper.

353 A, range extensions of 10 genera in time slices a to e. B, phylogenetic relationships of the 10

354 genera (they belong to two distant clades in this example). C, determination of the ghost

355 lineage durations according to the rules described in figure ESM1, with the value of the

356 duration for each genus [in number of time slice]. The age of each of the two major clades is

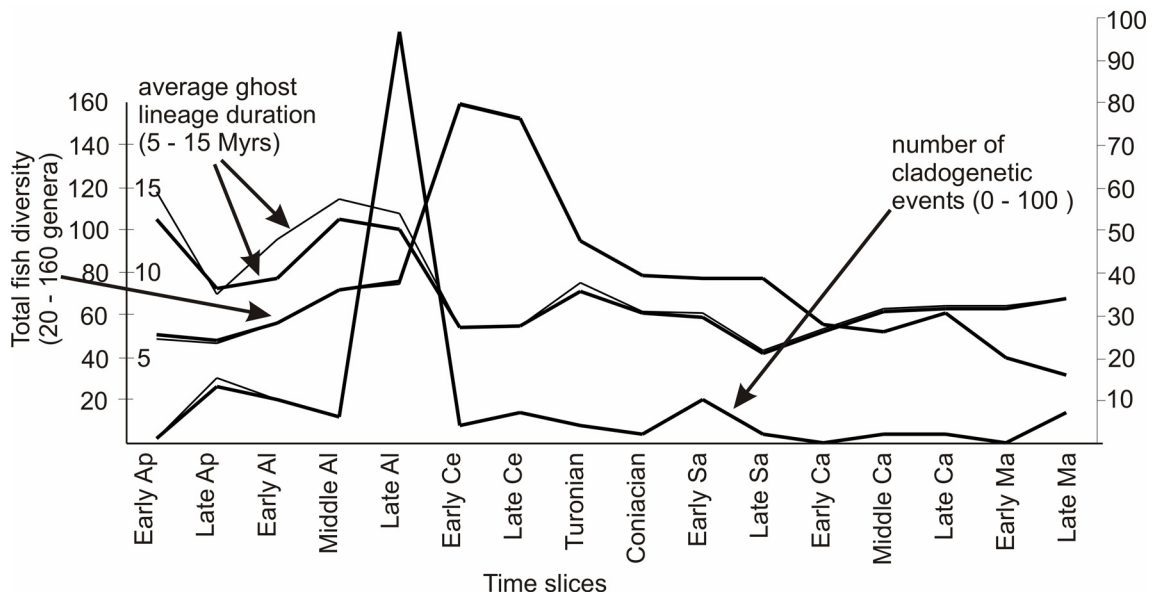
357 projected back through three time slices. D, metrics for time slices a to e with SD: standard

358 diversity (observed occurrences); TD, total diversity (observed plus ghost occurrences); TG,

359 total ghost lineage duration (sum of the values in C); AG, average ghost lineage duration

360 (TG/SD); CE, number of cladogenetic events (white circles).

361



362

363 Figure ESM3

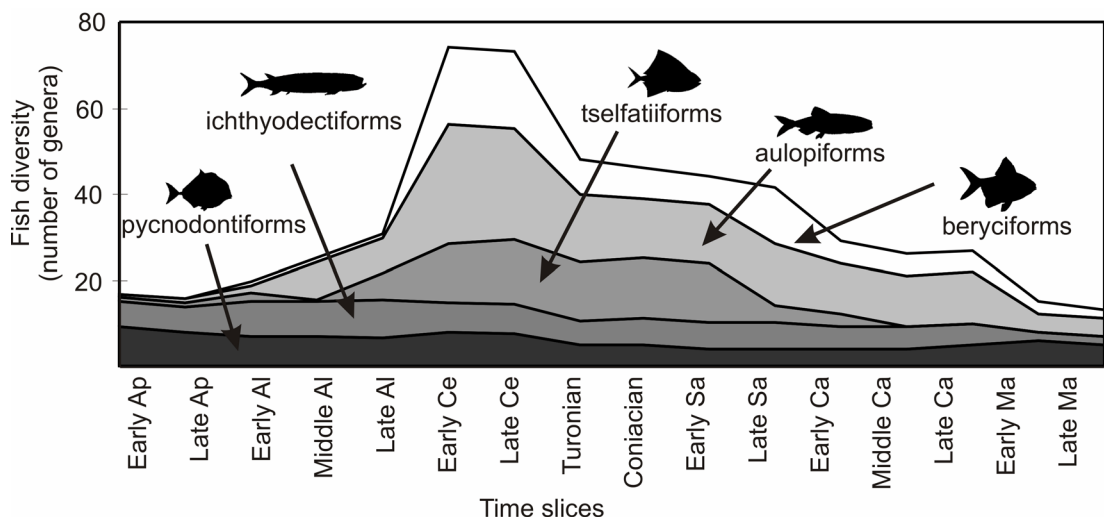
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364 Some metrics as in Fig. 2b (thin curves) and metrics computed with an alternative  
 365 phylogeny (thick curves). See text for the changes in phylogenies.

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368 Figure ESM4

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369 Chart of the cumulative total numbers of genera (observed, Lazarus and ghost) from five  
 370 Cretaceous actinopterygian orders. Note the almost constant numbers of genera of  
 371 pycnodontiforms and ichthyodectiforms, while the tselfatiiforms, aulopiforms and  
 372 beryciforms thrived in the Late Albian – Cenomanian.

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