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Growth rate, extinction and survival amongst late Cenozoic

bivalves of the North Atlantic

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ABSTRACT

Late Cenozoic bivalve extinction in the North Atlantic and adjacent areas has been attributed

to environmental change (declines in temperature and primary production). Within scallops

and oysters—bivalve groups with a high growth rate—certain taxa which grew exceptionally

fast became extinct, while others which grew slower survived. The taxa which grew

exceptionally fast would have obtained protection from predators thereby, so their extinction

may have been due to the detrimental effect of environmental change on growth rate and

ability to avoid predation, rather than environmental change *per se*. We investigated some

glycymeridid and carditid bivalves—groups with a much lower growth rate than scallops and

oysters—to see whether extinct forms from the late Cenozoic of the North Atlantic grew

faster than extant forms, and hence whether their extinction may also have been mediated by

increased mortality due to predation. Growth rate was determined from the cumulative width

of annual increments in the hinge area; measurements were scaled up to overall shell size for the purposes of comparison with data from living species. Growth of the extinct glycymeridid *Glycymeris subovata* was at about the same rate as the slowest-growing living glycymeridid and much slower than in late Cenozoic samples of extant *G. americana*, in which growth was at about the same rate as the fastest-growing living glycymeridid. Growth of extinct *G. obovata* was also slower than *G. americana*, and that of the extinct carditid *Cardites squamulosa ampla* similarly slow (evidently slower than in the one living carditid species for which data are available). These findings indicate that within bivalve groups whose growth is much slower than scallops and oysters, extinction or survival of taxa through the late Cenozoic was not influenced by whether they were relatively fast or slow growers. By implication, environmental change acted directly to cause extinctions in slow-growing groups, rather than by increasing susceptibility to predation.

KEYWORDS: Growth rate, extinction, *Glycymeris*, *Cardites*, late Cenozoic, North Atlantic

Introduction

According to Stanley (1986), of the 361 marine bivalve mollusc species present in the Pliocene of the US Atlantic and Gulf Coastal Plain, 78% have become extinct. This percentage is far higher than for Pliocene marine bivalve species of California and Japan, where it is assumed that extinction was at a background rate, and equates to some 65% 'excess' extinction in the area, sufficient for recognition of a regional mass extinction event in the western North Atlantic Ocean. In the eastern North Atlantic (including Mediterranean Sea) a total of 45% of Pliocene marine bivalve species have become extinct (Raffi et al. 1985), a figure not much above the background rate. Temperature decline (the onset of the

Pleistocene ice age) has been invoked as the cause of late Cenozoic extinctions on both sides

of the Atlantic (Raffi et al. 1985; Stanley 1986) but extinctions in the western Atlantic have

been ascribed alternatively to a decline in primary production from high levels in the

Miocene and Pliocene (e.g. Allmon 2001). A problem with both these explanations is that in

at least some cases extinction took place long after the inception of pronounced

glacial/interglacial cyclicity (e.g. Ward et al. 1991), and also well after primary production

had fallen along much of the US eastern seaboard (Johnson et al. 2019).

A lag between production decline and extinction has also been noted for late Cenozoic

marine invertebrates of the Caribbean (O'Dea et al. 2007; O'Dea and Jackson 2009).

Amongst bryozoans, those species destined to become extinct suffered an immediate

reduction in abundance on production decline, suggesting that the lag represents no more than

the time required to extirpate the last individuals (O'Dea and Jackson 2009). A second

possibility is that it reflects the existence of refugia provided by local upwelling systems

(Leigh et al. 2014). A third, applicable in principle to bivalves of the US eastern seaboard

(Thomas 1976; Dietl et al. 2004), is that it reflects coincident changes in the nature of

gastropod predation. While a recent study (Sime and Kelley 2016) failed to confirm an initial

report (Kelley and Dietl 2011) of a late Cenozoic decline in the abundance of gastropod

predators in this area, predation should not be ruled out as an influence on the timing of

extinction given its enormous role in bivalve mortality, including through agents whose

abundance may be poorly reflected in the fossil record (e.g. Myers et al. 2007).

The scallop genus *Placopecten*, common in the early Pliocene of the US Atlantic Coastal

Plain, has persisted to the present-day. From its restriction to relatively cool-water Pliocene

deposits (Ward et al. 1991; Johnson et al. 2017) and modern range from the Gulf of St

Lawrence, Canada, only as far south as Cape Hatteras in the US (Naidu 1991), it clearly had,

and still has, a preference for low temperatures. This seems to provide a reason for its

76 survival of the intensely cold conditions of the Pleistocene and suggests as a corollary that

77 these might have caused the extinction of two other scallop genera, *Carolinapecten* and

78 *Chesapecten*, which are unusually large forms occurring in warmer-water Pliocene deposits

79 (Ward et al. 1991; Johnson et al. 2017, 2019). Unlike *Placopecten*, which has a minimally

80 ornamented shell, *Chesapecten* and *Carolinapecten* exhibit strong radial plication, indicative

81 of a predominant 'siege' (resistance) strategy towards predators (Johnson et al. 2019). At

82 least some representatives of *Chesapecten* and *Carolinapecten* grew at a much faster rate

83 than Pliocene and modern *Placopecten* (Goewert and Surge 2008; Johnson et al. 2017, 2019),

84 no doubt in part because of favourable environmental conditions (high temperature and/or

85 production) but also because of the benefit (early achievement of large size) to a siege

86 strategy. By virtue of its relatively streamlined shape, together with other adaptations (Gould

87 1971), *Placopecten* is able to escape predators by 'flight' (swimming) to a size greater than in

88 plicate scallops (Johnson et al. 2019). Rapid growth would curtail the time over which this

89 strategy is available and so would probably be of no benefit to this genus even if permitted by

90 environmental conditions. The survival of *Placopecten* from the Pliocene to present might

91 not therefore be due to its supposed ability to tolerate the intervening cold conditions but

92 because declines in both temperature and production, and their detrimental effects on growth,

93 were of no consequence for its ability to avoid predation. By contrast, *Chesapecten* and

94 *Carolinapecten*, with their use of a strategy benefitted by rapid growth, might have suffered

95 higher predation. This would probably not have caused the demise of the last individuals

96 ('final' extinction) because by their very rarity the rate of loss to predators would have been

97 reduced. However, higher predation might have caused population sizes to decline to a level

98 insufficient for long-term survival, given the likelihood of density-independent mortality

99 events. Infrequent occurrence of such events would be worth considering as an explanation

100 for the lag noted between environmental change and extinction, but our concern here is to

101 investigate how environmental change was involved in extinction: whether it acted directly

102 or, as suggested above, through its effect on growth potential and ability to avoid predation.

103   Kirby and Jackson (2004) have demonstrated that the large, extinct Miocene and

104 Pliocene oyster *Crassostrea cahobasensis* from the Caribbean area grew much faster than

105 Pliocene–Holocene congeners (*C. virginica*, *C.* aff. *virginica*, *C. columbiensis*) from the same

106 region. These latter forms occupied marginal-marine settings, in which they would have

107 suffered relatively little attention from marine predators, whereas *C. cahobasensis* was fully

108 marine. As immobile bivalves, oysters only have the option of resistance if attacked by

109 predators, so the rapid growth of *C. cahobasensis* can be viewed as a response to the high

110 likelihood of this in the marine environment. Correspondingly, its extinction can be seen as a

111 consequence of late Cenozoic environmental changes in the Caribbean area, which, as in the

112 adjacent western North Atlantic, included a fall in primary production that might have

113 prevented rapid growth (Kirby and Jackson 2004). Indications therefore exist from two

114 bivalve groups that environmental change acted to cause extinction through its effect on

115 growth potential and ability to avoid predation. However, these groups constitute only a small

116 proportion of the late Cenozoic bivalve fauna of the western North Atlantic and Caribbean

117 area (where also many taxa became extinct; Jackson et al. 1993; Jackson and Johnson 2000;

118 Smith and Jackson 2009). Moreover, by the standards of bivalves as a whole, all scallops and

119 oysters are fast-growing (typically tens of millimetres per annum in early ontogeny) so the

120 now-extinct exceptionally fast-growers within these groups might have been nearer the limits

121 of what could be sustained by the environment than the fastest growers in other marine

122 groups. The growth rate and ability to withstand predation of the latter might not therefore

123 have been impacted by environmental deterioration. We decided to investigate this possibility

124 (and hence the generality of the rapid growth/extinction relationship amongst marine

125 bivalves) by a study of late Cenozoic glycymeridids, a group exhibiting slower growth than

scallops and oysters (typically a few millimetres per annum in early ontogeny) but in which

large size can be achieved through greater longevity (e.g. Bušelić et al. 2015). Glycymeridids

are infaunal (living at a shallow depth within seafloor sediment; Thomas 1975) but, like

epifaunal scallops and oysters, subject to predation (e.g. Sime and Kelley 2016). Amongst

glycymeridids (principally *Glycymeris americana*; Fig. 1A) in the late Cenozoic of the US

Atlantic Coastal Plain, the frequency of drill holes produced by predatory gastropods is lower

in large individuals (B. Kelly, pers. comm. 2019), indicating the existence of a 'size refuge'

and of a growth rate sufficient (even if lower than in scallops and oysters) for some

individuals to achieve it. That environmental deterioration did not jeopardise this growth rate

and lead to an unsustainable rate of predation is shown by the survival of *G. americana* to the

present. However, *G. subovata* (Fig. 1B), a species found alongside *G. americana* in some

fossil assemblages, did become extinct, its last occurrence being in the Early Pleistocene

Chowan River Formation according to Campbell (1993). Perhaps *G. subovata* grew relatively

rapidly? To test this we determined growth rate in fossil populations of each species by a

study of annual increment widths in the hinge plate. We expanded the investigation by

incorporating data from a supposedly (see later) extinct late Cenozoic glycymeridid (*G.

obovata*; Fig. 1C) from eastern England, together with data from a co-occurring and also

supposedly extinct carditid (*Cardites squamulosa ampla*; Fig. 1D). Like glycymeridids,

carditids are shallow-burrowing bivalves (Stanley 1970), and the limited available evidence

indicates that they also grow more slowly than scallops and oysters (Moss et al. 2016).

FIGURE 1 ABOUT HERE

Material

153

154   The geographic provenance and stratigraphic position of the material described below is

155   shown in Figures 2 and 3, respectively. We investigated samples of *G. americana* from the

156   early Pleistocene James City (JC) and Waccamaw (WM) formations in North Carolina.

157   ALAJ collected material from the former at Lee Creek Mine, Aurora, Beaufort County, and

158   from the latter at Clyde Moore Quarry, Columbus County. The material from the Waccamaw

159   Formation was supplemented by a specimen (thought to be from Old Dock, Columbus

160   County) kindly supplied by PH Kelley. *G. obovata* material (MH) was collected by ALAJ

161   from the late Pliocene Moore House Member of the Yorktown Formation at Riddick Pit,

162   Chuckatuck, Suffolk City, Virginia. Ideally we would have investigated samples of each

163   species from the same horizon and location to exclude local environmental effects. However,

164   the species seldom co-occur in any numbers (Thomas 1976). On the basis of their ostracod

165   (Hazel 1971, 1988) and/or molluscan (Ward et al. 1991) faunas the units supplying *G.*

166   *americana* represent warmer ('subtropical') conditions than the unit supplying *G. subovata*

167   ('warm temperate'). However, oxygen isotope (δ^{18}O) temperatures from scallop shells of the

168   James City Formation at Lee Creek (Johnson et al. 2019) are lower than from scallop shells

169   of the Moore House Member at Riddick Pit (Johnson et al. 2017), although the former

170   temperatures derive from calculations using a significantly lower value for water δ^{18}O, which

171   may be inappropriate.

172

173   FIGURE 2 ABOUT HERE

174

175   *C. squamulosa ampla* specimens (CCC) were collected by ALAJ from the early Pliocene

176   Ramsholt Member of the Coralline Crag Formation at Sudbourne Park, county of Suffolk.

177   One specimen of *G. obovata* was also collected from this unit and site, and another from the

178   same unit at Sutton Knoll (also known as Rockhall Wood), 13 km to the south-west. The

179   sample of this species from the Coralline Crag (CCG) was supplemented by specimens from

180   the Gedgrave area loaned by the Sedgwick Museum, Cambridge. Within the Coralline Crag,

181   aragonitic bivalves such as *Glycymeris* are usually only preserved in the Ramsholt Member

182   (Balson et al. 1993; Long and Zalasiewicz 2011), so the *G. obovata* specimens from

183   Gedgrave almost certainly derive from this specific unit. A further sample of *G. obovata*

184   (RC) was obtained from a collection at the University of Derby (Geological Collections)

185   deriving from the late Pliocene Red Crag Formation ('Waltonian'/Walton Crag) at Walton-

186   on-the-Naze, county of Essex. Assemblage evidence (Wood et al. 2009) suggests that the

187   Walton Crag was deposited under slightly cooler conditions than the Coralline Crag, thus the

188   two samples of *G. obovata* from eastern England perhaps afford a means of judging the

189   sensitivity of growth to temperature in *Glycymeris*. However, oxygen isotope temperatures

190   from the Coralline Crag are lower than suggested by the taxonomic composition of some

191   elements of the biota (Johnson et al. 2009; Vignols et al. 2018) so the Walton Crag may not

192   represent a significantly different environment. Whether or not the temperature regimes of

193   the Coralline and Walton Crag were different, the latitude of these deposits (52° N) suggests

194   that conditions would have been cooler than during deposition of the units sampled in the US

195   (34–37° N), a supposition borne out for summer temperature by isotopic data (Johnson et al.

196   2009, 2017, 2019; Vignols et al. 2018). One would not therefore expect growth within the US

197   samples to have been slower than in the English material (at least glycymeridid samples),

198   given the tendency for growth to be faster at higher temperatures in bivalves (Moss et al.

199   2016).

200

202

203   Newly collected specimens have been accessioned at the University of Derby (Geological

204   Collections) and those used from existing collections returned to their respective repositories

205   (see above), in each case with acetate peels produced for the investigation (see below).

206   Accession numbers are given in the online Supplemental Material.

207

208   **Methods**

209

210   As well as through other techniques (Peharda et al. 2012; Brocas et al. 2013; Beaver et al.

211   2017), it has been shown by oxygen isotope ($\delta^{18}O$) sclerochronology that the prominent

212   growth lines in a number of modern *Glycymeris* species are annual structures (Berthou et al.

213   1986; Bušelić et al. 2015; Yamaoka et al. 2016; Peharda et al. 2017). These lines therefore

214   enable identification, counting and measurement of annual increments in this genus, although

215   the occurrence of supernumerary lines creates a potential for slight uncertainty/inaccuracy

216   (Royer et al. 2013). No oxygen isotope sclerochronology has been conducted on modern

217   *Cardites* but isotopic sampling of *C. squamulosa ampla* at intermediate temporal resolution

218   has provided sufficient evidence to conclude that the growth lines in this taxon are annual

219   (Vignols et al. 2018).

220   Berthou et al. (1986), Yamaoka et al. (2016) and Peharda et al. (2017) isotopically

221   sampled the shell exterior of *Glycymeris* but other isotopic work on modern examples of this

222   genus has been on shell cross-sections. Growth lines are visible in cross-sections but are

223   much less distinct in the main part of the shell than in the hinge plate, which supports the

224   taxodont teeth. Consequently, most of the numerous recent studies based on growth lines in

modern *Glycymeris* (not so far including modern *G. americana*) have used data from this structure (Brocas et al. 2013; Reynolds et al. 2013; Bušelić et al. 2015; Peharda et al. 2016, 2017; Featherstone et al. 2017; Reynolds, Hall, et al. 2017; Reynolds, Richardson, et al. 2017). We found in our material that growth lines could be seen in the hinge plate (and heterodont hinge teeth of *C. squamulosa ampla*) and also noted that the hinge area was largely free of domichnial borings, whose presence in the main part of some shells (Fig. 4B) partially obliterated the less-distinct growth lines there. We therefore identified, counted and measured annual growth increments in the hinge plate/teeth (hereafter referred to as the hinge), using cumulative values for maximum width (Fig. 4A) as a measure of hinge size in successive years. We wished to check that hinge size is a good proxy for overall size and did so by investigating the relationship between the total cumulative width of hinge increments and anatomical length (Fig. 4C; measured with vernier callipers to a precision of 1 mm) in the studied shells. We scaled up our hinge measurements ([cumulative hinge width/total cumulative hinge width]*anatomical length) to obtain year-by-year values for overall size through ontogeny in order to enable comparison with overall-size/age data from living taxa. However, we decided (see below) that relative growth rate was best determined amongst the fossil samples from the raw (hinge-size/age) data.

FIGURE 4 ABOUT HERE

We chose for investigation 6–7 shells (favouring the largest) from each of the samples, stabilising them by encasement in Buehler EpoThin 2 resin before sectioning with a Buehler Isomet rock-saw at 100 rpm along the line of maximum growth (Fig. 4C; dorsal-ventral in *Glycymeris*, anterodorsal-posteroventral in *C. squamulosa ampla*). Cut surfaces were hand-ground to remove scratches using silicon carbide grits (600 grade to finish) and then briefly

250   etched in 10% hydrochloric acid. Earlier trials on Pliocene *Arctica islandica* had not shown

251   any enhancement of growth-line prominence by staining with Mutvei's solution, in

252   agreement with results from other fossil shells (Schöne et al. 2005). We experimented with

253   Alizarin red S and found that in some of the present shells this did improve visibility.

254   Acetate-peel replicas were made of the prepared surfaces (Richardson and Walker 1993).

255   These were mounted between glass plates and digitally photographed under an optical

256   microscope. Images were imported into the bespoke measuring software Panopea (© Peinl

257   and Schöne, 2004) and the widths of successive annual increments in the hinge measured to a

258   precision of 10^{-6} μm (recorded to a precision of 1 μm in Table 1).

259   Each set of specimens was ground, etched, stained (where beneficial), peeled and

260   photographed by one of the URSS students, who then obtained measurements. The images

261   used were then remeasured by at least three other students (each student measuring a total of

262   at least four sets of images). This produced somewhat discrepant initial hinge-size/age plots

263   for individual specimens, attributable to differing judgements on the status of growth lines

264   (annual or supernumerary; Fig. 4A) and to differing measurement trajectories. The initial

265   replication exercise was used to develop more uniform standards for recognition of annual

266   growth lines and to decide upon a common measurement trajectory (the line of maximum

267   growth in the hinge cross-section; Fig. 4A). Fresh measurements made with the revised

268   approach were entered in version 3.20 of the free statistical software PAST

269   (http://folk.uio.no/ohammer/past; Hammer et al. 2001) for calculation of von Bertalanffy

270   regressions from the combined cumulative-increment-width and age data for each sample.

271   Regressions were similarly calculated from the (up-scaled) overall size and age data.

272   Although not always providing the best fit (e.g. Pace et al. 2017), von Bertalanffy regressions

273   are widely used to characterise growth within populations of organisms. The *k* parameter of

274   the von Bertalanffy equation can be used as an indicator of growth rate and accurately

275 reflects differences between bivalve groups, e.g. the slower growth of glycymeridids and

276 carditids compared to scallops and oysters (Moss et al. 2016). However, it did not adequately

277 reflect differences between the samples investigated herein and so was not used as a metric

278 for comparison, relative growth rates being determined by visual inspection of graphed

279 regressions.

280

281 **Results**

282

283 ***Introductory remarks***

284

285 　　Growth lines in the hinge had been largely obliterated by domichnial borings in specimen

286 MH5 and were difficult to distinguish from elements of the crossed-lamellar microstructure

287 in CCG3 (Fig. 5F). All other specimens were sufficiently well preserved to provide increment

288 data, and of these all but RC4 were complete enough for measurement of anatomical length.

289 A summary of the raw data is provided in Table 1; information for each individual is given in

290 the online Supplemental Material.

291

292 TABLE 1 ABOUT HERE

293

294 　　Notwithstanding our ability to obtain increment data from the hinge of all but the two

295 specimens indicated above, the clarity of growth lines was not uniformly high, creating

296 uncertainty over the definition of annual increments in some cases. Figure 5 shows some of

297 the variation. Increment recognition was generally quite easy in *Glycymeris* (Fig. 5A–E, H, I)

298 and particularly straightforward in the JC sample (Fig. 5A–C). In some instances, annual

299 growth lines may have been incorrectly judged to be supernumerary (e.g. Fig. 4A), resulting

300   in a local overestimate of increment width and underestimate of age, while in others

301   supernumerary lines may have been incorrectly judged to be annual, resulting in the reverse.

302   However, we do not think that such local errors will have had a significant cumulative effect

303   on data from *Glycymeris* specimens. Recognition of growth lines, and distinction between

304   annual and supernumerary structures, was more difficult in *C. squamulosa ampla* (Fig. 5G),

305   so the data from this taxon may be somewhat inaccurate.

306

307   FIGURE 5 ABOUT HERE

308

309   Sectioning revealed notable differences in shell thickness between specimens of similar

310   size, both within samples (e.g. the thicker shell of JC4 compared to JC3; Fig. 6) and amongst

311   samples (e.g. thicker shells in the CCG sample of *G. obovata* compared to the RC sample,

312   and in the sample of *C. squamulosa ampla* compared to *Glycymeris* samples).

313

314   FIGURE 6 ABOUT HERE

315

316   ***Hinge size in relation to overall size***

317

318   A plot of total cumulative increment width against anatomical length (Fig. 7) shows that

319   hinge size is a reasonably good proxy for overall size ($r = 0.84$) in the studied glycymeridid

320   and carditid material.

321

322   FIGURE 7 ABOUT HERE

323

324   ***Hinge size and overall size in relation to age***

Of the twelve *G. americana* specimens, six were over forty years old at death (JC1: 42;

JC4: 89; WM1: 46; WM2: 49; WM4: 42; WM6: 46), compared with only one of five *G.*

subovata (MH1: 52), one of 13 *G. obovata* (RC2: 57) and one of six *C. squamulosa ampla*

(CCC2: 45). The figures for maximum age in *G. subovata* and *G. americana* are close or very

close, respectively, to those reported by Moss et al. (2017). The six relatively old *G.*

americana specimens were also relatively large, all being above 70 mm in anatomical length

(maximum 107 mm; JC1, WM1), compared with a maximum of 68 mm (CCG1) in other

species.

Ontogenetic plots of hinge size against age (Fig. 8) reveal an ontogenetic decline in

growth rate in most individuals (as typical of bivalves), with divergence of hinge-size/age

profiles through ontogeny, both within and amongst samples. *G. americana* individuals (Fig.

8A, B) generally show higher growth rates (i.e. larger hinge size for a given age) than *G.*

subovata (Fig. 8C) in early ontogeny, and above age 20 there is no overlap between the data

for *G. americana* and *G. subovata*. Within *G. americana*, individuals in the JC sample (Fig.

9A) generally show higher growth rates than in the WM sample (Fig. 8B). *G. obovata*

individuals (Fig. 8D, E) generally show similar growth rates to *G. subovata* but one specimen

from the CCG sample (Fig. 8E) shows a rather higher growth rate, within the range of both

the WM and JC samples of *G. americana*. Some *C. squamulosa ampla* individuals (Fig. 8F)

show slower growth than in *G. subovata* and the RC sample of *G. obovata*, and nearly all

individuals show a lower growth rate than in the CCG sample of *G. obovata*.

FIGURE 8 ABOUT HERE

The von Bertalanffy regressions for hinge size against age (Fig. 9A) make plain the

pattern of growth within (i.e. ontogenetic decline in growth rate) and the differences in

350 growth rate between samples, with the exception of the regression for the *C. squamulosa*

351 *ampla* (CCC) sample. The almost straight form of this contrasts with the convex-up shape of

352 most individual growth curves (Fig. 8F) and is clearly an artefact resulting from a chance

353 combination of individual growth rates and ages at death. The CCC regression is, however,

354 adequate to show the low growth rate of *C. squamulosa ampla*.

355

356 FIGURE 9 ABOUT HERE

357

358   The von Bertalanffy regressions for overall size against age (Fig. 9B) have broadly similar

359 relative positions to those for hinge size against age. However, there are differences in detail

360 between the plots: in the overall-size/age plot the JC regression cross-cuts the WM

361 regression, the CCG and RC regressions occupy similar positions, and the CCC regression

362 lies substantially below all the other regressions. The reason for these differences between the

363 plots is indicated by Figure 10, which shows individual growth curves for overall size in the

364 JC sample, together with the von Bertalanffy regression for the full set of data (as in Fig. 9B)

365 and another for all except the data from specimen JC4, which was long-lived and has an

366 unusually thick shell for its size (Fig. 6). The influence of this specimen on the overall-

367 size/age regression is very clear. Its hinge growth was like that of other JC specimens (Fig.

368 8A) but evidently it accreted a disproportionate amount of material to the internal surface

369 (increasing thickness) compared to the shell periphery (increasing anatomical length). A

370 fairer way of measuring overall size in this specimen would have been to include shell

371 thickness. Had this been done (and indeed measurements of anatomical length and shell

372 thickness combined with anatomical height; cf. Kirby and Jackson 2004) it seems very likely

373 that the growth of overall size in JC4 would have been like that of other specimens in the JC

374 sample. In the absence of such additional data the best strategy is to fall back on the hinge-

15

375   size/age regression to compare growth in the JC sample with the WM sample of *G.*

376   *americana* (and other samples). We believe that overall size has been similarly

377   underestimated in the CCG sample of *G. obovata* (thick-shelled relative to the RC sample)

378   and the sample of *C. squamulosa ampla* (thick-shelled relative to the *Glycymeris* samples),

379   and that therefore the hinge-size/age regressions (Fig. 9A) provide the best indication of

380   relative growth rate amongst all the samples. On the basis of these the fastest growth amongst

381   the *Glycymeris* material is shown by the *G. americana* samples (JC>WM), followed by *G.*

382   *obovata* (CCG>RC) and then *G. subovata* (MH; only marginally slower than the RC sample

383   of *G. obovata*). It is impossible to precisely rank the growth rate of *C. squamulosa ampla*

384   (CCC) because the von Bertalanffy regression cross-cuts those for the MH and RC samples

385   and is anyway not an accurate reflection of growth in the individuals concerned (see above).

386   However, as already stated, growth in *C. squamulosa ampla* was clearly slow (roughly the

387   same as the MH and RC samples in terms of hinge size at the maximum age).

388

389   FIGURE 10 ABOUT HERE

390

391   Although the overall-size/age regressions do not provide the best picture of relative

392   growth rate amongst the studied samples they do enable (cautious) comparison with

393   equivalent data from living glycymeridid and carditid species. Included in Figure 9B are

394   regressions for the glycymeridids *Glycymeris bimaculata* and *G. nummaria* from the

395   Mediterranean, and *G. fulgurata* and *G. vestita* from the western Pacific, and for the carditid

396   *Carditamera affinis* from the eastern Pacific. To our knowledge, these are the only

397   glycymeridid and carditid species for which von Bertalanffy parameters have been published.

398   While there is a possibility that the regressions do not adequately represent overall size (i.e.

399   that their positions relative to each other and to regressions for the fossil samples might alter

400 somewhat if other measures of overall size were incorporated), it is fair to conclude that the

401 growth rate of *G. americana* was at about the upper end of the range in living glycymeridids

402 (i.e. similar to *G. bimaculata*) and that of *G. subovata* at about the lower end of the range (i.e.

403 similar to *G. fulgurata*). The growth rate of *Cardites squamulosa ampla* was evidently lower

404 than that of *Carditamera affinis.*

405

406   **Discussion**

407

408   The slower growth of extinct *G. subovata* than extant *G. americana* is opposite to the

409 pattern identified amongst extinct and extant late Cenozoic scallops and oysters of the

410 western North Atlantic and Caribbean area. Before drawing conclusions from this it is as well

411 to consider whether the results are a reflection of the local environments of the sampled

412 populations. Assemblage evidence from the unit supplying *G. subovata* indicates somewhat

413 cooler conditions than during deposition of the units supplying *G. americana*, and the same

414 type of evidence indicates that the RC sample of *G. obovata* experienced somewhat cooler

415 conditions than the CCG sample (see Material). Growth rate was lower in the RC than the

416 CCG sample of *G. obovata*, perhaps signifying some influence of temperature on the growth

417 of glycymeridids. It is, however, doubtful whether this factor is sufficient to account for the

418 much greater difference in growth rate between *G. subovata* and *G. americana*, the former

419 growing at a rate lower than the RC sample of *G. obovata*, which is from a higher-latitude,

420 cooler location. That *G. subovata* lived under cooler conditions than *G. americana* is, in any

421 case, questionable (see Material) so one must accept that its slower growth is not a reflection

422 of local environment, and that the US glycymeridid species do not conform to the pattern of

423 extinction/survival in relation to growth rate identified amongst contemporaneous scallops

424 and oysters. Extinction of *G. obovata,* which also grew slower than *G. americana*, is likewise

425 contrary to this pattern, though in this case slower growth is more reasonably attributable to

426 cooler conditions. Extinction of the co-occurring, ecologically similar, and slow-growing *C.*

427 *squamulosa ampla* is also counter to the view that the pattern seen in scallops and oysters

428 extends to groups with a lower growth rate.

429   Interpretation of the data from *G. obovata* and *C. squamulosa ampla* is complicated by the

430 possibility that neither taxon is extinct. We have followed the recent taxonomy of Vignols et

431 al. (2018) for our material from England but in the past forms here referred to *G. obovata*

432 have been placed in the extant species *G. glycymeris* (e.g, Raffi et al. 1985), and *C.*

433 *squamulosa ampla* is so similar to the modern species *C. antiquatus* as to be almost certainly

434 its ancestor (Vignols et al. 2018)—i.e. *C. squamulosa ampla* may be pseudoextinct. Until

435 such time as it is shown that the English samples are from taxa that are not (truly) extinct we

436 must rest with the interpretation of growth-rate data from them given above.

437

438   **Summary, conclusions and further work**

439

440   Growth in extinct *G. subovata* and supposedly extinct *G. obovata* was not as fast as in late

441 Pleistocene samples of the extant species *G. americana*. Growth in *G. americana* was at a

442 rate comparable to the fastest-growing living glycymeridid, whereas growth in *G. subovata*

443 was at a rate comparable to the slowest-growing. The supposedly extinct carditid *C.*

444 *squamulosa ampla* grew at a rate similar to *G. subovata* and *G. obovata*, and evidently slower

445 than the one living carditid species for which data are available. These facts indicate that

446 within bivalve groups having a lower growth rate than scallops and oysters, extinction or

447 survival of taxa through the late Cenozoic was not influenced by whether they were relatively

448 fast or slow growers—the growth rate of relatively fast growers in these groups was

449 presumably not close to the limit of what could be supported by the environment and hence

18

450   not jeopardised by environmental changes. By implication, predation did not make a

451   significant contribution to the demise of those taxa in slow-growing groups that became

452   extinct, or at least it made no greater contribution following late Cenozoic environmental

453   changes. These themselves probably played the major part in extinctions within slow-

454   growing groups but given the undoubted existence of potential refugia (e.g. for western North

455   Atlantic species, Caribbean locations offering high primary production and/or water

456   temperature; Stanley 1986; Leigh et al. 2014) inability to migrate to such locations must have

457   been a factor. Perhaps those taxa that became extinct had larvae that were too short-lived to

458   reach refugia across areas unfavourable for colonisation by adults? The duration of the larval

459   stage could be determined from prodissoconch size in extinct taxa (Smith et al. 2003), and

460   data from the same approach applied to fossil examples of extant taxa could be supplemented

461   by directly obtained data from living forms to see if larval longevity in survivors is higher

462   than in extinct taxa. As well as this work on representatives of slow-growing bivalve groups

463   it would be worth seeking to confirm the relationship between extinction/survival and growth

464   rate in fast-growing groups by investigating other members of them (e.g. other genera of

465   scallops and oysters) in the late Cenozoic. Equally, it would be worth attempting to

466   corroborate evidence (Kirby 2000, 2001) of a relationship between extinction/survival and

467   growth rate within fast-growing groups in the earlier Cenozoic. Investigation of

468   environmental influences on growth (cf. Moss et al. 2017, 2018; Fancher et al. 2018; Palmer

469   et al. 2019) would be a necessary part of such work, as would measurement of several

470   dimensions of overall size (cf. Kirby and Jackson 2004). A solid phylogenetic framework

471   would also be required to enable distinction between true extinction (lineage termination) and

472   pseudoextinction (phyletic evolution). It has been claimed that phyletic evolution is limited in

473   importance (e.g. Stanley 1979) but there is evidence of its significant occurrence in bivalves

474   (e.g. Johnson 1984, 1985, 1993, 1994; Johnson and Lennon 1990).

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683

684 <div align="center">FIGURE CAPTIONS</div>

685

686 Fig. 1. External views of left valves of A) *Glycymeris americana* (JC1), B) *G. subovata*

687 (MH2), C) *G. obovata* (CCG4) and D) *Cardites squamulosa ampla* (CCC2).

688

689 Fig. 2. Position of collection locations in the eastern United States (1–3) and eastern England

690 (4–7): 1 = Clyde Moore Quarry and Old Dock (WM); 2 = Lee Creek Mine (JC); 3 = Riddick

691 Pit (MH); 4 = Walton-on-the-Naze (RC); 5 = Sutton Knoll (CCG); 6 = Gedgrave (CCG); 7 =

692 Sudbourne Park (CCC, CCG).

693

Fig. 3. Stratigraphic position of samples (bold letters in parentheses). Ages of units (Ma) in North Carolina and Virginia are from Ward et al. (1991), with refinement for the Waccamaw Formation from Akers (1972); ages of units in Essex and Suffolk are from Wood et al. (2009), except for the Coralline Crag Formation (from Vignols et al. 2019, fig. 2). Alternative interpretations of the ages of units in the eastern USA, and an alternative correlation with the sequence in eastern England, are given in Johnson et al. (2019, Supplemental Data File 1) and Vignols et al. (2019, fig. 2), respectively.

701

Fig. 4. A) Cross-section of the hinge plate of *Glycymeris americana* (WM3), enlarged from B), a cross-section of the entire shell (left valve), sectioned along the line (axis of maximum growth) shown in C), interior view. A is an acetate peel showing bubbles (white spots) and the resin mounting-medium (top and right); B has been digitally processed to remove the resin 'background'; lower scale bar applies to both B and C. Alternating black and white lines in A demarcate successive annual increments (27), bounded by annual growth lines, along the measurement-trajectory (line of maximum increment width in the hinge cross-section) adopted after the initial (trial) measuring exercise; arrows show the positions of two lines considered to be supernumerary, one or both of which was/were taken to be annual in three of the four initial sets of measurements. A shows growth lines of about average clarity (slightly obscured by shell-microstructural elements) for the hinges of the specimens used in this study. B shows examples of the domichnial borings (probably made by non-predatory annelid worms) commonly seen in the main part of the shell. C illustrates the parameter of overall size (anatomical length) employed in the study; in *Cardites squamulosa ampla* the line of section (maximum growth) was oblique to the line of measurement of anatomical length, in correspondence with the posterior elongation of the shell in this taxon (see text and Fig. 1D).

718

Fig. 5. Examples of hinge cross-sections from each sample, showing variation in the clarity

of growth lines. A, B, C) JC1, JC6, JC4, respectively; D) MH1; E) WM1; F, H) CCG3,

CCG5, respectively; G) CCC2; I) RC5. All parts are greyscale images of acetate peels from

specimens mounted in resin; A-C are from specimens stained with Alizarin red S; white spots

are bubbles.

724

Fig. 6. Resin-encased and sectioned shells of *Glycymeris americana* specimens JC3 (A) and

JC4 (B). Note the much thicker shell and much larger hinge in JC4 despite the very similar

overall size to JC3.

728

Fig. 7. Scatter plot and *y*-on-*x* linear regression ($y = 104x + 1033$; $r = 0.84$) for total

cumulative increment width versus anatomical length in the studied glycymeridid (crosses)

and carditid (crosses on grey background) material. Note that the carditid data can be viewed

as an extension of the glycymeridid data towards smaller sizes.

733

Fig. 8. Ontogenetic plots of hinge size (cumulative maximum width of annual increments)

versus age for individuals within each sample. JC = *G. americana*, James City Formation,

North Carolina; WM = *G. americana*, Waccamaw Formation, North Carolina; MH = *G.*

subovata, Moore House Member, Yorktown Formation, Virginia; CCG = *G. obovata*,

Coralline Crag Formation, Sufolk*;* RC = *G. obovata*, Red Crag Formation, Essex; CCC =

Cardites squamulosa ampla, Coralline Crag Formation, Suffolk. The anomalously thick-

shelled specimen JC4 (see Fig. 6) is indicated by larger markers in A.

741

Fig. 9. A) Von Bertalanffy regressions for the combined data for hinge size (cumulative maximum width of annual increments) relative to age from each sample. B) Von Bertalanffy regressions for the combined data for overall size (length; scaled up from hinge-size data as explained in Methods) relative to age from each sample, together with regressions for living glycymeridid and carditid species based on parameters supplied by Peharda et al. (2012; *G. nummaria*), Bušelić et al. (2015; *G. bimaculata*), Moss et al. (2016; *C. affinis* during and after La Niña phases in the El Niño Southern Oscillation) and Yamaoka et al. (2016; *G. fulgurata*, *G. vestita*). The regressions for *G. fulgurata* and *G. vestita* are derived from ones for anatomical height relative to age, with values for height multiplied by an appropriate factor (1.1; derived from Yamaoka et al. 2016, fig. 1A, C) to convert to length. JC = *G. americana*, James City Formation, North Carolina; WM = *G. americana*, Waccamaw Formation, North Carolina; MH = *G. subovata*, Moore House Member, Yorktown Formation, Virginia; CCG = *G. obovata*, Coralline Crag Formation, Sufolk*;* RC = *G. obovata*, Red Crag Formation, Essex; CCC = *Cardites squamulosa ampla*, Coralline Crag Formation, Suffolk.

Fig. 10. Ontogenetic plots of hinge size (length; scaled up from hinge-size data as explained in Methods) versus age for individuals within the JC sample of *G. americana* (thick-shelled specimen JC4 indicated by larger markers), together with von Bertalanffy regressions for the combined data including (thick continuous line without markers) and excluding (thick dashed line without markers) the data from JC4.

TABLE CAPTION

Table 1. Summary of raw data (italic figures in brackets are sample sizes).

767   [8537 words in total]

10 mm

FIGURE 1
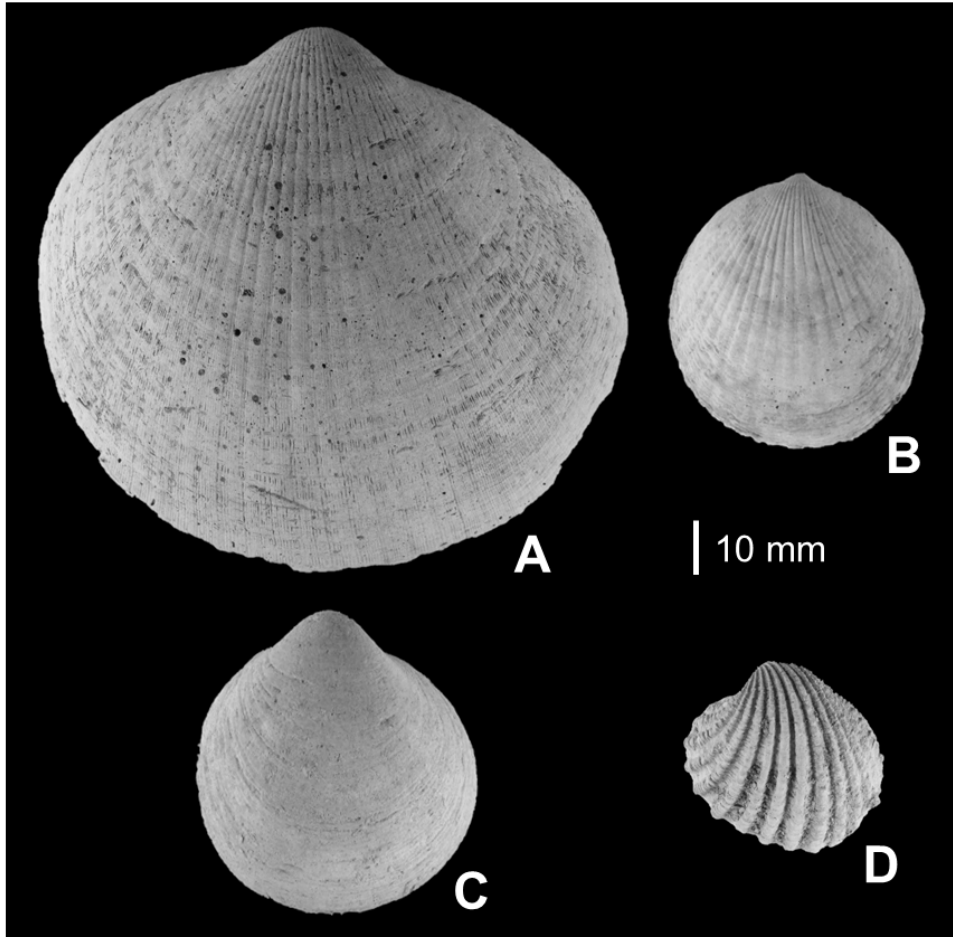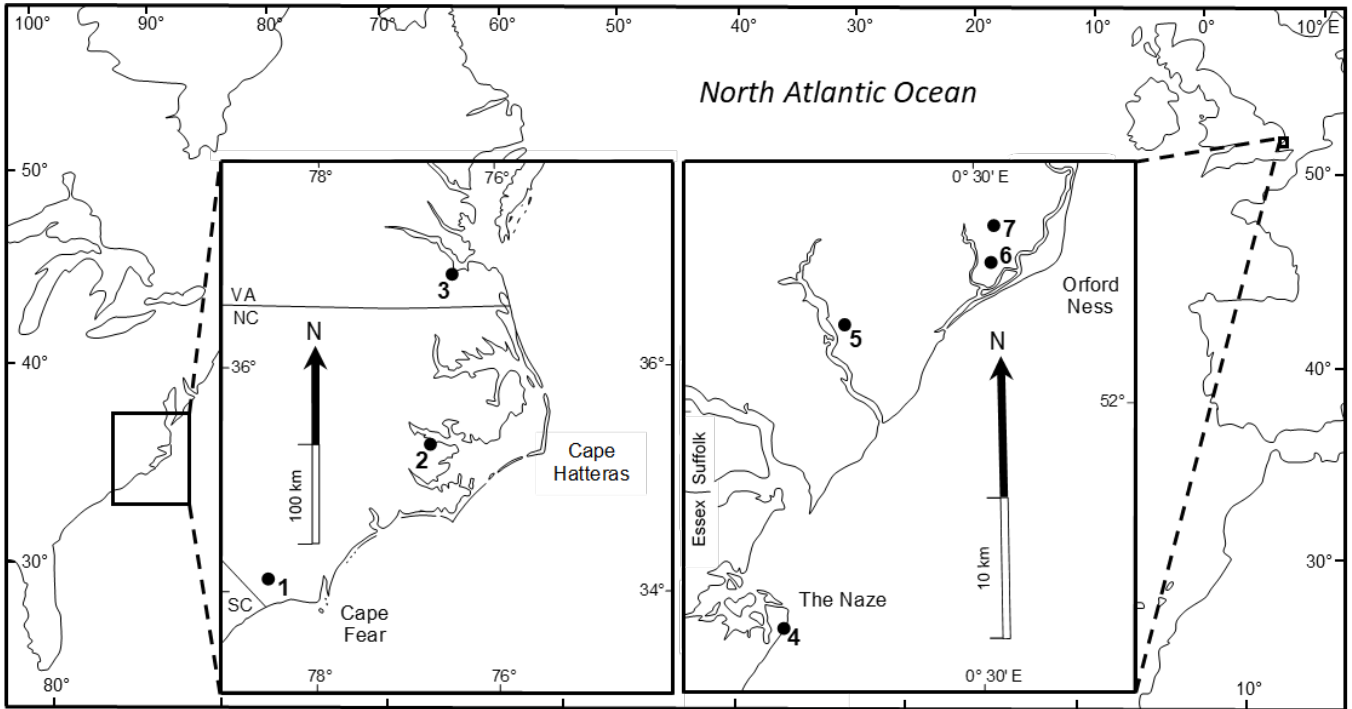
FIGURE 2

	N. Carolina / Virginia	Essex / Suffolk

Chart columns (left to right): PLEISTOCENE/PLIOCENE epoch, stage (Calabrian, Gelasian, Piacenzian, Zanclean), age scale (1.5–4.0 Ma).

N. Carolina / Virginia:
- Waccamaw Formation (WM)
- James City Formation (JC)
- Chowan River Formation
- Yorktown Formation:
  - Moore House Member (MH)
  - Morgarts Beach Member
  - Rushmere Member
  - Sunken Meadow Member

Essex / Suffolk:
- Wroxham Crag Formation:
  - How Hill Member
  - Sidestrand Member
- Norwich Crag Formation
- Red Crag Formation:
  - Ludham Member
  - Thorpness and Sizewell members
  - Walton Crag (RC)
- Coralline Crag Formation:
  - Sudbourne and Aldeburgh members
  - Ramsholt Member (CCC, CCG)
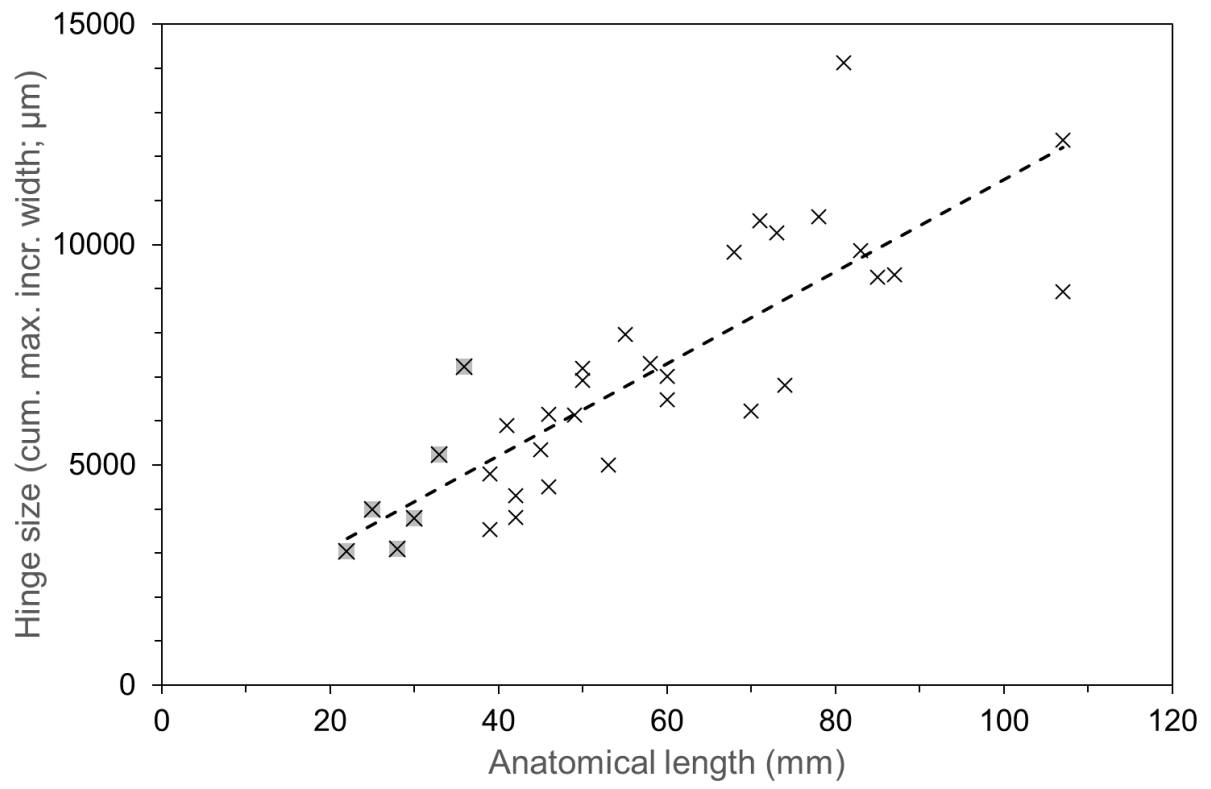
FIGURE 3

FIGURE 4

1000 µm

A

B

C

D

E

F
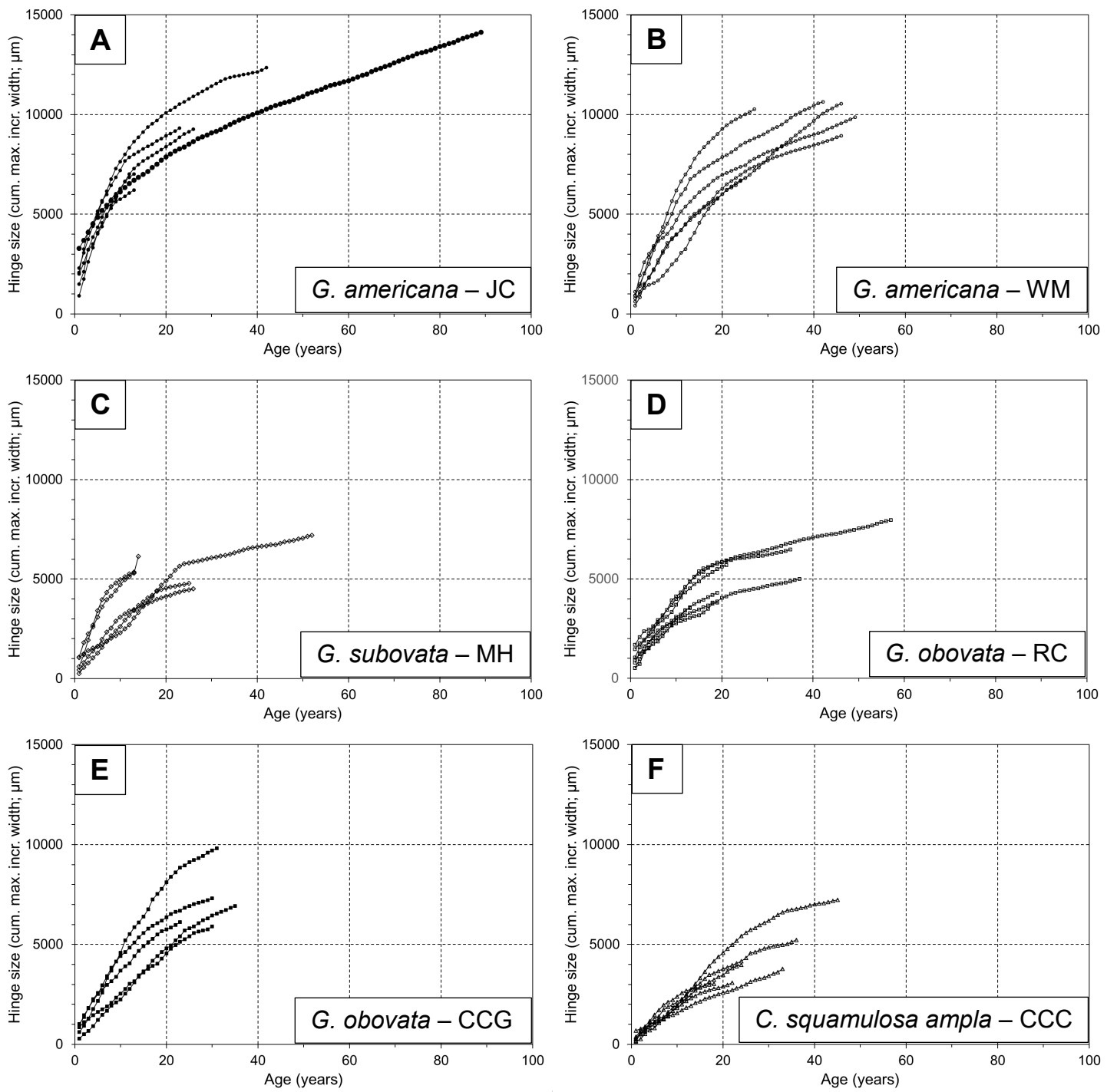
G

H

I

FIGURE 5

10 mm

A

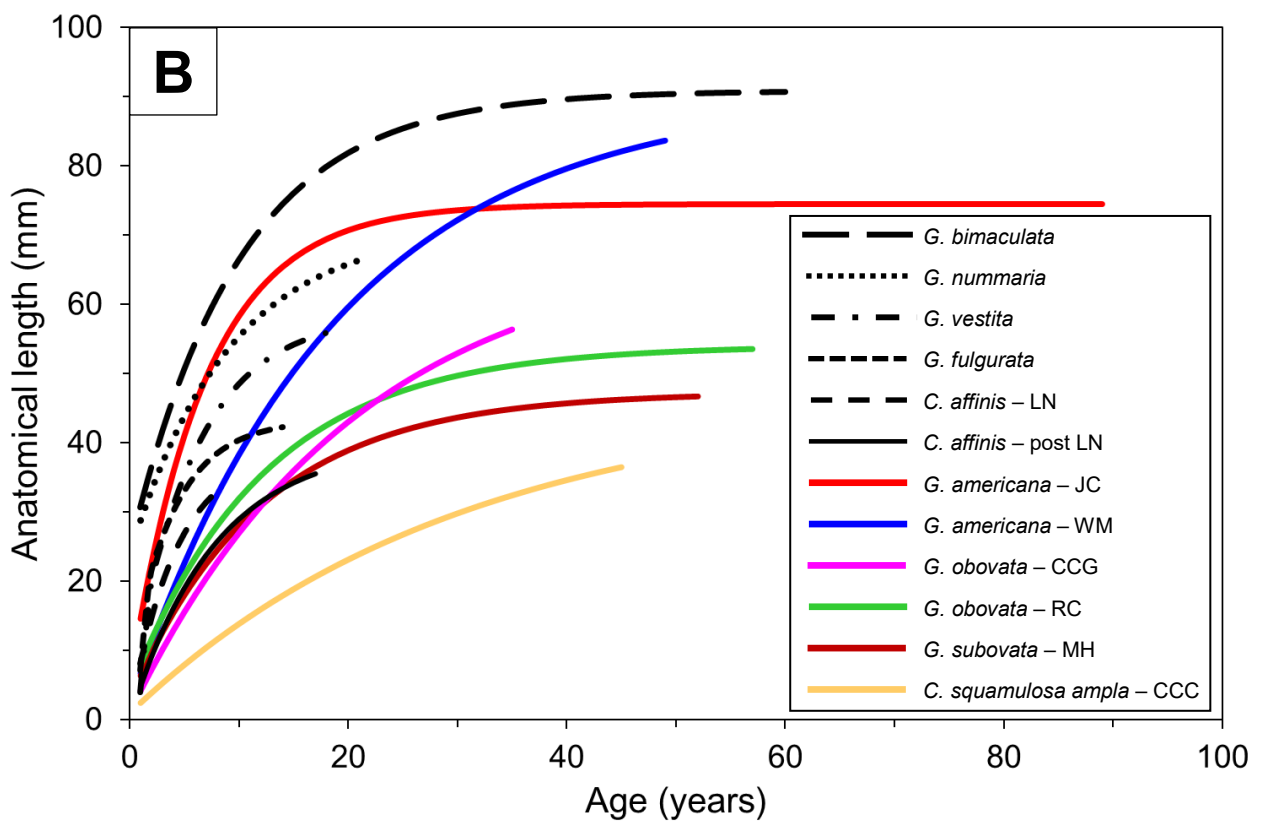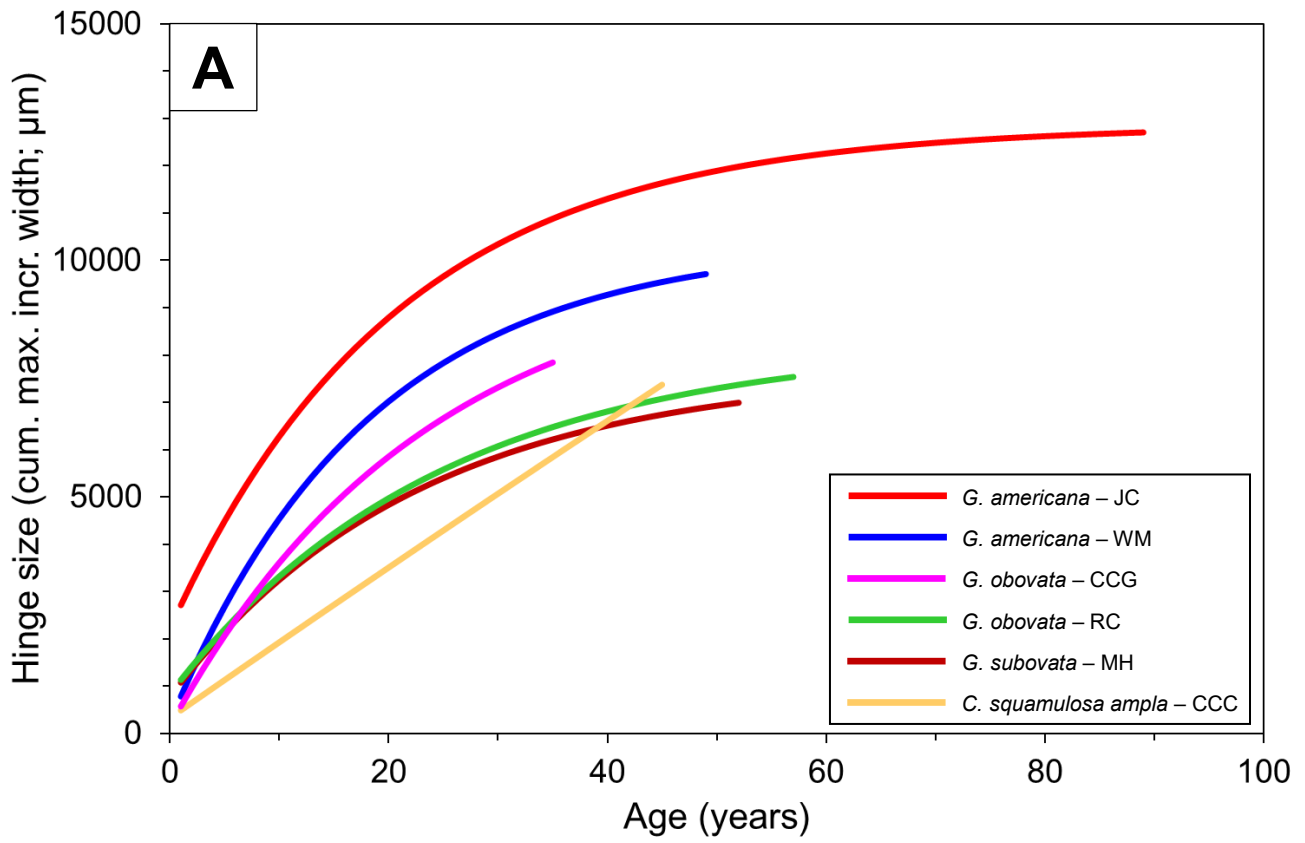B
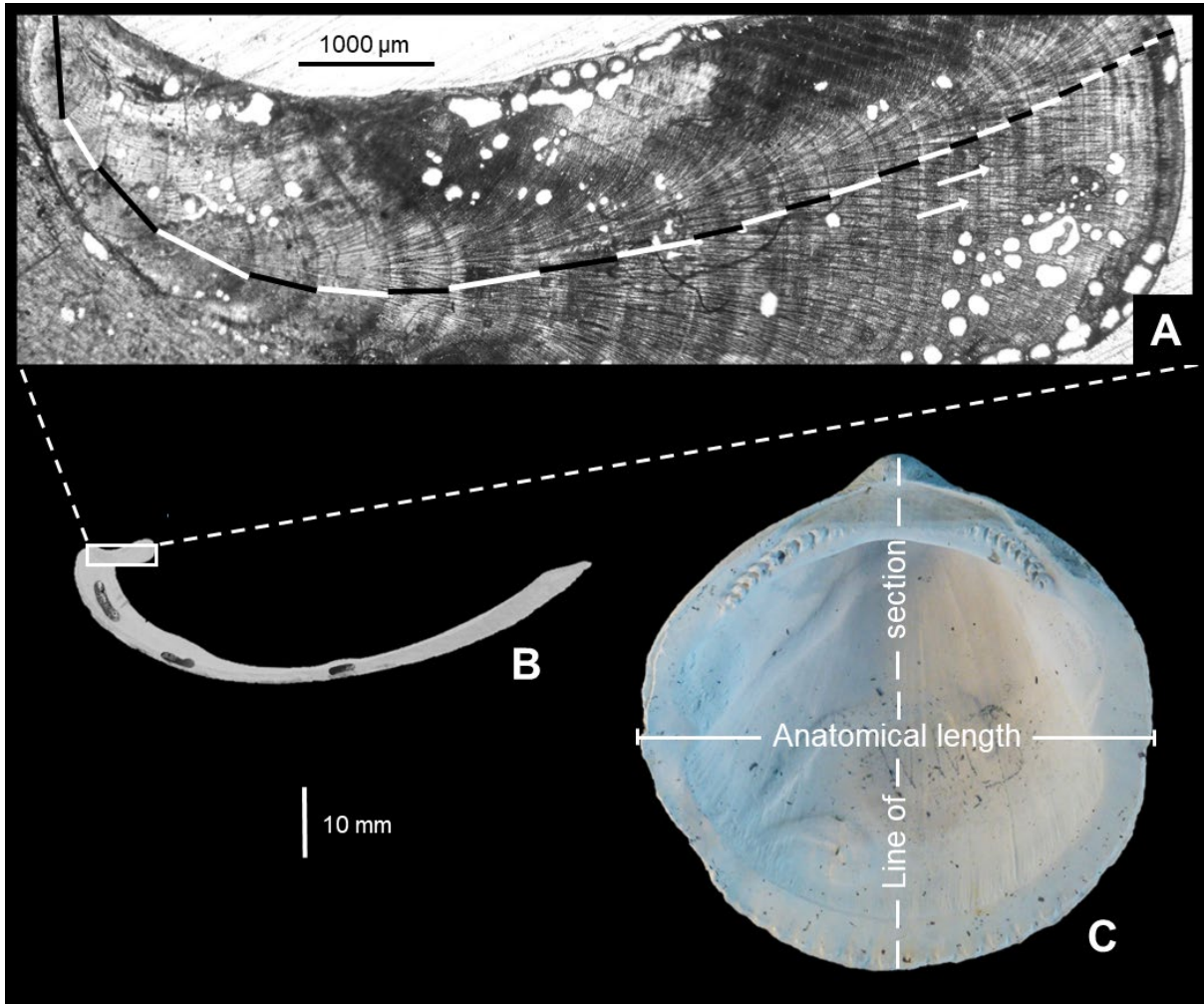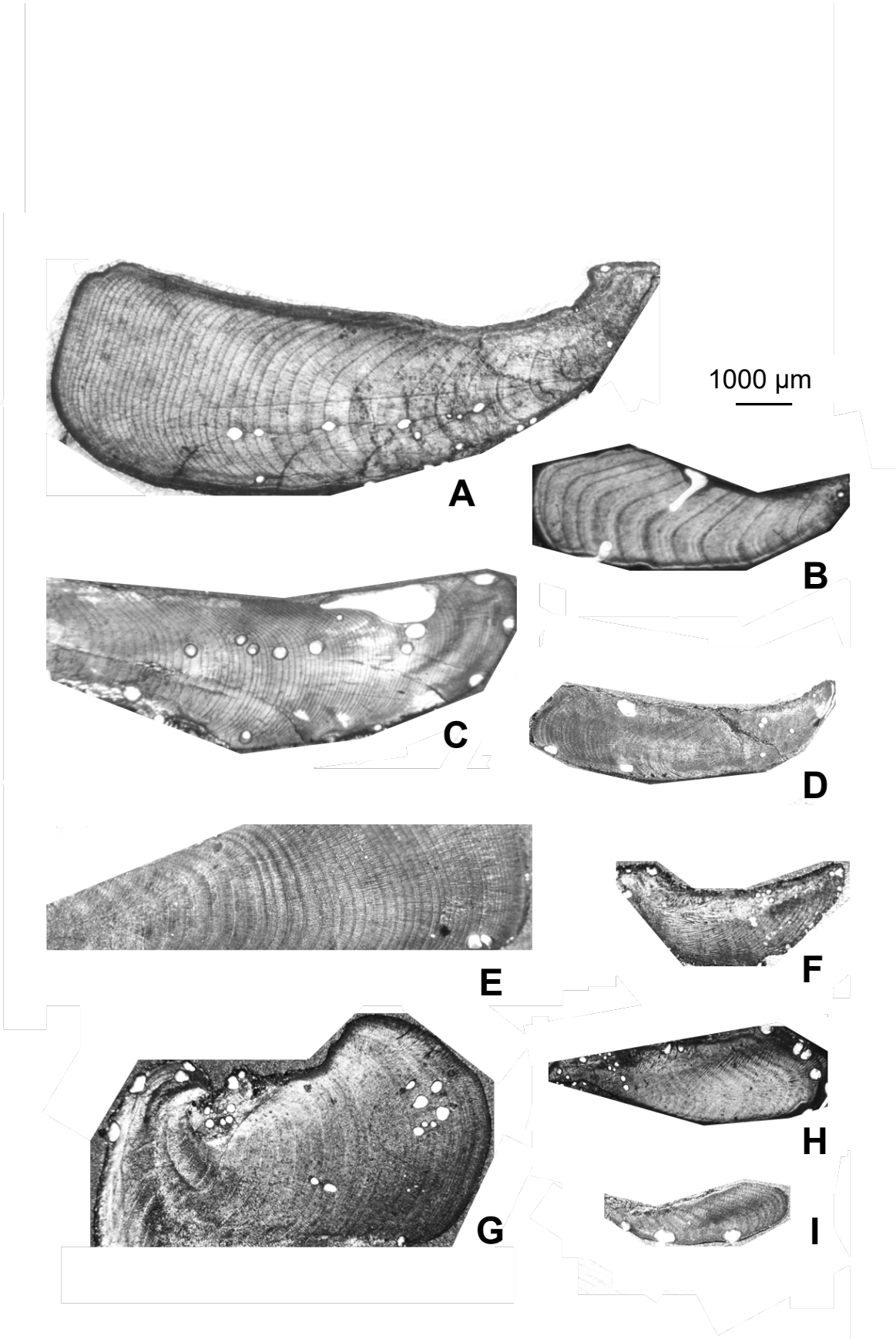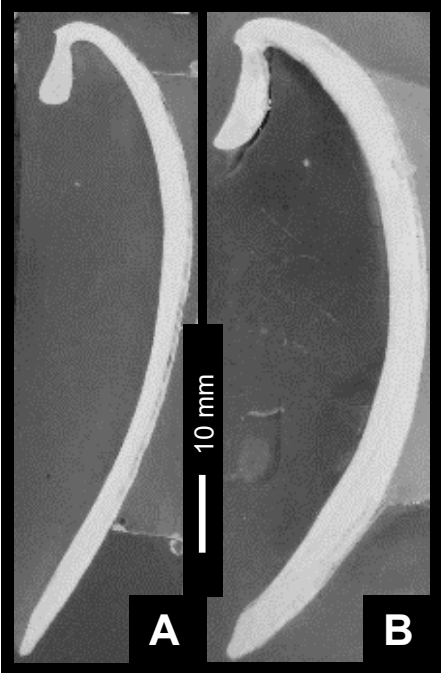
FIGURE 6

FIGURE 7

FIGURE 8

FIGURE 9
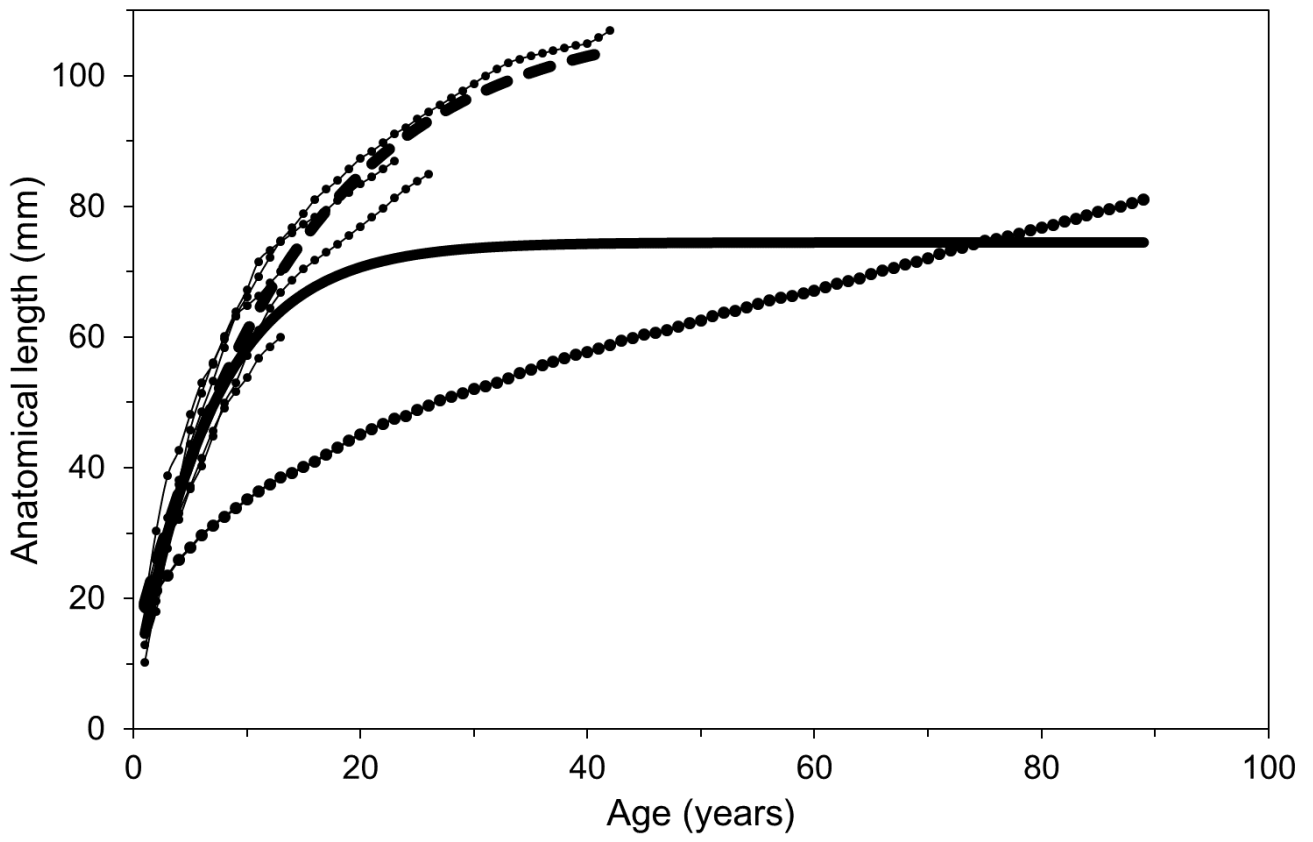
FIGURE 10

TABLE 1

Sample	Range in age (years)	Range in total cumulative hinge-increment width (μm)	Range in anatomical length (mm)
JC	13-89 (*6*)	6219-14135 (*6*)	60-107 (*6*)
WM	25-49 (*6*)	6810-10631 (*6*)	71-107 (*6*)
MH	13-52 (*5*)	4503-7195 (*5*)	39-50 (*6*)
RC	13-57 (*7*)	3538-7968 (*7*)	39-60 (*6*)
CCG	23-35 (*5*)	5903-9822 (*5*)	41-68 (*6*)
CCC	18-45 (*6*)	3031-7228 (*6*)	22-36 (*6*)