

1 **Effectiveness of micromorphy against drilling predation: Insights from early Miocene**
2 **faunal assemblage of Quilon limestone, India**

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15 **Abstract**

16 The nature of drilling predation, although well documented for molluscan fossils, is
17 understudied for micromolluscs (<5mm). Studying predation in micromolluscs is especially
18 critical in evaluating the adaptive significance of micromorphy against predation and
19 assessing the importance of predator-prey size relationship (PPSR). This study documents
20 drilling predation event in microbivalves from early Miocene (Burdigalian) fossil assemblage
21 of Quilon limestone from Kerala, India. Our sample of ~2000 valves represent nine families
22 with an average drilling frequency (DF) of 0.06 and an incomplete drilling frequency (IDF)
23 of 0.26. The characteristic drillhole morphology and occurrence of five genera of modern
24 drilling gastropods (Naticid: *Natica*, *Tanea* and *Polinices*; Muricid: *Triplex* and
25 *Dermomurex*) from the same locality reveals the predator identity. Predation in the studied
26 assemblage is found to be highly selective in terms of prey taxa, size, mobility and site
27 selection. Six out of nine families show evidence of predation indicating taxon selectivity.
28 Poor correlation between DF and abundance further supports this view. Failed attacks are
29 strongly correlated with morphological features such as surface ornamentation (Lucinidae),
30 presence of conchiolin layers (Corbulidae). Drilling occurs primarily on medium size class
31 and prey outside this size range show lower rate of attack. This indicates the existence of an
32 “inverse size refugia” for extremely small prey along with the classical size refugia existing
33 for large prey. Mobility is found to be a deterrent to drilling predation and it also increases
34 failure.

35 Microbenthos of Quilon limestone shows a lower predation intensity in comparison
36 to the Miocene macrobenthos worldwide including coeval formation of the Kutch Basin. The
37 interaction in microbenthos is more strongly size-dependent in contrast to the Kutch fauna.
38 Reduced predation intensity in microfauna and existence of “inverse size refugia” support the

39 claim of micromorphy acting as a defense mechanism and highlights the role of size-
40 dependent predation in marine benthos.

41

42 **Introduction**

43 Predation is considered as one of the primary ecological processes that drives natural
44 selection [1-3]. Predator-prey interactions are inherently dependent on size [4]. Consequently,
45 body size of interacting predator and their prey are one of the vital predictors in controlling
46 the feeding relationship within food web [5-7]. Based on global data on body size, Brose et al
47 (2006) suggested that predator-prey size relationships (PPSRs) may systematically differ
48 among habitats, such as terrestrial and marine [8]. The nature of PPSRs of marine
49 invertebrates in deep time is especially interesting because of its impact on major
50 evolutionary breakthrough driven by predation [1].

51 Drilling predation is one of the unique scenarios where the signature of the predatory
52 event is preserved and various aspects of predator-prey dynamics can be reconstructed by
53 evaluating non-random attacks based on species identity, ecological character, and size of the
54 prey (see [9] for review). Such records are found in the recent [10-13] as well as in the fossil
55 ecosystems dating as far back as Cambrian. The predation intensity varied during
56 Phanerozoic, often in sync with diversity [14] and shows a significant increase from Late
57 Mesozoic with the appearance of two modern predatory gastropod families, namely Muricid
58 and Naticid [9, 15, 16].

59 It has long been recognized that predators are generally larger than their prey [17, but
60 see 18], especially in highly size-structured marine ecosystem [19-21]. Size selectivity is
61 largely true for drilling predator-prey system [22- 24] with some exceptions [25]. The prey
62 selection by a drilling predator is a balance between invested energy (through foraging,
63 drilling and consumption) and energy gain (dependent on prey size) [22, 26]. As predator size

64 increases, metabolic demand becomes more resulting in an increase in the rate of food intake
65 to match the energetic demands [27]. Such increase in energy requirement can be tackled by
66 choosing either a larger prey or attacking multiple smaller preys; the decision depends on the
67 availability and distribution of prey-size in a community [28]. Prey often develops anti-
68 predatory strategies as a response to an increase in predation pressure. Increase in effective
69 size and attaining a “size refugia” is one of the common anti-predatory strategies exploited by
70 marine invertebrates [29-33]. Such “size refugia” is often a result of handling limit of the
71 predator [22]. Interestingly, prey smaller than the “size refugia” are not always attacked with
72 equal frequency. It has been observed that the medium size class are often attacked the most,
73 making them the preferred size class for predation [13, 25]. This points to an apparent
74 predation-resistance of extremely small sized prey. If the attacks on extremely small prey
75 significantly reduces the net energy gain of the predator, it would be expected to find a low
76 predation pressure in smaller sized prey [27]. This may lead to an “inverse size refugia” in
77 the smaller size class and shield the extremely small prey from predation. Harper and Peck
78 [34] also demonstrated low intensity of durophagous predation in tropical brachiopods and
79 attributed the micromorphic nature of tropical brachiopods as a defense against durophagous
80 predation. Unfortunately, the drilling predation dynamics in juveniles and extremely small
81 molluscan prey are rarely studied and hence, not well understood to test the existence of
82 predation resistance in smaller prey.

83 The Quilon limestone of early Miocene, exposed in southern state of Kerala, India
84 preserves a molluscan assemblage, dominated by bivalves and gastropods. This fauna is
85 characterized by extremely small size (<5mm) in comparison to the bivalve fauna of coeval
86 Chhasra formation of the Kutch Basin, India representing the same biogeographic province
87 namely Western Indian Province (WIP) [35]. Both of these fauna displays abundance of

88 predatory drillholes. Using these two fauna, we attempted to evaluate predator-prey dynamics
89 in extremely small size class, addressing the following questions:

- 90 i. What is the nature of prey-predator dynamics (in terms of prey selectivity, size
91 selectivity, site selectivity) in the extreme size class?
- 92 ii. Does the micromorphy provide any adaptive advantage against drilling
93 predation?

94

95 **Materials and methods**

96 **Geological setting and collection**

97 All the specimens are collected from an extended cliff section of Asthamudi Lake (N
98 08°58'36", E 076°38'08") near Padapakkara village, Kerala, India (Fig 1). It corresponds to
99 the Quilon limestone outcrop studied by Dey [36], Menon [37,38], and Reuter et al [39]. This
100 unit is represented by fossiliferous hard greenish limestone and interpreted as a seagrass
101 habitat of Burdigalian (early Miocene) age [39]. The diverse fauna shows exquisite
102 preservation of various invertebrate groups (including gastropod, bivalves, cephalopod,
103 scaphopod, ostracodes, foraminifera and crabs) and dominated by individuals of small body
104 size (<5 mm). Bulk sample was collected from the vertical face of the exposure.

105

106 **Fig 1.** Map of Indian subcontinent with the Kerala and the Kutch Basin demarcated by a star
107 and a circle respectively (inset). The detailed map of studied locality with exposures of
108 Quilon limestone. The locality of collection is marked by a star.

109

110 Bulk sample of loose sediments (~230gm) were soaked for 2-3 days in normal water.
111 Repeated heating and thawing was used to separate specimens from the limestone matrix.

112 The processed samples were then sieved using a stacked sieve of five mesh sizes (63, 60, 35,
113 25, 18 μ m). Sediments below 25 μ m sieve size did not contain any fossil. A total of 2032 intact
114 bivalve specimens were studied under microscope and identified upto family level. Using the
115 digitized images, the specimens were measured with the help of Image J. We measured all
116 drilled specimens and 20 random undrilled specimens from each of the family for size
117 analysis (Data File S1). We used SEM image to document representative specimens. We also
118 compared our data with previously published predation data from the bivalve fauna of coeval
119 formations including Chhasra formation of Kutch, India [25] (Fig 1).

120

121 **Analysis**

122 Using the standard criteria for identifying predatory drillhole [16], we identified the
123 predatory drillholes. We also found a few very small, cylindrical drillholes. The morphology
124 of these drillholes is significantly different from the predatory drilling and hence, excluded
125 from our analysis. We considered families that are represented by more than ten individuals
126 for this study.

127 Because all the bivalve specimens in our collection are disarticulated valves, drilling
128 frequency (DF) was calculated by dividing the number of drilled valves by the half of total
129 number of valves in the collection [40].

$$130 \quad \text{Drilling frequency (DF)} = N_D / (N * 0.5)$$

131 Where

132 N_D = number of valves with complete drillhole

133 N = total number of valves.

134 The incomplete drilling frequency (IDF) was calculated by dividing the total number
135 of incompletely drilled valves by the total number of drilled valves (complete and
136 incomplete) present in the collection [25].

137 Incomplete drilling frequency (IDF) = $N_{ID} / (N_{ID} + N_D)$

138 Where

139 N_{ID} = number of valves with incomplete drillhole

140 N_D = number of valves with complete drillhole.

141 Because there is no incidence of multiple drillholes for single specimen in our
142 specimens, the calculated IDF is comparable to prey effectiveness (PE) proposed by Vermeij
143 [1].

144 To reconstruct the predator size from a drill hole, we used following formulas
145 proposed for Naticid [22] and Muricid [24] gastropods.

146 For Naticid, $\log(Y_{nat}) = -0.372 + 0.552 (\log X_{nat})$

147 Where

148 Y_{nat} = Drillhole diameter

149 X_{nat} = Predator size

150

151 For Muricid, $\log_e(Y_{mur}) = 0.82 \log_e(X_{mur}) - 2.46$

152 Where,

153 Y_{mur} = Maximum outer diameter of the drillhole

154 X_{mur} = Maximum predator size.

155 We found it difficult to follow the standard protocols using sector grids [41] to assign
156 location of the drillhole in the small specimens of the studied fauna. Instead, we divided each
157 valve into three concentric regions (umbonal, middle and edge) and assigned the locations to
158 the drillholes. The division of the sites was maintained consistently for all the drilled
159 specimens.

160 We used Mann-Whitney U-test to compare response (in terms of size, drilling
161 frequency) between various groups based on species identity, ecological character. To

162 compare between different ecological groups and different size classes (small, medium,
163 large) we used Chi² test. To compare the size distribution of various categories (i.e. drilled,
164 undrilled), we used Kolmogorov-Smirnov (K-S) test. To assess the relationship between
165 predator and prey size, we used Pearson correlation test. All the analysis is done on R
166 software [42].

167

168 Results

169 Predation intensity and success

170 A total of 2032 valves represent nine families of bivalves, dominated by Cardiidae
171 (Fig 2, Fig 3A). A total of 62 valves show drillholes representing six families; Arcidae,
172 Veneridae and Tellinidae does not have any drilled individuals (Table 1). The pooled DF is
173 0.06 and IDF is 0.25. We did not find incidence of multiple drillhole in any specimen. The
174 majority of the drillholes are created by Naticid gastropods (84%).

175

176 **Fig 2.** SEM pictures of the drilled bivalve families of Kerala, India. Complete drillholes are
177 present in Cardiidae (A), Corbulidae (B), Glycymerididae (C), Cardiidae (D), Lucinidae (E),
178 Anomidae (F) and incomplete drillhole on Lucinidae (G), Corbulidae (H).

179

180 **Table 1.** Taxonomic summary of drill hole data with ecological information of Kerala, India.

181

Family	Abundance	Undrilled	Complete Drill holes	Drill holes at umbo	Drill holes at middle	Drill holes at edge	Naticid	Muricid	Incomplete Drill holes	DF	IDF	Substrate	Mobility
Corbulidae	271	246	16	1	12	3	9	7	9	0.12	0.36	Infaunal	Immobile
Veneridae	147	147	0	0	0	0	0	0	0	0	-	Infaunal	Mobile

Cardiidae	1298	1264	34	1	28	5	32	2	0	0.05	0	Infaunal	Mobile
Tellinidae	23	23	0	0	0	0	0	0	0	0	-	Infaunal	Mobile
Lucinidae	181	164	5	1	3	1	4	1	12	0.06	0.71	Infaunal	Mobile
Anomidae	47	43	4	3	0	1	4	0	0	0.17	0	Epifaunal	Immobile
Arcidae	34	34	0	0	0	0	0	0	0	0	-	Epifaunal	Mobile
Glycymerididae	29	27	2	1	0	1	2	0	0	0.14	0	Infaunal	Mobile
Overall	2030	1948	61	7	43	11	51	10	21	0.06	0.26	-	-

182

183

184 The relative abundance of prey family varies and is not showing any control on DF or
 185 IDF (Fig 3A-C). DF and IDF vary significantly between families (Fig 3B, C). Anomidae
 186 shows highest DF (0.17) followed by Glycymerididae, Corbulidae, Lucinidae and Cardiidae
 187 (Table 1). Lucinidae shows highest incidence of incomplete drillholes (0.7) followed by
 188 Corbulidae.

189 Majority of the drillholes are located in the middle (71%), followed by edge drilling
 190 (18%) and umbonal drilling (11%) (Table 1). Except for Anomidae and Glycymerididae, all
 191 the families show rarity of umbonal and edge drilling (Fig 3D).

192

193 **Fig 3.** Plots showing families in the studied assemblage with their individual abundance (A);
 194 drilling frequency (DF) (B); incomplete drilling frequency (IDF) (C) and site selectivity (D).

195

196 We did not find any significant difference in DF or IDF between infauna and epifauna
 197 (Fig 4; Table 2). However, the families with incomplete drilling are all infaunal. All the
 198 complete drillholes in epifaunals are created by Naticids; Muricid drillings are observed only
 199 on infaunals (Fig 4A; Table 2). DF is significantly higher in immobile families and IDF in

200 mobile families (Fig 4B; Table 2). Naticid drillings are significantly higher in mobile families
 201 and Muricids drillings in immobile families (Table 2).

202

203 **Fig 4.** Barplots showing pooled drilling frequency (DF) for various ecological groups based
 204 on their substrate relationship (A) and mobility (B).

205

206 **Table 2.** Results of Chi² test to evaluate the difference in DF between various ecological
 207 groups. Significant results are in bold.

	Undrilled valves	Drilled valves	Chi ²	P	Complete drillhole	Incomplete drillhole	Chi ²	P	Naticid drillhole	Muricid drillhole	Chi ²	P
Infauna	1871	78	0.18	0.67	57	21	1.45	0.23	47	10	0.84	0.36
Epifauna	77	4			4	0			4	0		
Mobile	289	29	25.1	0	20	9	14.6	0	38	3	7.52	0.006
Immobile	1659	53			41	0			13	7		

208

209

210 Size selectivity

211 We found a significant difference in size distribution between groups with and
 212 without drilling (complete and incomplete) (Fig 5A- C; Table 3). At the family level
 213 analyses, three families (Anomidae, Cardiidae, Lucinidae) showed a significant difference in
 214 size distribution between groups with and without drilling (Fig 5D- F; Table 3). Moreover,
 215 the smaller and larger size classes showed a significantly lower incidence of drilling (Fig 6,
 216 Table 4). The three families without any drilling (Arcidae, Veneridae and Tellinidae) show
 217 significant difference in size distribution in comparison to pooled size distribution of all the
 218 drilled individuals (Fig 7A-C). Individuals are significantly larger in Arcidae (K-S test
 219 statistic D=0.57, p<0.05) than the average size of the drilled ones. Both Veneridae (K-S test

220 statistic $D=0.54$, $p<0.05$) and Tellinidae (K-S test statistic $D=0.44$, $p<0.05$) are smaller than
 221 the drilled ones size.

222

223 **Fig 5.** Boxplot showing comparison between prey-size of drilled (complete and incomplete)
 224 and undrilled (A); complete and incomplete (B) and undrilled and complete (C) for pooled
 225 data. Lower panel shows the same for individual families (D-F). The boxes are defined by
 226 25th and 75th quantiles; thick line represents median value.

227

228 **Table 3.** Results of K-S test to evaluate the difference in prey size for overall and various
 229 families. Significant results are in bold.

	Overall		Anomidae		Cardiidae		Corbulidae		Glycymerididae		Lucinidae	
	D	p	D	p	D	p	D	p	D	p	D	p
Drilled vs Undrilled	0.21	0.02	0.8	0.03	0.43	0.02	0.17	0.9	0.55	0.64	0.45	0.05
Complete vs Incomplete	0.3	0.12	-	-	-	-	0.26	0.79	-	-	0.45	0.48
Undrilled vs Complete	0.2	0.05	0.8	0.03	0.43	0.02	0.21	0.82	0.55	0.64	0.7	0.04
Undrilled vs Incomplete	0.26	0.17	-	-	-	-	0.2	0.95	-	-	0.34	0.4

230

231

232 **Fig 6.** Barplot showing the proportion of drilled valves in three different size classes- small
 233 ($>1\text{mm}$), medium (1-2mm) and Large ($<2\text{mm}$).

234

235 **Table 4.** Results of Chi^2 test to evaluate the difference in proportion of drilled valves in three
 236 different size classes. Significant results are in bold.

	Undrilled valves	Drilled valves	Chi ²	p
Small ($>1\text{mm}$)	28	1	10.45	0.001
Medium (1-2mm)	115	56		
Large ($<2\text{mm}$)	29	5	4.42	0.04

237

			2.3	0.13
Small (>1mm)	28	1		

238

239

240

241 **Fig 7.** Boxplot showing comparison between pooled prey-size of drilled valves in contrast to
 242 the undrilled families including Arcidae (A), Veneridae (B) and Tellinidae (C). The boxes are
 243 defined by 25th and 75th quantiles; thick line represents median value.

244

245 There is a significant positive correlation between prey size with OBD (and inferred
 246 predator size) for Naticid attacks (Fig 8A, B; Table 5), but not for Muricid attacks. However,
 247 this positive relationship does not exist for Naticid attacks on Cardiidae and Corbulidae (Fig
 248 8C, D; Table 5). The inferred size of the Muricids is significantly larger than that of the
 249 Naticids.

250

251 **Fig 8.** Scatterplot showing relationship between prey size and outer borehole diameter (OBD)
 252 (A) and inferred predator size (B) for pooled data. Lower panel shows the prey-predator size
 253 relationship for Cardiidae (C) and Corbulidae (D). The open circles represent Naticid attack
 254 and the solid triangles represent Muricid attacks.

255

256 **Table 5.** Results of Pearson correlation test to evaluate the relationship between predator and
 257 prey size of studied locations. Significant results are in bold.

Location	Relationship	Pearson correlation coefficient	p
Kerala_Overall	Prey size vs OBD	0.25	0.04
Kerala_Overall	Prey- predator size	0.4	0
Kutch_Overall		0.12	0.41
Kerala_Naticid		0.34	0.01
Kerala_Muricid		-0.24	0.51

Kerala_Naticid	prey/predator vs predator size	-0.85	0
Kerala_Muricid		-0.93	0
Kutch_Naticid		-0.57	0

258

259

260 Comparison with macro fauna

261 The DF and IDF of the microscopic bivalves are significantly lower than those of
 262 larger bivalves of Kutch (Fig 9A, B, Table 6). The site selectivity between two provinces
 263 were also compared (Fig 9C, Table 6). In comparison to Kutch, the umbonal proportion of
 264 drillholes is significantly lower in Kerala. Unlike Kerala, Kutch fauna shows complete
 265 absence of Muricid predation.

266

267 **Fig 9.** Barplots showing comparison between Kerala and Kutch drilling frequency (DF) (A);
 268 incomplete drilling frequency (IDF) (B) and site selectivity (C).

269

270 **Table 6.** Comparison of drilling frequencies between Kerala and Kutch data.

271

Location	DF	IDF	Umbonal drilling	Middle drilling	Edge drilling
Kerala	0.061	0.2	0.3617	0.4043	0.234
Kutch	0.253	0.41	0.1333	0.68889	0.1778

272

273

274 The two fauna show different size selectivity. Unlike microfauna of Kerala,
 275 distribution of drilled and undrilled prey size are not significantly different in Kutch fauna
 276 (K-S test statistic $D=0.21$, $p=0.07$, Fig 10A). Moreover, it does not show a significant
 277 correlation between size of prey and Naticid predator – a trend that is observed in microfauna
 278 of Kerala (Fig 10B, Table 5). Both the regions, however, show significant negative

279 correlation between predator size with prey/predator ratio (Fig 10C, Table 5). When we
280 compared the data with three models of increasing, decreasing and constant prey size with
281 increasing predator size (Data File S2), both the regions matched the model corresponding to
282 constant and increasing prey-size with increasing predator-size.

283

284 **Fig 10.** Plots showing comparison of prey size distribution between the Kerala and Kutch
285 fauna (A), relationship between PPSRs (B) and the comparison based on the cost-benefit
286 model (C). The open circles represent Naticid attack and the solid triangles represent Muricid
287 attacks.

288

289 In a family specific comparison with global data of Miocene (Data File S3),
290 microbivalves demonstrate a low DF in comparison to the mean DF in all instances except
291 for Anomiidae; the observed DF of microbivalve is often lower than the lowest reported
292 value of DF for corresponding family (Fig 11).

293

294 **Fig 11.** Plots showing comparison of DF for individual families between globally reported
295 data for macrobivalve specimens (>5mm) and the present study. The boxes are defined by
296 25th and 75th quantiles; thick line represents median value.

297

298 **Discussion**

299 Record of predatory drillhole is one of the unique instances where predator-prey
300 dynamics can be studied quantitatively in deep-time. Among the studied prey taxa, bivalves
301 are one of the major contributors [9]. Yet, documentation of predation on bivalve
302 microfossils are largely absent except for a few brief reports [43, 44]. Consequently, the

303 nature of drilling predation in extremely small bivalves is largely unknown. Present study is
304 the first detailed attempt to understand the predator-prey dynamics at extreme size class.

305

306 **Nature of prey and predator**

307 Microbivalves, primarily defined based on their small size (<10mm) [45], are
308 enigmatic in their identity. Although some micromolluscs belong to families in which large
309 species predominate, the majority occur in relatively few families that are composed
310 exclusively of small species [45, 46]. On the other hand, juveniles of all families of bivalve
311 also contribute to the microscopic size spectrum of bivalve population and they often lack
312 adult characteristics. The studied fauna shows a number of families outside the exclusively
313 micromolluscan families [47]. Few species found in this assemblage, are represented by
314 larger megascopic individuals collected from the same formation [36]. The microscopic
315 bivalves of our study, therefore, probably represent the smaller individuals of available
316 species.

317 Majority of drilling in the present study is similar to those created by predatory
318 gastropods. The exact identification of predatory family is more complicated for
319 microbivalve community. The identification criteria for Muricid vs Naticid drillholes are
320 primarily developed based on the morphological nature of drillings on thick shelled molluscs.
321 With thin shelled microbivalves, the drillhole morphology is often uncharacteristic. However,
322 many of them represent characteristic marks of muricid and naticid drilling. The existence of
323 three genera of Naticid (*Natica*, *Tanea* and *Polinices*) and two genera of Muricid (*Triplex* and
324 *Dermomurex*) from the same locality supports our identification [48]. Majority of the
325 individuals of these predatory gastropod genera are quite small (<10mm), making them
326 potential predators for microfauna. Experimental studies demonstrated that juveniles of both
327 muricids and naticids create drillholes where the diameters are less than 0.1mm [49, 50],

328 often with irregular outline [51]. Although, some of the holes in our studied material match
329 this description (Fig 2E,G), many are quite regular in form. Moreover, a few studies claimed
330 that gastropods are not always able to drill immediately after hatching. Muricid gastropod
331 *Nucella lapillus* does not drill their usual prey barnacle upon hatching [52]. Instead, they feed
332 on unfertilized eggs, small polychaetes before finally switching to their usual diet of bivalves
333 and barnacles after attaining a minimum shell height of ~8mm. Juvenile Naticids are also
334 found to prey upon other groups such as ostracods [53] and foraminifera [54], instead of
335 bivalves. Considering the dominantly smooth outline and high average value of OBD
336 ($\gg 0.1\text{mm}$) of the studied drillholes, smaller individuals of the reported genera are more
337 likely to be the predators over the juveniles.

338 Muricid gastropods attack and drill primarily epifaunally. However, they may scour
339 shallow infaunal prey [16]. This explains the Muricid drillings on infaunal bivalves in the
340 assemblage. Naticid is much more versatile; although primarily it hunts infaunally, it can
341 perform the entire predatory action on the sediment surface [55]. Absolute dominance of
342 Naticid drilling in both infauna and epifauna of the studied assemblage shows such versatility
343 of Naticids.

344

345 **Prey selectivity in extreme size class**

346 Leighton (2003) [56] showed a positive correlation exists between relative abundance
347 of each species and their predation intensity for brachiopod group. However, results from
348 other studies challenge the generality of this observation [16, 25, 41]. Our data also shows
349 that abundance of taxa is not a good predictor of drilling frequency. We found Cardidae to be
350 the most abundant taxa and the highest DF is observed in Anomidae indicating prey
351 selectivity.

352 Incomplete drillholes are the signature of failed attacks caused by effective defensive
353 morphology of the prey (such as large size, ornamentation), presence of secondary predators,
354 competition etc [57-59]. Our data shows strong association between IDF and the
355 morphological defense of the prey taxa. Incomplete drillholes occur only in two families,
356 Lucinidae and Corbulidae, characterized by unique morphological feature. Lucinidae species
357 have heavy ornamentation on the shell surface which is known to impart resistance against
358 drilling [60]. Concentric ribs of Lucinids that increase effective thickness, can provide
359 effective resistance against drilling only when selected as the drilling location. The fact that
360 majority of the incomplete drillholes located on the ribs and not in between, supports this
361 argument (Fig 2G). Drilling predation is claimed to be inhibited in Corbulidae due to the
362 presence of conchiolin layers within corbulid valves [41, 61-63] along with other
363 antipredatory morphology such as increased valve thickness, increased inflation [64]. The
364 lower success rate in Corbulidae points to the morphological defence. We also found average
365 prey size with incomplete drillholes are larger than those with complete ones for both of the
366 cases; this supports the claim of bigger size as responsible factor for producing incomplete
367 drillholes in these two families.

368 Ecological selectivity plays a major role in drilling predation. In general, epifauna are
369 more susceptible to predation by epibenthic than infauna [1, 65]. Our results, however, does
370 not support this notion of increased protection for infauna at such small size class. This may
371 be due to the fact that depth of infauna at such size class is not enough to offer effective
372 protection against predators including epifaunal predators. Abundance of Muricid drilling in
373 the infaunal prey in our sample supports this. Mobile behavior of bivalves has been claimed
374 to be an efficient strategy to evade predators [13, 66, 67]. Mobility seems to be an effective
375 defense even at such small size class, especially fending Muricid gastropods that succeeded
376 more attacking immobile prey. Mobile prey even at small size seems to either achieve

377 complete evasion (low DF) or escape after being attacked (high IDF); this pattern indicates
378 that mobility offers predation refuge for extremely small sized bivalves.

379 The position of the drillhole on the prey shell is indicative of the degree of behavioral
380 stereotypy of the predator. Non-random siting of drillholes is primarily related to
381 manipulation technique of the predator [68] and dependent on the morphology of the prey
382 [69-71]. Such site preference is widely reported, especially for Naticids [22, 72-75]. Such
383 high level of stereotypic behavior of Naticids may be due to the fact that they completely
384 cover their prey inside the mantle and has lesser flexibility. Muricids, on the other hand,
385 crawl across bivalve prey before initiation of drilling, and thus may show more variation in
386 drillhole position [76]. We did not, however, find any difference in degree of stereotypy
387 between Muricid and Naticid. Majority of our specimens show central position of drillhole
388 irrespective of the predator identity. The location of the drillholes also provide important
389 information on predation dynamics. Umbonal drilling, although common among bivalves in
390 general, is not profitable for the predator because of the high thickness of area. This thickness
391 increases substantially with increasing size of the prey and may pose deterrence to drilling.
392 The common occurrence of umbonal drilling is probably due to the fact that it offers the
393 predator some advantage in handling the prey more effectively. At extremely small size,
394 umbonal thickness is not substantially different from the rest of the shell and hence should be
395 preferred. Our specimens, however, do not show a significant dominance of umbonal drilling.
396 Edge drilling, on the other hand is considered a faster technique albeit risky; a prey can
397 damage the feeding organ (proboscis) by clamping down [77]. Edge-drilling was used when
398 competition was intense [78]. We also found a significant number of edge drilling in our data
399 indicating to probably a competitive scenario [12]. This is not unlikely considering the large
400 number of young individuals after spawning season of predator that exponentially decrease
401 with time before reaching a plate near adulthood.

402

403 **Size selectivity in extreme size class**

404 Size is a crucial factor in controlling prey selection by drilling predators. Drillhole
405 size is indicative of the size of the drillers for both Muricid and Naticid gastropods [22, 79].
406 Well accepted equations to derive predator size from OBD are primarily developed from
407 feeding experiments using extant gastropods of normal size; the applicability of these
408 equations to smaller size class has not been tested explicitly. The inferred gastropod size
409 using the drillholes of our study matches the general size spectrum of gastropods reported
410 from this locality [48] confirming the generality of these relationships even at such smaller
411 size class.

412 The positive correlation between Naticid predator and prey size in microbivalve
413 assemblage indicates a size dependent prey choice. This relationship has been explained as an
414 energy maximizing strategy that balance the energy gain associated with the large food items
415 and the energy spend associated with capturing and boring that large prey item [22]. For
416 Muricid, the size relationship between prey and predator does not show any significant
417 correlation. Unlike Naticids, energetically viable attacks by Muricids are often associated
418 with insignificant correlation between predator and prey size [26, 57].

419 Previous studies reported the existence of a handling limit for a specific predator,
420 beyond which the attacks are likely to fail and prey larger than this handling limit is immuned
421 from successful attacks [22, 26]. Size emerges as an important factor when we evaluate the
422 taxa without any drillholes. Both Arcidae and Veneridae are significantly different in size
423 than the families with drillhole. The larger size of Arcidae supports the idea of a “size refuge”
424 [1, 22]. The smaller size of Veneridae is also probably protecting it by offering limited
425 nutritional value and hence providing a “inverse size refugia”. Although Tellinidae did not

426 show any size difference, extremely low abundance (low encounter rate) of this taxon may be
427 responsible for lack of drilling.

428

429 **Nature of prey-predator size dynamics**

430 Prey preference by the predator is best evaluated using cost-benefit model developed
431 on the tenets of optimal foraging theory. Such models have been used to correctly predict the
432 prey choice for both Naticid [22, 41, 80] and Muricid [26]. For these models, cost-benefit
433 ratio is estimated by the ratio of shell thickness and internal volume of the prey. Due to the
434 small size of our specimen, it was not realistic to measure the thickness of the shell. In
435 absence of this information, ratio of prey and predator has also been used to evaluate the
436 relative change of predatory behavior [81]. Predators always prefer the prey item with lowest
437 cost-benefit ratio in the size range that can be handled [16]. Cost: benefit ratio of a particular
438 prey taxon generally decreases with ontogeny due to relatively higher energetic yield of the
439 biomass [22]. Consequently, for a specific predator size prey with larger size ought to be
440 beneficial if thickness does not change significantly. Because of the extremely small size and
441 early ontogenetic stage, we do not expect significant variation in thickness in the
442 microbivalve population. Our study, however, shows a very high prey: predator size ratio for
443 small predators and the ratio decreases with increasing size of the predator. To give rise to
444 this apparent counterintuitive decreasing prey-predator size ratio, the predator needs to
445 exercise one of the following options with increasing size: a) maintain a constant prey size
446 choice, b) choose smaller prey or c) choose larger prey, but not proportionally large. Our
447 models show that, the declining ratio of prey:predator is achieved by maintaining a constancy
448 of prey size or choosing inadequately large prey. Interestingly, Muricids tend to show a
449 preference towards lower size in comparison to Naticids. In comparison to megabenthic
450 community of Kutch, the macrobenthos is characterized by a higher prey-predator ratio

451 although the change in prey choice by increasing size of the predator shows similar trend.
452 The relatively lower value of prey-predator ratio for larger predators of Kutch is still probably
453 energetically viable because energetic yield of the prey increases exponentially with
454 increasing prey size ([22], Fig. 1)

455

456 **Possible effect of taphonomy and depositional environment**

457 Comparison might be affected by the fact that these two regions represent two
458 different depositional environments. Kerala has been interpreted to represent a seagrass
459 environment [39] that is often characterized by low of predation pressure [82, 83]. The
460 emergent seagrass blades cause decrease in the mobility of predators and the visual detection
461 of prey [82, 84] and the roots and rhizomes of the seagrass act as a barrier to digging
462 predators from attacking the infaunal preys [83, 85]. Thus, the predation refuge which the
463 seagrass offers to the bivalves causes the decrease in overall predation pressure. However, the
464 infauna in the microbivalves of the studied locality does infact show slightly higher predation
465 intensity. Moreover, the low family-specific DF of microbivalves in comparison to global
466 record of Miocene makes it unlikely that the depositional environment alone is creating such
467 low predation intensity.

468 Taphonomic attributes are different for macro and micro invertebrates. Generally
469 smaller individuals shelly invertebrates are poorly preserved [86] and are often affected more
470 by other taphonomic attributes such as hydrodynamic sorting, that may even alter drilling
471 signature [12, 87]. Considering the relatively pristine state of preservation of macrobenthos of
472 our study, however, it is unlikely to assume taphonomy to be the primary contributor of
473 generating the pattern.

474

475 **Evolutionary implication**

476 In a study on modern brachiopods, Harper and Peck [33] found a significant
477 proportion of micromorphic brachiopods in the tropics. All three extant clades of brachiopods
478 from tropical ocean are micromorphic. Brachiopods found till 17° in the southern hemisphere
479 are characterized by the complete absence of large (>10mm) species [88]. The micromorphic
480 individuals were often better protected against durophagous predation. In a study on the
481 predation intensity of temperate rhynchonelliforms, Harper et al [32] found the existence of
482 both classical size refugia for larger individuals as well as “inverse size refugia”. Along with
483 low frequency of repair scars in large individuals, the micromorphic ones (<5 mm) showed
484 almost complete absence of predation. The preferred target group appeared to be the medium
485 size class (20- 40 mm) with the frequency of repair scars normally distributed around that
486 class validating the prediction of optimal foraging theory [89]. Apart from the low energetic
487 yield of the small brachiopods, the low intensity of durophagous predation in small
488 brachiopods could be because of their inaccessibility due to cryptic life habit [90]. Based on
489 these, Harper and Peck [34] hypothesized that micromorphy of brachiopods is a likely
490 outcome of intense durophagous predation in the tropics and proposed micromorphy to be an
491 adaptive response to increasing durophagy at lower latitudes. Our study finds evidence of
492 effective defense rendered by micromorphy against drilling predation. The observed DF is
493 the lowest in comparison to majority the reported DFs from Miocene [25] pointing to the
494 rarity of such low predation intensity. Because of the effective defense in large and small
495 groups, we can expect an evolutionary trend towards increasing variance in the size of the
496 prey. Phanerozoic nature of predator-prey size ratio shows an increase without significant
497 change in prey size [91]. The variance in prey size is not showing recognizable directional
498 trend either (Fig.2A, [90]). However, it is known that the preservation potential of small
499 shells is significantly lower than the larger shells [86]. This makes it hard to comment on the
500 evolutionary trend of predation in extremely small prey. Moreover, we do not know if the

501 intensity of predation changed inhomogenously across size classes. It would be, therefore,
502 important to focus on relative proportion of drilling frequency across size classes through
503 time to appreciate the advantage of micromorphy against predation in evolutionary
504 timescale.

505

506 **Conclusions**

507 Our study documents the drilling predation dynamics in the extreme size class of
508 micromolluscs from Early Miocene deposits of India. Our analyses demonstrate that the
509 drilling predation in extreme size class is highly selective in terms of prey taxa, size, mobility
510 and site selection. Drilling occur primarily on medium size class (0.83- 2.32 mm) and prey
511 outside this size range are less likely to be attacked. This indicates the existence of an
512 “inverse size refugia” for extremely small prey along with the classical size refugia existing
513 for large prey. Mobility is found to be deterrent to drilling predation and it also increases
514 failure. In comparison to the predation in macrobenthos of the same biogeographic province
515 of coeval formation, microbenthos shows a lower level of predation intensity and rate of
516 failure. The interactions in microbenthos seems to be more strongly size-dependent compared
517 to those among the macrobenthos that are often characterized by a lack of prey-predator size
518 relationship. In comparison to the drilling predation in macrobenthos of global occurrences
519 during Miocene, microbenthos shows a lower level of predation intensity in a family specific
520 analyses. Prey-predator interaction in extreme size class highlights the importance of size in
521 determining the nature of predation dynamics. Considering the plasticity of body size in
522 response to environmental triggers, changing predation dynamics would be expected during
523 times of environmental change and would have significant effect in shaping the natural
524 selection of a group in deep time.

525

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529

530 **Supplementary materials**

531 **Data File S1. Dataset used for present study**

532 Family : Family names of bivalves; Prey size: Length of the prey; Drill hole morphology:
533 morphology of the drill holes/ Predator identity; Drill hole diameter: Outer borehole
534 diameter of the drill hole; Position: Position of the drill hole; Completion: Completion of
535 drill hole; Drilling: Type of prey (drilled or undrilled); Predator size: Length of the predator,
536 Kerala; Location: Name of the location from where specimens were collected; Size class:
537 small, medium or large.

538

539 **Data File S2. Dataset used for present study**

540 Prey1_increasing (mm): Prey size in increasing order keeping minimum and maximum
541 values same as original data; Prey1_decreasing (mm): Prey size in decreasing order keeping
542 minimum and maximum values same as original data; Prey1_constant (mm): Mean prey size
543 of original data; Predator1_increasing (mm): Predator size in increasing order keeping
544 minimum and maximum values same as original data; Location: Name of the location from
545 where specimens were collected.

546

547 **Data File S2. Dataset used for present study**

548 Authors: Name of the authors of the published literature from where DF is collected; Year:
549 Year of publication; Title: Title of the literature; Prey: Type of Prey item; Prey family: Name
550 of the famies; DF: Drilling frequency; Age: Age of the formation from where species are
551 collected.

552

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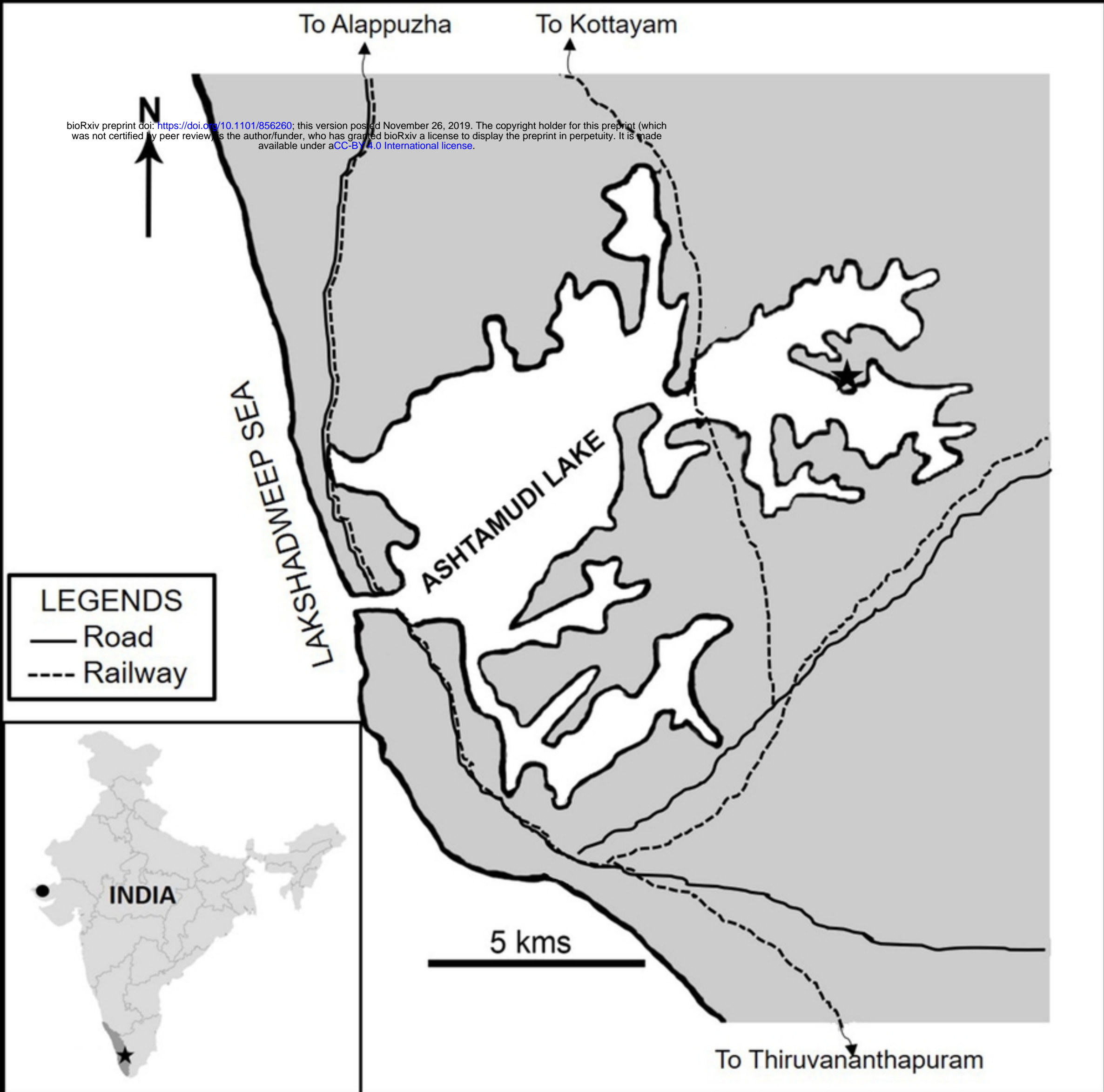


Figure 1

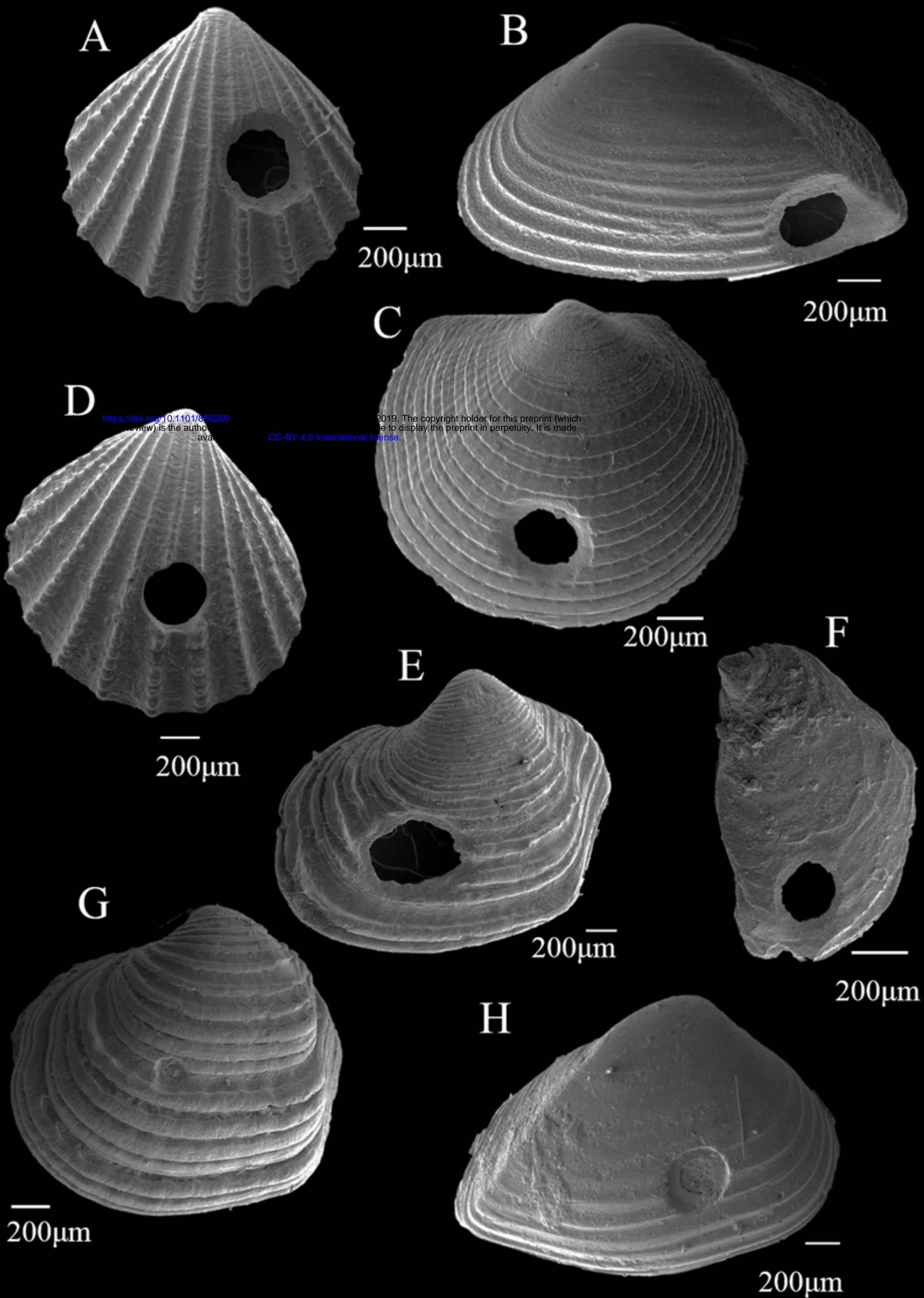


Figure 2

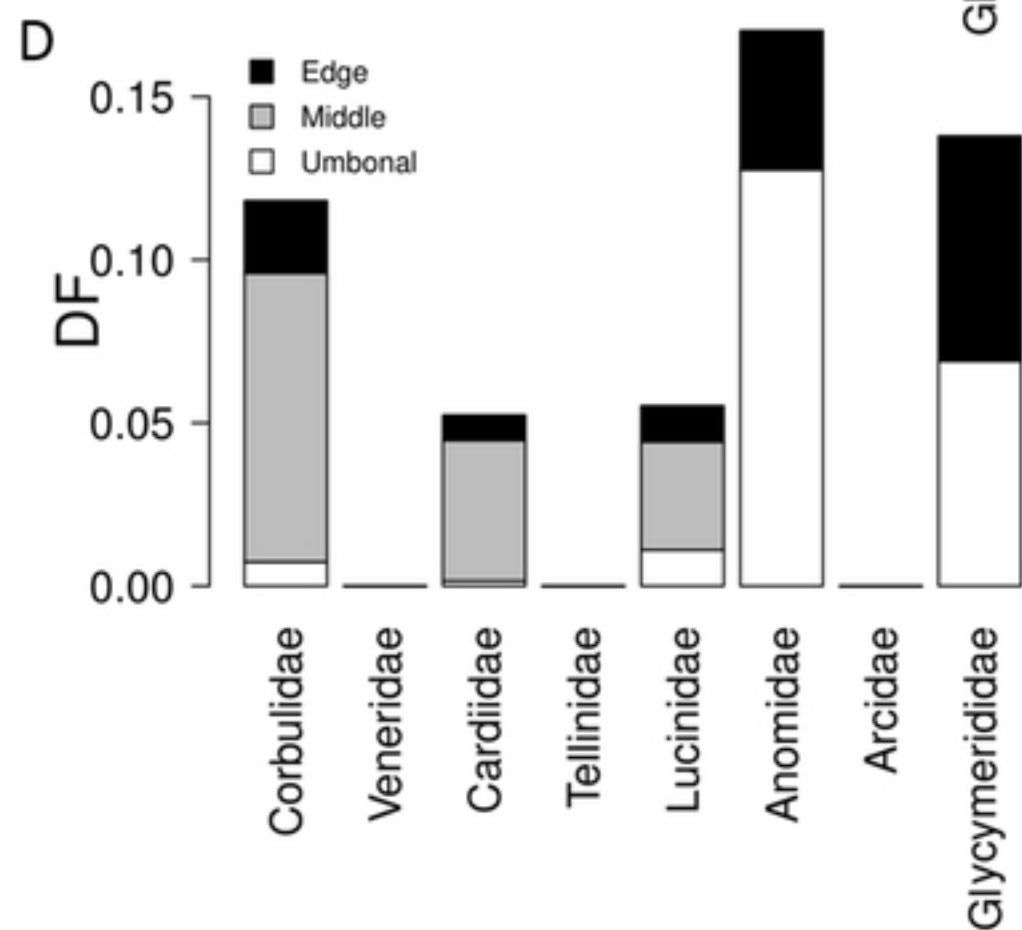
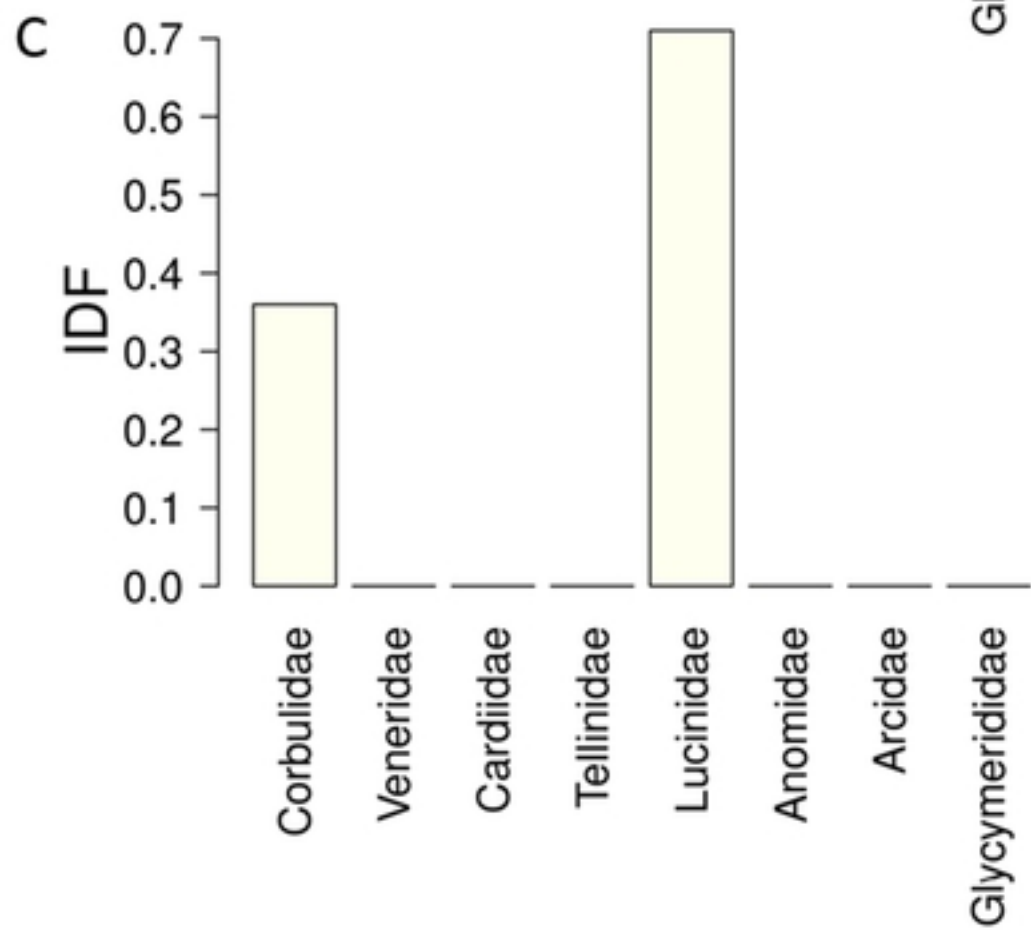
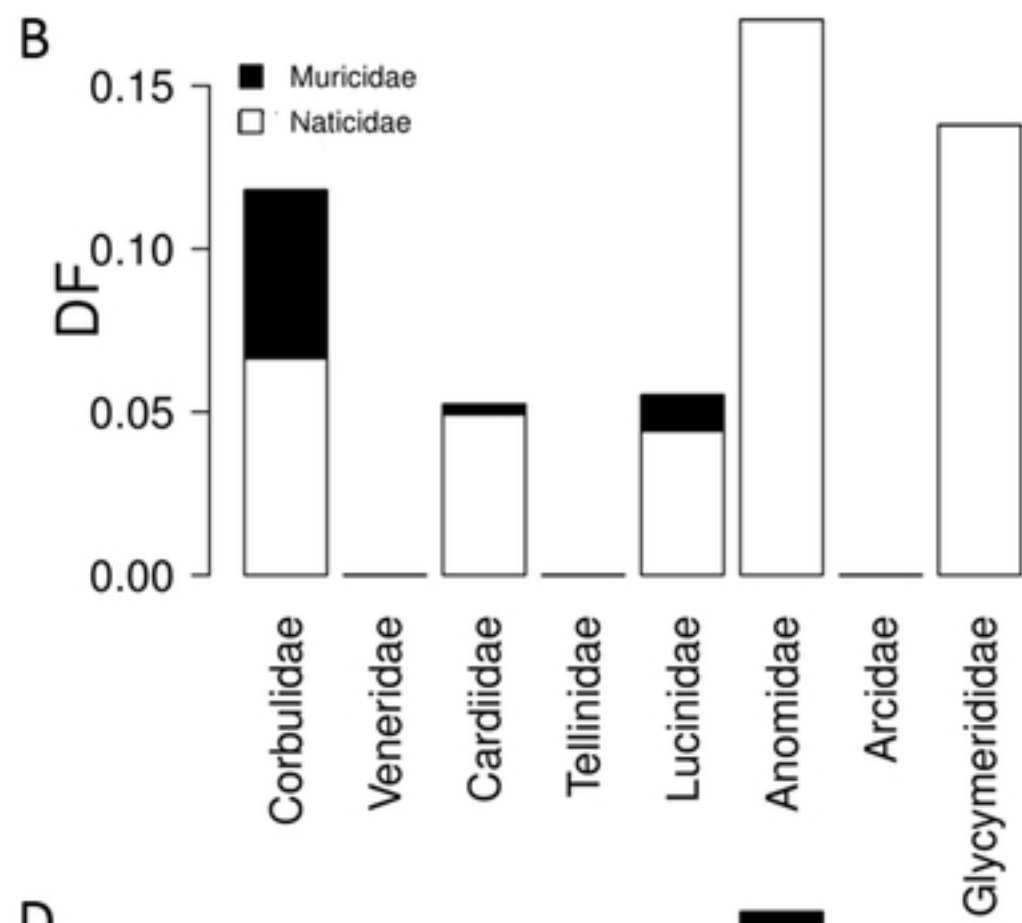
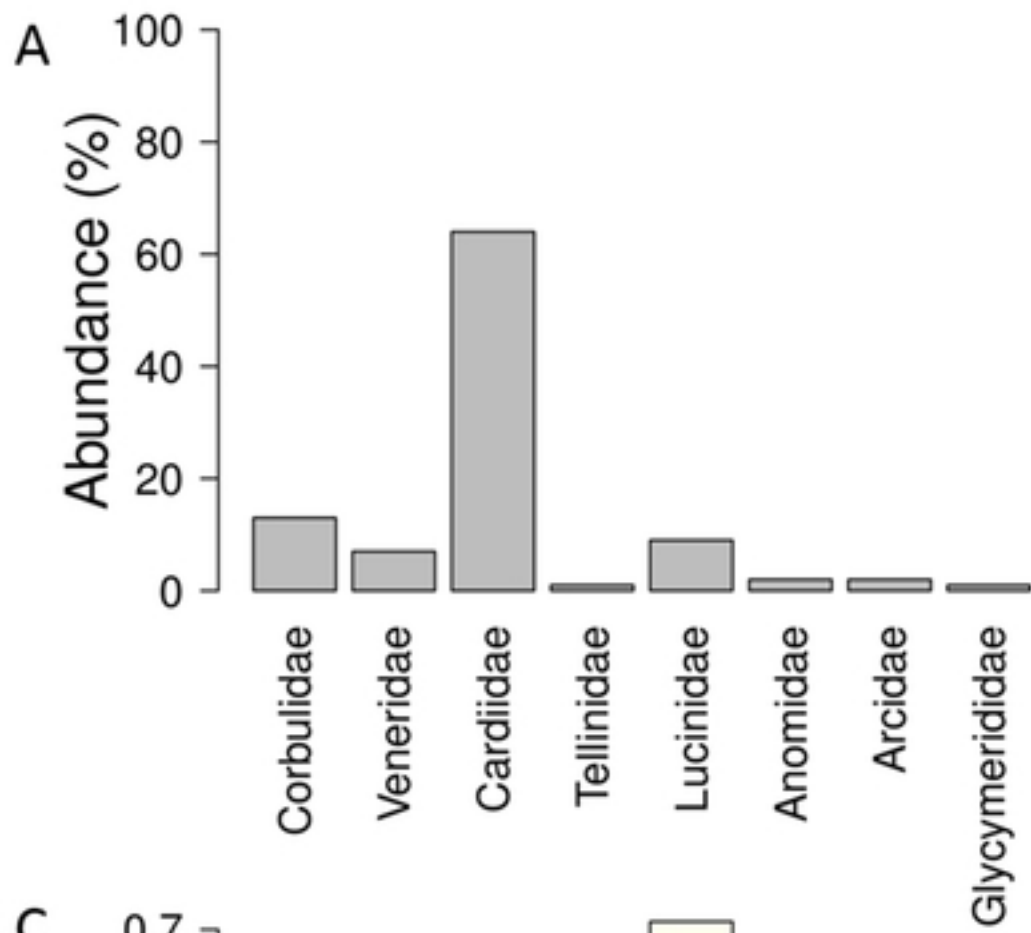


Figure 3

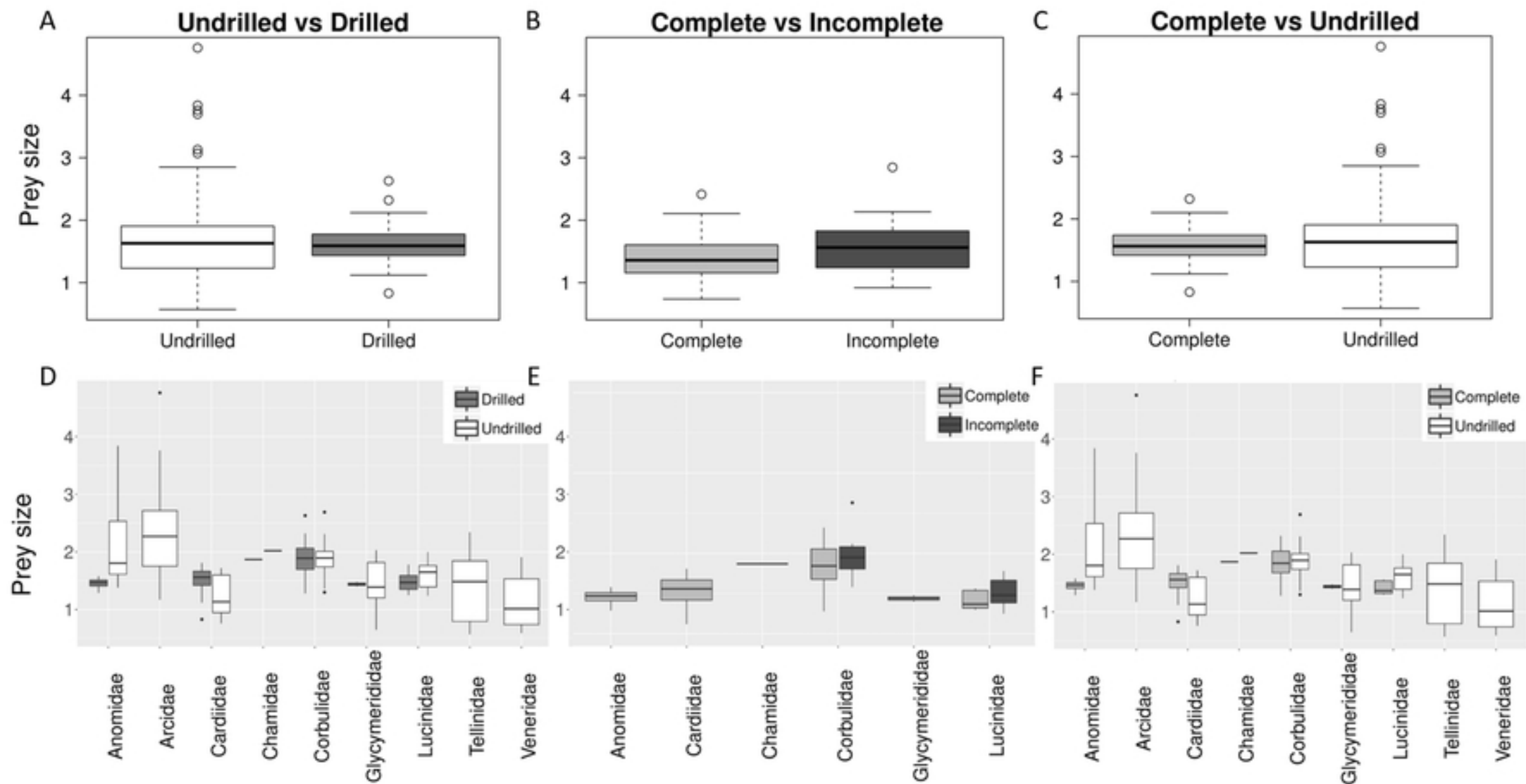


Figure 5

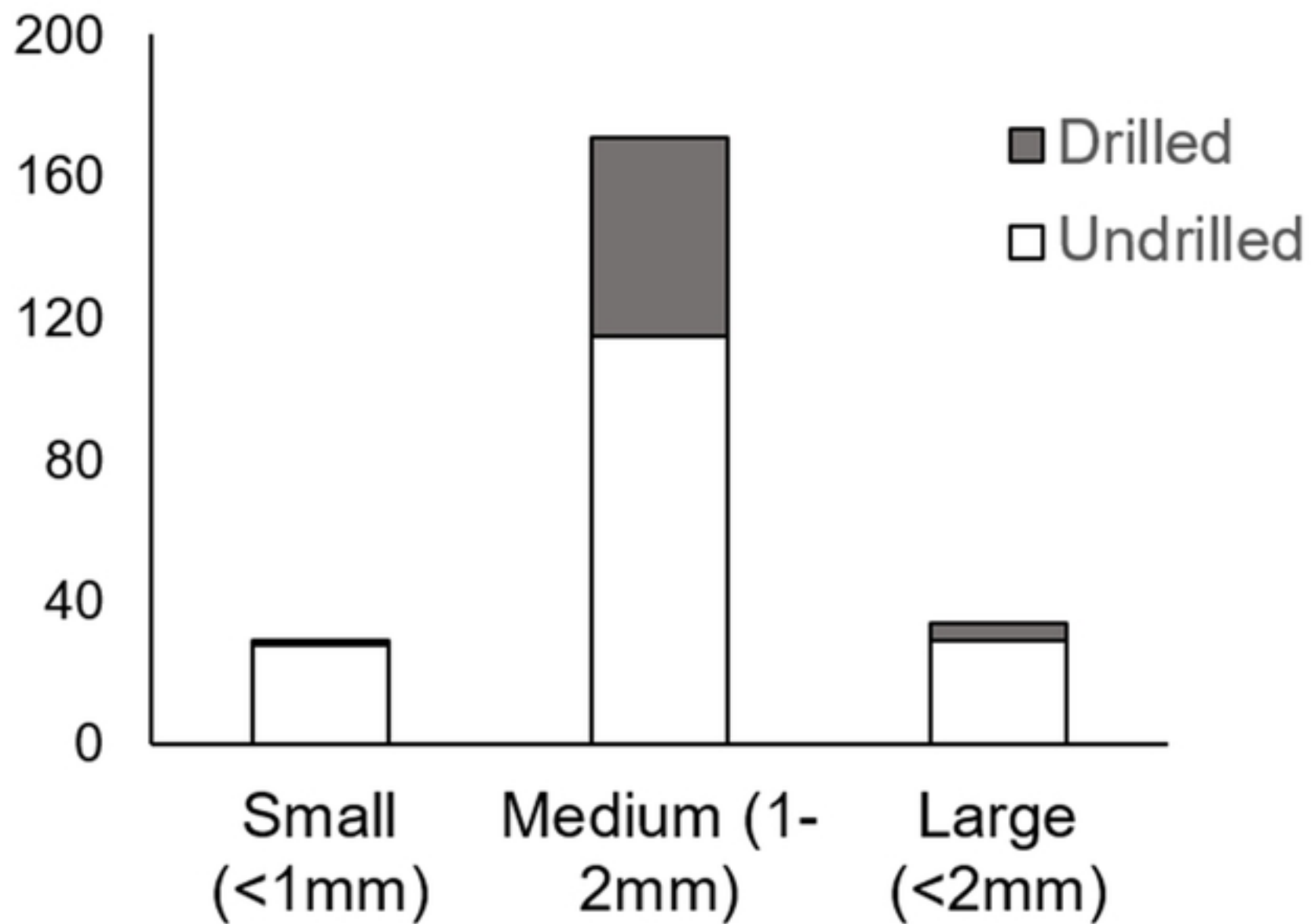


Figure 6

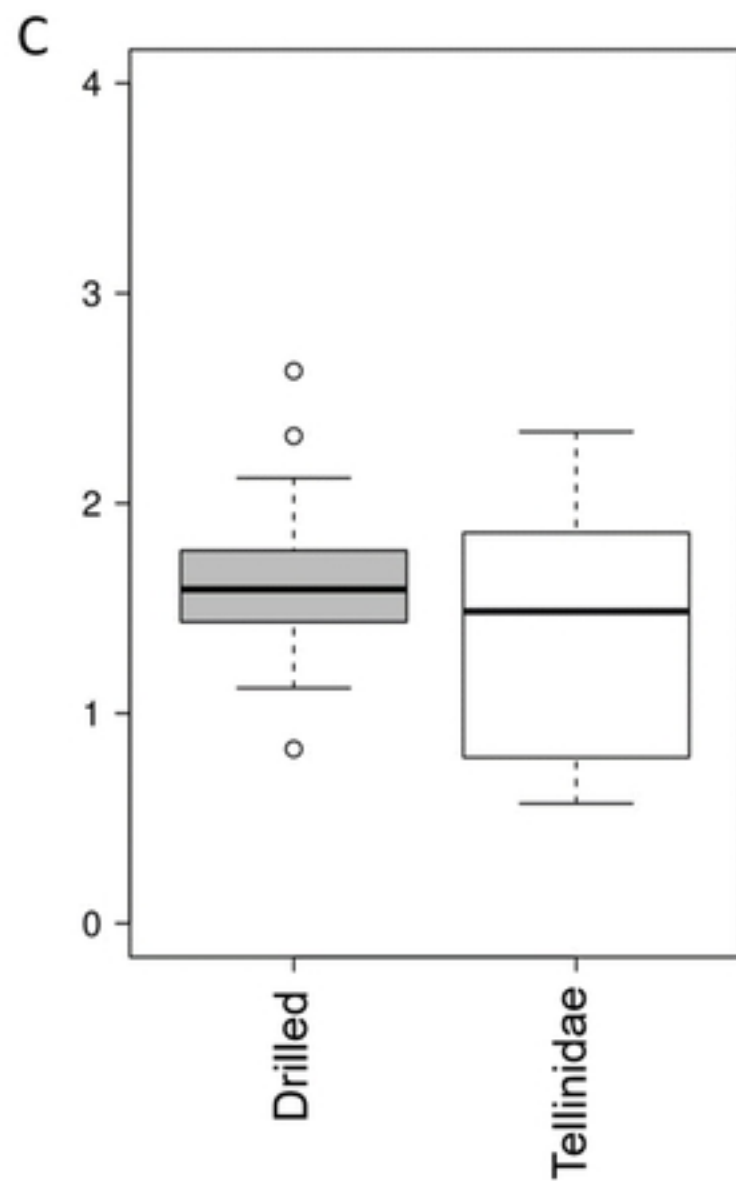
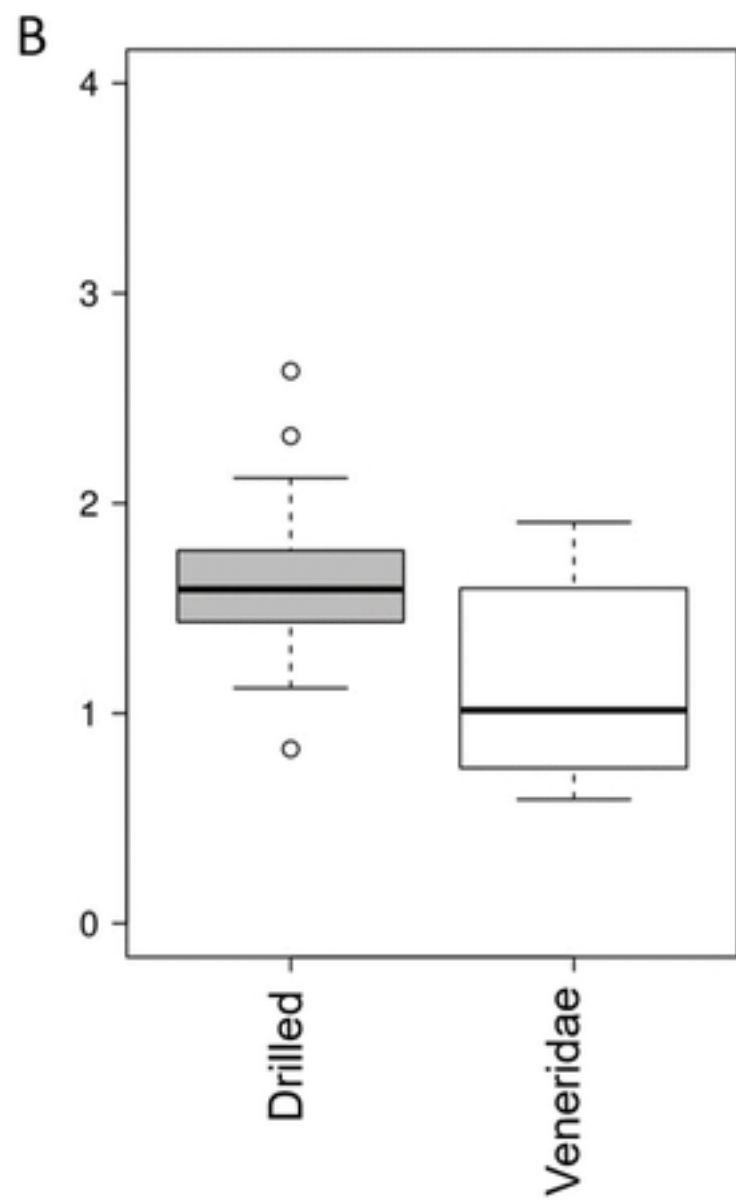
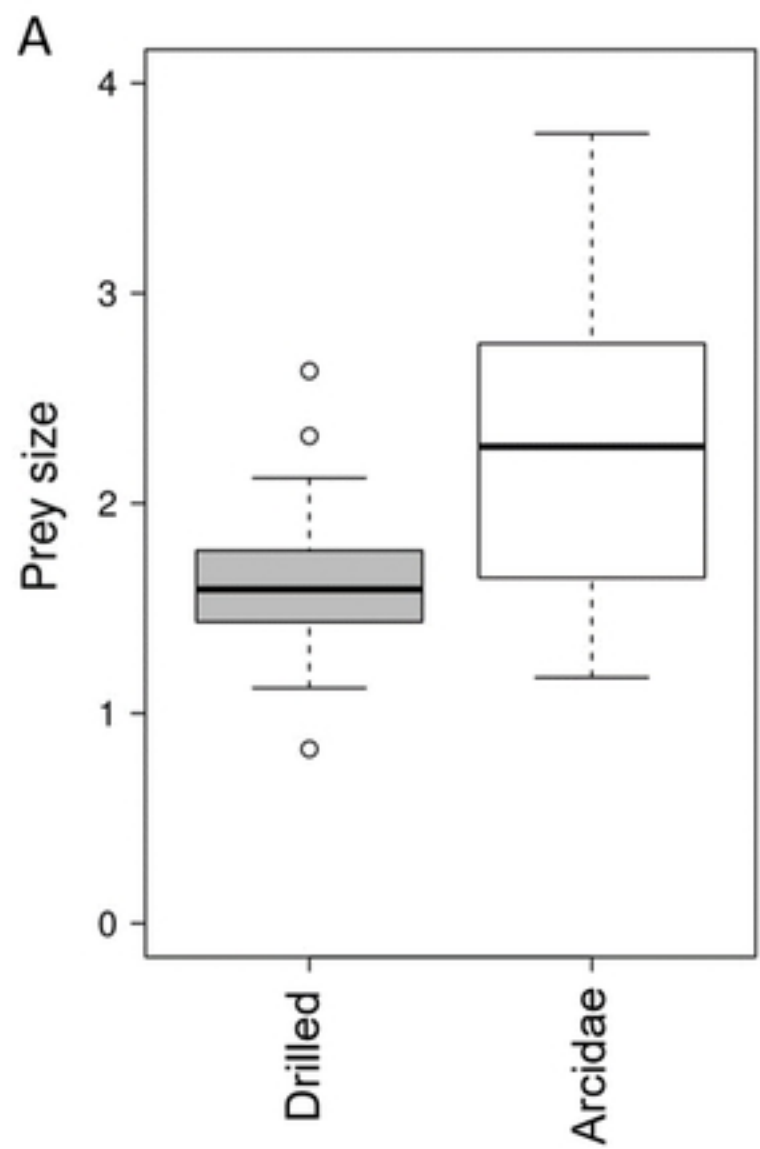


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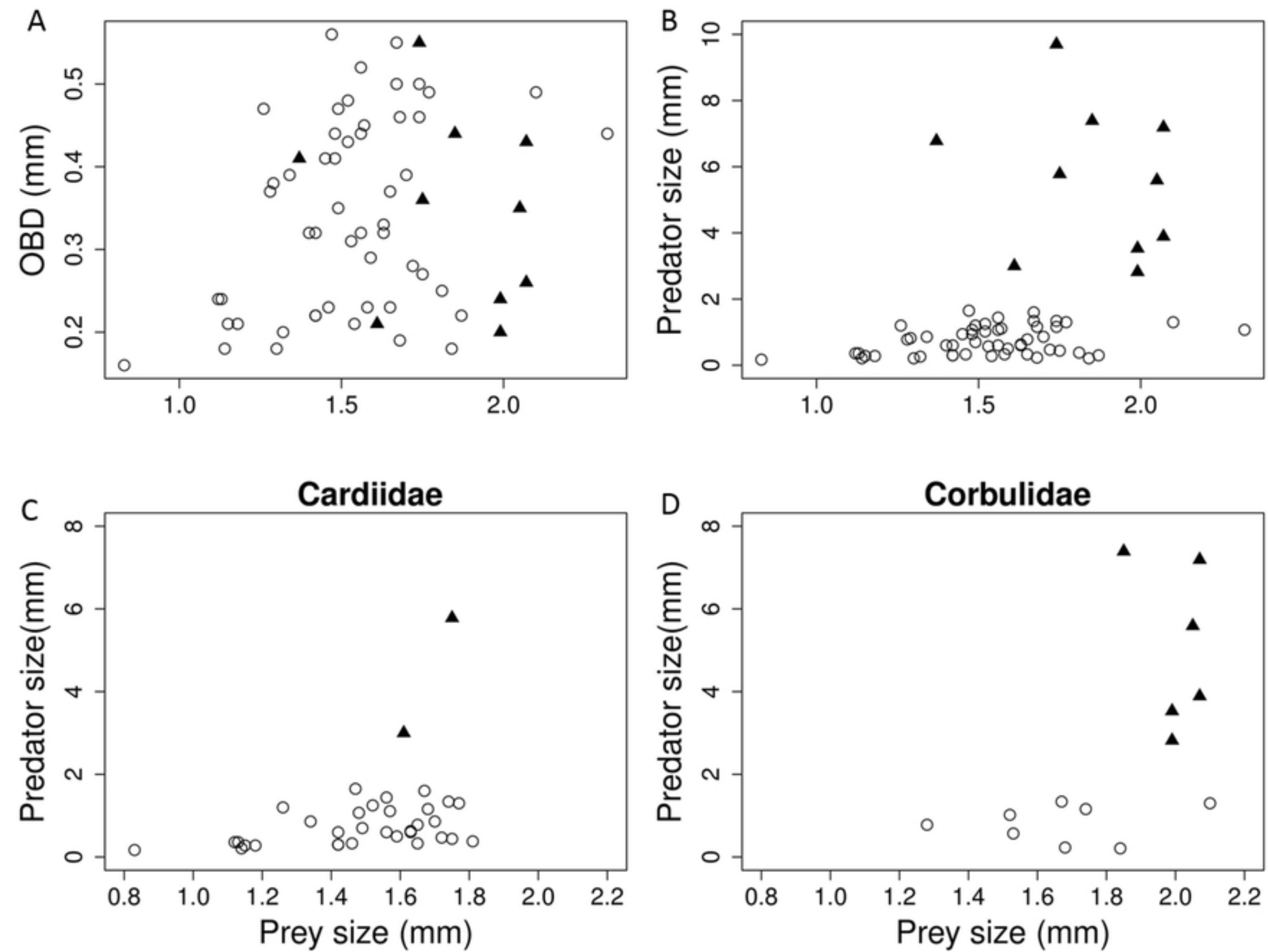


Figure 8

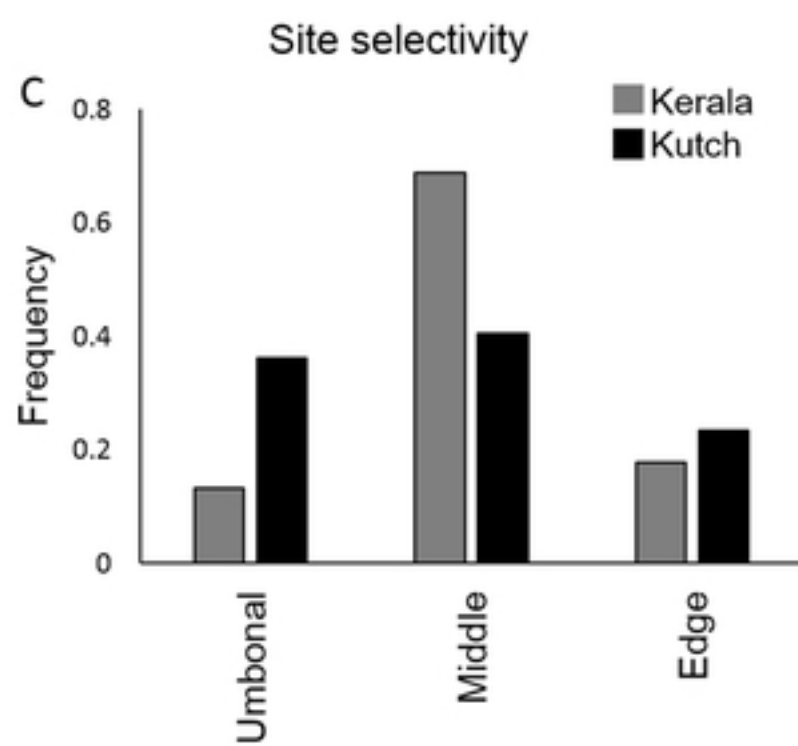
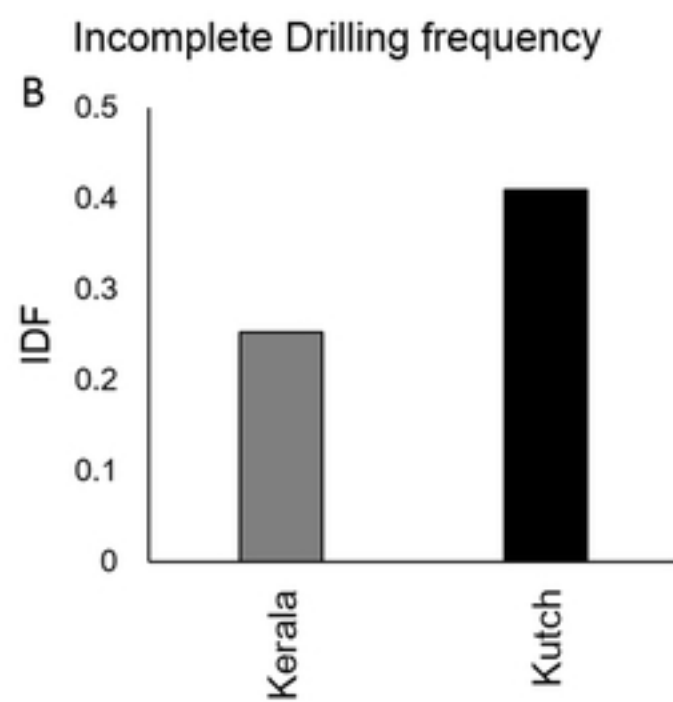
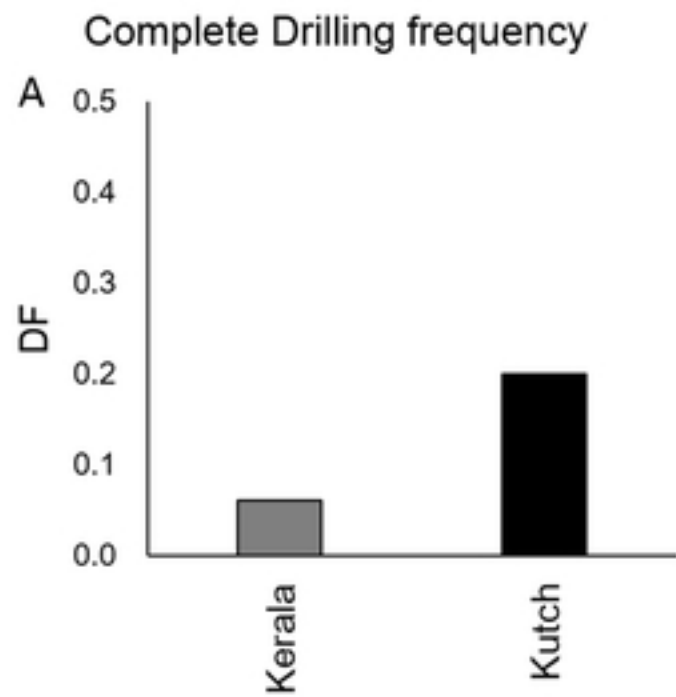


Figure 9

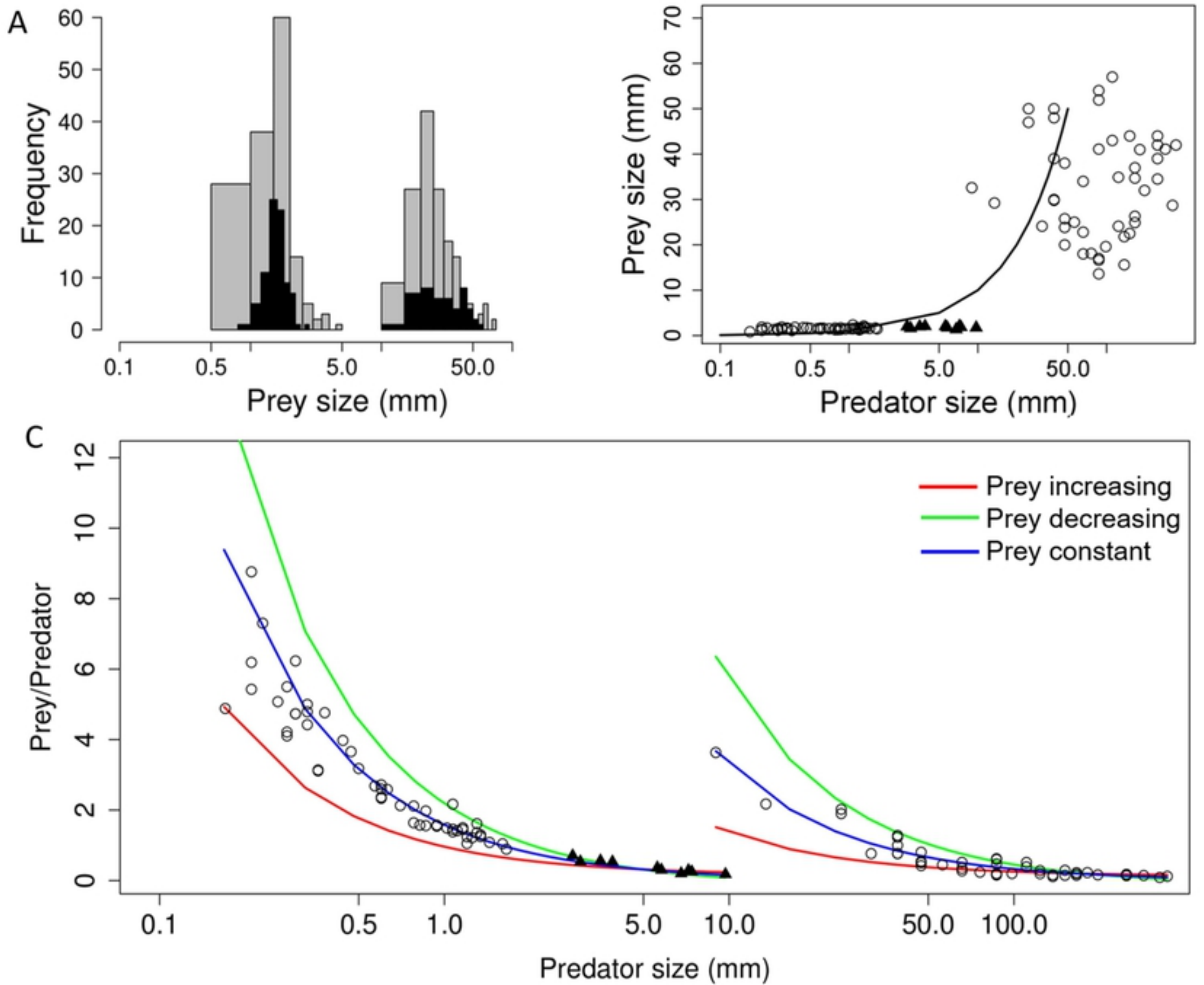


Figure 10

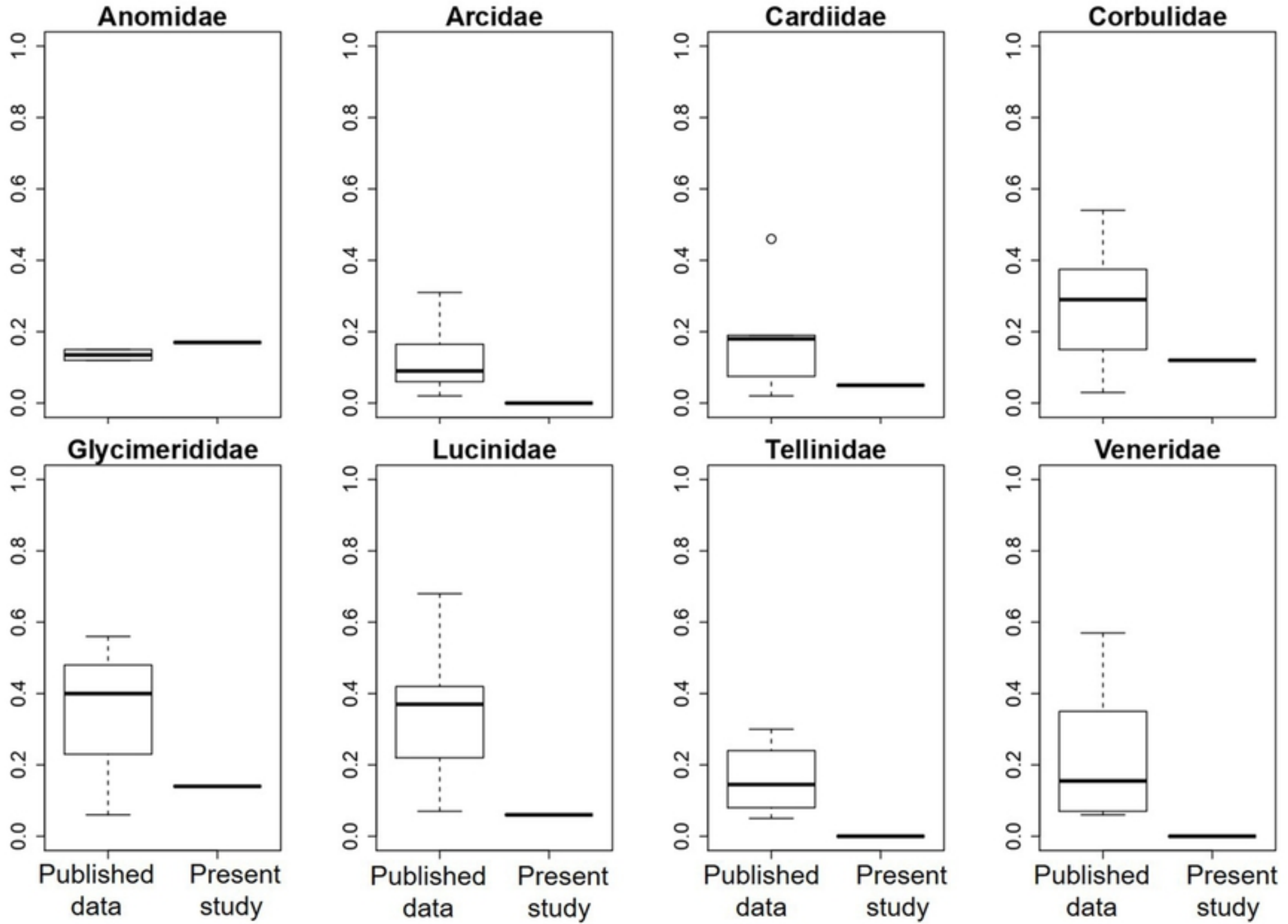


Figure 11

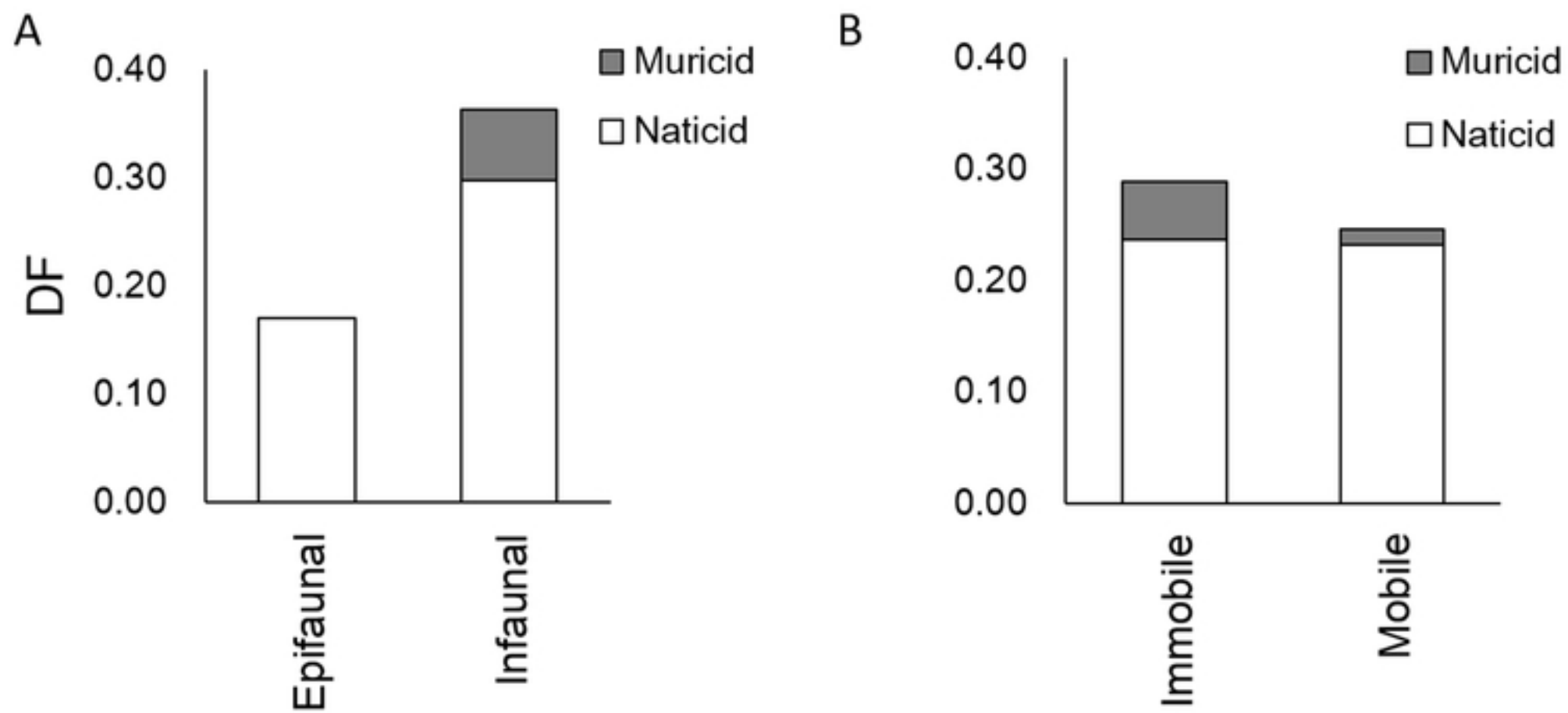


Figure 4