1     **Effectiveness of micromorphy against drilling predation: Insights from early Miocene**

2     **faunal assemblage of Quilon limestone, India**

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# 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

# Materials and methods

## 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 Kerela 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, 18μm). Sediments below 25μm 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

## 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  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 Chi$^2$ 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 | - | - |

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

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

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

We did not find any significant difference in DF or IDF between infauna and epifauna (Fig 4; Table 2). However, the families with incomplete drilling are all infaunal. All the complete drillholes in epifaunals are created by Naticids; Muricid drillings are observed only 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 Chi$^2$ 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

# 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 Inomplete | 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    (>1mm), medium (1-2mm) and Large (<2mm).

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 (>1mm) | 28 | 1 | | |
| | | | **10.45** | **0.001** |
| Medium (1-2mm) | 115 | 56 | | |
| | | | **4.42** | **0.04** |
| Large (<2mm) | 29 | 5 | | |

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 inclusing 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 | | **0.4** | **0** |
| Kutch_Overall | Prey- predator size | 0.12 | 0.41 |
| Kerala_Naticid | | **0.34** | **0.01** |
| Kerala_Muricid | | -0.24 | 0.51 |

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

258

259

## 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

## Discussion

299        Record of predatory drillhole is one of the unique instances where predator-prey

300    dynamics can be studied quantitatively in deeptime. 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

## 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   (>>0.1mm) 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

## 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

## 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 handing 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

## 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

## 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

## 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 again 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

# 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

# Acknowledgements

# Supplementary materials

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

Family : Family names of bivalves; Prey size: Length of the prey; Drill hole morphology:

morphology of the drill holes/ Predator identity; Drill hole diameter: Outer borehole

diameter of the drill hole; Position: Position of the drill hole; Completion: Completion of

drill hole; Drilling: Type of prey (drilled or undrilled); Predator size: Length of the predator,

Kerala; Location: Name of the location from where specimens were collected; Size class:

small, medium or lage.


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

Prey1_increasing (mm): Prey size in increasing order kepping minimum and maximum

values same as original data; Prey1_decreasing (mm): Prey size in decreasing order kepping

minimum and maximum values same as original data; Prey1_constant (mm): Mean prey size

of original data; Predator1_increasing (mm): Predator size in increasing order kepping

minimum and maximum values same as original data; Location: Name of the location from

where specimens were collected.


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

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

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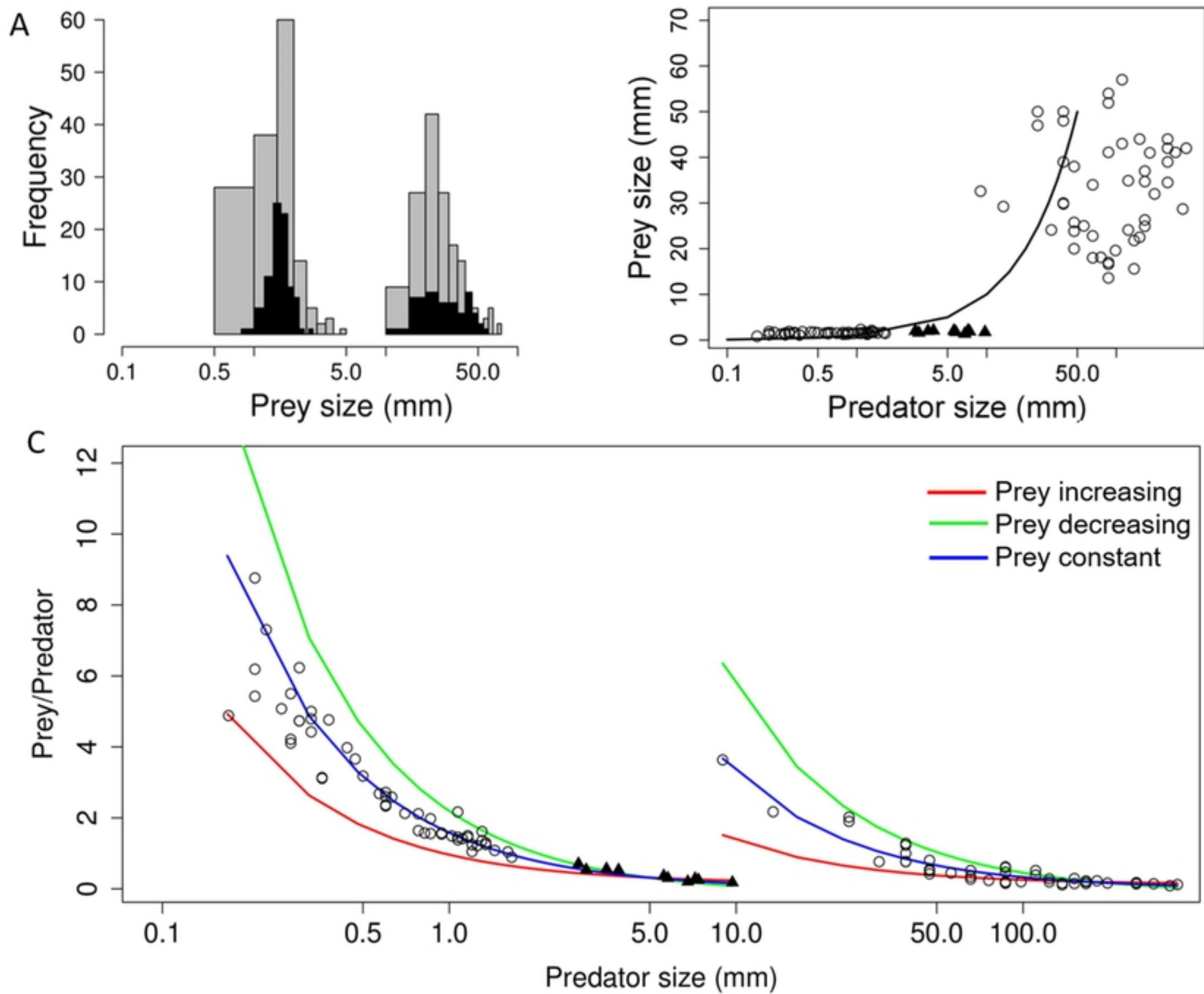
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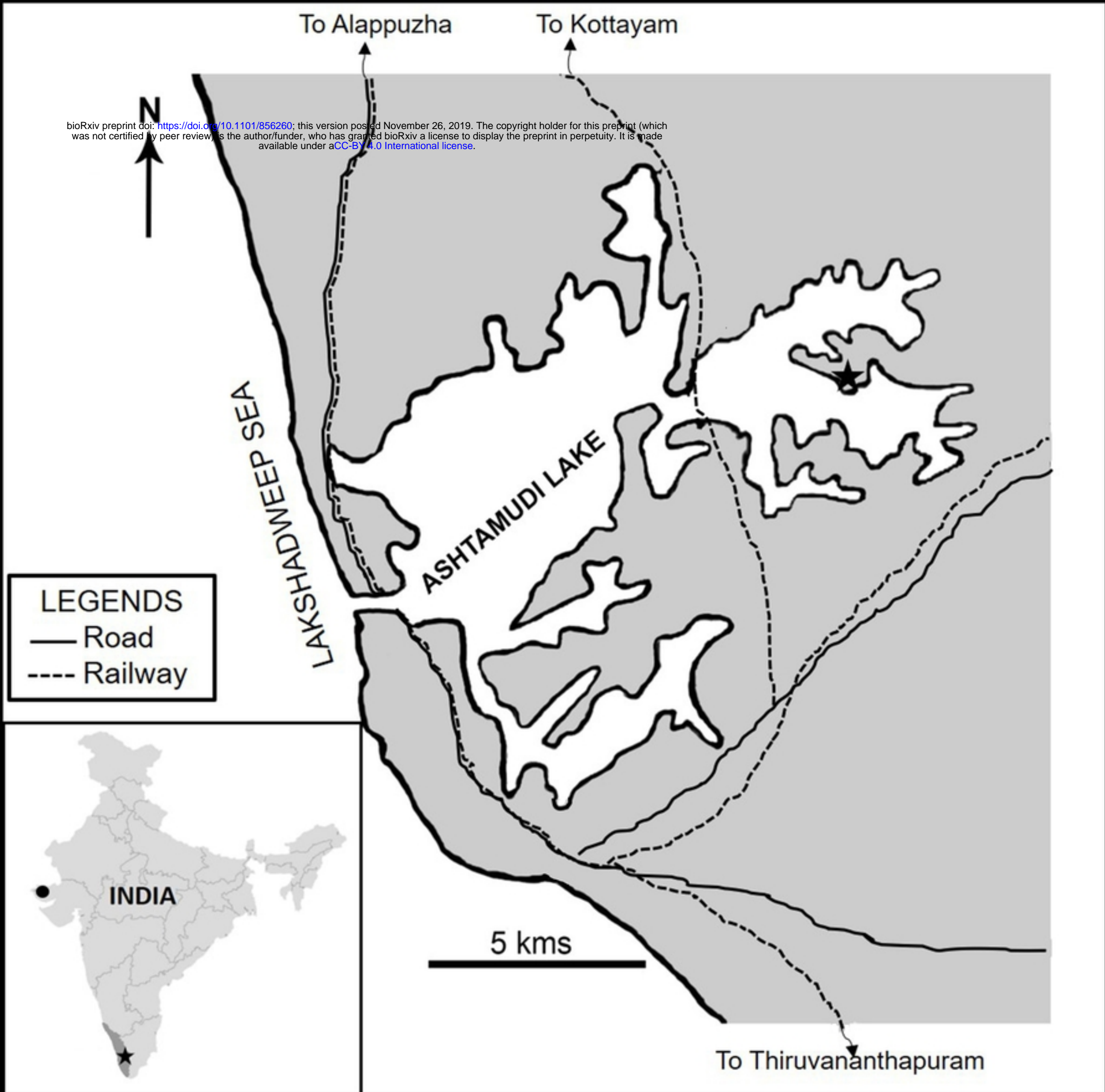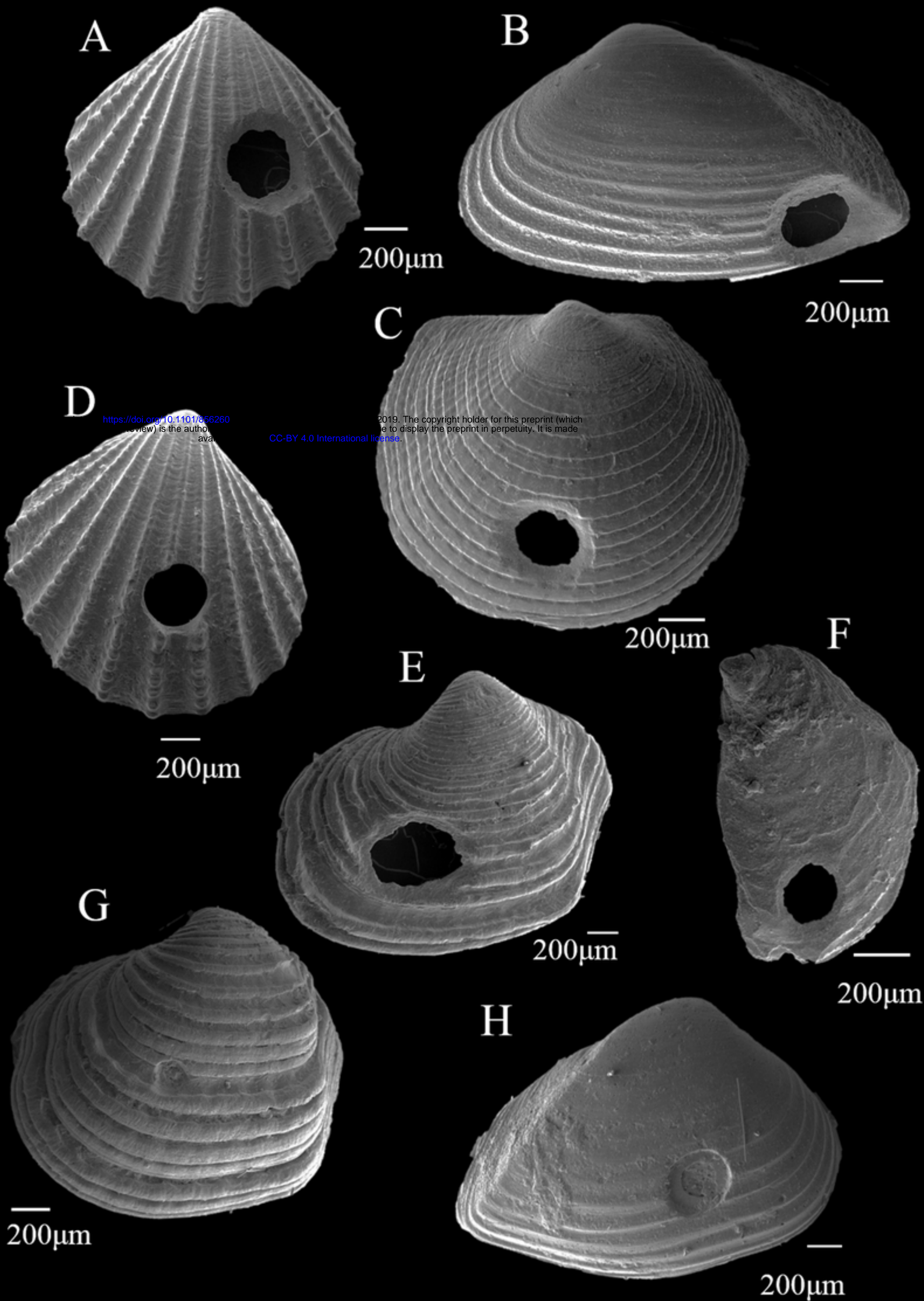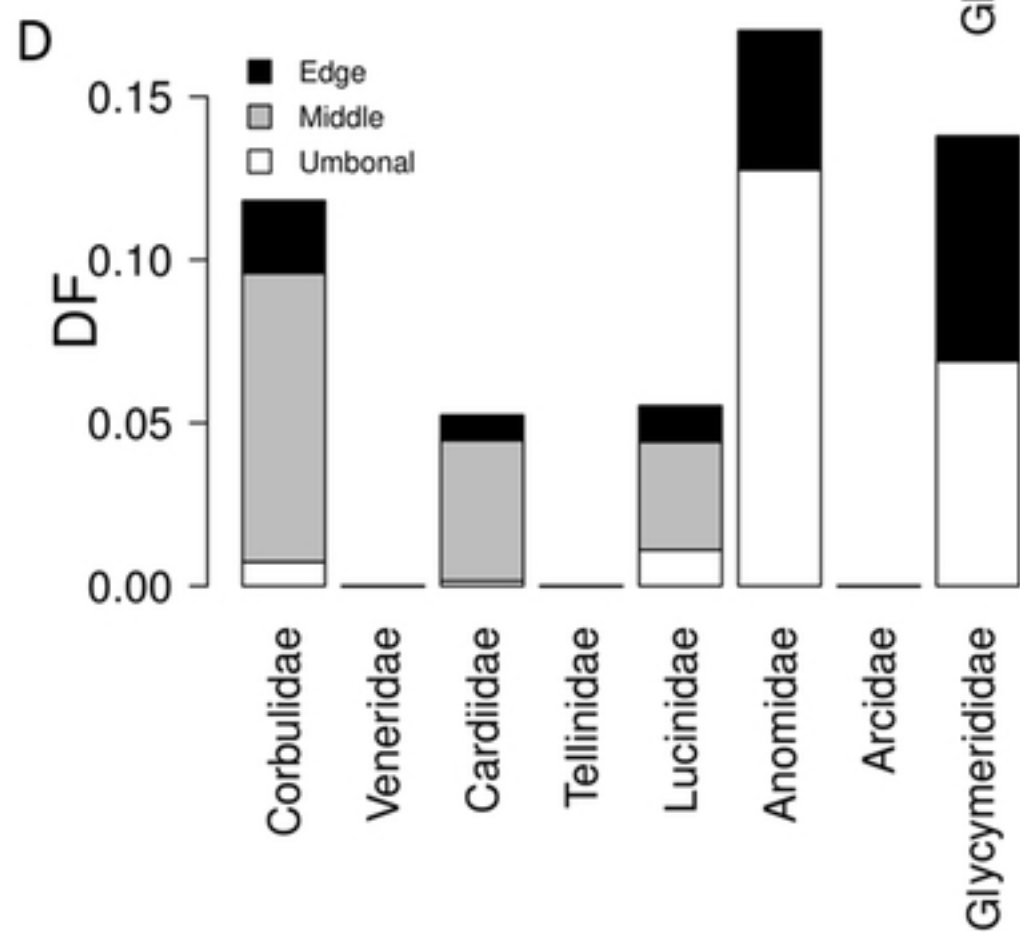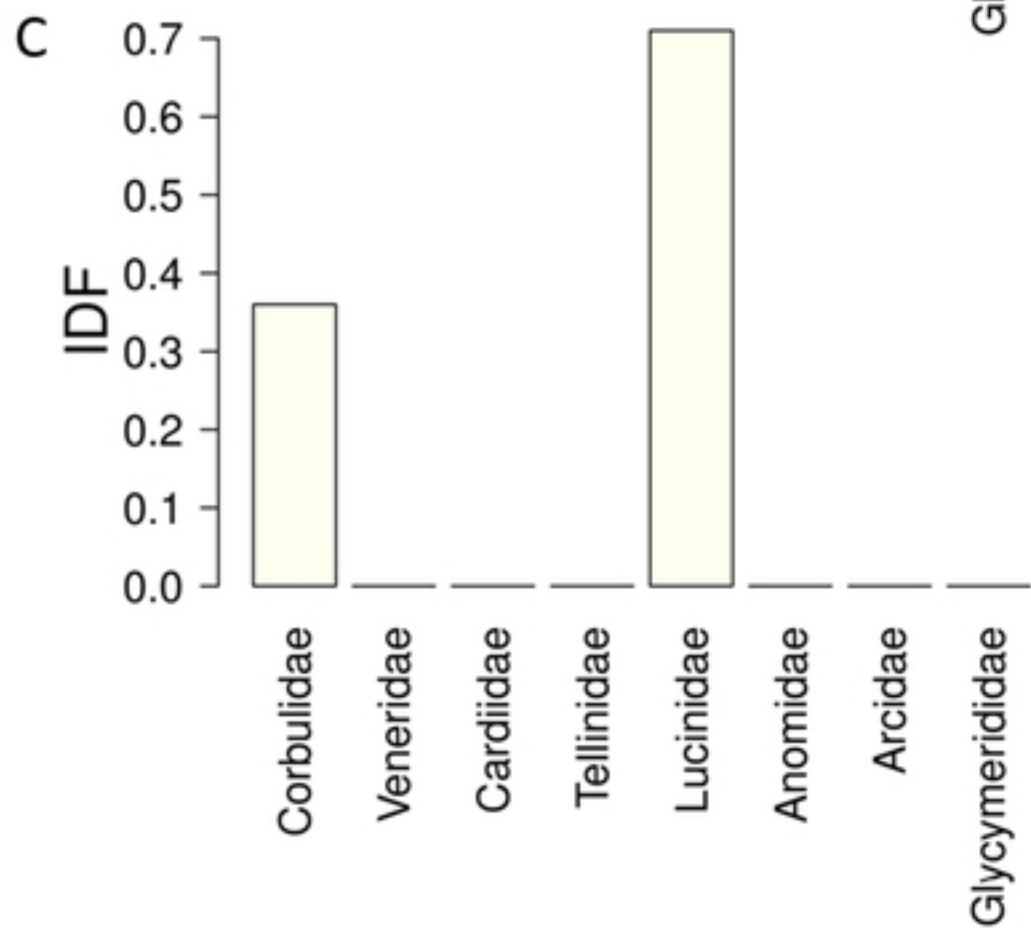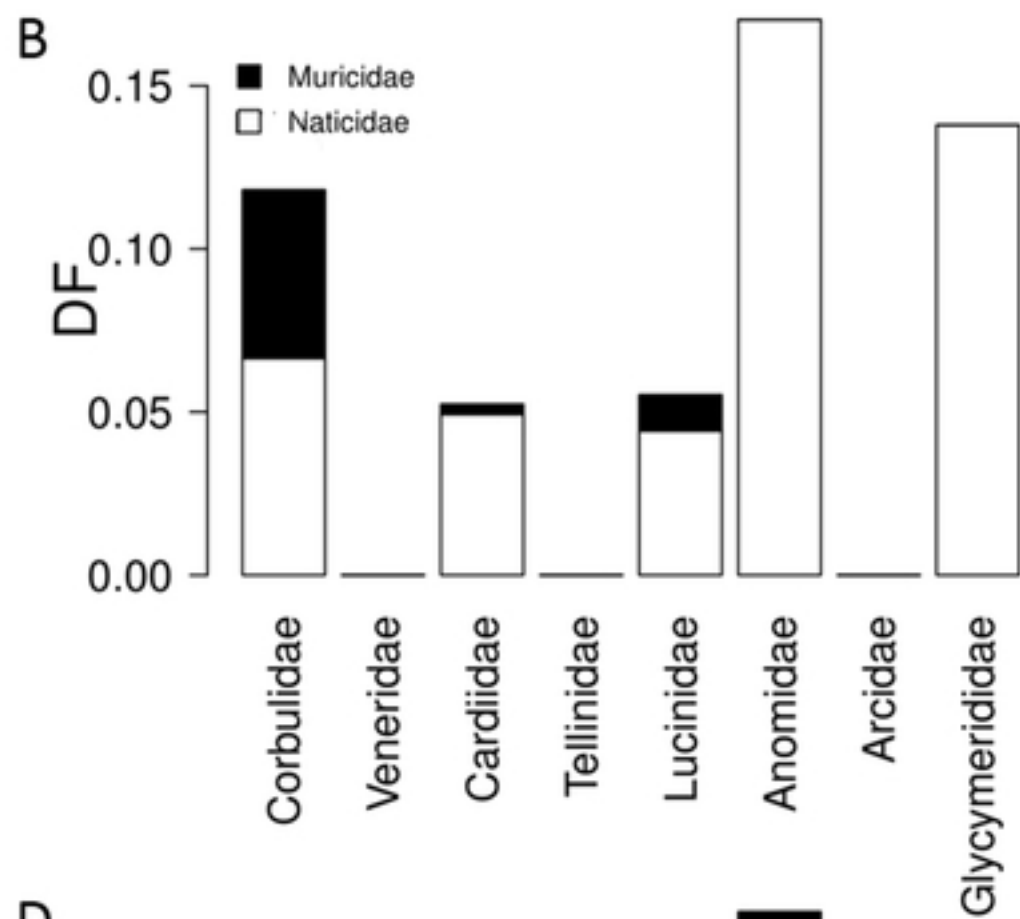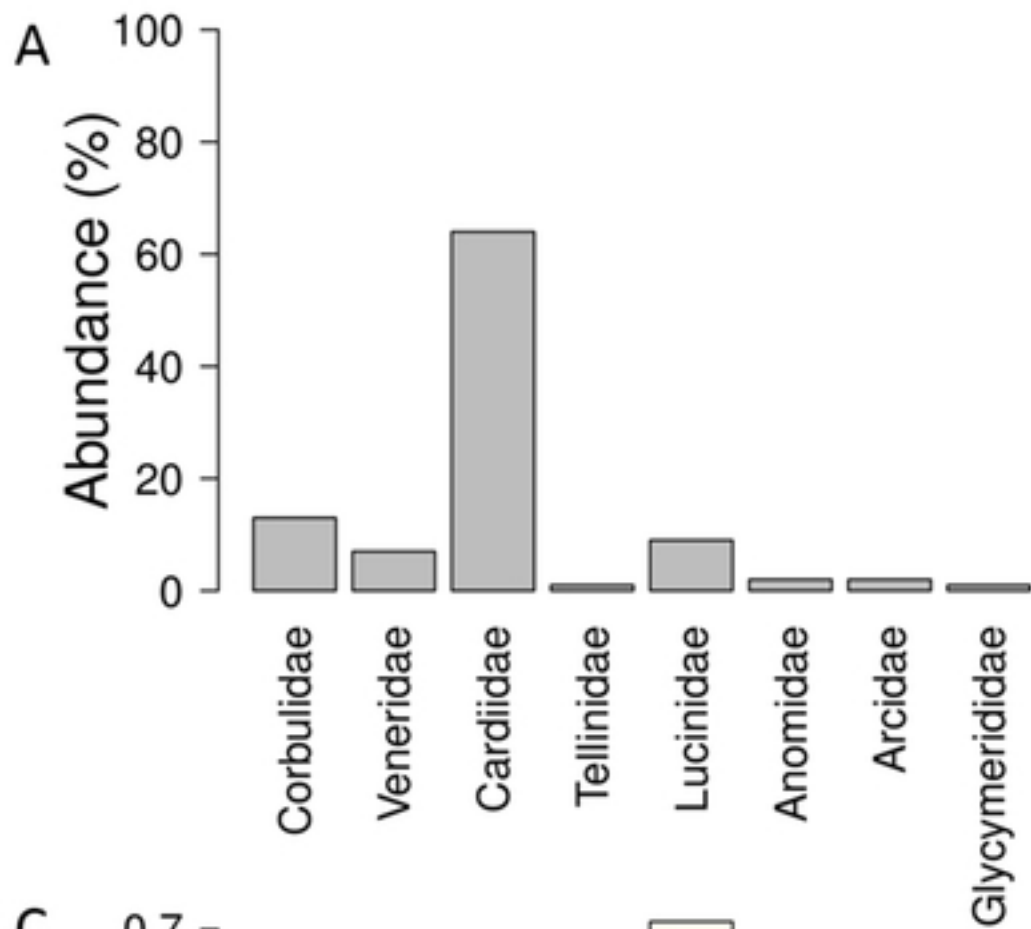
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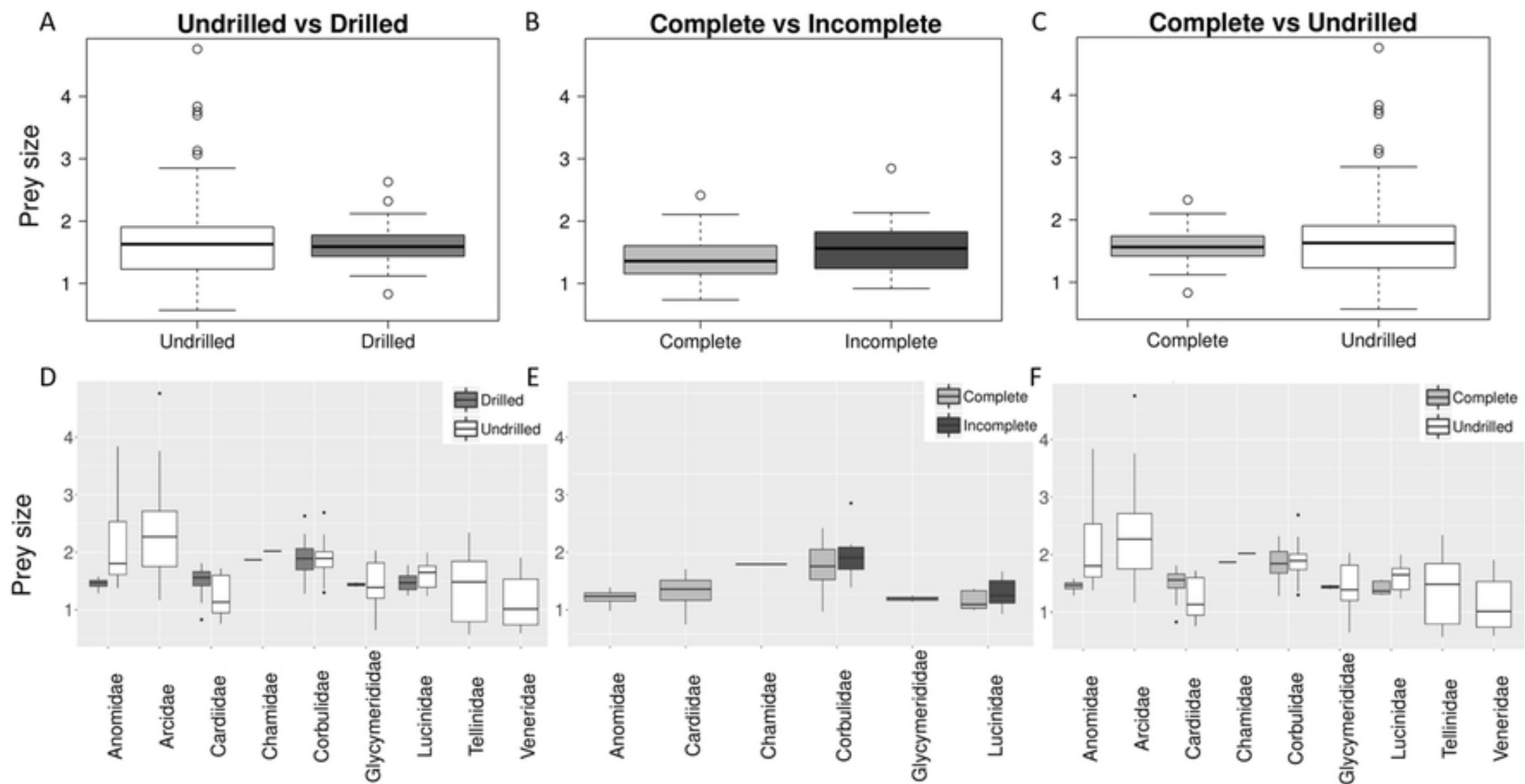
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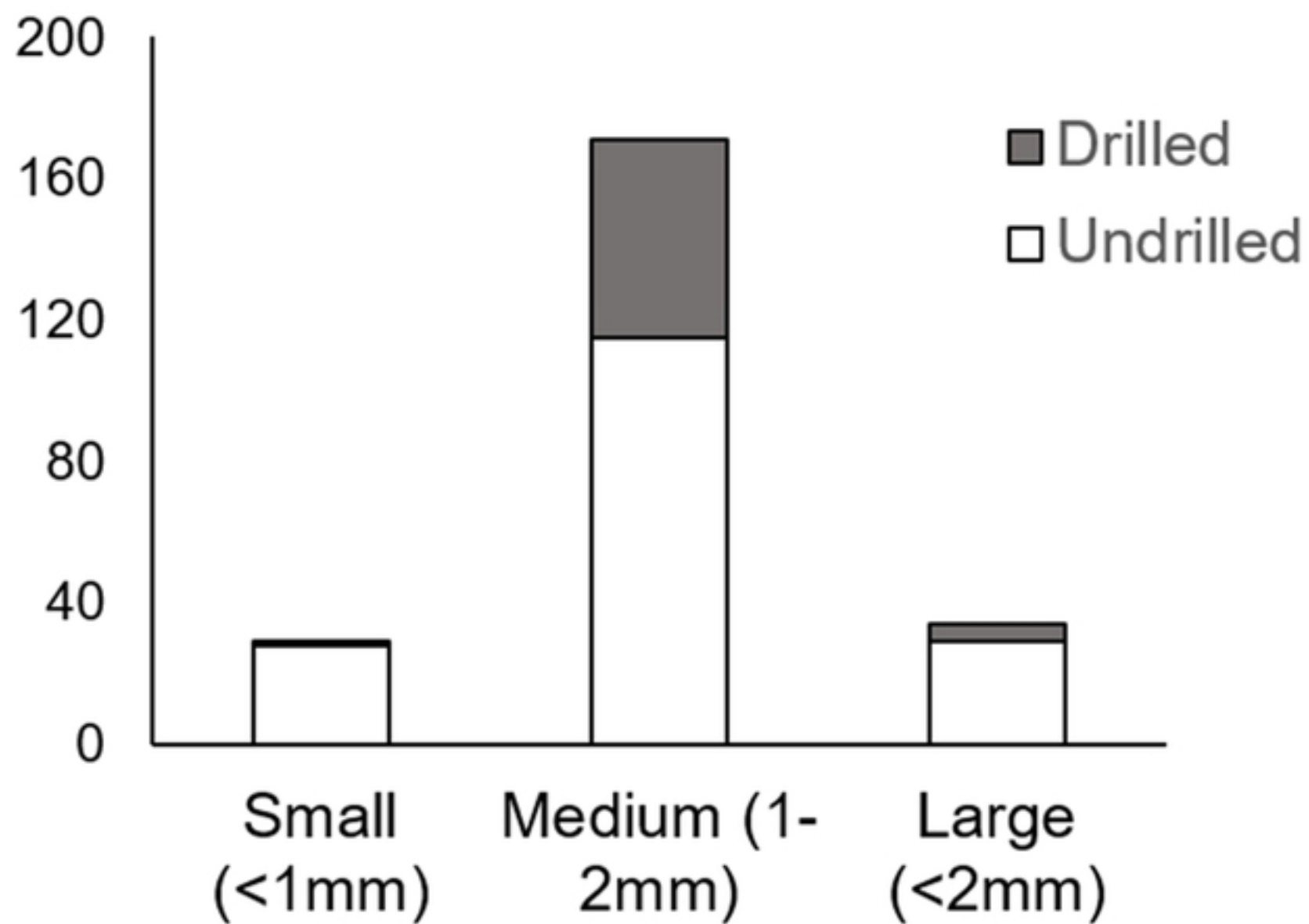
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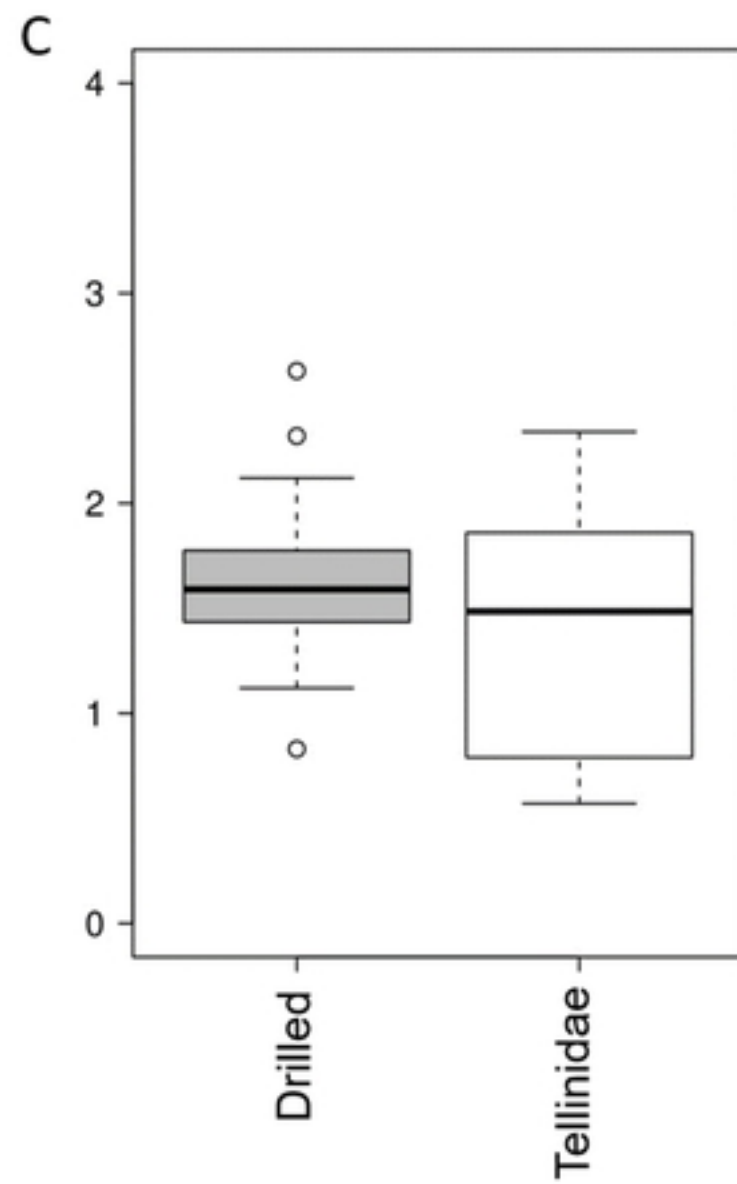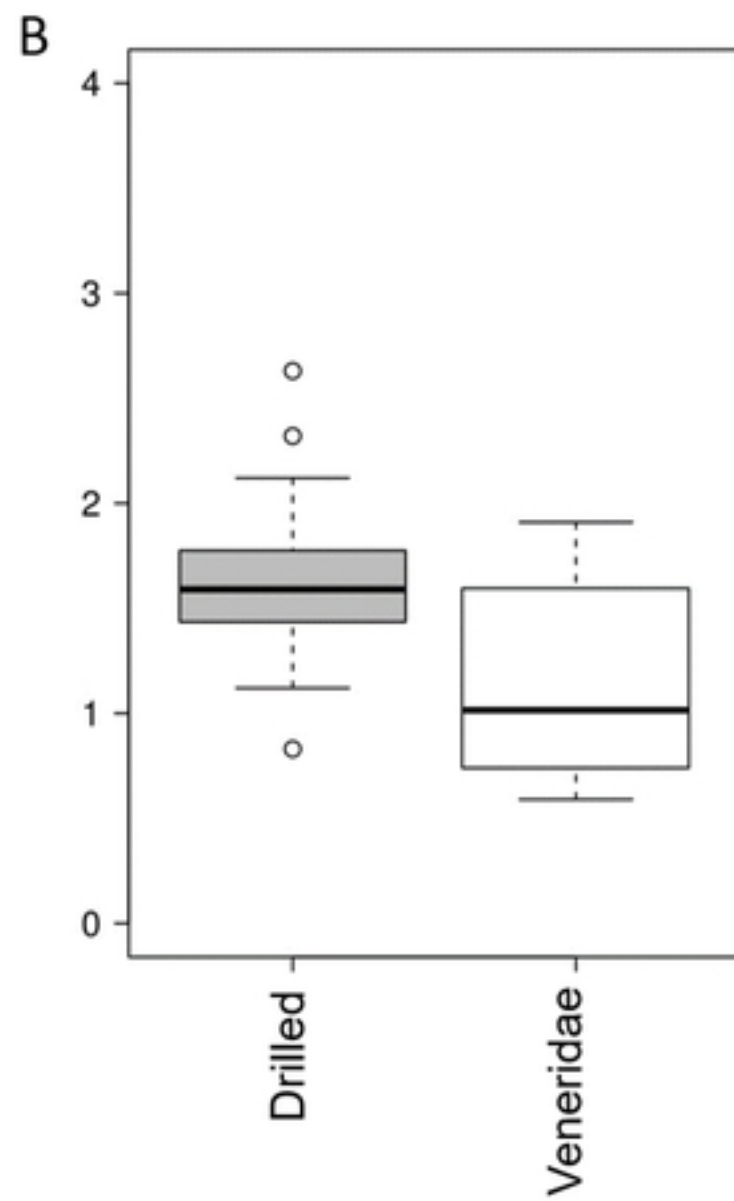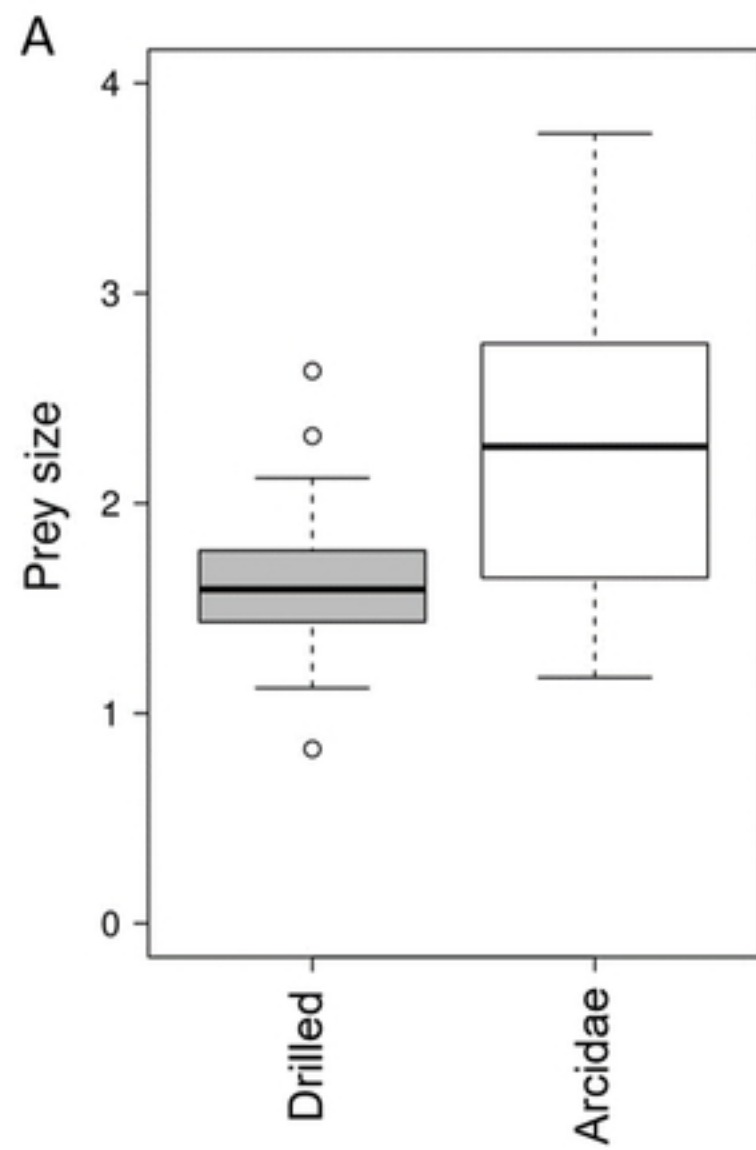
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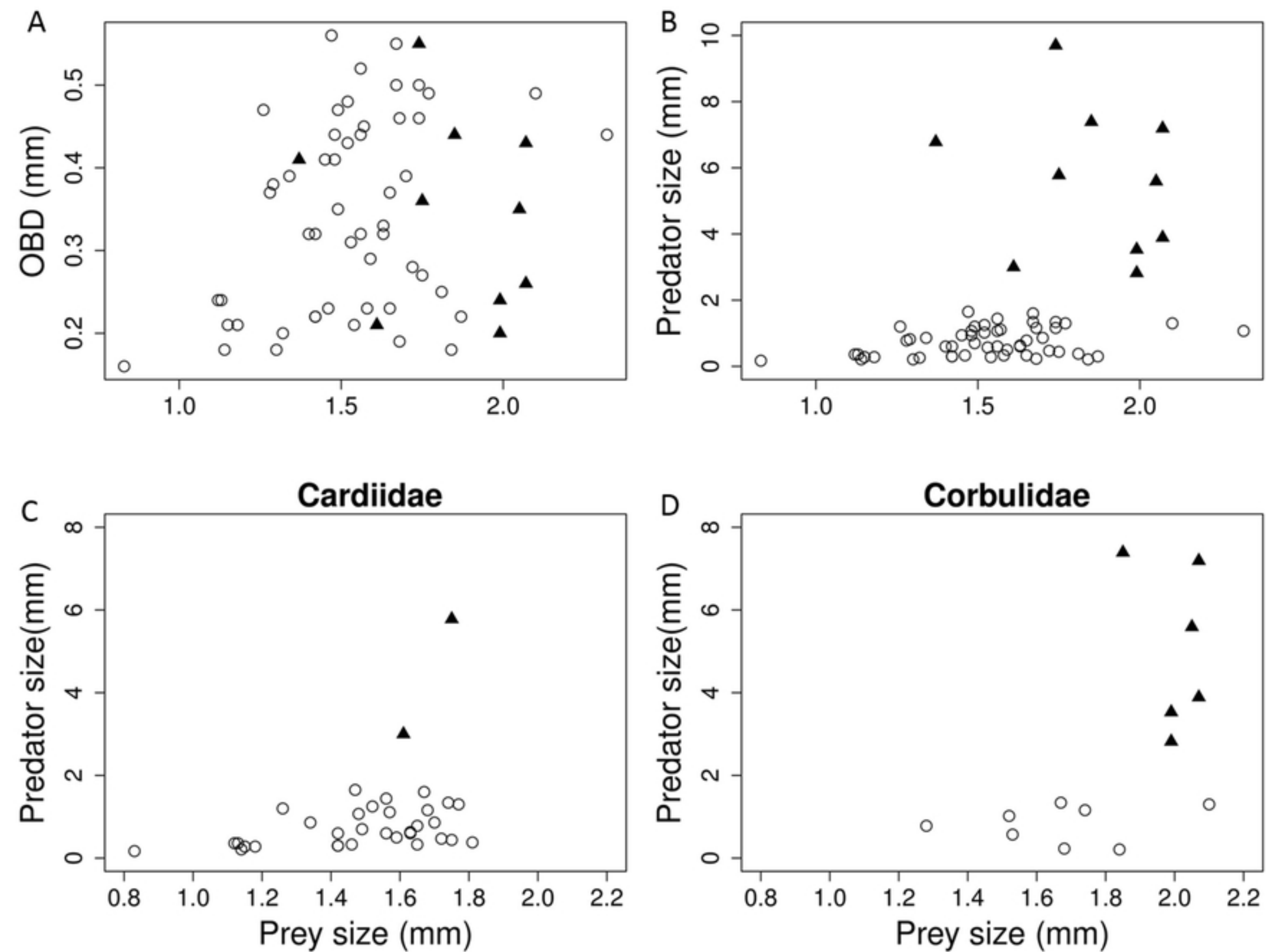
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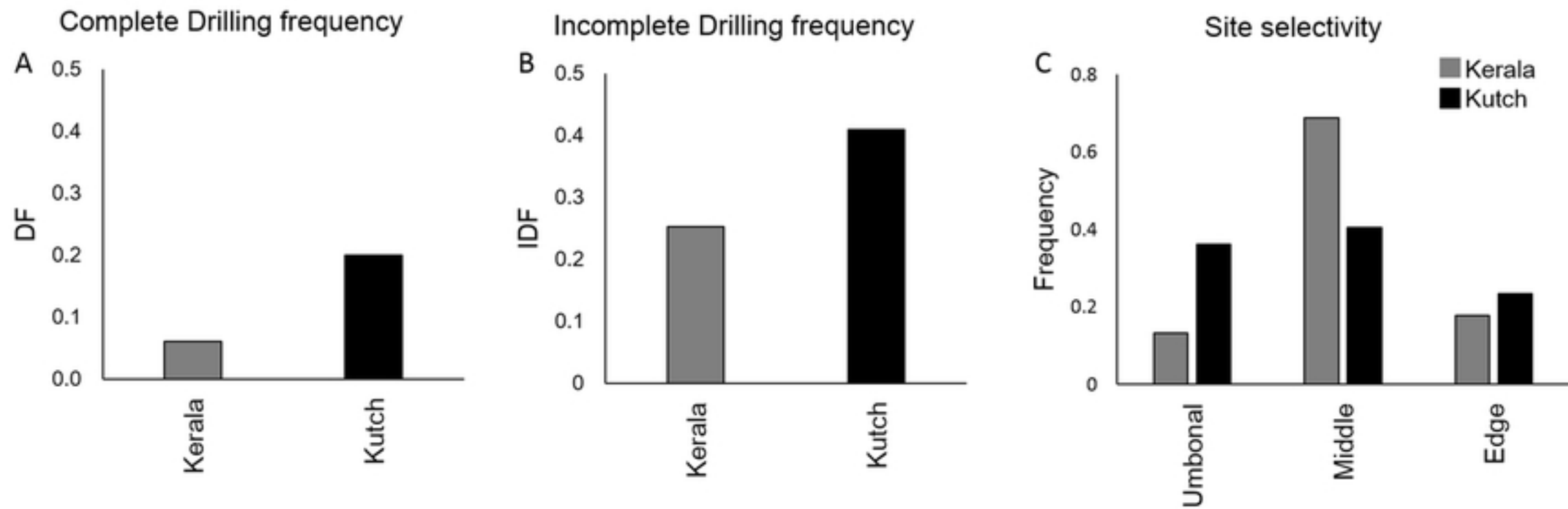
Figure 9

Figure 10

Figure 11

Figure 4