

1 Crustaceans as hosts of parasites throughout the Phanerozoic

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24

25 Abstract

26

27 The fossil record of crustaceans as hosts of parasites has yielded three confirmed associations: epicaridean
28 isopod-induced swellings on Jurassic–Recent decapod crustaceans, feminization of Cretaceous and
29 Miocene male crabs possibly caused by rhizocephalan barnacles, and presumed pentastomids on/in
30 Silurian ostracods. Cestode plathyhelminth hooks and swellings by entoniscid isopods may be recognized
31 in the future. Relative to 2014, we report an increase of 41% to 124 fossil decapod species with
32 epicaridean-induced swellings in the branchial chamber (ichnotaxon *Kanthylooma crusta*). Furthermore,
33 using a Late Jurassic (Tithonian) decapod assemblage from Austria, we find (1) no correlation between
34 genus abundance and prevalence of *K. crusta*, (2) host preference for some galatheid taxa (as for a mid-
35 Cretaceous assemblage from Spain), and (3) a larger median size of parasitized versus non-parasitized
36 specimens for two selected species. The latter result may be caused by infestation throughout ontogeny
37 rather than exclusively in juveniles and/or possible selection for the larger sex.

38

39 Keywords: barnacle, biotic interaction, Bopyridae, Cirripedia, coevolution, Crustacea, Decapoda,

40 Isopoda, Ostracoda, parasitism

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42

43 1. Introduction

44

45 Extant crustaceans (or pancrustaceans) act as both parasites and hosts of parasites (e.g., Yamaguti 1963;
46 Cressey 1983; Boxshall et al. 2005; Boyko and Williams 2011; Trilles and Hipeau-Jacquotte 2012; Smit
47 et al. 2014; Klompmaker and Boxshall 2015; Boxshall and Hayes in press). For this paper, we define
48 parasitism as a symbiotic relationship in which the parasite is nutritionally dependent on the host for at
49 least part of its life cycle and has a negative impact on the fitness of the host (cf. Combes 2001; Tapanila

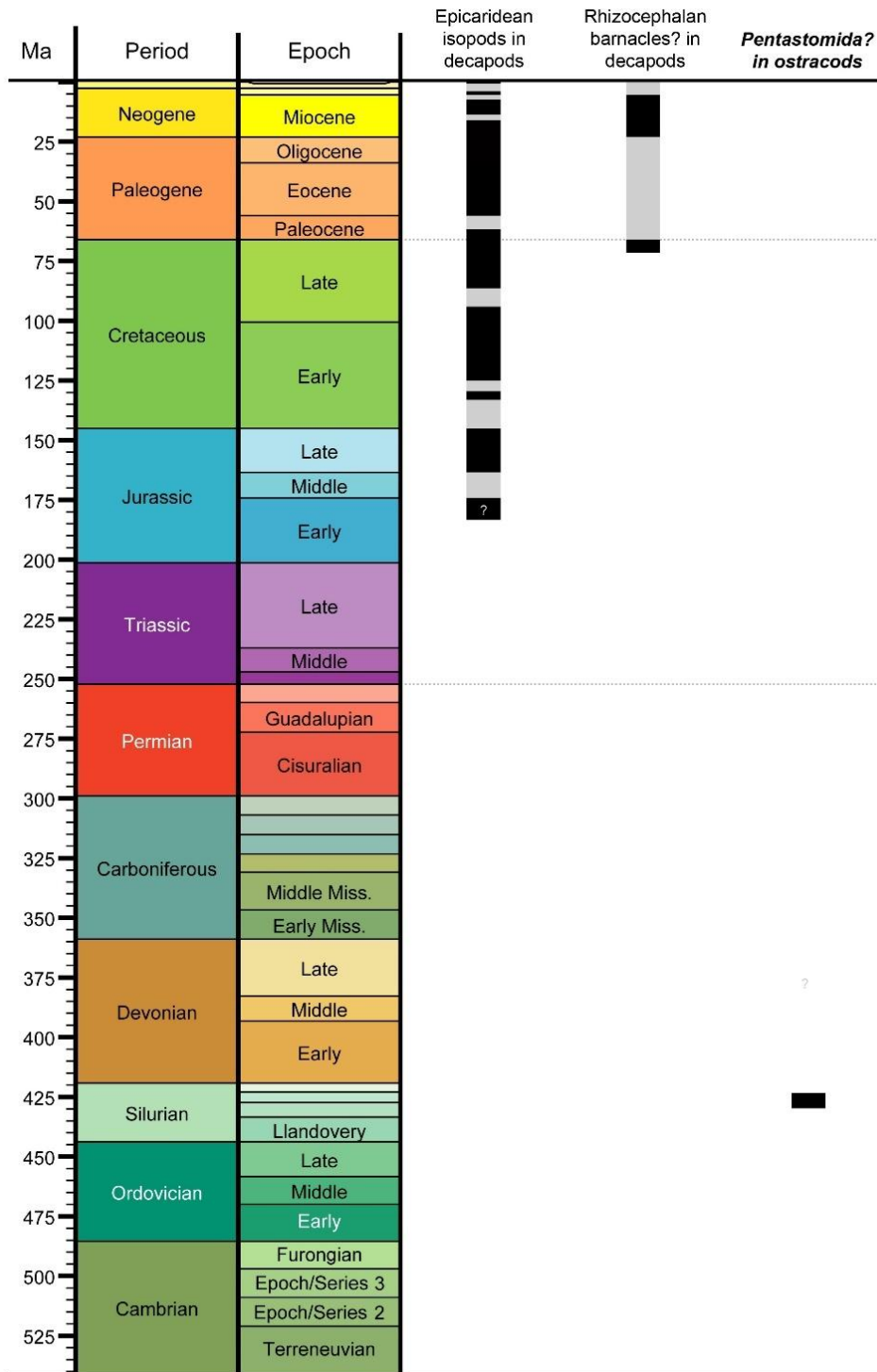
50 2008). Over 7000 extant crustaceans are intermediate and final hosts to parasites from diverse clades such
51 as acanthocephalans, cestodes, crustaceans (e.g., copepods, cirripedes, isopods, Tantulocarida), digenean
52 trematodes, monogeneans, nematodes, and protists (e.g., Boxshall et al. 2005; Klompmaker and Boxshall
53 2015; Boxshall and Hayes in press). Representatives of nearly all to all major clades of crustaceans serve
54 as hosts today, including amphipods, branchiopods, cirripeds, copepods, decapods, euphausiaceans,
55 mysidaceans, ostracods, peracarids, and stomatopods (e.g., Boxshall et al. 2005; Klompmaker and
56 Boxshall 2015; Boxshall and Hayes in press). The impact of parasitism on crustaceans is likely to be
57 enormous, but understudied in the context of whole ecosystems.

58 The fossil record of parasitism involving crustaceans has been reviewed recently (Klompmaker
59 and Boxshall 2015, for crustaceans as parasites and hosts; Haug et al. this volume, for crustaceans as
60 parasites). Three instances of parasites in crustacean hosts have been reported thus far (Fig. 1). This low
61 number and the fact that the stratigraphic coverage of two of these records is spotty can be ascribed to a
62 combination of the small size of parasites, the low preservation potential of parasites due to their general
63 lack of a hard skeleton, not all parasites leave recognizable traces, and the lack of targeted research. One
64 notable exception is epicaridean isopods, which cause characteristic swellings on decapod crustacean
65 carapaces. This association represents a nearly continuous record since the Jurassic (Klompmaker et al.
66 2014; Klompmaker and Boxshall 2015), presenting an ideal model system to study various aspects of
67 parasitism through time.

68 The goal of this paper is to re-review the fossil record of crustaceans as hosts of parasites because
69 ample new evidence has been found in recent years. We focus primarily on evidence of epicaridean
70 isopod parasites in decapod crustaceans by (1) presenting a substantially expanded list of infested
71 decapod species and (2) using a vast Late Jurassic assemblage to test the relationship between taxon
72 abundance and infestation percentage, assess host preference, and evaluate the size of parasitized versus
73 non-parasitized specimens for two species. Subsequently, we briefly review the claimed evidence for
74 parasitism of (1) rhizocephalan barnacles in fossil decapod crustaceans, (2) ciliates on ostracods, and (3)
75 pentastomids on ostracods. Finally, modern parasitism on crustaceans with preservation potential are
76 discussed.

77
78 Institutional abbreviations: MAB = Oertijdmuseum, Boxtel, The Netherlands; MCV = Museo Civico D.
79 Dal Lago, Valdagno, Vicenza, Italy; NHMW = Naturhistorisches Museum Wien, Vienna, Austria; UF =
80 Florida Museum of Natural History at the University of Florida, Gainesville, Florida, USA.

81



82
 83 Figure 1. Stratigraphic ranges of crustaceans as hosts of parasites. Black parts represent known
 84 occurrences, while grey parts are inferred occurrences. Black occurrences have been plotted at the stage-
 85 level where possible. The category in bold italic font is based on body fossils of the parasite; others are
 86 based on morphologies inferred to have been caused by parasites in the host taxon. Timescale on left
 87 produced with TSCreator 6.3 (<http://www.tscreator.org>). Modified and updated from Klompmaker and
 88 Boxshall (2015: fig. 12).

89

90 2. Isopod swellings in decapod crustaceans

91

92 2.1. General information

93

94 Epicaridean isopods (Bopyroidea and Cryptoniscoidea) parasitize calanoid copepods as intermediate hosts
95 and other crustaceans as final hosts, following two larval stages (e.g., Williams and Boyko 2012).
96 Approximately 800 species are known and they are found today in all oceans (e.g., Williams and Boyko
97 2012). The phylogenetic relationship of epicaridean families has recently been clarified using 18S rDNA,
98 resulting in five accepted families to date (Boyko et al. 2013). Unlike the endoparasitic Cryptoniscoidea
99 (Dajidae and Entophilidae), Bopyroidea (Ionidae, Bopyridae, and Entoniscidae) are ectoparasitic and their
100 female individuals often create swellings in the cuticle of one or rarely both branchial chambers of
101 decapod crustaceans (e.g., Markham 1986; Boyko and Williams 2009; Williams and Boyko 2012).
102 Epicaridean females feed on hemolymph and ovarian fluids after piercing the inner cuticle of the host
103 (e.g., Bursey 1978; Lester 2005), while the much smaller, less deformed, less modified males attach
104 themselves to females subsequently for reproduction and do not form swellings in the cuticle. Effects on
105 the host are manifold and can be dramatic (Table 1).

106

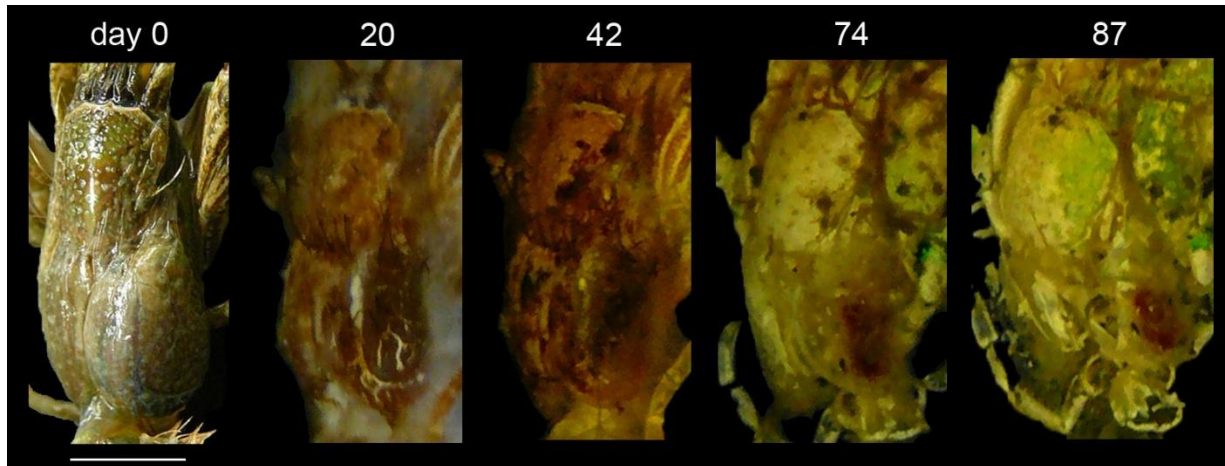
107 Table 1. Parasitic epicarideans cause a variety of negative effects on their decapod hosts. Sources are not
108 comprehensive.

Effect of bopyroid isopods on decapod host	Source(s)
lower fecundity	Van Wyk 1982; Calado et al. 2006; Hernáez et al. 2010
castration	McDermott 1991; González and Acuña 2004; Markham and Dworschak 2005; Sherman and Curran 2013 O'Brien and Van Wyk 1985; Markham and Dworschak 2005; Petrić et al. 2010; Romero-Rodríguez and Román-Contreras 2011; Yasuoka and Yusa 2017
feminization of males	
altered sexual characters of females	Lee et al. 2016; Yasuoka and Yusa 2017
gill damage and scar tissue development	Bursey 1978; McDermott 1991; Corrêa et al. 2018
reduced molt frequency	Van Wyk 1982; O'Brien and Van Wyk 1985
(unintended) mortality	Anderson 1990
increased predation risk	Brinton and Curran 2015
lower activity levels	Bass and Weis 1999; McGrew and Hultgren 2011
lower oxygen consumption	Anderson 1975; Neves et al. 2000
different host sex ratios	Somers and Kirkwood 1991; McDermott 2002; Cericola and Williams 2015

109

110 The body fossil record of epicarideans is nearly non-existent. No adults have been found in decapod body
111 chambers thus far due to their low preservation potential, as also shown experimentally (Klompemaker et
112 al. 2017; Fig. 2). Only some epicaridean larvae have been found in Miocene and Late Cretaceous amber
113 (Serrano-Sánchez et al. 2016; Néraudeau et al. 2017; Schädel et al. 2018). However, the swellings in the
114 oft-calcified cuticle of decapod hosts can be preserved and detected relatively easily in the fossil record
115 (e.g., Wienberg Rasmussen et al. 2008; Ceccon and De Angeli 2013; Robins et al. 2013; Klompemaker et
116 al. 2014; Klompemaker and Boxshall 2015; Hyžný et al. 2015). These swellings are referred to the
117 ichnotaxon *Kanthyloma crusta* Klompemaker et al., 2014 (see also Klompemaker and Boxshall 2015). The
118 earliest known swelling is in a lobster from the Early Jurassic (Toarcian) of Indonesia, but this record is
119 somewhat doubtful (Wienberg Rasmussen et al. 2008; Klompemaker et al. 2014). The Late Jurassic
120 (Oxfordian) yields the first definite examples, suggesting coevolution between epicarideans and their
121 decapod host for at least 160 million years. Most infested fossil species are brachyurans and galatheoids,

122 taxa that today are parasitized primarily by Ionidae and Bopyridae, respectively (Markham 1986; Boyko
123 and Williams 2009).
124



125
126 Figure 2. Decay of the carapace of the modern hermit crab *Clibanarius vittatus* (Bosc, 1802) and its
127 parasitic bopyrid [most likely *Bopyrissa wolffi* Markham, 1978, see Markham (1978) and McDermott et
128 al. (2010)] in the swollen right branchial chamber. The carapace is tilted to the left to better observe the
129 decay of the parasite. The bopyrid body outline is still visible on day 20, but much less so subsequently
130 when a smaller red spot is observed. For experimental setup and conditions see Klompmaker et al. (2017).
131 1st, 2nd, and 4th image modified from same reference. Scale bar: 5.0 mm wide.
132

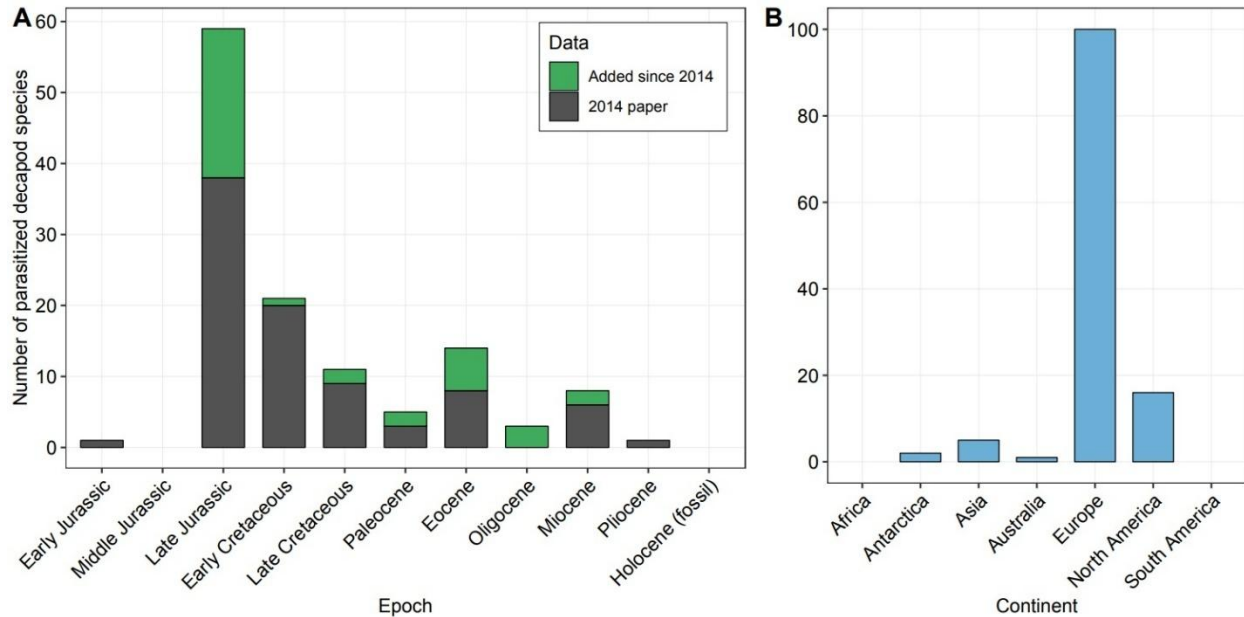
133 2.2. Global Meso- and Cenozoic data

134
135 Fossil decapod crustacean species with at least one specimen containing a swelling in the branchial region
136 attributed to an epicaridean parasite have been listed previously (Van Straelen 1928: p. 51; Van Straelen
137 1931: p. 56; Houša 1963: p. 110; Förster 1969: p. 53–54; Markham 1986: table 2; Wienberg Rasmussen
138 et al. 2008: table 2; Klompmaker et al. 2014: table 3). The most recent report identified 88 parasitized
139 species. Targeted research on Meso-Cenozoic decapod assemblages for evidence of *Kanthylooma crusta*
140 since the summer of 2017, published research since 2014, and new discoveries of infested species in older
141 literature has led to an increase of 41% of known infested fossil species, totaling of 124 infested species
142 (Fig. 3, for examples of new and some known occurrences). This remarkable rise and the total number of
143 infested decapod species today exceeding 550 (Boyko and Williams 2009: fig. 6, and subsequent papers)
144 suggest that more infested fossil taxa are to be expected.

145 Most infested fossil species represent Brachyura and Galatheoidea, and are primarily found in
146 Europe (100/123 or 81%, Fig. 4B). The highest number of infested species on the epoch-level is known
147 from the Late Jurassic (Fig. 4A). A Late Jurassic peak was also shown for the percentage of infested
148 decapod species per epoch in the Mesozoic (Klompmaker et al. 2014: fig. 6). Although they argued that
149 elevated collecting and reporting of *Kanthylooma* in the Late Jurassic may explain part of the peak, they
150 found a biological explanation more likely. Variable reporting may indeed be a factor because there are
151 multiple papers specifically dedicated to this type of parasitism in the Late Jurassic (Remeš 1921;
152 Bachmayer 1948; Houša 1963; Radwański 1972), while only two papers have focused on *Kanthylooma*
153 from younger, pre-Holocene epochs (Ceccon and De Angeli 2013: Eocene; Klompmaker et al. 2014: mid-
154 Cretaceous). Whether this type of parasitism is truly reaching its peak in the Late Jurassic can only be
155 assessed by studying the infestation prevalence on the finest possible scale using specimens from many
156 assemblages across time and space. This study is currently ongoing.
157



158
159 Figure 3. Fossil decapod crustacean carapaces with isopod-induced swellings (ichnotaxon *Kanthylo-*
160 *crusta*) in one of the branchial chambers. A. *Galathea valmaranensis* De Angeli and Garassino, 2002,
161 from the Oligocene (Rupelian) of Sant'Urbano, Italy (left side), MCV.17/0049. B. *Pithonoton*
162 *marginatum* von Meyer, 1842 [sensu Wehner (1988: pl. 6.1)] (right side), NHMW 1990/0041/1373. C.
163 *Pithonoton* cf. *P. rusticum* Patruilius, 1966 (right side), NHMW 2017/0089/0028. D. *Longodromites*
164 *angustus* (Reuss, 1858) (right side), NHMW 1990/0041/2600. E. *Cyclothyreus cardiacus* Schweitzer and
165 Feldmann, 2009a (left side), NHMW 2017/0089/0026. F. *Distefania oxythyreiformis* (Gemmellaro, 1869)
166 (right side), NHMW 2017/0089/0002. G. *Cycloprosopon* cf. *C. octonarium* Schweitzer and Feldmann,
167 2010 (left side), NHMW 1990/0041/1455. H. *Coelopus hoheneggeri* (Moericke, 1889) (left side),
168 NHMW 1990/0041/1519. I. *Abyssopthalmus spinosus* (von Meyer, 1842) from the Late Jurassic
169 (Kimmeridgian) of the Plettenberg, Germany (right side), MAB k3612. J. *Galatheites* cf. *G. diasema*
170 Robins et al., 2016 (right side), NHMW 1990/0041/0163. K, L. *Panopeus nanus* Portell and Collins,
171 2004, from the early Miocene of Jamaica (right side), UF 288470. C–H, J from the Late Jurassic
172 (Tithonian) near Ernstbrunn, eastern Austria. All dorsal views, except for L (frontal view). Scale bars: 5.0
173 mm wide.
174



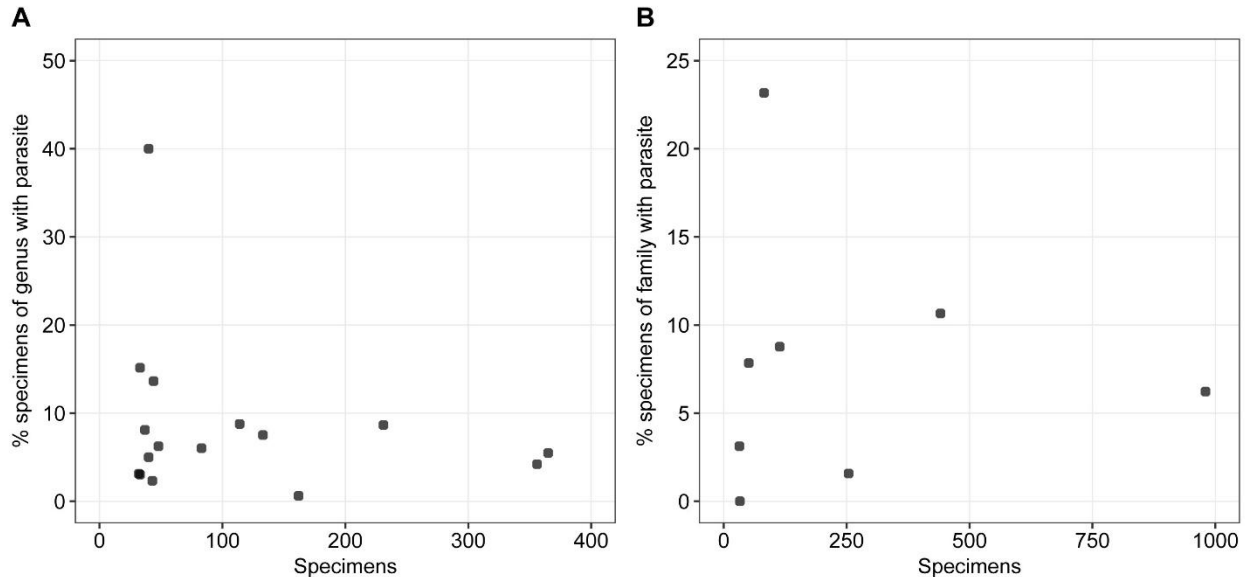
175
 176 Figure 4. The number of decapod crustacean species parasitized by epicaridean isopods. A. Raw epoch-
 177 level data split before and after Klompaker et al. (2014: table 3), total n = 124. Targeted research has
 178 led to 41% more decapod species that were infested. B. Data split by continent.
 179

180 2.3. Abundance vs infestation percentage per taxon

181
 182 Multiple studies have shown that host density positively affects the transmission rate of parasites. For
 183 example, there is a positive correlation between mammal host density across many species and strongylid
 184 nematode parasite abundance in modern ecosystems (Arneberg et al. 1998). For decapods, host
 185 abundance was the best predictor of bopyrid infestation prevalence in modern carid shrimp from Florida
 186 (Briggs et al. 2017). An Early Cretaceous decapod assemblage from Koskobilo in northern Spain yielded
 187 a significant correlation between taxon abundance and epicaridean infestation percentage on the species-
 188 and genus-levels (Klompaker et al. 2014: fig. 4A, 4B). These fossil specimens were collected
 189 predominantly from the southern wall of the Koskobilo quarry, minimizing the influence of possible
 190 spatial and temporal variation. However, they called for more research because of the limited sample size
 191 of specimens of many taxa and the fact that the correlation appears driven by one taxon.

192 To address these issues, the latest Jurassic – earliest Cretaceous Ernstbrunn coral-associated
 193 assemblage (also called the Bachmayer Collection) from eastern Austria (e.g., Schneider et al. 2013) was
 194 used. This decapod collection consists of ~6900 specimens according to the latest counts (pers. comm. A.
 195 Kroh to AAK, November 2018). Bachmayer (1945) listed four localities in the Ernstbrunn Limestone in
 196 which decapods were found (Dörfles I, Dörfles Werk II, Klafnerbrunn I, and Klement I), but decapods
 197 were only abundant in Dörfles I and rare in the other three localities. The Dörfles exposures are
 198 considered to be middle to late Tithonian in age based on ammonite stratigraphy (Zeiss 2001; Schweitzer
 199 and Feldmann 2009b). All specimens of this collection were identified to the genus- and family-levels,
 200 where possible. Species-level assignments were not consistently possible for all taxa because not all
 201 brachyurans species have been studied in detail. As in Klompaker et al. (2014), both branchial sides
 202 needed to be preserved to confirm that specimens were not infested, whereas this was not a requirement
 203 for specimens with *Kanthyloma*. Our results show that there is no significant relationship between taxon
 204 abundance and infestation percentage on both the genus- and family-levels (Fig. 5). Similar results apply
 205 when genus-level data is split into Anomura (n = 6; r = -0.28, two-tailed t-test p = 0.59) and Brachyura (n
 206 = 10; r = -0.09, two-tailed t-test p = 0.80). Sample size is not adequate for such analyses on the family-
 207 level. Decapods from the Ernstbrunn Limestone assemblage were, however, not all collected at the same

208 location or stratigraphic level (Bachmayer 1945). The precise locality and stratigraphic position are not
209 known for all Ernstbrunn specimens. In situ collected assemblages from a single bed and small spatial
210 scale with a relatively high proportion of parasitized specimens would be needed to further test the
211 relationship between abundance and prevalence. Brachyurans and galatheoids from the Tithonian
212 Štramberk Limestone in the active Kotouč Quarry (Czech Republic, Fraaije et al. 2013) may be
213 most suitable because decapods from this limestone are occasionally infested (Houša 1963; pers. obs.
214 AAK, CMR). Due to the generally low prevalence of epicarideans within large, diverse decapod
215 assemblages today (Williams and Boyko 2012, and references therein), modern assemblages may not be
216 suitable for this purpose.
217



218
219 Figure 5. The percentage of parasitized specimens per taxon versus taxon abundance for decapods from
220 the Ernstbrunn Limestone assemblage (Late Jurassic, Tithonian, Austria). A. Genera, $n = 16$; $r = -0.23$,
221 two-tailed t-test $p = 0.39$. B. Families, $n = 8$; $r = -0.04$, two-tailed t-test $p = 0.93$. Minimum number of
222 specimens per taxon = 30.

223 224 2.4. Host preference

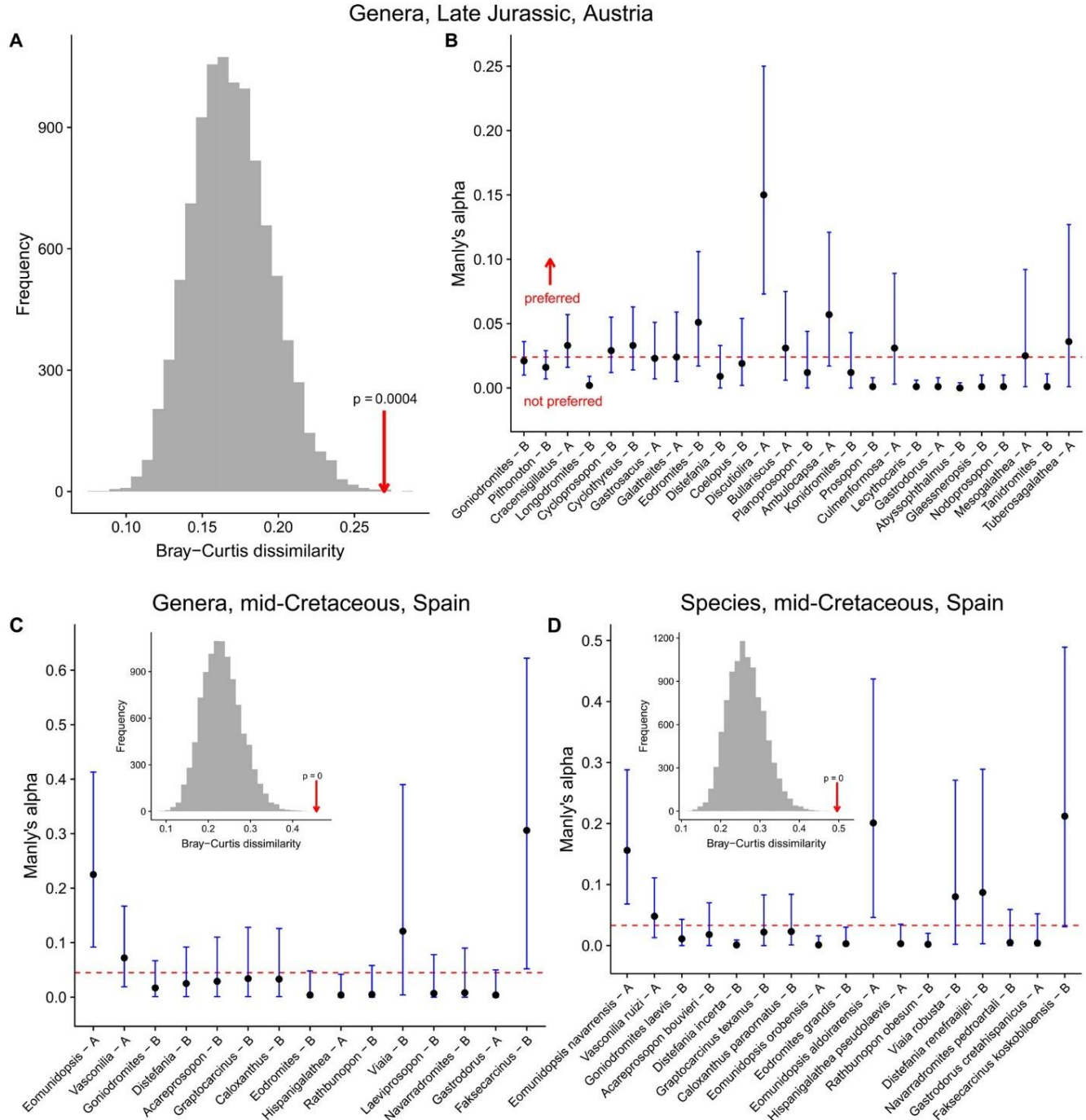
225
226 Host preference is likely to result in non-random patterns of parasite prevalence. Some generalizations
227 have been made concerning epicaridean parasites: Markham (1986) mentioned that host-species
228 specificity appears to be rare among Bopyriodea; McDermott (1991) remarked that most branchial
229 bopyroids infest particular crab families; and Boyko and Williams (2009) noted that some bopyroids
230 infested multiple paguroid hosts, whereas others have been found only on one species thus far. Data in
231 systematic studies on epicarideans echo variability in host specificity: An et al. (2009: table 1) showed
232 that most *Progebiophilus* spp. were restricted to one thalassinidean host species and both An et al. (2015)
233 and Boyko et al. (2017) noted epicaridean species infecting only a single host species, whereas other
234 epicaridean species were found on multiple, often related host species. For carid shrimp from Florida,
235 each bopyrid species was found only on one host genus (Briggs et al. 2017). The fact that multiple species
236 from the same genus or family can be infested by the same parasite species does not imply a lack of
237 preference because parasitized hosts can have very different infestation percentages (e.g., Owens and
238 Glazebrook 1985; González and Acuña 2004; Brockerhoff 2004).

239
240 Host specificity of individual parasite species is impossible to address because epicarideans tend
241 not to preserve as fossils due to their low preservation potential (Klompaker et al. 2017; Fig. 2), but it is
possible to assess host preferences for all epicaridean-induced swellings combined. Very little is known

242 thus far. From the Late Cretaceous (Campanian-Maastrichtian) of Greenland, species-level infestation
243 percentages have been reported from a lobster-brachyuran assemblage preserved in siliciclastic rocks,
244 primarily in shales (Collins and Wienberg Rasmussen 1992; Wienberg Rasmussen et al. 2008). The
245 raninoid crab species *Macroacaena rosenkrantzi* (Collins and Wienberg Rasmussen, 1992) was infested
246 more frequently than the congeneric *M. succedana* (Collins and Wienberg Rasmussen, 1992) (73/1295 =
247 5.6% vs a few out of 193 = < 2%). Species-level data is also known from the mid-Cretaceous reefal
248 limestones (late Albian) from Spain (Klomp maker et al. 2014). The galatheoid *Eomunidopsis navarrensis*
249 (Van Straelen, 1940) was heavily infested (21/174 = 12.1%) relative to other common species (< 5%).

250 To evaluate host preference for the Jurassic for the first time, the Tithonian Ernstbrunn Limestone
251 decapod assemblage was used again and the same specimen selection criteria as above were used with
252 specimens determined to the genus-level. We studied host preference in a more quantitative framework
253 than was done previously, testing host preference against a null model as described in Smith et al. (2018).
254 To test for host preference in the entire assemblage, the observed number of infested specimens per taxon
255 was compared to the expected number in the null model (i.e., random distribution) using the Bray-Curtis
256 index of dissimilarity based on 10,000 iterations. Subsequently, preference for individual host genera are
257 assessed using Manly's alpha to identify which genera are more and less frequently infested than would
258 be expected by chance. The results indicate that evidence for *Kanthyloma crusta* is distributed non-
259 randomly across the genera because only 0.05% of the simulated Bray-Curtis dissimilarity values is
260 greater than the observed Bray-Curtis dissimilarity value (Fig. 6A). The only taxon that is preferentially
261 infested is the moderately common genus *Discutiolira* Robins et al., 2016, whereas *Longodromites*
262 Patru lius, 1959, *Prosopon* von Meyer, 1835, *Lecythocaris* von Meyer, 1858, *Gastrodorus* von Meyer,
263 1864, *Abyssopthalmus* Schweitzer and Feldmann, 2009b, *Glaessneropsis* Patru lius, 1959, and
264 *Nodoprosopon* Beurlen, 1928, are less frequently infested than expected by chance (Fig. 6B). To compare
265 the results to the mid-Cretaceous Koskobilo assemblage (Klomp maker et al. 2014: table 1), the same tests
266 were run on the genus- and species-levels from that assemblage. Bray-Curtis dissimilarity analyses
267 indicate that *Kanthyloma crusta* is distributed non-randomly (insets Fig. 6C, D). The very abundant
268 *Eomunidopsis* Vía Boada, 1981, and the less common *Faksecarcinus* Schweitzer et al., 2012, are
269 preferential host taxa, while *Eodromites* Patru lius, 1959, appears avoided by epicarideans (Fig. 6C). On
270 the species-level, *Eomunidopsis navarrensis* and *E. aldoirarensis* Klomp maker et al., 2012, are targeted,
271 but *E. orobensis* (Ruiz de Gaona 1943), *Eodromites grandis* (von Meyer, 1857), *Distefania incerta* (Bell,
272 1863), and *Rathbunopon obesum* (Van Straelen, 1944) are less frequently infested than would be expected
273 by chance (Fig. 6D).

274 Host specificities can be compared across assemblages by different methods. Basic host
275 specificity considers the number of taxa infested (Poulin et al. 2011), which is higher for Ernstbrunn (22
276 genera) than for Koskobilo (9 genera). However, the Ernstbrunn Limestone assemblage contains more
277 genera (42 vs 22). To remedy this issue, the percentage of genera that is parasitized can be compared.
278 This method yields a higher percentage for Ernstbrunn (52%) than for vs Koskobilo (41%). A caveat here
279 is that many of the non-infested genera are represented by a low number of specimens. Other indices
280 compare the prevalence per host taxon or structural specificity (Poulin et al. 2011). Rohde's modified
281 index takes into account the percentage of parasitized specimens per taxon and corrects for a different
282 number of host genera (Rohde 1980; Rohde and Rohde 2005). This index ranges from 0 to 1 with a
283 higher value implying a higher level of host specificity among the infested hosts. Using genus-level data,
284 the mid-Cretaceous Koskobilo assemblage yield a higher host specificity value than the Late Jurassic
285 Ernstbrunn Limestone assemblage (0.49 vs 0.39). Another specificity measure combines prevalence and
286 phylogenetic distance to compare host specificity (Poulin and Mouillot 2005), but the phylogenetic
287 structures of the Ernstbrunn and Koskobilo assemblages differ substantially, rendering any comparisons
288 using this method uninformative.



289
 290 Figure 6. Parasite host preference analyses for decapods from the Ernstbrunn (Late Jurassic, Tithonian,
 291 Austria) and Koskobilo (mid-Cretaceous, late Albian, Spain) assemblages. A–B. Genera from Ernstbrunn,
 292 $n = 42$. C. Genera Koskobilo, $n = 22$. D. Species Koskobilo, $n = 30$. Histogram panels: grey histograms
 293 show randomized Bray-Curtis dissimilarity values assuming no host preference; red arrows indicate
 294 actual value for the assemblage. P-value is the chance of getting a higher value than the actual value.
 295 Panels with dots and error bars: Manly's alpha values with 95% confidence intervals for brachyuran (B)
 296 and anomuran (A) taxa, ordered by decreasing abundance. Dashed line is the expected alpha value for
 297 each taxon ($1/n$), assuming no host preference. Only taxa with at least ten specimens are shown.
 298

299 2.5. Size of parasitized versus non-parasitized specimens

300

301 Parasitism by epicaridean isopods poses a metabolic drain on the decapod host because female parasite
302 individuals feed on host hemolymph and ovarian fluids after piercing the host's cuticle (Burseley 1978;
303 Lester 2005). For example, a bopyrid parasite can consume up to 25% (Walker 1977) or up to 10%
304 (Anderson 1977) of hemolymph volume per day, for a species of carid shrimp. Consequently, a lower
305 growth rate leading to smaller average and maximum sizes within parasitized specimens may be
306 expected. Multiple studies have indeed shown that modern parasitized decapods are smaller on average
307 than uninfected specimens of the same taxon (e.g., Roccatagliata and Lovrich 1999, for a lithodid
308 anomuran; González and Acuña 2004, for a galatheoid; Petrić et al. 2010, for a galatheoid), but other
309 studies found that infested individuals are of similar size (e.g., Mantelatto and Miranda 2010, for
310 porcellanid anomuran) or even larger (e.g., McDermott 1991, for a brachyuran; Lee et al. 2016, for a carid
311 shrimp). For maximum size, many examples exist in which the non-parasitized individuals were larger
312 (O'Brien and Van Wyk 1985, and references; Roccatagliata and Lovrich 1999), but one study showed no
313 difference (O'Brien and Van Wyk 1985).

314 No study has compared body sizes of parasitized versus non-parasitized fossil decapods of the
315 same taxon thus far. To that end, we examined two species of the Ernstbrunn Limestone assemblage
316 introduced above. Both the galatheoid *Cracensigillatus acutirostris* (Moericke, 1889) and the brachyuran
317 *Goniodromites bidentatus* Reuss, 1858, are abundant species in this assemblage, specimens of these taxa
318 are fairly well-preserved, and multiple specimens are infested, making them suitable target species. Using
319 digital calipers, the maximum width (without spines and without the additional width due to the parasitic
320 swelling) and maximum length (without the long, often incomplete rostrum for *C. acutirostris*) was
321 measured for all infested specimens where possible. For non-parasitized specimens, the same
322 measurements were taken for 43 and 36 randomly chosen individuals of *C. acutirostris* and *G. bidentatus*,
323 respectively. Length (L), width (W), and the geometric mean of length and width ($\sqrt{L \times W}$) are used to
324 compare the sizes of parasitized and non-parasitized specimens for both species using a Mann-Whitney
325 test and a significance level of 5%.

326 For the geometric mean (Fig. 7), the median size is significantly larger for parasitized specimens
327 of *C. acutirostris* ($p = 0.008$), while the median appears also larger for *G. bidentatus*, but not significantly
328 so ($p = 0.057$). Results are similar for the length ($p = 0.030$ and $p = 0.060$, resp.), but the median widths
329 are statistically larger for parasitized specimens of both species ($p = 0.002$ and $p = 0.018$, resp.). Larger
330 size classes contain a higher proportion of infested specimens, although sample size is limited for some
331 size classes (Fig. 7).

332 For maximum size, the samples of non-infested specimens contain the largest specimen for both
333 species (see Fig. 7), but non-infested specimens are more numerous than infested specimens in both cases.
334 To test the effect of unequal sample size on the maximum size, bootstrap analyses without replacement
335 were carried out. The maximum size was determined 10,000 times from random sampling without
336 replacement from the pool of non-infested specimens with the total number of infested specimens for that
337 species as the number of specimens to be sampled from the pool of non-infested specimens. The
338 distribution of maximum sizes was then compared to the maximum size of the infested sample for both
339 species, with a p-value representing the chance of getting a larger non-parasitized specimen than the
340 largest parasitized specimen here. For both species, the maximum sizes of the infested specimens fall well
341 within the distribution of bootstrapped maximum sizes for non-infested specimens ($p > 0.05$, Fig. 8),
342 indicating that the maximum sizes of parasitized and non-parasitized taxa do not differ statistically.

343

344 How can the larger median size of infested specimens be explained for both species? We will
345 discuss the following hypotheses: (1) swellings in small specimens were not recognized, (2) parasitized
346 specimens represent a different assemblage consisting of larger specimens on average, (3) small
347 specimens with a swelling have a relatively low preservation potential compared to similar-sized
348 specimens that are not infested and/or small specimens have a lower preservation potential than large
349 infested carapaces, (4) the larger swollen specimens represented specimens of which the parasite was lost

350 at an earlier stage but the swelling remained present, (5) parasites have an equal probability of infesting
351 their host at any point during the life of the host, (6) parasites are more likely to infest larger hosts, (7)
352 complete or partial castration of the host leads to increased growth and/or longevity of parasitized hosts,
353 (8) juvenile hosts have a higher probability of dying than adult infested specimens, (9) parasites selected
354 for the larger sex within species, and (10) a combination of several factors.

355 It is unlikely that swellings in small specimens were not noted or were too small to be
356 distinguished from possible post-mortem deformations. We (AAK, CMR) studied specimens for
357 swellings with 10x magnification hand lenses and from different angles in case of doubt.

358 Not all specimens from the Ernstbrunn Limestone assemblage were collected in the same locality
359 and possibly the same stratigraphic level (see above), which may affect host size and parasite prevalence
360 (e.g., McDermott 1991). Bachmayer (1948) reported on parasitic swellings in nine individuals across
361 three species, six from Dörfles I and three from Dörfles Werk II, and Bachmayer (1964) showed another
362 specimen from Dörfles Werk II with *Kanthylooma*. Analyzing the specimens per locality is not possible
363 because the exact locality is unknown for most specimens. Given that Dörfles I and Dörfles Werk II are
364 only ~100 m apart (Bachmayer 1945; Schneider et al. 2013), the hypothesis that the parasitized specimens
365 represent a very different assemblage consisting of larger individuals appears unlikely.

366 No experiments have explored whether small corpses and/or molts containing a swelling have a
367 lower preservation potential than equally-sized specimens without a swelling. However, a galatheoid host
368 cuticle was much thicker on the swelling due to a thicker epidermis/connective tissue layer relative to a
369 non-infested conspecific, but the calcified layers were of equal thickness (Burse 1978). For non-infested
370 specimens, the decay rate of small specimens is not markedly different than in large specimens for most
371 marine arthropods, including brachyurans (Klompaker et al. 2017). Thus, a relatively low preservation
372 potential for small specimens exhibiting *Kanthylooma* is unlikely to explain the larger size of infested
373 specimens.

374 Not all decapods exhibiting a swollen branchial region harbor an isopod parasite permanently,
375 with the isopod leaving the branchial region prior to the death of the host. Such occurrences, however,
376 cannot be identified in fossil specimens because the preservation potential for epicaridean isopods is low
377 (Klompaker et al. 2017; Fig. 2). Decapods can lose the parasite during the molting phase either after the
378 death of the parasite or when the living parasite gets dislodged (e.g., Van Wyk 1982; Anderson 1990;
379 Somers and Kirkwood 1991; Cash and Bauer 1993; Roccatagliata and Lovrich 1999), but the swelling in
380 the carapace can remain present even after a new molting phase for at least one molting cycle for a
381 porcellanid or even four to five cycles for a carid shrimp (Van Wyk 1982). Such empty swellings can
382 dominate large size classes of infested specimens (Van Wyk 1982; Roccatagliata and Lovrich 1999), but
383 they make up only a small portion of all specimens in those size classes (Van Wyk 1982; Cash and Bauer
384 1993; Roccatagliata and Lovrich 1999). Conversely, no marked increase of empty swellings with
385 carapace size were found for a galatheoid (Wenner and Windsor 1979) and a porcellanid (Oliveira and
386 Masunari 1998). Thus, carapaces with these “ghost parasites” are unlikely to result in a substantial
387 increase in the median sizes of fossil specimens with swellings.

388 Regarding the timing of infestation, infestation of many modern decapods by bopyroids is
389 suggested to occur almost exclusively in juvenile hosts based on (1) a positive and often significant
390 relationship between parasite size and host size (e.g., Allen 1966; Beck 1980; Abu-Hakima 1984; Cash
391 and Bauer 1993; Oliveira and Masunari 1998; Roccatagliata and Lovrich 1999; González and Acuña
392 2004; Mantelatto and Miranda 2010; Román-Contreras and Romero-Rodríguez 2013; Baeza et al. 2018),
393 (2) the observation that immature parasites are found in small hosts only (Van Wyk 1982; Oliveira and
394 Masunari 1998, both for a porcellanids), and (3) small specimens are shown to be more readily infested
395 than large specimens (Anderson 1990, for a carid shrimp). Consequently, swellings should be visible
396 early on in the life of infested decapod hosts and, all else being equal, the proportion of specimens that is
397 infested would remain about the same or decrease due to the adverse effects of parasitism on the host (see
398 above) as host size increases. Such patterns are indeed shown in papers that also report on parasite
399 prevalence per size class (e.g., Oliveira and Masunari 1998; Roccatagliata and Lovrich 1999; González
400 and Acuña 2004; Mantelatto and Miranda 2010; but see Román-Contreras and Romero-Rodríguez 2013).

401 On the other hand, epicarideans can also infest their host throughout host ontogeny as shown by a
402 relatively weak or lack of correlation between parasite size (including immature specimens) and host size
403 (Brockerhoff 2004; Smith et al. 2008; Griffen 2009; Rasch and Bauer 2015). Research using only mature
404 female parasites to test for an expected correlation between parasite size and host size (e.g., McDermott
405 1991; Roccatagliata and Lovrich 1999; Jordá and Roccatagliata 2002) should not be taken into account in
406 this case because all epicarideans should be used to assess the timing of infestation. All else being equal,
407 an increase in prevalence with host size is expected when infestation takes place throughout host
408 ontogeny or primarily in larger size classes. As this pattern matches the size-prevalence results herein
409 (Fig. 7), infestation throughout ontogeny or preferential infection of larger specimens rather than solely in
410 juveniles can explain the larger median size of infested individuals. This hypothesis is consistent with the
411 lack of epicarideans in small host size classes in some studies (Mantelatto and Miranda 2010; Lee et al.
412 2016).

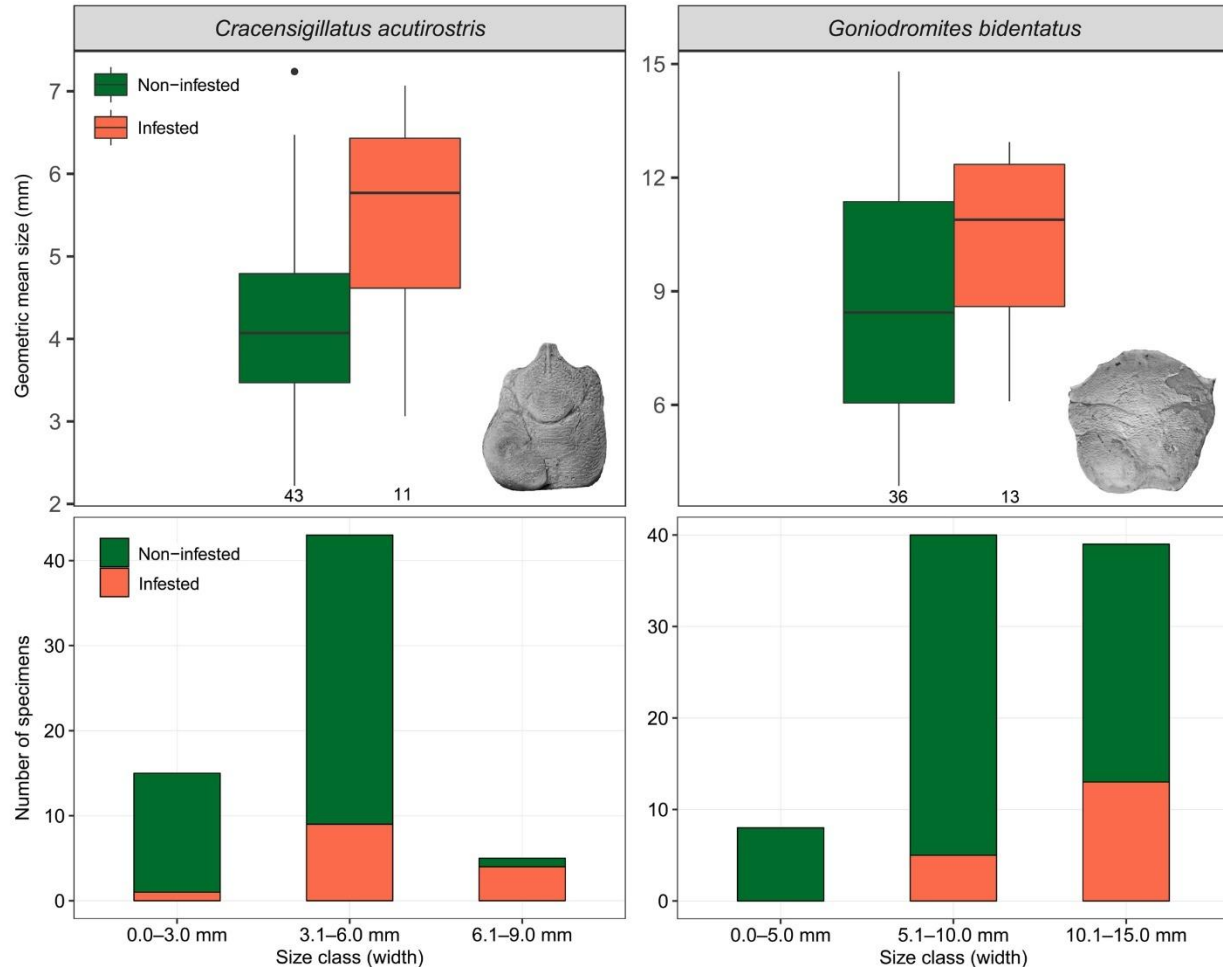
413 Castration may provide another explanation for the larger median size of infested specimens, if
414 the energy that would have been spent on host reproduction is directed toward growth of the host
415 specimen (cf. Poulin 2011: fig. 5.7) instead of to the growth of the parasite and the parasite's reproductive
416 efforts. Host gigantism may be (1) a strategy of the parasite because parasite fecundity is positively linked
417 to host size and host survival may perhaps be improved or (2) an adaptation of the host to counterbalance
418 the negative impact of parasitism (Poulin 2011). Parasite fecundity is often positively correlated with
419 some measure of bopyroid parasite size (e.g., Jay 1989; McDermott 2002; Romero-Rodríguez and
420 Román-Contreras 2008; Román-Contreras and Romero-Rodríguez 2013; Cericola and Williams 2015;
421 Baeza et al. 2018) or host size (Beck 1980); thus, a larger host would be beneficial to the parasite
422 population. However, not all epicarideans castrate their host and host growth rates are inhibited relative to
423 non-infested specimens for many decapods when the epicaridean becomes mature, perhaps because more
424 energy is diverted to the parasite at that point (O'Brien and Van Wyk 1985, and references; Romero-
425 Rodríguez et al. 2016). Castrated hosts that outlive non-parasitized conspecifics would also result in
426 relatively large parasitized specimens. However, at least some species live shorter lives (Romero-
427 Rodríguez et al. 2016, for a carid shrimp) and the multiple negative effects of parasitism (see above)
428 render the castration hypothesis unlikely.

429 A larger median size of infested individuals may be explained by young hosts having a higher
430 probability of dying than older infested specimens, particularly when a branchial swelling has yet to form
431 in small specimens. For those that do survive, a swelling may appear only in larger size classes. High
432 mortality of primarily young hosts infested by a bopyrid is known for a carid shrimp during the one-to-
433 two-week endoparasitic stage before becoming ectoparasitic in the gill chamber (Anderson 1990).
434 Mortality of infested vs non-infested individuals was equal after five weeks (Anderson 1990), but
435 specimen sizes were not provided. Others also hinted at a high mortality of young, infested individuals
436 (Roccatagliata and Lovrich 1999; Lee et al. 2016). As little is known about how much time it takes for an
437 epicaridean to cause a swelling in small and large hosts, it is difficult to further evaluate this hypothesis.

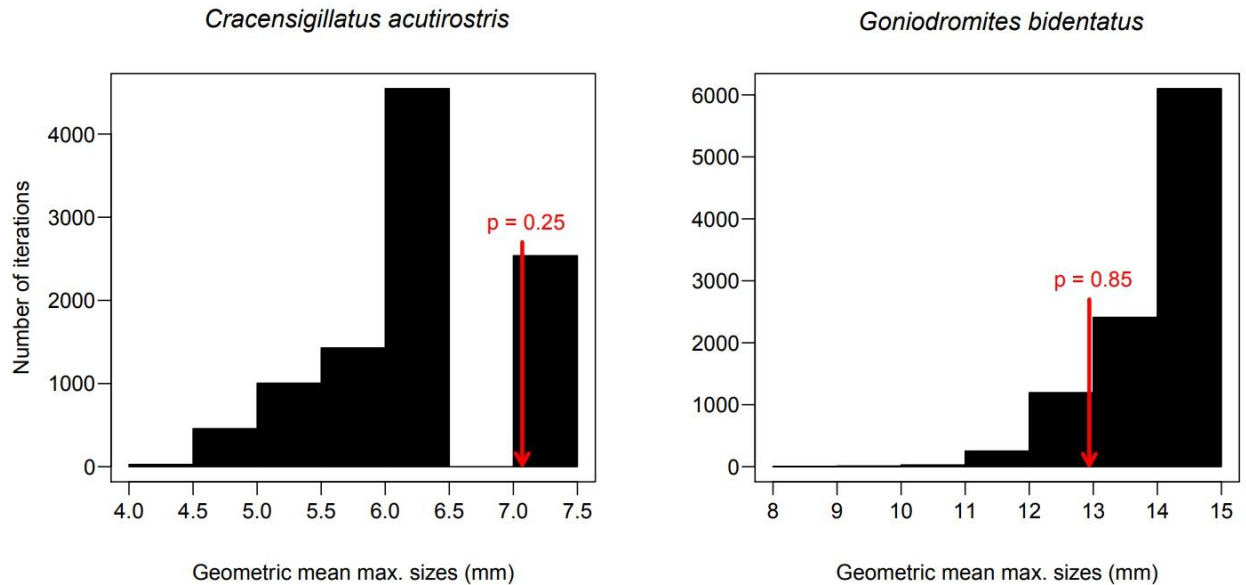
438 Selection of the larger sex of a species, which would have a positive effect on parasite fecundity
439 (see above), could result in a larger median size for infested specimens. For a galatheoid, Petrić et al.
440 (2010) found that the larger male specimens were infected more frequently despite being less common.
441 Our analysis of Petrić et al's data indicates that males are significantly more infested than females ($\chi^2 =$
442 4.7, $p = 0.03$). Beck (1979) mentioned several more examples of bopyroids infecting the larger sex,
443 although results were not always consistent and sexes do not always differ in size (e.g., McDermott
444 1991). If both fossil *Cracensigillatus acutirostris* and *Goniodromites bidentatus* had differently-sized
445 sexes, it is possible that the larger sex was selected by epicarideans. Unfortunately, sex determination is
446 not possible for the fossil specimens because only dorsal carapaces were available.

447 In sum, despite a possible slower growth rate for infested specimens, infestation throughout
448 ontogeny rather than exclusively in young individuals and, possibly, selection for the larger sex appear
449 the most likely explanations for the larger median sizes of infested specimens of *C. acutirostris* and *G.*
450 *bidentatus*. This study adds to the rare examples from the fossil record testing the relative sizes of infested
451 and non-infested specimens. Other examples include Paleozoic crinoids parasitized by platyceratid

452 gastropods that were either larger (Baumiller and Gahn 2018) or smaller (Rollins and Brezinski 1988;
 453 Gahn and Baumiller 2003) than non-parasitized crinoids, and Holocene and possibly Pleistocene bivalves
 454 infested by trematodes that were larger than non-infested specimens (Ruiz and Lindberg 1989; Huntley
 455 and Scarponi 2012).
 456



457
 458 Figure 7. Upper panel: boxplots of geometric mean sizes of non-infested vs infested specimens of two
 459 decapod species from the Ernstbrunn Limestone assemblage (Late Jurassic, Tithonian, Austria).
 460 Geometric mean size = $\sqrt{[\text{maximum carapace length (excluding rostrum for } C. \text{ acutirostris)} \times \text{maximum}$
 461 $\text{carapace width excluding spines}]}$. Infested galatheoid *Cracensigillatus acutirostris* (photo = NHMW
 462 2007z0149/0315, modified from Robins et al. 2013: fig. 16.12): Mann-Whitney $p = 0.008$. Infested
 463 brachyuran *Goniodromites bidentatus* (photo = NHMW 2017/0089/0012): Mann-Whitney $p = 0.057$.
 464 Lower panel: per size class stacked bar diagrams of non-infested and infested specimens for the two
 465 decapod species. Maximum width is used to maximize sample size.
 466



467
468 Figure 8. Comparison of the maximum size of a parasitized specimen versus bootstrapped maximum sizes
469 of non-parasitized specimens for two decapod species from the Ernstbrunn Limestone assemblage (Late
470 Jurassic, Tithonian, Austria). Bootstrapping without replacement (number of iterations = 10,000)
471 was performed because the sample size of non-parasitized specimens was larger than that of parasitized
472 specimens in both cases (sample sizes as in previous figure). Red arrow represents the maximum size of
473 parasitized specimens within the sample. P-value is the chance of getting a larger non-parasitized
474 specimen than the largest parasitized specimen.

475 476 **3. Rhizocephalan barnacles in decapod crustaceans**

477
478 Rhizocephalan barnacles infest modern decapods and castrate their host, cause feminization of male
479 individuals, and reduce host growth rates (e.g., Reinhard 1956; O'Brien and Van Wyk 1985; Takahashi
480 and Matsuura 1994; Høeg et al. 2005; Nagler et al. 2017b). Feminization of male individuals is seen in
481 true crabs (e.g., Reinhard 1956), but not in squat lobsters (Boyko and Williams 2011). The fossil record
482 of evidence for rhizocephalans parasitizing decapods has been discussed in detail recently (Klompaker
483 and Boxshall 2015). In short, feminization of male crab specimens from the Late Cretaceous of South
484 Dakota, USA (Bishop 1974; Bishop 1983b; Jones 2013) and the Miocene of New Zealand (Feldmann
485 1998) is known, with the latter specifically attributed to Rhizocephala. However, epicarideans may also
486 cause feminization of male specimens (e.g., Reinhard 1956; Rasmussen 1973; O'Brien and Van Wyk
487 1985). No new records of feminized fossil decapods have been reported since 2015, but a 5 mm large
488 nauplius larva, perhaps close to Rhizocephala, was found in the Late Jurassic of Germany (Nagler et al.
489 2017a). Collections of decapods with ventral sides and appendages preserved would be suitable for
490 additional studies on this type parasitism. Anomura have been suggested as the ancestral hosts of
491 Rhizocephala because four basal rhizocephalans all infested anomurans and an ancestral host
492 reconstruction also pointed toward anomurans (Glenner and Hebsgaard 2006; Scholtz et al. 2009).

493 494 **4. Ciliates on ostracods**

495
496 Phosphatized stalked peritrichid ciliates (Ciliophora) have been found attached to ostracods within an
497 Early Triassic ammonoid from Svalbard (Spitsbergen) (Weitschat and Guhl 1994). The specimens were
498 up to 0.2 mm long and attached to the inner part of the shell and on the epipodal appendages. These
499 specimens were not considered parasitism in the strict sense because the specimens were filter feeding

500 rather than feeding directly on the host (Klompaker and Boxshall 2015). More specimens may only be
501 found in Konservat-Lagerstätten.

502

503 **5. “Pentastomids” on ostracods**

504

505 Four 1–4 mm long specimens identified as Pentastomida associated with a Silurian ostracod were
506 reported from the Herefordshire Lagerstätte in England (Siveter et al. 2015). Whether these specimens
507 represent true pentastomids was called into question (De Baets et al. 2015; De Baets and Littlewood
508 2015; Klompaker and Boxshall 2015). A re-evaluation rejects a pentastomid affinity because the snout
509 and trunk are in different planes, unlike for true pentastomids in which they are in the same plane; the
510 paired limbs are proportionally longer than in extant pentastomids; and no apical hooks were found, a
511 feature characteristic of true pentastomids (Boxshall and Hayes in press). Regardless of the taxonomic
512 identity, two specimens occurred jointly on the carapace, suggesting that these specimens may not have
513 been nutritionally dependent on the ostracod (not parasitism in the strict sense), but two others were found
514 within the ostracod at the position of the gills near eggs, and may have fed on eggs (parasitism).
515 Specimens were identified as adults, suggesting that the ostracods may have served as the final host
516 (Siveter et al. 2015).

517

518 **6. Modern evidence with preservation potential**

519

520 Many modern crustaceans serve as hosts of parasites sometime during the life cycle of parasites, but most
521 are unlikely to be found in the fossil record (e.g., Klompaker and Boxshall 2015). The reasons are: (1)
522 the parasite does not leave a (recognizable) trace (e.g., Vannier and Abe 1993, for ostracod hosts); (2) the
523 parasite is unlikely to be found as body fossils associated with the crustacean host because the parasite
524 has a low preservation potential and/or is extremely small (e.g., Boxshall and Lincoln 1983, for
525 tantulocarid parasites on other crustaceans); and/or (3) the body fossils of the host are unlikely to fossilize
526 (e.g., Poinar et al. 2010, for amphipod hosts).

527 Some associations only found in modern ecosystems thus far have the potential to be found in the
528 fossil record. First, the endoparasitic entoniscid isopods can cause swellings/asymmetries in the carapaces
529 of decapod crustaceans including anomuran, brachyuran, and shrimp hosts (Miyashita 1941: p. 251;
530 Shiino 1942: p. 62, 68; Shields and Kuris 1985: fig. 1; Mushtaq et al. 2016: p. 1608). These swellings
531 may be less prominent than those caused by the primarily ectoparasitic Bopyridae and Ionidae and not
532 always at the same spot in the branchial chamber because entoniscids are found in the visceral cavity of
533 their host and may even cause a swelling of the cardiac region (Adkison 1990; Williams and Boyko 2012:
534 fig. 1F; Mushtaq et al. 2016: fig. 1). Although not all entoniscid cause malformations (McDermott 2009,
535 for pinnotherid crabs), gentle bopyrid/ionid-induced swellings may be confused with swellings caused by
536 entoniscid in fossil material. Thus, it is possible that some examples of *Kanthylooma crusta* ascribed to
537 bopyrids/ionids are caused by entoniscids.

538 Second, Hosie (2008: fig. 12A) showed a barnacle *Smilium zancleanum* (Seguenza, 1876), with
539 swelling up to 1 cm made by a cryptoniscoid isopod. The swellings are located in the muscular peduncle
540 or at the base of the capitulum, where they can cause a disruption in the alignment of plates. Exceptional
541 preservational circumstances are necessary for such swellings to preserve in the fossil record.

542 In addition to small (0.02–0.40 mm) hooks of likely platyhelminth (?Monogenea) origin found in
543 fish, platyhelminth hooks have also been found in association with two crustacean specimens from the
544 Late Devonian (Frasnian) of Latvia (Upeniec 2001; Upeniece 2011; De Baets et al. 2015). Two hooks
545 were found near a specimen of Mysidacea (a member of Peracarida), whereas another hook was found
546 near a clam shrimp (Conchostraca). Recent work has suggested that parasitism by platyhelminthes of
547 these crustacean specimens is unlikely because of the large size of the hooks relative to the crustacean
548 specimens (De Baets et al. 2015) and the rarity of hooks among the thousands of mysidacean specimens
549 (Klompaker and Boxshall 2015). Monogeneans parasitize nearly exclusively fish today, but another
550 group of platyhelminthes, Cestoda, also uses hooks for attachment to crustacean host, including their

551 larvae (e.g., Xylander 2005). Cestodes have been recorded from modern decapods such as true crabs
552 (Dollfus 1976; Torchin et al. 2001), hermit crabs (McDermott et al. 2010), and shrimps (Dollfus 1976;
553 Georgiev et al. 2007). Cestode hooks are mineralized (e.g., Collin 1968; Ambrosio et al. 2003). Thus,
554 minute platyhelminth hooks may be found associated with fossil crustaceans in the right preservational
555 settings in the future.

556

557 **Acknowledgements:** AAK and CMR thank Thomas Nichterl and Andrea Krapf (both Naturhistorisches
558 Museum Wien, Austria) for help with handling loans, and Andreas Kroh (Naturhistorisches Museum
559 Wien) for facilitating a wonderful research stay in Vienna in 2017. René Fraaije (Oertijdmuseum, The
560 Netherlands) made his fossil decapod collection available for study. This research was supported by a
561 Paleontological Society Arthur J. Boucot research grant to AAK and, in part, by a Palaeontological
562 Association research grant (PA-RG201401) to AAK.

563

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