

Becoming a limpet: An 'intermittent limpetization' process driven by host features in the kleptoparasitic gastropod family Capulidae

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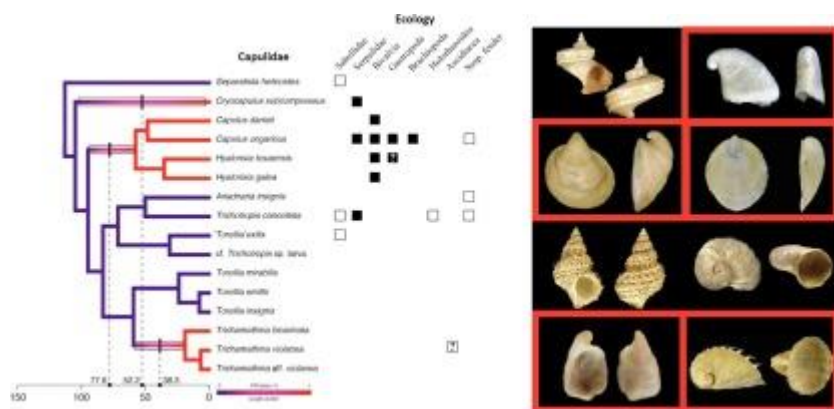
Abstract :

A coiled shell is the most evident feature of the typical Bauplan of a gastropod mollusc. However, at least 54 families independently evolved an apparently simplified shell morphology: the limpet. Species with this largely uncoiled, depressed shell morphology occur in almost every aquatic habitat and are associated to a number of different lifestyles and diets. The marine gastropod family Capulidae includes 18 recognised genera, the large majority of which are coiled, but with a number of limpet-like species. Capulid shell plasticity is also associated to a broad range of feeding ecologies, from obligate suspension feeders to kleptoparasites.

To investigate the evolution of the limpet-like shell in the family Capulidae we performed an ancestral state reconstruction analysis on a time-calibrated phylogenetic tree (COI, 16S, and ITS2) including 16 species representing a good deal of its morphological diversity.

Our results identified at least three capulid lineages that independently evolved limpet-like shells, suggesting that a recurrent limpetization process characterizes this family. One of the limpet-like genera was undescribed and was here named *Cryocapulus* n. gen. We suggest that capulids evolved from a coiled suspension feeder lineage and that the shift to kleptoparasitism, which occurred in the family ancestor, may have represented a strategy to save energy through the exploitation of the water current produced by the host. Probably the major drivers of shell evolution in capulids are related to their ecology, most of them being kleptoparasites, include the shape and the kind of host substrate, and lead to the repeated acquisition of a limpet-like shape.

Graphical abstract



Highlights

► We investigated limpet-like shell evolution in the marine gastropod family Capulidae. ► At least three capulid lineages independently evolved limpet-like shells. ► One limpet-like capulid lineage was certainly undescribed: *Cryocapulus* n. gen. ► The capulid ancestor was likely a coiled kleptoparasite. ► The host features may have favoured the repeated evolution of limpet-like shells.

Keywords : Limpetization, Kleptoparasitism, Capulidae, Divergence time estimation, Ancestral state reconstruction

47 **1. Introduction**

48

49 The classic Bauplan of a gastropod mollusc normally corresponds to a dextrally coiled shell.
50 Interestingly enough, the Patellogastropoda or “true limpets”, the first offshoot of the extant
51 Gastropoda, have a coiled larva but a secondarily uncoiled adult shell, which maximises the surface
52 of the foot and thus their ability in resisting to dislodgement from hard substrates. A limpet-like
53 shell is generally cap-shaped, sometimes partially coiled and with an expanded last whorl. This
54 apparently simplified morphology has convergently evolved, from the Early Cambrian to the
55 Neogene, in at least 54 gastropod families (Vermeij, 2017). Overall, limpet-like molluscs can be
56 found in almost all habitats, including freshwater and the deep sea, where this shape evolved
57 independently at least 10 times (Vermeij, 2017). Geographically, the maximum diversity of
58 uncoiled taxa has been registered along the temperate shores of Australasia, while the minimum
59 was reported for the Indo-West Pacific area and at the poles (Knox, 1963; Vermeij, 2017). A
60 limpet-like shell has been found associated to very different lifestyles and diets, from herbivory
61 (e.g. abalones), to filter feeding and parasitism (e.g. calyptraeids, capulids, and certain eulimid
62 genera), and even predation (e.g. the muricid genus *Concholepas* Lamarck, 1801).

63 The large majority of the studies about limpet-like taxa focused on the acquisition and loss of this
64 shell character, while little is known about the subtended evolutionary processes. Albrecht et al.
65 (2004) found that two limpet-like groups of African freshwater gastropods traditionally assumed to
66 belong in the same family were instead a paradigmatic example of convergent limpet-like shell
67 evolution in two distinct lineages: the genus *Burnupia* B. Walker, 1912 (currently ascribed to a
68 family on its own, Burnupiidae Albrecht, 2017) and the subfamily Ancyliinae Rafinesque, 1815 in
69 the family Planorbidae Rafinesque, 1815. Albrecht et al. (2004) hypothesized that different factors,
70 or a combination of them, may have played a role in these independent acquisitions of a limpet-like
71 shell, including: (a) resistance to thermal and desiccation stress due the ability to mould shell edges
72 to the surface, (b) increased survival in low oxygen regimes due to an enlarged pallial cavity, (c)
73 reduced predation risk thanks to a flat surface that makes crashing the shell more difficult, and (d)
74 resistance to hydrodynamic forces such as currents and waves due to a proportionally larger foot.
75 According to Albrecht et al. (2004), the high frequency of independent limpet-like shell evolutions
76 in gastropods suggests a relatively simple underlying genetic mechanism, probably controlled by
77 one or few genes, as suggested for other traits, like the single-locus genotype of coiling chirality
78 (Davison et al., 2016; Sturtevant, 1923). Collin and Cipriani (2003) reported for the family
79 Calyptraeidae Lamarck, 1809, mainly comprising uncoiled limpet-like species, at least one case of
80 re-evolution of a coiled shell, in the genus *Trochita* Schumacher, 1817. According to Collin and

81 Cipriani (2003) the genetic and developmental pathways for shell coiling may have been retained in
82 the larval stages of all calyptraeids, and secondarily re-expressed heterochronically in the adult shell
83 of *Trochita*. Finally, one recent study (Yamamori and Kato, 2018) compared genetic,
84 morphological, and ecological data to investigate evolutionary trends accompanying shell-flattening
85 in the trochid subfamily Fossarininae Bandel, 2009. The coiled shell of the genus *Fossarina* A.
86 Adams & Angas, 1864, which uses narrow refugia in intertidal rock reefs, resulted to be the
87 ancestral state of the subfamily. Two closely related species evolved a limpet-like shell, probably as
88 the result of different selective pressures: the extremely flattened shell of *Broderipia iridescens*
89 (Broderip, 1834) is thought to be linked to its lifestyle, as obligate inquiline in the pits occupied by
90 a non-boring sea urchin (Yamamori and Kato, 2017); the ribbed and less flat shell of *Broderipia*
91 *eximia* G. Nevill & H. Nevill, 1869 may be an adaptation to a life moving between wave-swept
92 rock surfaces and refugia inside vacant barnacle shells.

93 Among marine gastropod lineages that evolved limpet-like shells, the worldwide-distributed family
94 Capulidae J. Fleming, 1822 includes species with normally coiled shells, and others that are limpet-
95 like, having undergone a “limpetization” process (*sensu* Simone, 2018). According to the currently
96 accepted systematics, coiled genera are more numerous than limpet-like ones (15 out of 18) and
97 comprise species like the common NE Pacific *Trichotropis cancellata* Hinds, 1843 (Fig. 1E) or the
98 much less common Indo-West Pacific *Separatista helicoides* (Gmelin, 1791) (Fig. 1A). Among the
99 uncoiled groups, the most widespread genus is *Capulus* Montfort, 1810 (Fig. 1B, C, G), which
100 based on current taxonomy, includes at least 20 Recent species (MolluscaBase, 2020). According to
101 Simone (2002, 2018), among gastropods Capulidae have reached the maximum level of
102 limpetization (degree 3 – “secondary true limpets” in Simone, 2018), characterized by a symmetrical
103 shell, a horseshoe-shaped columellar muscle, and an uncoiled visceral mass, as exemplified by
104 *Capulus*.

105 The feeding ecology of the Capulidae is peculiar among gastropods. Capulids may exploit the water
106 currents generated by their host, being obligate suspension feeding, as the coiled species *Ariadnaria*
107 *insignis* (Middendorff, 1848) (Iyengar, 2008). Others directly steal the food particles from a host
108 using a pseudoproboscis consisting in a dorsally split, tube-like extension of the mouth (Fretter and
109 Graham, 1962; Ponder, 1998) – a strategy termed kleptoparasitism; these kleptoparasitic species
110 live on various filter-feeding organisms (notably bivalves and sedentary polychaetes), generally
111 several times larger in size (Ponder, 1998; Yonge, 1938). The Indo-West Pacific capulid *Capulus*
112 *danieli* (Crosse, 1858) is even known to drill a hole in the shell of its scallop host, over or near its
113 mouth, to insert the pseudoproboscis directly in the host mantle area with the highest concentration
114 of food (Orr, 1962) (Fig. 2C).

115 Because most capulid species are rare and hardly collected alive, only two studies made an attempt
116 to produce a molecular phylogeny of the family Capulidae. Fassio et al. (2015) produced the first
117 capulid phylogeny and investigated the larval ecology of Antarctic species. More recently, Fassio et
118 al. (2020) produced a new phylogenetic hypothesis with a wider taxonomic framework (6 genera) to
119 address the Indo-West Pacific diversity of the genus *Hyalorisia* Dall, 1889.
120 Given the plasticity of shell shapes and array of feeding strategies of the Capulidae, this family is an
121 ideal model for our study, aimed to investigate (a) the evolution of a limpet-like shell, (b) the
122 evolution of kleptoparasitic feeding strategies and (c) the relationship between the two traits,
123 through divergence time estimation and ancestral state reconstruction analyses.

124

125

126 **2. Materials and Methods**

127

128 *2.1 Molecular dataset*

129

130 The analysed capulid dataset included 16 species, representing 6 (4 coiled and 2 limpet-like) of the
131 18 living genera (MolluscaBase, 2020): the coiled *Ariadnaria insignis* (Middendorff, 1848),
132 *Separatista helicoides* (Gmelin, 1791) (Fig. 1A), *Torellia exilis* (Powell, 1958), *Torellia insignis* (E.
133 A. Smith, 1915), *Torellia mirabilis* (E. A. Smith, 1907) (Fig. 1F), *Torellia smithi* Warén, Arnaud &
134 Cantera, 1986, *Trichotropis cancellata* Hinds, 1843 (Fig. 1E), and *Trichotropis* sp.; and the limpet-
135 like *Capulus bicarinatus* (Pease, 1861) (Fig. 2A), *Capulus danieli* (Crosse, 1858) (Fig. 2C),
136 *Capulus subcompressus* Pelseneer, 1903 (Figs 1B, 2E–F), *Capulus ungaricus* (Linnaeus, 1758)
137 (Figs 1C, 2B), *Capulus violaceus* Angas, 1867 (Fig. 1G), *Capulus* aff. *violaceus*, *Hyalorisia galea*
138 (Dall, 1889) (Fig. 2D), *Hyalorisia tosaensis* (Otuka, 1939) (Fig. 1D). In terms of shell shape
139 diversity, this dataset covers the whole variation in the family, from the clearly coiled *Trichotropis*
140 to the dorso-ventrally flattened *Hyalorisia*. In terms of taxonomic diversity, we have included 16%
141 of the current capulid species diversity (MolluscaBase, 2020), which is acceptable considering the
142 rarity of most species and the scarcity of samples preserved for molecular analyses. Three species
143 of the Calyptraeidae, a closely related family (Ponder and Lindberg, 2008) also showing different
144 degree of shell coiling, were included in the dataset: the coiled *Sigapatella novaezelandiae* (Lesson,
145 1831), and the limpet-like *Crepidula unguiformis* Lamarck, 1822 and *Crucibulum lignarium*
146 (Broderip, 1834). For all these species, COI, 16S rDNA, and ITS2 sequences were retrieved from
147 the GenBank (mostly based on our own earlier work: Fassio et al., 2015, 2020; Table 1).

148

149 *2.2 Phylogenetic analyses*

150

151 Geneious v.11 (<https://www.geneious.com>) was used to align COI sequences, while MAFFT v.7
152 (E-INS-i algorithm; Katoh & Standley, 2013) was used for 16S rDNA and ITS2. Phylogenetic
153 analyses were performed on the combined dataset (COI partitioned by codon+16S rDNA+ITS2,
154 after checking for incongruence among genes) with Maximum Likelihood (ML) and Bayesian
155 inference (BA) methods. JModeltest v.2 (Darriba and Posada, 2012) was used to choose for each
156 gene the best fitting nucleotide substitution model (COI codon 1st=GTR+I+G, 2nd=F81,
157 3rd=GTR+G; 16S rDNA= GTR+I+G; ITS2=HKY+G). ML analyses were carried out using W-IQ-
158 TREE online v.1 (bootstrap pseudoreplicates = 1,000, other parameters as default; Trifinopoulos et
159 al., 2016) while BA analyses were performed using MrBayes v.3 (10⁷ generation, 25% burn-in,
160 other parameters as default; Ronquist et al., 2011) on CIPRES Science Gateway Portal (Miller et
161 al., 2010). MCMC convergence was checked with Tracer v.1.7 (Rambaut et al., 2018). The same
162 criteria were used for interpreting the node value of ultrafast bootstrap (UFb), obtained from the
163 ML analysis (Minh et al., 2013), and of the posterior probability (PP): a node was considered highly
164 supported with values ≥ 0.98 , and moderately supported with values >0.95 and <0.98 .

165

166 2.3 Divergence time estimation

167

168 BEAST v. 1.8 (Drummond and Rambaut, 2007) was used to generate an ultrametric tree from the
169 same alignment used in the phylogenetic analysis (10⁸ generation, 25% burn-in, 2 runs). The tree
170 was calibrated at 5 points based on fossil data, set under exponential prior (Ho and Phillips 2009),
171 and with the 95% of the distribution set within the range of the fossil age. The heterogeneity of the
172 mutation rate across lineages was set under uncorrelated, lognormal distributed relaxed clocks for
173 the five partitions. As tree prior the Birth-Death incomplete sampling was used.

174 The age of the node corresponding to the origin of the family Capulidae was calibrated following
175 Tracey, Todd & Erwin (1993) who identified the first appearance of the ‘Trichotropidae’ (currently
176 included in the family Capulidae) during the Albian?/ Aptian (Lower Cretaceous, 125-100.5 Ma)
177 based on the following fossils: ?*Atresius cornuelianus* (d’Orbigny, 1843)† (Vaucluse, France), and
178 *Atresius lallierianus* (d’Orbigny, 1843)† (Yonne, France). For the origin of the genus *Capulus* s.s.
179 (in our dataset represented by the clade *Capulus ungaricus*+*Capulus danieli*) we referred to the
180 oldest species confidently ascribable to this genus, *Capulus onyxoides* Cossmann, 1879† (Paris
181 Basin, France) from the Ypresian (Lower Eocene, 56-47.8 Ma). The origin of the genus *Hyalorisia*
182 was dated with the fossil *Capulus (Hyalorisia) nettlesi* Robinson, 1983† from the Moodys Branch
183 Formation, Mississippi, USA (Upper Eocene, 41.2-33.9 Ma). The following two calibration points,

184 concerning single-species lineages, were set as STEM, to impose that the age of the stem nodes of
185 these lineages must be at least as old as the fossils (minimum age constraint) (Sauquet, 2013). The
186 origin of the lineage leading to *Trichotropis cancellata* was calibrated with the first appearance of
187 *Trichotropis cancellaroides* (Deshayes, 1861)[†] (Paris Basin, France) from the Ypresian (Lower
188 Eocene, 56-47.8 Ma) considering that the genus and family attribution of “*Trichotropis?* sp.” from
189 the Palaeocene Faxe formation of Denmark by Lauridsen & Schnetler (2014: fig. 42), are highly
190 questionable. The origin of the species *Capulus ungaricus* was dated at the lower Pliocene (5.0-4.4
191 Ma) based on fossils from Kallo, East Flanders, Belgium (Marquet, 1998); records from the
192 Miocene ascribed to *Capulus ungaricus*, are actually to be ascribed to other species.

193

194

195 2.4 Ancestral state reconstruction

196

197 To investigate the evolution of a limpet-like shell in the family Capulidae we performed an
198 ancestral state reconstruction (ASR) on the calibrated ultrametric tree generated with BEAST using
199 the R package phytools (model=ARD, nsim=1000, Q=mcmc; Revell, 2012). The species were
200 categorised as limpet-like or coiled following Collin et al. (2003) and Simone (2018). Based on the
201 observation that a coiled shell is the general ancestral state of most caenogastropod families
202 (Vermeij, 2017), we set it as prior for the state at the root of capulids.

203 The ancestral state reconstruction analysis in phytools is performed by a stochastic mapping
204 procedure on a given phylogenetic tree (the ultrametric dated tree), by sampling from a chosen
205 number of generations (in our case 10^5) every 100. The probability of having a limpet-like shell on
206 every point along the branches of the tree is obtained as the proportion of the sampled trees that had
207 that state on that point. This is graphically reported (with ‘densitymap’ in phytools) with a colour
208 gradation and a corresponding colour scale from blue to red, representing the increasing probability
209 of having the state “limpet-like shell”. To estimate the date of the transitions in the state of
210 character across the dated tree, we have derived, from the trees sampled in the stochastic mapping,
211 the cumulated distribution of all changes along all branches (with ‘markchanges’ in phytools). On
212 the densitymap tree we have located the medians of each distribution of changes between every two
213 consecutive points across the tree with different state, i.e. two consecutive points with probability
214 for a limpet-like shell being 0 and 1 (or 1 and 0), respectively; these were the branch segments
215 along which the character state was assumed to have changed. The medians were used as the
216 estimated dates for the changes of state, along with the relevant 95% confidence intervals
217 (Supplementary Materials: ScriptS1).

218

219

220 3. Results

221

222 3.1 Phylogenetic reconstruction

223

224 The phylogenetic analyses confidently reconstructed the relationships among capulid taxa (Fig. 3),
225 and the three markers did not show any phylogenetic incongruence (Supplementary Materials: Figs
226 S1-S6). Both BA and ML analyses supported the monophyly of the family, two early-diverging
227 lineages, the coiled *Separatista helicoides* and the limpet-like '*Capulus*' *subcompressus* followed by
228 two major lineages: (A) including limpet-like species of the genera *Capulus* s.s. (*Capulus ungaricus*
229 and *Capulus danieli*) and *Hyalorisia*, and (B) including a diverse group of coiled species ascribed to
230 the genera *Torellia*, *Trichotropis*, *Ariadnaria*, and *Capulus*-like limpets. This second clade can be
231 further divided in (B1) grouping '*Torellia*' ('*Torellia*' *exilis*), an unidentified capulid larva from the
232 Southern Ocean, *Trichotropis cancellata*, and *Ariadnaria insignis* (originally described in
233 *Trichotropis*), and (B2) including the Indo-Pacific specimens ascribed to '*Capulus*' *bicarinatus*,
234 '*Capulus*' *violaceus*, '*C.*' aff. *violaceus*, and the rest of the Antarctic *Torellia* s.s. (*Torellia*
235 *mirabilis*, *Torellia insignis*, and *Torellia smithi*). While all the nodes between and within the
236 lineages A and B were supported (with the exception of the *C. ungaricus* + *C. danieli* clade), the
237 positions of *S. helicoides* and '*C.*' *subcompressus* differed between BA and ML. The BA tree
238 positioned *S. helicoides* as sister to the clade including '*C.*' *subcompressus* and the rest of the
239 family, even if with a low support value (0.83). Based on these results, the capulid genera *Capulus*
240 and *Torellia*, as traditionally conceived, are not monophyletic.

241

242 3.2 Calibrated tree

243

244 The origin of the family Capulidae was estimated at 112.87 Ma (95% HPD: 137.85-100.4), at the
245 beginning of the Albian (Lower Cretaceous), and the split between the lineage leading to '*Capulus*'
246 *subcompressus* and the rest of the family at the end of same age (104.7 Ma, 95% HPD: 130.71-
247 86.74) (Fig. 4). The divergence between clades A and B was estimated at the end of the
248 Cenomanian (Upper Cretaceous) (94.7 Ma, 95% HPD: 117.96-77.57). The split between the
249 lineages leading to the limpet-like '*Capulus*' and the coiled *Torellia* was dated at the boundary
250 between Selandian and Thanetian (59.19 Ma, 95% HPD: 79.74-39.5). The beginning of the

251 diversification of the two Antarctic clades including species morphologically ascribed to *Torellia*
252 s.l. was dated at 30.86 Ma (*Torellia* 'exilis' + capulid larva) and 23.7 Ma (the other *Torellia* spp.).

253

254 3.3 Ancestral state reconstruction

255

256 According to the results of the ancestral state reconstruction, the shift from a coiled to an uncoiled
257 shell occurred independently at least three times during capulid evolution (Fig. 5). The first event
258 was estimated to have occurred along the branch leading to the *Capulus* s.s. + *Hyalorisia* clade in
259 the 93.6-58 Ma interval, with a median in the Campanian (77.6 Ma, Upper Cretaceous); the second
260 was along the branch leading to the Antarctic '*Capulus*' *subcompressus*, in the 102.15-2.77 Ma
261 interval, with a median in the Ypresian (52.25 Ma, Lower Eocene); lastly, the most recent event
262 occurred on the branch leading to the '*Capulus*' clade, in the 57.8-19.4 Ma interval, with a median
263 in the Bartonian (38.3 Ma, Middle Eocene). The same ASR analysis without setting the coiled shell
264 as the capulid root ancestral state was not able to clearly attribute the basal node to either state,
265 making the analysis completely uninformative, probably due to the limited dataset.

266

267

268 4. Discussion

269

270 4.1 Systematics of Capulidae

271 Based on our results *Torellia* as traditionally conceived is not monophyletic. Pending the molecular
272 analysis of the type species (*Cyclostoma delicatum* Philippi, 1844 = *Torellia vestita* Jeffreys, 1867)
273 we cannot delimit with certainty the genus (although we suspect that *Torellia insignis*, *T. smithi* and
274 *T. mirabilis* may belong to the same lineage as *T. delicata*: see also Fassio et al., 2015).

275 The genus *Capulus* has been employed to accommodate species with limpet-like shells (with
276 *Hyalorisia* earlier considered a subgenus or a full genus). However, our phylogenetic analysis
277 demonstrated (as shown also by Fassio et al., 2020) that also *Capulus* as traditionally conceived is
278 not monophyletic. *Capulus* s.s. should therefore be restricted to the lineage including the type
279 species (*C. ungaricus*), which is the sister lineage to *Hyalorisia* (Fassio et al., 2020). There is a need
280 for two further distinct genera, one for the clade represented by '*Capulus*' *violaceus*, '*Capulus*' cf.
281 *violaceus*, and '*Capulus*' *bicarinatus* which we conservatively ascribe to the genus *Trichamathina*
282 Habe, 1962 (Fig. 1H), and another to accommodate the Antarctic '*Capulus*' *subcompressus*.

283

284 Class Gastropoda

285 Subclass Caenogastropoda
286 Order Littorinimorpha
287 Superfamily Capuloidea
288 Family Capulidae
289
290 Genus *Capulus* Montfort, 1810
291 **Type species:** *Patella ungarica* Linnaeus, 1758 (Northeastern Atlantic, Mediterranean), by original
292 designation.
293 **Diagnosis:** Shell of average to large size for the family (9-60 mm), limpet-like, depressed dorso-
294 ventrally, thick, whitish-yellowish background, aperture rounded to ovoidal, with yellowish-
295 brownish periostracum. Protoconch of 1.25–1.4 whorls. Foot rounded, pseudoproboscis long,
296 longitudinally curved to form a dorsally open canal.
297 **Remarks:** *Capulus* is similar to *Hyalorisia* in its general shell features, but has a dorso-ventrally
298 less depressed shell and lacks the glossy lamella inside the posterior part of the aperture.
299 Based on our results, *Pileopsis danieli* Crosse, 1858, certainly belongs to *Capulus*. Additionally, we
300 suggest that, based on morphological similarity (dorso-ventrally depressed shell, large and rounded
301 aperture, no internal glossy lamella), the following extant species also likely belong to *Capulus* as
302 restricted here (listed alphabetically by specific epithet):
303 *Capulus californicus* Dall, 1900
304 *Roya devexa* May, 1915
305 *Capulus dilatatus* A. Adams, 1860
306 *Capulus elegans* Tapparone Canefri, 1877
307 *Capulus huangi* S.-I Huang & Y.-F. Huang, 2012
308 *Capulus kawamurai* Habe, 1992
309 *Capulus ngai* Thach, 2016
310 *Capulus novaezelandiae* Dell, 1978
311 *Amalthea (Malluvium) otohimeae* Habe, 1946
312 *Capulus sericeus* J. Q. Burch & R. L. Burch, 1961
313 *Capulus simplex* Locard, 1898
314 *Capulus spondylicola* Habe, 1967
315 *Pileopsis ungaricoides* d'Orbigny, 1841.
316
317 If our morphological criterion will prove valid after testing with genetic data, then, among the fossil
318 taxa, we suggest that the following may also belong to *Capulus*:

319 *Capulus deurganckensis* Marquet & Landau, 2006†

320

321 *Capulus partimsinuosus* S. V. Wood, 1848†

322

323 *Patella sinuosa* Brocchi, 1814†

324

325 *Capulus uncinatus* (Hutton, 1873)† (see Dell, 1964 for details).

326

327 Genus *Hyalorisia* Dall, 1889

328 **Type species:** *Capulus (Hyalorisia) galea* Dall, 1889 (from the Louisiana Slope to Barbados and
329 the Caribbean coast of Colombia), by monotypy.

330 **Diagnosis:** Shell of small to average size for the family (4–25 mm), limpet-like, thin, strongly
331 depressed dorso-ventrally, white semi-transparent, rounded to ovoidal, with yellowish
332 periostracum; glossy lamella inside posterior part of aperture. Protoconch of 0.7–1.2 whorls. Foot
333 rounded; head large, swollen; cephalic tentacles subulate; pseudoproboscis elongated, flattened,
334 rounded at tip, longitudinally curved to form a dorsally open canal.

335 **Remarks:** see Fassio et al. (2020) for a taxonomic revision of the extant species. *Hyalorisia* differs
336 from *Capulus* in its more strongly depressed shell, and the glossy lamella inside the posterior part of
337 the aperture. We suggest that also *Capulus fragilis* E. A. Smith, 1904 (a junior homonym of
338 *Capulus fragilis* Meek & Hayden, 1856, from the Cretaceous of South Dakota) may also belong to
339 *Hyalorisia*.

340

341 Genus *Cryocapulus* Schiaparelli, Bouchet, Fassio, & Oliverio n. gen.

342 <http://zoobank.org/xxx>

343 **Type species:** *Capulus subcompressus* Pelseneer, 1903 (Southern Ocean).

344 **Diagnosis:** Shell of small size for the family (1–9 mm), limpet-like, thin, laterally strongly
345 compressed, smooth, whitish, aperture ovoidal. Protoconch of 2.25–2.4 whorls, sculptured with
346 spiral cordlets. Foot oval, laterally compressed, pseudoproboscis elongated, longitudinally curved to
347 form a dorsally open canal.

348 **Etymology:** From the Greek *cryo*, cold, and the genus name *Capulus*, with reference to the
349 Antarctic distribution of the type species.

350 **Remarks:** Based on a similar, limpet-like but not depressed shell, we suggest that also the South
351 American *Capulus compressus* E. A. Smith, 1891 (from 43°S southward in the Pacific, and from

352 28°S southward in the Atlantic) (Cárdenas et al., 2008) belongs to this genus. The gross anatomy
353 and ecology of the type species was described by Schiaparelli et al. (2000).

354

355 Genus *Trichamathina* Habe, 1962

356 **Type species:** *Amathina nobilis* A. Adams, 1867 (Japan), by original designation.

357 **Diagnosis:** Shell: size small to average for the family (3–40 mm), limpet-like, thick, from laterally
358 compressed to dorso-ventrally depressed, white/orange/red/violet in colour, with or without narrow
359 longitudinal ridges, aperture ovoidal to round. Number of protoconch whorls unknown. Foot oval to
360 round, pseudoproboscis elongated, longitudinally curved to form a dorsally open canal.

361 **Remarks:** The shell shape of *Trichamathina* can be considered intermediate between that of
362 *Capulus* and *Cryocapulus*. It is similar to *Capulus* in its limpet-like shell but can have narrow
363 longitudinal ridges and being laterally compressed. It differs from *Cryocapulus* in its shell shape,
364 less compressed laterally, and colour, that in *Cryocapulus* it is always white. Pending the genetic
365 analysis of samples of the type species *T. nobilis* (A. Adams, 1867) and/or of the closely related *T.*
366 *buccinula* (Golikov in Golikov & Scarlato, 1967), and based on the strong morphological similarity
367 in their shell, we ascribe our samples of *Capulus violaceus* Angas, 1867, *C. cf. violaceus*, and *C.*
368 *bicarinatus* (Pease, 1861), to *Trichamathina*. Likewise, we suggest that also *Capulus japonicus* A.
369 Adams, 1861 and *Capulus badius* Dunker, 1882, from the Indo-West Pacific, belongs to this genus.

370

371 4.2 Evolution of capulid feeding strategies

372

373 Because of the high amount of missing data of capulid trophic ecology (see Fig. 5), it was not
374 possible to statistically test the evolution of this character, as for the shell shape. However, our data
375 still allow drawing some evolutionary hypotheses. The first diverging lineages of the capulids are
376 represented in our dataset by *Separatista helicoides* and *Cryocapulus subcompressus*, both
377 kleptoparasitic on polychaetes of the order Sabellida: *S. helicoides* (coiled) is reported to live on
378 sabellids (Okutani, 2000) and *C. subcompressus* (limpet-like) on the serpulid *Serpula narconensis*
379 Baird, 1864 (Schiaparelli et al., 2000) (Fig.2). Polychaetes may thus likely represent the ancestral
380 host of kleptoparasitic capulids, shared by both coiled and uncoiled species. Three other capulid
381 species are known to live on tube-worms: ‘*Torellia*’ *exilis* on the sabellid *Perkinsiana* sp. (Fassio et
382 al., 2015), and the two more generalist species *Capulus ungaricus*, reported to feed, among other
383 hosts, also on serpulids (Graham, 1988), and *Trichotropis cancellata*, which is associated to both
384 serpulids and sabellids (Pernet and Kohn, 1998).

385 Our data suggest that clade A established a close kleptoparasitic relationship with bivalves, that
386 represent the only host of *Hyalorisia* species, living on Propeamussiidae (Matsukuma, 1978, Fassio
387 et al., 2020) (Fig. 2C), and of *Capulus danieli*, living on Pectinidae (Garrard, 1961; Orr, 1962;
388 Matsukuma 1978; this paper) (Fig. 2B). *C. ungaricus* is instead a true generalist, being able to
389 establish kleptoparasitic interactions with a variety of hosts such as bivalves, gastropods,
390 polychaetes, and brachiopods (Graham, 1988; Schiaparelli et al., 2000; Sharman, 1956; Thorson,
391 1965), or live as a free suspension feeder (Sharman, 1956). A similar generalist ecology is also
392 reported for the NE Pacific *Trichotropis cancellata* that has been observed both as kleptoparasite on
393 polychaetes and holothurians (Iyengar, 2008, 2002; Pernet and Kohn, 1998), and as a free
394 suspension feeder (Iyengar, 2008; Yonge, 1962). On the other hand, some capulids are thought to
395 be obligate suspension feeders as in the case of the NE Pacific *Ariadnaria insignis* (Iyengar, 2008)
396 and *A. borealis* (Graham, 1954). The anatomy of these two *Ariadnaria* species was described in
397 detail (Graham, 1954; Simone, 2002) and shows several peculiar features, among which at least the
398 short proboscis (which is used to convey to the mouth the food collected within the mantle cavity)
399 seems to be related to a non-parasitic life-style.

400 Feeding ecology information about the *Trichamathina* lineage is scarce. Specimens of *T. nobilis*
401 were reported to kleptoparasitize the bivalve *Chlamys behringiana* (Middendorff, 1849), and to
402 have a negative impact on the growth rate of the host (Alexeyev, 2006). A photographic record of
403 *T. violacea* on a sea squirt from Taiwanese waters (by Huang Qixiong
404 <https://blog.xuite.net/tmc701038/wretch/130736418-2012>), if confirmed by further data, would
405 represent the first record of a capulid on ascidians, and would fit with the ability of this family to
406 potentially adapt to a vast array of filter feeders as hosts. However, the indented shell aperture of
407 this species may suggest its adaptation to less flat surface, for example a worm tube, and that the
408 finding on an ascidian may represent an occasional event.

409 In summary, we hypothesize that the first capulids were kleptoparasites, probably of polychaetes, as
410 suggested by the preferences of the two oldest capulid lineages. Taking into consideration that their
411 sister family, Calyptraeidae, is composed of filter feeders living on hard substrata (from rocks to
412 several marine invertebrate taxa) (Beesley et al., 1998), we can further hypothesize that the
413 common ancestor of these two families was a suspension feeder. Subsequently, the evolution of
414 kleptoparasitism in capulids may have represented a strategy to save energy: for instance, a higher
415 growth rate was observed in individuals of *T. cancellata* living on a host, compared to free living
416 ones, regardless of body size (Iyengar, 2002). The presence of at least two generalist capulid
417 species, one coiled and one limpet-like, able to live on different hosts as well as free suspension

418 feeders, underlines the high ecological and morphological plasticity of this family, that may have
419 re-evolved a free-living style.

420

421 4.3 *From coiled to limpet-like*

422 Our results suggest that a plesiomorphic coiled shell in capulids is not only concordant with a
423 common pattern in most caenogastropod families, and in particular in limpet-like ones (Vermeij,
424 2017), but it also represents the most parsimonious scenario. In fact, a limpet-like capulid ancestor
425 would require at least three independent cases of re-evolution of a coiled shell (an unlikely event,
426 whereas limpetization processes are rather common). Therefore, at least three capulid lineages
427 independently evolved limpet-like shells (*Cryocapulus*, *Capulus* s.s. + *Hyalorisia*, and
428 *Trichamathina*) suggesting that a limpetization process intermittently occurred in this family. The
429 real diversity of limpet-like capulid genera is then higher than thought so far, especially considering
430 that at least 21 limpet-like Recent species were included in the genus *Capulus* as traditionally
431 conceived, which has instead been retrieved as polyphyletic.

432 Linking paleoenvironmental dynamics with character state changes may actually be rather
433 speculative at this level of the analysis. However, the first shift to a limpet-like shell (in the lineage
434 leading to *Capulus* s.s. + *Hyalorisia*) was estimated to have occurred during the Campanian stage,
435 an age of warm climate conditions and world-wide rising of the sea level (Jarvis et al., 2002), which
436 likely produced new shallow water habitats available for colonization by benthic invertebrates. The
437 second shell shift (in the lineage leading to the Antarctic *C. subcompressus*) occurred shortly after
438 the Early Eocene Climatic Optimum (~51–53 Ma), another period characterized by a long-term
439 maximum of global temperatures, ocean acidification, and rising of the sea level (Zachos et al.,
440 2008). The third shift (in the lineage leading to *Trichamathina* spp.) was estimated after what is
441 considered the major Cenozoic climatic change: a rapid global cooling occurred around 13.8 Ma,
442 immediately after the warm period of the Mid-Miocene Climate Optimum (~17–15 Ma) (Zachos et
443 al., 2008). This relatively rapid mutation of the climatic conditions probably promoted dramatic
444 changes in the faunal composition of many habitats, likely creating new evolutionary opportunities.
445 Such paleoenvironmental dynamics may have favoured the transition to a limpet-like shell, by
446 affecting host availability opportunities and predator pressure (e.g. appearance of new shallow
447 water species, disappearance of species unable to cope with sea water acidification). A limpet-like
448 shell may have been the key to exploit newly available ‘flat’ hosts, or at the same time, an increased
449 predatory pressure may have favoured species with higher capacity to resist dislodging.

450 The stem capulids were probably coiled, subsequently, some of them underwent different degrees
451 of shell uncoiling, frequently to the extent of a limpet-like one. Several combinations of factors may

452 have indeed favoured limpet-like shell against coiled ones. One hypothesis is that the parasite-host
453 interaction acted as a major driver. In fact, a limpet-like shell, that maximises the attaching surface
454 and minimises the effects of potential dislodging forces, represents a clear advantage (Yonge, 1962)
455 and can result particularly suited for an obligate sedentary parasitic life-style. This may have been
456 the case of the shell shape shift in the lineage leading to *Capulus* s.s. + *Hyalorisia*, probably
457 associated with the exploitation of a new type of host, the bivalves, predominant in the species of
458 this clade. Moreover, limpet-like capulids have mainly hosts with a solid and rigid test (calcareous
459 tube of polychaetes, shells of bivalves and brachiopods); even *Capulus ungaricus*, a generalist in
460 the host choice, always selects calcareous substrates. This may suggest that shell shape of capulids
461 can be associated not only to the shape of the hosts (e.g. slender annelid tubes or relatively flat
462 bivalve shells), but also to the kind of attaching substrate that they provide. In fact, among capulids
463 parasitizing marine worms, the limpet-like ones live on the calcareous tube of serpulids rather than
464 on that of sabellids, which is made of non-calcareous materials and often covered by sand grains of
465 different sizes. Conversely, coiled species were found on both calcareous and non-calcareous hosts,
466 as in the case of *Trichotropis cancellata*. The solid tube of serpulids, made of calcium carbonate,
467 may have represented an optimal surface for adhesion, making it more difficult to be dislodged by
468 predators or even, in the case of association with pectinoid bivalves, by the dragging due to host
469 swimming. On the other hand, host choice in coiled species is not necessarily optimised to improve
470 adhesion, and may have been driven by other factors, such as the power of the water current
471 produced by the host. Additionally, it should be considered the need for the capulid to optimize its
472 position relatively to that of some hosts, which may rotate inside the tube under changing water
473 flow direction, to intercept food particles.

474 Other factors may have concurred to favour a limpet-like shell, and may even offer alternative
475 hypotheses. For instance a limpet-like shape results in a stronger adhesion to the substrate, but also
476 offers a large surface area for respiratory exchange and suspension-feeding (Vermeij, 2017). It is
477 therefore possible that the suspension-feeding capulids were favoured in the shift to a limpet-like
478 shell when associated with hard substrates. In fact, there are capulids with a coiled shell
479 (*Separatista* and '*Torellia*'), which are kleptoparasites of annelids with a non-calcareous tube. A
480 combination of specialization to hard substrates and suspension-feeding might have been an
481 important driver of the evolution of limpet-like shells and the shift to calcareous tubes may have
482 been promoted for the optimal surface to adhesion.

483 However, these hypothetical frameworks need to be investigated on a dataset with a denser
484 taxonomic sampling and, most important, including sound observations on the ecology of a larger
485 proportion of species.

486 Capulids emerged as a group that actually explored a broad ecological spectrum, ranging from free-
487 living to kleptoparasitism, in association with a high shell plasticity that allowed to intermittently
488 shift from a coiled to a more host-adapted limpet-like form.

489
490

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502

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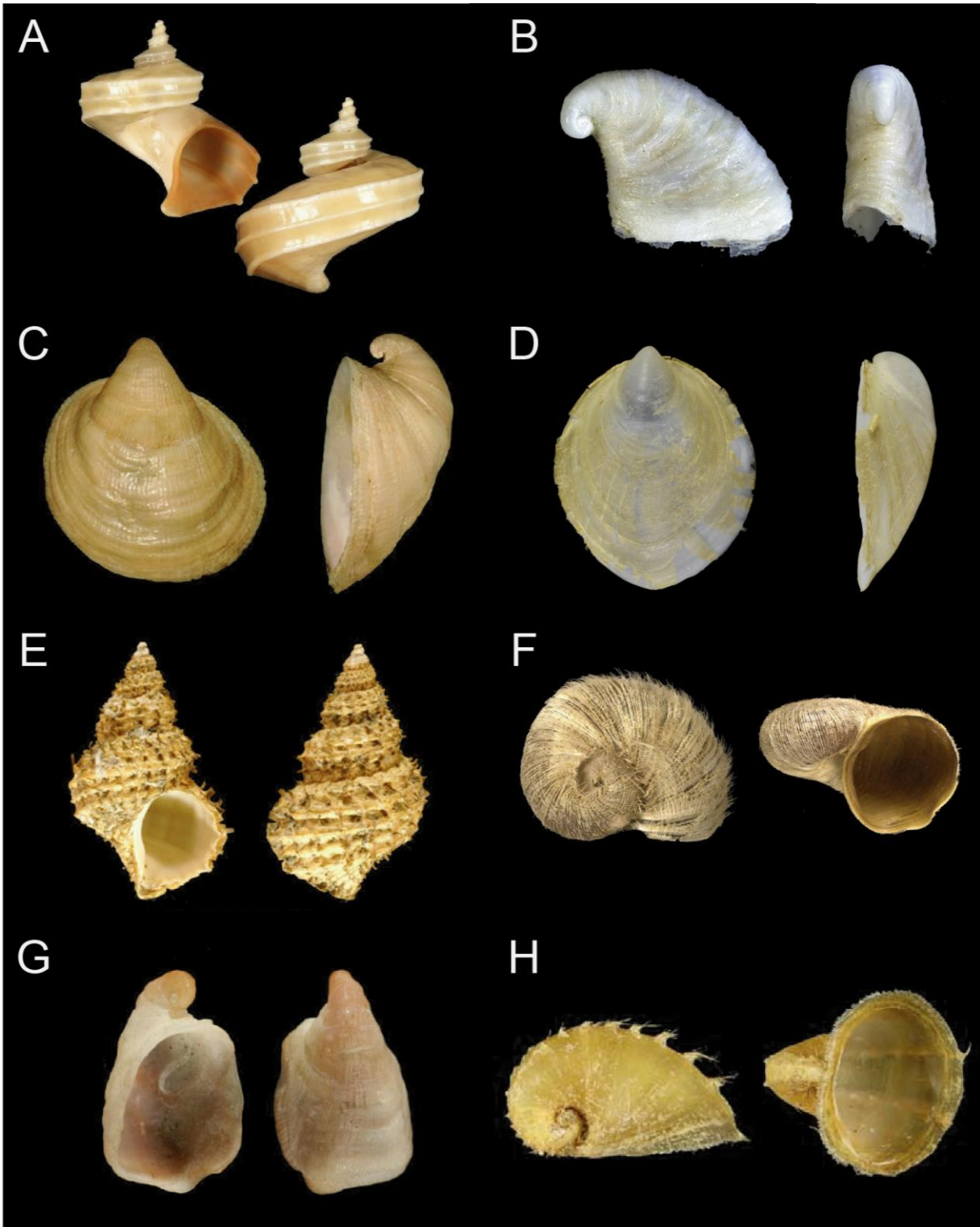
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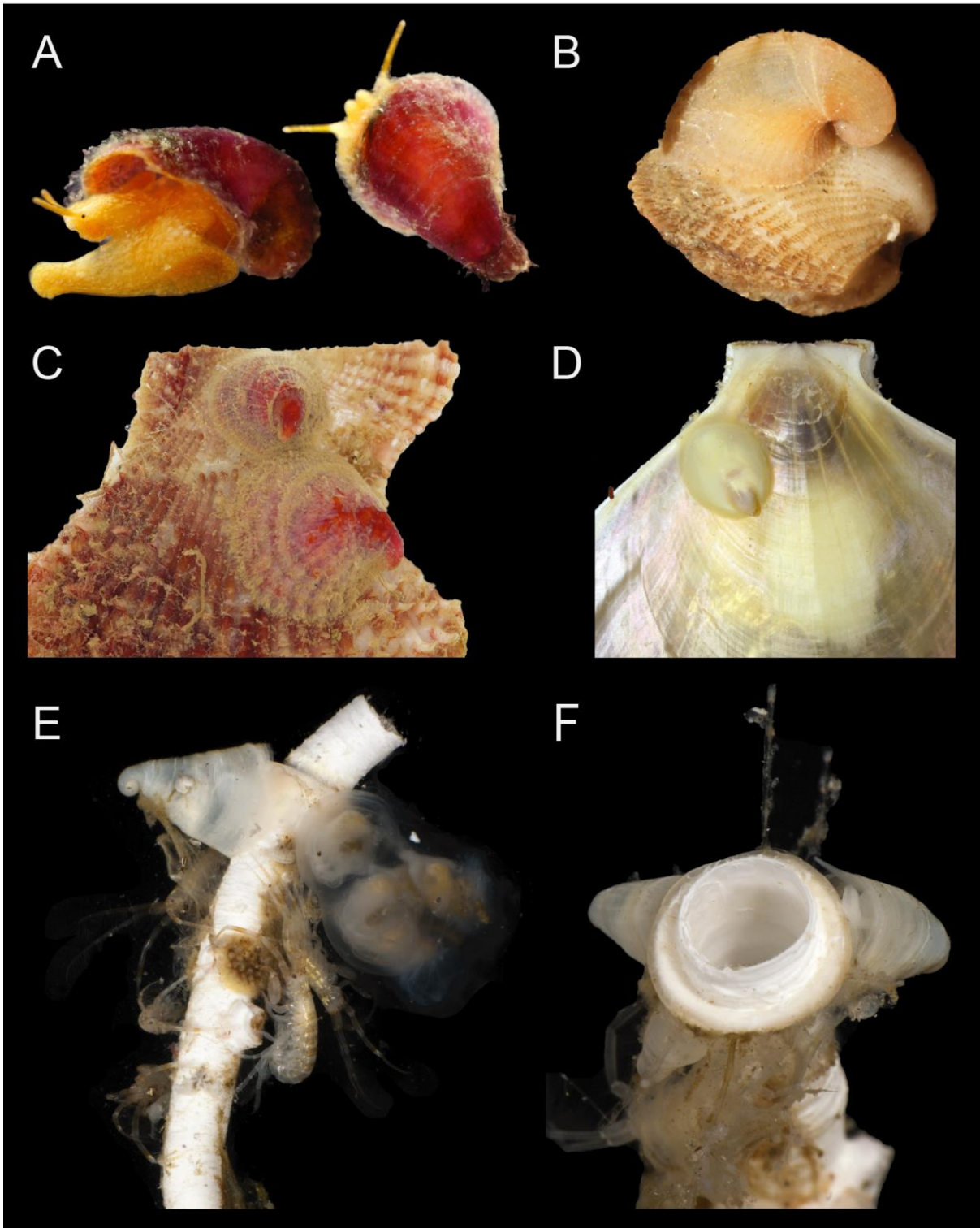
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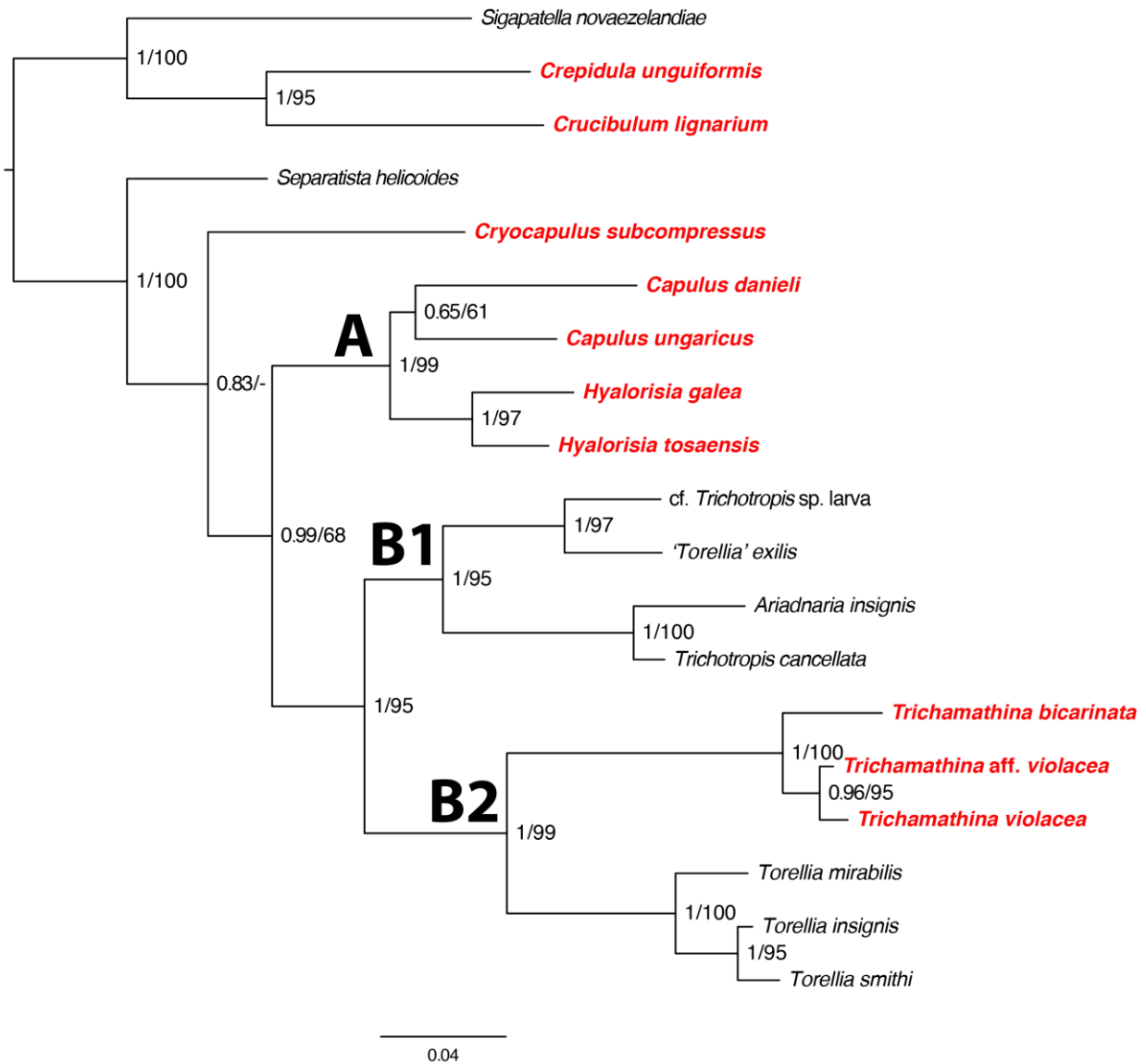
621
 622 **Fig. 1.** Shell diversity in the family Capulidae. **A**, *Separatista helicoides* 1117020 (l = 13.9 mm), **B**,
 623 *Cryoapulus subcompressus* USNM 881933 (l = 7 mm), **C**, *Capulus ungaricus* NMR993000033407 (l = 38
 624 mm), **D**, *Hyalorisia galea* holotype USNM 508724 (l = 18 mm), **E**, *Trichotropis cancellata*
 625 NMR993000056168 (l = 19 mm), **F**, *Torellia mirabilis* USNM 894573 (l = 16 mm), **G**, *Trichamathina*
 626 *violacea* NMR993000053570 (l = 9 mm), **H**, *Trichamathina nobilis* (l = 15 mm). Photo credits: © G. & P.
 627 Poppe (A, H); USNM (B, D, F); collection Natural History Museum Rotterdam, taken by Joop Trausel and
 628 Frans Slieker (C, E, G).



629
630

631 **Fig. 2.** Living specimens of Capulidae: **A**, *Trichamathina bicarinata* MNHN-IM-2019-8859, Koumac, New
632 Caledonia; **B**, *Capulus ungaricus* MNHN-IM-2019-5198 attached on *Striarca lactea* MNHN-IM-2019-
633 4842, off Bastia, Corsica; **C**, two *Capulus danieli*, MNNH-IM-2019-3869 and MNNH-IM-2019-3870,
634 attached on *Mimachlamys gloriosa* MNNH-IM-2019-7541, Koumac, New Caledonia; **D**, *Hyalorisia galea*
635 MNHN-IM-2013-60195 attached on *Propeamussim dalli* MNHN-IM-2013-60196, N Grande-Terre,
636 Guadeloupe; **E**, a typical Antarctic “microcosm” of interacting species on a *Serpula narconensis* tube where
637 it is possible to recognize *Cryoapulus subcompressus* (MNA-13163), in a subterminal position and partially

638 lifted by the serpulid prominent collar, and the mucous tubes produced by the amphipod *Jassa goniamera*
639 Walker, 1903; **F**, three *C. subcompressus* specimens (MNA-13162), located close to *S. narconensis* collar,
640 with the specimen on the right showing a semi extended pseudoproboscis. Photo credits: MNHN, taken by
641 Laurent Charles (A-D); Stefano Schiaparelli © PNRA (Italian National Antarctic Program) (E-F).

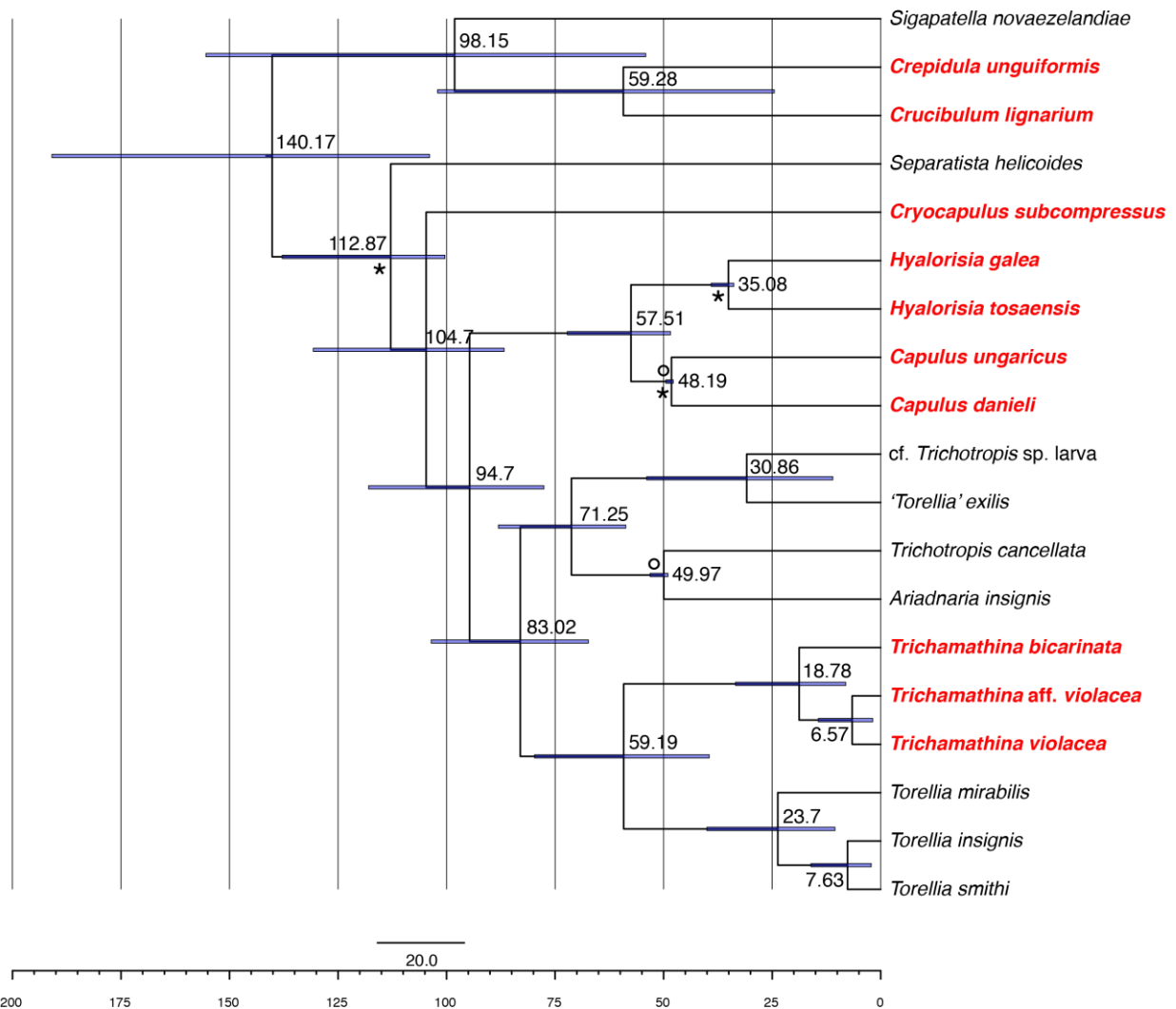


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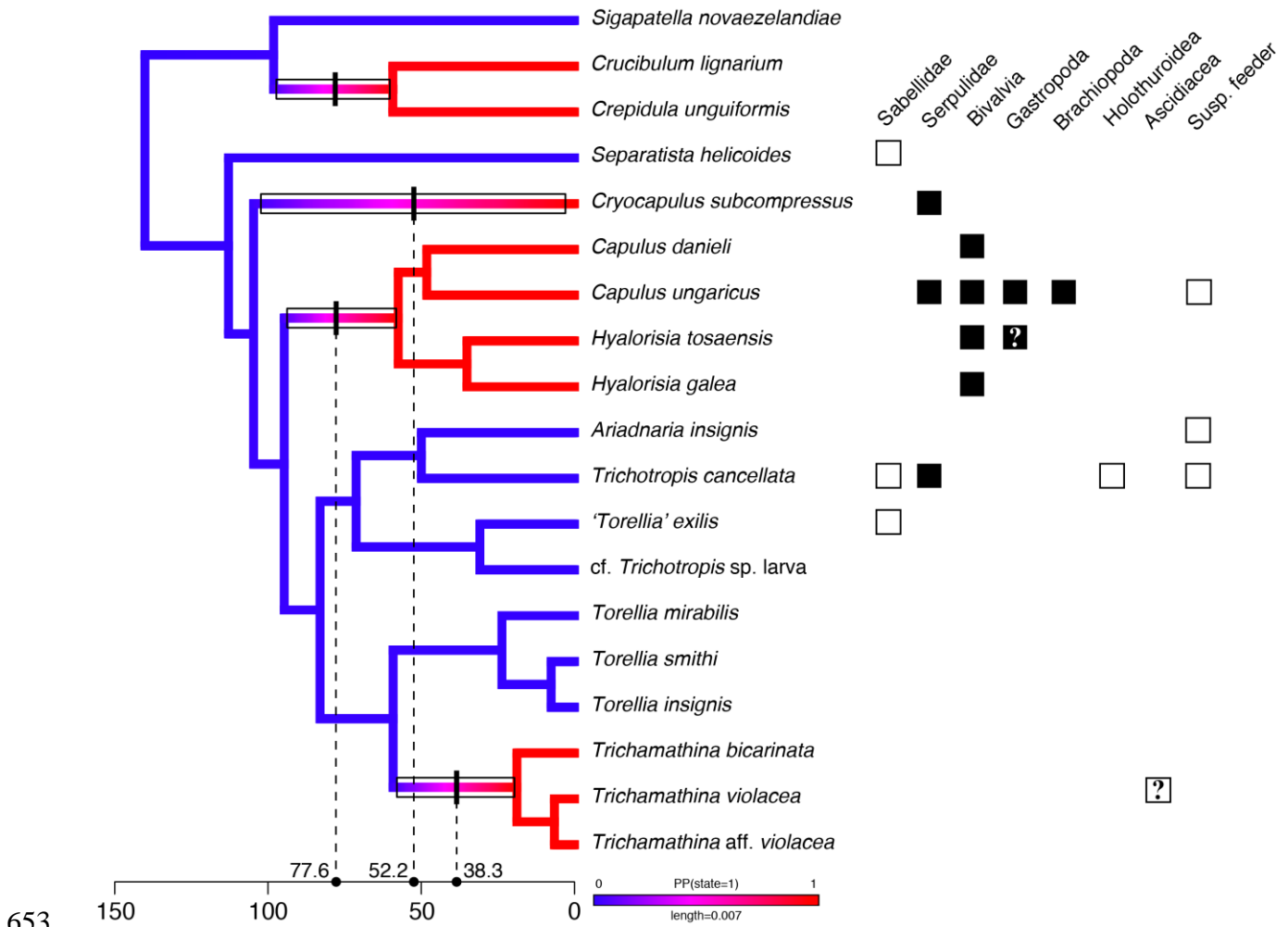
644 **Fig. 3.** Phylogenetic relationships (Bayesian inference, on the combined dataset) of the family Capulidae.

645 Letters indicate the three major lineages (A, B1, and B2). Numbers at nodes are PP and UFb support values,

646 respectively. In bold/red the species with limpet-like shell, in black those coiled.



647
 648 **Fig. 4.** Time calibrated tree of the family Capulidae, inferred from BEAST analysis of the combined
 649 molecular dataset. Coloured bars indicate 95% highest posterior density intervals for node ages (Ma), and
 650 number at node the median (Ma). Asterisks and circles indicate divergence points calibrated with fossils,
 651 circles specify when a point was calibrated with the STEM function. In bold/red the species with limpet-like
 652 shell, in black those coiled.



653
 654 **Fig. 5.** Stochastic mapping of shell shape states along the branches of the time calibrated tree (Ma). Branch
 655 colours indicate the probability of the character state (blue=0, coiled; red=1, limpet-like). For the branches in
 656 which state changes occurred, the median (vertical black bars) and 95% confidence interval (black rectangle)
 657 of the distribution of changes are indicated. On the right, available information on capulid ecology are
 658 reported: either the host or the free life-style as suspension feeder (see the Discussion section for references).
 659 Black square=host surface made of calcium carbonate, white square=other building materials, ?=uncertain
 660 data.
 661

662 **Table 1.** Voucher ID, collecting localities, and sequences GenBank accession numbers.

Species	Voucher	Collection Data	COI	16S	ITS2
<i>Hyalorisia galea</i>	MNHN-IM-2013-60195	Guadeloupe, N of Grande-Terre, KARUBENTHOS 2015, CP4524, 16°29'N, 61°42'W, 500-550 m	MT491359	MT525835	MT525781
<i>Hyalorisia tosaensis</i>	AORI_YK2262	Japan, Kagoshima, off Nomaike, 410 m	MT491390	MT525849	
<i>Ariadnaria insignis</i>	11BIOAK-0379	USA, Alaska, Hesketh Island, Cook Inlet	KF644079		
<i>Capulus danieli</i>	MNHN-IM-2019-3870	New Caledonia, Koumac, KOUMAC 2.3, KR1019, 20°35.1'S, 164°16.3'E, 7 m	MT491384	MT525841	MT525787
<i>Cryocapulus subcompressus</i>	MNA6631	Antarctica, Weddell Sea, PS81/185_4, 63°52'S, 55°41'W, 255 m	KR364819	KR364850	MT525793
<i>Capulus ungaricus</i>	BAU-2379	Italy, Chioggia	MT491300		MT525752
<i>Capulus ungaricus</i>	BAU-2382	Italy, Chioggia		MT525803	
<i>Trichamathina violacea</i>	MNHN-IM-2007-35260	Philippines, Panglao I., Momo Beach, PANGLAO 2004, B10, 09°36.5'N, 123°45.6' E, 3-14 m	MT491304	MT525806	MT525755
<i>Trichamathina aff. violacea</i>	MNHN-IM-2007-35241	Philippines, Panglao I., Napaling, PANGLAO 2004, B8, 09° 37.1'N, 123°46.1'E, 3 m	MT491303	MT525805	MT525754
cf. <i>Trichotropis</i> sp. larva	C5gastrop03	Antarctica, Ross Sea, Cape Hallet	GU227117	GU226997	
<i>Trichamathina bicarinata</i>	MNHN-IM-2019-8859	New Caledonia, Koumac, KOUMAC 2.3, KB513, 20°40.1' S, 164°15.4' E, 0 m	MT491389	MT525846	MT525791
<i>Crepidula unguiformis</i>	BAU-3593	Italy, Taranto, Torre Colimena	MT491302	MT525804	MT525753
<i>Crucibulum lignarium</i>	-	Chile, Valdivia, Corral Bay. 39°51' S, 73°26' W	JX661559		
<i>Crucibulum lignarium</i>	FMNH299434	Chile, Chiloe, Ancud. 41°53' S, 73°50' W		AF550465	
<i>Separatista helicoides</i>	YK1615	Japan, Kagoshima, Marukihama	AB930472		
<i>Sigapatella novaezelandiae</i>	FMNH282186	New Zealand, South Island, Portabello	AF546068	AF546008	
' <i>Torellia</i> ' <i>exilis</i>	MNA48	Antarctica, Ross Sea, TAN0402 Stn 94, 71°31.8' S, 170°06.6' E, 220 m	KR364814	MT525847	MT525795
<i>Torellia insignis</i>	MNA6663	Antarctica, Bransfield Strait, PS81/197_4, 62°44.4'S, 57°25.9'W, 285 m	KR364810	KR364865	MT525797
<i>Torellia mirabilis</i>	MNA6646	Antarctica, Bransfield Strait, PS81/118_8, 62°27.1'S, 56°16.8'W, 419 m	KR364856	KR364856	MT525799
<i>Torellia smithi</i>	MNA6666	Antarctica, Bransfield Strait, PS81/227_2, 62°56'S, 58°41'W, 564 m	KR364811	KR364868	MT525802
<i>Trichotropis cancellata</i>	FMNH282220	USA, Washington state, Friday Harbor. 48°20' N, 123°01' W	AF546069	AF546009	

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