

1 **Decapod crustaceans from the Lower Cretaceous of Spain,**
2 **with an account of new occurrences in Barremian-Aptian**
3 **strata of the Maestrazgo Basin**

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27 HIGHLIGHTS

- 28 • A revision of all currently known decapod crustaceans from the Lower
29 Cretaceous of Spain is provided
- 30 • Systematic descriptions comprise Barremian–Aptian decapod crustaceans from
31 the Galve subbasin (Maestrazgo Basin)
- 32 • Seven taxa are described, three of which are new
- 33 • The environmental distribution of these taxa is discussed
- 34 • Comparison with other subbasins suggests extrinsic factors to have been the
35 main drivers of faunal distribution

37 A B S T R A C T

38 Decapod crustaceans are rare in Early Cretaceous invertebrate assemblages from the
39 Iberian Peninsula; however, current knowledge does allow differences in taxonomic
40 composition between different basins and subbasins to be recognised. In order to
41 understand the distribution of Barremian–Aptian decapod crustaceans of Iberia better,
42 seven new localities in the Galve subbasin (Maestrazgo Basin, north-east Spain) have
43 been sampled. Seven taxa are here described, including the anomurans *Cretacocalcinus*
44 *fortis* sp. nov. and *Viapagurus* gen. nov. (type species: *Pagurus avellanedai* Vía, 1951),
45 one indeterminate axiidean, the astacidean *Hoploparia* sp., plus the brachyurans
46 *Ariecornibus* sp., *Pithonoton lluismariaorum* Ossó, van Bakel, Ferratges-Kwekel and
47 Moreno-Bedmar, 2018 and *Palaeodromites pimientai* sp. nov. Assemblages are
48 characterised by low abundance, being found in formations that represent depositional
49 settings ranging from shallow-marine platforms to deeper marine bottoms. Some taxa,
50 such as *V. avellanedai* nom. corr. and *P. lluismariaorum*, are also known from other
51 subbasins of the Maestrazgo Basin but, in general, most appear endemic, suggesting that
52 regional changes in facies distribution may potentially have affected differences in
53 taxonomic composition.

54 *Keywords:*

55 Galve subbasin

56 Decapoda

57 Tethyan

58 Benthos

59 Diversity

60 New taxa

61

62 **1. Introduction**

63

64 Recent studies of decapod crustaceans of Mesozoic age have indicated that major peaks
65 in diversity during the Late Jurassic and mid-Cretaceous were related to the
66 development of reefs (Klompaker et al., 2013; Schweitzer and Feldmann, 2015). The
67 global collapse of reefs during the Late Jurassic saw decapod crustacean diversity
68 decline dramatically; worldwide, the Lower Cretaceous is characterised by low-
69 diversity faunas (Klompaker et al., 2013; Luque et al., 2019). Despite this global drop
70 in diversity, local sponge-dominated habitats like those from the Aptian of the Salou-
71 Garraf Basin in eastern Spain (Moreno-Bedmar et al., 2008; Ossó et al., 2022) provided
72 refuges for some assemblages dominated by dromioid and necrocarcinid crabs. In
73 contrast, proximal parts of the Maestrazgo Basin and the Oliete subbasin in particular
74 (Canérot et al., 1982; Salas et al., 2001; Liesa et al., 2019) were dominated by
75 siliciclastic environments during the Early Cretaceous. These yield assemblages with
76 common axiidean shrimp and glypheid lobsters, and subsidiary glypheids, astacoids and
77 anomurans (Ferratges et al., 2020). In the Basque-Cantabrian Basin, the situation during
78 the Aptian was rather different, with assemblages having an admixture of elements,
79 with frequent macrurans and dromioids (López-Horgue and Bodego, 2017; Ossó and
80 Moreno-Bedmar, 2020; Ossó et al., 2021). These differences reflect how the various
81 basins and subbasins in Iberia record specific faunal assemblages during the Early
82 Cretaceous, which probably reflect abrupt changes in facies distribution and the
83 influence of both Atlantic and Tethyan faunas.

84 In order to understand the diversity and composition of decapod assemblages
85 prior to their diversity peak in the Albian better (Klompaker, 2013; Klompaker et
86 al., 2013), field work in the Galve subbasin, a westerly marginal depocentre of the
87 Maestrazgo Basin, has been carried out. This has resulted in the discovery of seven new

88 localities that have yielded decapod crustaceans ranging in age from late Barremian to
89 late Aptian. Unlike other Lower Cretaceous Iberian basins and subbasins in the
90 Maestrazgo Basin, the Galve subbasin had not previously been sampled for decapod
91 crustaceans.

92 The main aim of the present study is to describe the new material collected from
93 the Galve subbasin. A detailed comparison of all decapod crustaceans from pre-Albian
94 Lower Cretaceous strata of Spain is also provided, shedding light on the diversity and
95 palaeoenvironmental distribution of this group prior to the widespread development of
96 reefs during the Albian.

97

98 **2. Geological setting and stratigraphy**

99 The Galve subbasin is a small marginal subsiding domain located in the north-western
100 corner of the Maestrazgo Basin (Fig. 1). The Maestrazgo Basin is part of the larger
101 Iberian Rift System which developed in eastern Iberia during the Mesozoic as a result of
102 extensional stresses inflicted on the Iberian Plate by the continued breakup of Pangaea
103 and the opening of the western Tethys and North Atlantic oceans (e.g., Salas et al.,
104 2001; Aurell et al., 2019; Martín-Chivelet et al., 2019).

105 Extensional stresses during the second rifting stage in the Iberian Rift System
106 (latest Jurassic–Early Cretaceous) led to the breakup of extensive carbonate platform
107 systems that had developed during the previous Jurassic post-rift stage and divided the
108 Maestrazgo Basin into seven subsiding domains (Salas et al., 2001; Martín-Chivelet et
109 al., 2019). The extensional structure of the Galve subbasin is characterised by two
110 orthogonal fault systems with a NNW–SSE and WSW–ENE strike. The WSW–ENE
111 fault family has a listric geometry; it was probably generated by Early Cretaceous
112 extensional stresses, while the NNW–SSE faults present steeper and more constant fault
113 plane dips and correspond to reactivated Variscan structures. This fault configuration
114 has important implications for the geometry and spatial distribution of the Lower
115 Cretaceous sedimentary record of the Galve subbasin, which exhibits pronounced
116 syntectonic features such as fan-shaped geometries, angular unconformities and
117 substantial sedimentary gaps (e.g., Liesa et al., 2006; Aurell et al., 2016). The
118 sedimentary record of the upper Barremian to upper Aptian interval of the Galve
119 subbasin includes six lithostratigraphical units (Fig. 2A), as follows:

120 1 – the transitional Artoles Formation, consisting of marls alternating with
121 sandstone and limestones with abundant oysters and calcareous algae; this has been
122 interpreted as a semi-restricted lagoon to tidal flat depositional system (e.g., Díaz-
123 Molína and Yébenes, 1987);

124 2 – the continental-transitional Morella Formation, comprising clays containing
125 terrestrial and marine palynomorphs, channelised sandstones with vertebrate remains
126 and dinosaur footprints, and marginal-marine limestones containing abundant marine
127 macro- and microfauna (e.g., Santisteban et al., 2012; Villanueva-Amadoz et al., 2014);

128 3 – the marine Chert Formation, consisting of massive limestones and
129 sandstones representing a mixed carbonate-siliciclastic, shallow homoclinal ramp with
130 an abundant microfossil record including orbitolinid blooms (Vennin and Aurell, 2001;
131 Embry et al., 2010);

132 4 – the Forcall Formation, comprising marls and limestones with abundant
133 orbitolinids, bivalves, gastropods and ammonites, which record the early Aptian
134 Oceanic Anoxic Event 1a (OAE1a) (Moreno-Bedmar et al., 2009; Bover-Arnal et al.,
135 2011, 2016);

136 5 – the predominantly calcareous Villarroja de los Pinares Formation, which
137 corresponds to platform-top carbonates dominated by rudists and corals (e.g., Vennin
138 and Aurell, 2001; Embry et al., 2010; Bover-Arnal et al., 2010, 2016);

139 6 – the Benassal Formation, which consists of an alternation of marls and
140 limestones with abundant rudists, colonial corals, bivalve/gastropod associations and
141 rare ammonites, interpreted as a distal-to-proximal shallow ramp (Tomás et al., 2008;
142 Bover-Arnal et al., 2010; Martín-Martín et al., 2013).

143 The decapod crustacean material presented herein has been recovered from
144 seven individual sections which range from the base of the Chert Formation to the base
145 of the Benassal Formation and range in age from upper Barremian to upper Aptian (Fig.
146 2).

147

148 3. Biostratigraphy

149 The oldest levels with decapod crustaceans in the Maestrazgo Basin are situated in the
150 lowermost part of the Chert Formation (Loc.1) near Allepuz (Fig. 3D), where only
151 *Cretacocalcinus fortis* sp. nov. has been collected. Another level located in the top of

152 this formation has provided solely the paguroid *V. avellanedai* nom. corr. and
153 indeterminate axiideans (Loc. 2). Bover-Arnal et al. (2016) indicated that the onset of
154 sedimentation of marine carbonates of the Chert Formation in the Galve subbasin
155 occurred during the late Barremian. In particular, the presence of the ammonite genus
156 *Martelites* Conte, 1989 suggests that this unit spans the uppermost Barremian *Martelites*
157 *sarasini* ammonite Zone (Fig. 2A).

158 Localities 3 and 4 are located in the upper part of the Forcall Formation, the age
159 of which ranges from latest Barremian (uppermost part of the *Martelites sarasini*
160 ammonite Zone) to early Aptian (lower part of *Dufrenoyia furcata* ammonite Zone)
161 (Moreno-Bedmar et al., 2010; Garcia et al., 2014; Bover-Arnal et al., 2016). The
162 assignment of Locality 3 to the *D. forbesi* ammonite Zone is based on regional
163 correlation. Locality 4 is found in the classic outcrop of “Barranco de las Calzadas”
164 (Fig. 3A). This section has been extensively studied for stratigraphy, chemostratigraphy
165 (OAE 1a), ammonite record and *Lithocodium* crusts (Moreno-Bedmar et al., 2009,
166 2010, Bover-Arnal et al., 2010, 2011). The ammonites *Deshayesites deshayesi*
167 (d’Orbigny, 1841) and *Deshayesites* sp. have been collected here (Fig. 3B). At Locality
168 4, two beds have yielded decapod crustaceans, namely bed 11 (Level 137; Fig. 3A) and
169 19 (Level 141) (*sensu* Moreno-Bedmar et al., 2010). Both beds are within the
170 *Deshayesites deshayesi* ammonite Zone (see Moreno-Bedmar et al., 2010, fig. 5). Bed
171 11 has yielded a single specimen of *Hoploparia* sp., while bed 19 holds the richest
172 decapod crustacean assemblage, including *Viapagurus avellanedai* nom. corr.,
173 *Ariecornibus* sp., *Pithonoton lluismariaorum*, indeterminate axiidean, and *Hoploparia*
174 sp. Bed 19 corresponds to the highest level within the *D. deshayesi* ammonite Zone.

175 Localities 5 and 6 are found in the same stratigraphical interval at the base of the
176 Benassal Formation near Allepuz. Locality 6 has yielded ammonites identified as
177 *Dufrenoyia dufrenoyi* (d’Orbigny, 1840) (Fig. 3E), belonging to the *Dufrenoyia furcata*
178 ammonite Zone. The age calibration of the lowermost Benassal Formation to the
179 uppermost part of the *Dufrenoyia furcata* ammonite Zone is based on Moreno-Bedmar
180 et al. (2012); it has been adopted in several subsequent papers (e.g., Garcia et al., 2014;
181 Bover-Arnal et al., 2016). Moreno-Bedmar et al. (2012) reported *D. dufrenoyi* also from
182 the same stratigraphical position in the Mola de la Vila section (Morella subbasin). In
183 the Galve subbasin, one specimen of *Dufrenoyia* sp. has been noted in an outcrop close
184 to the town of Villarroya de los Pinares (locality 6). The new ammonite finding at
185 locality 6 confirms the age calibration of the lowermost part of the Benassal Formation

186 to the uppermost lower Aptian. Locality 7, in the classic “Las Mingachas” outcrop (Fig.
187 3C), occupies the same stratigraphical position as localities 5 and 6, and therefore
188 corresponds to the same age. Localities 5, 6 and 7 have yielded *V. avellanedai* nom.
189 corr. and indeterminate axiideans.

190

191 **4. Material and methods**

192 All specimens recovered for the present study were picked up during surface screening.
193 There are no specific levels with fossil concentrations, and the common occurrence in
194 the field is as isolated macrofossils. Abundance is taxon-dependent. For example, the
195 paguroid *V. avellanedai* nom. corr. is by far the commonest taxon and always appears
196 isolated in marly levels. This is also the case for indeterminate axiideans; they are
197 common in levels of the Benassal Formation as well. The remaining taxa are very rare
198 and restricted to one or two specimens each. Disarticulated elements of the lobster
199 *Hoploparia* sp. were found inside a burrow. In such a case, the specific environment
200 inside the burrow favoured the preservation of these remains.

201 Specimens were prepared using a Micro Jack 2 air scribe (Paleotools) under a
202 binocular microscope. In some cases, potassium hydroxide (KOH) was used to remove
203 the matrix. Specimens were photographed using a Nikon D7100 camera equipped with
204 AF-S Micro NIKKOR 60 mm objective, following coating with ammonium chloride to
205 enhance contrast.

206 Repository and institutional abbreviations: Specimens are deposited in the
207 palaeontological collection of the “Museo de Ciencias Naturales de la Universidad de
208 Zaragoza” under the acronym MPZ.

209

210 **5. Systematic palaeontology** (by F.A. Ferratges and S. Zamora)

211 The higher-level classification of principal groups is based on Tshudy et al. (2018) for
212 astacideans, McLaughlin (2003) and McLaughlin et al. (2007, 2010) for paguroids and
213 Guinot et al. (2013) and Jagt et al. (2015) for brachyurans. Alternative classifications
214 can be found in Karasawa et al. (2011) and Luque et al. (2019). The following
215 abbreviation (for decapod crustacean anatomy) is used below: P1 – first pereopod.

216 Order Decapoda Latreille, 1802

217 Suborder Pleocyemata Burkenroad, 1963

218 Infraorder Axiidea de Saint Laurent, 1979

219 **Axiidea indet.**

220 Fig. 4A-D

221

222 *Remarks.* The morphology of cheliped P1 recorded herein (see below), with a relatively
223 elongate propodus and long and narrow fingers is too fragmentary to be attributed to
224 any concrete family. Unfortunately, no carapaces and other elements are preserved and
225 the material shares characteristics of Callianassidae, Callianideidae or Axiidae. We are
226 placing the material as Axiidea indet. pending the discovery of better preserved material
227 and further investigation.

228

229 *Material.* One specimen (MPZ2022/618), preserving a complete claw with fingers,
230 cheliped and propodus.

231 *Horizon and locality.* Forcall Formation at Locality 3, Barranco de las Calzadas
232 (Miravete de la Sierra, Teruel).

233 *Description.* Cheliped (P1) merus not well preserved (fig. 4A), suboval; carpus
234 elongated, subrectangular in outline, unarmed, upper and lower margins rimmed,
235 distal/lower margin forming continuous round margin; palm approximately twice longer
236 than tall, upper and lower margins slightly converging distally; fixed finger slightly
237 shorter than palm, unarmed, fixed fingertip bent slightly upwards; dactylus slightly
238 longer than palm, unarmed, tip slightly bent downwards. Both fingers with abundant
239 setal pits.

240 Infraorder Astacidea Latreille, 1802

241 Superfamily Nephropoidea Dana, 1852

242 Family Nephropidae Dana, 1852 (*sensu* Tshudy and Babcock, 1997)

243 Genus *Hoploparia* M'Coy, 1849

244 *Type species.* *Astacus longimanus* Sowerby, 1826, by the subsequent designation of
245 Rathbun (1926).

246 ***Hoploparia* sp.**

247 Fig. 5

248 *Material.* Two incomplete carapaces and two chelipeds (MPZ2022/615, 621, 622 and
249 640). One of the carapaces (MPZ2022/615) is found within the burrow of a thalassinoid
250 mud shrimp, associated with several isolated propodi and abundant broken fragments.
251 The propodus show predation marks.

252 *Horizon and locality.* Forcall Formation at Locality 3, Barranco de las Calzadas
253 (Miravete de la Sierra, Teruel).

254 *Remarks.* The genus *Hoploparia* is a well-known, extinct clawed lobster that ranged
255 from the Valanginian (Lower Cretaceous) to the Miocene (see Tshudy et al., 2005; El-
256 Shazly, 2015). It is considered a “wastebasket” genus due to an ambiguous diagnosis
257 and the fact that cladistic analyses indicate that it is paraphyletic (Tshudy and
258 Sorhannus, 2003; Tshudy et al., 2018). The present material is assigned to this genus
259 because observable features match its current diagnosis (see also Tshudy, 1993).
260 However, due to the fragmentary nature of the present material we prefer to keep it in
261 open nomenclature pending further work.

262 Infraorder Anomura MacLeay, 1838

263 Superfamily Paguroidea Latreille, 1802

264 Family ?Diogenidae Ortmann, 1892

265 Genus *Cretacocalcinus* Ferratges, Hyžný and Zamora, 2021

266 *Type species.* *Cretacocalcinus josaensis* Ferratges, Hyžný and Zamora, 2021, by
267 original designation.

268 *Discussion.* The present material is assigned to *Cretacocalcinus*, because observable
269 characteristics match those of this genus (for details, reference is made to Ferratges et
270 al., 2021).

271 ***Cretacocalcinus fortis* sp. nov.**

272 Fig. 6A, B, D

273

274 Zoobank ID code: urn:lsid:zoobank.org:act:B40DDC52-7BE3-4BFB-AEDE-
275 F471E2DEEB65

276

277 *Diagnosis.* Palm height exceeding length; outer surface covered with small, densely
278 arranged granules; upper margin with a crest; one row of setal pits on inner lateral
279 occlusal margin, both in pollex and dactylus; cutting edges of dactylus and fixed finger
280 consisting of massive molariform tooth row in external view.

281

282 *Etymology.* From Latin *fortis*, meaning strong.

283

284 *Material.* Only the holotype, an isolated left chela, is currently known (MPZ2022/612).

285 *Horizon and locality.* Base of the Chert Formation at Locality 1 in Allepuz (Teruel).

286 *Description.* Palm of left propodus subquadrate, slightly taller than long, with oval
287 transverse cross section; maximum height in distal part; gently curved inwards; outer
288 and inner sides convex, strongly convex at centre of inner side; outer and inner surface
289 densely covered by small rounded granules. Upper margin convex, with a slightly acute
290 crest. Lower margin weakly convex; distal margin at a 25° angle to upper margin. Fixed
291 finger strong, long, equalling more than a third of palm, subtriangular in section, very
292 tall proximally and narrowing abruptly distally; occlusal margin with lateral cutting
293 edge, formed by blunt molariform teeth decreasing in size proximally. Dactylus
294 subtriangular in section, as long as fixed finger, narrow, arched, laterally depressed
295 forming a ridge in upper margin, covered by granules; teeth on occlusal surface strong
296 and rounded; one row of large setal pits on inner lateral occlusal margin both in pollex
297 and dactylus.

298 *Remarks.* A comparison between *Cretacocalcinus fortis* sp. nov. and the type species,
299 *C. josaensis*, has revealed certain differences, although both forms share a very similar
300 general morphology. The new species lacks spines on the upper margin and the fixed
301 finger is much more robust, as are the teeth of the occlusal margins which are also
302 rounded. The new species is less laterally compressed and much larger in size than *C.*
303 *josaensis*.

304 Family Paguridae Latreille, 1802

305 Genus *Viapagurus* nov.

306 Zoobank ID code: urn:lsid:zoobank.org:act:4E9103DC-BBC9-4697-83AC-
307 E4FC399745B5

308 *Type species. Pagurus avellanadae* Vía, 1951.

309 *Diagnosis.* Chelipeds markedly unequal (heterochelous), right one larger, palm
310 subquadrate, width exceeding height; maximum length in distal part; curved inwards.
311 Upper margin convex, acute, with two irregular rows of spines. Lower margin convex.
312 Outer and inner surface convex, covered with conical tubercles; transverse section
313 ovoid. Palm of left propodus subquadrate, wider than tall; maximum length in proximal
314 end; transverse section ovoid; outer and inner sides convex; covered by acute tubercles.
315 Upper margin convex, with two irregular rows of spines. Lower margin straight, with
316 row of forwardly directed spiny tubercles. Pollex of both chelipeds triangular in section,
317 strong; occlusal margin longitudinally sunken, with lateral cutting edge. Dactylus
318 subtriangular in section, strong, curved downwards, with a lateral ridge in upper margin;
319 outer side of cutting edge with proximal tooth; one row of setal pits in outer surface,
320 near occlusal margin, both in pollex and dactylus. Walking leg dactylus long, arched,
321 with capsulated setal pits.

322 *Etymology.* Named after the late Luis Vía Boada, in recognition of a lifetime dedicated
323 to the study of fossil brachyurans from Spain.

324 *Remarks.* This species, based on a single isolated right propodus lacking fingers, was
325 originally assigned to the genus *Pagurus* Fabricius, 1775. Later authors (e.g., Ossó et
326 al., 2018, p. 97) complemented the description of chelae of this form on the basis of
327 newly collected material from the type locality and considered that, ‘The general
328 morphology of the chelae of the present species matches characters of *Pagurus* (*sensu*
329 *lato*) well, in that the right propodus is much larger than the left, with a convex lower
330 margin and a short, strong fixed finger with hollow occlusal margin’. However, the
331 genus *Pagurus* is considered a “wastebasket” genus due to an ambiguous diagnosis,
332 which is unfortunate since it is the most abundant and diverse taxon within the family
333 Paguridae Latreille, 1802 (McLaughlin et al., 2010; Komai and Rahayu, 2014), now
334 considered polyphyletic (Fraaije et al., 2015). Around 200 species are accepted as valid
335 (McLaughlin et al., 2010; Osawa, 2012; Komai et al., 2013; Komai and Rahayu, 2014),

336 but actually only fewer than a dozen of these match the diagnosis based on the type
337 species (McLaughlin et al., 2007; Fraaije et al., 2015). For this reason, during recent
338 years, several extant species that were previously assigned to *Pagurus* have been
339 transferred to other genera, and occasionally even to other families (McLaughlin, 2003;
340 McLaughlin et al., 2010 and references therein). Of note is the fact that some extinct
341 species originally assigned to *Pagurus* have later been reassigned to the family
342 Callianassidae (see e.g., Mertin, 1941; Hyžný and Summesberger, 2019).

343 In the fossil record, the problem is exacerbated because most of the taxonomically
344 diagnostic features are not preserved (e.g., Jagt et al., 2006; Fraaije, 2014; Fraaije et al.,
345 2014; Fraaije and Polkowsky, 2016; Ferratges et al., 2020) and numerous (markedly
346 heterogeneous) extinct taxa have been placed in this genus; a modern revision is thus
347 required (Schweitzer and Feldmann, 2001).

348 Modern representatives of the genus *Pagurus* have certain features in common
349 that are not seen in '*Pagurus*' *avellanedai*, such as a flat outer surface of the right chela
350 (major cheliped), usually with a longitudinal ridge in the centre of the palm, generally
351 rhomboid in cross section, with more or less sharp margins, capsulated setae (see
352 Fraaije et al., 2015) and a much less robust build than is seen in '*P.*' *avellanedai*. They
353 also have markedly flat regions on the surface of the chela (i.e., on inner and lower
354 surfaces) which serve to fit the different segments during a defensive posture, when
355 entering a host shell.

356 In view of the fact that the present material includes only chelipeds, we cannot
357 use the list of characters supplied by McLaughlin (2003) or Tudge et al. (2012).
358 Because only chelae and leg fragments are available and the major cheliped is the right
359 one, we tentatively include the new taxon in the Paguridae *sensu lato*. However, '*P.*'
360 *avellanedai* clearly differs from other Cretaceous pagurid genera (such as
361 *Palaeopagurus* van Straelen 1925, *Paguristes* Dana 1851, or *Striadiogenes* Garassino,
362 De Angeli and Pasini 2009) in the general outline of the chelae, the distribution and
363 type of ornamentation, the cross section, the shape of the fingers, occlusal margin, and
364 the morphology of the dactylus of walking legs. Thus, we consider it warranted to erect
365 a new genus and also correct the specific name to *avellanedai*, as suggested by Vía
366 himself in the 1988 paper.

367

368 ***Viapagurus avellanedai*** (Vía, 1951)

369 Fig. 6C, E–H

370 1943 “fragmento de pata”; Bataller, p. 547.

371 1951 *Pagurus Avellaneda* Vía, p. 171, text-fig. 11; pl. 1, fig. 11, 11a.

372 1982 *Pagurus avellaneda* Via, 1951; Whetstone and Collins, p. 1219.

373 1988 *Pagurus avellanedai* Via, 1951; Vía, pp. 344, 350, fig. 344.

374 1988 *Pagurus avellanedai* Via, 1951; Solè and Via, p. 26.

375 2010 *Pagurus avellaneda* Vía, 1951; Schweitzer et al., p. 56.

376 2015 *Pagurus avellaneda* Via, 1951; Fraaije et al., p. 356.

377 2018 *Pagurus avellaneda* Via, 1951; Ossó et al., p. 97, figs 4–6.

378 *Material*. Thirty-one specimens (MPZ2022/584, 585, 590–595, 599–603, 607, 611, 616,
379 617, 619, 620, 624–636) with cuticle preserved, as follows: 14 right propodi, 5 left
380 propodi and four fragments of walking legs.

381 *Remarks*. The new material matches the descriptions of *P. avellaneda* by Vía (1951)
382 and Ossó et al. (2018) well. Four other Cretaceous hermit crab forms have been
383 assigned to *Pagurus*, but these are easily differentiated from the present one: *Pagurus*
384 *convexus* Whetstone and Collins, 1982, from the Upper Cretaceous of Alabama (USA),
385 differs considerably in general outline, with a much more convex lower margin and
386 clearly different distribution and shape of tubercles, while *P. banderensis* Rathbun,
387 1935, from the Albian of Texas (USA), shows certain similarities in terms of robustness
388 and ornamentation. However, it differs in that the lower margin of the pollex is concave
389 (*vs* convex), longer and with better-defined molariform teeth; it also has large setal pits
390 that are clearly visible on the inner margin. *Pagurus travisensis* Stenzel, 1945, from the
391 middle Albian of Texas (USA) has a more globose outer side, while *P. texensis*
392 Franțescu, 2014 from the upper Albian of Texas (USA) cannot be compared because it
393 refers to an individual that preserves an incomplete shield, but lacks chelae.

394

395 Infraorder Brachyura Latreille, 1802

396 Superfamily Dromioidea De Haan, 1833

397 Family Dromiidae De Haan, 1833

398 Subfamily Goniodromitinae Beurlen, 1932

399 Genus *Pithonoton* von Meyer, 1842

400 *Type species. Pithonoton marginatum* von Meyer, 1842, by original designation.

401 *Species included. Pithonoton cardwelli* Armstrong, Nyborg, Bishop, Ossó-Morales and
402 Vega, 2009; *P. campichei* (de Tribolet, 1874); *P. elongatum* von Meyer, 1860; *P.*
403 *laevimarginatum* Lörenthey and Beurlen, 1929; *P. lluismariaorum* Ossó, Van Bakel,
404 Ferratges-Kwekel and Moreno Bedmar, 2018; *P. marginatum* von Meyer, 1842; *P.*
405 *obtusum* (von Meyer, 1857); *P. rusticum* Patruilius, 1966 and *P. simplex* (von Meyer,
406 1837).

407 ***Pithonoton lluismariaorum*** Ossó, Van Bakel, Ferratges-Kwekel and Moreno Bedmar,
408 2018

409 Fig. 7A, B

410 *Material.* A single, near-complete carapace, lacking the rostrum (MPZ2022/596).

411 *Horizon and locality.* Forcall Formation at Locality 3, Barranco de las Calzadas
412 (Miravete de la Sierra, Teruel).

413 *Remarks.* This species has recently been described by Ossó et al. (2018) on the basis of
414 three specimens from La Cova del Vidre (north-east Spain), having been recovered
415 from the lower part of the *D. deshayesi* ammonite Zone within the Margas de Forcall
416 Formation. The specimen described herein comes from the *Deshayesites forbesi*
417 ammonite Zone within the same unit, but in a different sub-basin. Our specimen is
418 assigned to *P. lluismariaorum* on account of similar carapace morphology, development
419 of gastric regions and ornamentation pattern.

420

421 Superfamily Homoloidea De Haan, 1839

422 Family Homolidae De Haan, 1839 (see Guinot et al., 2013, p. 301).

423 Genus *Ariecornibus* Frantescu, 2014

424 *Type species. Ariecornibus schweitzerae* Franțescu, 2014, by original designation.

425 *Remarks.* The present material is assigned to *Ariecornibus* because of a similar carapace
426 surface, with well-defined and delineated regions; a surface ornamented with low nodes
427 and tubercles; a large subtriangular cardiac region, with three nodes; and a slightly
428 concave posterior margin, rimmed and with a row of small granules (see Franțescu,
429 2014, for comparison).

430 *Ariecornibus* sp.

431 Fig. 7C

432

433 *Material.* A single, partial carapace (MPZ2022/608).

434 *Description.* Carapace ornamented with nodes and granules; posterolateral margins
435 convex; posterior margin concave, with thin, granular rim. Postcervical groove deep,
436 sinuous; branchiocardiac groove well defined, lateral of cardiac region branches,
437 anterior branch recurving towards lateral margins, posterior branch shallow, defining
438 cardiac region. Small epibranchial regions, defined as shallow depressions;
439 metabranchial regions large, inflated.

440

441 *Horizon and locality.* Forcall Formation at Locality 3, Barranco de las Calzadas
442 (Miravete de la Sierra, Teruel).

443 *Remarks.* The present specimen shows important similarities to the type species,
444 *Ariecornibus schweitzerae*. However, its rather poor state of preservation precludes a
445 detailed description, but small differences may be noted, such as: a more convex lateral
446 margin and a more concave posterior margin; the posterior groove of the epibranchial
447 region is convex instead of concave and the branchial lobe is well defined by grooves.
448 For these reasons, we tentatively assign this specimen to this genus, but not to the type
449 species.

450 Superfamily Homolodromioidea Alcock, 1900

451 Family Goniidromitidae Beurlen, 1932

452 Genus *Palaeodromites* A. Milne-Edwards, 1865

453 *Type species.* *Palaeodromites octodentatus* A. Milne-Edwards, 1865, by original
454 designation.

455 *Other species included.* *Palaeodromites crypticus* Jagt, Van Bakel and Fraaije, 2007; *P.*
456 *transiens* Wright and Collins, 1972 and *P. xestos* Schweitzer, Feldmann, Rader and
457 Franțescu, 2016.

458 *Remarks.* The present material is assigned to *Palaeodromites* because all observable
459 characteristics match the diagnosis of this genus (see A. Milne-Edwards, 1865).

460 ***Palaeodromites pimientai*** sp. nov.

461 Fig. 7D, E

462 Zoobank ID code: urn:lsid:zoobank.org:act:70765EAD-49A9-45F2-9162-
463 CD9508C30077

464

465 *Diagnosis.* Carapace subcircular, vaulted, finely granular, as long as wide. Maximum
466 width at level of epibranchial region. Front subtriangular, almost straight in dorsal view,
467 axial lobe slightly projected. Entire lateral margin convex, rounded; anterolateral
468 margins broadly arched; posterolateral margin shorter than anterolateral margins,
469 bearing a small node; posterior margin weakly concave. Orbits wide and directed
470 obliquely; cervical and postcervical grooves well defined axially; branchiocardiac
471 groove not visible. Epigastric regions moderately inflated.

472

473 *Etymology.* The specific name honours Juan Carlos García-Pimienta (Cultural Heritage
474 Division, Government of Aragon), who found the material and assisted during field
475 work.

476

477 *Material.* The holotype, a near- complete carapace (MPZ 2022/641), is the sole known
478 example to date.

479 *Horizon and locality.* Forcall Formation at Locality 3, Barranco de las Calzadas
480 (Miravete de la Sierra, Teruel).

481 *Description.* Carapace subcircular, transversely and longitudinally vaulted, slightly
482 wider than long, ornamented with fine granules. Maximum width at level of

483 epibranchial region, over half the distance posteriorly on carapace. Front downturned,
484 subtriangular and flat, weakly sulcate, almost straight in dorsal view, axial lobe slightly
485 projected. Orbits directed obliquely, appearing to have been wide; outer-orbital angle
486 produced into short, triangular, spine. Entire lateral margin convex, rounded;
487 anterolateral margins broadly arched, bearing crested, complex node divided into four
488 blunt spines (excluding outer-orbital angle); posterolateral margin shorter than
489 anterolateral margins, bearing a small node; posterior margin weakly concave, with
490 narrow, granular rim. Cervical and postcervical grooves shallow, but well defined
491 axially; branchiocardiac groove not visible. Epigastric regions moderately inflated.
492 Mesogastric region with long anterior process, two marked swellings posteriorly;
493 protogastric and hepatic regions confluent, broadly inflated. Postcervical groove
494 straight, crossing axial regions, not well developed laterally. Branchiocardiac groove
495 obsolete. Cardiac region broadly triangular; intestinal region somewhat inflated but
496 poorly defined. Epibranchial region flattened.

497

498 *Remarks.* *Palaeodromites pimientai* sp. nov. bears a superficial similarity to other
499 species included in the genus. The type species, *P. octodentatus*, has a wider posterior
500 margin, more prominent anterolateral spines and more concave posterolateral margins,
501 while *P. xestos* can be differentiated by its more elongated outline, with slightly more
502 inclined orbits. In addition, the anterolateral spines are more pointed than in the new
503 species, with the posterior margin straight instead of concave. *Palaeodromites transiens*
504 also shows important similarities to the new form, but has a wider-than-long outline and
505 is rhomboidal in shape. Finally, *P. crypticus* differs from the new species by presenting
506 a carapace that is wider than long, with some larger spines on the dorsal surface; lateral
507 margins bear several spines and the cervical groove is much more pronounced.

508

509 **6. Discussion**

510 *Pre-Albian palaeoenvironmental distribution of decapod crustaceans in the* 511 *Maestrazgo Basin*

512 Here we present a compilation of known and new decapod crustacean records from
513 Spain, in stratigraphical order. Special emphasis is put on a comparison (Fig. 8; Table 1)

514 between known and newly recorded sites of the Galve subbasin and the known decapod
515 crustacean record of the Oliete subbasin (Ferratges et al., 2021).

516 In the Maestrazgo Basin, decapod crustaceans of early late Barremian age are
517 restricted to the Oliete and Salzedella subbasins. Along the western margin of the Oliete
518 subbasin, near the village of Obón, a single level containing carbonate nodules with
519 well-preserved specimens of the glypheid lobster *Atherfieldastacus rapax* (Harbort,
520 1905) has been recorded from the middle part of the Blesa Formation (García-Penas et
521 al., 2022b). This level is found within a marly facies containing oysters, serpulids,
522 gastropods, hybodontid shark spines, durophagous fish teeth and occasional characeans
523 and quartz silt to fine sand, representing a shallow, low-energy, restricted bay with a
524 narrow and unstable connection with the Maestrazgo Basin (Aurell et al., 2018).
525 Towards the west (basinwards), in the Salzedella subbasin, the lower upper Barremian
526 is represented by the Artoles Formation, which illustrates proximal, shallow, coastal-to-
527 open-marine environments contrasting with the restricted bay deposits represented by
528 the middle Blesa Formation in the more marginal Oliete subbasin. Near the locality of
529 Ares del Maestrat, specimens of *Atherfieldastacus rapax* have been described from the
530 middle part of the Artoles Formation (González-León et al., 2017). The lobsters appear
531 in two limestone-dominated stratigraphical intervals with packstone to floatstone
532 textures and containing abundant oysters as well as ooids, peloids, intraclasts, bivalves,
533 gastropods, echinoderms and dasycladacean algae. These deposits represent an
534 energetic and proximal, near-coastal, marine environment.

535 The latest Barremian represents the start of a long-term transgressive event
536 recognised across the Tethyan Realm. In most of the Maestrazgo Basin, this interval is
537 represented by the Chert Formation, which documents proximal to distal settings in a
538 carbonate ramp environment (Vennin and Aurell, 2001; Bover-Arnal et al., 2010, 2016).
539 In the Oliete subbasin, however, this interval is represented by the Alacón Formation
540 (Aurell et al., 2018), which shows a marked long-term, upwardly transgressive trend,
541 from intertidal to shallow and relatively energetic ramp environments (García-Penas et
542 al., 2022a). Both units yield frequent *Palorbitolina lenticularis* blooms as well as
543 episodic terrigenous input, mainly along the western margin of the Maestrazgo Basin.

544 In the Oliete subbasin, the lower part of the Alacón Formation is highly
545 terrigenous, oyster-dominated and shows evidence of environmental stress, probably
546 related to lowered salinity levels caused by riverine (freshwater) input. In these deposits,

547 which represent a very shallow bay with fluctuating salinity, axiidean remains are very
548 abundant. The effects of these burrowing organisms on the sediment can also be
549 observed throughout the unit, especially at 4th-order sequence boundaries, where
550 bedding is frequently disturbed by the burrowing intensity and high concentrations of
551 *Thalassinoides* traces, occasionally associated with abundant axiidean remains, can be
552 found (García-Penas et al., 2022a).

553 In the Galve subbasin, the base of the Chert Formation consists of marls and
554 bioturbated marly limestones with abundant irregular echinoids and bivalves,
555 interpreted as a distal ramp environment under the fair-weather wave base (Peropadre,
556 2011). This interval has yielded a single specimen of *Cretacocalcinus fortis* sp. nov.
557 The top of the Chert Formation at the same locality preserves the first record of
558 *Viapagurus* gen. nov. and axiideans in distal ramp limestones.

559 The latest Barremian–earliest Aptian represented a stage of generalised marine
560 transgression across the Maestrazgo, Salou-Garraf and Basque-Cantabrian basins,
561 coeval with the drowning of many Barremian shallow platforms in the western Tethys
562 (Hardenbol et al., 1998; Bover-Arnal et al., 2016).

563 In the Galve and Oliete subbasins, the lower Aptian is represented by marl and
564 clay-dominated transgressive deposits. In the Galve subbasin, the upper part of the
565 Forcall Formation has yielded a diverse decapod crustacean assemblage comprising
566 nephropids (*Hoploparia* sp.), pagurids (*Viapagurus avellanedai* nom. corr.), homolids
567 (*Ariecornibus* sp.), goniodromitids (*Pithonoton lluismariaorum*, *Palaeodromites*
568 *pimientai* sp. nov.) and axiideans. The specimens have been recovered from a marl-
569 dominated interval (Fig. 8) containing ammonites, solitary corals and orbitolinids,
570 deposited in a low-energy distal platform environment (Bover-Arnal et al., 2010;
571 Peropadre, 2011). In the Oliete subbasin, the sedimentology of the lower Aptian is
572 unique relative to the Galve subbasin, and its base is diachronic due to the existence of a
573 condensed interval associated to an important sedimentary gap spanning most of the *D.*
574 *oglanlensis* and *D. forbesi* ammonite zones (Fig. 8) (Moreno-Bedmar et al., 2010;
575 García-Penas et al., 2022a). This unit is sedimentologically quite homogeneous across
576 the subbasin. Its lower interval is dominated by thick marl and clay intervals with scarce
577 intercalations of fine sandstone with occasional hummocky cross-lamination, deposited
578 under the fair-weather wave base in an offshore ramp environment subjected to
579 occasional storm influence (Vennin et al., 1993). These levels have yielded one of the
580 most diverse Aptian decapod crustacean associations in Spain (Ferratges et al., 2021),

581 dominated by the glypheid *Atherfieldastacus magnus* (M'Coy, 1849), but also including
582 axiideans (*Aptaxiopsis longimanus* Ferratges, Hyžný and Zamora, 2021, *Crosniera*
583 *forcallensis* Ferratges, Hyžný and Zamora, 2021, *Meticonaxius monodon* Ferratges,
584 Hyžný and Zamora, 2021, *Aptanacalliax enigma* Ferratges, Hyžný and Zamora, 2021),
585 Paguroidea (*Cretacocalcinus josaensis* Ferratges, Hyžný and Zamora, 2021) and
586 Homoloidea (*Mithracites vectensis* Gould, 1859). The succession deposited around the
587 lower–upper Aptian transition is characterised by the progressive appearance of
588 sandstone and sandy limestone levels with articulated and disarticulated bivalves
589 (mostly trigoniids and oysters) and, eventually, microconglomeratic levels with trough
590 cross-lamination, reflecting the progressive shallowing of the depositional system.
591 These upper levels, which represent a lower shoreface environment, have yielded
592 isolated specimens of *Atherfieldastacus magnus*. It is interesting to note that the basal
593 offshore deposits near the locality of Obón contain monospecific carbonate nodules
594 bearing well-preserved specimens of *Atherfieldastacus magnus*. These nodules do not
595 appear to be associated to burrow systems and could have been reworked from a
596 shallower environment (García-Penas et al., 2022a).

597 Other parts of Iberian were also affected by the latest Barremian–earliest Aptian
598 transgression. In the Basque-Cantabrian Basin, for example, the lower Aptian is
599 represented by several shallow-marine siliciclastic units. In Cuchía (Cantabria), the
600 lower Aptian Patrocinio Formation represents the progradation of a delta system
601 (Najarro et al., 2011). The basal siliciclastic prodelta deposits of this unit represent a
602 low-energy environment quite similar to the lower Aptian offshore clays in the Oliete
603 subbasin and have yielded specimens of *Atherfieldastacus magnus*, callianassids and the
604 brachyuran *Cuchiadromites jadeae* (see López-Horgue and Bodego, 2017; Ossó et al.,
605 2021). Near Cuchía, this unit has also yielded Homoloidea (*Mithracites vectensis*) and
606 Homolodromioidea (*Rathbunopon viai* González-León, Ossó, Moreno-Bedmar and
607 Vega, 2016a).

608 In the Perelló subbasin, marls and limestones from the middle part of the Forcall
609 Formation, representing open-marine environments, have yielded Paguridae
610 (*Viapagurus avellanedai* nom. corr.), Prosopidae (*Rathbunopon tarraconensis* Ossó,
611 van Bakel, Ferratges and Moreno-Bedmar, 2018) and Dromiidae (*Pithonoton*
612 *lluismariaorum*) (Ossó et al., 2018).

613 The upper lower Aptian is represented in most of the Maestrazgo Basin by the
614 regressive shallow platform carbonates of the Villarroya de los Pinares Formation,

615 which have not yielded any decapod crustacean remains. During the latest early Aptian,
616 a significant eustatic sea level drop of *c.* 60 metres exposed the carbonate platform of
617 the Villarroya de los Pinares Formation, which underwent localised incision in the
618 Galve subbasin (Bover-Arnal et al., 2010, 2016, 2022). This incised surface transits
619 westwards into an iron-stained regressive surface, which can be recognised across the
620 Maestrazgo Basin and marks an abrupt lithological change to the marl-dominated lower
621 interval of the Benassal Formation, which spans the uppermost lower to upper Aptian.
622 The Benassal Formation extends across the Maestrazgo Basin, and represents a complex
623 array of sedimentary environments. In the Galve subbasin, the lower interval of this unit
624 consists of bluish marls with calcareous nodules representing a low-energy distal
625 platform environment (Bover-Arnal et al., 2010; Martín-Martín et al., 2013). Other
626 authors have interpreted these levels to document relatively deep lagoon deposits
627 (Peropadre, 2011). Two localities in the same stratigraphical position within this lower
628 interval have yielded *Viapagurus avellanedai* nom. corr. and indeterminate axiideans. In
629 the Basque-Cantabrian Basin, near Sestao (Basque Country), upper Aptian marine
630 siliciclastic distal ramp deposits of the Bilbao Formation have yielded indeterminate
631 remains of Callianassidae. Near Zaramillo (Basque Country), similar prodelta deposits
632 have yielded *Atherfieldastacus magnus* (see López-Horgue and Bodego, 2017).

633

634 ***Factors controlling decapod crustacean diversity***

635 During the late Barremian to late Aptian, the Maestrazgo Basin evolved from a
636 disjointed array of subbasins, each representing geographically restricted
637 palaeoenvironments ranging from continental to open marine, to a mostly unified
638 sedimentary domain characterized by proximal-to-open-marine sedimentary settings.
639 This homogenization was driven by successive transgressive stages of possible eustatic
640 origin during the latest Barremian to early Aptian (e.g., Bover-Arnal et al., 2010, 2022;
641 García-Penas et al., 2022a), as well as by the linkage of major fault systems associated
642 to the maturation of the Iberian Rift System, which caused a progressive delocalization
643 of tectonic subsidence (Salas et al., 2001)

644 The transition from continental or restricted depositional environments to marine
645 carbonate platforms across the Maestrazgo Basin is linked to a progressive
646 diversification of the decapod crustacean faunas. A notable exception is the Oliete
647 subbasin, which developed during the Early Cretaceous as a very shallow and relatively

648 enclosed bay with varying degrees of connection with the more open-marine
649 environments of the adjacent Morella and Galve subbasins. This bay received elevated
650 terrigenous and nutrient inputs, and experienced high salinity fluctuations linked to
651 riverine discharges (García-Penas et al., 2022a). The decapod crustacean faunas of the
652 Oliete subbasin are dominated by burrowing detritivore forms such as glypheid lobsters
653 and axiidean shrimp, which can thrive in restricted environments with fluctuating
654 salinity and oxygenation (e.g., Hyžný et al., 2015), that other groups cannot tolerate.

655 Maximum decapod crustacean diversity in the Oliete subbasin is associated to
656 siliciclastic platform facies, and in the Galve subbasin to carbonate platform facies; both
657 diversity peaks are approximately coeval and present many similarities between high-
658 rank groups, while species appear endemic. It has been proposed that maximum
659 diversities tend to correlate with transgressive events (e.g. Sepkoski, 1976; Hallam,
660 1987; Brett, 1998; Smith and Benson, 2013), as rising sea levels increase the
661 availability of favourable shallow marine habitats. However, it seems that in many cases
662 the relationship between species diversity and habitable area is complex and non-linear
663 (e.g. Smith, 2001; Holland, 2012). In the Oliete and Galve subbasins, where this study
664 focuses, diversity peaks are linked to an early-Aptian third-order transgressive
665 maximum (Bover-Arnal et al., 2016; 2022). In the case of the Oliete subbasin, this
666 transgressive maximum is linked to thick clay intervals generated in an open-marine
667 siliciclastic platform with normal marine salinity and good marine circulation, as
668 evidenced by the co-occurrence of high-diversity decapod associations and stenohaline
669 groups such as brachiopods, echinoderms, ammonites and solitary corals. Furthermore,
670 nutrient availability in this environment is thought to have been high, as there is
671 evidence of high riverine freshwater inputs, and this is another environmental factor that
672 has been linked to generalized increases in productivity and biodiversity (Martin, 2003).
673 In the Galve subbasin, the levels recording maximum decapod crustacean diversity
674 correspond to a stratigraphic interval interpreted as relatively shallow but open-marine
675 carbonate platform deposits, which are also characterized by abundant and diverse
676 ammonites and orbitolinids (Bover-Arnal et al., 2010; Moreno-Bedmar et al., 2010).

677 This generalized transgression represents the onset of relatively deep open-
678 marine conditions across the western Maestrazgo Basin, and is assumed to have been
679 accompanied by enhanced marine circulation between subbasins, which would have
680 facilitated the dispersal of the planktotrophic larvae of decapod crustaceans, thus driving
681 colonization of the newly available environments and speciation. Endemism may have

682 been fostered by the retention of subbasin-specific palaeoenvironmental conditions due
683 to geographical restriction even during peak transgression (e.g. high detrital and nutrient
684 input in the Oliete subbasin).

685 In view of the palaeoenvironmental distribution of decapod crustacean groups in
686 the Oliete and Galve subbasins, it can be asserted that maximum diversities of decapod
687 crustaceans in the western Maestrazgo Basin are related to stable open-marine
688 environments characterized by moderate depth (and its associated favorable taphonomic
689 conditions), good water oxygenation, normal marine salinities and possibly to increased
690 nutrient availability. In contrast, regressive stages are dominated by low-diversity
691 eurytopic groups, as geographical restriction caused by sea-level fall made individual
692 subbasins prone to ecologically limiting variations in palaeoenvironmental factors.

693 Endemism is also high across the rest of Maestrazgo Basin, with the exception
694 of widespread groups such as glypheid lobsters and the brachyuran *Mithracites*
695 *vectensis*. *Atherfieldastacus magnus* is a widespread lobster that has been recorded from
696 several countries (see details in Ferratges et al., 2021). The brachyuran *M. vectensis* is a
697 common taxon in the Maestrazgo and Basque-Cantabrian basins and the British Isles
698 (see Ossó et al., 2015, González-León et al., 2016a, b).

699 The shallow open carbonate platforms of eastern Spain (Salou-Garraf Basin)
700 also yield a high diversity of decapod crustaceans related to the development of sponge
701 meadows (Ossó et al., 2022). This reef-like environment contains the forerunners of
702 taxa that would later predominate reef environments during the Albian (see López-
703 Horgue and Bodego, 2017, table 1), suggesting that the environmental conditions for
704 decapod diversification in the mid- and Late Cretaceous were pre-established in the
705 Aptian.

706

707 **7. Conclusions**

708

709 Aptian decapod crustaceans are a minor component in invertebrate fossil assemblages
710 of Spain. The Maestrazgo Basin, in northeast Spain, comprises an array of sub-basins
711 separated by major faults which controlled Lower Cretaceous deposition. Fossil
712 crustaceans have been extensively studied in the Oliete subbasin, one of the most
713 environmentally restricted domains. Sampling in the nearby Galve subbasin has resulted
714 in the description of seven new localities yielding fossil decapod crustaceans. We
715 describe the anomurans *Cretacocalcinus fortis* sp. nov. and *Viapagurus* gen. nov. (type

716 species: *Pagurus avellanedai* Vía, 1951), one indeterminate axiidean, the astacidean
717 *Hoploparia* sp., plus the brachyurans *Ariecornibus* sp., *Pithonoton lluismariaorum*
718 Ossó, van Bakel, Ferratges-Kwekel and Moreno Bedmar, 2018 and *Palaeodromites*
719 *pimienti* sp. nov.

720 Integration of stratigraphic and paleontological data sets suggests that variations
721 in decapod diversity and abundance in the Oliete and Galve subbasins were in tune with
722 third-order transgressive-regressive cycles. Diversity and abundance peaks are coeval in
723 both domains, and coincide with a third-order transgressive maximum recognizable
724 basinwide in the Maestrazgo Basin. Favorable environmental factors such as good water
725 oxygenation, normal marine salinity and mesotrophic conditions prevailed in both
726 subbasins during peak transgression, promoting speciation. Different subbasins retained
727 particular paleoenvironmental conditions, fostering endemism. This study also provides
728 an overview of the Lower Cretaceous, pre-Albian paleoenvironmental distribution of
729 decapods in Spain, which may prove to be useful for future research.

730

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738

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1181 **CAPTIONS**

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1183 **Fig. 1. A.** Palaeogeography and palaeoenvironmental distribution of the Western
 1184 Tethys. The location of the Maestrazgo (Mb), Garraf (Gb) and Basque-Cantabrian (B-
 1185 Cb) basins is indicated, including their record of Aptian decapod crustaceans (modified
 1186 from Steuber et al., 2005). **B.** Location of the seven Lower Cretaceous subbasins (sb) of
 1187 the Maestrazgo Basin (Mb) and their palaeoenvironmental distribution during the early
 1188 Aptian. Ol: Oliete sb.; Mo: Morella sb.; Per: El Perelló sb.; Pa: Las Parras sb.; Ga:
 1189 Galve sb.; Sa: Salzedella sb.; Pen: Penyagolosa sb. The Aptian decapod crustacean
 1190 record of each subbasin is indicated. The green rectangle indicates the location of Figure
 1191 2A.

1192 **Fig. 2A.** Stratigraphical chart of the Galve subbasin, with emphasis on the Barremian–
 1193 Aptian interval, indicating the stratigraphical position of the decapod crustacean-
 1194 yielding sites surveyed in the present study (adapted from García et al., 2014; Bover-
 1195 Arnal et al., 2016 and Aurell et al., 2016). Iberian rift stages are those from Salas et al.
 1196 (2001). **B.** Geological map of the study area, including the locations of the sites
 1197 sampled. Stratigraphical units follow the colour code shown in Figure 1A.

1198 **Fig. 3.** Photographs of field localities and ammonites collected from the localities
 1199 studied. **A.** Forcall Formation at Barranco de las Calzadas (Miravete de la Sierra, Loc.
 1200 3). **B.** Ammonites: *Deshayesites dehayesi*, left, *Deshayesites* sp., right, from level 137 at
 1201 Barranco de las Calzadas (Miravete de la Sierra, Loc. 3). **C.** Las Mingachas outcrop
 1202 (Miravete de la Sierra, Loc. 7). The star indicates the level with *Viapagurus avellanedai*
 1203 nom. corr. **D.** Locality 1 at Allepuz (Teruel), the square indicating the level where the
 1204 specimen of *Cretacocalcinus fortis* sp. nov. was collected. **E.** Ammonite, *Dufrenoyia*
 1205 *dufrenoyi* from the Benassal Formation, locality 6; scale bar represents 5 mm.

1206 **Fig. 4A.** Axiidea indet. from the Forcall Formation at Locality 3 (MPZ2022/618); **B–D.**
 1207 Axideans from the Chert (D; MPZ2022/637) and Benassal (B, C; MPZ2022/597 and
 1208 MPZ2022/598, respectively). Scale bars represent 2 mm.

1209 **Fig. 5.** *Hoploparia* from the Forcall Formation. **A–F.** Partially disarticulated specimen
 1210 (MPZ2022/615) collected from within the same burrow. A. part of the burrow with two
 1211 disarticulated chelae; B. partial carapace; C. detail of right cheliped; D. cross section of

1212 right cheliped of C; E. left cheliped; F. complete right cheliped. **G.** Partial carapace
1213 (MPZ2022/621). Scale bars represent 2 mm in D; and 5 mm in A-C, E-G.

1214 **Fig. 6.** Paguroids. **A, B, D.** *Cretacocalcinus fortis* sp. nov., complete left cheliped
1215 (MPZ2022/612, **holotype**). **C, E, F–H.** *Viapagurus avellanedai* (Vía, 1951) nom. corr.,
1216 complete right cheliped, lacking moveable finger (MPZ2022/607) and walking leg
1217 (MPZ2022/603), respectively. Scale bars represent 5 mm.

1218 **Fig. 7.** Brachyurans from the Forcall Formation. **A, B.** *Pithonoton lluismariaorum* Ossó,
1219 Van Bakel, Ferratges-Kwekel and Moreno Bedmar, 2018 (MPZ2022/596), complete
1220 carapace, lacking rostrum. **C.** *Ariecornibus* sp. (MPZ2022/608), posterior part of
1221 carapace preserved. **D, E.** *Palaeodromites pimientai* sp. nov. (MPZ2022/641,
1222 **holotype**), complete carapace. Scale bars represent 5 mm.

1223 **Fig. 8.** Comparison between decapod crustacean records in the Oliete and Galve
1224 subbasins of the Maestrazgo Basin.

1225 **Table 1.** Decapod crustacean taxa known to date from the Barremian–Aptian of the
1226 Iberian Peninsula.

1227 **Table 2.** Occurrence of decapod crustacean species at the various localities. X=
1228 present; -- = absent.

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Locality	Taxa						
	<i>Pithonoton lluismariaorum</i>	<i>Hoploparia</i> sp.	<i>Cretacocalcinu s fortis</i>	<i>Viapagurus avellanedai</i>	<i>Palaeodromites pimientai</i>	<i>Axiidea</i> indet.	<i>Ariecornibus</i> sp.
1	-	-	X	-	-	-	-
2	-	-	-	X	-	X	-
3	X	X	-	X	X	X	X
4	-	-	-	X	-	-	-
5	-	-	-	X	-	X	-
6	-	-	-	X	-	X	-
7	-	-	-	X	-	X	-

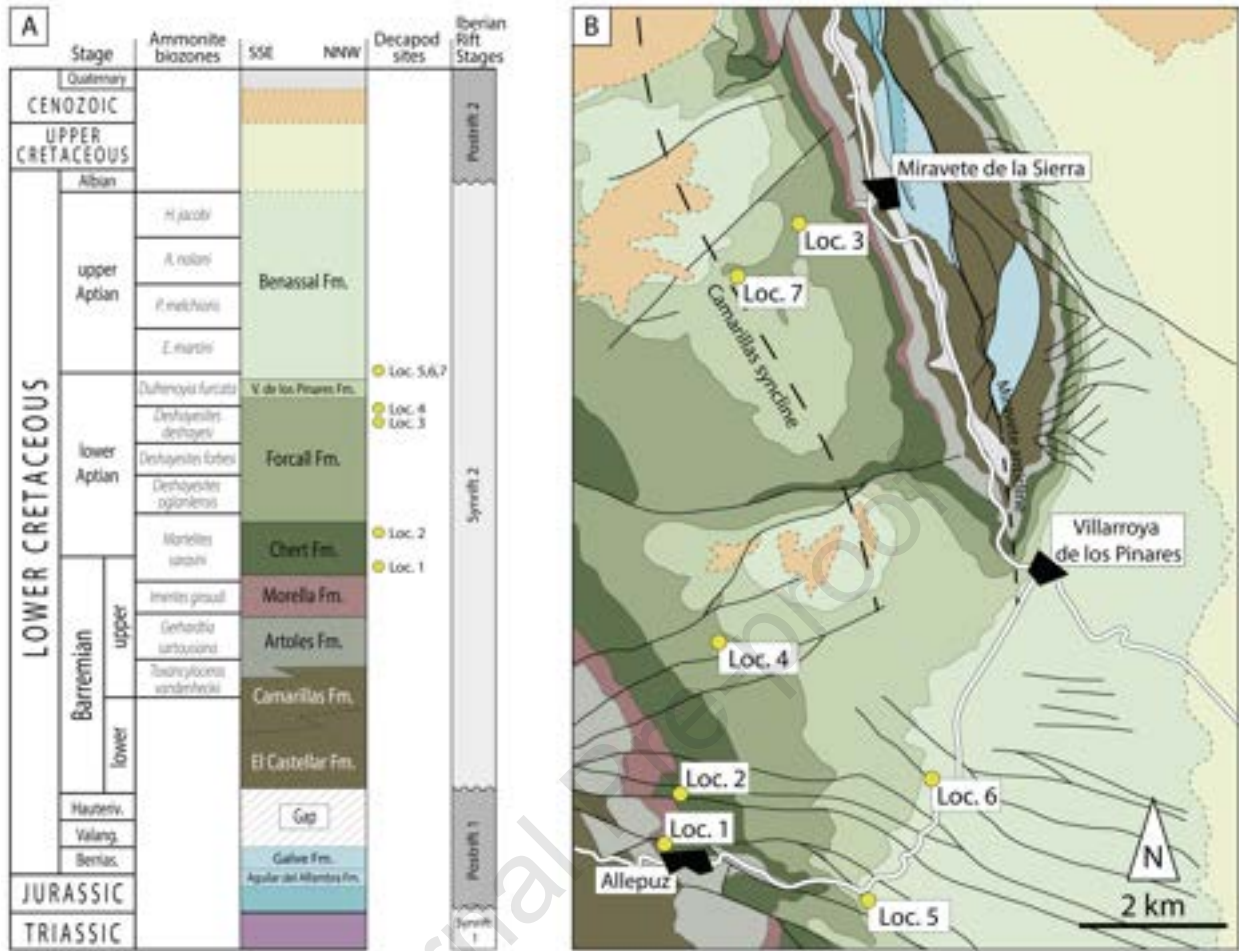
Table 2. Occurrence of decapod crustacean species at the various localities. X= present; -- = absent.

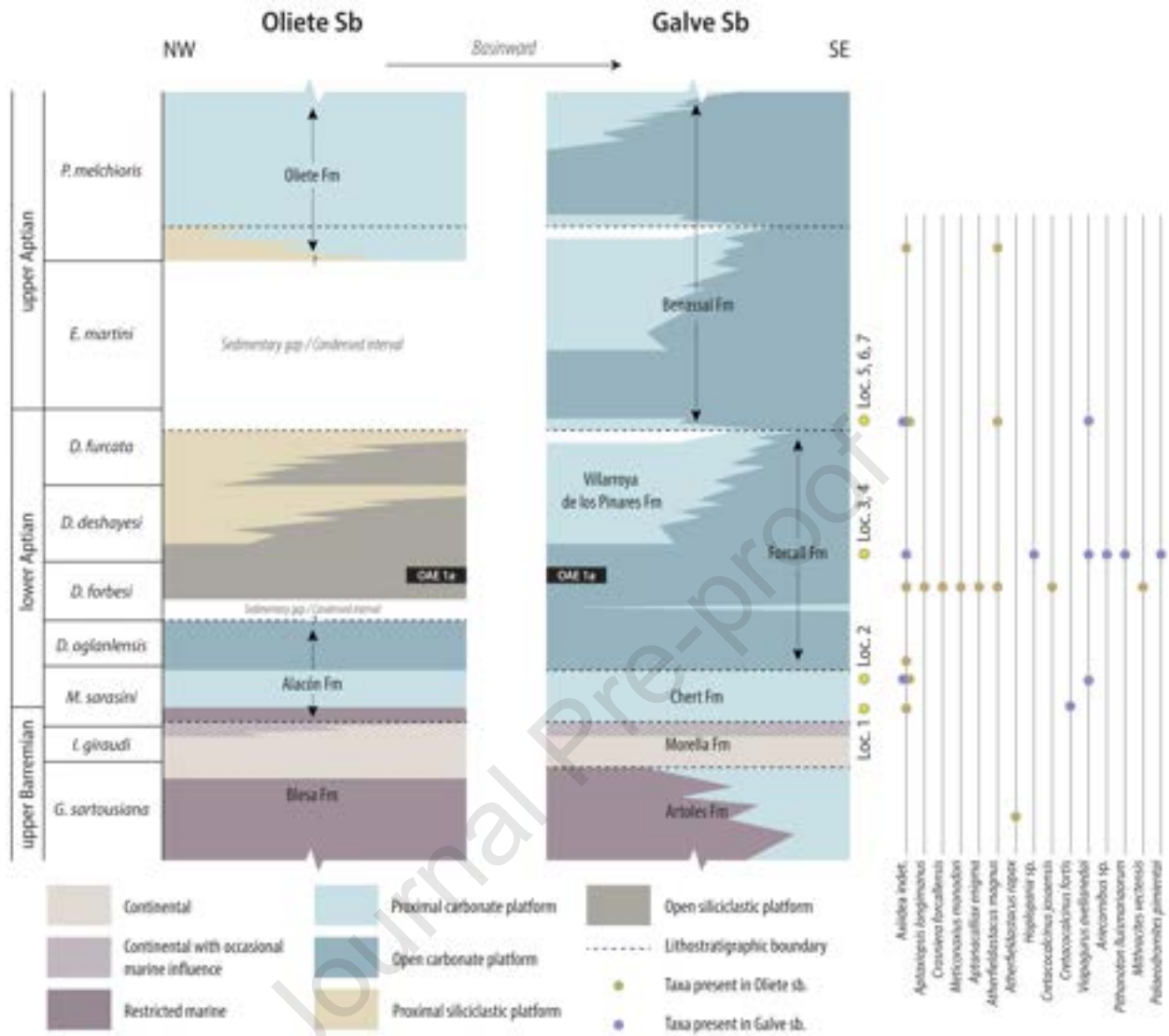
Table 1. Decapod crustacean taxa known to date from the Barremian–Aptian of the Iberian Peninsula.

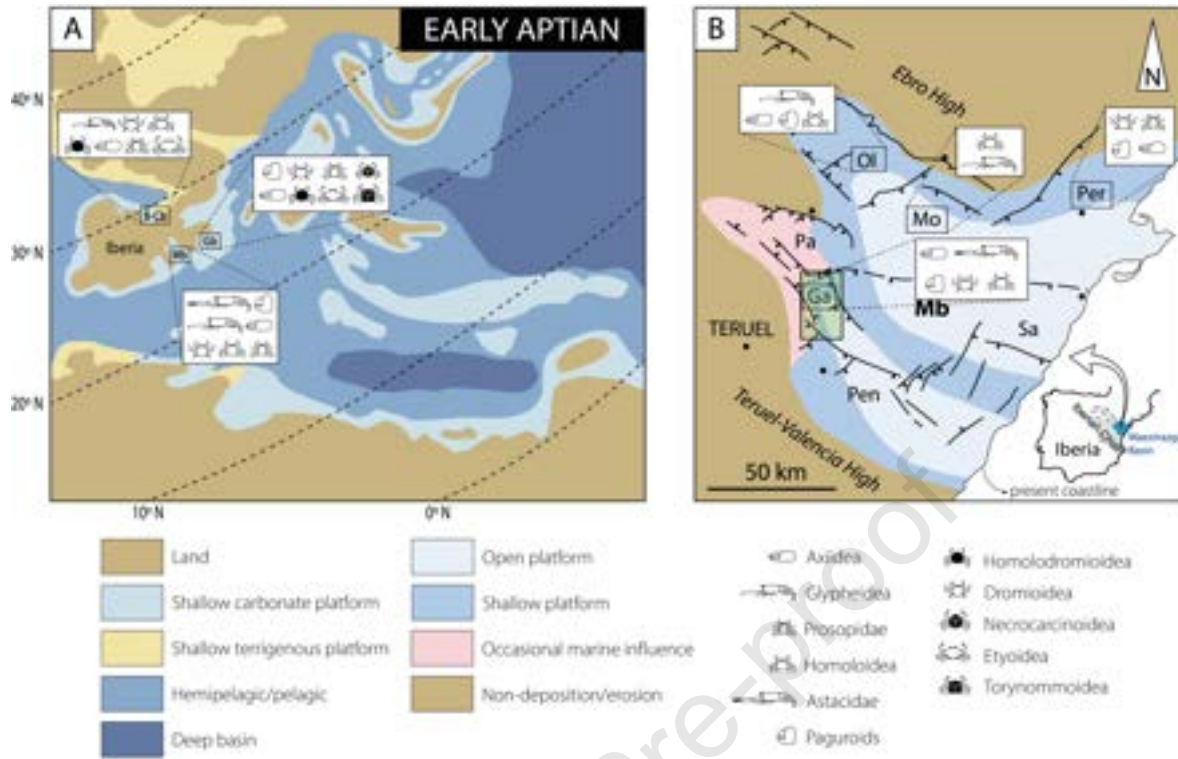
Infraorder	Superfamily	Species	Environment	Basin	Formation (Age)	Reference
Caridea Dana, 1852	Atyoidea De Haan, 1849	<i>Delclosia almeni</i>	Very shallow coastal lagoon	Basque-Cantabrian Basin	Aroco (Hauterivian-Barremian)	López-Horgue et al., 2017
		<i>Delclosia martinelli</i>	Lacustrine environments	La Serranía de Cuenca Basin	Huérquina (Barremian)	Rabadà, 1993; Garassino, 1997
Axiidea de Saint Laurent, 1979		<i>Aptaxiopsis longimanus</i>	Marine open platform	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Ferratges et al., 2021
		<i>Aptanacalliax enigma</i>	Marine open platform	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Ferratges et al., 2021
		Callianassidae indet. 1	Shallow marine prodelta	Basque-Cantabrian Basin	Ereza (Aptian)	Lopez-Horgue et al., 2017
		Callianassidae indet. 2	Marine open platform (likely prodelta)	Basque-Cantabrian Basin	Bilbao (Aptian)	Lopez-Horgue et al., 2017
		<i>Callianassa infracretacea</i>	-	Salou-Garraff Basin (Viladellops)	Aptian	Bataller, 1943; Vía, 1951
		<i>Callianassa</i> cf. <i>michelotti</i>	-	Maestrazgo Basin (Castellote, Teruel)	Aptian	Vía, 1951
		“ <i>Callianassa</i> ” sp.	Sponge meadows?	Salou-Garraff basins	Margas de Valcarca (Aptian)	Ossó et al., 2022
		<i>Crosniera forcallensis</i>	Marine open platform (likely prodelta)	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Ferratges et al., 2021
		<i>Meticonaxius gracilis</i>	Marine open platform (likely prodelta)	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Ferratges et al., 2021
		Axiidea indet. 1	Marine distal platform	Galve subbasin (Maestrazgo Basin)	Forcall, (Aptian)	Herein
		Axiidea indet. 2	Marine distal platform	Galve subbasin (Maestrazgo Basin)	Chert, Benassal (Barremian-Aptian)	Herein
Astacidea Latreille, 1803	Astacoidea Latreille, 1802	<i>Austropotamobius llopisi</i>	Lacustrine environments	La Serranía de Cuenca Basin	Huérquina (Barremian)	Vía, 1971; Garassino, 1997
	Nephropoidea Dana, 1852	<i>Homarus edwardsi</i>	Sponge meadows?	Salou-Garraff basins	Margas de Valcarca (Aptian)	Vía, 1951
		<i>Hoploparia</i> sp.	Marine distal platform	Galve subbasin (Maestrazgo Basin)	Forcall (Aptian)	Herein
Glypheide von Zittel, 1885	Glypheoidea von Zittel, 1885	<i>Atherfieldastacus magnus</i>	Marine distal platform	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Vía, 1951, 1975; Bover-Arnal et al., 2010; Ferratges et

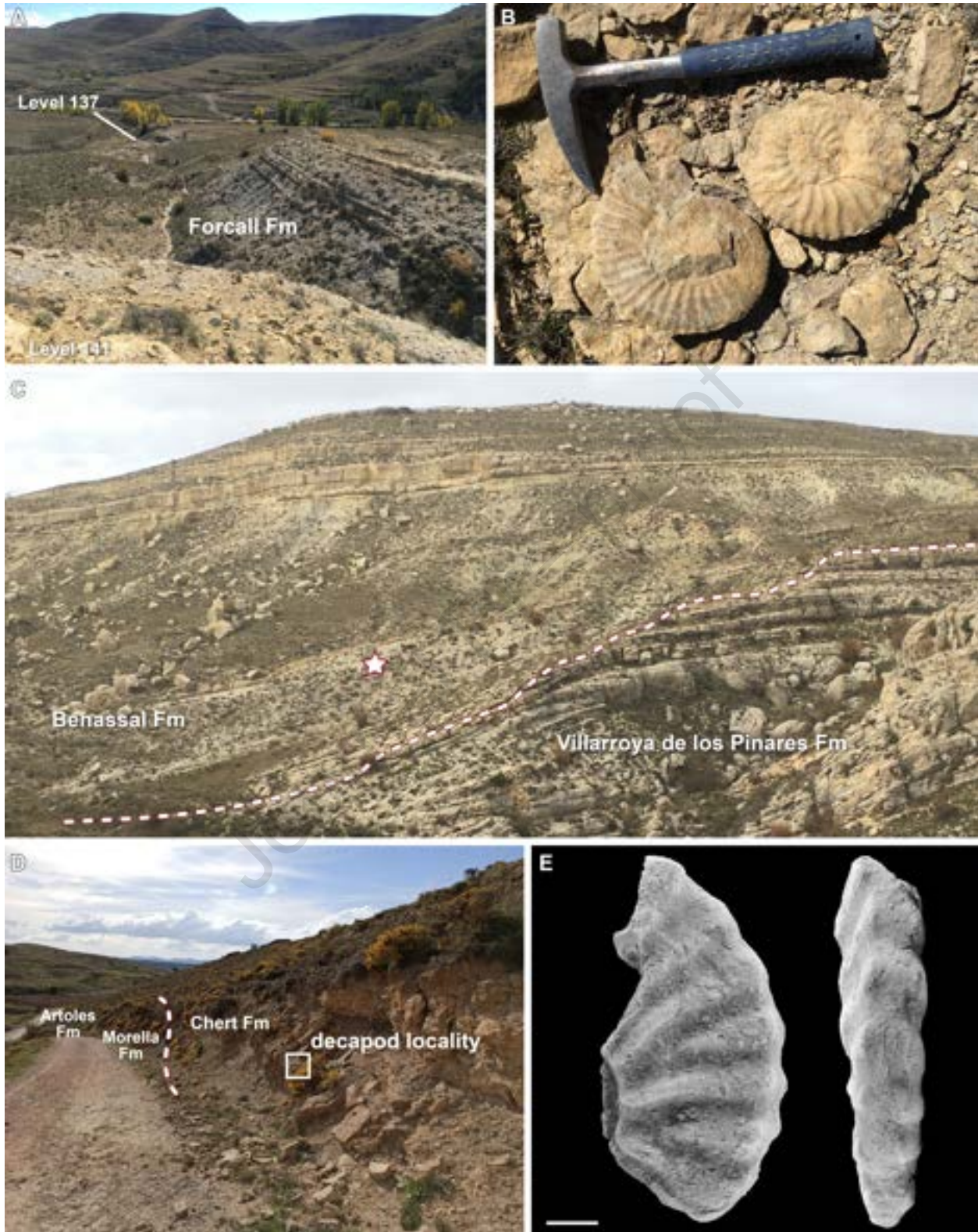
						al., 2021	
			-	Salou-Garraff basins	Aptian	Calzada and Urquiola, 1999	
			Shallow marine prodelta marls	Basque-Cantabrian Basin	Ereza (early Aptian)	Lopez-Horgue et al., 2017	
			Shallow marine prodelta marls	Basque-Cantabrian Basin	Caranceja (early Aptian)	López-Horgue, 2009;	
			Marine distal platform	Basque-Cantabrian Basin	Patrocinio (Aptian)	Najarro et al., 2011	
			Marine distal platform	Basque-Cantabrian Basin	Tellamendi (early late Aptian)	Lopez-Horgue et al., 2017	
			<i>Atherfieldastacus rapax</i>	Shallow-marine environment.	Maestrazgo Basin	Artoles (Barremian)	González-León et al., 2017
Anomura MacLeay, 1838	Paguroidea Latreille, 1802		Mecochiridae indet.	Freshwater shallow lakes	Basque-Cantabrian Basin	Aroco (Berriasian)	Lopez-Horgue et al., 2017
			<i>Meyeria ornata</i>	Marine distal platform	Oliete subbasin (Maestrazgo Basin)	“Forcall”, Aptian	Ferratges et al., 2021
			<i>Cretacocalcinus fortis</i> sp. nov.		Galve subbasin (Maestrazgo Basin)	Chert (Barremian)	Herein
			<i>Cretacocalcinus josaensis</i>	Marine distal platform	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	Ferratges et al., 2021
		<i>Viapagurus avellanedai</i> (nov. comb.) nom. corr.	Marine distal platform	Maestrazgo Basin	Forcall (Aptian)	Vía, 1951, and herein	
		<i>Pagurus</i> sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022	
Brachyura Latreille, 1802	Dromioidea De Haan, 1833		<i>Eomunidopsis</i> cf. <i>navarrensis</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
			<i>Pithonoton lluismariaorum</i>	Open-marine, muddy environment	Maestrazgo/Salou-Garraff basins and Galve subbasin (Maestrazgo Basin)	Forcall (Aptian)	Ossó et al., 2018, and herein
			<i>Cuchiadromites jadeae</i>	?Mixed siliciclastic-carbonate platform	Basque-Cantabrian Basin	Patrocinio (Aptian)	Ossó et al., 2021
			<i>Vectis</i> sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
			<i>Distefania incerta</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
			<i>Eodromites</i> sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
			<i>Goniodromites laevis</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
	<i>Mesodromilites</i> sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022		

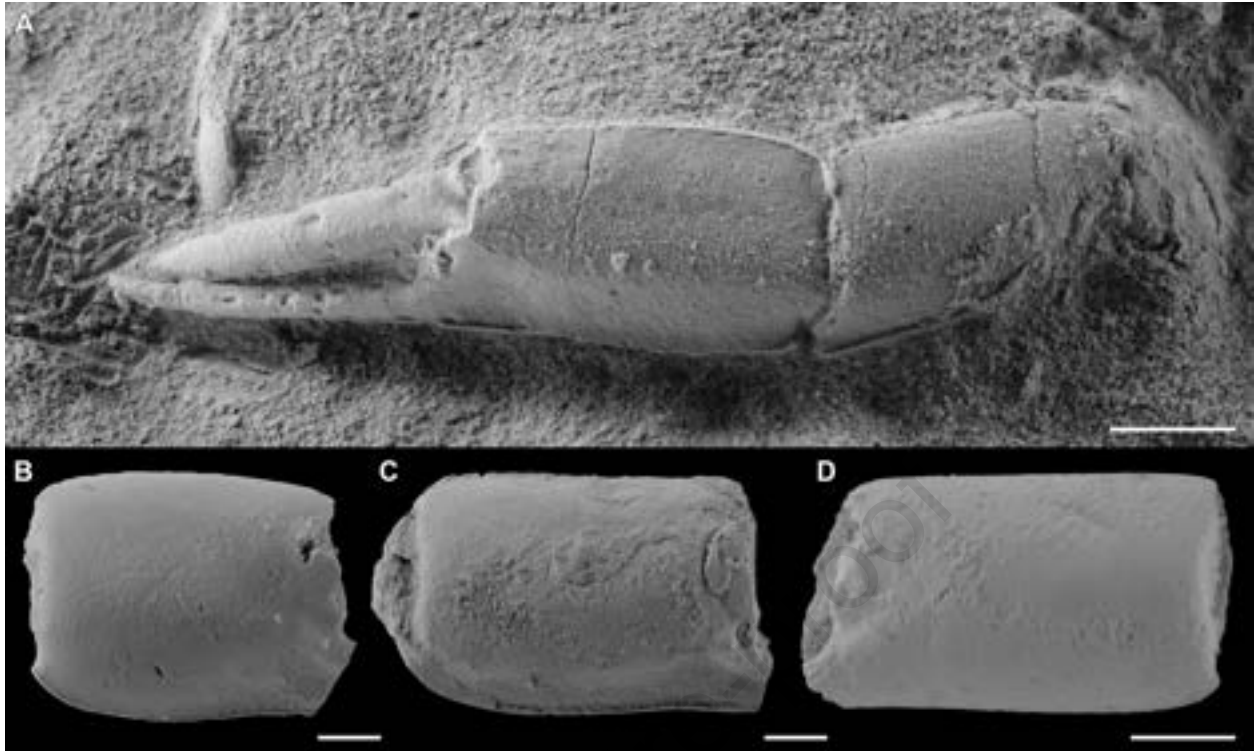
Homoloidea De Haan, 1839	<i>Ariecornibus</i> sp.	Marine distal platform	Galve subbasin (Maestrazgo Basin)	Forcall (Aptian)	Herein
	<i>Mithracites vectensis</i>	Marine distal platform	Oliete subbasin (Maestrazgo Basin)	“Forcall” (Aptian)	González-León et al., 2016a; Ferratges et al., 2021
		Marine distal platform	Maestrazgo Basin	Chert (late Barremian)	Ossó et al., 2015
		Marine distal platform	Basque-Cantabrian Basin	Patrocinio (Aptian)	González-León et al., 2016b
Homolodromioidea Alcock, 1900	<i>“Glaessnerella” angusta</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
	<i>Palaeodromites pimientai</i> sp. nov.	Marine distal platform	Galve subbasin (Maestrazgo Basin)	Forcall (Aptian)	Herein
	<i>Rathbunopon tarraconensis</i>	Open-marine, distal environment	Maestrazgo/Salou-Garraff basins	Forcall (Aptian)	Ossó et al., 2018
	<i>Rathbunopon viai</i>	Prodelta	Basque-Cantabrian Basin	Patrocinio (Aptian)	González-León et al., 2016
Necrocarcinoida Förster, 1968	<i>Necrocarcinus</i> sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
	<i>Pseudonecrocarcinus</i> ? sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
	<i>Paranecrocarcinus</i> ? sp.	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
Etyoidea Guinot and Tavares, 2001	<i>Etyxanthosia fossa</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022
	<i>Etyus tresgalloi</i>	Prodelta	Basque-Cantabrian Basin	Patrocinio (Aptian)	Ossó and Moreno-Bedmar, 2020
Torynommoidea Glaessner, 1980	? <i>Withersella</i>	Sponge meadows?	Salou-Garraff basins	Margas de Vallcarca (Aptian)	Ossó et al., 2022

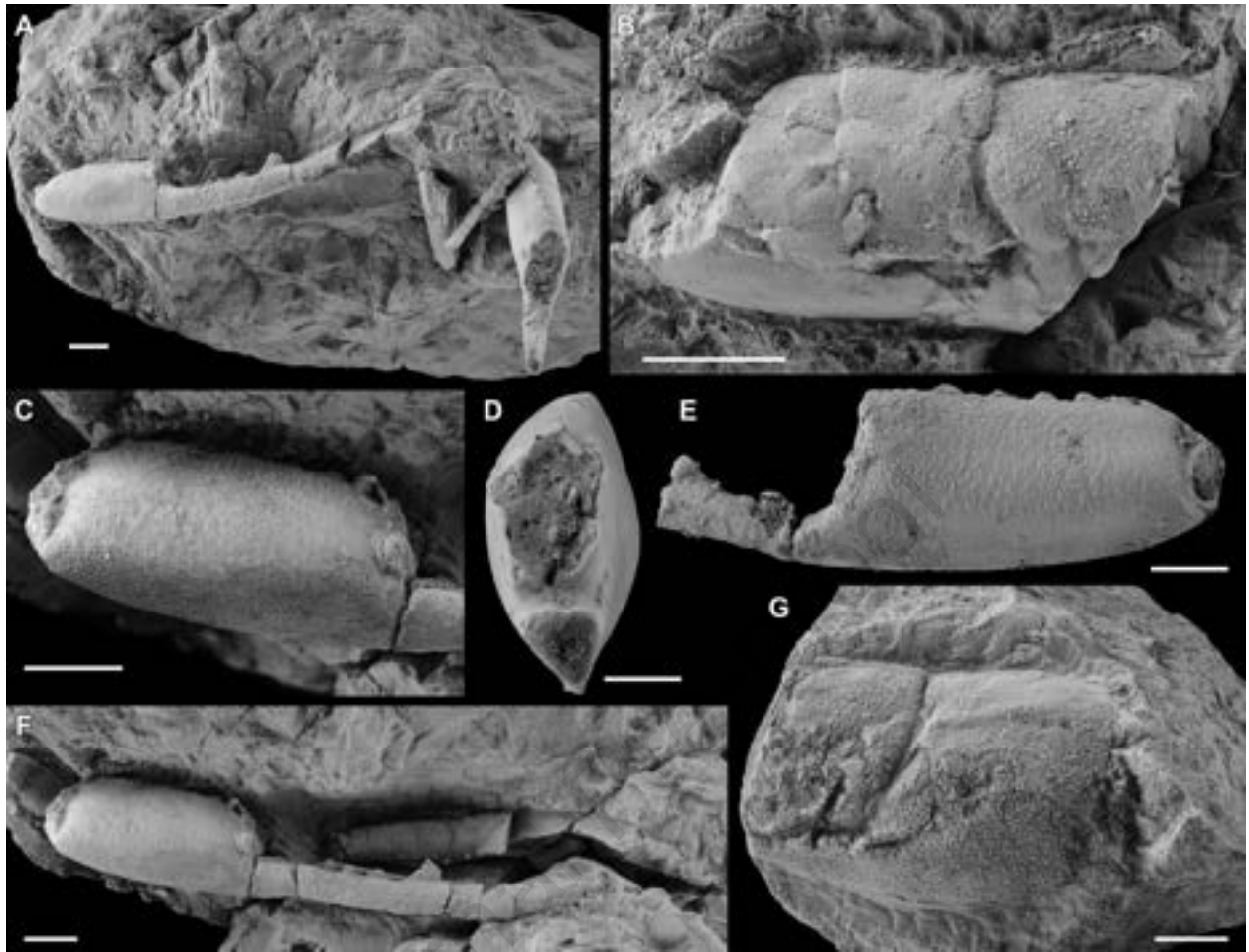


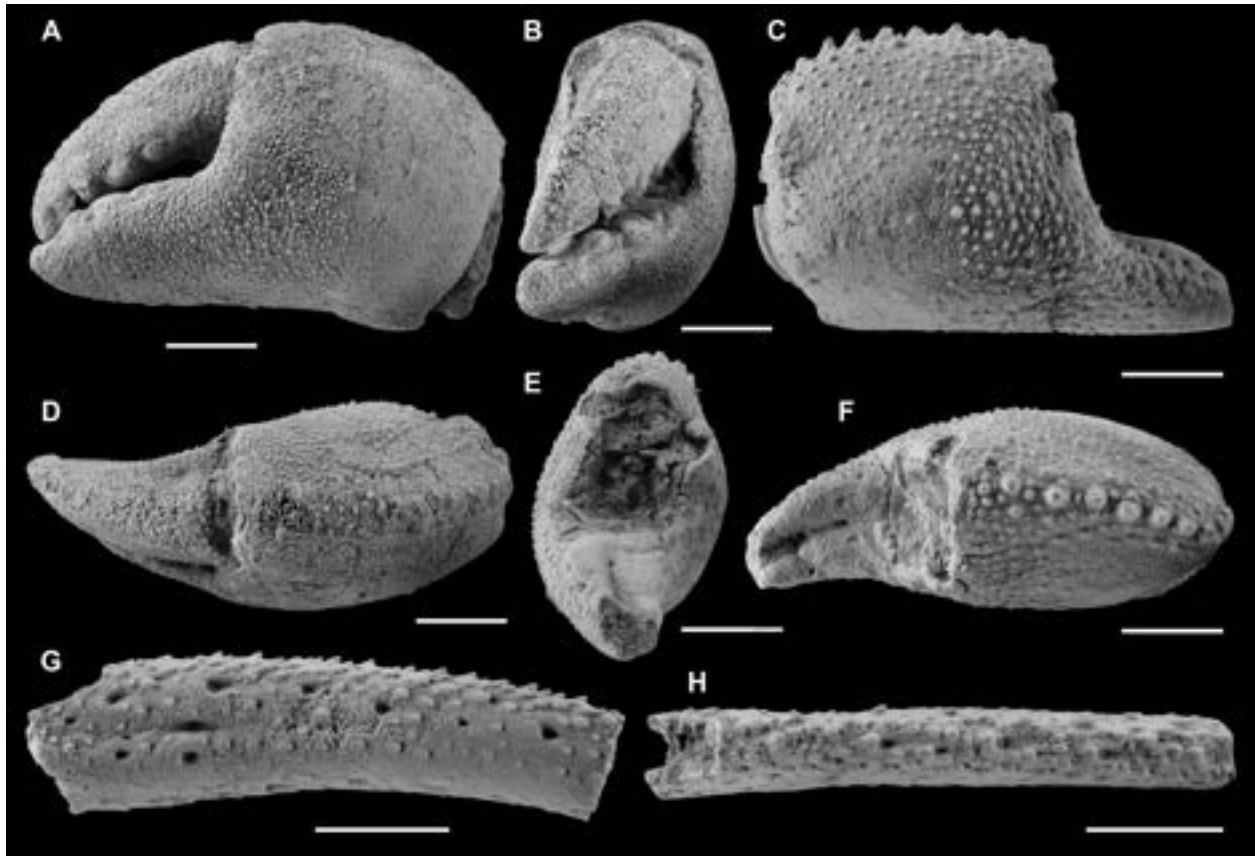




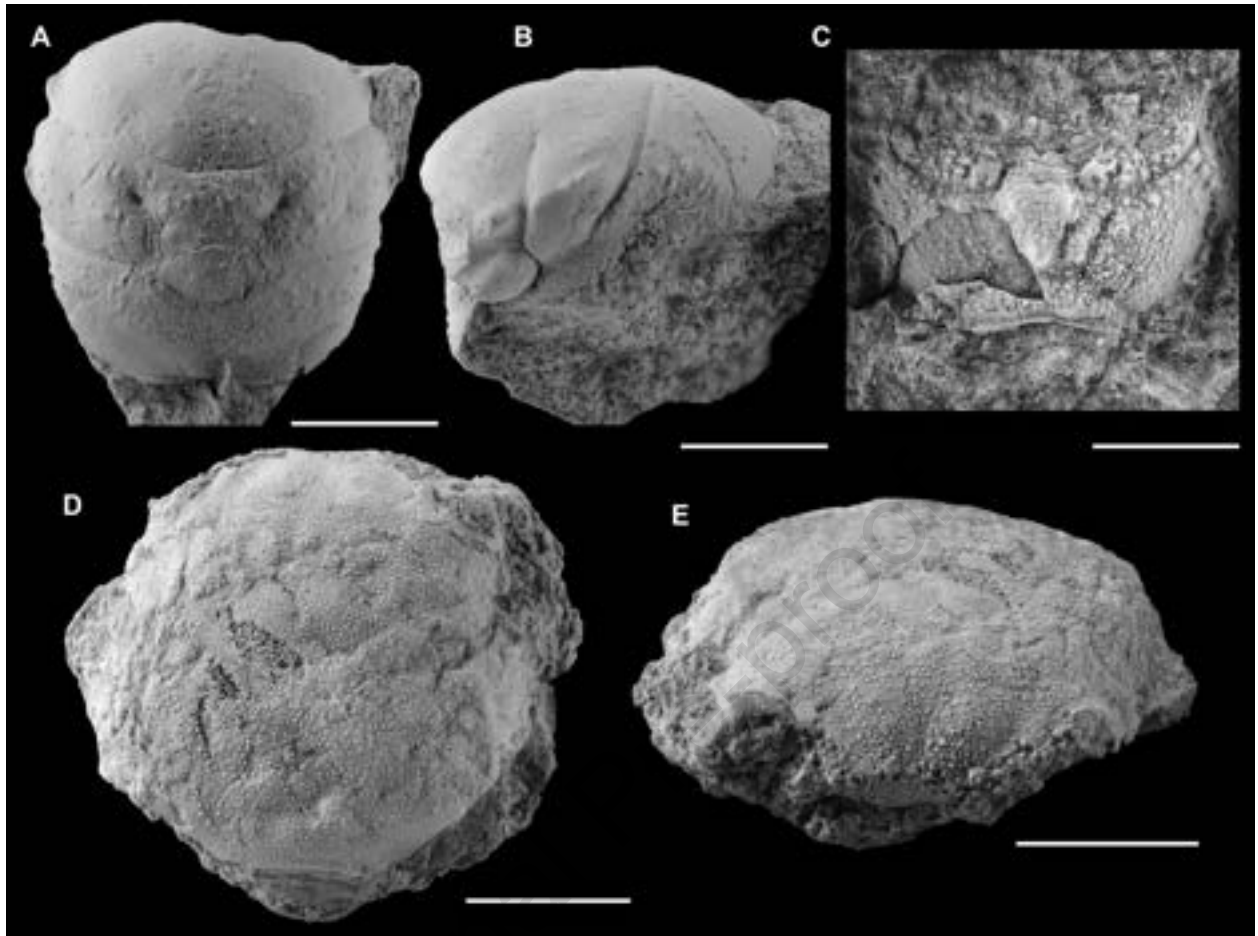








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Author statement

S.Z., A.G.P. and M.A. conceived the study. S.Z., F.A.F., A.G.P. and J.M.G. collected the material. F.A.F. and S.Z. did the systematic work. J.M.B. studied the ammonites. All authors drafted the manuscript and analyzed and interpreted data. All authors critically revised the manuscript, gave final approval for publication and agree to be held accountable for the work performed therein.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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