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1 **A Palaeozoic open shelf benthic assemblage in a protected marine environment**

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17

18

19 ABSTRACT

20

21 A Late Ordovician benthic assemblage containing trilobites (*Colpocoryphe*, *Onnia*)
22 and diploporid echinoderms (*Aristocystites*) taxa that are usually typical of open shelf
23 environments is preserved in protected marine settings in the lower part of the Kermeur
24 Formation (Armorican Massif, NW France). A facies analysis carried out on the Veryac'h
25 section (Crozon Peninsula) allows identification of four sedimentary facies (SF), ranging from

26 the bay/lagoon domain (SF1 and SF2) to the back-barrier (SF3) and barrier (SF4) domains. A
27 benthic fauna comprising trilobites, brachiopods and diploporids is found in the SF1 and SF2.
28 In SF1, fossils are randomly scattered in sediments (taphofacies 1, TF1) showing two
29 different preservation stages: TF1a with complete articulated skeletons and TF1b with
30 disarticulated shells. These two preservation stages can be related either to the different
31 modes of life of the taxa (i.e., recumbent, burrowing or nektobenthic) or to a composite
32 assemblage with both autochthonous and allochthonous taxa. In this benthic assemblage,
33 some trilobites and echinoderms taxa are mostly preserved either as complete exoskeletons
34 and exuviae (*Colpocoryphe grandis*) or complete thecae (*Aristocystites* sp.), indicating an
35 autochthonous origin. These taxa are usually found in low-energy open shelf settings. Their
36 occurrence in a protected environment results from the combination of both allocyclic factors
37 (i.e., change in sea level) and local conditions (i.e., shelf morphology, environmental
38 conditions). Indeed, the lower part of the Kermeur Formation was deposited during a
39 transgressive phase following a significant sea-level fall (Sandbian–Katian boundary). During
40 the transgressive phase, barrier-lagoon systems were formed on the flat surface inherited from
41 the sandbian shelf. Under non-restricted ecological conditions (i.e., normal oxygenation and
42 salinity) in the protected settings, the new ecological niches were suitable for benthic
43 organisms accustomed to open shelf environments. The settlement of these open shelf benthic
44 species in coastal and protected environments may represent an offshore–onshore expansion,
45 contrary to that described in the onshore–offshore diversification model of Phanerozoic shelf
46 communities (Jablonski et al., 1983 ; Sepkovski, 1991).

47
48 *Keywords:* Barrier-lagoon environments; taphonomy; facies analysis; Katian (Ordovician);
49 Armorican Massif.

50

51 **1. Introduction**

52

53 Numerous studies have been carried out on Ordovician shelf successions belonging to
54 the northern Gondwana margin in order to explain the relationships between benthic fauna
55 distributions and related depositional environments. Results from these studies have led to the
56 recognition of "biofacies" or benthic associations along an open shelf profile, especially for
57 trilobites (Fortey and Owens, 1978, 1987; Henry and Destombes, 1991; Vidal, 1998; Zhou
58 Zhiyi et al. 2001, 2003; Turvey, 2005) and brachiopods (Villas, 1985, 1992, 1995; Havlíček,
59 1989; Havlíček et al., 1987). These biofacies are valuable tools for palaeogeographic
60 reconstructions (Fortey and Owens, 1987; Henry, 1989; Henry et al. 1997; Fortey and Cocks,
61 2003).

62 The present work shows that, in some particular contexts, benthic taxa that are
63 generally associated with open shelf environments can also be associated with marine
64 protected depositional settings. The Upper Ordovician succession studied here is located on
65 the Crozon Peninsula (Armorican Massif, western France). Sediments were laid down during
66 the sea-level rise following the major sea-level fall recorded in the *foliaceus* graptolite zone
67 (Sandbian–Katian boundary; Webby et al., 2004). This regressive event is recognized in
68 several areas of the northern Gondwana Domain, from the Armorican Massif (Robardet,
69 1981) to the Iberian Domain (Portugal: Henry et al., 1974; Paris, 1979, 1981; Spain: Villas,
70 1992), as well as the Algerian Sahara and central Morocco (Videt et al., 2010) and other
71 palaeogeographic domains such as Baltoscandia (Nielsen, 2004) and Laurentia (Turinian–
72 Chatfieldian boundary: Ross and Ross, 1992). In the northern Gondwana Domain, the fall and
73 successive rise of the sea-level coincided with a decline in the endemism of benthic fauna
74 and the arrival of taxa from Avalonia, Laurentia and Baltica (Havlíček, 1989; Cocks and
75 Fortey, 1990; Young, 1990). In the Armorican Massif, the transgressive phase led to the
76 deposition of nearshore successions yielding a poorly diversified benthic fauna (Robardet et

77 al., 1994).

78 The aims of the present study are to (1) identify the depositional environments of these
79 successions, (2) investigate the origin, either autochthonous or allochthonous, of the benthic
80 taxa, and (3) understand the mode of settlement of organisms during the transgressive phase.
81 The analysed successions comprise the upper part of the Postolonnec Formation (Sandbian)
82 and the lower part of the Kermeur Formation (Katian). An integrated approach involving
83 facies analyses combined with palaeontological and taphonomic observations (e.g., faunal
84 content and preservation mode) is carried out.

85

86 **2. Geological context**

87

88 In the Armorican Massif (Fig. 1), the lower Palaeozoic terrains are subdivided into
89 two palaeobiogeographic units: the Medio-North Armorican Domain (MNAD) and the South
90 Armorican Domain (SAD). In the MNAD, several transgressive-regressive cycles occurred in
91 the Ordovician (Paris et al., 1999; Paris et al., 2007; Dabard et al., 2009). The first
92 transgressive phase began in the Floian (Early Ordovician) with the deposition of continental
93 and/or coastal plain facies, and then several cycles succeeded each other in the overlying silty
94 clayey formations until the late Sandbian regressive phase. In the Crozon Peninsula (Fig. 2),
95 the Floian is characterized by thick sandstones of the Grès Armoricain Formation that were
96 deposited in nearshore settings (Durand, 1985). These sandstones are overlain by silty-clayey
97 shelf facies of the Postolonnec Formation, which is Dapingian to Sandbian in age (Paris,
98 1990). Then, the clastic sedimentation continued into the Katian with micaceous sandstones,
99 quartz-arenites and mudstones of the Kermeur Formation (90 to 450 m thick; Plusquellec et
100 al., 1999). In the studied area, this formation is overlain by the Cosquer Formation, dated as
101 Hirnantian (Bourahrouh, 2002), and interpreted as glacio-marine deposits (Hamoumi et al.,

102 1981). The Postolonnec, Kermeur and Cosquer formations were deposited under stable
103 platform conditions and were affected by weak deformation (Rolet et al., 1986; Darboux,
104 1991) and low-grade metamorphism (Paradis, 1981) during the Late Devonian–Early
105 Carboniferous.

106 The diversity of the benthic fauna is variable in these Ordovician sediments. The
107 Postolonnec Formation yields numerous and well-known macrofossil assemblages (Mélou
108 and Plusquellec, 1975a) comprising trilobites (Henry, 1980), brachiopods (Botquelen and
109 Mélou, 2007), bivalves (Babin, 1966), ostracods (Vannier, 1986a, 1986b), graptolites
110 (Philippot, 1950; Henry et al., 1976), echinoderms (Chauvel, 1941; Chauvel and Nion, 1969)
111 and gastropods. This diversity is reduced to only a few species in the overlying Kermeur
112 Formation, including brachiopods and trilobites (trinucleids and dalmanitids; Henry, 1980)
113 that are reported only from the upper part of the formation. The lower part is characterized by
114 abundant bioturbation with few brachiopods and echinoderm plates (Mélou and Plusquellec,
115 1975a, 1975b, 1980). New material sampled by the authors reveals a higher benthic diversity
116 than previously known.

117

118 **3. Stratigraphic context**

119

120 The upper part of the Postolonnec Formation (Fig. 3) consists of clayey silty facies
121 containing sandy beds with hummocky cross-stratifications or siliceous and/or phosphatic
122 concretion-bearing beds and shellbeds. It was deposited in a shelf environment dominated by
123 storm wave action, between the median part of the inner shelf and the outer shelf (Loi et al.,
124 1999; Loi and Dabard, 2002; Dabard et al., 2007). The bioturbation structures are small and
125 primarily represented by *Planolites*. Macrofaunas are either randomly dispersed in the clayey
126 siltstones or concentrated in shellbeds. Two types of shellbeds *sensu* Botquelen et al. (2004)

127 can be distinguished: (1) type A, 1 to 5 mm thick, lenticular and made up of a single coquina
128 level; and (2) type B, up to 20 cm thick, continuous and composed of several superposed and
129 amalgamated coquina levels. Trilobites (*Marrolithus bureaui*) and chitinozoans
130 (*Lagenochitina ponceti*, *L. deunffi* and *L. dalbyensis* biozones; Paris, 1990; Paris et al., 1999)
131 yield a Sandbian age for the upper part of the Postolonnec Formation.

132 The Kermeur Formation overlies the Postolonnec Formation without apparent angular
133 discordance at the outcrop scale. The lower bounding surface is sharp and erosional. It is
134 overlain by a conglomeratic unit, 40 to 70 cm thick, containing numerous ferruginous (Fe)
135 oolites and phosphatic (P) pebbles (Deunff, 1958; Henry et al., 1974; Paris, 1981). The
136 chitinozoans present in the conglomerate matrix belong to the *Euconochitina tanvillensis*
137 biozone (Paris, 1981; Bourahrouh, 2002) from the lower Katian (Webby et al., 2004).
138 Different chitinozoan assemblages of Sandbian age have been observed in the P-pebbles
139 (Henry et al., 1974; Paris, 1981); some belong to the *L. deunffi* biozone and others to the *L.*
140 *dalbyensis* biozone. These microfauna data indicate a partial reworking of the upper part of
141 the Postolonnec Formation linked to the late Sandbian–early Katian sea-level fall (Paris and
142 Le Hérissé, 1992).

143

144 **4. Material and Methods**

145

146 The Postolonnec and Kermeur formations crop out in the Crozon Peninsula along the
147 Mort-Anglaise, Veryac'h and Poul sections (Fig. 1). This study was carried out at the
148 Veryac'h beach, where these formations are both continuous and exposed in the sea-cliff. The
149 high quality of exposure allows a facies analysis to be performed, including logging at the
150 1/40 scale. At the same time, palaeontological material was collected in the Kermeur
151 Formation by excavation favoured by recent cliff-slides. Although macrofossils are rare and

152 scattered in these facies, about 90 specimens were collected. The diversity of the collected
153 samples is similar to that obtained by amateurs over a period of a several years (M. Le Duff,
154 personal communication, 2005). All specimens are housed in collections at the Geology
155 Department at Brest University (prefix LPB), France. As most of the collected taxa have been
156 previously described by Henry (1980) and Botquelen and Mélou (2007), only a few species
157 are briefly discussed here at the end of this paper.

158

159 **5. Facies analysis**

160

161 Five sedimentary facies, SF0 to SF4, occur in the lower part of the Kermeur
162 Formation.

163

164 *5.1. Description*

165

166 SF0: the basal conglomeratic facies contains Fe-oolites (mainly chamosite) and
167 phosphatic pebbles (P-pebbles) in a bioturbated clay-sandy matrix made up of detrital quartz
168 grains (150 to 250 μm in size) and phyllosilicates. The size of the Fe-oolites varies between
169 250 and 700 μm . They are deformed with a maximum elongation direction parallel to the
170 bedding and some of them are broken. The P-pebbles, 0.1 to 2 cm in size, show an ovoid
171 shape and display various compositions; some consist of microcrystalline apatite with detrital
172 silt-sized grains of quartz and phyllosilicates and others contain coquinas with P-cement.

173 SF1: this bioturbated facies overlies SF0. It consists of beds with a constant thickness
174 of approximately 1 m, made up of fine- to medium-grained clayey sandstones of a dark-grey
175 colour ("dirty" sandstone); the argillaceous matrix makes up about 50% of the rock
176 (Hamoumi, 1981). These sandstones are rich in quartz and contain micas and organic matter.

177 They are intensely bioturbated and the primary sedimentary structures have been destroyed.
178 The bioturbation is less abundant in places, which leads to the preservation of some sandy
179 layers (Fig. 4 A), 1 to 3 cm thick with flaser bedding, and some thin layers of black mudstone
180 (approximately 1 cm thick). The well-diversified trace fossils are large (up to 3 cm in
181 diameter). Most of them belong to the ethological categories of domichnia and equilibrichnia,
182 (e.g., *Bifungites* and *Arenicolites*; Mélou and Plusquellec, 1975b), as well as some spiral
183 systems (Fig. 4 B). In this facies, the fauna is scattered and scarce with the occurrence of
184 some trilobites, diploporid echinoderms and very rarely, brachiopods. Some trilobite
185 exoskeletons and diploporid thecae that are still articulated are preserved (see part 6.1).

186 SF2: this facies forms beds, 0.5 to 1 m thick, made up of intensively bioturbated sandy
187 mudstones. The matrix (about 60% of the total rock) and organic matter are more abundant
188 here than in SF1. Locally, the bioturbation is less abundant and primary structures can be
189 observed. They are represented by thin (a few centimetres thick) black mudstones layers (Fig.
190 4 D) that can extend laterally over several decimetres and also by roughly laminated clayey-
191 sandy beds with diffuse basal and top surfaces. Flaser bedding also occurs. The bioturbation,
192 which is less diversified than in SF1, is dominated by numerous equilibrichnia structures
193 (*Teichichnus*, 0.1 to 1 cm in width) that are distributed along the stratification (Fig. 4 C). This
194 facies yields brachiopods, diploporids and only a few trilobite sclerites. Although the fauna is
195 generally disarticulated and scattered, some rare lenticular shellbeds, made up of a single
196 coquina layer, are present.

197 SF3: the bioturbated heterolithic facies is made up of well-sorted fine- to medium-
198 grained sandy beds, several centimetres to 1 dm thick, that alternate with lenticular to flaser
199 bedding (Figs. 5 A, C, D, E, F, G). The sandy beds show planar to subhorizontal laminations
200 with very flattened hummocky cross-stratification (HCS) locally. The basal surface of the
201 sandy beds is slightly erosive (Figs. 5 B, C) and preserves the crawling structures produced in

202 the underlying clay. Locally, weakly incised gutters and furrows are observed (Fig. 5 B). 2D
203 current ripples (with a wavelength of several centimetres to 1 dm) and wave ripples
204 (sometimes at the top of the sandy beds with HCS) are present in the lenticular to flaser
205 bedding (Figs. 5 A, D, E). Current ripples showing opposite palaeocurrent directions (e.g.,
206 Fig. 5 E) and clay drapes within ripples (Figs. 5 A, D, E, G) are visible. Some wave ripples
207 have flattened crests. Bioturbation is abundant but the stratification is preserved. It mainly
208 consists of crawling structures (repichnia) that are preserved as hyporeliefs at the bases of the
209 sandstone beds as well as numerous burrows (*Skolithos*) filled with clayey material (Figs. 5
210 F). This facies is devoid of body fossils.

211 SF4: this sandstone facies consists of medium- to coarse-grained and well-sorted
212 quartz-arenite beds (1 dm to 1 m thick) with planar and low-angle laminations (Figs. 6 A, B).
213 The beds contain numerous concave scours, draped by thin silty to fine-grained sandy beds,
214 with a lateral extension from 1 to several metres (Figs. 6 B, C). Swaley cross-stratification
215 (SCS) is observed locally (Fig. 6 D). The top surfaces of the sandy beds are flat and smooth,
216 but wave ripples (wavelength of about 1 dm) occur within some sub-circular depressions
217 (about 1 to 3 m in diameter; Fig. 5 H). At the outcrop scale, some beds pass laterally into
218 layers with a flattened HCS belonging to SF3 (Fig. 6 C). Bioturbation (mainly *Skolithos*) is
219 very sparsely developed. This facies is devoid of body fossils.

220

221 5.2. Interpretation

222

223 The P-pebbles of SF0 were provided from the underlying deposits. The late Sandbian
224 sea-level fall led to a partial emergence of the shelf as well as the erosion of the nodule-
225 bearing clayey siltstones occurring in the upper part of the Postolonnec Formation. During
226 this regressive phase, the P-nodules were concentrated by winnowing and made up of pebbles

227 of lag deposits. Then, during the transgressive phase, these pebbles were integrated into the
228 first Katian sediments.

229 In SF1 and SF2, the sandy fraction is relatively abundant (the mean values range from
230 40 to 50%), however no storm-related structures (e.g., HCS, silty laminae, coquina storm bed;
231 Aigner, 1985; Botquelen et al., 2004) have been observed in the rare non-bioturbated
232 intervals. Rather, the mudstone layers and flaser bedding in these intervals reflect alternating
233 periods of quiescence and low-energy currents. Furthermore, some skeletons (carapaces or
234 thecae) preserved in SF1 are still articulated or slightly dislocated (see part 6.1). These
235 characteristics, together with the intense bioturbation affecting the deposits as a whole, are
236 incompatible with sudden supply of sediments, yet imply low depositional rates with regular
237 inputs. All these features argue against storm-dominated sedimentation in an open shelf
238 setting, as can be observed in the underlying Postolonnec Formation (Dabard et al., 2007).
239 Instead, they suggest a restricted environment, protected from storm influences, where sandy
240 inputs are related to unidirectional currents or fair-weather waves.

241 HCS and SCS occurring in SF3 and SF4 are structures related to storm wave action
242 (Leckie and Walker, 1982; Aigner, 1985; Brenchley et al., 1986). SCS (SF4) have only been
243 described from shoreface environments (Leckie and Walker, 1982), whereas HCS (SF3)
244 occur in spillover lobes in coastal lagoons (Shirai and Tada, 2000), open-coast tidal flats
245 (Yang et al., 2005, 2006) and on open storm-wave-dominated shelves from the shoreface to
246 the median part of the inner shelf (Dott and Bourgeois, 1982; Aigner, 1985; Guillocheau and
247 Hoffert, 1988). In SF3, the wave ripples at the top of the sandy beds with HCS rule out inner
248 shelf settings and are in agreement with nearshore settings. On the other hand, the occurrence
249 of 2D ripples in lenticular to flaser beddings (SF3) and the preservation of clay drapes within
250 current ripples imply alternations of periods of current activity and periods of quiescence.
251 Such features are generally associated with environments submitted to tidal and/or fair-

252 weather wave processes (Reineck and Wunderlich, 1968; Sultan and Plink-Björklund, 2006;
253 Billeaud et al., 2007). A tidal influence is consistent with the opposite current directions (Figs.
254 5 E) observed in SF3. Moreover, it explains the preservation of wave ripples in sub-circular
255 depressions (SF4), which can be interpreted as puddles linked to a tidally-driven emergence in
256 a shoreface barrier. In these two facies, the association of storm-related structures with tidal-
257 related structures suggests a barrier context (e.g., Boyd et al., 1992; Dalrymple et al., 1992;
258 Cattaneo and Steel, 2003), where SF4 is interpreted as a barrier facies and SF3 as a back-
259 barrier facies (see the model in Fig. 7). The sandy beds, with planar and subhorizontal
260 laminations and very flattened HCS associated with small wave ripples (SF3), represent
261 deposits laid down when storm waves cut through and spilled over the barrier. These last
262 processes are emphasized in SF4 by concave scours draped by silt and fine-grained sand (Fig.
263 6 B). SF1 and SF2, deposited in an environment protected from storm influences, thus
264 correspond to bay/lagoon deposits (e.g., MacCarthy, 1987; Plint, 1988). In these facies, sandy
265 particles were supplied by continental areas (fluvial system) and barriers (spillover lobes)
266 and were secondarily reworked by low-energy currents in the lagoon. The central location of
267 SF2 in the protected setting is supported by (1) the higher clay/sand ratio, which is consistent
268 with an environment far from a direct continental influence and (2) the occurrence of
269 disarticulated shells and rare lenticular shellbeds, which provide evidence of winnowings on
270 the bottom. The lack of evidence for restrictive conditions (e.g., hypersaline or anoxic
271 conditions) suggests extensive connections with an open marine environment, probably linked
272 to the discontinuity of the barrier and/or to submerged barrier portions. No indication of depth
273 (e.g., desiccation marks, wave ripples) has been found in SF1 and SF2. Bioturbation occurring
274 in the successive facies (SF1: *Bifungites*, *Arenicolites*; SF2: *Teichichnus*; SF3 and SF4:
275 *Skolithos*) is consistent with such depositional settings (e.g., marine lagoons and open bays;
276 Ekdale et al., 1984; Frey et al., 1990; Mangano and Buatois, 2004; MacEachern et al., 2007).

277

278 5.3. Stratigraphic evolution

279

280 The sharp-based contact and reworking of the underlying deposits characterize the
281 transition between the Postolonnec and Kermeur formations. The lack of regressive facies is
282 in agreement with a rapid and/or forced regression that led to the emersion and erosion of a
283 segment of the shelf. Then, the first transgressive deposits were laid down during the Katian
284 (*E. tanvillensis* biozone) on a flat surface inherited from the Sandbian shelf (the transgressive
285 surface, TS in Fig. 8). This type of gently sloping shoreface-shelf profile allows the formation
286 of coastal barriers (e.g., Beets et al., 2003; Dillenburg et al., 2004; Loi et al., 2010), which are
287 built up from wave transport and sand accumulation along the coastline. In the Kermeur
288 Formation, the basal transgressive deposits are represented by the bioturbated SF0, SF1 and
289 SF2 laid down on a bay/lagoon setting. The superposition of back-barrier (SF3) and barrier
290 sediments (SF4) indicates a landward barrier migration. This vertical facies evolution, from
291 protected marine to open marine environments, is integrated into a transgressive evolution
292 associated with a long-term sea-level rise (e.g., Heward, 1981; MacCarthy, 1987; Plint, 1988;
293 Swift et al., 1991; Cattaneo and Steel, 2003; Yang et al., 2006). Higher up in the formation,
294 several oscillations between protected marine and shoreface barrier environments can be
295 identified (Fig. 3), gradually leading to an open marine environment later in the Katian
296 (*Belonechitina robusta* biozone; Gorini et al., 2008).

297

298 6. Faunal assemblages and taphofacies

299

300 6.1. Description

301

302 In the lower part of the Kermeur Formation, fossils are only present in SF1 and SF2.

303 Two different taphofacies are recognized, TF1 and TF2.

304 TF1: preserved in SF1, the fossil assemblage of this taphofacies (Fig. 9 A) includes
305 trilobites, diploporids (echinoderms) and very rarely, brachiopods. The trilobites are assigned
306 to *Colpocoryphe grandis*, *Onnia seunesi* ?, *Zeliskella (Zeliskella) sp.*, *Phacopidina sp.* and
307 *Eccoptochile sp.* The diploporids are assigned to *Aristocystites sp.*, and the brachiopods to
308 *Drabovia pentagonomya* (see below for systematic assignments; Botquelen and Mélou, 2007,
309 for the brachiopods). The bioclasts are isolated and randomly dispersed throughout the
310 thickness interval of SF1, without any ordered arrangement in the bedding plane and
311 unrelated to sedimentary events. In this taphofacies, two different preservation stages (or
312 taphonomic grades) for the fossils are distinguished, denoted as TF1a and TF1b, accounting
313 for 60% and 40% of the material, respectively (out of a total of 46 specimens).

314 In the first grade (Fig. 9 A, TF1a), skeletons belonging to three taxonomic groups are
315 preserved with different skeletal parts that are still articulated, each of them occurring as a
316 single species. The trilobites include numerous complete exoskeletons and *in situ* exuviae
317 (most of the specimens identified as moults correspond to a joined thorax and pygidium with
318 overturned librigenae in the immediate vicinity; Figs. 10 A, B); this material is all assigned to
319 *Colpocoryphe grandis*. The diploporids (Fig. 11), identified as *Aristocystites sp.*, are
320 preserved as scattered but complete thecae and a few isolated thecal plates. The brachiopods
321 are represented by very scarce articulated *Drabovia pentagonomya* valves. These fossils are
322 all preserved as internal and external moulds, without abrasion or bioerosion marks.

323 The second grade of this taphofacies (Fig. 9 A, TF1b) is characterized by a high degree
324 of shell disarticulation, which are nevertheless always randomly dispersed; most of the
325 material is composed of trilobite exoskeleton fragments, including trinucleids (*Onnia seunesi*
326 ?, Figs. 10 E–H) and dalmanitids (*Zeliskella (Zeliskella) sp.*, Fig. 10 G; *Phacopidina sp.*, Fig.

327 10 F), along with less abundant taxa such as *Eccoptochile* sp. (Fig. 10 I), as well as scarce
328 brachiopod valves (*Drabovia pentagonomya*, Figs. 10 L–M). These taxa are preserved only as
329 isolated exoskeletal parts, and some specimens were broken before burial.

330 In summary, *Drabovia* occurs in both grades of this taphofacies, and *Aristocystites* and
331 *Colpocoryphe* are mostly preserved as complete remains with different parts of their skeletons
332 in articulated or slightly dislocated arrangements (Fig. 9 A; TF1a). *Onnia*, *Phacopidina*,
333 *Zeliskella* and *Eccoptochile* are always disarticulated and/or fragmented (Fig. 9 A; TF1b).

334 TF2: preserved in SF2, the faunal assemblage of this taphofacies (Fig. 9 B) consists
335 mainly of brachiopod valves, diploporid thecal plates (*Aristocystites* sp.) and very rarely,
336 trilobite sclerites (Calymenidae, consistent with *Colpocoryphe grandis*). The brachiopods
337 include three species: *Drabovia pentagonomya*, which is clearly predominant, *Tafilaltia*
338 *destombesi* and *Triplexia* cf. *T. simplex*. This taphofacies is characterized by the preservation
339 of fossils as lenticular shell concentrations on a single bedding plane. The lateral extent of
340 these lenses varies from 1 dm to 1 m and their thickness can reach 3 to 5 cm. These lenses
341 have a slightly erosive basal surface and consist of either a single thin coquina layer or
342 scattered shells in a silty-sandy matrix. Bioclasts are preserved as internal and external
343 moulds. All the specimens are disarticulated with a fragmentation rate of about 40% (based
344 on 44 specimens), showing slight differences from one species to another (only the valves for
345 which more than one half of the specimen is preserved were taken into account). No erosion,
346 bioerosion or abrasion mark was observed on these fossils; however, their preservation as
347 internal and external moulds in medium-grained sandstones makes it difficult to observe these
348 features.

349

350 6.2. Interpretation

351

352 In the first bioturbated facies (SF1), the two taphonomic grades are associated but
353 show two different preservation stages: TF1a with complete skeletons in an articulated
354 position and TF1b with disarticulated shells. Grade TF1a contains trilobite exuviae preserved
355 *in situ* and shows a very low degree of disarticulation, even when the skeletons are composed
356 of numerous easily disconnected skeletal parts or plates. The physical integrity of arthropod
357 carapaces belonging to grade TF1a indicates that the sediments were not disturbed (Plotnick,
358 1986; Speyer, 1991). These features, along with the scattering of fossils in the sediments,
359 provide strong evidence that these fossils are preserved in their life environment. The
360 assemblage of this grade is made up of *Colpocoryphe*, a trilobite burrower with
361 predator/scavenger feeding habits (Hammann, 1983; Fortey and Owens, 1999a), and
362 *Aristocystites*, a recumbent suspension feeder (Parsley, 1990). After death, the pre-burial
363 position of *Colpocoryphe* provided protection from disturbance and disarticulation. A similar
364 taphonomic result is observed for *Aristocystites*, whose complete thecae occur in the same
365 habitat. This diploporid displayed a reclining mode of life on the sea-floor and its preservation
366 was probably favoured by regular sediment inputs.

367 Conversely, grade TF1b is characterized by shell disarticulation. This cannot be linked
368 to storm reworking because the shells are scattered in the sediments and coquina storm beds
369 have not been observed. Two hypotheses can be proposed to explain this grade. The first one
370 considers the modes of life. The disarticulated exoskeletons belong to epibenthic trilobites,
371 (Fortey and Owens, 1999a, 1999b) including *Onnia*, *Phacopidina* and *Z. (Zeliskella)*, and
372 very rarely, epifaunal brachiopod (*Drabovia*). The mode of life of these taxa exposes them to
373 post-mortem disarticulation by scavengers, bioturbation and bacterial decomposition before
374 burial. In some cases, the high proportion of disarticulation may be related to the morphology
375 of the exoskeletons. For example, the distal tips of the trinucleid thoracic segments (such as in
376 the genus *Onnia*) do not exhibit imbricated structures (Fortey and Owens, 1999b). These

377 trinucleid morphological characteristics favour rapid disarticulation compared to other
378 trilobite families. Thus, the two taphonomic grades (TF1a and TF1b) of the benthic
379 assemblage in SF1 can be interpreted as being related to the different modes of life of the
380 taxa. A second hypothesis can be proposed to explain the occurrence of these disarticulated
381 and partially fragmented shells. They could be allochthonous and transported by currents from
382 open marine settings. In that case, these shells would be distributed in both fossiliferous
383 facies, yet they were not observed in SF2; their relative scarcity can explain the lack of data in
384 this facies. In this second hypothesis, the benthic assemblage of TF1 corresponds to a
385 composite assemblage with allochthonous and autochthonous species.

386 In TF2, the coquinas are disarticulated and accumulated in lenticular bodies with a
387 slightly erosive basal surface. This arrangement can be related to type A-shellbeds, as
388 described by Botquelen et al. (2004), produced by the winnowing of the water-sediment
389 interface that reworks the finer particles and leads to a concentration of shell debris. Two
390 hypotheses can be proposed for TF2: 1) it corresponds to either a within-habitat time-
391 averaged assemblage (*sensu* Walker and Bambach, 1971; Kidwell, 1998), considering the
392 evidence for a low energy setting in this facies, or 2) to a para-autochthonous to allochthonous
393 assemblage, considering the high degree of disarticulated shells and their accumulation in
394 lenticular bodies. It is difficult to assess the degree of transport, but the interpretation of SF2
395 is compatible with limited reworking. In this case, the fauna could have drifted from more
396 open environments such as inlets.

397 There are other differences between the faunal assemblages of the two taphofacies.
398 Some taxa, although occurring in TF2, are either absent from TF1 (*Triplesia* and *Tafilaltia*) or
399 significantly less abundant (*Drabovia*). These differences argue for a different origin for these
400 assemblages, such as two different biotopes. This is especially relevant for the brachiopods,
401 the abundance of which in SF2 could be linked to the substrate composition. Indeed, the

402 bioturbated sandy mudstones facies (SF2) could represent loose ground substrate, which is
403 more favourable for epifaunal soft-substrate brachiopods than the bioturbated clayey
404 sandstones facies (SF1). The latter facies is probably more closely comparable to soft ground
405 in the terminology proposed by Goldring (1995).

406

407 **7. Discussion and conclusion**

408

409 This study reveals a higher benthic diversity than that described by previous authors in
410 the lower part of the Kermeur Formation, especially for trilobites, which have not been
411 reported before. According to the benthic association models proposed for the Ordovician
412 (Fortey and Owens, 1978, 1987; Henry, 1989; Vidal, 1998), the taxonomic composition and
413 diversity of the complete assemblage (TF1) implies open shelf settings. Assuming that this is
414 a composite assemblage, the very low diversity of the autochthonous fraction (i.e.,
415 *Colpocoryphe* and *Aristocystites*) could be consistent with a nearshore assemblage (Henry,
416 1989; Westrop and Adrain, 1998; Turvey, 2005; Botting and Muir, 2008) but not with this
417 taxonomic composition. In fact, the genus *Colpocoryphe*, which is numerically dominant in
418 grade TF1a, usually occurs in relatively deep open shelf environments characterized by fine-
419 grained sediments (Hammann, 1983; Vidal, 1998). Certain species with reduced eyes, such as
420 *Colpocoryphe taylorum* or *C. inopinata*, were even adapted to the more distal environments
421 of the outer shelf (Fortey and Owens, 1987; Henry, 1989). On the Crozon Peninsula, the
422 species *C. grandis* is present in the upper part of the Postolonnec Formation (Henry, 1980) in
423 silty clayey facies that are related to a distal shelf environment (i.e., the median part of the
424 inner shelf and the outer shelf; Dabard et al., 2007). Moreover, these trilobites co-occur with
425 *Aristocystites*, a diploporid echinoderm related to low-energy environments in some areas
426 (Parsley, 1990). The other part of the assemblage (grade TF1b), which is either allochthonous

427 or not according to the interpretation, is an epifaunal assemblage dominated by trinucleids
428 (*Onnia*). This association with numerous trinucleids and dalmanitids is reminiscent of the
429 assemblages described from either the upper part of the Postolonnec Formation (*Crozonaspis*
430 *chauveli* faunizone, Veryac'h section in Henry, 1980, p. 232) or the upper part of the Kermeur
431 Formation (*Crozonaspis dujardini* faunizone, Aber section, in Henry, 1980, p. 234). In both
432 cases, the sedimentary facies yielding these assemblages are consistent with distal open shelf
433 environments (Loi and Dabard, 2002; Gorini et al., 2008). The present study shows that, in
434 the Kermeur Formation, these species are present in a bay/lagoon context.

435 This paradox can be explained by a wider range of environmental tolerance (i.e., depth
436 and granulometry) for these taxa, especially for *Colpocoryphe* and *Aristocystites*, and by
437 environmental conditions that were probably similar to those of deeper open environments. In
438 fact, during the early Katian transgression, the construction of a coastal barrier in neashore
439 settings allowed the establishment of turbidity and hydrodynamic conditions that were close
440 to those of deeper open-shelf environments. Moreover, if the barrier was discontinuous or
441 partially submerged, the chemical conditions (i.e., salinity and oxygenation) in the protected
442 area could be similar too. Thus, the formation of lagoon-barrier systems produced new
443 ecological niches available for colonization by organisms accustomed to deeper shelf
444 environments. This colonization may represent an example of offshore–onshore expansion,
445 which is the inverse of the migration described in the onshore–offshore diversification model
446 of Phanerozoic shelf communities (Jablonski et al., 1983; Sepkovski and Sheehan, 1983;
447 Sepkovski and Miller, 1985; Sepkovski, 1991). In this model, new species originate in
448 shallow settings before spreading into deeper environments.

449

450 **8. Systematic palaeontology**

451

452 8.1. *Trilobita*

453

454 Family Calymenidae BURMEISTER, 1843

455 Subfamily Colpocoryphinae HUPÉ, 1955

456 Genus *Colpocoryphe* NOVÁK in PERNER, 1918

457 *Colpocoryphe grandis* (ŠNAJDR, 1956)

458 **Figs. 10 A–D Material:** numerous specimens preserved as internal and external moulds,
459 complete in most cases; only a few were numbered: LPB 14792 to LPB 14799.

460 **Discussion:** the large size of the specimens (8 to 10 cm in length on average, and up to 12
461 cm), the shape of the terminal axial piece of pygidium with lateral expansions, and the large
462 but shallow vincular furrows on pygidial pleurae that become larger forwards, allow this
463 material to be assigned to *Colpocoryphe grandis* (see Henry, 1980). *Colpocoryphe grandis*
464 occurs in the upper part of the Postolonnec Formation and in the lower part of the Kermeur
465 Formation on the Crozon Peninsula, without apparent variation in morphology between these
466 two different formations. In the Kermeur Formation, this taxon occurs as complete
467 exoskeletons and exuviae scattered in SF1, and scarce disarticulated sclerites in lenticular
468 shell concentrations of SF2.

469

470 Family Trinucleidae HAWLE and CORDA, 1847

471 Subfamily Marrolithinae HUGHES, 1971

472 Genus *Onnia* BANCROFT, 1933

473 *Onnia seunesi* ? (KERFORNE, 1900)

474 **Figs. 10 E, H**

475 **Material:** six cephalae, preserved as incomplete internal and external moulds. LPB 14800 to
476 LPB 14805.

477 **Discussion:** in spite of the missing pygidium and thorax, the shape of the fringe and the
478 position of the girder on the lower lamella allow this material to be assigned to the genus
479 *Onnia* (see Ingham, 1974): from the postero-lateral angle, the girder begins between the first
480 and second row of pits, then curves inward and runs between the second and third row of pits.
481 Among the two *Onnia* species described from the Upper Ordovician of the Armorican Massif
482 (see Lebrun, 1994), *O. seunesi* is most closely related to material from the Kermeur
483 Formation, as the latter shows an occipital spine. Nevertheless, the assignment to *Onnia*
484 *seunesi* remains doubtful as all studied specimens are broken. They occur in sedimentary
485 facies SF1 in the lower part of the Kermeur Formation, Veryac'h section.

486

487 Family Dalmanitidae VOGDES, 1890

488 Subfamily Zeliskellinae DELO, 1935

489 Genus *Zeliskella* DELO, 1935

490 *Zeliskella (Zeliskella)* DELO, 1935

491 *Zeliskella (Zeliskella)* sp.

492 **Figs. 10 G–J Material:** one cephalon, preserved as incomplete internal and external moulds,
493 LPB 14806 a, b, and one pygidium, internal mould, LPB 14807.

494 **Discussion:** the shape of the glabella (Fig. 10 G) and glabellar furrows (S2, S3), as well as the
495 size and position of eyes, the pit on the frontal lobe of the glabella, the apparent lack of genal
496 spines and tubercle on the occipital ring, are all characteristics shared with *Z. (Zeliskella)*,
497 particularly the slightly earlier species *renaudae* HENRY, 1980. Nevertheless, the posterior
498 furrow of the cephalon stops laterally in the case of *Z. renaudae* (see Henry, 1980), whereas it
499 continues on the free cheek of the single cephalon collected from the base of the Kermeur
500 Formation. Considering this difference and the lack of some exoskeleton parts (particularly,
501 the anterior part of the cephalon and the end-part of the pygidium), a specific assignment is

502 not possible. Although the internal mould of the pygidium (Fig. 10 J) is poorly preserved, its
503 morphology is compatible with the species cited above. *Zeliskella* (*Zeliskella*) sp. occurs as
504 scarce exoskeleton parts that are isolated and scattered in SF1.

505

506 Subfamily uncertain

507 *Phacopidina* BANCROFT, 1949

508 *Phacopidina* sp.

509 **Fig. 10 F**

510 **Material:** two cephalae preserved as internal moulds, LPB 14808 and 14809 (incomplete).

511 **Discussion:** the glabellar furrows S2 and S3 are shallow and less marked than the S1 furrows;

512 S2 furrows are concave backward in the shape of an arc; the S3 furrows are sinuous and

513 convergent backward. These features, added to the shape of the glabella, the position and size

514 of the eyes, as well as the course of the preocular suture - slightly in front but closely

515 following the frontal lobe of the glabella - are consistent with the genus *Phacopidina*. This

516 material is consistent with *Phacopidina micheli* (TROMELIN, 1877), Llanvirn–Lower

517 Caradoc from the Armorican Massif (Henry, 1980), but more material (especially pygidia) is

518 needed to propose a reliable specific assignment. In the Kermeur Formation, *Phacopidina* sp.

519 occurs as scarce exoskeleton parts that are isolated and scattered in SF1.

520

521 Family Cheiruridae SALTER, 1864

522 Subfamily Eccoptochilinae LANE, 1971

523 Genus *Eccoptochile* HAWLE and CORDA, 1847

524 *Eccoptochile* sp.

525 **Fig. 10 I**

526 **Material:** one incomplete pygidium, internal mould, LPB 14810.

527 **Discussion:** this pygidium, collected from the base of the Kermeur Formation, in SF1, is
528 referred to *Eccoptochile*. The species of this genus described either in the Armorican Massif
529 (Henry, 1980) or Spain (Hamman, 1974, 1976) are chiefly distinguished by their cephalic
530 morphology, therefore a specific assignment is not possible from this single specimen.

531

532 8.2. Echinodermata

533 Class Diploporita MÜLLER, 1854

534 Superfamily Aristocystitida NEUMAYR, 1889

535 Family Aristocystitidae NEUMAYR, 1889

536 Genus *Aristocystites* BARRANDE, 1887

537 *Aristocystites* sp.

538 Fig. 11 A–C

539 **Material:** four thecae preserved, one as an internal mould LPB 14811, and three as
540 incomplete external moulds LPB 14812 to 14814.

541 **Discussion:** on the external moulds, the thecae are ovoid in shape and more than 10 cm long.
542 The thecal plates are well sized (≥ 5 mm), relatively hexagonal in shape and more or less
543 regularly arranged. They show dense vermicular openings but no tubercle is observed. These
544 features indicate that the specimens from the base of the Kermeur Formation should be
545 assigned to the genus *Aristocystites*, and are particularly reminiscent of *A. bohemicus*
546 BARRANDE, 1887 (see Parsley, 1990). Since neither holdfasts nor oral faces are observed on
547 the collected specimens, the specific assignment remains uncertain. In the Kermeur
548 Formation, *Aristocystites* sp. is preserved as complete thecae and isolated thecal plates
549 scattered in the highly bioturbated SF1, and then only as thecal plates in lenticular shell
550 concentrations of SF2 together with brachiopod valves.

551

552

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558

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844

845 **Figures captions**

846

847 **Fig. 1.** Location of the Kermeur Formation outcrops in the Armorican Massif (Crozon
848 Peninsula).

849

850 **Fig. 2.** Ordovician deposits in the Veryac'h section (Crozon Peninsula), with global and
851 British stratigraphic stages (assigned from Paris, 1990; Bourahrouh, 2002; Webby et al.,
852 2004).

853

854 **Fig. 3.** Lithostratigraphic column of the Veryac'h section, from the upper part of the
855 Postolonnec Formation to the lower part of the Kermeur Formation. Vertical evolution of
856 sedimentary environments from SF0 to SF4. Location of the fossiliferous levels (shown by a
857 grey line) and related taphofacies.

858

859 **Fig. 4.** Bioturbated clayey sandstone SF1 with some preserved sandy layers (arrows in A) and
860 bioturbation (B). Bioturbated sandy mudstone SF2 with equilibrichnia structures (C) and
861 preserved black clayey mudstone (arrow in D).

862

863 **Fig. 5.** Bioturbated heterolithic SF3. General views (A and C) and details showing lenticular
864 to flaser beddings (D, F, G), current ripples with clay drapes on the top surface of a sandy bed
865 (B), current ripples with opposite directions (E), waves ripples with flattened crests overlain
866 by current ripples at the top of a sandy bed (D). Bioturbated heterolithic (SF3) and quartz-
867 arenite (SF4) facies (F, G). Skolithos burrows filled with clayey material (arrow in F). Puddle
868 with wave ripples (arrow) in the quartz-arenite SF4 (H).

869

870 **Fig. 6.** General view of the quartz-arenite SF4 (A) and details showing the concave scours in

871 the sandy beds (arrows in B) and swaley cross-stratification (D). Lateral transition from SF3
872 to SF4 (C).

873

874 **Fig. 7.** Depositional model for the lower part of the Kermeur Formation. Distribution of the
875 sedimentary (SF) and taphonomic (TF) facies from continental (X) to open marine (Y)
876 domains.

877

878 **Fig. 8.** Evolution in space (X–Y) and time of the distribution of sedimentary facies in the
879 Veryac’h section during the transgressive phase. P1, P2 and P3 represent the adjustment
880 barrier-lagoon profiles related to the sea-levels (L1, L2, L3) at different times. The SF0
881 occurs in the transgressive surface.

882

883 **Fig. 9.** Taxonomic and taphonomic composition of fauna from the lower part of the Kermeur
884 Formation. (A) Taphofacies 1, strictly associated with SF1, is characterized by a random
885 dispersion of specimens. Depending on the taxa, skeletons are either preserved whole and
886 articulated (grade TF1a) or, on the contrary, systematically disarticulated and often
887 fragmented (grade TF1b). (B) In taphofacies 2, strictly associated with SF2, fossil remains are
888 disarticulated and preserved in lenticular shell concentrations.

889

890 **Fig. 10.** Selected specimens from the lower part of the Kermeur Formation (SF1 and SF2),
891 Veryac’h section, Crozon Peninsula, France. Scale bar: 0.5 cm.

892 (A–D) *Colpocoryphe grandis* (ŠNAJDR, 1956);

893 (A) internal mould of a complete exoskeleton, LPB 14792; (B) internal mould of a moult,
894 with dorsal view of the connected thorax and pygidium and ventral view of the librigenae,

895 (the cranidium is under librigenae), LPB 14795; (C) internal mould of a pygidium, LPB
896 14793; (D) rubber cast of an external mould of a pygidium, LPB 14794.
897 (E, H) *Onnia seunesi* ?;
898 (E) internal mould of cephalon, LPB 14804; (H) internal mould of cephalon, LPB 14800.
899 (F) *Phacopidina* sp., internal mould of cephalon, LPB 14808.
900 (G, J) *Zeliskella (Zeliskella)* sp.; (G) internal mould of incomplete cranidium, LPB 14806a;
901 (J) internal mould of incomplete pygidium, LPB 14807.
902 (I) *Eccoptochile* sp., internal mould of pygidium, LPB 14810.
903 (K) *Triplesia* cf. *T. simplex* HAVLÍČEK, 1971, internal mould of ventral valve, LPB 14126.
904 (L, M) *Drabovia pentagonomya* HAVLÍČEK, 1971; (L) internal mould of dorsal valve, LPB
905 14110; (M) internal mould of ventral valve, LPB 14108.
906 (N, O) *Tafilaltia destombesi* HAVLÍČEK, 1970; (N) internal mould of dorsal valve, LPB
907 14092; (O) internal mould of ventral valve, LPB 14091.
908
909 **Fig. 11.** *Aristocystites* sp., diploporid from the lower part of the Kermeur Formation,
910 Veryac'h section, Crozon Peninsula, France. Scale bar: 0.5 cm.
911 (A) internal mould of theca, LPB 14811;
912 (B) one isolated thecal plate with filling of diplopores, dichotomous at each end, LPB 14812;
913 (C) external mould of theca, LPB 14813.
914

Fig.1

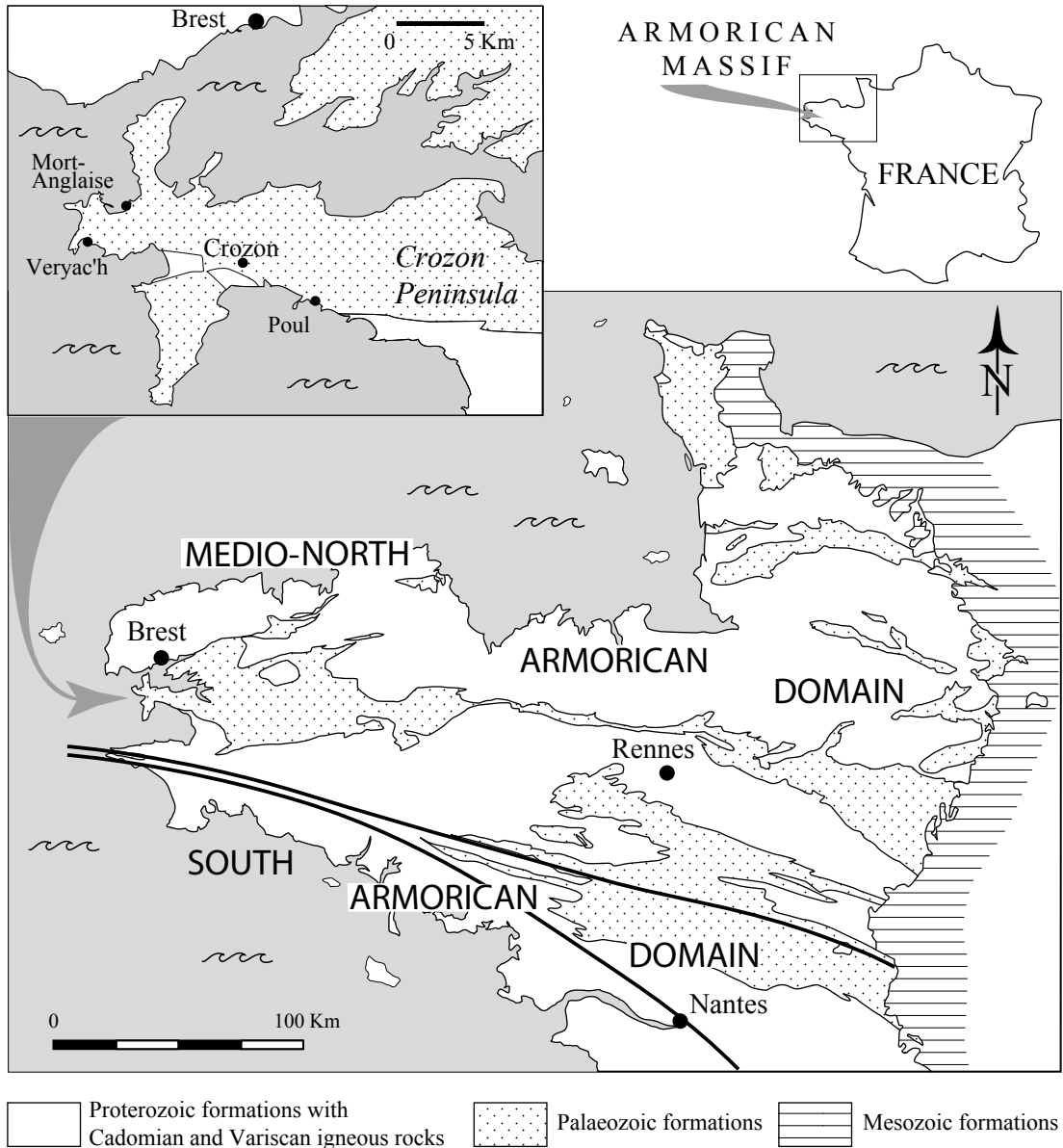


Fig. 2

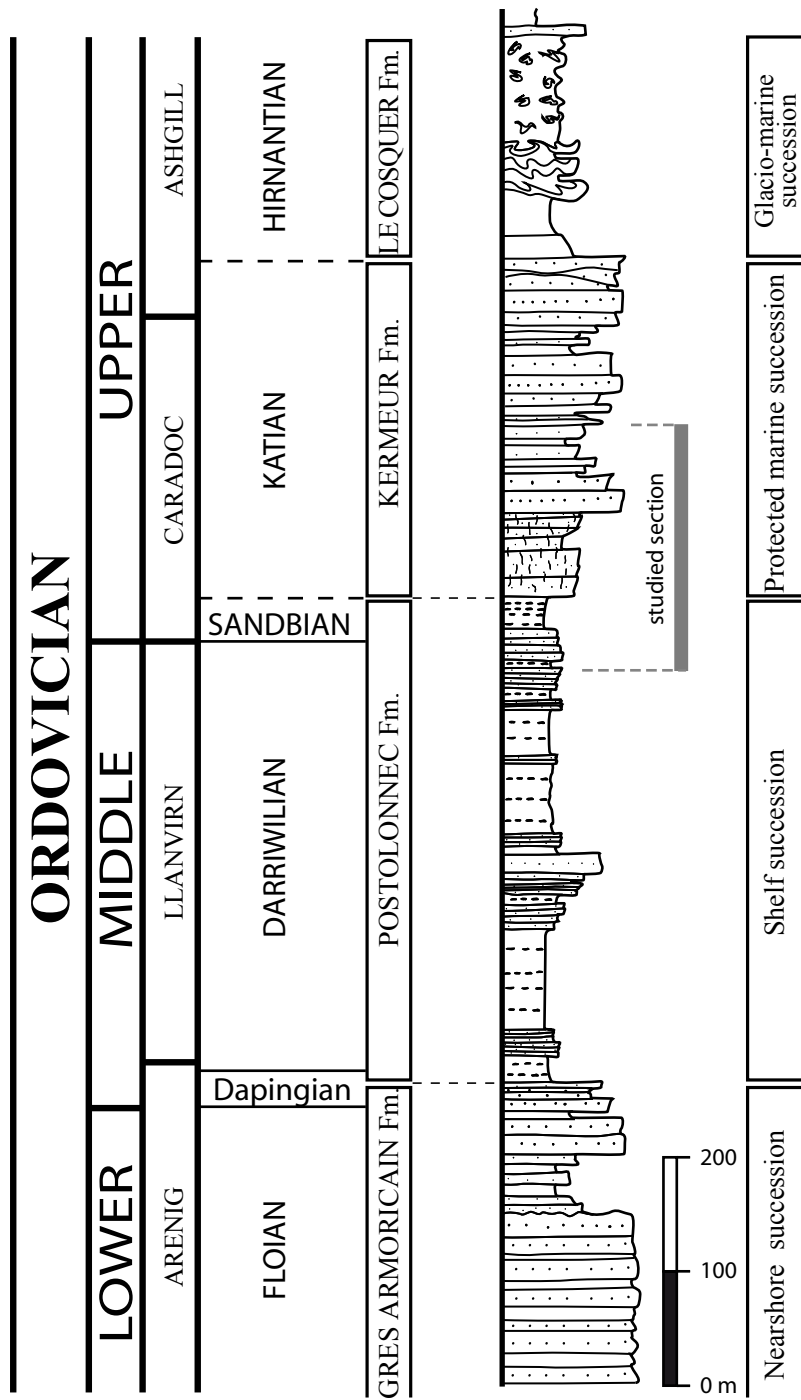
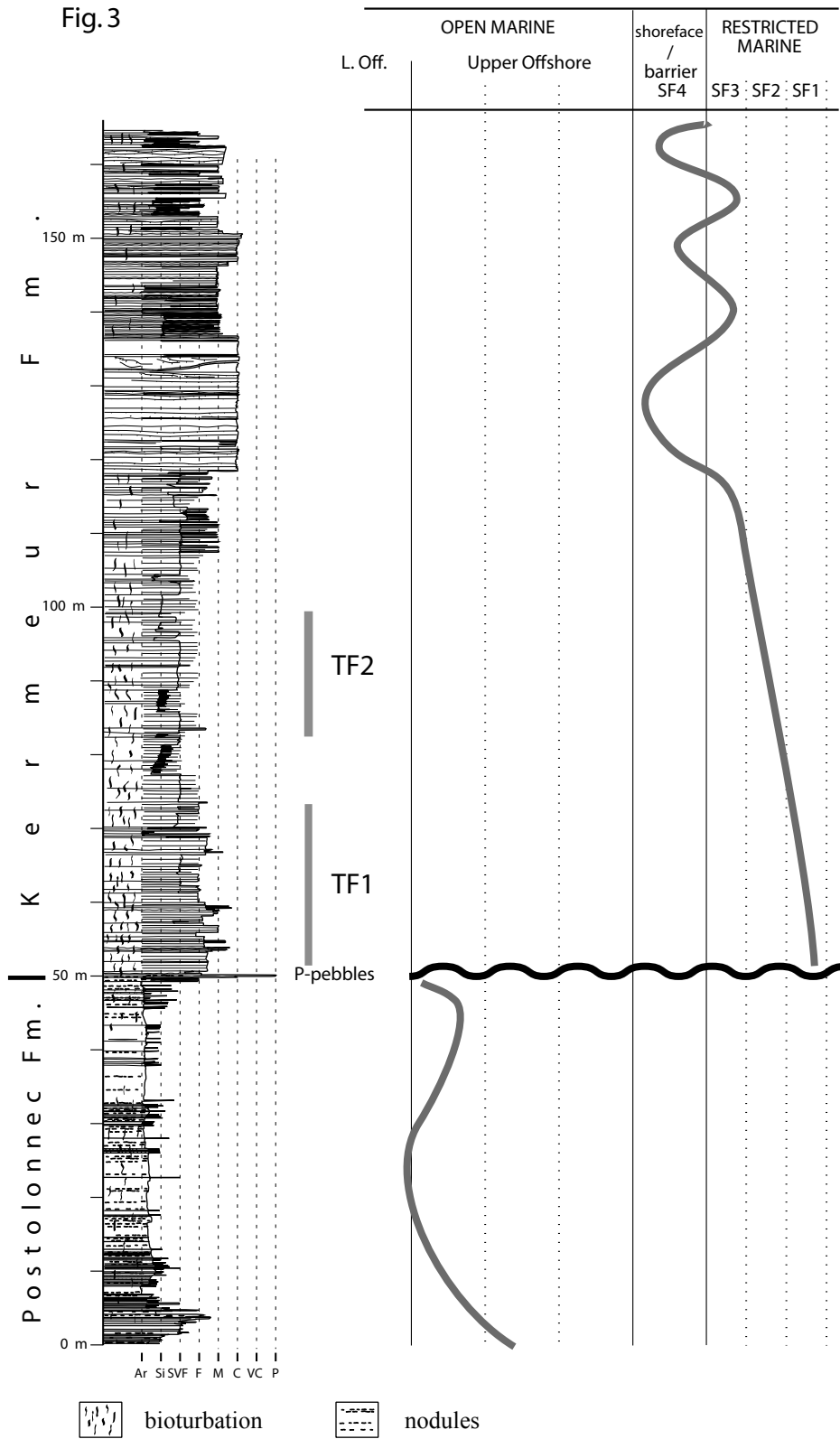


Fig. 3

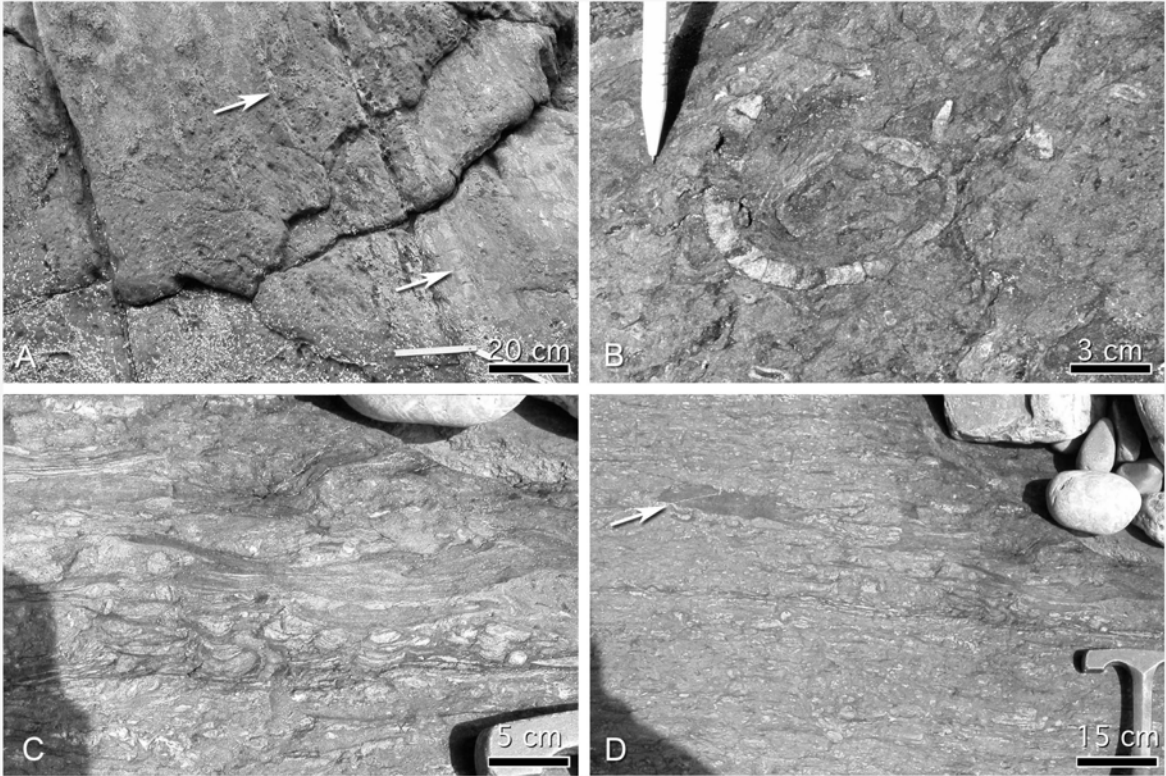


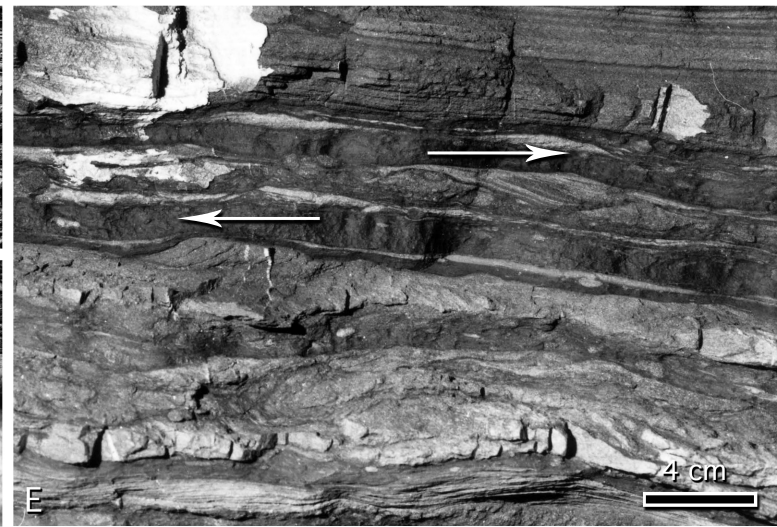
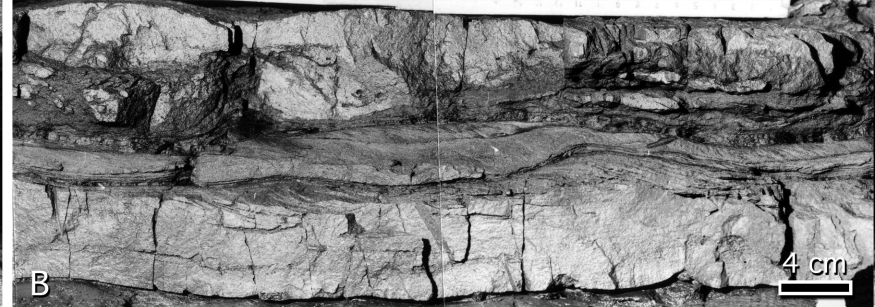
bioturbation



nodules

Fig. 4





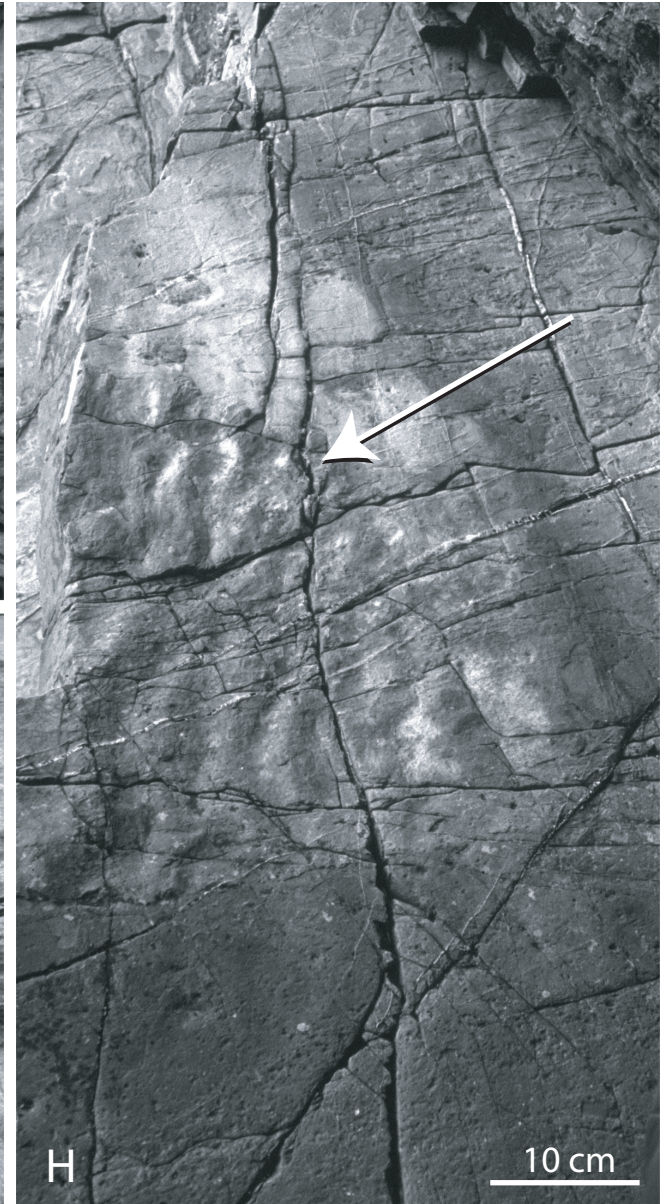
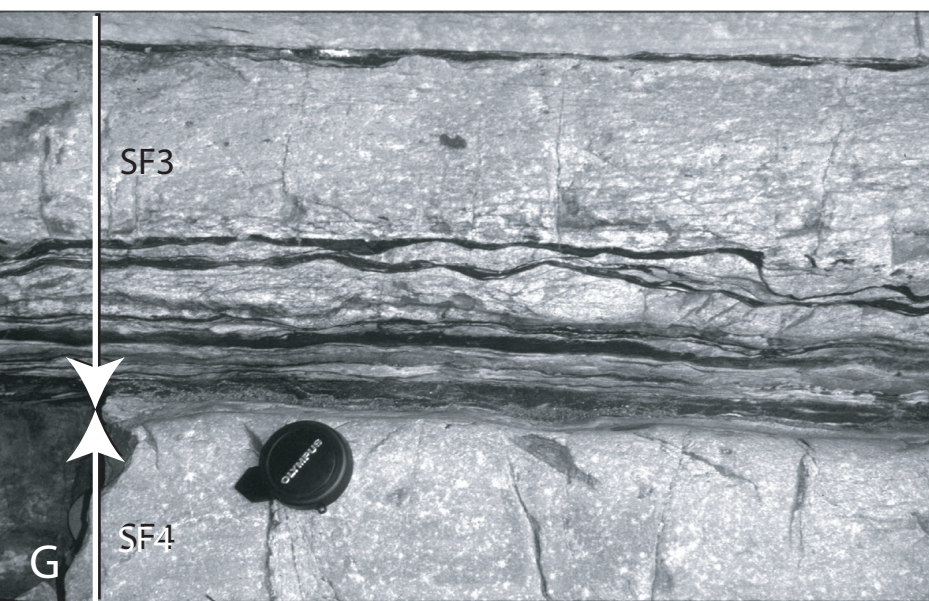
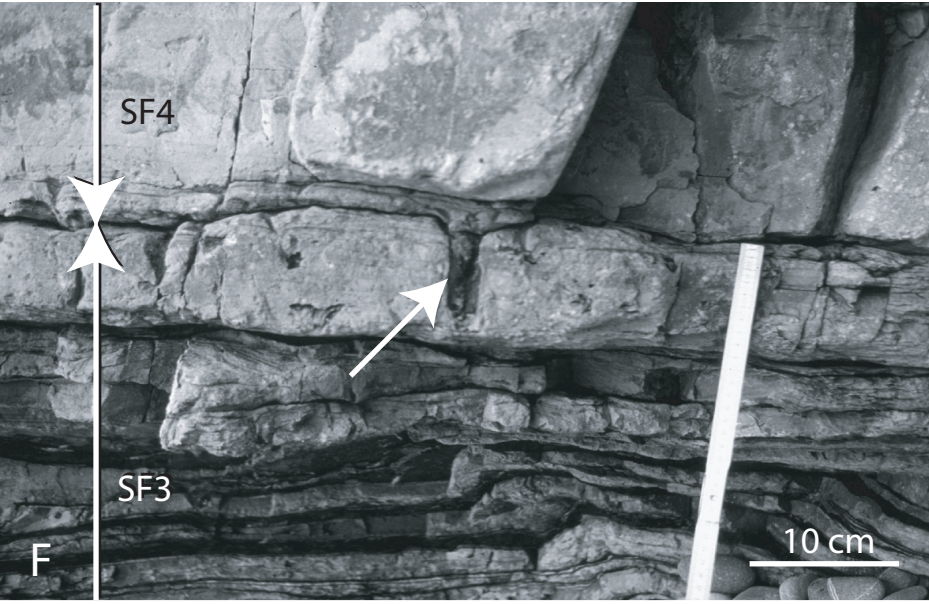


Fig. 6

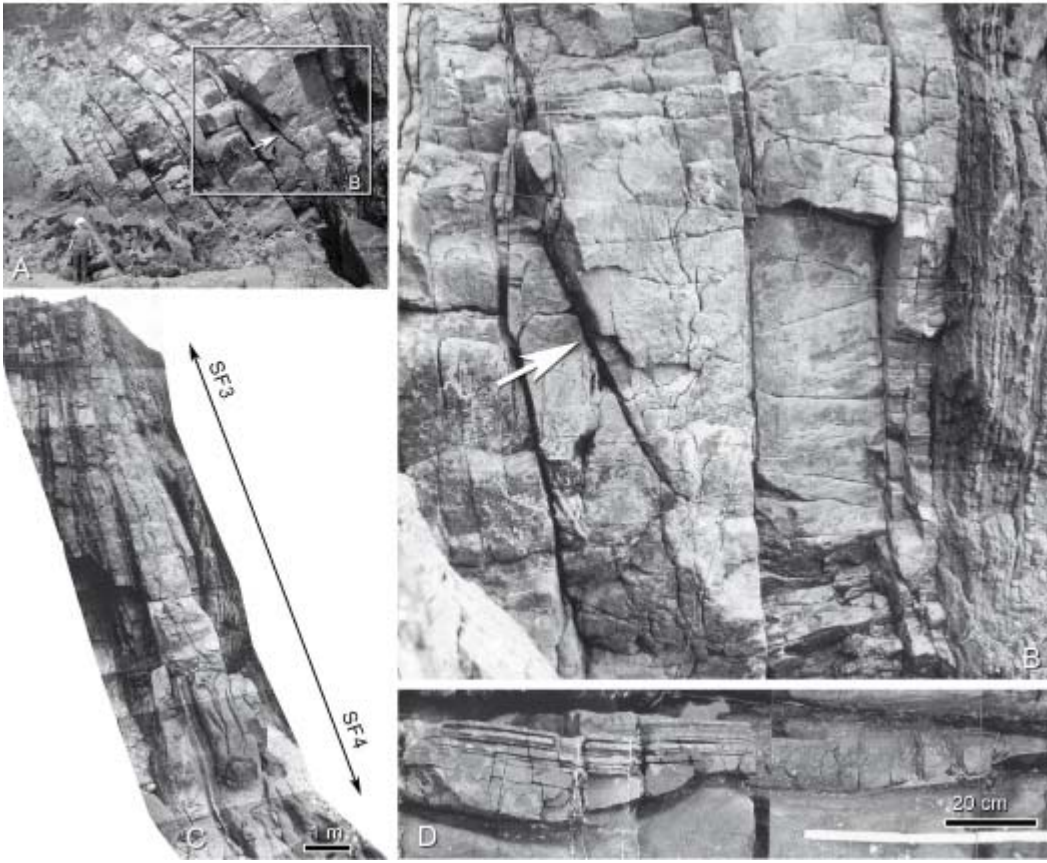


Fig. 7

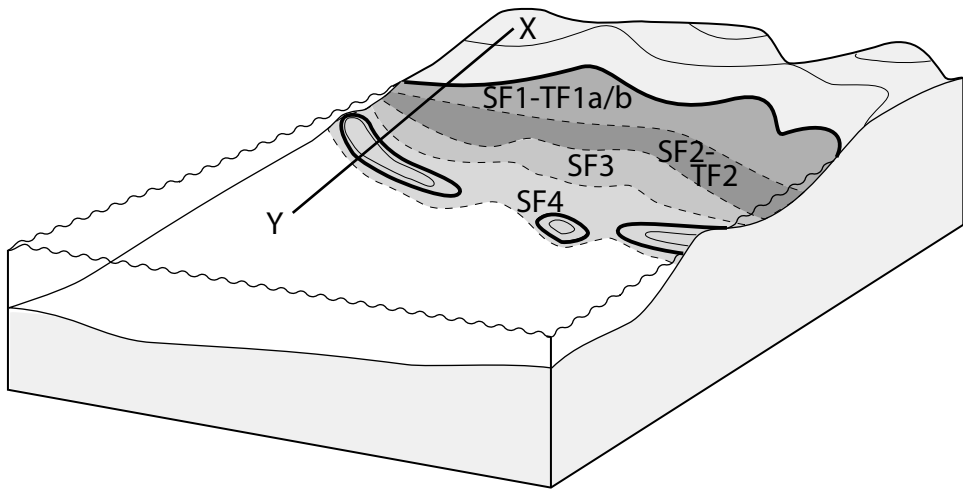
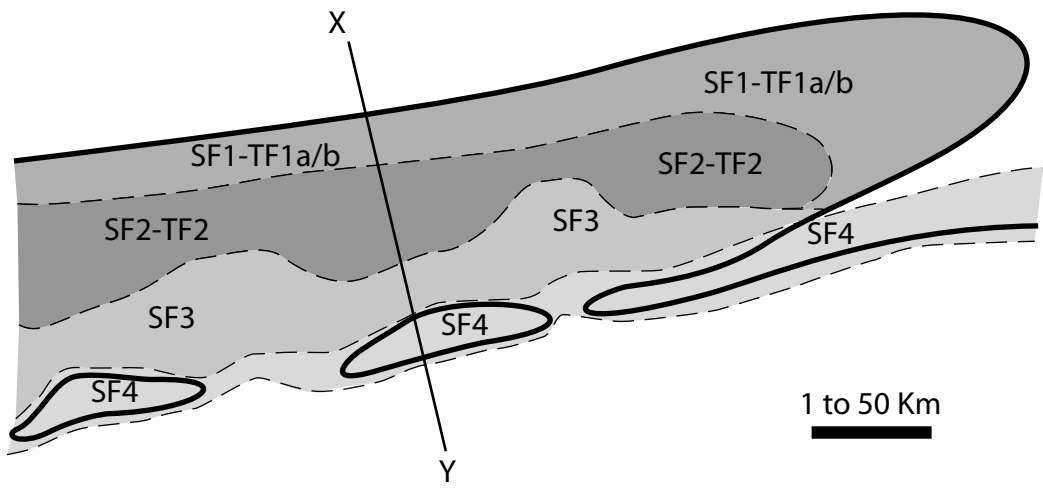


Fig.8

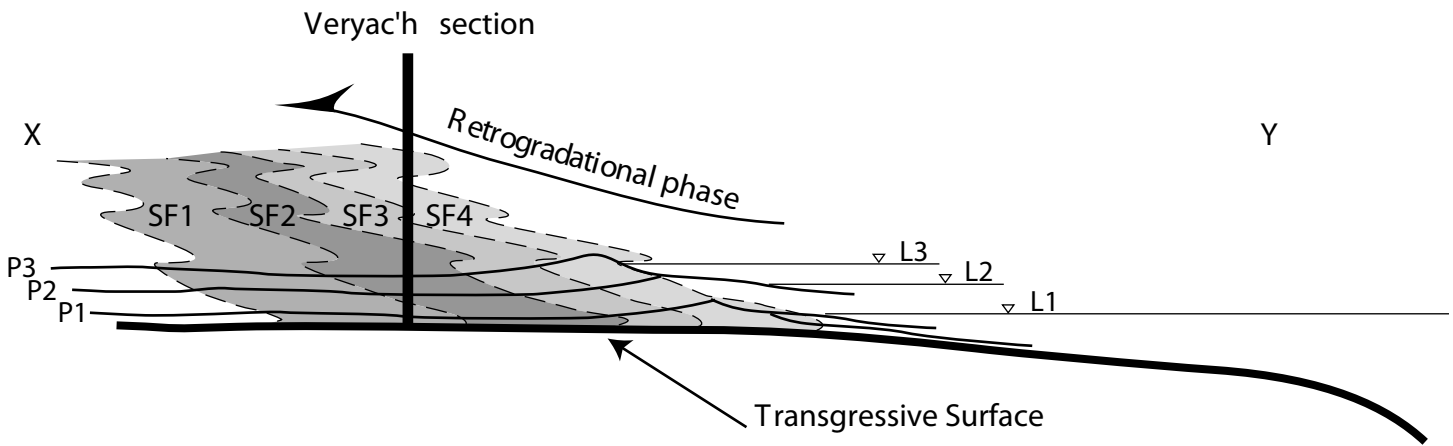


Fig. 9

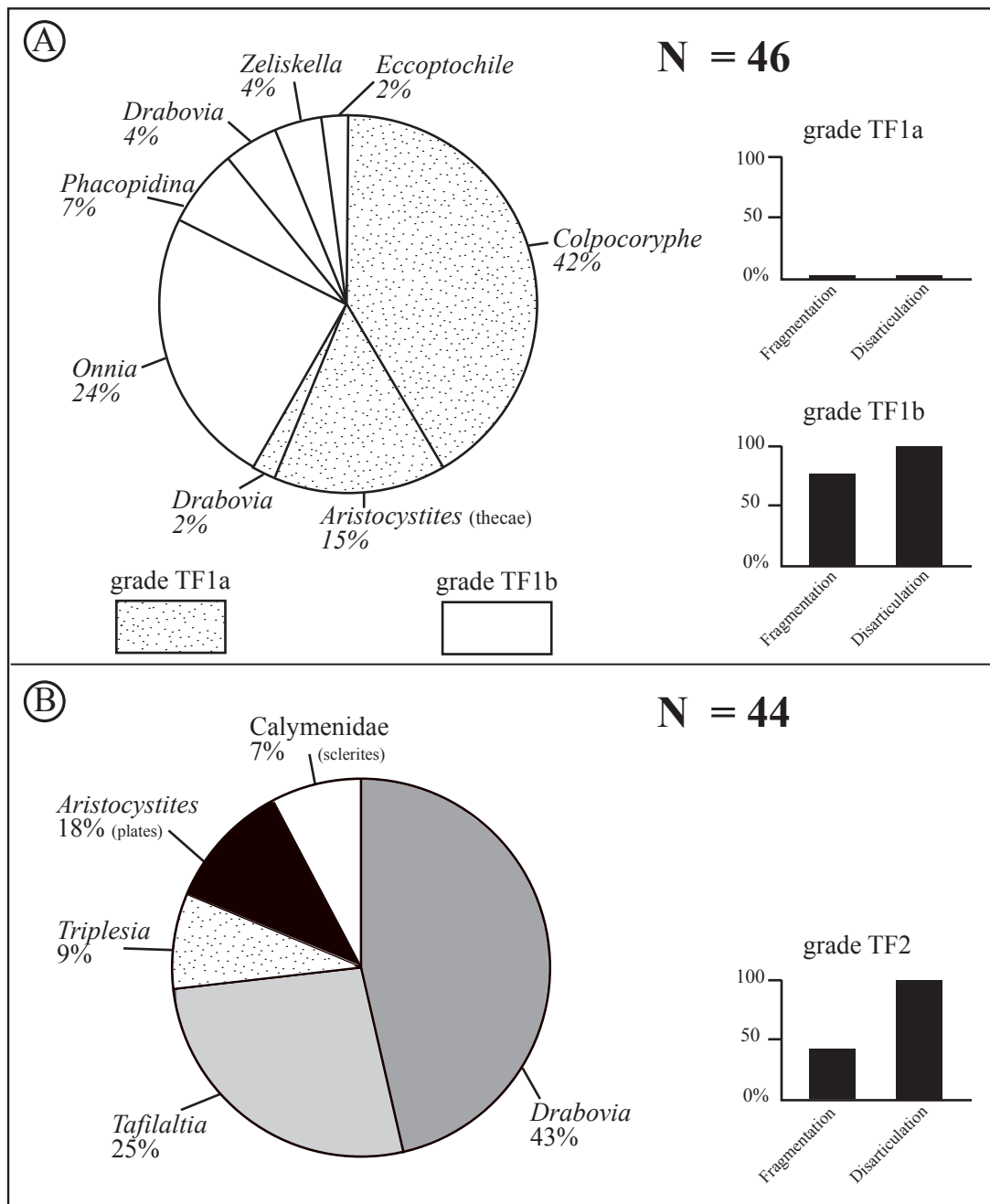


Fig. 10

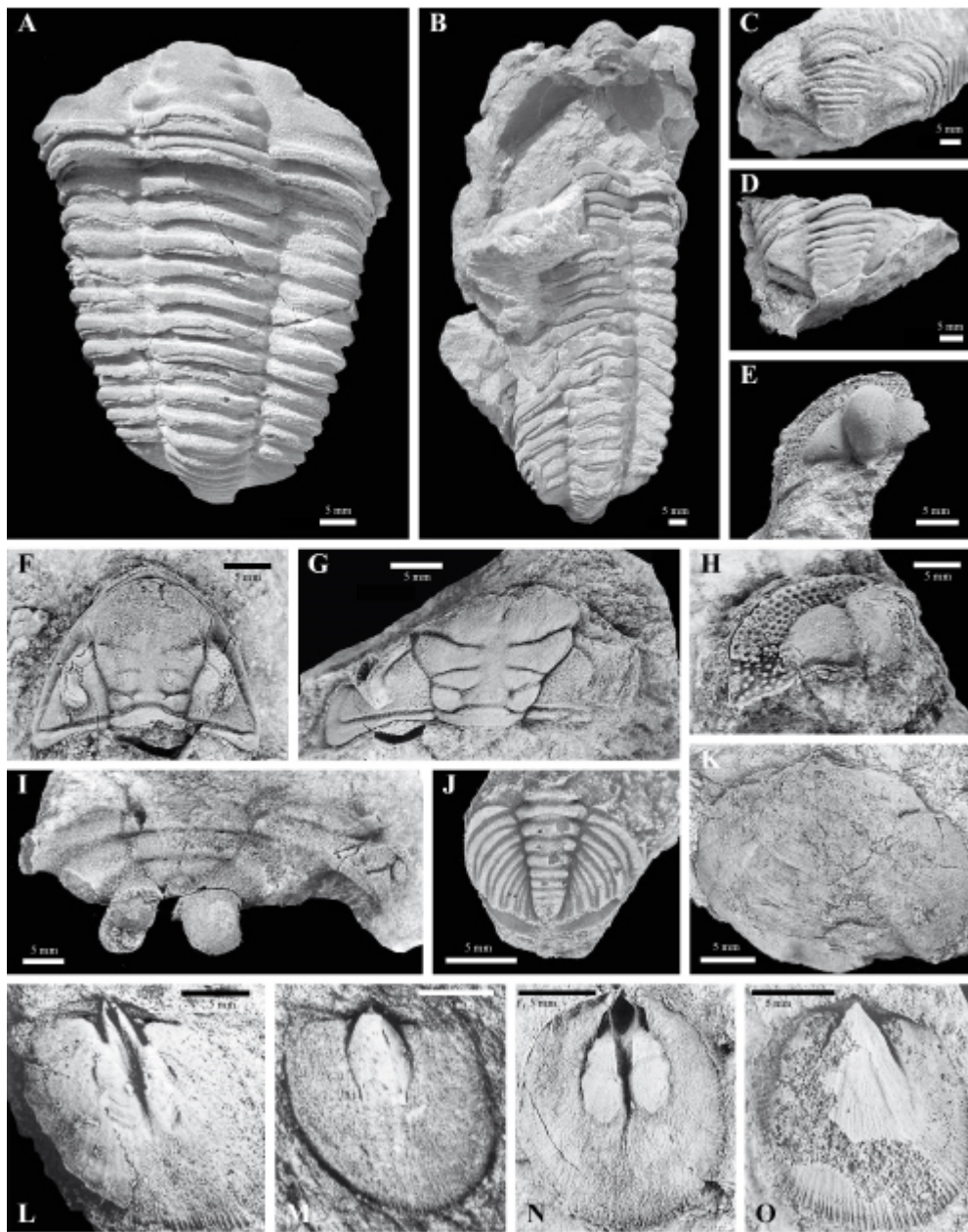


Fig. 11

