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Muriel Vidal, Alfredo Loi, Marie-Pierre Dabard, Arnaud Botquelen. A Palaeozoic open shelf benthic assemblage in a protected marine environment. Palaeogeography, Palaeoclimatology, Palaeoecology, 2011, 306 (1-2), pp.27-40. 10.1016/j.palaeo.2011.03.025 . insu-00609440

HAL Id: insu-00609440 https://insu.hal.science/insu-00609440

Submitted on 19 Jul 2011

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1	A Palaeozoic open shelf benthic assemblage in a protected marine environment
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19	ABSTRACT
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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).

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

50

51 **1. Introduction**

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 recognition of "biofacies" or benthic associations along an open shelf profile, especially for 56 57 trilobites (Fortey and Owens, 1978, 1987; Henry and Destombes, 1991; Vidal, 1998; Zhou Zhiyi et al. 2001, 2003; Turvey, 2005) and brachiopods (Villas, 1985, 1992, 1995; Havlíček, 58 59 1989; Havlíček et al., 1987). These biofacies are valuable tools for palaeogeographic reconstructions (Fortey and Owens, 1987; Henry, 1989; Henry et al. 1997; Fortey and Cocks, 60 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 (Sandbian-Katian boundary; Webby et al., 2004). This regressive event is recognized in 67 several areas of the northern Gondwana Domain, from the Armorican Massif (Robardet, 68 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 endemicity of benthic fauna 74 and the arrival of taxa from Avalonia, Laurentia and Baltica (Havlíčcek, 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

In the Armorican Massif (Fig. 1), the lower Palaeozoic terrains are subdivided into 88 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 (Philippot, 1950; Henry et al., 1976), echinoderms (Chauvel, 1941; Chauvel and Nion, 1969) 110 111 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.

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118 **3. Stratigraphic context**

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The upper part of the Postolonnec Formation (Fig. 3) consists of clayey silty facies containing sandy beds with hummocky cross-stratifications or siliceous and/or phosphatic concretion-bearing beds and shellbeds. It was deposited in a shelf environment dominated by storm wave action, between the median part of the inner shelf and the outer shelf (Loi et al., 1999; Loi and Dabard, 2002; Dabard et al., 2007). The bioturbation structures are small and primarily represented by *Planolites*. Macrofaunas are either randomly dispersed in the clayey 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 <i>L. deunffi</i> biozone and others to the <i>L</i> .
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 μ m in size) and phyllosilicates. The size of the Fe-oolites varies between
169	250 and 700 μ m. 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.

SF3: the bioturbated heterolithic facies is made up of well-sorted fine- to mediumgrained sandy beds, several centimetres to 1 dm thick, that alternate with lenticular to flaser
bedding (Figs. 5 A, C, D, E, F, G). The sandy beds show planar to subhorizontal laminations
with very flattened hummocky cross-stratification (HCS) locally. The basal surface of the
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

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

of lag deposits. Then, during the transgressive phase, these pebbles were integrated into thefirst 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 (fluviatile 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).

278 5.3. Stratigraphic evolution

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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 protected marine to open marine environments, is integrated into a transgressive evolution 291 292 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

303

In the lower part of the Kermeur Formation, fossils are only present in SF1 and SF2. 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 single species. The trilobites include numerous complete exoskeletons and *in situ* exuviae 316 317 (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.

The second grade of this taphofacies (Fig. 9 A, TF1b) is characterized by a high degree of shell disarticulation, which are nevertheless always randomly dispersed; most of the material is composed of trilobite exoskeleton fragments, including trinucleids (*Onnia seunesi* ?, 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

- brachiopod valves (*Drabovia pentagonomya*, Figs. 10 L–M). These taxa are preserved only as
 isolated exoskeletal parts, and some specimens were broken before burial.
- In summary, *Drabovia* occurs in both grades of this taphofacies, and *Aristocystites* and
 Colpocoryphe are mostly preserved as complete remains with different parts of their skeletons
 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 Triplesia 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

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; Spever, 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 allochtonous 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 composite assemblage with allochthonous and autochthonous species. 385

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.

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

bioturbated sandy mudstones facies (SF2) could represent loose ground substrate, which is
more favourable for epifaunal soft-substrate brachiopods than the bioturbated clayey
sandstones facies (SF1). The latter facies is probably more closely comparable to soft ground
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 cephala, 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

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 cephala 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

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 (Hammann, 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 (\geq 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
- scattered in the highly bioturbated SF1, and then only as thecal plates in lenticular shell
- 550 concentrations of SF2 together with brachiopod valves.
- 551

553	Acknowledgments
554	The authors are indebted to M. Robardet and Y. Plusquellec for helpful scientific
555	discussions, to B. Dattilo and J. Botting for constructive comments on earlier version. The
556	editorial work made by F. Surlyk greatly improved the manuscript. Dr. S. Mullin provided
557	writing assistance. This work is a contribution to the ECLIPSE 2 programme (CNRS, France).
558	
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- 844
- 845 **Figures captions**

Fig. 1. Location of the Kermeur Formation outcrops in the Armorican Massif (CrozonPeninsula).

849

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

853

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

sedimentary environments from SF0 to SF4. Location of the fossiliferous levels (shown by a

857 grey line) and related taphofacies.

858

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

862

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

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

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

873

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

877

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

882

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

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);

(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,

- (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 ?;
- (E) internal mould of cephalon, LPB 14804; (H) internal mould of cephalon, LPB 14800.
- (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





	ORDOVICI	AN	
LOWER	MIDDLE	UPPE	R
ARENIG	LLANVIRN	CARADOC	ASHGILL
FLOIAN	DARRIWILIAN	NUTIAN	HIRNANTIAN
GRES ARMORICAIN Fm.	POSTOLONNEC Fm.	KERMEUR Fm.	LE COSQUER Fm.
200 200 100 0 m		studied section	All to a so
Nearshore succession	Shelf succession	Protected marine succession	on Glacio-marine succession

Fig. 2





Fig.4





















Fig.8









Fig. 11

