A spectacular *Cruziana* trace fossil site from the Lower Ordovician of Brittany (Crozon Peninsula, NW France)

Olaf Elicki & Florentin Paris

From the Cap de la Chèvre Formation (Fm.) of the Crozon Peninsula (Beg-Ar-Gwin locality, Brittany, northwestern France) an exceptional trace-fossil site is described and discussed. A mass occurrence of remarkably large-sized trilobite trails of *Cruziana furcifera* d'Orbigny, 1842, is reported for the first time in France. An additional layer exposes *Cruziana barriosi* Baldwin, 1977, which represents the only trilobite trace of this second assemblage, and occurs in large numbers. *Cruziana barriosi* is first reported from Europe outside Iberia. The *Cruziana furcifera* and *Cruziana barriosi* trace-fossil assemblages from Beg-Ar-Gwin, which both represent the *Cruziana rugosa* group, show very low ichno-diversity (n = 2–3). The ichnocoenoses and the sedimentological characteristics of the host rock suggest an ecologically unstable, transitional marginal-marine depositional system exposed to elevated ecological stress. Palaeogeographically situated in high southern latitudes, the assemblages and deposits show close relations to similar Gondwanan occurrences, as on the Iberian Peninsula and in the Middle East. The *Cruziana rugosa* group, in particular, is confirmed as a valuable tool for stratigraphic correlation, as well as for refining palaeoecological–palaeogeographic reconstruction models for this part of Gondwana. The stratigraphic position of the Cap de la Chèvre Fm. is evaluated. Based on the Beg-Ar-Gwin trace fossil assemblages, a depositional age of early to middle Floian (Early Ordovician) is most likely, at least for the fossil-bearing upper part of the Cap de la Chèvre Fm. • Key words: Ordovician, *Cruziana furcifera*, *Cruziana barriosi*, Cap de la Chèvre Formation, Beg-Ar-Gwin, Brittany.

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Ordovician sediments are well exposed in Brittany (northwestern France; Fig. 1). The palaeontological and sedimentological context and stratigraphy of the strata, as well as their palaeogeographic interpretation, have been extensively investigated and discussed in numerous publications, Ph.D. theses and research projects (*e.g.* Dabard 1983, Bonjour 1988, Bonjour & Chauvel 1988, Bonjour *et al.* 1988, Robardet *et al.* 1994, Dabard *et al.* 2009, Vidal *et al.* 2011), and were recently summarized by Dabard *et al*. (2015, 2021), Paris (2016), and Lefebvre *et al*. (2023).

The Crozon Peninsula is of particular interest for discussion of the timing and nature of the onset of Palaeozoic sedimentation. Because the sedimentary column in several places begins with continental facies of the lower Cap de la Chèvre Fm. (or regional equivalents), this unit is of particular interest with respect to any stratigraphically significant information (see the stratigraphy chapter below), such as the first intercalations of marine strata within the formation. Evidence for initial marine conditions comes from the first occurrence of relevant marine trace fossils (trilobite traces). Trilobite traces are the most prominent fossils in many Palaeozoic siliciclastic successions worldwide (Seilacher 2007, Mángano & Buatois 2016, Gutiérrez-Marco *et al*. 2017a, b). They represent essential palaeoecological indicators of various shallow marine environments and provide important data for inferring depositional processes and models, reconstructing palaeoecological architectures, and stratigraphical and palaeogeographical correlation (*e.g.* Seilacher 2007, Buatois & Mángano 2011, Knaust & Bromley 2012, Mángano & Buatois 2016). One of the most widely recognised representatives of this type of trace fossil in shallow marine systems of the early Palaeozoic is *Cruziana*, which, for such systems, is commonly accepted to represent a trace predominantly produced by ploughing trilobites (for a detailed discussion, see Seilacher 2007). Seilacher (1970) developed a scheme of ethological groups of *Cruziana* ichnospecies, characterised by distinct morphological features they share (e.g. *Cruziana rugosa* Group, *Cruziana fasciculata* Group, *Cruziana dispar* Group, *etc.*). The *Cruziana rugosa* Group is particularly

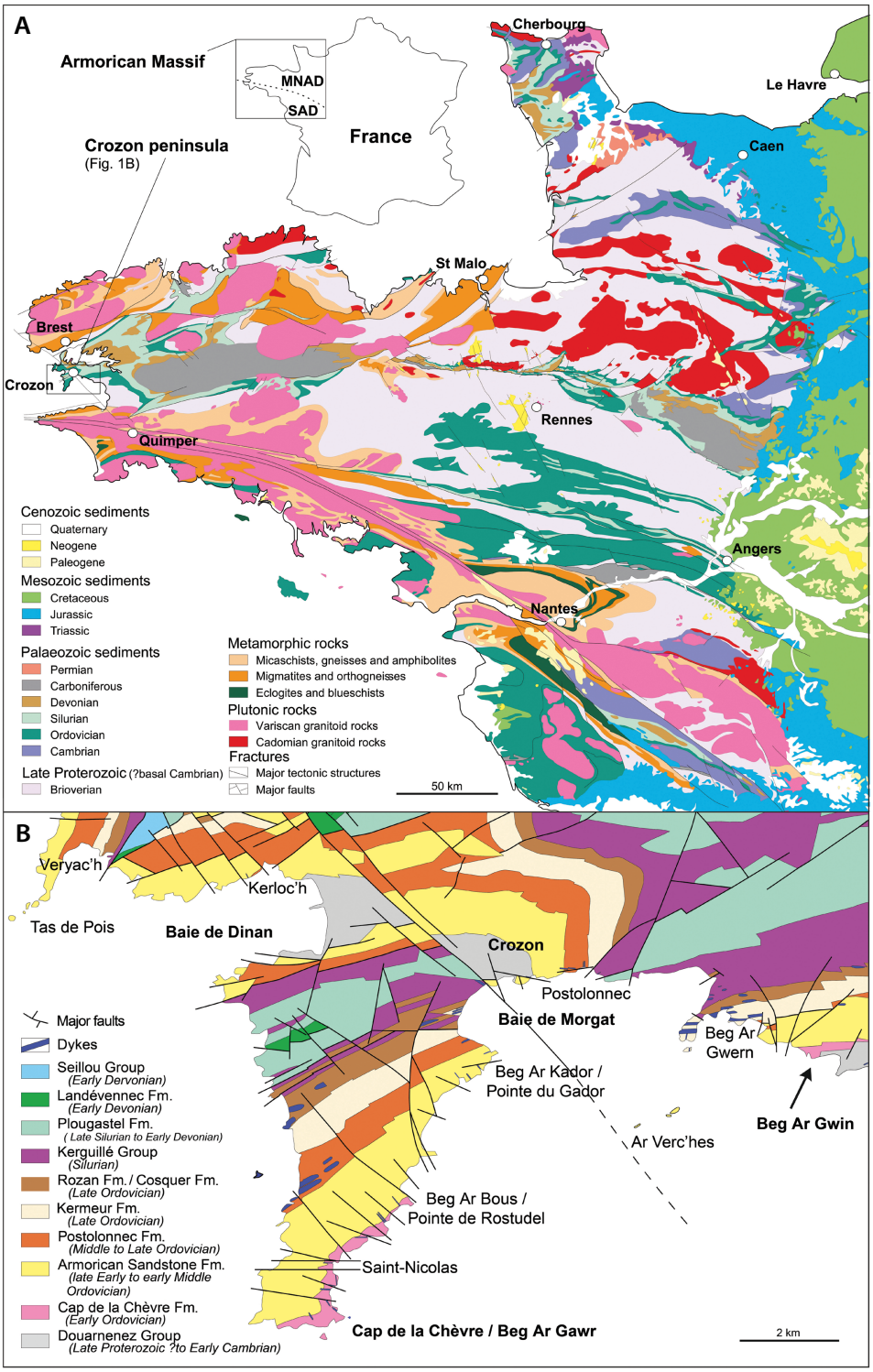
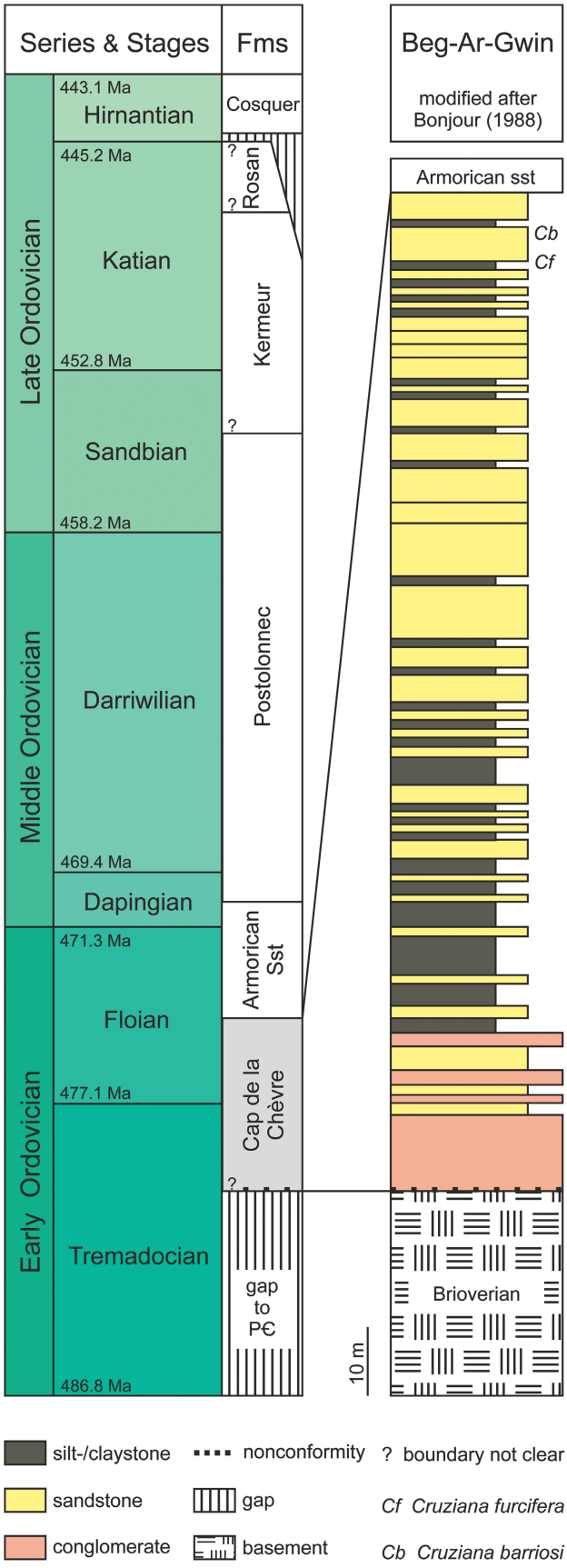


Figure 1. Geological maps of the working area. • A – geological overview of the Armorican Massif in Northwestern France (Brittany and marginal areas of the adjacent Normandy and Pays de la Loire regions), adapted from geological maps at various scales 1:1,000,000, 1: 320,000, and 1: 50,000 of the Bureau de Recherches Géologiques et Minières, France; modified after Paris (2016). The insert shows the geographic position of the Armorican Massif in France, as well as the Medio-North Armorican (MNAD) and South Armorican domains (SAD). The Crozon Peninsula working region is indicated by a rectangle (illustrated in more detail in Fig. B). • B – geology of the southern Crozon Peninsula, modified after Kerdreux & Paris (2023); position of the investigated fossiliferous outcrop of the Cap de la Chèvre Fm. at the Beg-Ar-Gwin locality is indicated by a black arrow.

characteristic of parts of the Gondwana palaeocontinent, where it can also attain some biostratigraphic significance (Seilacher 1992, Buatois & Mángano 2011, Mángano & Buatois 2016, Meischner *et al.* 2020).

From the Beg-Ar-Gwin locality (Crozon Peninsula), Bonjour (1988, pl. 1, fig. 2) reported and illustrated a single large specimen that he assigned to *Cruziana rugosa*, which, in fact, represents *Cruziana furcifera* (see discussion below). This trace fossil was seemingly the only *Cruziana* specimen exposed on site at that time. About four decades later, a re-inspection of Bonjour's trace fossil locality by one of the authors (FP) revealed



a much more extensive, spectacular, large-scale *Cruziana* horizon due to the extensive weathering (Fig. 3). This new opportunity for investigation, together with the considerable importance of the marine trace fossil assemblage of the Cap de la Chèvre Fm. regarding interpreting the depositional conditions, its stratigraphic position, and the palaeogeographic value of this oldest Palaeozoic succession in the area, motivated the here presented research.

Geological background

Brittany, located in northwestern France (Fig. 1), is part of the Armorican Massif, a classic region of early Palaeozoic research. This area, where Palaeozoic sedimentary successions are widely exposed, belongs to the so-called North Armorican Domain (NAD), the Median (or Medio) Armorican Domain (MAD), and the South Armorican Domain (SAD) of the Armorican Massif (Lefebvre *et al*. 2023). Some authors combine the first two regions mentioned as the Medio-North Armorican Domain (MNAD) (Robardet *et al.* 1994, Dabard *et al.* 2021). Palaeozoic sedimentation began in the Early Ordovician, probably locally in the Cambrian, and ended in the late Carboniferous. In the Early Palaeozoic, the region was part of a terrane collage (Armorican Terrane Assemblage) at the austral rim of the Gondwana palaeo-continent (Paris & Robardet 1990, 1994; Cocks & Torsvik 2021), most likely situated at approximately 75–80° south of the equator (Torsvik & Cocks 2013, Scotese 2023).

In the MAD, the Palaeozoic strata are well accessible through numerous artificial features (such as quarries) and natural outcrops, especially along the Atlantic coast. The Crozon Peninsula (western Brittany, Département Finistère), the area of the present research, represents the westernmost part of MAD with exposures of early Palaeozoic successions in spectacular coastal outcrops. Here, Early Ordovician strata (Cap de la Chèvre Fm., up to more than 100 m thick, overlain by the Armorican Sandstone Fm., 20–700 m thick) were unconformably deposited on top of the Precambrian rocks (so-called

Figure 2. Stratigraphic scheme (according to ICS 12/2024 correlation chart) and Ordovician formations developed in the Crozon Peninsula region (modified after Vidal *et al.* 2011, Paris 2016, Lefebvre *et al.* 2023). Simplified lithological succession of the Cap de la Chèvre Fm. at Beg-Ar-Gwin locality (based on Bonjour 1988) is illustrated to the right. The stratigraphic positions of the investigated trace fossil horizons (*Cf – Cruziana furcifera*, *Cb – Cruziana barriosi*) are indicated. Note that the positions of the bases of the Cap de la Chèvre, Kermeur, Rosan, and Cosquer formations are not well known due to erosional gaps and missing biostratigraphic data. Minor differences in the completeness of the succession between the northern and the southern Crozon regions are not considered.

Figure 3. Beg-Ar-Gwin outcrop (southern Crozon Peninsula). • A – view from the sea showing the complete Cap de la Chèvre Fm., from base (right) to top (left). White arrow marked by "a" points to the lower formation boundary to the Precambrian basement, white arrow at "b" marks the boundary to the overlying Armorican Sandstone Fm. The horizontal arrows indicate the position of the two investigated trace fossil horizons (*Cf* – *Cruziana furcifera* layer, *Cb* – *Cruziana barriosi* layer). • B – view from the distance to the large sedimentary (lower) surface exposing the investigated mass occurrence of large *Cruziana furcifera* traces (white encircled). Note that accessibility is only from the sea.

Brioverian series = regional term of late Proterozoic to possibly earliest Cambrian strata; Néraudeau *et al*. 2024) as a result of a transgressive pulse, caused by rifting processes in this part of Gondwana ("*brevis* transgressive event" according to Paris 1990, Paris *et al*. 2007, Dabard *et al.* 2021) (Figs 2, 3). The Cap de la Chèvre Fm. represents a temporarily marine-influenced red-bed sequence of alluvial to fluvial and deltaic siliciclastic deposition (Bonjour 1988). Permanent marine conditions, established with the onset of the Armorican Sandstone Fm., persisted for most of the Ordovician with some minor sea level fluctuations, including some minor stratigraphic gaps (for details see Babin *et al*. 1976, Durand 1985, Bonjour 1988, Paris & Le Hérissé 1992, Paris *et al*. 1999, Vidal *et al*. 2011, Dabard *et al*. 2015, Paris 2016, Lefebvre *et al.* 2023).

The geology of the Beg-Ar-Gwin area (southern Crozon Peninsula, Fig. 1) is characterised by the Cap de la Chèvre Fm. (Fig. 2), which is exposed in stratigraphic contact with the Precambrian basement. According to Bonjour (1988), the formation rests unconformably on the Brioverian rocks with a conglomerate ("Membre conglomératique de base": 25 m thick), followed by an intermediate, red siltstone-dominated lithology ("Membre intermédiaire à siltstones rouges": 45 m thick), and finally by a heterolithic sandstone subunit ("Membre gréseux supérieur": about 75 m thick). The first indication of sporadic marine conditions comes from sparse marine trace fossils (*Skolithos*, *Cruziana*) near the base of the middle subunit; further occurrences of these ichnotaxa are found in some layers within the upper subunit (Bonjour 1988). According to depositional patterns and trace-fossil content, Bonjour (1988) concluded that the Cap de la Chèvre Fm. represents a transgressive succession initially deposited under alluvial conditions, and followed by fluvial/deltaic environments; only the succeeding Armorican Sandstone Fm. marks fully marine, nearshore conditions.

Materials and methods

This study is based on field work in the Beg-Ar-Gwin coastal area situated in the western Département du Finistère, north-eastern coast of the Baie de Douarnenez (48° 13′ 10″ N, 04° 23′ 4″ W). The trace fossils are observed on two surfaces. One is exposed for approximately 40 square metres (Fig. 4), while the other is exposed for less than 1 square metre (Fig. 6). Both represent weathered lower surfaces of a tectonically overturned heterolithic succession on steep cliffs. Not all trace fossils were directly accessible due to very challenging natural outcrop conditions (rugged, dangerous vertical cliffs), but in these cases, they were extensively photographed in detail from a short distance, enabling appropriate ichnological evaluation. From both surfaces, more than a hundred individual arthropod trails have been observed. Since sampling was neither possible nor permitted by law in this protected natural park area, the measurements, descriptions, and determinations were made based on photographic documentation.

Results

Ichnogenus *Cruziana* d'Orbigny, 1842

Type ichnospecies. – *C. rugosa* d'Orbigny, 1842 (see Häntzschel 1965, p. 27).

Cruziana furcifera d'Orbigny, 1842

Figures 4, 5A–G

1842 *Cruziana furcifera*; d'Orbigny, p. 21, pl. 1, fig. 2-3.
1970 *Cruziana furcifera*. – Seilacher, p. 464.
1977 *Cruziana furcifera*. – Baldwin, p. 19, fig. 3e.
1985 *Cruziana furcifera*. – Durand, p. 46, pl. 2, figs 2, 5; pl. 3, figs 3, 6.

? 1988 *Cruziana furcifera*. – Bonjour, p. 31.
1988 *Cruziana rugosa*. – Bonjour, pl. 1, fig. 2.
2005 *Cruziana furcifera*. – Aceñolaza & Milana, p. 634, fig. 3.
2007 *Cruziana furcifera*. – Egenhoff *et al*., p. 291, figs 3e, 4b.
2009 *Cruziana furcifera*. – Gibb *et al*., p. 700, fig. 2c–g.
2014 *Cruziana furcifera*. – Rodríguez-Tovar *et al*., p. 544, fig. 5a–f.
2015 *Cruziana furcifera*. – Stachacz *et al*., p. 13, fig. 5-4.
2020 *Cruziana furcifera*. – Meischner *et al*., p. 7, fig. 3d–f; 4a, b.

Material and locality. – About 70 trails in positive convex hyporelief on the lower surface of a tilted microconglomeratic sandstone bed of the heterolithic upper Cap de la Chèvre Fm. (about 11.4 m below its top); coordinates: 48° 13′ 15.24″ N, 04° 24′ 6.12″ W, Beg-Ar-Gwin, Crozon Peninsula, Brittany.

Diagnosis. – Long bilobate furrows with clearly developed median ridge; regular endopodal scratches and some criss-crossing (in a faint rhombic pattern) at acute angles and not clearly separated; scratches may swing towards parallelism with the median line in a median posterior direction; no pleural furrows (Seilacher 1970, Fillion & Pickerill 1990).

Description. – No preferred orientation of the *Cruziana* trails is observed; their course is mostly straight, and there is only a minor change of direction in a few cases. Criss-crossing of traces is common. The width of each trail is relatively constant (in general, the width of trails varies within 8–15 cm, for the majority within 9–11 cm). The trails can be followed for up to 230 cm in some cases. Fresh non-weathered traces show depth of up to 5 cm. A clear and deep groove separates the two lobes. Lateral ridges have not been observed. The scratches are coarse and clear (Fig. 5C, F, G) and arranged in sets with changing angles relative to the median groove, ranging from 30° to 60°. Criss-crossing of scratches is common, resulting in a rhomboid pattern (Fig. 5G). In rare cases, *Cruziana furcifera* shows indistinct corrugations at the end of a trail – a morphological feature typical of *Cruziana rugosa* (Fig. 5D–F).

Remarks. – The exposed, overturned lower surface has the dimension of about 40 square metres and is partly covered

Figure 4. Investigated spectacular sedimentary (lower) surface within the upper Cap de la Chèvre Fm. at Beg-Ar-Gwin with mass occurrence of large *Cruziana furcifera* trails (for details see Fig. 5). View is to the Northeast. The middle part of the surface is still covered by fine volcanoclastics. Whereas the northwestern part (to the upper left) is comparatively fresh-weathered, the southeastern part (to the lower right) was, in contrast, already exposed to distinctly longer-lasting weathering effects. Scale in the centre (folding yardstick) is 1 m.

by remains of a (originally underlying) fine-grained volcanoclastic bed (Fig. 4). The arthropod ichnofauna consists exclusively of the large *Cruziana furcifera* specimens (Fig. 5A–G). The few other trace fossils are represented by scattered tube-shaped burrows of *Skolithos* and *Monocraterion* (clear discrimination finally not possible in some cases due to poor preservation, for discussion see Jensen 1997, Schlirf & Uchman 2005, Knaust 2025), and by undefined worm-like simple traces (Fig. 5C). Preservation of details (scratches *etc*.) is somewhat poor in the eastern part of the outcrop due to advanced weathering (Fig. 5B), but it is excellent in the left-hand (western) fresh-weathered part of the surface (Fig. 5A).

According to Seilacher (1970), Fillion & Pickerill (1990), and Egenhoff *et al*. (2007), *Cruziana furcifera* can be clearly distinguished from similar ichnospecies by the type and orientation of the scratches (including the reticulate pattern when criss-crossing) and by the absence of marginal ridges. Rodríguez-Tovar *et al*. (2014), however, noted that the latter attribute may be of limited diagnostic value because, in the type material of the ichnospecies, the marginal ridges are present or not within the same specimen. A particular taxonomic problem may generally exist when morphological transitions between the very similar ichnospecies *Cruziana furcifera*, *Cruziana rugosa*, and *Cruziana goldfussi* occur within the same trail. Such transitions (if not taphonomically induced), indicating a change in the type of trilobite movement, are reported by several authors from various regions worldwide (*e.g*. Rodríguez-Tovar *et al*. 2014, Neto de Carvalho & Baucon 2016, Kesidis *et al*. 2018, Elicki & Altumi 2019, Meischner *et al*. 2020). This led some authors to combine these ichnospecies into a single ichnospecies, with *Cruziana furcifera* and *Cruziana goldfussi* as subjective synonyms of *Cruziana rugosa*, or in the rank of sub-ichnospecies (*Cruziana rugosa rugosa*, *Cruziana rugosa furcifera*, *Cruziana rugosa goldfussi*; see Aceñolaza *et al*. 2015 and Mángano & Buatois 2016). The occurrence of transitional forms, however, poses a challenge for the systematics of ichnology, where differences in special trace characters mainly reflect variations in ethological behavior rather than differing body constructions. Today, most authors apply the classical approach, treating *Cruziana furcifera*, *Cruziana rugosa*, and *Cruziana goldfussi* as discrete ichnospecies, defined by the aforementioned criteria. Here, we follow this approach. *Cruziana furcifera* is a typical element of the *Cruziana rugosa* Group according to Seilacher (1970).

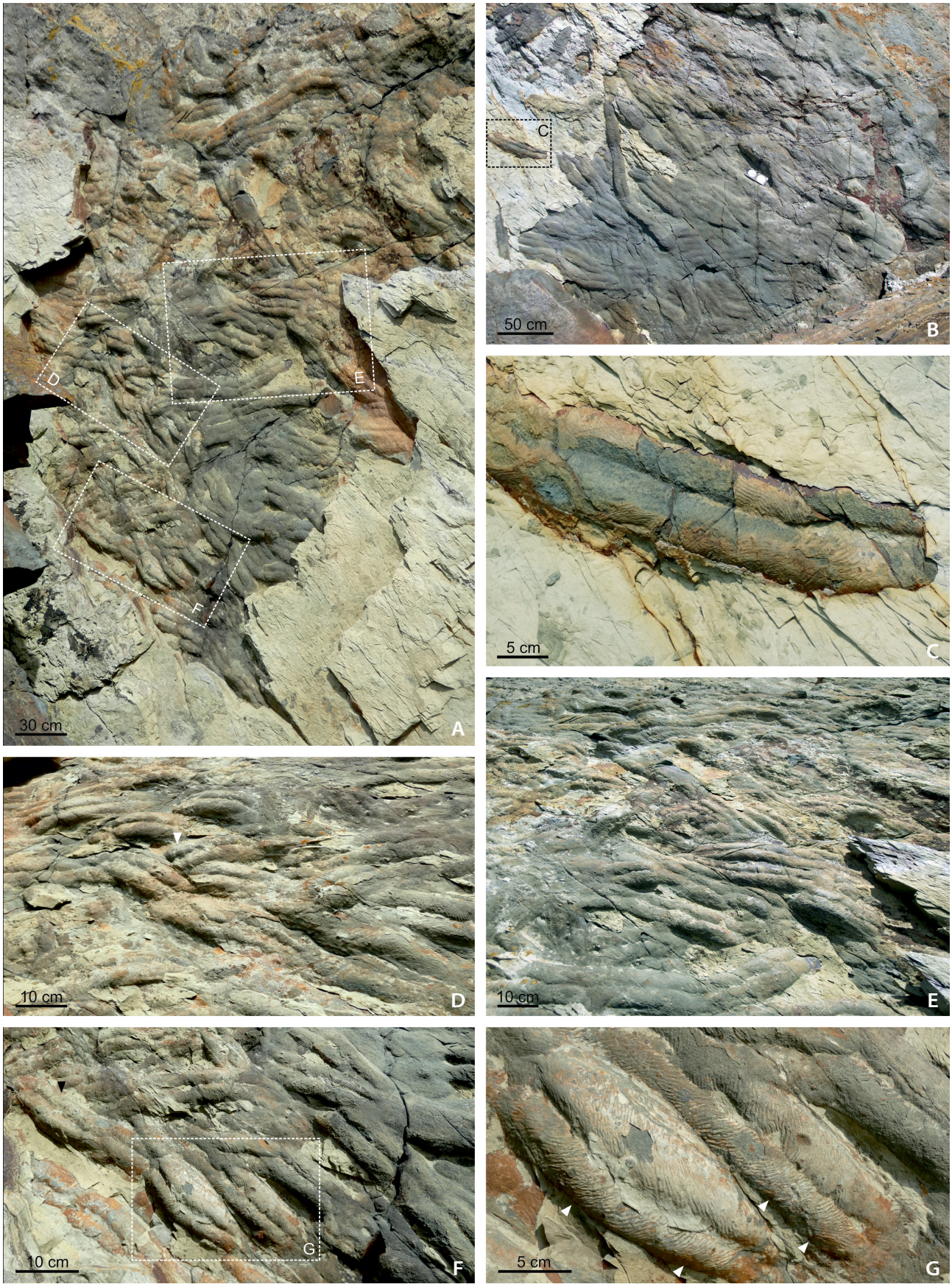
***Cruziana barriosi* Baldwin, 1977**
Figure 6A, B

1977 *Cruziana barriosi*; Baldwin, pp. 17–19, pl. 1c.
1990 *Cruziana barriosi*. – Fillion & Pickerill, p. 24, pl. 2, fig. 6.
2007 *Cruziana* cf. *barriosi*. – Sá *et al*., p. 437, fig. 3d.
2009 *Cruziana barriosi*. – Gibb *et al*., p. 699, fig. 2a, b.
2020 *Cruziana almadenensis*. – Meischner *et al*., p. 8, fig. 5a, b.

Material and locality. – More than 30 specimens on a lower bed surface within a heterolithic succession (about 4 m above the *Cruziana furcifera* surface described above); upper part of the Cap de la Chèvre Fm. (about 7 m below its top, as adopted by Bonjour 1988); coordinates: 48° 13′ 15.48″ N, 04° 24′ 7.37″ W, Beg-Ar-Gwin, Crozon Peninsula, Brittany.

Diagnosis. – Bilobate furrows without lateral grooves; lobes are flat-topped; scratches run mostly parallel to the long axis of the trace, sometimes showing very slight

Figure 5. Detailed views of the large sedimentary (lower) surface within the upper Cap de la Chèvre Fm. at Beg-Ar-Gwin (as shown in Fig. 4). • A – northwestern part of the outcrop showing nicely preserved large *Cruziana furcifera* trails within the heterolithic succession. Note that the fine-grained volcanoclastics still covering the trace fossil assemblage represent the underlying stratum (the section is overturned). Sectors of special interest are outlined by white rectangles and displayed enlarged in the labelled figures. • B – southeastern part of the outcrop. The *Cruziana* trace fossil trails show a length of more than 2.30 m (and seem to continue below the fine-grained cover). The ichnofossils in this part of the outcrop are rather poorly preserved due to a significantly longer-lasting exposure to weathering than the northwestern portion of the outcrop. The black rectangle indicates the *Cruziana* trace specimen previously observed by Bonjour (1988); most of the large surface area, with many other specimens visible today, was apparently entirely covered at that time. It was only the coastal weathering over the following decades that revealed the multitude and details exposed today. The indicated *Cruziana* specimen is shown in detail in (C). • C – close-up of the specimen of *Cruziana furcifera* already observed by Bonjour (1988) about 40 years ago. The surface of the lobes shows a characteristic reticulate scratch pattern typical of *Cruziana furcifera*. The surrounding fine-grained sediment is truncated by several *Monocraterion* (with concentric rings) and *Skolithos* burrows. • D – close-up of the northwestern part of the outcrop showing the common criss-crossing of many *C. furcifera* specimens. The white triangle points to an individual *C. furcifera* trace showing some corrugate-like features similar to *rugae* as known for *C. rugosa*. • E – close-up of the southeastern part of the outcrop with the same characteristics as in the Northwest (D), but in different, rather poor preservation. • F – close-up of the northwestern part of the outcrop with many *C. furcifera* specimens. Black triangle points to a few of the *rugae*-like structures, pointing to some degree of transition from *C. furcifera* to *C. rugosa* within the same trail. The white rectangle marks the area illustrated enlarged in (G). • G – close-up of (F) showing well-preserved details of large *C. furcifera* specimens. White triangles point to the particularly nice preservation of the reticulate scratch pattern, which is a typical diagnostic character of *C. furcifera*. Note that a morphological transition from cruzianiform to rather rusophyciform traces is vaguely indicated in some cases. The trilobite trails are subsequently penetrated by *Skolithos* and *Monocraterion* tubes.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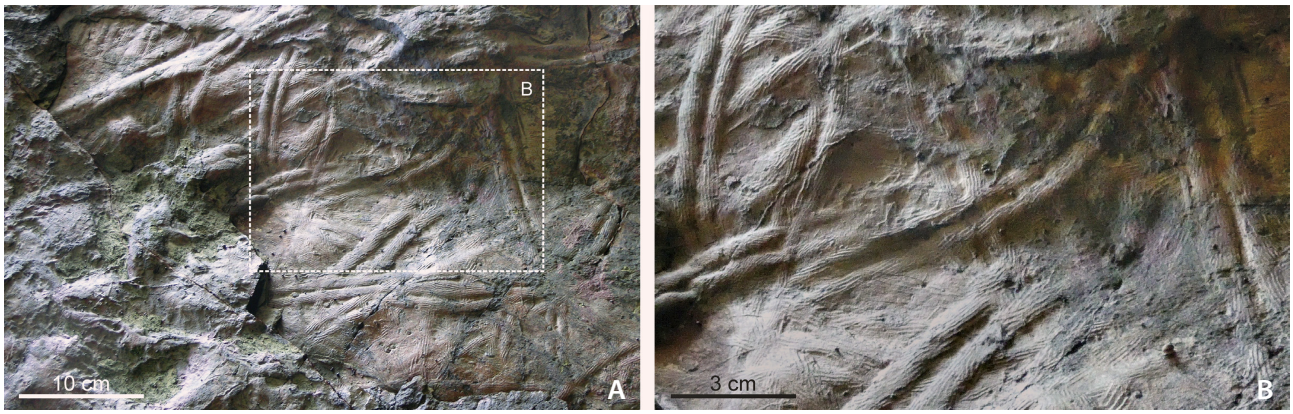

Fig. 6. *Cruziana barriosi* trails from the upper Cap de la Chèvre Fm. at Beg-Ar-Gwin. • A – largely monospecific assemblage of *Cruziana barriosi*; note some additionally occurring *Skolithos* specimens. The white rectangle displays the area of the detailed view shown in (B). • B – several trails of *Cruziana barriosi*; note that there is no preferred orientation of the trails. The striae (scratches) on the lobes are parallel to sub-parallel with the trace axis (the slight angle never exceeds about 10°). Some of the *Cruziana* specimens are penetrated by *Skolithos*.

divergence (V-angle); at least five scratches per lobe; median ridge may be wide (Baldwin 1977).

Description. – *Cruziana barriosi* represents the only arthropod trace on this surface (Fig. 6A). The only other, but non-arthropode trace fossils are represented by a few *Skolithos* and rare *Monocraterion* (see remarks given above), and undefined worm-like simple traces (Fig. 6B). Preservation is in positive hyporelief. The trails run more or less straight, with only occasional slight curves; their running direction is not consistent, and overcrossing is common. The width of the traces varies within 1.5–3.5 cm (mostly 2–3 cm), but is constant within a single trail. The number of striae is 5–6 per lobe, and they are straight, nearly parallel, with only a slight divergence and well-defined; a slight inclination of the parallel-running ridges can be observed, but this never exceeds 10°. The median groove, separating the two lobes, is broad, deep, and distinct. There are no lateral ridges.

Remarks. – *Cruziana barriosi* Baldwin, 1977, was erected as an ichnospecies based on material from northern Spain. Later, trace fossil findings from Newfoundland (Fillion & Pickerill 1990), Australia (Gibb *et al*. 2009), and Portugal (Sá *et al*. 2011) were assigned to this ichnotaxon. According to the original diagnosis the characteristic features of this cruzianiform bilobate trace fossil is in the general trail morphology, in the usually broad and flat topped lobes, in the absence of lateral ridges, in the sets of grouped striae (at least 5 ridges per set) that run more-or-less parallel with the trace axis, and, often, with a wide median ridge that separates the two lobes. It has to be stressed that there are significant differences between the hitherto reported specimens regarding their size (width of 7–12 cm in Spain and Newfoundland *versus* 2–3 cm in Portugal and Australia), and also in the number of striae per lobe (5–6 in Spain *versus* 9–12 in Portugal and Australia). The described specimens from Brittany are within this general size range. Here, we follow the opinion of Gibb *et al*. (2009) that a distinct size and a strict number of the striae are of minor taxonomic significance and do not legitimize the creation of several very similar ichnospecies.

Additionally, there is a remarkable congruence between the definition of the ichnotaxon *Cruziana barriosi* Baldwin 1977 and a *Cruziana* trace interpreted by Seilacher (1970) as the cruzianiform variant of his (rusophyciform) *Cruziana almadenensis* (*Rusophycus almadenensis* according to Mángano *et al*. 2016). Both Ordovician cruzianiform traces are known from only a few reports and regions, and descriptions and illustrations have been published in much smaller numbers, especially for *Cruziana almadenensis* Seilacher, 1970. In its original diagnosis, *Cruziana barriosi* Baldwin, 1977 is identical to the cruzianiform version of *Cruziana almadenensis*, as understood by Seilacher (1970). Until the systematic relationship between the two trace fossils is clarified through a detailed reinvestigation of the few original materials and sampling of additional specimens from the two type areas (which is beyond the scope of the present paper), some systematic confusion will remain.

Discussion

Stratigraphic aspects

The only fossil content of the Cap de la Chèvre Fm. comes from trace fossils. The diagnosed *Cruziana furcifera* d'Orbigny, 1842 and *Cruziana barriosi* Baldwin, 1977 are typical Ordovician ichnospecies. Both represent index trace fossils of the so-called *Cruziana rugosa* Group.

The stratigraphic occurrence of *Cruziana furcifera* is equivalent to what is known from the eponymous *Cruziana rugosa*. In his widely accepted stratigraphic scheme of Gondwanan *Cruziana* stratigraphy, Seilacher (1992, 2007) synonymised both ichnotaxa and mentioned only *Cruziana rugosa*. According to him, this ichnotaxon is typical of the Lower Ordovician (Seilacher has subdivided the Ordovician system into only lower and upper stages). It should be noted that Seilacher (1970, 1992) emphasized that the stratigraphic resolution of his scheme must be understated due to the usually missing body index fossils or radiometric geochronological control, and due to the resulting strongly limited correlation with other stratigraphic schemes. Trace fossils, in general, are facies-controlled and of limited stratigraphic significance, often being the only fossils in the sedimentary successions in which they occur. Seilacher's scheme, albeit quite rough in its temporal resolution, provides a general stratigraphic orientation applicable to the Gondwanan realm, rather than a detailed stratigraphic determination. This may explain why *Cruziana rugosa* and *Cruziana furcifera* have not been exclusively reported from Lower Ordovician deposits, but also from distinctly younger Ordovician strata (*e.g*. Egenhoff *et al.* 2007, Gibb *et al.* 2009, Aceñolaza *et al.* 2015, Neto de Carvalho & Baucon 2016). It should be noted, however, that Seilacher's *Cruziana* ichnostratigraphy is, nevertheless, of great value. Because of the limited range of the geographic dispersal of the early Palaeozoic trilobite trace makers (only a few hundred kilometres maximum according to Seilacher 2007), their much wider or even transcontinental dispersal was not possible. However, a gradual stratigraphic shift across the shelfal areas of the same palaeocontinent is conceivable but would lead to some stratigraphic diachrony. In the case of *Cruziana furcifera* and *Cruziana rugosa*, this means their stratigraphic occurrence on the northern Gondwanan shelf, which is largely equivalent to the region north of Africa (including the terranes there), is focused on the late Early to Middle Ordovician. In the more distant South American shelf sector, in contrast, both ichnotaxa are reported from Middle to Late Ordovician strata (Egenhoff *et al*. 2007).

In Brittany, *Cruziana furcifera* and *Cruziana rugosa* are best known from the Armorican Sandstone Fm., which ranges stratigraphically from late Floian to Dapingian (late Early to early Middle Ordovician; Durand 1985, Paris 2016, Dabard *et al*. 2021). Their presence already in the underlying Cap de la Chèvre Fm. points to an age somewhat older than late Floian for the here-discussed occurrence at Beg-Ar-Gwin. Given the relatively low lithostratigraphic distance between the *furcifera*-bearing layers of the Cap de la Chèvre Fm. and the Armorican Sandstone Fm., a generally Floian age (late Early Ordovician) for these trace fossils at Beg-Ar-Gwin might be reasonable. This is comparable to equivalent Ordovician deposits in Spain and Portugal – regions palaeogeographically closely related to Brittany (Paris & Robardet 1977; Noblet 1984; Gutiérrez-Marco *et al.* 2002, 2017a, b; Ballèvre *et al.* 2009; Sá *et al.* 2011, Neto de Carvalho & Baucon 2016). In southern Jordan (Arabian Plate), the same trace fossils occur in early Floian strata (Meischner *et al*. 2020, Elicki 2025).

For *Cruziana barriosi* from the type area in northern Spain (Barrios Fm.), Baldwin (1977) originally assigned a late Tremadocian age. Based on palynological data and regional correlations, a Floian age for the trace-fossil-bearing upper Barrios Fm. was, however, later suggested (Toyos & Aramburu 2014, Palacios 2015, Gutiérrez-Marco *et al*. 2019), although a late Tremadocian age could not be fully ruled out. Gutiérrez-Alonso *et al.* (2016) published zircon ages from volcanoclastics of the upper Barrios Fm. in the Cantabrian Zone (northern Spain) corresponding to the Tremadocian–Floian boundary. In Newfoundland, *Cruziana barriosi* occurs in the Arenig (= Floian to Dapingian; Fillion & Pickerill 1990), in Australia (Stairway Sandstone) in the middle to late Darriwilian (Gibb *et al*. 2009), and in Jordan (lower Dubaydib Fm.) in the late Darriwilian ?to earliest Sandbian (Meischner *et al*. 2020, Elicki 2025). In summary, for all currently known occurrences of *Cruziana barriosi*, it appears that the ichnospecies is most common in the Floian to late Darriwilian? but it generally spans an Early to Middle Ordovician stratigraphic range.

At Beg-Ar-Gwin, the stratigraphic occurrence of *Cruziana furcifera* and *Cruziana barriosi* from the Cap de la Chèvre Formation is more or less identical, because the lithostratigraphic position of both host layers within the sedimentary succession is in very close vertical distance (3.5–4 m). A more detailed estimation of the stratigraphic age of this depositional interval remains, however, problematic. This is because the fossil-bearing layers of the Cap de la Chèvre Fm. are positioned between the Armorican Sandstone Fm. above, and the geochronologically dated volcanic rocks of the lower Cap de la Chèvre Fm. below. For the Armorican Sandstone Fm., the oldest biostratigraphic evidence comes from late Floian chitinozoans (from the middle part of this unit; *brevis* Biozone; Paris 1990, 2016), supported by accompanying graptolite control for this chitinozoan biozone from several northern Gondwana regions (Paris 1990). From the lower Cap de la Chèvre Fm., a volcanoclastic layer sampled from the type area (that is approximately 13 km southeast of the Beg-Ar-Gwin locality and situated approximately 100 m below the base of the Armorican Sandstone Fm.), yielded a radiometric U-Pb age of 465 ± 1 Ma (Bonjour *et al.* 1988). The authors concluded an Arenigian coincidence with the palynological data from the Armorican Sandstone. According to the present refined international stratigraphic

scheme (ICS 2024, Cohen *et al.* 2013 updated), the geochronological age of 465 ± 1 Ma is Darriwilian (upper Middle Ordovician). This would mean, however, that the dated volcanoclastics of the lower Cap de la Chèvre Fm. would represent a middle Darriwilian age, whereas the overlying Armorican Sandstone Fm. should be late Floian to Dapingian in age, and therewith older than its underlying strata! It was already referred by Vidal *et al*. (2011) that an earlier published radiometric Rb-Sr-age of 472 ± 5 Ma (= late Floian) produced by Auvray *et al*. (1980) from volcanics in northern Brittany (Plouézec volcanics of the upper part of the Cambro-Ordovician so-called "Série Rouge", Went 2017), which they interpret as partly equivalent to the Cap de la Chèvre Fm., seems to be rather appropriate. Bonjour *et al*. (1988) questioned the accuracy of this radiometric data. For the Cap de la Chévre Fm. at the Beg-Ar-Gwin locality, there is additional geochronological information. Dabard *et al*. (2021) analysed a detrital zircon grain coming from a subarkose layer about 80 m above the base of the unit, which is approximately 55 m below the *C. furcifera* surface discussed here. They obtained an age of 484.7 Ma ± 7 Ma, which corresponds to the Furongian–Tremadocian boundary interval. In the course of our current research on a sample from a volcanoclastic bed directly below the *C. furcifera* surface at Beg-Ar-Gwin, we can preliminarily report comparable zircon ages (publication in preparation). Combining the recent stage of knowledge and until clarification of the stratigraphic inconsistency between biostratigraphic and chronostratigraphic data (possibly through re-sampling and re-investigation of the volcanoclastics, as well as probable additional palynological research), the stratigraphic position of the trace fossil assemblages of the Cap de la Chèvre Fm. at Beg-Ar-Gwin can be best estimated as early to middle Floian; only slightly older or younger ages – albeit less likely – cannot fully be ruled out.

Palaeoecological aspects

According to Mángano & Buatois (2016), a remarkable turnover in the character of trilobitic ichnofaunas is observed in the peri-Gondwanan realm at the beginning of the Ordovician period. Assemblages of the typical late Cambrian to early Ordovician *Cruziana semiplicata* Group were replaced by those of the *Cruziana rugosa* Group (Crimes 1975, Seilacher 1992). This change was relatively rapid (with some overlap) and occurred within the Tremadocian–Floian boundary interval of the middle Early Ordovician. The mentioned authors highlight changes (onshore–offshore relocation) in the taxonomic inventory of trilobite trace makers from shallow-marine heterolithic environments, which are the preferred areas for preserving trilobite traces. Such relocation of trace makers due to changes in the favoured habitats may reflect an evolutionary aspect. Late Ordovician trace fossil assemblages, in contrast, do not show such a distinct dominance of trilobite ichnotaxa as they do in the early and middle Ordovician (Mángano & Buatois 2016). This may further reflect (at least partly) the radiation of other organism groups during the Ordovician biodiversification event, and – due to increasing bioturbation – also a related increase in the loss of firmground substrates needed for preservation, especially of this kind of trilobite traces (Mángano & Buatois 2016).

Neto de Carvalho (2006) summarized the current state of knowledge and opinions regarding possible trace makers that produced the trilobite traces of the *Cruziana rugosa* Group. According to him, some *Cruziana furcifera* and *Cruziana goldfussi* specimens in the Penha Garcia Ichnological Park (Portugal) were produced by the same trilobite, but some *Cruziana rugosa* specimens should be attributed to a different species. Other observations from the same area, as well as from other regions and authors (*e.g*. Bergström 1976, Meischner *et al*. 2020), show morphological transitions among *Cruziana furcifera*, *Cruziana rugosa*, and *Cruziana goldfussi*, indicating that they were created by the same trilobite individual. Thus, all three ichnospecies seem to represent morphological variants of traces of the same animal, only depending on changes in its behaviour. This behaviour may also have been influenced by movement-related changes (such as changes in motion speed or feeding movements) and by environmental changes (including changes in grain size, water content in the substrate, water agitation, and population density). The *Cruziana furcifera* trace fossils from Berg-Ar-Gwin show delicate preservation of scratches and, sometimes, deep burrowing. Such preservation indicates a distinct stability of the substrate, which would otherwise have collapsed to some extent immediately after burrowing. The somewhat cohesive, muddy ground was subsequently quickly filled with overlying sand. In ichnology, this kind of cohesiveness is usually attributed to the presence of stabilising microbial organic matter around the sand grains (*e.g*. Hofmann *et al*. 2012, Mángano *et al.* 2013). The microbes secrete extracellular polymeric substances (biofilms), which, among other things, enable them to fix sediment (Noffke *et al*. 2025). This mucilage is an essential factor in the formation and preservation, especially of arthropod tracks and resting traces, produced in siliciclastic sediments. Such a relationship was also concluded by Neto de Carvalho (2006) for Ordovician trace fossil sites in Portugal, which are largely similar to the *Cruziana furcifera* assemblage at Beg-Ar-Gwin. This author further suggested that the common criss-crossing of trilobite trails may be partly explained by post-depositional compaction processes within the heterolithic succession, which combined trilobite traces originally

created at slightly different lithostratigraphic levels. Such a diagenetic effect may not be excluded to some extent in the Beg-Ar-Gwin trace fossil site, too. This means that recurring episodes of colonisation of rather fine-grained, microbially stabilised substrates, each followed by sudden deposition of coarser sandy layers, have enabled such excellent preservation. Depositional environments characterised by this kind of sedimentation, as well as the observed heterolithic depositional patterns (Bonjour 1988), are typical of shallow-marine areas with unstable conditions, such as in deltaic, estuarine, or marginal marine coastal regions. Other sedimentary textures, necessary for a more detailed determination, were not recognisable at Beg-Ar-Gwin due to the small outcrop size and severely limited accessibility of the strata. According to more detailed sedimentological observations by Bonjour (1988), the Beg-Ar-Gwin section of the Cap de la Chèvre Fm. generally represents a transition from alluvial to fluvial, and finally to deltaic conditions characterized by distributary systems. The investigated trace-fossil-bearing portion represents its uppermost part. In this part of the succession, Bonjour (1988) has not provided a detailed analysis. But he mentioned wide channel deposits and sandbars and suggested proximal-deltaic (possibly tidally influenced) and transitional conditions progressing. If the position of the upper boundary of the Cap de la Chèvre Fm. at Beg-Ar-Gwin is accepted in the understanding of Bonjour (1988), then the fully marine conditions are finally reached within only a small vertical distance by the onset of the overlaying Armorican Sandstone Fm. Comparable environmental conditions (as water depth, water agitation, temperature) have been assumed for stratigraphically more or less equivalent north Gondwanan successions that include comparable assemblages of remarkably large trace fossils of the *Cruziana rugosa* Group, *e.g.* from Spain (Baldwin 1977, Rodríguez-Tovar *et al*. 2014), Portugal (Neto de Carvalho *et al*. 2021), Saudi Arabia (Masri *et al*. 2014 and unpublished data of one of the authors, O.E.), Oman (Heward *et al.* 2016), United Arab Emirates (Fortey *et al.* 2011), Jordan (Meischner *et al*. 2020), and Turkey (unpublished data of one of the authors, O.E.).

For Brittany, the increasing number of trace fossil horizons in the upper part of the Cap de la Chèvre Fm. and the frequent, regular lithological changes (heterolithics) are consistent with an explanation of increasing tidal effects toward the top of this unit, as implied by Bonjour (1988). The limited diversity of the ichnofauna may additionally support this interpretation: only a few producer species were able to colonise the temporarily suitable niches. Their high abundance, however, suggests challenging palaeoecological conditions (such as unstable water levels and water agitation) and/or biological advantages for colonisation (*e.g.* ecological flexibility or colonisation speed). Although the trace-producing trilobite species cannot be precisely identified, for the distinctly large *Cruziana* traces of the *Cruziana rugosa* Group, asaphid trilobites are commonly assumed to be the most likely trace makers (Baldwin 1977, Fillion & Pickerill 1990, Neto de Carvalho 2009, Gutiérrez-Marco *et al.* 2017a, b). Earlier assumptions have also considered illaenid species (Seilacher 1990) or calymenids (Fortey & Morris 1982).

Concluding remarks

A striking general feature of ichnospecies in the *Cruziana rugosa* Group is the often-reported large size of these trilobite traces. Widths of around 10 cm are usual; those of up to 15 cm are observed at Beg-Ar-Gwin, and more than 20 cm in Portugal and Jordan (Neto de Carvalho & Baucon 2016, Meischner *et al*. 2020). Remarkably large widths of Ordovician trilobite traces (sometimes of more than 30 cm!) are reported from other palaeoregions, too, as from eastern Canada's St. Lawrence Lowland, from eastern Newfoundland, and from western Siberia (see compilation in Neto de Carvalho & Baucon 2016). Neto de Carvalho (2009) discussed a possible relationship between gigantism in *Cruziana* from Penha Garcia (Portugal) and palaeogeographic latitudes. During the Ordovician, this part of Gondwana was situated near the South Pole. Thus, the remarkable size in some trilobite taxa could represent the effect of "polar gigantism" that is also known today, *e.g.* from invertebrates and especially arthropods (*e.g.* De Broyer 1977, Moran & Woods 2012, Shishido *et al.* 2019). Albeit the theory of the occurrence of larger organisms in cold oceanic waters due to higher oxygen rates ("oxygen temperature hypothesis") is controversely debated (Woods & Moran 2020), a combination with other stress factors in high-latitude oceans, or of both mutual and taxon-specific factors (*e.g.* less predators, more extended time of individual growing, different biological conditioning between taxa *etc*.) might be speculated also for early Palaeozoic seas (Saleh *et al.* 2021). The giant Ordovician cruzianids from southern Jordan, the Arabian Peninsula, and the Middle East (see citations above) share the same palaeogeographic position in high southern latitudes as those found in Portugal and Brittany. Additionally, in southern Jordan, the Ordovician co-occurrence of monospecific bivalve assemblages with a general unusual large size of the individuals (Elicki 2025) seems to support a "polar gigantism" phenomenon. If true, then the extremely large size of the *Cruziana* traces from Siberia (Siberia palaeocontinent) and from Canada (Laurentia palaeocontinent) – albeit, most probably produced by different trilobite species – must be explained by other reasons due to their palaeoposition in the vicinity of the palaeoequator (Torsvik & Cocks 2017).

Because dispersal of mobile benthic organisms over a distance of a few thousand kilometres on the same shelf would produce only little stratigraphic diachrony, the Beg-Ar-Gwin trace fossils can be used as an effective stratigraphic tool, and thus for correlation opportunities with palaeogeographically adjacent regions at least. The Beg-Ar-Gwin trace fossil assemblage provides an important jigsaw piece that helps fill a gap in the Gondwanan shelf correlation before the widely distributed Armorican sandstone unit. It shows that this special kind of palaeoecosystems formed a distinct, continuous stripe along the northern Gondwanan shelfal regions.

Based on the here presented observations, further research is encouraged notably with regard to (1) biostratigraphic indications, *e.g.* from palynological investigation of the dark, fine-grained portions of the heterolithics of the Cap de la Chèvre Fm., (2) modern radiometric geochronology from syngenetic volcanic intercalations in the earliest Ordovician strata at Beg-Ar-Gwin (work is in progress by the authors), and (3) related research in comparable, but still underinvestigated deposits of adjacent Gondwanan regions.

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