# Running crabs, walking crinoids, grazing gastropods: behavioral diversity and evolutionary implications of the Cabeço da Ladeira Lagerstätte (Middle Jurassic, Portugal)

Caranguejos que correm, crinóides que caminham, gastrópodes que se alimentam: diversidade comportamental no Lagerstätte do Cabeço da Ladeira e suas implicações evolutivas (Jurássico Médio, Portugal)

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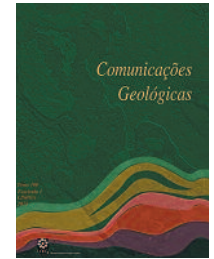
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Abstract: Ichnology is a powerful tool for understanding the evolutionary paths of animal clades, through the paleobiology of behavior preserved in Lagerstätten such as the Cabeço da Ladeira (Portugal) site. Here, the peritidal carbonates of the Chão das Pias Formation (Middle Jurassic, upper Bajocian) record the development of microbial mats in a tidal flat. Episodically, the flat was expanded during periods of equinoctial spring tides that may have been responsible for the *in situ* killing of several members of echinoderm clades, and the fine preservation of their endoskeleton, in addition to the behavior of an arthropod-dominated endo- and epifauna. Mat-preserved shallow tiers with a moderate ichnodiversity attributed to the *Cruziana* ichnofacies include trackways of crabs (*Laterigradus lusitanica* igen. nov., isp. nov.) and shrimps (*Diplopodichnus* isp.); trails of fishes (?*Undichna*), gastropods (*Archaeonassa fossulata*), isocrinid crinoids (*Krinodromos bentou* igen. nov., isp. nov.) and insects (*Haplotichnus indianensis*); and burrows of shrimps or lobsters (*Thalassinoides suevicus*) and other arthropods (*Asterosoma ludwigae*, *Gyrochorte comosa*), or polychaetes (*Rhizocorallium commune*). This is implied already above (igen. nov., etc.) and seems not needed. The crab trackways and gastropod bulldozing trails, extending up to 12.3 m, are among the longest invertebrate cursorial traces ever found in the fossil record. The mortichnial crawling trail of a crinoid is the first evidence of locomotion for this group in the fossil record, and a rare unambiguous example of this ethology. Extensive continuous trackways attributed to amphibious crabs record, with great detail, typical gaits of underwater punting and walking sideways on dry land. The earliest evidences of sidewalking behavior may also be evidence for the development of the crab form during their rise in the Jurassic.

Keywords: Ichnology; tidal flat; walking sideways; amphibious brachyurans; crinoid mortichnion; Bajocian.

Resumo: A Icnologia é um poderoso instrumento para a compreensão das etapas evolutivas de clados de animais através da paleobiologia do comportamento inscrito em sítios paleontológicos excepcionais, como o Cabeço da Ladeira (Portugal). O Jurássico Médio (Bajociano superior) da Formação de Chão das Pias é formado por uma sequência de carbonatos peritidais que regista o desenvolvimento de tapetes microbianos numa planície de maré. Episodicamente, esta terá tido um desenvolvimento extraordinário através de marés equinociais que poderão ter sido responsáveis pela morte *in situ* de diversos grupos de equinodermes e pela preservação com excelente detalhe dos seus esqueletos articulados, além das formas de comportamento de uma endo- e epifauna dominada pelos artrópodes. Os níveis superficiais, com uma moderada icnodiversidade preservada pelos tapetes microbianos e atribuível à icnofácies de Cruziana, incluem trilhos de caranguejos (*Laterigradus lusitanica* nov. igén.) e de outros crustáceos (*Diplopodichnus* isp.), assim como eventualmente de peixes (?*Undichna*),

pistas de gastrópodes (*Archaeonassa fossulata*), crinóides isocrinídeos (*Krinodromos bentou* nov. igén.) e insectos (*Haplotichnus indianensis*), além de galerias de lagostins ou de lagostas (*Thalassinoides suevicus*), e de outros artrópodes (*Asterosoma ludwigae*, *Gyrochorte comosa*) ou poliquetas (*Rhizocorallium commune*). *Laterigradus lusitanicus* e *Krinodromos bentou* são novos icnogéneros e icnoespécies definidos neste trabalho. Os trilhos de caranguejos e as pistas de gastrópodes são algumas das mais extensas evidências de locomoção encontradas no registo fóssil dos invertebrados até ao momento. A "marcha para a morte" de um crinóide é o primeiro registo fóssil de locomoção para este grupo, e um raro exemplo desta categoria etológica. Extensos trilhos contínuos também evidenciam com grande detalhe os estilos de locomoção "salto com vara" subaquático e "caminhada de lado" em terra emersa característicos dos caranguejos anfíbios. Os mais antigos indícios da locomoção "de lado" poderão ser também a evidência da evolução da forma de caranguejo com a diversificação dos Brachyura durante o Jurássico, um clado bem-sucedido que culminou com a colonização de habitats terrestres devido às suas exaptações motoras.

Palavras-chave: Icnologia; planície de maré; locomoção lateral; caranguejos anfíbios; mortichnion de crinóide; Bajociano

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1. Introduction

Since the founding times of ethology by Niko Tinbergen and Konrad Lorenz, behavior is considered in a complementary way as a mixture of immediate (or mechanical) causes and evolutionary purposes (Alcock, 2013). At the immediate level, actions taken by

an organism are the result of internal physiological mechanisms (demand) that are the by-product of a particular developmental process depending on interactions between genotype and environmental variables. However, even in completely different groups of organisms, convergent behaviors are generated in an equivalent pool of genetic solutions under similar environmental conditions (universality *sensu* Barzel and Barabási, 2013). Nevertheless, each animal species possesses its own neural mechanism which, for pattern-selective processes, means subtle differences in the mode of reaction to stimuli from related species. On the other hand, behavior may evolve divergently when subjected to different selection pressures through time. The substantial modification of behavior due to constant adaptation to ecological changes through time and coevolution, may generate a functional change by aptation, if this increases reproductive success of the species (Vermeij, 1987; Boucot, 1990). Biological behavior, whenever preserved in the fossil record, was impacted by genetic adaptations, by the original environmental and ecological parameters, diagenetic overprints and even, in some ancient cases, tectonic strain (Neto de Carvalho, 2011). Ichnology, the discipline coping with the analysis of organism-sedimentary environment interactions (description, classification and interpretation), is a fundamental link between biological mechanisms and geological processes (Plotnick, 2012). Trace fossils combine functional morphology and behavior of producers, but also the physical-chemical properties of the original environment-related substrate. Only in remarkable examples of those, it is possible to obtain substantial data on the ecology, functional morphology and behavior that ultimately lead to detailed knowledge of the soft-bodied or light-armored (behavioral or behavior is spelled the American way consistently producer. Therefore, ichnosites with an extraordinary quality and quantity of ichnological information are known as ichnolagerstätten (Savrda, 2007).

Recently, an exceptional new site was identified in the Middle Jurassic of Portugal, and has been studied by a multidisciplinary team. On about 4000 m² quarry exposure, some of the longest and continuous crawling trails and trackways ever described in the invertebrate fossil record were found. Large numbers of fully-articulated echinoderms are the most common macrofauna at this site (Pereira *et al*., 2014a,b; Pereira, 2015). Both trace and body fossils hold high paleobiological importance, due to their remarkable fine preservation, age, rarity on rocks from similar age and their high abundance. Cabeço da Ladeira records a shallow-tier preservation of trackways and trails, and different echinoderm clades in anatomical full- or semi-articulation, due to the presence of extensive microbial mats whose evidences are also widespread at the site (see below).

The aim of this paper is to report on various horizontal trace fossils predominantly preserved on the bedding plane that are present at the same beds as the well-preserved echinoderms. We discuss their evolutionary and behavioral implications, namely the acquisition of morphological exaptations that enabled new modes of locomotion and ultimately, the colonization of new habitats. The moderately diversified ichnoassemblage is composed mostly of arthropod trackways, trails and burrows. They include the earliest trackways indicating the presence of amphibious true crabs walking sideways in the Middle Jurassic, very long and almost linear bulldozing trails attributed to gastropods moving in the ebb tide, and the very first locomotion trails left by stalked crinoids in the fossil record.

2. Stratigraphy of the Cabeço da Ladeira fossil site

The site of Cabeço da Ladeira is located about 2 km to the north of the locality of São Bento, municipality of Porto de Mós, in the

Serras de Aires e Candeeiros Natural Park (Fig.1). This area lies within a regional structure called Maciço Calcário Estremenho, located in the central area of the Lusitanian Basin. The Lusitanian Basin is located along the western Iberian margin and resulted from extension related to the opening of the North Atlantic. The sedimentary record of this rift basin is oriented NNE-SSW along 200 km and 100 km wide, with a maximum thickness of 4 to 5 km. The Maciço Calcário Estremenho was uplifted by compressive tectonic forces, associated with the Alpine Orogeny (Kullberg *et al*., 2013). Its tectonic structure is generically divided into three elevated regions separated by elongated fault-related depressions, cropping out rocks from the Jurassic. The Lower Jurassic is restricted to narrow salt walls where Hettangian evaporites occur. On the other hand, the Middle Jurassic consists of bright colored limestones, exposed on the top of the elevated regions. They were formed in different paleoenvironments at a carbonate ramp depositional system (inner ramp: Azerêdo, 1998, 2007). The Upper Jurassic is characterized by limestones and marls, with colors varying from brown to grey, appearing on tectonically controlled, depressed areas. With the exception of the rocks in the vicinity of the main faults, beds are sub-horizontal. The geosite *Cabeço da Ladeira* is within
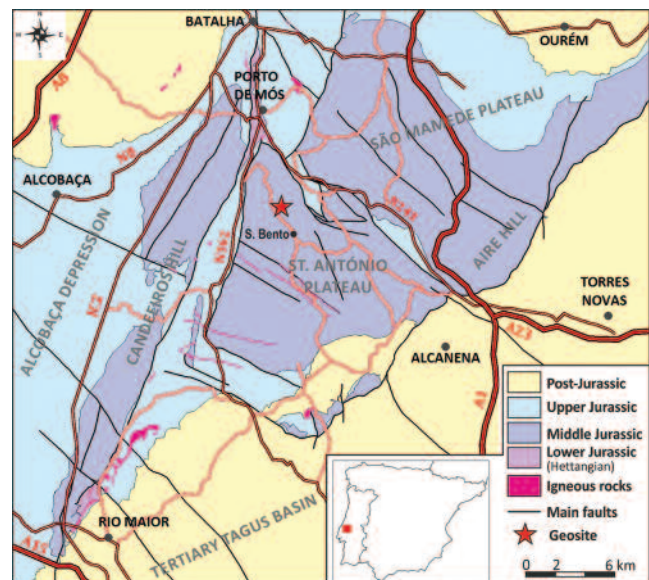

Fig. 1. Geological map of Maciço Calcário Estremenho with the location of the site under study (adapted from Carvalho, 2013; Pereira *et al*., 2014a).

Fig. 1. Mapa geológico do Maciço Calcário Estremenho com a localização do local em estudo (adaptado de Carvalho, 2013; Pereira *et al*., 2014a).

one of those elevated structures, known as the *Santo António* plateau, exposing rocks from the Middle Jurassic period.

According to Azerêdo (2007), it is possible to observe, from the base to the top, the Barranco do Zambujal Formation (Aalenian-lower Bajocian), the Calcários de Vale da Serra Member (upper Bajocian) from the Chão das Pias Formation and the Codaçal Member (lower Bathonian) from the Santo António-Candeeiros Formation. The Cabeço da Ladeira succession is exposing upper Bajocian sediments from the Vale da Serra Member of the Chão das Pias Formation (Sauzei biozone; Ruget-Perrot, 1961). With a thickness of 50-to-60 m, the sequence is formed by greyish yellow marly limestones and clayish limestones (mudstone and wackestone micrites and biomicrites with ammonoids and echinoderms) in the lower part. Towards the top, a gradual transition to calciclastic and dolomitic limestones, wackestone and packstone intrapelmicrites and biopelmicrites occur (Azerêdo, 1998). The increasing intercalation, from east to west and from the base of the sequence

to its upper part, of dolomitized oobioclastic, massive dolomite and dolomite laminated levels, testimony a regressive trend in facies, with progradation of shallower conditions with microbial-algal mats (Azerêdo *et al.*, 2003).

At the quarry, the succession is composed of seven different cm-scale limestone beds (Fig. 2) deposited under very shallow subtidal-to-intertidal conditions, with episodic short-term aerial exposure without evidence for the development of soils. Newly exposed rock has a white to beige color, but acquires a dark grey and yellow-to-orange color due to the exposure to weathering agents and the growth of lichens. Thin clay layers are also present between some of these limestone layers and filling some epichnial trails. The rocks, mostly limestones, range from mudstone to wackestone, with a variable component of peloids, bioclasts and intraclasts (Fig. 3).

The clast size varies between and within layers. Intralayer variations are often very sharp and associated with erosion surfaces. Erosion surfaces and truncations are also quite evident, with a normal grading. Laterally, grain size can vary rapidly. Nevertheless, it is possible to observe a slight decrease in layer thickness and overall grain size towards the top of the section. On the upper surface of some limestone layers there are beautifully preserved ripple marks. These ripples occupy a significant area of this locality, being separated in two groups, with parallel or anastomosing crests (Fig. 3A). The parallel ripples appear to have symmetric sides, and are mostly oriented NNW-SSE. Microbial-mat-related structures (Seilacher, 2008; Noffke, 2010) are abundant, represented by a lower, mineral-rich layer: big wrinkle structures are preserved in bed 6 (Fig. 3G) and palimpsest, multidirectional ripples are found in bed 2; elephant skin, mud (mat) chips, "foam" structures and shrinkage cracks are spread all over the fine iron-rich laminate levelling structures that partially covers long trackways in bed 3 (Fig. 3D). The recurrent presence of microbial mat-related structures in the sequence shows that the deposition took place in very shallow conditions of the carbonate mudflat. However, echinoderms are abundant and indicative of subtidal environments. Nevertheless, sudden environmental changes were responsible for their death mostly in life position and the preservation of almost intact articulated skeletons (Fig. 3A). Rill marks cut the microbial mat structures and cross the ripple marks in mainly SW direction. They are good indicators of the lower foreshore above the low tide (Fig. 3H). Deep-imprinted trails and trackways crossing the mudflat show episodes of aerial exposure that may have been related to spring tides that periodically exposed wider areas from the lower intertidal-upper subtidal. Growth of biomats usually occurs in harsh and hypersaline environments uninhabitable for most burrowing organisms (Knaust *et al.*, 2012) and therefore provides excellent substrate conditions, through the formation of leathery semi-rigid top layers, for survivorship and preservation of those delicate trackways (De, 2014; Fig. 3F) and shallow-tiered burrows.

More than a hundred echinoderm specimens have been identified at this locality, with the potential for increasing the number (Pereira, 2015). The echinoderms appear more or less scattered evenly throughout the exposed rock area. All seven beds exposed in the quarry are bioturbated, and beds 1, 2, 3, 4 and 7 have echinoderm fossils. So far, beds 5 and 6 did not yield any echinoderm fossils. However, the exposed area of these two layers is substantially smaller than the other beds, so they may also contain fossils. In the vast majority of the cases, echinoderms are preserved semi-articulated, with rare cases of isolated spines and disassociated plates of echinoids. In many cases, only the external molds of echinoderms are present, with the actual fossil no longer present either due to erosion or rock quarrying activity. The echinoderm fossils found on that site belong to four distinct echinoderm classes (by order of abundance): the Echinoidea, including *Heterocidaris* sp. nov., *Stomechinus bigranularis* (Lamarck, 1816), *Stomechinus*
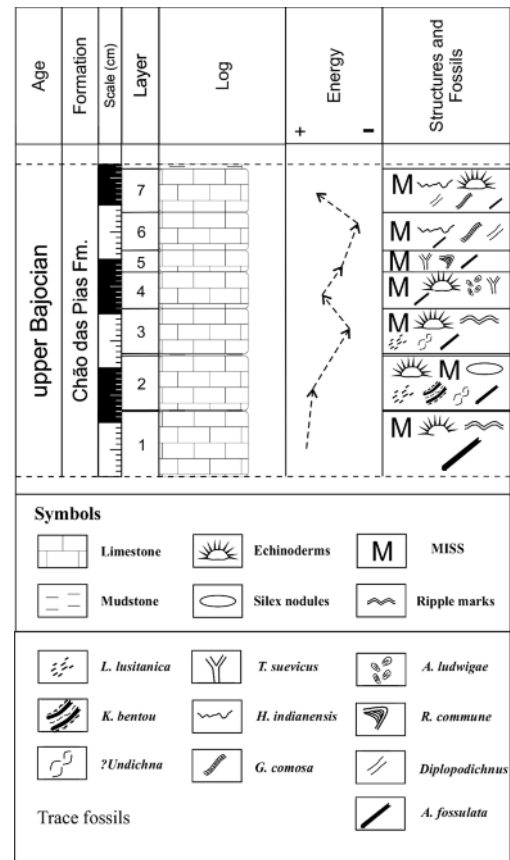

Fig. 2. Simplified lithostratigraphy of the Cabeço da Ladeira site (modified from Pereira *et al.*, 2014a).

Fig. 2. Litostratigrafia simplificada do sítio de Cabeço da Ladeira (modificado de Pereira *et al.*, 2014a).

sp., ?*Gymnodiadema hessi* Smith, 2011, *Paracidaris spinulosa* (Cotteau, 1875) and *Rhabdocidaris* spp.; the Asteroidea, with *Noviaster* sp. nov. and indetermined goniasterid; the Crinoidea, showing few isocrinid and possible ?comatulid representatives; and Ophiuroidea indet. (Pereira, 2015). Along with fossil echinoderms, rare bivalves and brachiopods are also present. The extraordinary preservation of these echinoderms, which are not commonly resistant to post-mortem processes, is typically associated with high sedimentary rates and rapid burial, as well as little transport (Baumiller *et al.*, 2008).

Following the observations of Mángano and Buatois (2004) for bioturbation in tidal flats, the Bajocian open-marine tidal flat of Cabeço da Ladeira developed on a carbonate ramp characterized by: 1) moderate ichnodiversity; 2) marine trace and body fossils of stenohaline forms, such as echinoderms and the elements of the *Cruziana* ichnofacies; 3) the presence of both infaunal (burrows) and epifaunal traces (trackways and trails); 4) the presence of both trophic generalists (*Archaeonassa*) and specialists (*Thalassinoides, Asterosoma*); 5) the dominance of horizontal trace fossils of the *Cruziana* ichnofacies, such as *Thalassinoides, Rhizocorallium* and *Gyrochorte*; 6) the presence of multispecific ichnoassociations; 7) the high levels of bioturbation, especially for *Thalassinoides* and *Archaeonassa*; and 8) the wide size range, as can be found for small and large types of *Thalassinoides*.

The remarkable preservation of trackways may be explained by stress factors that may have isolated the mixed layer from subsequent bioturbation (Pirrie *et al.*, 2004). The associated ichnofauna shows the common development of firmgrounds in a shallow-tiered *Glossifungites*-type ichnofacies (MacEachern *et al.*, 1992).
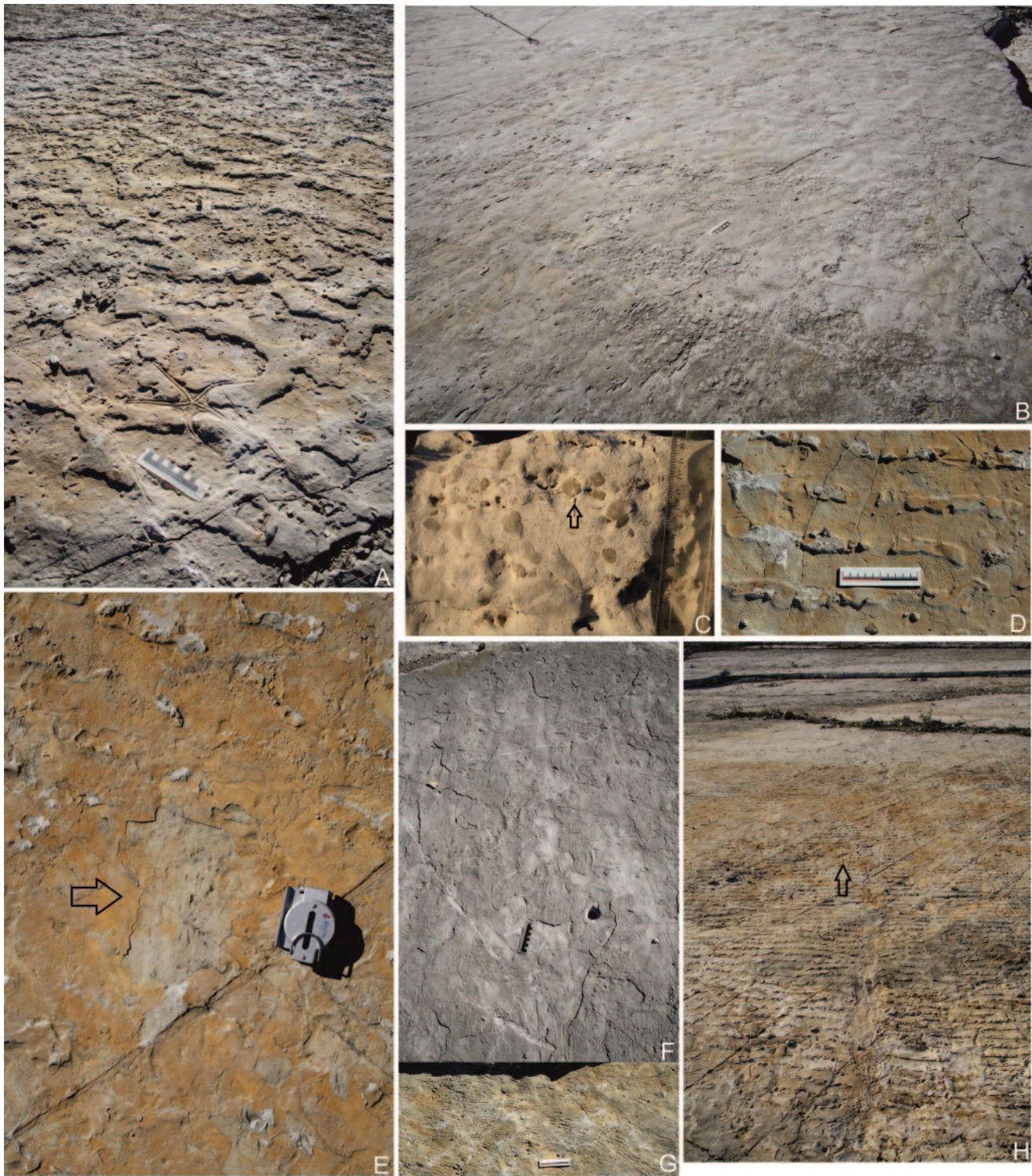
Fig. 3. Tidal flat sedimentary structures. A – Asteroid preserved resting on the rippled surface of bed 1; B – Oncoidal patches covered by the microbial mat (bed 2); C – Bioclastic concentrations; D – Laminae coated by oxides showing shrinkage cracks and "elephant skin"; E – Erosional pockets in the oxide-rich laminae revealing trail preserved underneath (bed 6); F – Microbial mat overgrown on a trailed surface; G – Wrinkle structures; H – Rill marks crossing the rippled-flat.

Fig. 3. Estruturas sedimentares de planície de maré. A – Asteróide preservado entre ripples na superfície da camada 1; B – Agregados de oncóides cobertos por tapete microbiano (camada 2); C – Concentrações bioclásticas; D – Lâmina de óxidos exibindo fendas de retracção e estruturas em "pele de elefante"; E – Bolsas de erosão na lâmina rica em óxidos revelando um trilho subjacente (camada 6); F – Crescimento de um tapete microbiano sobre uma superfície com trilhos; G – Estruturas pregueadas; H – Marcas de escoamento erodindo a planície com ripples.

3. The earliest sideways walking crab trails

3.1 Evidences for a crab-form tracemaker and the evolution of sideways locomotion

The Cabeço da Ladeira site possesses a remarkable preservation of very long trackways and trails crossing the microbial-mat related structures and ripple-marks that cover some of the beds, especially beds 2 and 3. Trackways represent single and fast excursions across the tidal flat by a multi-legged animal. The longest one measures 12.30 m and may be the longest fossil invertebrate trackway known in the world (Fig. 4A,B; see below). The trackway slightly curves along its course. It is composed by sets of up to four footprints, externally measuring 65 mm wide (Fig. 4C). Footprints are pit- to sigmoid-shaped, 3 to 25 mm long, showing different preservational conditions and depths related with heteropody (Seilacher, 2008). Along the trackway sets of up to twelve prints sometimes occur, forming a circular pattern that can be interpreted as probing behavior, through the use of sharp dactyls for chemoperception (*sensu* Schäfer, 1972; Fig. 4D). Together with the four-footprint sets, the stride lengths of 40-80 mm and metachronal gait clearly suggest an aerial style of locomotion. Based on the evidences presented, these trackways were most likely made by an amphibious decapod crustacean morphologically adapted for walking and running sideways (Fig. 5).

In the morphology of decapod crustaceans, thorax elongation is the most important feature, together with leg length, lateral flattening and placement at rest, to reflect the walking preference (Vidal-Gadea *et al.*, 2008). The most successful evolutionary trend of crabs and some crab-like anomurans (*e.g.*, Porcellanidae) was the progressive reduction of the long and vulnerable abdomen, which reduces drag and greatly hinders faster locomotion, alongside the inflexion of the reduced abdomen against the sternum (Förster, 1985), which favored the development of the crab form and sideward locomotion. Supported by phylogenetic analysis of DNA sequences, and gene rearrangements, Morrison *et al.* (2002) suggested that the evolution of the crab-like form and, therefore walking sideways, had five independent origins in bottom-dwelling crustacean decapods, the most successful one in the Brachyura, and four others in the Anomura (Porcellanidae, Paguroidea, Coenobitoidea and *Lomis*). Sideward walking provided crabs the unique advantage of being equally fast in opposite directions through increasing multilegged stride length (Vidal-Gadea *et al.*, 2008). Actually, the ecological dispersion of brachyurans to land habitats may have been aided by the use of sideways octopedal locomotion (Full and Herreid, 1984). Not all brachyuran crabs can walk sideways. In such gait, pairs of the four leading limbs are used in combination with alternating pairs of trailing limbs, which may result in longer, sigmoidal imprints in the substrate. The leg joints articulate along consecutively perpendicular planes. This possibly was an exaptation for the evolution of walking sideways (Vidal-Gadea *et al.*, 2008).

The main trail attributed to gastropods (Fig. 4) is followed at least for half of its length by a crab trackway more than 4 m long and 65 mm wide. This trackway is composed of sets of 2-3 elongated footprints with a stride length of 140-170 mm (Fig. 4G). Besides this example, there are at least two more trackways in Cabeço da Ladeira showing evidence of a punting gait under water (*sensu* Martinez *et al.*, 1998; see Fig. 9G). Crabs walking sideways experience drag forces perpendicular to their longitudinal axis. On land, crabs never have fewer than three legs in contact with the ground at any time. Drag forces are partially offset by lifting forces underwater due to buoyancy. Thus, legs touch the bottom less frequently moving under water compared to locomotion on land, as observed during lab experiments by Martinez *et al.* (1998). In underwater punting locomotion, only 2-3 legs are in contact with the ground at any time and leg kinematics is much more variable than on land. This thrust and gliding motion can be clearly followed in some of the Cerro da Ladeira trackways (Fig. 4G, 5).

The crab trackways and the crawling trails attributed to gastropods show the same orientation of the rill marks perpendicular to the rippled microbial mat surface. According to the asymmetry of the imprints in the longest trackway, the crab may have walked in the opposite direction of the tide. The substantial depth of the footprints, the use of at least four legs in walking or running, and the carcasses of many echinoderms also suggest the aerial exposure of the flat during a low tide. Several faint parallel trackways were also found under the microbial-mat layer (Fig. 4). In some places of the tidal flat it is possible to find circular mounds with a central crater measuring 28-50 mm in diameter (Fig. 4E). These may be interpreted as simple crab burrows used to protect the crab during the low tide cycle, as we can find nowadays for the Similar-sized side-runner *Carcinus maenas* (Linnaeus, 1758) (Fig. 4F). The Green crab is active during high tide, foraging on prey and grazing the algal and microbial mats that develop at the sediment surface (Baeta *et al.* 2006; CNC, pers. obs.). During low tide, they look for protection from predators and dehydration in simple burrows excavated by the leading limbs, using the wedge-shaped carapace to shovel the sediment above them. These transient burrows are abandoned every time they feel endangered after which a new one is built. However, we cannot exclude the possibility that these mounds may be related with the *Thalassinoides* producer, whose burrow mazes are also common in the succession.

This study implements previous works on the application of ichnology for understanding the evolution of crustaceans (Baucon *et al.*, 2014). This shows that trace fossils with a distinctive bioprint (Kopaska-Merkel and Rindsberg, 2015) are useful for interpreting the evolutionary history of organisms with a relatively low preservation potential, such as arthropods with lightly mineralized exoskeletons.

3.2 The earliest evidences of true crabs

The Early and Middle Jurassic fossil record of crabs is not very rich. Using molecular phylogenetics, Tsang *et al.* (2014) suggested that Brachyura, as its sister group Anomura, would have been present together over 180 Ma ago. The superfamily Majoidea has the oldest lineage diverging 254 Ma ago, according to Porter *et al.* (2005), but the oldest majoid fossils thus far are only mid-Cretaceous (late Albian) in age (Klompmaker, 2013). Divergence time estimates for Brachyura by Tsang *et al.* (2014) are more conservative and suggest around 170-171 Ma. Nevertheless, the first brachyurans in the fossil record appeared in the Lower Jurassic (Pliensbachian; see Schweitzer and Feldmann, 2010; Haug and Haug, 2014). Krobicki and Zatón (2008) suggested that the evolution of prosopid crabs apparently began in Early Jurassic on shallow, soft bottom marine environments. Brachyuran diversification started slowly during the Middle Jurassic (Müller *et al.*, 2000; Klompmaker *et al.*, 2013). No crab species are known from the Toarcian or Aalenian. The earliest crabs living in the subsequent Bajocian times were *Pithonoton, Eodromites, Gabriella, Tanidromites, Abyssophthalmus, Planoprosopon, Eoprosopon* and *Foersteria*, all based on European occurrences. While most of them have elongated carapaces and most likely walked forward, members of the genus *Pithonoton* show an ovoid or sub-pentagonal carapace that that may suggest a sideward locomotion. However, one of the largest Jurassic crab, *Eodromites grandis* (von Meyer, 1857) hardly exceeds 30 mm (dataset, Klompmaker *et al.*, 2015), which is significantly small to have produced the observed trackways. In the Lusitanian Basin, the earliest record of brachyuran body fossils thus far occurs much later in the Late Jurassic (mid-Oxfordian; Mateus *et al.*, 2013).

Reports of fossil brachyurans preserved *in situ* with their trace fossils are limited to the longusorbiid *Longusorbis cuniculosus* (Richards, 1975) from the upper Campanian to lower Maastrichtian of British Columbia, Canada (Richards, 1975); *Icriocarcinus xestos*

Fig. 4. Sideways running and water punting tracks as evidences for the presence of amphibious true crabs. A – The longest crab trackway crossing the Middle Jurassic tidal flat of Cabeço da Ladeira; B – Idem. Initial cast of the trail to give an idea of the extension and orientation of the trackway; C – Sets of four dactyl prints showing short stride length; D – Sets of 8-12 imprints evidencing resting places and possibly chemoperception along the trackway; E – Simple burrows attributed to sheltering behavior of crabs during the low tide; F – Locomotion and burrowing traces of *Carcinus maenas* during the low tide at the mouth of Aljezur river, SW Portugal; G – Water punting gait revealed by a lower number of imprints per set, longer imprints and increased stride length; H - Several sub-parallel trackways oriented N30ºW, sometimes intersecting each other, more than 20 mm wide.

Fig. 4. Trilhos de corrida "de lado" e de "salto com vara" subaquático como evidência da presença de verdadeiros caranguejos anfíbios. A – O mais longo trilho de caranguejo cruzando a planície de maré do Cabeço da Ladeira (Jurássico Médio); B – Idem. Início da moldagem do trilho dando a ideia da extensão e orientação do mesmo; C – Conjuntos de quatro impressões das patas exibindo um curta passada; D – Conjuntos de 8-12 impressões mostrando locais de descanso e possível quimio-receção ao longo do trilho; E – Galerias simples atribuídas ao hábito de refúgio dos caranguejos durante a maré baixa; F – Marcas de locomoção e de enterramento de *Carcinus maenas* durante a maré baixa na foz do rio Aljezur, SO de Portugal; G – Estilo de locomoção "salto com vara" subaquático evidenciado pelo menor número de impressões por conjunto, impressões mais longas e aumento do comprimento da passada; H – Diversos trilhos sub-paralelos orientados segundo N30ºW, por vezes intersectando-se entre si, com mais de mais de 20 mm de largura.

(Bishop, 1988) from the upper Campanian or lower Maastrichtian of California, USA (Bishop, 1988), the carpiliid crabs from the Oligocene of Kachchh, Gujarat, India (Gurav and Kulkarni, 2016), and the goneplacid *Ommatocarcinus corioensis* (Cresswell, 1886) from the lower Miocene-Pliocene of Australia (Jenkins, 1975). The scarcity of fossil crabs is well-known, when compared to heavier calcified taxa. They are frequently overlooked and, mostly because they are rarely preserved in coastal and nearshore facies and are far less abundant in pre-Late Jurassic sequences (Stempien, 2005; Klompmaker *et al*., 2013). By the Bathonian times, amphibious crab-like animals may have been producing burrows in gregarious populations within supralittoral breccias-conglomerate and littoral in a closed and shallow, low-salinity to freshwater coastal-lagoon setting, attributed to the *Psilonichnus* Ichnofacies (Marshall, 2003). These trace fossils found in NW Scotland could potentially provide the earliest known record of crab activity and their physiological adaptation to survive in a semi-terrestrial environment. The explosive adaptive radiation of the short-tailed crab-like type took place in the Late Jurassic (Förster, 1985). Rapid diversification of mostly reef-swelling crabs during the Late Jurassic coincided with a major expansion of reefs (Klompmaker *et al*., 2013). The remarkable findings described for Cabeço da Ladeira, Portugal, of crab trackways produced on an emerged tidal flat may push the evolution of true crabs with amphibious adaptations into the Middle Jurassic (late Bajocian).
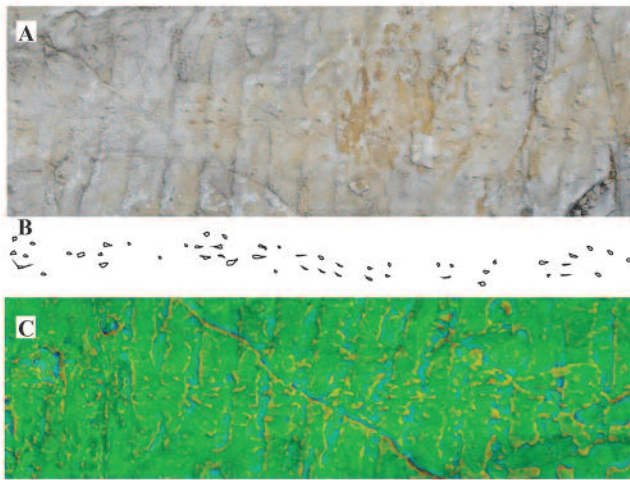

Fig. 5. 3D Model of *Laterigradus lusitanicus*. The trackway is clearly perpendicular to the ripple marks; only a section is represented to show the transition from aerial sideways running, with three to four long-shaped imprints, to an underwater punting gait where just two limbs are used, leaving circular pits behind. A – 2D orthophotography; B – Image interpretation by means of digital drawing; C – 3D model colored by an algorithm for curvature enhancing.

Fig. 5. Modelo 3D de *Laterigradus lusitanicus*. O trilho é claramente perpendicular às ripple marks; representa-se unicamente uma secção que demonstra a transição da corrida lateral aérea, com três ou quatro impressões de forma alongada, para um estilo de locomoção "salto com vara" subaquático onde unicamente dois membros são utilizados, deixando depressões circulares na retaguarda. A – Ortofotografia 2D; B – Interpretação da imagem através de desenho digital; C – Modelo 3D colorido através de um algoritmo para reforço por curvatura.

4. Among the longest invertebrate trackways and trails

At Cabeço da Ladeira there are several meter-long trackways attributed to crabs, trails that may be attributed to fishes (see below) and simple and straight furrows that may be compared with gastropod trails common to tidal flats. These latter trails consist of a central, flat furrow bordered by two narrow parallel ridges and almost vertical boundaries (Baucon, 2008; Fig. 6A). Two of the trails end in an elliptical-shaped pit (Fig. 6B). These burrows are

oriented towards the coastline and may be interpreted as if the producer looked for protection from dehydration or the phreatic level to keep the gills moist. The trail depth and sharpness may suggest that the animal was grazing the microbial mat during emersion episodes, cutting through the rippled surface by bulldozing the sediments in straight lines perpendicular to the estimated coastline (Fig. 6C). Gastropods are relatively slow crawlers (*e.g.*, Vermeij, 1987, and references herein). Following the shortest distance to water would significantly reduce the time exposed to the elements and predators. However, there are also more sinuous long trails showing the same bulldozing behavior (Fig. 6D). In fact, most of *Archaeonassa* occur as shallow epichnia, most of them covered with a thin veneer of white clay, and they are among the most common trace fossils in Cabeço da Ladeira stratigraphic sequence (Fig. 6F). Several long trails perpendicularly cut the ripples, paralleling others and seem to burrow under the stiff microbial mat leaving partially exposed tunnels behind (Fig. 6E). According to Mángano and Buatois (2015), *Archaeonassa fossulata* (Fenton and Fenton, 1937) may represent matground grazing of a microbially enriched surface. On the other hand, mat growth may progressively cover any trail or trackway crossing the flat.

Measuring 12.3 m *Laterigradus lusitanica* igen. nov., isp. nov. attributed to a crab trackway may be the longest described for invertebrates in the fossil record. Also the gastropod trails, straight or sinuous, are extremely long and continuous and can be followed by up to 11.5 m (Figs. 4A, 6A). Other examples of extensive invertebrate trackways in the literature are surprisingly rare. Lomax and Racay (2012) described a 9.7 m mortichnial trackway produced by *Mesolimulus walchi* in the lower Tithonian of the Solnhofen Lithographic Limestone. The longest fossil invertebrate trackway was claimed by De (2014), for a 10 m long crab trackway from the Eocene Mithakhari Group of Andaman island, and he provided a review of the longest invertebrate repichnia in the literature. However, some examples of very long trails and trackways may have not been taken into consideration in the review of De (2014), such as the very long trails attributed to *Climactichnites wilsoni* Logan, 1860, from the Middle-to-Late Cambrian of Blackberry Hill, Wisconsin, studied in detail for the last 20 years (Gass, 2015). Thus we may claim the continuous trackways and trails found at the Middle Jurassic of Cabeço da Ladeira are among the longest described in the fossil record. Apart from the relative interest that size may have for ichnology, continuous long trackways provide comprehensive information about behavioral variations from the general pattern related to ecospace heterogeneity (hydrodynamics, water depth and aerial exposure, substrate firmness, food distribution, etc.).

5. The first trail of a stalked crinoid in the fossil record

In the tidal flat of Cabeço da Ladeira, a stalked form of crinoid was found at the end of its trail (Fig. 7). Its course can be followed from a microbial mat patch identified by wrinkle structures. There, it shows the disruption of the mat around a shallow pit surrounded by small piles of broken sediment. The trail is very faint and large at the beginning, becoming sharper and as wide as the crinoid later on (Fig. 7A; Fig. 8 for photogrammetric interpretation). It consists of a flat to slightly disturbed central area resulting probably from stalk dragging. This central area is surrounded by two large and irregular furrows limited externally by ridges of sediment. The two large furrows were produced by the articulated moving arms of the crinoid in loose sediment. All the arms and cirri are bending backwards in locomotion position.

The columnal ossicles have more of less the same thickness throughout the length of the stalk. The cirri are present throughout the stalk, more or less regularly spaced, long, slender and ending on a little hook. Little is known about the calyx, appearing to be short

Fig. 6. Bulldozing trails attributed to gastropods. A – The longest linear trail crossing the tidal flat attributed to the locomotion behavior of gastropods; B – Burrow at the end of the trail (for reaching the phreatic level?); C – *Archaeonassa* showing bordering ridges of sediment resulting from a bulldozing-type movement; D – Long winding trail found in a quarry close to Cabeço da Ladeira location, but in the same unit; E – Parallel trails evidencing bioturbation in a microbial mat; F – Filling of the burrows by the overlying white clay layer.

Fig. 6. Trilhos tipo "Buldozer" atribuídos a gastrópodes. A – O mais longo trilho a cruzar a planície de maré atribuído ao comportamento de locomoção de gastrópodes; B – Galeria no final do trilho (para atingir o nível freático?); C – *Archaeonassa* evidenciando cristas laterais de sedimento expulso por um movimento tipo "Buldozer"; D – Longo trilho irregularmente sinuoso encontrado numa pedreira perto do Cabeço da Ladeira, na mesma unidade; E – Trilhos paralelos evidenciando bioturbação num tapete microbiano; F – Preenchimento de galerias por nível de argila branca sobrejacente.

and conical. The arms branch quite close to the calyx. The brachials appear to be massive. The preservation of the pinnules is poor, appearing to be relatively short. The presence of a stalk and the arrangement of the cirri along it suggest that these specimens belong to the order Isocrinida. This isocrinid trail is the only one of its kind found at Cabeço da Ladeira.

Isocrinid crinoids have a sessile life. Active crawling by stalked crinoids, a group generally thought to be sessile, was only recently

demonstrated (Baumiller and Messing, 2007). This study reveals that isocrinids could relocate by crawling with their arms, dragging the stalk behind them. However, the locomotion behavior of crinoids was never described from the fossil record. Speed is related to the length of the arms involved in the power stroke (Baumiller and Messing, 2007). The ability to detach the stalk and crawl may have evolved as escape strategy from benthic predators. Cidaroid echinoids occur in the same bed where the isocrinid crinoid trail

was found, and have been documented to prey on this kind of crinoids. The observed trace and maker suggest that this strategy might have been used by shallow-water crinoids to cope with sudden environmental changes, or instances of an abnormal low tide, which may have been the reason for the trail made by the crinoid at Cabeço da Ladeira. Several features that are necessary for crawling have been identified (Messing *et al*., 1988; Baumiller and Messing, 2007): a detachable stalk; some mode of reattachment of the stalk to the substrate, such as flexible cirri; and arms that are both flexible and strong enough to generate the power and recovery strokes to pull the animal along the bottom.

The elbow-crawling behavior may be described as the stalk being dragged behind the crown along the substrate, with the proximal part nearly horizontal. In this posture, only a portion of the strongly aborally flexed arms are in contact with the substrate (Baumiller and Messing, 2007), as we can see in the Middle Jurassic trail (Fig. 7B). In the power stroke, the arm base bends away from the mouth, pushing the more strongly flexed arm tip down and backward against the substrate. With the tide retreating and the flat being exposed, the crinoid had more difficulty in keeping the stalk uplifted and dragged it on the bottom. The result is expressed as the sharpening of the crawling effort, also due to dehydration of the sediment, and the piles of sediment pushed away by the arms' movement (Fig. 8). The trail becomes also more winding near the crinoids' final resting place. This is a fine example of a mortichnion: the isocrinid crinoid was caught by low tide in its death march (Seilacher, 2008). Examples of mortichnia are rare and some have
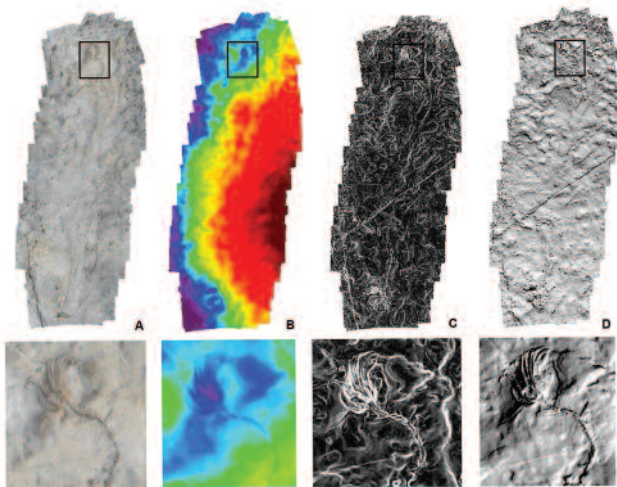

Fig. 7. *Krinodromos bentou* data integration, post-processing and analysis in GIS; the position of the isocrinid crinoid is detailed below in each resulting figure. A – Orthophotography with high spatial resolution showing the complete mortichnial trail that started from the living place (below); B – DSM representing the surface altimetry, red colors representing higher surfaces and blue colors lower ones. The crinoid shows continuous displacement (evidenced by the "trail" of blue colors crossing the red surface and connecting the starting point to the crinoid) before the final resting position; C –Surface slope map with the clear location of the site where the crinoid detached from the substrate, and the trail. The sharper impression of movements surround the crinoid; D – Shadow map that best pictures the dragged locomotion along the trail.

Fig. 7. Integração, pós-processamento e análise em SIG dos dados relativos a *Krinodromos bentou*; em cada uma das figuras encontra-se abaixo detalhado a posição do crinóide isocrinídeo. A – Ortofotografia de alta resolução espacial evidenciando a "marcha para a morte" que teve início no local de fixação em vida (abaixo); B – DSM representando a altimetria da superfície, vermelhos representando as cotas mais altas e azuis as cotas mais baixas. O crinóide mostra um deslocamento contínuo (evidenciado pelo "trilho" de cores mais frias cruzando a superfície a vermelho e ligando o ponto de partida ao crinóide) antes da posição final; C – Mapa de declives onde se observa claramente o local de onde o crinóide se desprendeu da superfície e o percurso tomado. À volta do crinóide é clara a impressão mais vincada dos seus movimentos; D – Mapa de sombras que melhor evidencia a locomoção arrastada ao longo do trilho.

been questioned recently (Vallon *et al*., 2015, 2016), but this find unequivocally confirms the validity of this ethological category.

6. Systematic ichnology

Ichnogenus *Laterigradus* igen. nov.

Diagnosis: Asymmetric trackway formed by up to four tracks distributed in discrete sets that may show different stride lengths adapted to distinct cursorial gaits expressed in water or land.

Laterigradus lusitanica isp. nov.
(Figs. 4, 5)

Etymology: Laterigradus comes from Latin and refers to the sideways steps; *lusitanica* indicates the territory of the Lusitani tribe that lived in Central Portugal before the expansion of the Roman Empire to Iberia; it gave also the name to the Lusitanian Basin.

Type locality and age: Cabeço da Ladeira, included in the Vale da Serra Member of the Chão de Pias Formation, upper Bajocian (Sauzei biozone; Ruget-Perrot, 1961); Maciço Calcário Estremenho (Lusitanian Basin, Portugal) coordinates: 8°47'57.307''W, 39°32'39.108''N.

Material: Numerous examples of such trackways in beds 4 to 6 of Cabeço da Ladeira site. The holotype is the longest and the best preserved trackway. A cast of the total length of this trackway was made and stored at the Geological Museum of Lisbon, number MG30474.

Diagnosis: The same as for the ichnogenus. Uniserial trackways with sets of up to four circular-to-sigmoidal tracks.

Remarks: This is a repichnion of crab-form decapods, most probably an brachyuran revealing a sideward locomotion. The trackways are straight to gently curved trackways and may reveal different stride lengths and number of tracks according to an underwater punting or octopedal walking gaits on land. The deepest part of dactyl imprints is located in the opposite direction to the locomotion, thus providing the direction of movement. The concentration of footprints in the trackway shows changes in speed of probing the sediment. The relatively low density of trackways shows that the crab producers were not gregarious, but territorial with large feeding areas in the flat.

Remarkably, there are few trackway ichnotaxa attributed to crustaceans. Pirrie *et al*. (2004) described the ichnogenus *Foesterichnus rossensis*, from the Coniacian Hidden Lake Formation, at James Ross Island, Antarctica, and revised the trackway fossil record of crustaceans. The diagnosis of the ichnogenus includes straight or curving trackways composed of paired rows of elongate to tear-shaped impressions, organized in series of three and four imprints. They clearly evidence forward walking of brachyuran crabs, and they were the first formally described and attributed to this group from the fossil record (Pirrie *et al*., 2004). As *Laterigradus lusitanicus* evidences a different locomotory, sideways walking and running behavior, that also has morphological implications for the crab-form producer responsible for them, we think it is useful to erect a new ichnogenus to include asymmetric trackways of brachyuran crabs.

Ichnogenus *Krinodromos* igen. nov.

Diagnosis: Trails composed of a narrow and flat central area with an irregular winding furrow, or almost no sedimentary disruption, bordered by shallow and large grooves externally limited by irregular piles of sediment.

Krinodromos bentou isp. nov.
(Figs. 7, 8)

Etymology: Krinodromos comes from the Greek "the course of the [sea] lily"; *bentou* refers to the closest village, S. Bento, close to which is located the quarry where the crinoid crawling trace was found.

Type locality and age: Cabeço da Ladeira, included in the Vale da Serra Member of the Chão de Pias Formation, upper Bajocian (Sauzei biozone; Ruget-Perrot, 1961); Maciço Calcário Estremenho (Lusitanian Basin, Portugal): coordinates: 8°47'57,307"W, 39°32'39,108"N.

Material: The holotype and only example was found with an isocrinid crinoid at its very end, which makes the attribution of the trail to a tracemaker much easier. A cast was made and stored at the Geological Museum of Lisbon, number MG30475.

Diagnosis: The same as for the ichnogenus.

Description: Very faint irregular trail with planar central area, or disrupted by an irregular curving furrow and bordered by two shallow, wide and irregular grooves that are limited by piles of sediment. The trail is mostly straight but narrows and curves abruptly (c. 50º) where the crinoid body fossil rests, becoming impressed more sharply (Fig. 8).

Remarks: Being a shallow and irregular trail, it is not easy to compare *Krinodromos bentou* to other examples from the fossil record if found without the associated producer. This trail is probably rare because we interpret this as an unusual locomotion on land resulting from flat exposure that ultimately caused the death of the crinoid. The most conspicuous ichnotaxobases that characterizes *Krinodromos bentou* are the two bordering grooves combined with pushed sediment piles, and a central flat area or a narrow winding furrow, depending on the firmness of the substrate. This trail can be explained as mortichnion of an isocrinid. In an abnormally low tide the crinoid crawled away from the microbial mat where it was anchored in a vertical hole surrounded by sediment pustules resulting from the effort to become free. The crinoid used sets of arms to create a bilateral symmetric locomotion by flexing the arms backwards pushing the sediment laterally, causing irregular piles. The bending termination of the trail could represent the climax of a stressed condition that coincided with the aerial exposure of the flat and the death of the crinoid. The animal was simply not fast enough to reach the water line. The width of the trace is similar to the width of the crinoids' bending arms in the final part, suggesting that it was produced as the body was dragged by the appendages throughout the sediment (Fig. 8).

Archaeonassa fossulata Fenton and Fenton, 1937
(Fig. 6)

Description: Unilobed narrow trails, having a median groove flanked by ridges, less than 10 mm to up to 40 mm wide. The trails can be winding or gently meandering, and linear. The longest linear trail is unilobed and can be followed for 11.2 m and is 20 mm wide. It is bordered by sediment ridges. Another long trail, measuring 8.4 m long and 20 mm wide, possesses an elliptical-shaped hole at one of the ends.

Remarks: These traces match the morphology of *A. fossulata* reviewed by Buckman (1994) and Yochelson and Fedonkin (1997). It is generally understood as recording the grazing behavior of gastropods. *Archaeonassa* may also be produced by preying gastropods (Baucon and Felletti, 2013a, 2013b).

Diplopodichnus isp.
(Fig. 9A)

Description: Two parallel grooves 1-3 mm wide, each in a straight, but mostly winding course, formed by discrete footprints or overlapping ones developing linear furrows. Prints are circular or elongated perpendicular to the trail course.

Remarks: These kinds of trails were described by Baucon (2008) as produced by the pereiopod prints and the dragging tail of mud shrimps. These axiidean shrimps are active during the low tide, grazing the algae and bacteria that develop at the sediment surface

(see Baucon, 2008, and references therein). *Diplopodichnus* are usually filled with sediment and cut by gastropod grazing trails, which indicates that these trackways were produced underwater. Axiideans, notably Axiidae, have a fossil record into the Early Jurassic (*e.g.*, Hyžný and Klompmaker, 2015).

Gyrochorte comosa Heer, 1865
(Fig. 9B)

Description: Winding bilobed burrows in convex epirelief, 4-18 mm wide, preserved as plaited ridges with bisserially arranged, chevron-shaped pads of sediment, separated by a median furrow.

Remarks: This is a burrow typical for the *Cruziana* Ichnofacies, produced within the sediments in a subtidal environment. The producer may be a polychaete-like worm (*e.g.*, Heinberg, 1973). However, the method of sediment transport and locomotion represented in *Gyrochorte* fit the physiology of an arthropod much better (see Schlirf, 2000).

Haplotichnus indianensis Miller, 1889
(Fig. 9C)

Description: Simple half-cylindrical trail, unbranched and horizontal, needle-like in size, running in straight or crooked lines, or crossing itself (Rindsberg and Kopaska-Merkel, 2005).

Remarks: Haplotichnus is interpreted to be the work of insects (Rindsberg and Kopaska-Merkel, 2005). The sharp turns are significant because short-bodied animals such as arthropods can change direction more easily than long-bodied worms. Due to its geotechnical properties, the mat is a protective environment for delicate juvenile insect forms. According to the observations of Baucon (2008), larvae of Diptera behave as undermat miners by excavating very shallow burrows parallel to the mat surface. The upper organic-rich layer would provide abundant nutrients and, at the same time, it guaranteed protection from predators and physical disturbance (Baucon, 2008), while the burrow was produced in the mineral-rich layer with microbial mat related structures.

Asterosoma ludwigae Schlirf, 2000
(Fig. 9D)

Description: Asterosoma with linear or curved elipsoidal bulbs, those seem to develop from an axial horizontal burrow. Bulbs are loosely grouped following the axial burrow that is in a lower level so bulbs are oblique and rise from the bedding plane. Burrow surface contains scratch marks and burrow fill is similar to the host bed.

Remarks: Asterosoma occurs in the same bed of *Thalassinoides suevicus*, with convex epirelief preservation. These burrows form the deepest tier in the ichnofabric, and were developed in subtidal conditions. They may share the same producer, in accordance with Neto de Carvalho and Rodrigues (2007).

Thalassinoides suevicus Rieth, 1932
(Fig. 9E)

Description: Burrow meshworks with unlined burrow walls, smooth lining, branching predominantly dichotomous, Y- to T- shaped typically enlarged at points of bifurcation. Sizes of *T. suevicus* differ between 7 and 40 mm in diameter.

Remarks: These burrows represent three-dimensional boxworks. Bed 4 is extensively bioturbated by small examples of *Thalassinoides*. Common intergradations between *Thalassinoides suevicus* and *Spongeliomorpha* Saporta, 1887, have been repeatedly described in the literature (see references in Schlirf, 2000). Outer burrow scratch marks are the result of digging in a firm substrate. The proposed producers of both size-scaled *Thalassinoides* could be small Axiidea

Fig. 8. Locomotion trail left behind by an isocrinid crinoid while trying to escape from death (Bed 2). A – The new trace fossil attributed to crinoid locomotion, *Krinodromos bentou* igen. nov., isp. nov.; B – Mortichnion of a isocrinid crinoid (more detailed view).

Fig. 8. Trilho de locomoção desenvolvido por crinóide isocrinídeo na tentativa de escapar da morte (camada 2). A – Novo icnofóssil atribuído a locomoção de crinóide, *Krinodromos bentou* igen. nov., isp. nov.; B – Mortichnion do crinóide isocrinídeo (vista mais detalhada).
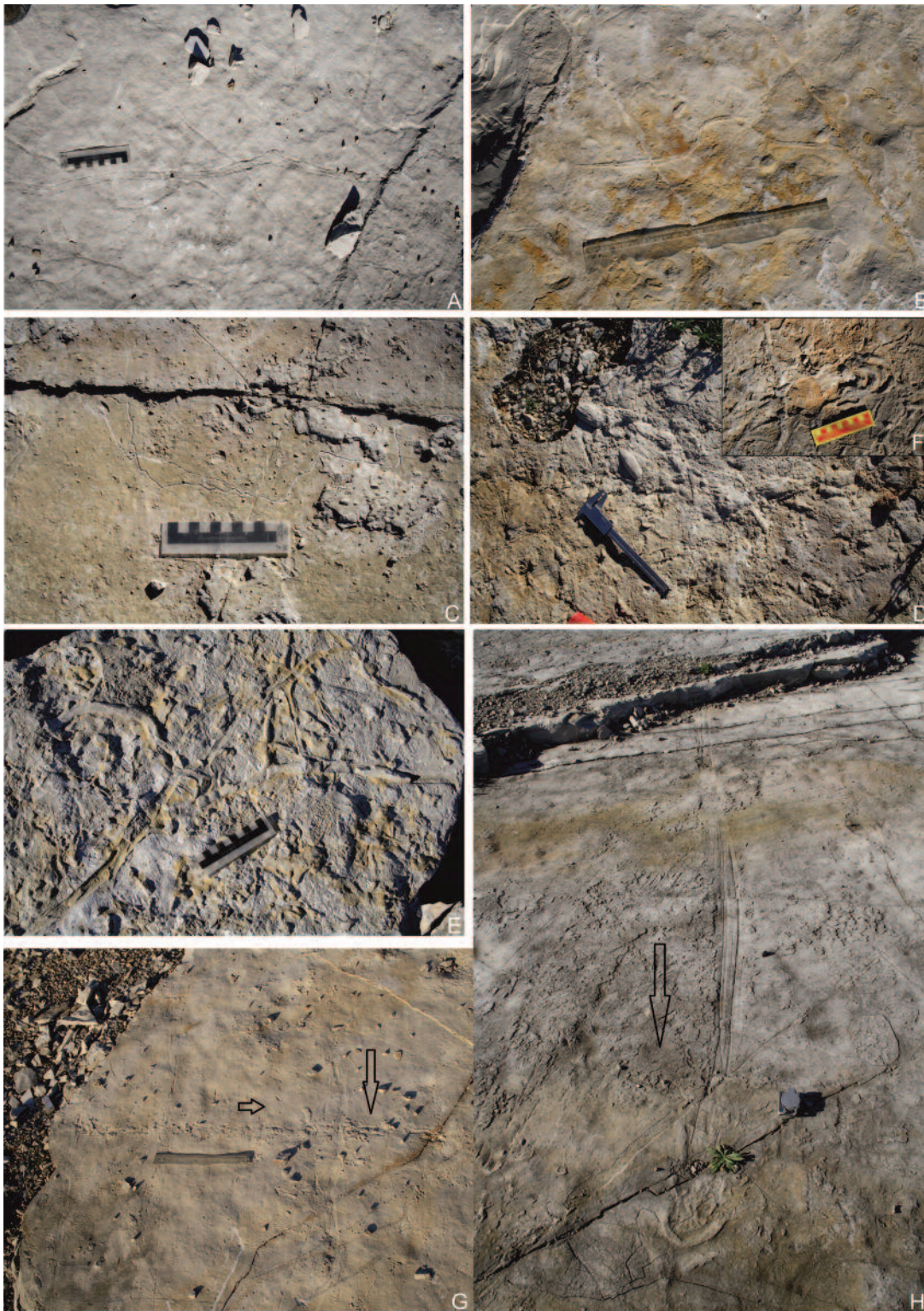
Fig. 9. Other trace fossils from the Bajocian of Cabeço da Ladeira. A – *Diplopodichnus* isp., one of the most abundant forms, most of the time filled with white clayish material; B – *Gyrochorte comosa*, more common in the upper levels of the sequence; C - *Haplotichnus indianensis* (bed 6) showing clearly sharp turning angles, and typically associated with microbial mat related structures; D – *Asterosoma ludwigae* with a dichotomous pattern of bulbs; E – *Thalassinoides suevicus* meshwork, large size; F – Horizontal spreite typical of *Rhizocorallium commune* in an elephant skin texture; G – Slightly sinusoidal ?*Undichna* set of grooves cut across by a crab trackway; H - ?*Undichna* with a cubichnion similar to *Crescentichnus* isp. of Romano and White (2015) at the end.

Fig. 9. Outros icnofósseis do Bajociano do Cabeço da Ladeira. A - *Diplopodichnus* isp., uma das formas mais abundantes, a maior parte das vezes preenchida com material argiloso; B - *Gyrochorte comosa*, mais comum nos níveis superiores da sequência; C - *Haplotichnus indianensis* (camada 6) mostrando estreitos ângulos de viragem muito evidentes e tipicamente associados a estruturas relacionadas com tapetes microbianos; D - *Asterosoma ludwigae* com um padrão dicotómico dos bolbos; E – Malha de *Thalassinoides suevicus* de grandes dimensões; F – *Spreite* horizontal típico de *Rhizocorallium commune* numa textura de "pele de elefante"; G – Conjunto de estrias ligeiramente sinusoidais de ?*Undichna* cortadas por um trilho de caranguejo; H - ?*Undichna* com um cubichnion semelhante a *Crescentichnus* isp. of Romano and White (2015) no final.

and Gebiidea shrimps or lobsters (Neto de Carvalho *et al*., 2007). Ghost shrimps inhabit predominantly intertidal and subtidal marine environments at tropical and subtropical latitudes, but their body fossil record goes back to Lower Cretaceous only (Hyžný and Klompmaker, 2015).

Rhizocorallium commune Schmid, 1876
(Fig. 9F)

Description: U-shaped spreiten burrows nearly parallel to the bedding plane; limbs are parallel and distinct.

Remarks: Rhizocorallium is rare in the Cabeço da Ladeira section, and occurs with abundant *T. suevicus* in bed 5. The ichnogenus *Rhizocorallium* was recently revised by Knaust (2013), who resumed to two valid ichnospecies, *R. jenense* and *R. commune*. The producer in this case is unknown, as *Rhizocorallium*-behavior may be produced by different worm and arthropod organisms. For Knaust (2013), the most likely producers for marine *Rhizocorallium* are polychaetes, based on their long-ranging occurrence, morphological features, associated body-fossil remains, and modern analogues. However Meyer (1988) cited the axiid *Protaxius* within *Rhizocorallium*. The common observation of scratch marks in the walls of *R. commune* in firmgrounds from different age across the Lusitanian Basin led Neto de Carvalho *et al*. (2010) and Mateus *et al*. (2013) to attribute this ichnospecies to the feeding behavior of crustaceans.

?*Undichna isp.*
(Fig. 9G,H)

Description: Trackways made of continuous, four or more, parallel furrows, 1-3+ m long in sets 70-100 mm wide. Grooves are mostly linear or curvilinear, or slightly sinusoidal. One of them is at least 3.2 m long and ends with a very shallow, resting trace with a crescent shape similar to the recently described *Crescentichnus* by Romano and White (2015) (Fig. 9H).

Remarks: Undichna is interpreted to be a fish-fin or fish-swimming trail left as an impression on the substrate (Trewin, 2000). They may have been produced during the low tide, when the water was retreating from the flat. Sets of grooves are usually sinusoidal with different wavelengths. In Cabeço da Ladeira, the furrows are mostly linear and can be traced for long distances, which is why we only attempt to compare those trails to *Undichna*. These traces are most common in bed 2; in bed 3 they are cut across by a crab trackway, suggesting that *Undichna* was made first. (Fig. 9G). In bed 2, two of them intersect each other, making a meander at the point of intersection.

7. Conclusions

Trace fossils are useful to decipher paleoenvironmental conditions and advance the knowledge about the evolutionary causes of behavior. The upper Bajocian limestone sequence from Cabeço da Ladeira, in the central part of Lusitanian Basin in Portugal, is composed of a repetition of environmental conditions prone to the development of microbial mats and oncolites in the carbonate tidal flat, that may have expanded substantially at low tide during the equinoctial spring tide. The result was the practically in situ killing of echinoderm specimens and their fine preservation together with delicate trackways and burrow details of a community dominated by cursorial arthropods and gastropods. A moderately diverse, shallow-tiered ichnoassemblage composed of ten ichnotaxa were described, among them the new ichnogenera and ichnospecies *Laterigradus lusitanica* and *Krinodromos bentou*. The first represent different gaits attributed to sideward walking and running of a crab-form animal. Underwater punting and aerial locomotion gaits were described and exemplify the dawn of true crabs and the first attempts of amphibious crabs in conquering terrestrial habitats. Together with straight bulldozing trails attributed to the grazing behavior of gastropods, Cabeço da Ladeira includes some of the longest invertebrate cursorial traces in the fossil record. *Krinodromos bentou* corresponds to the death march of an isocrinid crinoid in its attempt to crawl to the shore. The elbow-crawl behavior is the first record of stemmed crinoid locomotion from the fossil record.

Acknowledgements

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