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Roller Coaster Behavior in the *Cruziana Rugosa* Group from Penha Garcia (Portugal): Implications for the Feeding Program of Trilobites

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Trilobite burrows of the *Cruziana rugosa* group are common and well preserved in the Armorican Quartzite Formation (Lower to Middle Ordovician) of the Ponsul River gorge in Penha Garcia. Based on morphological and behavioral peculiarities, *Cruziana beirensis* is reinstated herein and included in the *rugosa* group. Apart from the broad range in morphology and size, *Cruziana* from Penha Garcia show higher behavioral diversity using food sources than has ever been documented in a single section. This behavioral diversity, mainly in circling behavior, has been analyzed using the Capacity Fractal Dimension by implementation of the box-counting theorem applied to the bedding plane. Fractal Dimension also suggests that *Cruziana rouaulti* can be included in the *rugosa* group, despite the obscurity of the scratch patterns, as products of juveniles. Circling, sinusoidal or *teichichnoid* behavior modifications reflect a generalist mode of sediment feeding, claimed mudtrophobacterivory, while most of the interactions with worm burrows originated previously or (mostly) later, by interpreted trilobite necrophagy and/or worm commensalism. Patchy exploitation of biomat grazing fields is inferred from *Cruziana* preservation styles, physical interactions with biomat-related sedimentary structures and area-limited high bioturbational indices in the explored tier.

Keywords   *Cruziana*, ethotype diversity, feeding management, biotic interactions, Lower to Middle Ordovician, Portugal

INTRODUCTION

Penha Garcia is the most accessible and one of the best places in Portugal to observe Ordovician "Armorican Quartzite" ichnocoenoses. Subvertically tilted heterolithic bedding planes, exposed over 400 meters thick sequence and exhibiting little weathering and low tectonic deformation, allow detailed ichnological studies to be made. The present paper deals only with the most common and most spectacular ichnofossils in the middle to upper Penha Garcia quartzite sequence: the *Cruziana*

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rugosa group. Closely related to *Cruziana,* and in some cases intergrading with it, are stationary *Rusophycus* burrows of at least 4 morphotypes including *R. pedroanus* (Seilacher), *R. didymus* (Salter), *R. morgati* Baldwin and *R. carleyi* James; Fig. 2f, either independent or as part of *Cruziana* burrows, *Diplichnites* (in some cases transitional to *Cruziana*), as well as *Monomorphichnus bilinearis* Crimes. These biogenic structures will be described elsewhere.

The new discoveries in Penha Garcia described in this paper emphasize the need for revision of one of the best known *Cruziana* groups (e.g., Delgado, 1886, 1888; Seilacher, 1970; Bergström, 1972, 1973; Kolb and Wolf, 1979; Durand, 1985; Fillion and Pickerill, 1990) with regard to taxonomy, tracemakers, ethological diversity and biological function, as well as interactions with other ichnofossils and sedimentary conditions that enhance the preservation of these fossil documents. The general epithet *roller coaster*, coined by Adolf Seilacher on a recent visit to the Penha Garcia *Cruziana*, expresses the ethological diversity that is so common for *Cruziana* in this area.

THE ICHNOLOGICAL PARK OF PENHA GARCIA: GEOLOGICAL SETTING

Idanha-a-Nova municipality is the centre of an area with 4600 km^2 ($\approx$5% of the total area of Portugal) around the High Tagus River Basin, where geotourism is expanding. Emphasis on paleontological and stratigraphic resources (particularly Palaeozoic) is expressed by the protection of fossils, outcrops and regional stratotypes as well as by the establishment of the Ichnological Park of Penha Garcia (Fig. 1), a beautiful river gorge where steeply overturned bedding planes exhibit delicately preserved Ordovician ichnocoenoses.

The Armorican Quartzite Formation of Penha Garcia lies within a syncline that extends into Spain (Ciudad Real Province) for hundreds of kilometers. It is composed of siliciclastic, shallow-marine tempestites dated as Arenigian to late Oretanian (Mediterranean chronostratigraphic table *sensu* Gutiérrez-Marco et al., 1995, equivalent to Lower to Middle
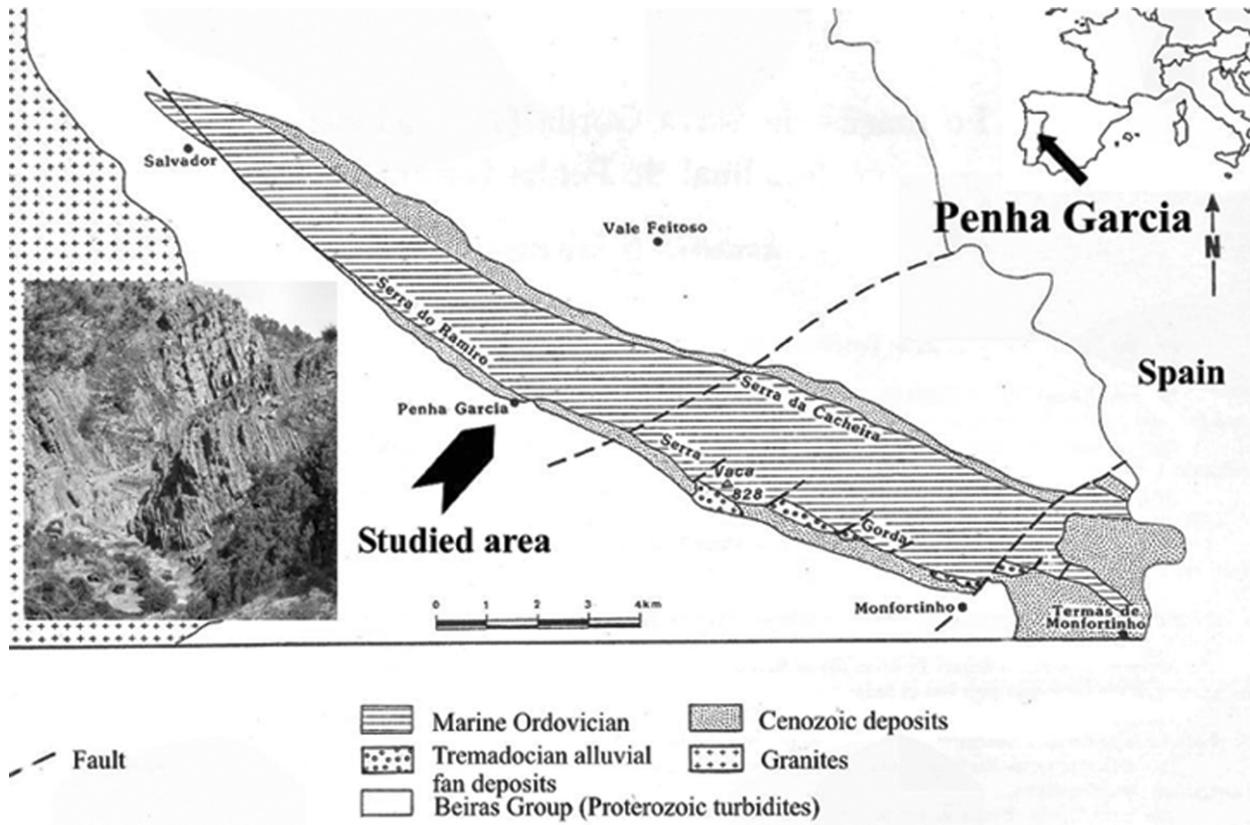
FIG. 1. Geological setting of Penha Garcia area (Idanha-a-Nova, Portugal), after Sequeira (1993). The studied section is positioned along the Ponsul river gorge that crosses all the 400 m thick Armorican Quartzite Formation.

Ordovician; Romano et al., 1986), deposited in foreshore to shallow offshore environments with frequent wave or bottom-current storm influence. In Portugal, the Armorican Quartzite Formation crops out in an area of more than 2500 km^2 as part of the European Armorican Massif. At Penha Garcia, the entire 400 m thick quartzite formation is exposed. It unconformably overlies a Neoproterozoic turbidite sequence (Beiras Group) or grades upward from coarse fan-delta deposits (Serra da Gorda Formation). Atop the Armorican Quartzite are black shales (Brejo Fundeiro Formation) in stratigraphic continuity, dated as late Oretanian to Dobrotivian (Middle Ordovician).

In the Armorican Quartzite, the almost complete absence of body fossils contrasts with the abundance and diversity of ichnofossils, which are most common in the more heterolithic (sand/silt to mud) offshore lithofacies of the middle and upper parts. Despite their palaeoenvironmental and palaeoecological significance to the Ordovician of Portugal, ichnofossils from Penha Garcia were known only from Nery Delgado's pioneer "*Bilobites*" studies (Delgado, 1886, 1888). A more systematic and thorough study of the Penha Garcia ichnofauna has been started (Neto de Carvalho et al., 1998, 2003, 2004a).

THE PENHA GARCIA *CRUZIANA* ICHNOFAUNA

Cruziana ispp. are common in the Armorican Quartzites from Southwestern Europe in equivalent rocks all around the northern margin of Gondwana. Five ichnospecies of *Cruziana* d'Orbigny 1842, most of them characteristic of the Gondwanan Lower Ordovician, occur in Penha Garcia. The occurrence of *Murchisoni* Biozone graptolites, a calymenid-dalmanitid biofacies (*Nava* Biozone) and the "*Cacemia* biofacies" in blackish slates 4 m above the Armorican Quartzite Formation confines the age of the *Cruziana rugosa* group to the Arenigian or to the late Oretanian for Penha Garcia section.

The elongate, ribbon-like *Cruziana furcifera* d'Orbigny, which has regular scratchmarks that criss-cross at an acute angle, is extremely abundant throughout the sequence (Fig. 2a). However, the lateral ridges typical of *Cruziana goldfussi* (Rouault, 1850) may also occur along specimens of *Cruziana furcifera*. Variants classified as *Cruziana goldfussi* have marginal ridges along the outer margins; they were produced by passive dragging of genal or pleural spines of the trilobite producer. There are close morphological and dimensional relationships (Fig. 3) between *Cruziana goldfussi* and *Cruziana furcifera,* including the acute V-angle and fine striae, in some cases with rhombic crisscrossing.
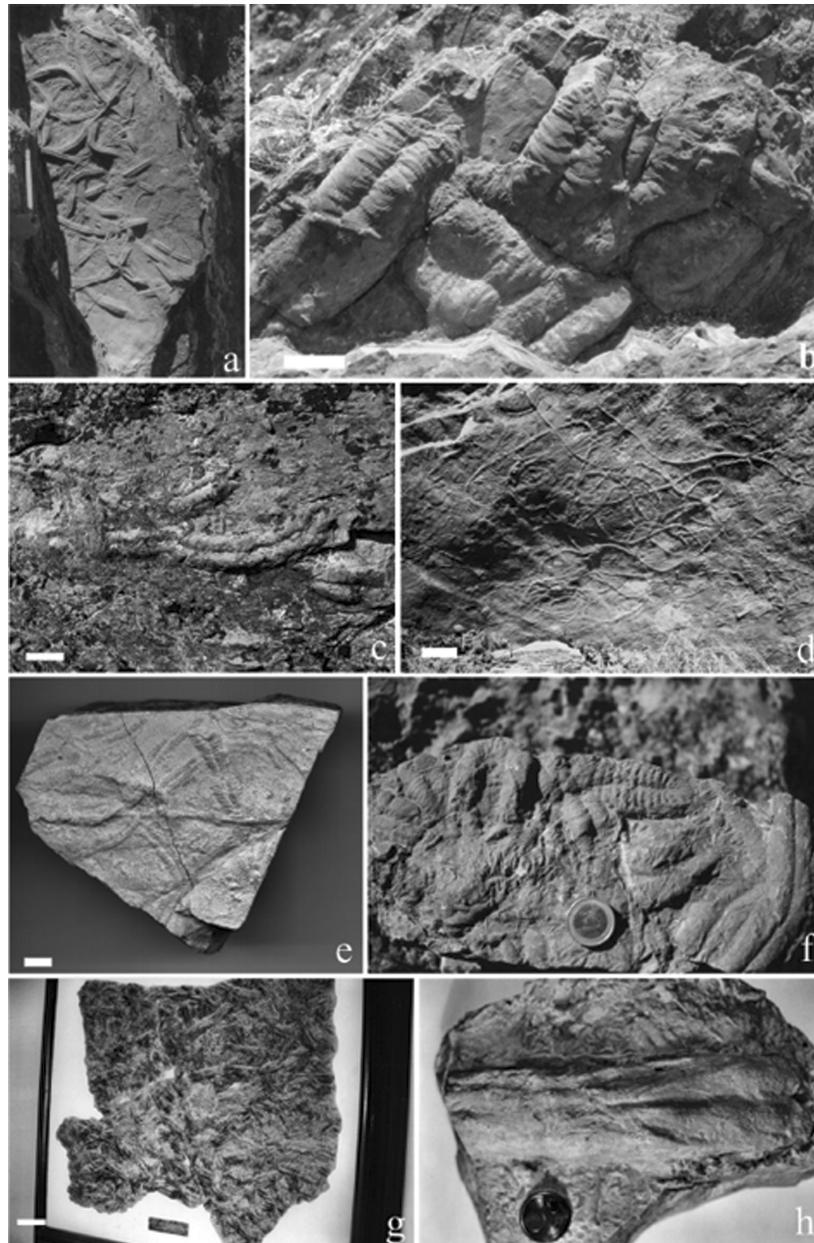
FIG. 2. *Cruziana rugosa*-group from central Portugal. **a**—*Cruziana furcifera* d'Orbigny (Penha Garcia); scale = 20 cm. **b**—U-shaped *Cruziana rugosa* d'Orbigny (Penha Garcia). It is shown *Cruziana* exquisite preservation of the bioimprints and the example of a curious alternation between motion directions, making 90°, reported in all specimens of this slab; scale = 10 cm. **c**—Band like *Cruziana rugosa* d'Orbigny (Serra do Ramiro, Penha Garcia); scale = 20 cm. **d**—Scribbling traces ascribed to *Cruziana rouaulti* (Lebesconte) from Penha Garcia; scale = 10 cm; **e**—*Cruziana problematica* associated with overlapping *Rusophycus biloba* (Vanuxem). Example from Venda quarry (Proença-a-Nova); scale = 1 cm. **f**—Examples of the *Rusophycus carleyi* group; scale = 20 mm. **g**—Highly bioturbated slab from Penedos de Góis with *Cruziana beirensis* Delgado and *Cruziana furcifera* d'Orbigny (see also Delgado, 1886: p. 49, est. 22); scale = 20 cm. **h**—Grupo Paleo collections at Lisbon Natural History Museum (162). *Cruziana beirensis* Delgado (Amêndoa, Mação); scale = 2 cm.

Cruziana rugosa d'Orbigny, characterized by strong transverse corrugations and comblike sets of up to 13 scratches (Fig. 2b), is abundant in Penha Garcia, reaching remarkable dimensions and degrees of preservation. A giant *Cruziana rugosa* up to 16.5 cm wide was followed for 3.2 m, crossing another specimen 19 cm wide and 2.9 m long (Fig. 2c). The record is held by a specimen *ex situ* that reaches a width of 26 cm. Specimens of *Cruziana rugosa* less than 8 cm wide are rare. Genal ridges may be present. In one specimen there is possible gradation with *Cruziana imbricata* Seilacher, 1970, passing from a corrugated to an imbricate-lunated series of scratchmarks in the same U-shaped structure. High-relief forms

are dominant, but depending on the undertrace level, almost flat structures or a single endopodal lobe revealed by the transverse corrugations may also occur.

The small *Cruziana rouaulti* (Lebesconte, 1883) is rarely associated with other ichnospecies of *Cruziana* (Fig. 2d). Usually, it shows smooth bilobation with marginal grooves. Where the sediment is finer, oblique bioglyphic patterns are preserved that resemble *Cruziana bagnolensis* Morière, 1878 (Durand, 1985). Even smaller variants (<1–5 mm) attributable to *Cruziana problematica* (Schindewolf) Bromley and Asgaard (1979), which differs from all the previous ichnospecies, can be observed by procline-induced scratches running transverse to the median furrow (Fig. 2e) as in modern feeding traces of *Triops cancriformis* (Schaeffer). For preservational problems involved in the distinction of *Cruziana rouaulti* and *C. problematica* see Jensen (1997: 46–48).

Cruziana beirensis Delgado, 1886 has previously been considered as a preservational variant of *Cruziana furcifera* (Seilacher, 1970; Durand, 1985; Fig. 2g). However, there are significant morphological differences to claim it as a distinct recurrent ethological pattern that should be maintained as a valid ichnospecies. It is a high-relief burrow characterized by vertical lateral walls and inner lobes that tend to widen towards the anterior end. This morphology results from *Teichichnus*-like burrowing, the burrow being enlarged in some cases by subsurface rupture of a previously probed volume as the tracemaker dug deeper (Fig. 2h).

THE *RUGOSA* GROUP TRACEMAKERS

Morphometric comparison of widths of the more common ichnospecies of *Cruziana* in Penha Garcia (Fig. 3) clearly shows three different dimensional types of producers. Contrary to Crimes (1970), the width here does not seem to increase stratigraphically. *Cruziana furcifera* and *Cruziana goldfussi*

FIG. 3. Width populations measured in *Cruziana* from Penha Garcia; n_{rugosa} = 181, $n_{\text{furcifera}}$ = 229, $n_{\text{goldfussi}}$ = 171, $n_{\text{rouaulti/problematica}}$ = 46.

were likely produced by the same kind of animals, as shown by their similar width ranges, behavior and preservation patterns. *Cruziana rugosa* is morphologically distinct and generally has a width range higher than that of associated ichnospecies, suggesting that it was produced by a different trilobite species. However, transitions between small *Cruziana rugosa-C. furcifera* are also preserved in Penha Garcia, as has already been described elsewhere (e.g., Bergström, 1976; Baldwin, 1977a; Kolb and Wolf, 1979). *Cruziana rouaulti* shows extremely reduced dimensions, but where scratches are preserved it does not differ except in small size from *Cruziana furcifera* and *C. goldfussi*. It could have been produced by an early ontogenetic (meraspid) stage of the same species. This agrees with the fact that *Cruziana rouaulti* tends to occur *en masse* along bedding planes separate from other *Cruziana* ichnospecies.

Cruziana rouaulti and *C. problematica* search patterns can also be related with other *Cruziana rugosa*-group burrows by Fractal Geometry tools (see methodology in the addendum; also Gibert et al., 1999; Neto de Carvalho, 2001). The Capacity Dimension (D_0) allows distinguishing inter-specific from ontogenetic differences (similar fractal dimension). Indeed, the data obtained from scribbling *Cruziana furcifera-goldfussi* are fairly constant ($D_0 = 1.60 \pm 0.08$, $n = 13$) and correlate well with those of *Cruziana rouaulti* ($D_0 = 1.63 \pm 0.05$, $n = 6$, $p < 0.05$) suggesting a similar behavioral program throughout ontogeny. Gregarious behavior in *Cruziana rouaulti* may represent a defensive strategy related to breeding colonies' behavior combined with breeding synchrony of vagile trilobites (cf. Schram, 1981; Foster and Treherne, 1981).

Dimensional, zoogeographical, stratigraphic and morphological comparisons with the fauna of giant trilobites in the slaty upper Arenig to lower Oretanian of Canelas (Valongo Formation; Guedes, 1999), lead us to infer that the makers of *Cruziana rugosa*-group burrows were asaphid trilobites (Neto de Carvalho et al., 1998) such as *Nobiliasaphus* Pribyl and Vanek, *Ogyginus* Raymond, and the common *Asaphellus* Calloway. Indeed, the last two genera have holaspid stages that span three orders of magnitude (millimeters to decimeters), are ubiquitous in Lower Ordovician siliciclastic facies (Seilacher, 1970) and can be correlated with the paleogeographic distribution of the *Cruziana rugosa* group. Furthermore, these trilobites have moderately vaulted rhachial rings facilitating bending backwards into an arch, which was a prerequisite for producing deep, U-shaped *Cruziana* burrows (cf. Seilacher, 1970, Fig. 5c). Rare examples of *Rusophycus* and *Cruziana* from Penha Garcia show impressions of genal spines, cephalic and parabolic pygidial doublures, antenniform cerci and coxae. Gigantism in *Cruziana* from Penha Garcia and asaphid trilobites from Canelas was possibly favored by the paleoantarctic geographic position of the Armorica plate during Ordovician time (Henry, 1988; Rabano, 1990; but see Geyer, 1993) or by high levels of dissolved CO_2 (Rudkin et al., 2003).
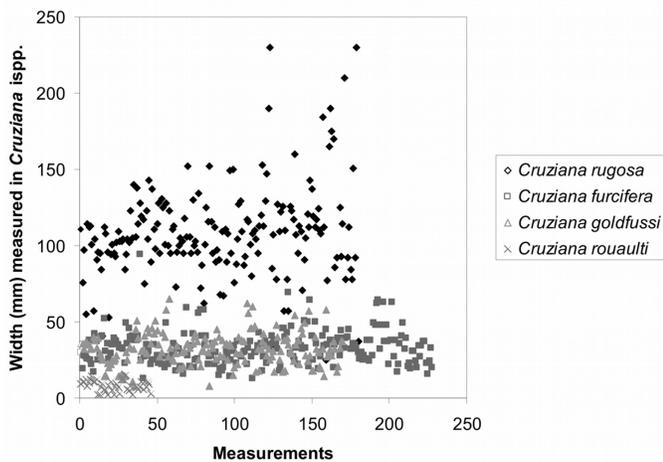
Asaphid trilobites have been proposed as the most likely producers of the *Cruziana rugosa* group (Bergström, 1972, 1973, 1976). However, Seilacher (1962, 1990) tentatively suggested the illaenid *Illaenus,* and Fortey and Morris (1982) the calymenid *Neseuretus,* as the producers. Fillion and Pickerill (1990) compared the size, morphology and stratigraphic range of specimens of the *rugosa* group with those of the asaphid *Ogyginus terranovicus* Dean. Baldwin (1977b) considered his *Rusophycus morgati* from the Grès Armoricain of France and Spain as an asaphid trace, associated with *Cruziana rugosa*-group ichnocoenoses. Fortey and Owens (1999) also recorded *Rusophycus* isp. associated with body fossils of *Ogyginus armoricanus* (Tromelin and Lebesconte) from the French Grès Armoricain. Most recently, Mángano et al. (2001) and Mángano and Waisfeld (2004) attributed *Cruziana rugosa* from northwest Argentina, including its ethological variants, to the asaphids *Ogyginus* or *Merlinia*. In fact, in the Alto del Condor section, remains of *Ogyginus* have been found in the same rocks that host *Cruziana rugosa*.

The comblike bioprints of *Cruziana rugosa* are historically viewed as having been made by multidigited inner leg branches (Seilacher, 1962, 1970, 1990; Baldwin, 1977a; Mángano et al., 2001) or setate outer branches (Bergström, 1972, 1973, 1976). Among the few known trilobite telopodites (e.g., Walcott, 1918; Harrington, 1959 and references cited therein; Seilacher, 1962; Bergström, 1969, 1972; Stürmer and Bergström, 1973; Cisne, 1975; Whittington, 1975, 1980; Bergström and Brassel, 1984), there is none that even loosely fits the inferred morphology of the legs recorded in *Cruziana rugosa*. Moreover, it is hard to believe that the multiclawed last podomere could reach more than 1/5 of the trilobite's width. Furthermore, scratches in each set may not be parallel, while unifid or bifid V-markings meet the median furrow with more relief and at an acute angle, and sets usually cross one another (see Fig. 5b). Instead they may show the forward metachronal activation of heterodimensional pole-like limbs imprinting their backward and downward movements. As observed in the burrowing behavior of the modern notostrachan *Triops cancriformis* (Schaeffer), the transverse corrugations and rhythmic variations in scratch angle found in *Cruziana rugosa* may result from a quasiperiodic change in opisthocline-procline body attitudes and burrowing intensity (Neto de Carvalho, 2004b). Outer leg branches as "the digging organ" interpretation of Bergström (1972, 1973, 1976), would explain the apparent regularity of the scratch pattern in the *Cruziana rugosa* group, but seems functionally difficult to reconcile with the tunnelling action regularly found in Penha Garcia.

BEHAVIORAL EXUBERANCE OF *CRUZIANA* PRODUCERS

The large number of bedding planes covered with well preserved trilobite burrows makes Penha Garcia a spectacular site. Patchy distribution is common, with mean bioturbation indices IB = 4–5 (*sensu* Miller and Smail, 1997; Fig. 4a) on areas

up to 20 m^2. These grazing fields contain contemporary burrows of a range of width and may relate to gregarious behavior, which has been previously suggested for trilobites (Speyer, 1990).

Diversity is also expressed by the broad range of behavioral programs employed in the search for food. As pointed out by Bergström (1976) and Jensen (1997), deep *Cruziana* burrows required too much energy to be explained by locomotion alone; their main purpose was food processing. Straight burrows more than 1 m long (Fig. 4b), meanders and dextral or sinistral circling behavior of large diameter (Figs. 4c, d) reflect different exploratory food strategies found in all the *Cruziana* ispp. described here. As can be shown by the Capacity Dimension, circling behavior in *Cruziana furcifera-goldfussi* provides fairly complete coverage ($D_0 = 1.60 \pm 0.08$) similar to the large scribbles of *Cruziana semiplicata* ($D_0 = 1.57$) from the Tremadocian of the Sierra de la Demanda, Spain (Seilacher, 1997). This reflects the convergent evolution of search programs in different groups of trilobites. Some specimens also show regular winding (Figs. 4e, f). *Teichichnoid*-style (see also Goldring, 1985) and deep-U structures with walls as steep as 87° (GPMNHN24) can be found in *Cruziana rugosa* (Figs. 2b, 4g) and *C. furcifera* (Fig. 4h). In some cases, U-shaped *Cruziana* structures merge in a "meeting point" with *Palaeophycus* or *Arthrophycus* (Fig. 4i) or diverge from a common point. These same ichnospecies may show *Arthrophycus*-like ramification (Fig. 4j).

Goldring (1985) demonstrated the intrastratal origin of *Cruziana* by studying sectioned specimens from Penha Garcia. In fact, almost all structures studied were produced below the sediment-water interface, although some epistratal furrows occur on decimeter-thick quartzite beds, mostly with faint inner lobes lacking scratchmarks. *Cruziana* relief varies significantly (Figs. 2a, 4e), indicating burrow formation within the sand layer and the intent to reach an organic-rich mud layer below. One specimen (GPMNHN34) shows typical *Cruziana furcifera* morphology incorporated in the base of a cylindrical tunnel generated by bulldozing which would have lifted and segmented cohesive sediment during its transit through the tier. This kind of trilobite tunneling was common in Penha Garcia, resulting in intense convex epirelief bioturbation atop the beds (Fig. 4k). Lebesconte (1883) long ago described full-relief *Cruziana*. Contradicting the ubiquity of intrastratal burrows in Penha Garcia, more than 20 *Cruziana rugosa* structures were found at the same level evidencing rheotropic alignment (*sensu* Baldwin, 1977c) relative to measured paleocurrent direction (now north) in asymmetric ripples (Fig. 4l).

CRUZIANA VS WORM BURROWS: PREDATION, NECROPHAGY OR COMMENSALISM?

Exposures with abundant *Cruziana rugosa* burrows frequently show worm burrows (*Palaeophycus* ispp.) crossing or cut by trilobite traces. In some cases the worm burrows follow the *Cruziana* median furrow or the inner lobes, with deeper
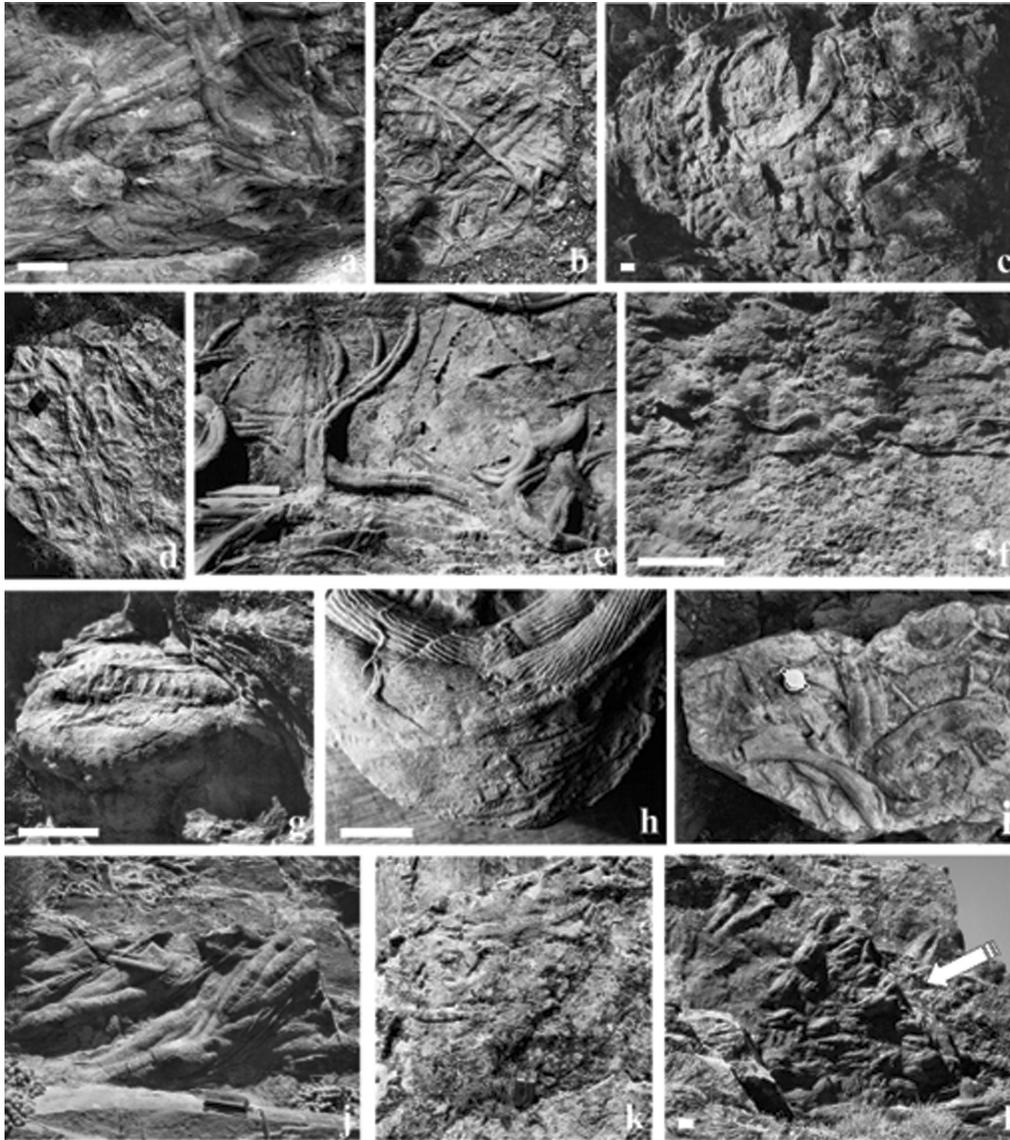
FIG. 4. Diversity in ecospace management by *Cruziana* producers at Penha Garcia. **a**—Bedding plane with *Cruziana* in a patchy IB = 4–5 distributed over 12 m². **b**—Highly bioturbated slab with 4 *Cruziana* morphotypes showing straight-ahead burrowing in *C. rugosa* d'Orbigny and *C. goldfussi* (Rouault) and circling behaviour for one *C. furcifera* d'Orbigny. **c**—Circling behaviour in *Cruziana furcifera* d'Orbigny with a diameter of 70 cm (Serra da Ribeirinha, Penha Garcia). **d**—Scribbling behaviour (dextral and sinister coiling in the same structure) in *Cruziana furcifera* d'Orbigny sometimes showing lateral (genal) ridges. **e**—Meandering *Cruziana furcifera* d'Orbigny with the deepest portion at the inflexion point (outer lobe). See arthrophycid fingering on top of central structure; scale = 20 cm. **f**—Sinusoidal behaviour in *Cruziana rouaulti* (Lebesconte). **g**—U-shaped *Cruziana rugosa* d'Orbigny in a *teichichnoid*-type of burrowing (Fonte do Cuco, Penha Garcia). **h**—*Cruziana goldfussi* d'Orbigny with the previous type of behaviour (Vila Velha de Ródão). Collections from the Geological Museum INETI (box 13); scale = 10 mm. **i**—*Cruziana beirensis* Delgado *meeting point* and *Arthrophycus alleghaniensis lateralis* (Seilacher) convergences (see Neto de Carvalho et al., 2003); scale = 4 cm. **j**—Arthrophycid-fan type of burrowing in *Cruziana rugosa* d'Orbigny. See the genal ridges at the right side of the structures. **k**—Convex epirelief trilobite tunnels cutting linguoid ripples at the top of a quartzite bed. **l**—Current oriented U-shaped *Cruziana rugosa* (paloeocurrent direction to present N given by asymmetric ripples; white arrow). Figures a–d, f, g, j–l have bar and compass scales = 10 cm.

telopodite claw marks normal to the worm burrow (Figs. 5a, 5b), suggesting active manipulation (Martinsson, 1965), or praedichnia (Bergström, 1973; Osgood and Drennen, 1975; Jensen, 1990, 1997; Brandt et al., 1995). Trilobites adopted a range of different feeding strategies (Fortey and Owens, 1999). Still, it is strange for a hunting burrow that neither defensive

tactics of the worm (escape structures) nor fight actions (sudden change in trilobite burrow directions or scratch pattern) are preserved in the ichnological record, which could be interpreted rather as trilobite necrophagy on dead burrowing worms. Furthermore, in Penha Garcia there is a negative correlation between the widths of worm burrows and of *Cruziana* ($r = 0.23$,
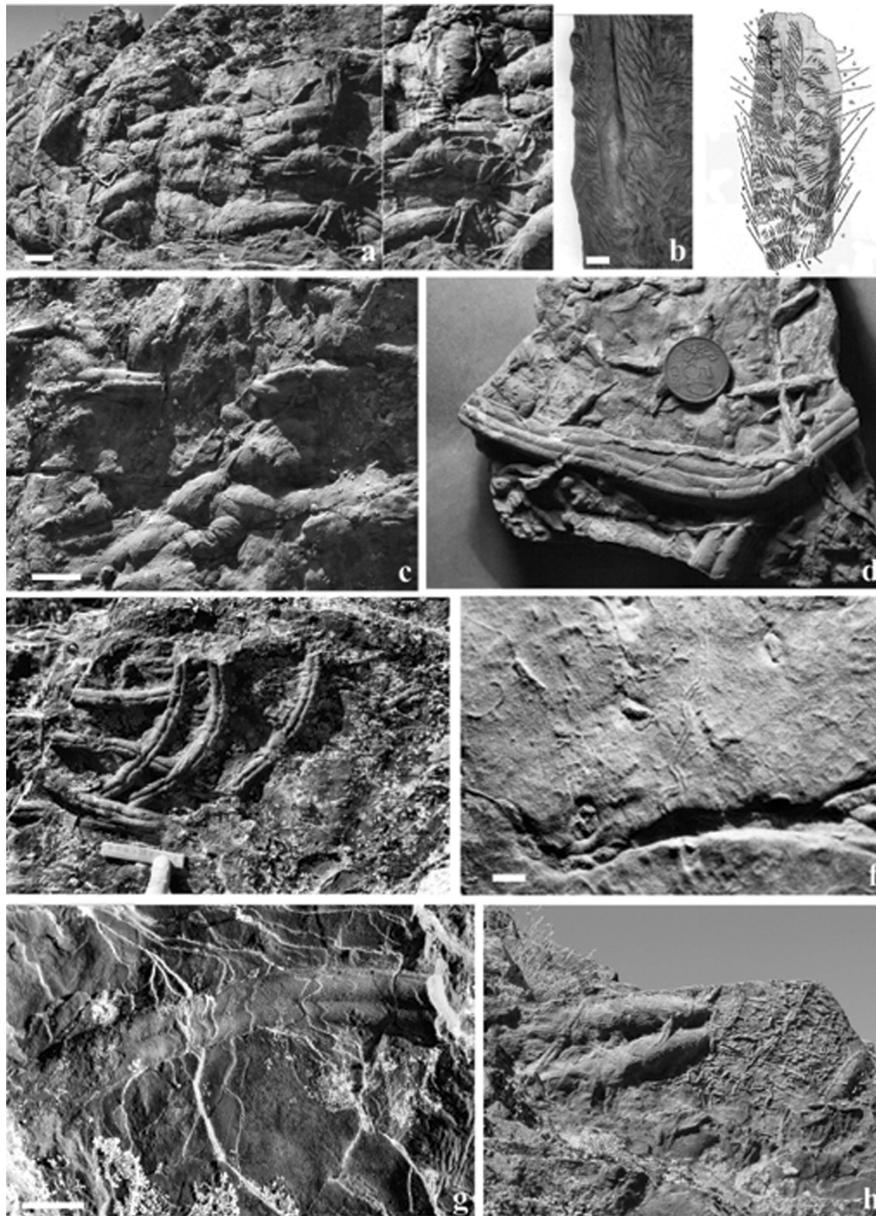
FIG. 5. Biotic and biologically mediated interactions with *Cruziana*. **a**—*Cruziana rugosa* d'Orbigny grazing field showing physical interactions between trilobite and worm burrows. Details from this slab in the right side: above, a worm burrow terminating below the *Cruziana* median furrow and intersected by transverse scratch-marks that emerge from the bioimprint pattern, homeomorphism with *Cruziana pectinata* Seilacher; below, worm burrow cluster crossing *Cruziana* (Serra da Ribeirinha, Penha Garcia); scale = 20 cm. **b**—*Cruziana rugosa* d'Orbigny (Poiares, Freixo de Espada à Cinta). Collections from the Geological Museum INETI 5832 (see Delgado, 1886: p. 46, est. 8). Criss crossing in the scratch pattern with variations at the claw formula and set angle; see set asymmetric angles at the worm burrow intersection (letters correspond to paired sets, photo at right for details); scale = 1 cm. **c**—Worm burrow accompanying the median furrow of a small *Cruziana furcifera* d'Orbigny (arrow signals direction) and following all stratinomic changes of the trilobite burrow for more than 50 cm (Penha Garcia); scale = 10 cm. **d**—Collections of the warehouse INETI 783. *Cruziana bagnolensis* Moriére mimicking *Cruziana goldfussi* (Rouault) motion under its right inner lobe (Carvoeiro, Mação); scale = 2,5 cm. **e**—Dextral circling behaviour in *Cruziana goldfussi* (Rouault) with previous structures being penetrated by later ones produced by the same animal without sediment mixing (Penha Garcia). **f**—Grupo Paleo collections at Lisbon Natural History Museum (116). *Cruziana problematica* (Schindewolf) deformed around worm tunnel without being destroyed by the burrowing procedure (Puerto de San Vicente, Guadarranque syncline, Spain); scale = 1 cm. **g**—*Cruziana goldfussi* (Rouault) obliquely crossing several silty-to-fine sand lamina maintaining the same preservation (Penha Garcia); scale = 10 cm. **h**—Giant U-shaped *Cruziana rugosa* d'Orbigny 24 cm wide within a level rich in seismically induced synaeresis cracks (Penha Garcia).

$p < 0.05$, $n = 27$) suggesting randomness. According to Fortey and Owens (1999) study about feeding variability among trilobites derived from exoskeletal functional morphology these animals made no difference between scavenging and predation. However, these authors assume that larger arthropods usually acquire macrophagic habits because of the high nutritive value of such food items. Despite the adaptive correlations between sediment feeding and necrophagy strategies, trilobites were predominantly microphagous (Seilacher, 1985; Rydell et al., 2001), feeding essentially of the microecosystems supported by bacteria in muds (mudtrophobacterivory).

In Penha Garcia, interactions between *Cruziana* and worm burrows occur only where the two were originally made in different tiers. In one example the worm burrow extended for 50 cm below the *Cruziana* median furrow, following all *Cruziana* stratinomic changes (Fig. 5c). This is the kind of behavior exerted in a deeper tier, detritus-feeding worm that commensally and systematically exploited secondary fabrics induced by trilobites bulldozing and their faecal accumulations. An analogous interaction was recorded in a small *Cruziana bagnolensis* Morière that followed for more than 10 cm the right lobe of a larger *Cruziana goldfussi* using the same type and direction of movement (judging by the similar opisthoclinal disposition and the angulation of chevroned scratches; Fig. 5d).

SUSPECTED BIOMAT-MEDIATED PRESERVATION OF BEHAVIOR DETAILS

As it was shown before, trilobite-related ichnofossils from Penha Garcia correspond to transient feeding epistratal furrows preserved in concave epirelief, intrastratal burrows in convex hyporelief (*sensu* Seilacher, 1955, 1970; Birkenmajer and Bruton, 1971; Goldring, 1985) and endichnial tunnels in convex epirelief, imprinted over or underlying fine sandy and silt-mud micaceous levels covered by arenaceous storm deposits. It is surprising how *Cruziana* from Penha Garcia can preserve delicate scratches (bioprints), considering the granulometry and the cohesion rate of disrupted substrates, but show no modification during the vertical transit (over 15 cm) on successive sediment layers representing shallower tiers (<15 cm) on proximal offshore environments dominated by benthic communities. Deep U-shaped specimens of *Cruziana,* particularly of *Cruziana rugosa* and *Cruziana furcifera,* show vertical lateral walls without evidence of collapse, even though the burrows lacked mucous binding or pelletal reinforcement (Fig. 4h). *Cruziana* intersections within the same tier may be simultaneous or sequential, cutting previously made structures like a knife without any kind of sedimentary disruption (Fig. 4i). Deposition of storm sand was preceded by erosion of several centimeters of predepositional mud. This implies the removal of the transitional layer and subsequent sealing of stiff mud rich in unoxidized organic components. Trilobites would tend to reach this organic-rich sedimentary horizon in order to feed, printing their attempts in the cohesive mud. But this preservational

process worked equally well in fine- to medium-grained sands without thixotropic properties, which could best be explained by the presence of microbial glue. This hypothesis could explain how the same organism could almost immediately intersect its own scribbles without deforming the sediment (Fig. 5e). Goldring (1985) showed *Cruziana* from Penha Garcia that had been exposed by penecontemporaneous erosion and became again filled without significantly erasing the trace. Later dehydration was so intense that *Cruziana* could be deformed by moulding subsequent but penecontemporaneous structures without destroying them (Fig. 5f). The makers of some *Cruziana* vertically penetrated several silty laminae while maintaining the same type of preservation (Fig. 5g). Bacterial biofilms would also favour the generation of synaeresis cracks a few decimeters beneath the sediment-water interface (Pratt, 1998) and cut through *Cruziana* that was crossed later by another trilobite burrow with no such shrinkage cracks (Fig. 5h). All preservational processes involving biological cohesion could be enhanced by diagenetic or tectonic compaction through a "stamp effect" which is responsible for the multiple undertraces coupled into several sediment layers and for the interpenetration without disturbance of burrows that were originally positioned at different levels.

CONCLUDING REMARKS

Trilobite burrows of the *Cruziana rugosa* group from Lower to Middle Ordovician quartzites in the Ichnological Park of Penha Garcia (Portugal) are analysed with respect to age, diversity, producer and behavior.

By its ethological particularities *Cruziana beirensis* is evaluated as a valid ichnospecies of the *rugosa* group.

Cruziana rouaulti also belongs to the *rugosa* group, because its bioprint preservation depends on grainsize (*C. bagnolensis* or *C. problematica*), whereas morphometric comparisons using the Capacity Fractal Dimension group it with *C. furcifera*. Monoichnospecific levels with *C. rouaulti* are interpreted as indicating clusters of juveniles.

Behavioral diversity in this ichnocoenosis is high and represents an acme in meandering, teichichnoid, arthrophycid and circling behaviors. Trilobite biogenic structures may be preserved as epistratal furrows and, most commonly, intrastratal burrows and tunnels.

Burrows of the *Cruziana rugosa* group are attributed to asaphid trilobites by their size and morphology, and by stratigraphic comparison with the Lower Ordovician asaphid-dominated fauna of northwest Gondwana. The burrowing process is reinterpreted based on the morphology of known trilobite appendages and functional analogies or behavioral homoplasies with modern *Triops cancriformis*.

Interactions between the makers of *Cruziana* and worm burrows suggest macrophagic enrichment of an essentially detritivorous (mudtrophobacterivorous) diet, although occasional, and the more usual commensally development of worm

communities occupying a deeper tier previously exploited by trilobites.

Preservation styles and the high degree of patchiness reflect social behaviour based on the management of trophic resources in organic-rich areas and horizons that may have a biomat origin.

SYSTEMATIC ICHNOLOGY

Cruziana beirensis Delgado, 1886
Figs. 2g–h, 4i

1884. *Cruziana furcifera* d'Orbigny, 1842. Delgado, p. 5, pl. II.
1886. *Cruziana beirensis*. Delgado, p. 49–51, pls. 22, 23 and 27.

Emended Diagnosis: *Cruziana* with steep lateral walls protruding vertically in an overlapping, teichichnoid fashion, by the increase in width of coffee bean-shaped lobes.

Holotype: Geological Museum INETI, specimen 13115; Delgado (1886: p. 50, pl. XXVII).

Material: Collection Nery Delgado (Geological Museum INETI): 3 specimens (all numbered 13115); Samples collection warehouse (Litoteca INETI): 7 specimens (469, 516, 551, 557, 783, 797, 824); National Natural History Museum UL (Grupo Paleo): 5 specimens (162, 177, 196, 198, 319). Localities: Penha Garcia; Vila Velha de Ródão; Serra de Águas Quentes and Carvoeiro (Mação); Penedo de Góis; Serra do Buçaco.

Description: Deep structure with vertical walls and a width range similar to those of *Cruziana furcifera* and *C. goldfussi*. Inner lobes progressively increase in width and depth from inside by overlapping and forming in the deepest part a more rusophyciform morphology merging steeply into the bedding plane. Unifid or bifid scratchmarks oblique to the median furrow, straight as in *Cruziana furcifera* and curving distally.

Discussion: This is an ichnospecies of the *Cruziana rugosa* group having bifurcated bioprints and producing compound structures together with *Cruziana goldfussi*. Delgado (1886) erected this ichnospecies pointing out intermediary features between *Cruziana furcifera* and *Cruziana goldfussi*. *Cruziana beirensis* was mentioned many times during the 20th century in papers on regional stratigraphy (Teixeira, 1981 and references therein). Seilacher (1970) and Durand (1985) assumed that *Cruziana beirensis* is a preservational variant of *Cruziana furcifera-C. goldfussi*. Analysing strictly morphological characters, we consider that *Cruziana beirensis* is sufficiently different from *furcifera-goldfussi* (1) by its protrusive teichichnoid style of displacement, (2) by the formation of a rusophyciform trace at depth by enlargement of the inner lobes and (3) by changing from opisthocline to isocline orientation during excavation.

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ADDENDUM

Fractal Methodology for *Cruziana* Analysis

For ichnology, one of the main interests of fractal geometry is that it is a descriptive method that simplifies the investigation of irregularly complex forms that could hardly be studied by Euclidean geometry. For this reason, ichnofossil fractal dimensions are potentially of interest in ichnotaxonomical studies (Jeong and Ekdale, 1996): the larger the fractal dimension, the higher the probability that an area has been covered by a portion of the producer's trace. Fractal Dimension represents the absolute value of sediment bioturbated by an organism. In this way, ichnofabrics reveal ecospace colonization with behavior strategies that can, recurring to fractals, be quantified and compared with samples from the same section, from the same depositional basin, or from spatiotemporally different basins and geodynamic contexts.

Despite the importance of fractal geometry inferred in several, mainly neoichnological, studies (e.g. Dicke and Burrough, 1988; Crist et al., 1992; With, 1994a, b; Nams, 1996; Jeong and Ekdale, 1996; Gibert et al., 1999; Neto de Carvalho, 2001, 2003, 2004; Jeong and Ekdale, in prep.), it remains an obscure analytical tool because of procedural difficulties and the time required (cf. Nams, 1996).

Capacity Fractal Dimension (D_0) is particularly useful in the study of ichnofossils with complex patterns (with displacement restrictions) and large bidimensional development, occurring well delimited in bedding planes. For calculation the *box-counting* theorem is employed (Feder, 1988). It is now well understood that box-counting is a powerful tool in fractal analysis because this allows a renormalization procedure, revealing the amount of persistence of autosimilarity properties and heterogeneity regardless of scale (Song et. al., 2005). This experimental method uses digitized images of ichnofossils. An image is covered by a grid with mesh size ε, counting the minimum number of squares $N(\varepsilon)$ that include part of the ichnofossil. The count must be repeated M times for different ε sizes (M > 2 magnitude orders). The absolute value of the regression line slope when fitted to the Richardson plot $\log N(\varepsilon)$ *versus* $\log \varepsilon$ is the Fractal Dimension by the relation

$$\log N(\varepsilon) \approx \log K. + D \log(1/\varepsilon).$$

The standard deviation of error describes the quality of the regression line adjustment. As ε approaches 0, $\log N(\varepsilon)$ and $\log(1/\varepsilon)$ reach a very high value in comparison with $\log K$. At the limit $\varepsilon \to 0$ is found the precise definition for Hausdorff Dimension

$$D_0 = \lim_{\varepsilon \to 0} \frac{\log N(\varepsilon)}{\log(1/\varepsilon)}.$$

Any physical structure has a minimum scale under which no scale-invariant structure is present. In a digitized image, this scale cannot be less than that of the pixel.