The extended Trilobite: 525 million years feeding imagination

A Trilobite estendida: 525 milhões de anos alimentando a imaginação

C. Neto de Carvalho[1,2]

1 Gabinete de Geologia e Paleontologia do Centro Cultural Raiano, Geopark Naturtejo Meseta Meridional – UNESCO European and Global Geopark. Avenida Joaquim Morão, 6060-101 Idanha-a-Nova. Portugal.
2 Centro de Geologia, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa. Portugal. carlos.praedichnia@gmail.com.

Abstract: Long-extinct trilobites had an important role on marine life evolution and escalation, but also marvelled Man for at least 15000 years. Trilobite-made burrows and tunnels represent an investment of energy to promote homeostasis in local environment conditions. So burrows can be understood as an adaptive extension of the animal to successfully cope with ecospace. Here we also expand the concept of extended physiology of trilobites by regarding *Cruziana* as a vehicle of cognitive communication through time, raising awareness of societies for involving geodiversity, and as a brand for new opportunities of community-based development.

Key-words: Trilobites, *Cruziana*, ecophenotypic behavior, "sense of place", geotourism.

Resumo: *As trilobites, há muito extintas, tiveram um desempenho importante na evolução e escalação da vida marinha, mas também maravilham o Homem há, pelo menos, 15000 anos. As escavações e túneis originados pelas trilobites representam um investimento de energia para promover a homeostasia nas condições ambientais locais. Deste modo, as escavações podem ser entendidas como extensões adaptativas do animal para uma gestão bem sucedida do ecospaço. Aqui pretende-se ir mais longe, expandindo o conceito de extensão fisiológica das trilobites, na análise de Cruziana como um veículo de comunicação cognitiva através dos tempos, relacionando as sociedades com a geodiversidade envolvente, e como marca para novas oportunidades de desenvolvimento local.*

Palavras-chave: *Trilobites, Cruziana, comportamento ecofenotípico, "sentido de lugar", geoturismo.*

THE CONCEPT OF EXTENDED PHENOTYPE

Behavior is primarily adaptation to the environment under sensory guidance. It takes the organism away from harmful events and towards favourable ones, or introduces changes in the immediate environment that make survival more likely.

D. O. Hebb
A Textbook of Psychology (1958)

An organism is a set of morpho-physiological characters (phenotype) determined by genome. Each single gene include different alternative forms, or alleles which, during the recombination process of *crossing-over*, may produce changes in the controlled characters, generating an immense number of possible genetic structures (genotypes) according to a self-organized process. In fact, from the interaction among alleles depends the effect on the proteins synthesis, making smallest modifications the cause of large phenotypic variation. In this way, some alleles generate morphological characters that may contribute to increase reproductive probability of the organism, leading to hereditary consolidation of genetic variability and, thus, to evolution. Other evolutionary processes to be taken into account result from genetic mutations and symbiogenesis.

Co-adaptation or adaptive adjustment of allele sets and their contribution for the evolutionary success strongly depends from environment surrounding phenotype. Adaptive process results from external stimuli that must have immediate feedback through the formulation of sensorial-motor reactions. This ecophenotypic interaction is related with the definition of ecological niche – environmental opportunities that can be exploited by proper organization of the phenotype. Better adapted phenotypes are those who possess more useful genomic variations operating vital functions, such as feeding, locomotion or reproduction, in a certain niche. Under this view, behaviour is all the strategic and flexible responses from a phenotype with the purpose of protecting and transmitting the genetic legacy. These responses allow the homeostatic development of the organism, exerting some control upon the ecosystem, which is intrinsically unpredictable.

Since the foundation times of Ethology by Niko Tinbergen and Konrad Lorenz, behaviour is considered in a complementary way as a mixture of immediate (or mechanical) causes and evolutionary purposes. At the immediate level, actions taken by an organism are the result of internal physiological mechanisms (needs) that are the by-product of a particular development process depending of interactions between genotype and

environmental variables. However, even in completely different groups of organisms, for similar environmental conditions are generated convergent behaviours in an equivalent pool of genetic solutions (universality). Nevertheless, each animal species possesses its own neural mechanism which, for pattern-selective processes, means subtle differences in the mode of reaction to stimuli for related species. On the other hand, behaviours may evolve divergently when subjected to different selection pressures through time. Their substantial modification due to constant adaptation to ecological changes succeeding through time and coevolution, may generate a functional change by coaptation, if this contributes decisively for the increasing reproductive success of the individual.

The biological behaviour, whenever preserved in the fossil record, was ruled and modified by genetic adaptations, by the original environmental and ecological prevailing parameters, to which overlaps diagenetical imprint and even, in some ancient cases, tectonic strain. Ichnology, as 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. Trace fossils represent functional morphology and behaviour of producers, but also the physical-chemical properties of the original environment-related substrate.

Cruziana is among the earliest trace fossils and was certainly one of the first attributed to behaviour of a specific producer, the trilobites. Its occurrence goes from the basal Cambrian, previous to the Atdabanian age of the first trilobites to far beyond the extinction of the group, coming to the present. So, not only trilobites produced *Cruziana* burrows, but any animal with convergent physiological behaviour (trilobitomorph). However the diversity trend of behaviours found at *Cruziana* follow the two main peaks, i.e. Upper Cambrian and Lower Devonian, of morphological diversification of trilobites. Also *Cruziana* foraging burrows are especially abundant in shallow marine settings from Lower Cambrian to Middle Ordovician.

More than 20500 species of trilobites were recently validated, and at least some of them are known to be able to do burrows and tunnels (e.g., Seilacher, 2007), establishing the foraging patterns of more than 40 ichnospecies of *Cruziana* and related stationary feeding programs of *Rusophycus*. So, what are the main palaeobiological implications of the trilobite-built *Cruziana* as an adaptive successful consequence of physiological demands? And how building behaviour of trilobites could come across Time to wonder Man for generations, and become a symbol for a new "sense of place" of communities and visitors?
For answering to seemly rather different questions, but here reunited under the sociobiological expansion of the extended phenotype concept of Richard Dawkins, we must show how to make it.

MAKE IT THE LARGEST (AND THE SMALLEST)

The *Cruziana rugosa* group are considered index fossils for the Lower Ordovician siliciclastic facies of peri-Gondwana. However, this group is present in the Armorican Quartzite Formation at the Centre Iberian Zone (CIZ), at least until Middle Ordovician (Neto de Carvalho, 2006), and may reach Upper Ordovician at Bolívia. *Cruziana rugosa* group was found at Penha Garcia Ichnological Park (Naturtejo Geopark, meridional CIZ) with remarkable abundance, diversity of foraging patterns and sizes, reaching 260 mm wide. But, who were the giants that made these burrows? *Rusophycus* found in the same units show ventral morphology, including hypostome prints, comparable with trilobites and the finding of part of a thorax of a very large trilobite point to giant asaphids (see also Neto de Carvalho, 2006), like Lower to Middle Ordovician *Asaphellus* or *Ogyginu*s species, also found as abundant complete forms and exuviae at contemporary Canelas fossil lagerstätte (Arouca Geopark; Gutiérrez-Marco et al., 2009). At Canelas, giant trilobites found in slates are sub-parallel to bedding and main schistosity plane. Changing morphology and size with deformation in giant asaphids and the once largest *Uralichas* was already noticed by Nery Delgado in his first studies of Covelo and Canelas slate quarries (both at Valongo anticline), at the end of 19th century. Here, diagenetic compaction of ductile shale deposits and Variscan-related transpressive heterogeneous regime combined with lateral escape (Dias and Ribeiro, 1994) was responsible for almost bidimensional flattening of the trilobites. Even taking into account lost of volume by escape of interstitial fluids and decreasing porosity by compaction, vertical shortening of trilobite internal moulds is the square of horizontal dilatation. So, smaller trilobites and trilobite sclerites, or other smaller animals may have comparably smaller flattening rates than bigger trilobites, such as the giant holaspid genus from Canelas, even if they come to appear altogether in the same slate bed. Still, decrease up to 30% of Canelas "giant" trilobites, for some authors, did not make them an average-sized trilobite community at all. So, what are the possible palaeobiological explanations for the evolution of communities of giant trilobites?

Large-sized trilobites from Ibero-Armorica have frequently been related to cold water adaptation, with the position of the area close to the South Pole during the Ordovician. This "polar gigantism" may be compared with recent boreal faunas of marine benthic arthropods. In fact, loss of heat by convection is accelerated in cold-water sea, so smaller body does need to produce more heat (per unite of mass) than a large one, in order to keep pace with surface-loss, meaning more energy spent, more food consumed and, thus, more work done. However, lower Middle Cambrian giant trilobite fauna from eastern Anti-Atlas is found in carbonates. The largest complete and undeformed trilobite found, the asaphid *Isotelus rex* with 720 mm, was found in Upper Ordovician competent carbonates at Canada, and is also an example of low-latitude

gigantism in trilobites (Rudkin et al., 2003). According to these authors, gigantism in arthropods is constrained by intrinsic biological factors (mechanical strength and composition of the cuticle, respiratory efficiency, complexity of moult cycle) and extrinsic (food resources, species interaction, temperature and oxygen availability). Low-latitude giant trilobites may evolve under conditions of ample food supply, elevated atmospheric CO_2 and a warm equatorial setting. In highly-variable dysaerobic cold-water conditions, such as in Canelas, gigantism might have been related with ample availability of food and lowered predation pressure that allowed also for niche partitioning by a diverse epifauna of mostly particle feeder trilobites.

Exoskeletons pose severe limitations to arthropod growth. Considering that the energy demand required to produce the *Cruziana* burrow is dependent on producer's volume (but also food quality and availability), this poses a scale-dependent constraint of energy supply relative to energy demand during growth, and thus evolution to large-size forms. During ontogenetic development trilobite post-embryonic development comprised constant rate of size increase, according to Przibram's Law, between moults, with addition of segments at the posterior part of the thorax and increase of body size. 200-fold increase in size can be expected to impose an almost tenfold reduction in animal's capacity to fuel its activity. *Cruziana* burrows from Penha Garcia may give some light about ontogenetic growth and energy demanding of the producer. Asaphid protaspides have an asaphoid planktic phase with a shift to an adult-like benthic form only at metamorphosis from protaspid to meraspid. *Cruziana rouaulti* and *C. problematica* with less than 2 mm found in Penha Garcia, evidencing the same foraging behaviours as the giant *Cruziana rugosa*, but with a smaller number of appendage imprints, mark the beginning of benthic life and meraspid stage with active exploitation of richer food patches.

So, does trilobite size matters? Taking cautiously diagenetic plus tectonic "gigantism" in orogenic terranes, there are still adaptive ecological, physiological and biomechanical questions remaining to explain size-limitations of trilobite growth.

MAKE IT IN GROUP

Gregarious behaviour can strongly affect individual fitness, as well as multidimensional (spatiotemporal) dynamics of populations. So, it is important to examine behavioural mechanisms and ultimate benefits by which organisms clump together. Trilobites may have grouped in mono- or polyspecific clusters for feeding, reproduction, moulting or protection and some have been mechanically arranged pre- or post-mortem (Paterson et al., 2008). In Portugal, trilobite clusters were long recognized by Nery Delgado (the *Placoparia* "nests" from Valongo). Neto de Carvalho (2006) discussed gregarious *Cruziana* feeding burrows, with uniform size distribution found in beds from Penha Garcia Ichnological Park, through aggregation around patchy food resources indicating limited range of instar classes of a single producer species.

Tightly packed linear patterns of monospecific and polyspecific, articulated or exuviae, single trilobite instars were also found at Canelas lagerstätte (Gutiérrez-Marco et al. 2009) and interpreted as cryptic behaviour to escape predation during collective moulting. But this model finds serious problems in a dysaerobic setting, with frequent fluctuation of Redox Potential Discontinuity above the sea bottom responsible for killing and preserving thousands of trilobites and no fodinichnia bioturbation at all. The linear groupings may be explained by schooling behaviour. Directional polarity rises from self-organization of directed motion (Edelstein-Keshet, 1997), particularly in arthropods. By random fluctuation, the number of individuals moving in some particular direction is slightly higher than in other directions, the unpredictability may be lightened by the presence of food resources or induced by increasing RPD. This may cause the entire traffic pattern to shift so that this direction becomes dominant, depending on the balance of competing environmental and behavioural influences. Trail following in trilobites might have been used for several (combined?) reasons: exploration of an oxygen-depleted environment, migration or foraging. Radwanski et al. (2009) reported for the first time migratory behaviour for trilobites induced by environmental stress that caused mass mortality.

MAKE IT EFFICIENT AS POSSIBLE

Trace fossils provide direct indication of the early evolution of sensory systems and of behavioural responses to environmental heterogeneity (Koy and Plotnick, 2007). Foraging behaviour includes all the methods by which an organism acquires and uses sources of energy and nutrients, the purpose of foraging is to create a positive energy rate for the organism. This must be related with ecospace efficiency in pascichnia, such as *Cruziana,* for energetically expensive burrowing and tunnelling strategies. *Cruziana rugosa* group from Penha Garcia shows higher behavioural diversity using food sources than has ever before been documented in a single section (Neto de Carvalho, 2006). This behavioural diversity, mainly in circling foraging behaviour, has been analysed using the Capacity Fractal Dimension by implementation of the box-counting theorem applied to the bedding plane. Circling, sinusoidal or *teichichnoid* behaviour modifications reflect a generalist mode of sediment feeding for trilobite producers. 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, both for juvenile meraspids and full grown holaspids.

MAKE IT POPULAR

For many thousands of years, Man introduced palaeobiological imprints in stone as landmarks into its

cognitive reasoning of a cultural landscape. Ordovician trilobites were incorporated into magic-religious believes in Central France, at least, 15000 years ago. In some cases, abundant and aesthetic trace fossils were also elevated to hierophanies, material symbols of the divine. *Cruziana* burrows were interpreted as *"painted snakes"* by several rural areas from Centre of Portugal and Extremadura, in Spain, and found as the central piece of many legends related with Moorish Princesses trapped by magic with fabulous gold treasures (Neto de Carvalho and Cachão, 2005). But, in the case of trace fossils, one needs a wider approach, integrating them in the sedimentary and palaeoenvironmental record, analysing preservation and ethological variants and even confronting with present natural and cultural landscape, to where they belong. In this ecological approach in space and time (palaeoecology), ichnofossil-bearing outcrops are elevated to the condition of exomuseums which do not enclose, but are opened to a permanent and dynamic dialogue with the memory of Life. The palaeontologist is the only one to establish the right bonds between past life modes and the present demands.

Ichnoanthropology and ichnoarchaeology are new approaches to understand how Man has been interacting with Nature (Baucon *et al.*, 2008). And Portugal has a remarkable cultural heritage based on trace fossils. Their mystic importance in the past is nowadays favoured by palaeobiological reinstatement and by implementing new strategies for tourism, which the Ichnological Park of Penha Garcia, with outstanding *Cruziana* ispp., is a well succeeded example visited annually by 12000 visitors, one *ex-libris* of Naturtejo Geopark.

Naturtejo is an intermunicipal major state-owned company, established in 2004, including also local private companies, aiming to create conditions for the economic development relying upon tourism. Naturtejo is the management organization of Geopark Naturtejo da Meseta Meridional – UNESCO European and Global Geopark. The municipalities forming the territory of Naturtejo Geopark, namely Castelo Branco, Idanha-a-Nova, Nisa, Oleiros, Proença-a-Nova and Vila Velha de Ródão, have a total area of 4617km^2, ruled by a cultural heterogeneity based on historical and even ecological criteria, where geodiversity appears as an umbrella for development projects. A Geopark intends to be a territory for excellence in three main task forces: conservation, education and (geo)tourism. Using 16 geomonuments (geological icons), the outstanding landscape of the Geopark is intended to be explained immersing visitors into 600 million years of Earth History.

Naturtejo Geopark was the first European and Global Geopark, under the auspices of UNESCO, from Portugal. The solid development of a Geopark must be built by the interplay of scientists, local communities and management authorities under a fractal approach to local development: knowledge, divulgation and promotion from the local to the global scales. In territories long forgotten by national development major plans a Geopark, as a well limited area of important geodiversity in historical interaction with local culture, can really make the difference only if Geopark foundations become deeply rooted in the actions and aspirations of locals, stakeholders and local decision makers. The partnership among local authorities, stakeholders and NGO's (youth-, development-, environment- and culture-related) as well as deep holistic knowledge of territory are essential for effective implementation of a Global Geopark. The annual calendar of geo-events mixing education and entertainment, constant interaction with local stakeholders, protection and management of geosites, educational programmes and development of geotrails, interpretive centres and exomuseums (geosite-based interpretation) physically reinforce the project under the local to national public opinion.

One of the most popular activities in Naturtejo Geopark is the Pedestrian Trails, nature-friendly edutainment activities made in natural or traditional paths. 450 km of signalized pedestrian trails cross all the Geopark, being 103 km with relevant geological interest - Geotourist Trails, which are explored by the educational programs and geotourist routes of the Geopark. They are mainly dedicated to geological themes, such as fossils, mines or landforms. It is possible to find several different experiences, such as at the Ichnological Park of Penha Garcia with the "Fossils Trail", where it is possible to be amazed by the aesthetic beauty of *Cruziana* foraging patterns or swim with floating trilobites and orthoceratid cephalopods that once lived there. Thousands of students come to the Ichnological Park, in the frame of educational programmes and annual projects developed with schools from the territory, to learn about Trilobite paleobiology. Being Naturtejo a special brand of the Tourism of Centre Region, responsible for the tourism incoming, *Cruziana* trace fossils from Penha Garcia are regarded as the icon of nature tourism in the entire region, as a strategy for developing an international-relevant tourism destination. The follow-up of national and international media and some awards including the ProGEO-Portugal Geoconservation Award for the Ichnological Park of Penha Garcia and the whole Naturtejo Geopark, as well as the Skål International Ecotourism Award for the Geopark Educational Programs, by one of the most important tourism associations, are attracting an increasing number of (eco)tourists.

MAKE IT BUSINESS

A European Geopark is a place of true geological landscape wonders with significant dimension to burst sustainable socio-economic development in the territory. This development may come passively with the increasing number of visitors but in areas far away from the main tourist routes cultural georesources prove to be marketing star-products able to attract not only publics but new opportunities for business. A strong promotional strategy must be directed towards the geological values for community in order to get a positive feedback chain reaction of the sense of

belonging that sustains any cultural icon as such for a long period of time. Community will be proud of its geological icon in such a way that they will protect and value it as a fundamental source of communication with the exterior, thus attracting tourism initiatives. At Naturtejo Geopark geological icons could be *Cruziana* or weird granite landforms, old mining works or waterfalls. Despite of many millennia of cultural affection or even religious devotion of Man upon rocks, geoscience issues stands here as in many countries all over the world: so important for the foundations of our civilization, so far from the knowledge of tax payers and decision makers. For local communities of the Geopark talking about geomonuments that attracts thousands of visitors every year is still awkward in comparison with historical and archaeological sites. Nature seems becoming far too distant of daily life even for rural-preponderant communities. But not so in order to feed our imagination with the right communication strategy.

Trilobite fossils are the dinosaurs of the invertebrate world, even if they became extinct 251 million years ago. Nowadays, one may find them as vacuum cleaner robots, Pokémon toys or giant kites. One may also taste trilobites…if coming to Naturtejo Geopark (Fig. 1). A young geologist couple came with the family to live in an almost deserted village called Salvaterra do Extremo. Here they invested their life savings in a new business: a Geo-bakery. From a ruined communitarian oven they built a high-quality guest-house and a traditional bakery reviving old recipes for braid and cookies. But the star-products are the trilobite and granite cookies as well as the "Earth Slices", orogenic toasts and pizza with names of plate tectonics to give a taste of Earth dynamics. Trilobite marketing is also getting attention in the village of Penha Garcia, where the Ichnological Park is devoted to trilobite daily life modes presented by *Cruziana* trace fossils. A trilobite is the logo of the outdoor company "Trilobite.Aventura". Two young entrepreneurs started a business one year ago that runs outdoor sports and medieval parties, a climbing school and the TriloPaint, a Paintball championship, not only in the region but all over the country. Also Arouca European Geopark, at the North of Portugal, is using the well-known giant trilobites from Canelas as umbrella for sustainable based-on community projects.

The impact of this marketing strategy, based on long-extinct trilobite fossils and trace fossils, on media and public opinion is impressive. In short, the close follow-up management of the Geopark with communities, in the field, can find the best opportunities for business with a sustainable approach that may differentiate the territory as tourism paradigm.

FIGURA 1. *President of the Republic of Portugal and his wife tasting the ancient flavours (trilobites) from the Casa do Forno geobakery during an official visit to the Naturtejo Geopark dedicated to "Innovative local communities".*

FINAL NOTES

For hundreds of millions of years as physiological built-up extensions of trilobites and for centuries as ichno-hierophanies, in the condition of identity symbols for communities, *Cruziana* is the foundation of a paradigm for socio-economic development based on Ecotourism, in Portugal, with Naturtejo Geopark under the auspices of UNESCO, included as first priority in the Tourism National Strategic Plan. Today and for the future, *Cruziana* from the Ichnological Park of Penha Garcia become geotourist referential which legitimate sustainable business opportunities and education for a citizenship closer to the condition of biological beings integrated in the Earth system.

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