Giant trilobites and trilobite clusters from the Ordovician of Portugal

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ABSTRACT

Large quarrying surfaces of roofing slate in the Arouca Geopark (northern Portugal), formed under oxygen-depleted conditions, have yielded a unique Ordovician fossil lagerstätte that reveals new information on the social behavior of trilobites. It provides several of the world's largest trilobite specimens (some reaching 70 cm), showing evidence of possible polar gigantism in six different species, as well as numerous examples of monotaxic and polytaxic size-segregated autochthonous trilobite clusters, some of which contain as many as 1000 specimens. These reveal a very diverse social behavior, which includes temporary refuge from predation and synchronous molting and reproduction, demonstrated for the first time in five contemporary families of three different trilobite orders from a single formation.

INTRODUCTION

Trilobites are among the most diverse and widespread arthropod fossils of the Paleozoic Era (Fortey, 2000), but complete specimens surpassing 30 cm in length are rare (Rudkin et al., 2003). Previous taphonomic studies have suggested that some autochthonous monotaxic trilobite clusters (Paterson et al., 2008) were the result of gregarious behavior related to synchronous molting and copulation (Speyer and Brett, 1985), temporary tunnel habitation (Cherns et al., 2006), or permanently cryptic lifestyles (Suzuki and Bergström, 1999; Chatterton et al., 2003). We present a remarkable Middle Ordovician fossil lagerstätte from northern Portugal that not only provides giant trilobite fossils, but contains some trilobite groups showing examples of the following behaviors: (1) en masse mating, with monotaxic body clusters of adult specimens killed by sporadic anoxic fluctuations; (2) epibenthic mass molting, with large assemblages of monospecific exuviae; and (3) hiding in burrows or under skeletal remains to escape predation while molting in a monotaxic to polytaxic cryptic behavior.

Middle Ordovician rocks rich in trilobite fossils were first described from the Arouca region 50 km southeast of Oporto in the mid-twentieth century (Thadeu, 1956) (Fig. 1). Recent reappraisal (Sá et al., 2007) shows that the main trilobite occurrences are toward the middle part of the Valongo Formation (see GSA Data Repository Fig. DR1[1]), which comprises roofing slates of commercial quality. The fossiliferous rocks are of middle Darriwilian age (*Didymograptus artus* graptolite biozone). The reopening of the old Canelas Quarry in 1990 provided the opportunity to collect thousands of new fossil specimens, which have been made available for scientific study through cooperation with the private company responsible for the exploitation.

STRATIGRAPHY

The Valongo Formation is a thick (310–425 m) monotonous sequence of cleaved gray mudstones with shelly and graptolitic horizons (Romano and Diggens, 1974) that accumulated in relatively shallow water clastic environments, as typified by its Reedocalymenine ("Calymenacean-dalmanitacean") trilobite fauna (Fortey and Cocks, 2003). However, in the Arouca area, peculiar extended periods of local anoxia alternated with normal oxygenation, intermittently producing exaerobic and dysaerobic conditions on the seafloor. Barren intervals of laminated shales suggesting anoxia alternate with monotypic concentrations of fossils on laminated shales (exoxia), increasingly bioturbated shales together with characteristic ichnofossils and sparse shelly fossils (dysoxia), and those bearing diverse infaunal and benthic fossils. Beds with concentric grazing traces (*Rotundusichnium*; Fig. DR2), previously restricted to bathyal and abyssal environments (Uchman, 1999), closely follow others with typical shallow-water trilobites (*Neseuretus*; Fig. DR3). These special local conditions are regarded as the result of a stratified-water basin within the Central Iberian shelf produced by extensional basement tectonics, the periodic stagnation being implicated in the formation of the lagerstätte.

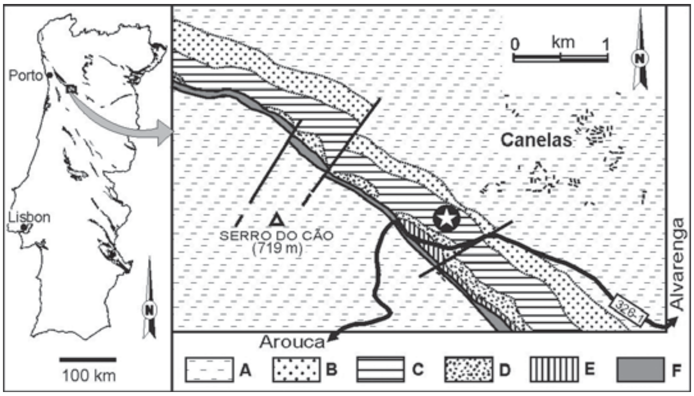

Figure 1. Geological sketch map showing outcrops of Ordovician rocks in Portugal (left, in black) and geological map of Canelas region. A: Neoproterozoic–Lower Cambrian rocks. B: Lower Ordovician rocks. C: Middle Ordovician rocks. D: Upper Ordovician rocks. E: Silurian rocks. F: Pennsylvanian rocks. Star indicates location of studied trilobites, Canelas Slate Quarry.

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[1] GSA Data Repository item 2009109, Figures DR1–DR4, stratigraphic log and supplementary fossil plates, is available online at www.geosociety.org/pubs/ft2009.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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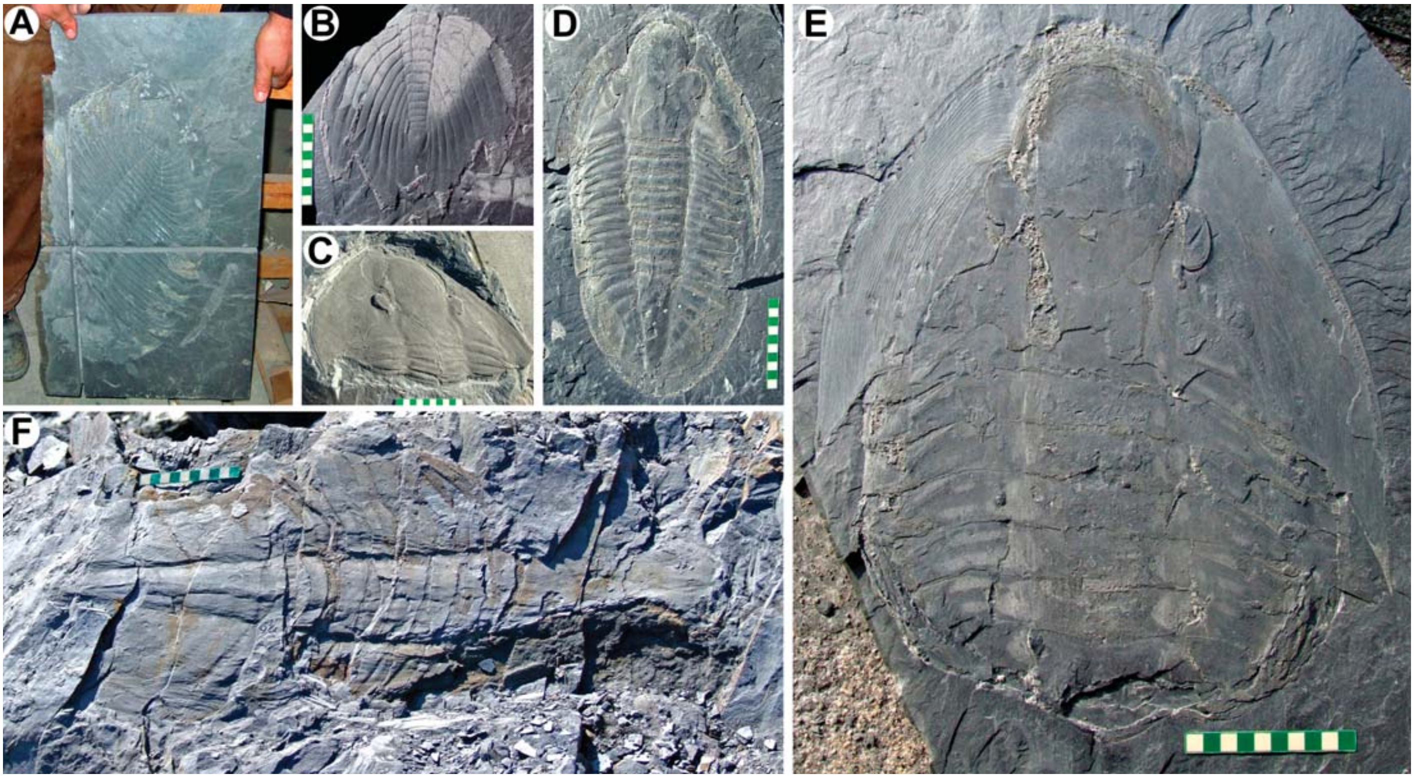

Figure 2. Some giant trilobite fossils from Darriwilian (Middle Ordovician) of Arouca, Portugal. A–B: *Hungioides bohemicus*; partially cut slate slab with 41-cm-long specimen. B: Pygidium with 21 cm sagittal length. C–F: *Ogyginus forteyi*. C: Enrolled specimen 33 cm wide. D: 44-cm-long specimen. E: Partially enrolled specimen 32 cm wide. F: 70-cm-long specimen photographed in situ. Scale bars = 10 cm.

TRILOBITE TAPHONOMY AND PALEOBIOLOGY

The mid-Darriwilian trilobite assemblage occurs between 90 and 240 m above the base of the Valongo Formation, and it includes 15 genera from four different orders (Sá and Gutiérrez-Marco, 2006; Sá et al., 2007), together with cephalopods and graptolites, and rare hyolithids, gastropods, bivalves, rostroconchs, brachiopods, and echinoderms that are only common in the upper beds. In the lower and middle parts of the fossiliferous interval (Fig. DR1), trilobites occur sparsely, and are found (isolated—as many as 3 specimens per 100 m^2—or in autochthonous clusters) showing a random distribution over successive exposed large bedding planes. The whole sequence shows, with episodic fluctuations, a general trend from anoxic to normal shelf oxygenation.

The quarried levels yield mainly large to giant-sized trilobites as partially disarticulated exuviae (Fig. DR4), and a few complete carapaces (Figs. 2A and 2D), including enrolled specimens (Figs. 2C and 2E), which accumulated in situ in the absence of bottom currents. There are four remarkable instances of isolated carcasses found together with their empty exuviae, which may be explained if they died immediately after molting (for illustrations, see Sá and Gutiérrez-Marco, 2006, p. 40). The giant trilobites are asaphids (*Ogyginus*, *Asaphellus*, *Nobiliasaphus*, and aff. *Nerudaspis*), dikelokephalids (*Hungioides*), and cheirurids (*Paterasspis*) in advanced holaspid stages, which alone were capable of surviving in these oxygen-depleted waters.

TRILOBITE GIGANTISM

The largest trilobite specimen ever recorded (*Isotelus rex*) has a reconstructed exoskeletal length of 72 cm (Rudkin et al., 2003). The Arouca lagerstätte has produced a 70-cm-long, almost complete fossil of *Ogyginus forteyi* (Fig. 2F); however, extrapolation from a 21-cm-long isolated pygidium of *Hungioides bohemicus* (Fig. 2B) suggests a total length of 90 cm. Giant articulated trilobites surpassing 30 cm in length are relatively common in our collection, after taking into account the rock compaction and unidirectional tectonic deformation (length increase up to 15%). Co-occurring pendent didymograptid graptolites show insignificant dilatation due to grain-boundary pressure solution or pressure shadows. The same trilobite species are also known from a number of coeval localities within the Central Iberian shelf, but are represented by small to medium-sized specimens (maximum of 25–40 cm in length) and completely disarticulated fragments of the large forms (Rábano, 1990). The giant size of these trilobites from a region at high southern latitudes on the margin of Gondwana, close to the Ordovician south pole (Fortey and Cocks, 2003), may be a cold-water adaptation, as suggested for some Ibero-Armorican trilobites in the Middle Ordovician (Henry, 1989).

TRILOBITE CLUSTERS

The trilobite clusters can be divided into those comprising dead animals and those dominated by exuviae. The former are found in the same levels as large isolated individuals, and include the asaphids *Ogyginus* and *Asaphellus*. Each monospecific cluster ranges from 7 to 17 similar-sized specimens, usually overlapping each other, and almost exclusively made up of carcasses—with hypostome in place—with some enrolled individuals (Fig. 3A). The exuviae clusters are also monotaxic, including smaller-sized genera *Ectillaenus*, *Placoparia*, and *Bathycheilus*, reaching numbers >100 (Fig. 3B), and occasionally >1000 (Fig. 3D). In a unique instance, a cluster of >18 complete exuviae of *Placoparia* occurs under the carapace of a giant asaphid (Fig. 3C). Trilobites in linear clusters are observed in straight, zigzag, or wavy patterns, and can be composed of partially disarticulated exuviae or complete specimens. They are mostly monospecific groups of *Bathycheilus* (Figs. 4A–4C), but some polytaxic clusters of this type also include similar-sized specimens of *Salterocoryphe* and/or *Retamaspis* (Fig. 4D). Complete specimens of *Bathycheilus* are found stretched or enrolled, and are mostly aligned single file and oriented along their sagittal axis. However, some linear clusters primarily representing exuviae are wider, have larger overlap, and generally have more transverse specimens.

DISCUSSION

The enrolled and outstretched trilobite carcasses, both isolated and in clusters, reveals repeated lethal events that may reflect a sudden rise of the oxycline above the sediment-water interface. The undisturbed laminated deposits show no evidence of rapid mudflows or other catastrophic sedimentary events. These temporarily dysaerobic environments were only inhabited by large opportunistic trilobites and occasionally by specialized burrowers (e.g., the producers of *Rotundusichnium* and *Phycodes noha*). Increasingly frequent elevations of oxygen levels upsection are related to basin infilling and the ensuing influx of shelf currents.

The clustering observed in Arouca trilobites can be recognized as gregarious behavior, and can be separated from mechanical aggregation because of the absence of preferred facing orientation, the monotaxic nature of the groups made of similar-sized individuals, and the lack of evidence of currents in the low-energy regime of this depositional environment. Gregarious behavior has been previously described for irregular (i.e., nonlinear) clusters of Cambrian–Devonian trilobites (Speyer and Brett, 1985; Paterson et al., 2007). There may be an analogy with extant horseshoe crabs, which seasonally congregate in large numbers for collective molting, prior to copulation and spawning (Shuster and Botton, 1985). The Arouca clusters include direct evidence of communal molting. The assemblages prove gregarious behavior among species belonging to five families of three different trilobite orders. Social clustering was evidently a common behavioral trait in these arthropods (Speyer and Brett, 1985; Karim and Westrop, 2002; Paterson et al., 2008).

The Portuguese trilobite clusters arranged in single file resemble those described from the Silurian of Canada (Chatterton et al., 2003) and the Ordovician of Morocco (Chatterton and Fortey, 2008), convincingly interpreted as showing cryptic behavior in trilobites. Individuals may have entered preexisting burrows for shelter during the vulnerable molting process; other trilobites have been found hiding inside empty shells (Babcock, 2003). Linear clusters found in the Canelas Quarry are only formed by individuals of the smaller species, which might suggest that the co-occurring giant trilobites did not hide during molting, most likely because they were not as vulnerable. Recent work suggests that some trilobites were able to excavate *Thalassinoides*-type tunnels and develop infaunal behavior (Cherns et al., 2006). It is interesting that an angular pattern observed in Portuguese and Canadian trilobites can be compared with partial occupation of the branches of T-shaped burrows like those of *Thalassinoides*, rather than *Planolites*-like burrows (Chatterton et al., 2003). The commonest trilobite found in linear arrangement is *Bathycheilus*, both as monospecific body and molt clusters. Biomechanical reconstructions of this long-spined genus suggest an epifaunal lifestyle (Hammann, 1983), so it is unlikely that it made the burrows. *Bathycheilus* has been found with *Retamaspis* and/or *Colpocoryphe* of similar size in single clusters, suggesting that they all sought the safety of empty tunnels. Although *Placoparia* has been described as forming cryptic linear clusters elsewhere (Mikuláš and Slavíčková, 2001), its cryptic behavior is here recognized in the form of an irregular molt cluster found under the partial remains of a large asaphid (Fig. 3C), used as a shelter from predation.

CONCLUSION

The unique taphonomic window offered by the Arouca fossil lagerstätte testifies to the great size reached by several Ordovician trilobites, including some of the largest trilobite fossils ever described. It demonstrates a wide array of ethology shown by trilobites, especially their gregarious behavior, which could have played a major role in the undisputed success of this, the most common group of Paleozoic arthropods.

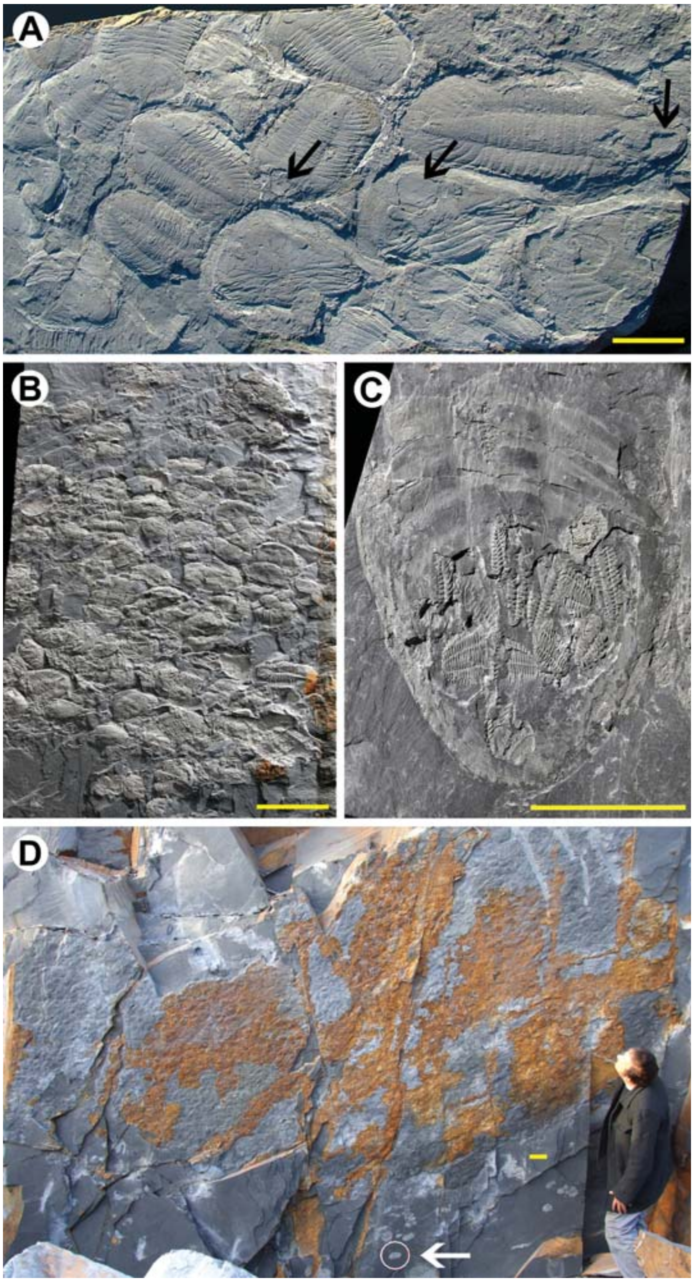

Figure 3. Nonlinear autochthonous trilobite clusters. A: Slab with at least 17 complete specimens of *Ogyginus forteyi*, some showing hypostome in place (arrows) and others enrolled. B: Molt assemblage with >100 specimens of *Ectillaenus giganteus*. C: Cluster of more than 18 articulated exuviae of *Placoparia cambriensis* under the carapace of giant *Ogyginus forteyi*. D: Quarry wall surface with discrete patch of >1000 partially articulated exuviae of *Ectillaenus giganteus*; single complete specimen is circled (arrow). Scale bars = 10 cm.

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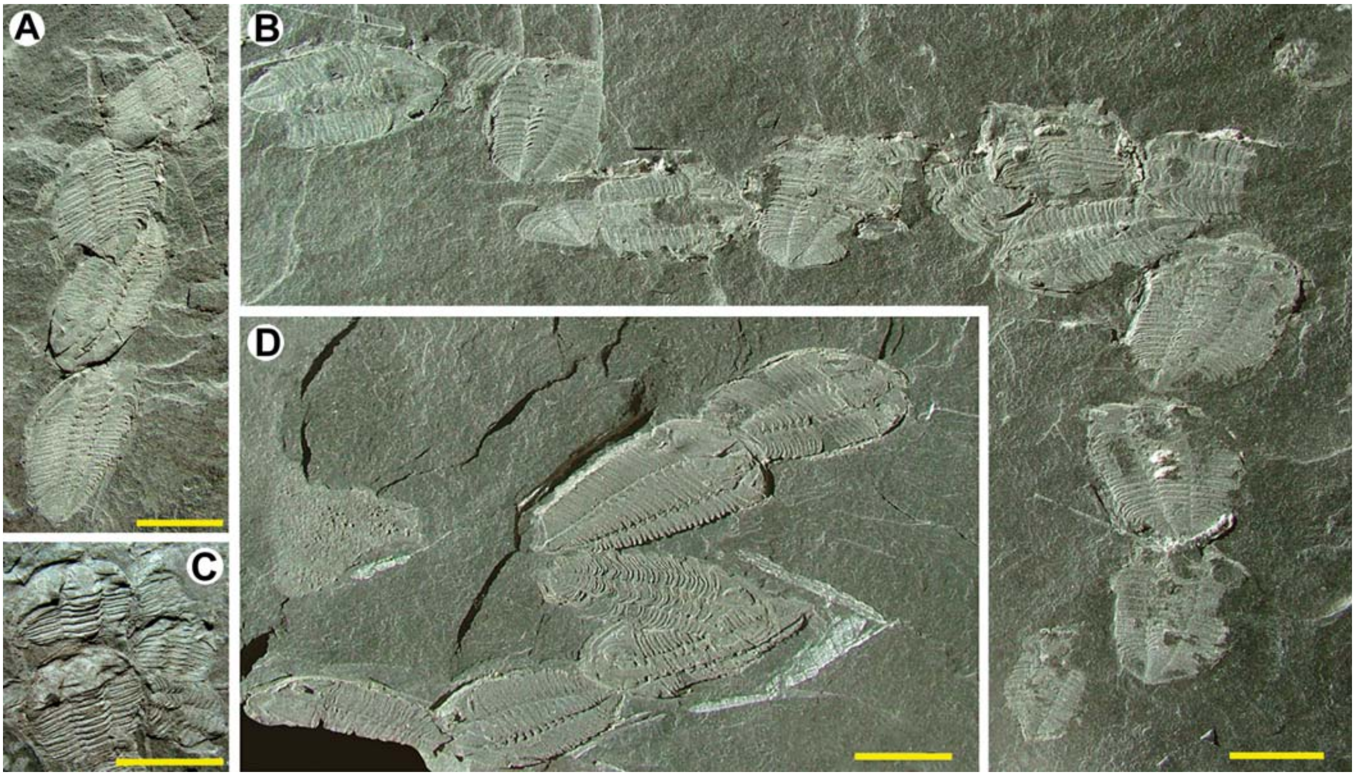

Figure 4. Linear autochthonous trilobite clusters. A–C: *Bathycheilus castilianus*. A: Row of specimens pointing in alternating directions. Specimen at top is enrolled. B: L-shaped cluster of complete and partially disarticulated specimens. C: Distal end of double row of specimens, pointed in same direction. D: Polytaxic zigzag pattern with six specimens. First and last two (starting from top right)—*Bathycheilus castilianus*; second—*Salterocoryphe* cf. *sampelayoi*; third and fourth—*Retamaspis melendezi*. Scale bars = 2 cm.

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