Trilobites in early Cambrian tidal flats and the landward expansion of the Cambrian explosion

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ABSTRACT

The timing of the early invasion of the continents, the routes to the land, and the environmental breadth of the Cambrian explosion are important topics because they are at the core of our understanding of early evolutionary breakthroughs. Illuminating some aspects of these problems are trilobite trace fossils in tidal-flat deposits from the lower Cambrian Rome Formation in the southern Appalachian Mountains of Tennessee (USA). Morphologic details and size range of the trace fossils suggest production by olenellid trilobites, which occur as body fossils in the same unit. The occurrence of this ichnofauna, together with physical structures indicative of periodic subaerial exposure (desiccation cracks) and deposition within the intertidal zone (flat-topped ripples), shows that trilobites forayed into the upper intertidal zone during the Cambrian. Our finding supports the migration of subtidal organisms into marginal-marine, intertidal settings at the dawn of the Phanerozoic, suggesting that trilobites contributed to the establishment of the intertidal ecosystem during the Cambrian. The sequence of events involved in the colonization of early Paleozoic tidal flats is consistent with the idea that most terrestrial taxa originated from marine rather than freshwater ancestors, and that direct routes to the land from marginal-marine ecosystems were involved in the colonization of continental environments early in the Phanerozoic.

INTRODUCTION

The origin of major animal bauplans during the Cambrian explosion took place in open, shallow-marine environments, although the subsequent seaward expansion is revealed by the presence of complex trace fossils in deep-sea deposits (Buatois and Mángano, 2003). However, the extent of the Cambrian explosion in marginal-marine and terrestrial environments is still controversial (MacNaughton et al., 2002; Mángano and Buatois, 2004; Davies et al., 2010; Kennedy and Droser, 2011; Hagadorn et al., 2011; Davies and Gibling, 2012; McIlroy, 2012; Rota-Stabelli et al., 2013). Integration of strong ichnologic and sedimentologic evidence presented herein shows that trilobites, the dominant elements of the Cambrian evolutionary fauna, used resources of the intertidal area by the early Cambrian. The aims of this paper are to (1) document the occurrence of trilobite trace fossils in intertidal deposits of the lower Cambrian Rome Formation of Tennessee (USA), and (2) discuss the implications in terms of the environmental breadth of the Cambrian explosion.

GEOLOGIC SETTING

The Rome Formation crops out through the Valley and Ridge Province in the southern Appalachian Mountains, Tennessee (Fig. 1), at the base of Alleghanian décollements that detached within lower Cambrian strata (Hatcher, 1989), forming part of the Ouachita embayment. Although body fossils are rare in the Rome Formation, a well-preserved olenellid fauna assigned to the *Bonnia-Olenellus* Zone occurs throughout the south-central Appalachians, suggesting a late early Cambrian age (Cambrian Stages 3 to 4) (Palmer, 1971). More recent age determinations based on strontium isotope ratios in interbedded evaporites in the southernmost Appalachian Mountains indicate a slightly older age of 525–520 Ma (Cambrian Stages 2–3; Thomas et al., 2001).

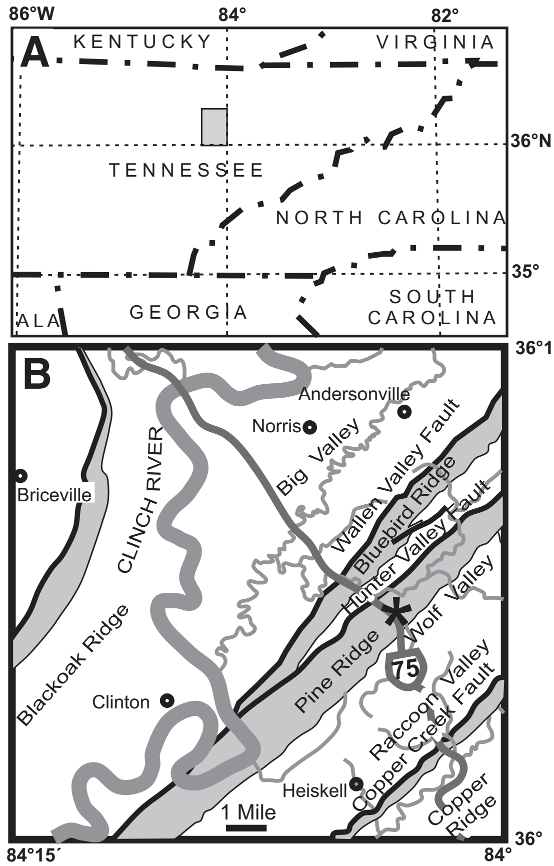

Figure 1. A: General map showing location of study area (detail of Briceville, Tennessee, 7.5′ quadrangle). B: Map showing outcrop belt of Rome Formation and trace-fossil site (asterisk; 36°7′58.96″N, 84°2′21.04″W).

The Rome Formation is a succession of maroon, red, green, and gray mudstone, siltstone, and sandstone, locally interbedded with limestone and dolostone. Much of the Rome Formation has been interpreted as representing tidal-flat deposition (e.g., Samman, 1975). McReynolds and Driese (1994) suggested a mixed carbonate-clastic broad tidal flat domain in eastern Tennessee, with transitions to restricted subtidal and supratidal environments and subordinate storm activity. Diverse symmetrical ripples (including interference patterns and flat-topped ripples), desiccation cracks (Figs. DR1A–DR1D in the GSA Data Repository[1]), rainprints (see

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[1]GSA Data Repository item 2014037, Figure DR1 and Table DR1 (summary of trilobite trace-fossil occurrences in intertidal deposits), is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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Rindsberg, 2005), and salt crystal casts indicate extremely shallow marine environments periodically exposed subaerially in a seasonally dry, probably subarid, climate (Samman, 1975; McReynolds and Driese, 1994; Thomas et al., 2001). Desiccation cracks are a few centimeters to >30 cm wide, narrowing downward and locally penetrating deeper than 10 cm. Polygons have three to six sides, with orthogonal angles, and are thus related to subaerial exposure in upper intertidal to supratidal environments rather than syneresis underwater (Samman, 1975). Crosscutting relationships among cracks demonstrate repeated episodes of desiccation.

OCCURRENCE OF TRILOBITE TRACE FOSSILS

The studied outcrop of the Rome Formation within the White Oak Mountain thrust is exposed at Moores Gap along Interstate Highway 75 west of Knoxville (Fig. 1), eastern Tennessee (Hatcher, 1989). The Rome Formation here is ~100 m thick, and is composed of sets of meter-scale, fining-upward parasequences characterized by shallow-subtidal thick-bedded, cross-bedded, grayish to yellowish sandstone, which passes upward into tidal-flat, thin-bedded flaser, wavy, and lenticular bedded sandstone and siltstone, and is capped by supratidal red shale (Fig. 2).

Trilobite trace fossils such as *Cruziana*, *Rusophycus*, *Monomorphichnus*, *Petalichnus*, and *Dimorphichnus* are common in the heterolithic middle to upper intertidal part of tidal-flat parasequences (Fig. 3). *Cruziana* in particular is crosscut by prominent desiccation cracks. Samman (1975) showed a bedding plane with abundant *Dimorphichnus* crosscut by mudcracks. Some trackways display intense overlap among specimens, forming dense palimpsest pavements. *Planolites*, *Palaeophycus*, and *Skolithos* are also present locally; the latter typically crosscut the trilobite trace fossils. Clusters of *Rusophycus* are locally preserved in subtidal medium- to thick-bedded sandstone and dolostone, together with *Phycodes* and *Bergaueria* (Samman, 1975).

Measurements of the studied trace fossils and those illustrated by Samman (1975) show maximum widths of ~9 cm, although the mean ranges between 2 and 4 cm. Olenellids are the only trilobites of comparable size recorded in the Rome Formation, and regression lines for width/length of Rome trilobite trace fossils (Samman, 1975, his figure 46) are similar to those of olenellids. Fine morphology of transverse striae and size range of the Rome specimens suggest inclusion of the continuous trails in *Cruziana irregularis*, a form originally described from the lower Cambrian Gog Group of the Canadian Rockies, and attributed to olenellids (Fenton and Fenton, 1937), the only arthropods known in that unit (Desjardins et al., 2010). As in the Rome Formation, continuous trails in the Gog Group are intergradational with short resting traces (*Rusophycus* isp.).

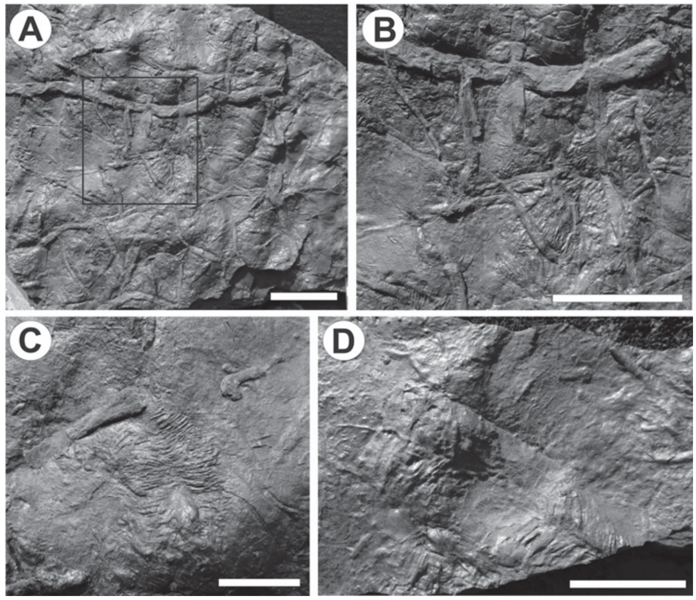

Figure 3. Trilobite trace fossils in tidal-flat deposits of Rome Formation (specimens are housed at Department of Earth and Environmental Sciences, University of Kentucky, Lexington, Kentucky, USA). All scale bars are 5 cm. A: General view of pavement of *Cruziana irregularis* crosscut by different sizes of desiccation cracks. B: Close up showing one of the specimens in A. C: Close up of *Cruziana irregularis* displaying diagnostic features. Transversal endopodal scratch marks are locally grouped in sets of as many as six elements. Note change in angle of different sets (70°–90°). D: *Cruziana irregularis* intergradational with slightly deeper *Rusophycus* isp. No clear marginal ridges or cephalic marks are observed.

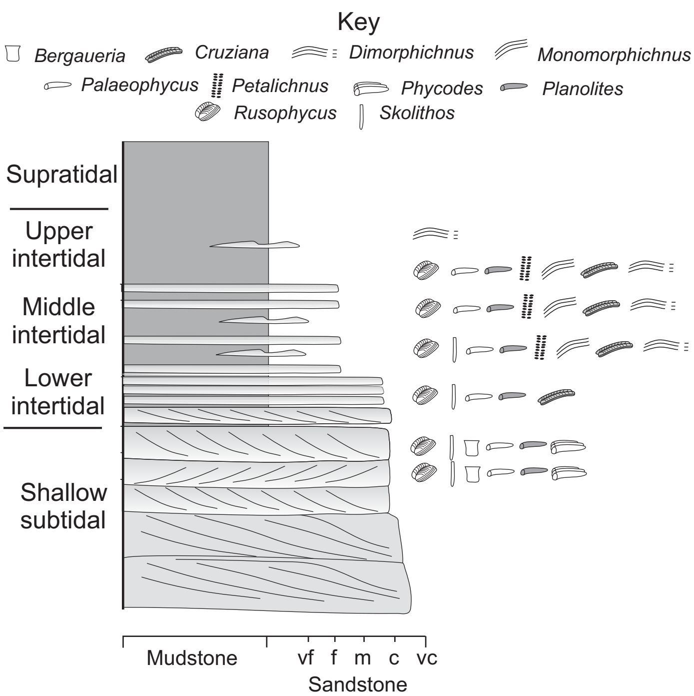

Figure 2. Idealized Rome Formation meter-scale parasequence showing trace-fossil distribution. Abbreviations: vf—very fine; f—fine; m—medium; c—coarse; vc—very coarse. Location of section indicated by asterisk in Figure 1B.

TIDAL-FLAT ECOSYSTEMS AND LANDWARD INCURSIONS OF THE CAMBRIAN EVOLUTIONARY FAUNA

Tidal flats are complex ecosystems rich in food sourced both from land and sea (Reineck and Singh, 1980; Reise, 1985; Palmer, 1995; Little, 2000; Mángano et al., 2002; Desjardins et al., 2012). In modern settings, many organisms migrate to tidal flats for food or protection, with flood and ebb tides transporting marine larvae, juveniles, and adults, and terrestrial organisms visiting the tidal flat at low tide. Some of these are periodic visitors that exploit intertidal resources and retreat to subtidal areas with the ebb flow, or to land during the high tide. Others are permanent residents of the intertidal area. Cambrian tidal flats were different from their modern counterparts; for example, terrestrial predators were absent and terrestrial organics may have been quite scarce, resulting in simpler food webs and community structures (Mángano and Buatois, 2004). Other than by the possible contribution of terrestrial microorganisms (Horodyski and Knauth, 1994; Prave, 2002), Cambrian intertidal trophic webs were probably based mostly on phytoplankton and mesozooplankton (Butterfield, 2001). Despite this, Cambrian tidal flats may have represented habitats of enriched food resources and protection from marine predators (Mángano and Buatois, 2004).

An ichnofauna dominated by trilobite trace fossils in deposits with evidence of tidal influence and subaerial exposure clearly indicates that the producers could migrate into intertidal areas. The presence of the same kind of *Rusophycus* in associated subtidal deposits indicates that the trilobite fauna occupied low-energy settings marginal to subtidal sandbodies, expanding their range periodically into the intertidal setting. Because trilobite trace fossils are typically crosscut by desiccation cracks, trilobites may have migrated into the intertidal zone with the flood tide, retreating to the subtidal zone with the ebb flow. Therefore, desiccation took place after bioturbation and the colonization window in these settings was controlled by the tidal cycle. The trilobite trace fossils record short-term incursions into the intertidal zone rather than membership in permanent intertidal communities. However, the common presence of trilobite trace fossils in upper intertidal deposits indicates that migration was not restricted to the more distal sand-flat portion of the intertidal zone.

Four hypotheses are invoked to explain trilobite incursions to intertidal areas: the trilobite nursery, trilobite pirouette, hunting burrow, and microbial garden hypotheses (Mángano and Buatois, 2004); the first reflects reproductive behavior, while the others are linked to feeding. The trilobite nursery hypothesis was proposed to explain the presence of clusters of *Rusophycus* in tidal-flat deposits, as an analogy with modern limulids laying eggs in modern tidal flats (Fenton and Fenton, 1937; Eldredge, 1970; Mángano et al., 1996). Numerous organisms nest in tidal flats (e.g., limulids, fishes, turtles), returning to subtidal environments after hatching, and therefore tidal flats are nursery sites in which eggs and juveniles are safe from marine predators (Reise, 1985). However, in the Rome Formation, clusters of *Rusophycus* occur only in subtidal deposits.

The trilobite pirouette hypothesis is based on the idea that trilobite trails displaying circular and scribbling patterns represent grazing rather than simple locomotion (Seilacher, 1970). The presence of these patterns in intertidal deposits suggests incursions to browse for organic detritus during the high tide. However, no scribbling patterns have been detected in Rome Formation trace fossils.

The hunting burrow hypothesis proposes that some deep *Rusophycus* may reflect predation on so-called worms (Jensen, 1990). In these examples, the axis of the *Rusophycus* is nearly but not quite parallel to the prey burrows, which follow the curvature of the trilobite trace fossil and commonly contact only one of its lobes. Possible worm burrows (*Planolites*, *Palaeophycus*) are present in the Rome Formation along with *Rusophycus*, but no consistent relationship between them has been detected, providing no evidence of predation.

The microbial garden hypothesis is based on the concept of promotion (*sensu* Reise, 1985), and envisions trilobites visiting the intertidal zone to feed from the enriched food resources resulting from activity of other infaunal organisms. In modern coasts, the activity of infauna (e.g., polychaetes, tellinid bivalves) significantly increases nutrients, promotes upward diffusion of nutrients, and enhances microbial growth (Reise, 1985). Cambrian tidal flats, particularly in the lower intertidal zone, were characterized by intense infaunal activity that may have concentrated organic detritus, microbiota, and meiofauna, promoting trilobite incursions on the rising tide. The widespread presence of trilobite and worm trace fossils in the Rome tidal flat argues for this hypothesis, suggesting that infaunal activity in intertidal sediments was already intense by the early Cambrian, reflecting the impact of the agronomic revolution (Seilacher, 1999).

DISCUSSION: THE ENVIRONMENTAL BREADTH OF THE CAMBRIAN EXPLOSION

The presence of trilobite trace fossils in intertidal deposits of the Rome Formation exhibiting strong evidence of periodical subaerial exposure shows that members of the Cambrian evolutionary fauna could migrate into extremely shallow-water environments, suggesting a significant landward expansion of the Cambrian explosion into marginal-marine ecosystems. Although trilobite trace fossils are usually regarded as indicators of open-marine offshore to nearshore settings, their presence in heterolithic facies can no longer be taken as an absolute indicator of subtidal deposition. In fact, the presence of trilobite trace fossils in intertidal deposits may have been more common than currently envisioned, involving different groups of trilobites during the early Paleozoic (Table DR1 in the Data Repository).

Colonization of tidal-flat environments may have been a protracted process that started near the beginning of the Cambrian. The earliest records of trace fossils in intertidal settings are from the earliest Cambrian (Fortunian), and consist of monospecific occurrences of *Treptichnus pedum* (Geyer and Uchman, 1995; Buatois et al., 2013), currently attributed to priapulids (Vannier et al., 2010). Later in the early Cambrian, other horizontal burrows and trails, vertical burrows, and trilobite trace fossils became common in tidal-flat deposits. By the middle Cambrian to Furongian, an ichnofauna consisting of the giant trail *Climactichnites*, its associated resting trace *Musculopodus*, and arthropod trails and trackways was present in tidal-flat deposits of eastern North America, commonly along with microbial matgrounds (e.g., Getty and Hagadorn, 2008; Collette et al., 2010). As in the Rome Formation, some of these trace fossils are associated with sedimentary structures indicative of sporadic subaerial exposure. In fact, some of the trackways were actually emplaced subaereally in eolian deposits, indicating that arthropods forayed into coastal dunes (MacNaughton et al., 2002; Hagadorn et al., 2011). This sequence of events is consistent with the idea that most terrestrial taxa originated from marine rather than freshwater ancestors and that direct routes to the land from marginal-marine ecosystems were involved (Buatois et al., 1998). The incursion of trilobites to intertidal settings suggests that these organisms contributed to the establishment of the intertidal ecosystem which may have provided food resources and acted as refugia for these migrants and other arthropods.

Moreover, an association of trace fossils and sedimentary facies identical to that of the Rome Formation occurs in the coeval lower Cambrian intertidal strata of the Precordillera of western Argentina (Astini et al., 2000). In this succession, trilobite trace fossils are associated with a set of physical sedimentary structures (flat-topped ripples and desiccation cracks, halite pseudomorphs) indicative of periodic subaerial emergence in a stressed hypersaline environment. This occurrence is of paleogeographic significance because the Argentinean Precordillera was the counterpart of the Ouachita embayment in southern Laurentia (Thomas and Astini, 1996, 2003); during the early Cambrian Tennessee and the Precordillera belonged to the same continent.

CONCLUSIONS

The occurrence of trilobite trace fossils in a setting with strong evidence of intertidal deposition in the lower Cambrian Rome Formation provides solid support for the idea that some of the dominant elements of the Cambrian evolutionary fauna extended their range into these environments. Because the establishment of a complex intertidal ecosystem may have provided food resources and acted as refugia for trilobites and other migrant arthropods, the Rome ichnofauna is an important piece of evidence for the history of the Cambrian explosion.

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