Paleoecology of the familiar trilobite *Elrathia kingii*: An early exaerobic zone inhabitant

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ABSTRACT

The ''ptychopariid'' *Elrathia kingii* is the most familiar and abundant trilobite in North America, but it occurs at only a few localities in the Middle Cambrian Wheeler Formation of Utah. *E. kingii*'s unusual abundance and typically monospecific community association resulted from a novel, opportunistic ecological strategy. We infer that the trilobite occupied the exaerobic zone, at the boundary of anoxic and dysoxic bottom waters. *E. kingii* consistently occur in settings below the oxygen levels required by other contemporaneous epifaunal and infaunal benthic biota and may have derived energy from a food web that existed independently of phototrophic primary productivity. Although other fossil organisms are known to have preferred such environments, *E. kingii* is the earliest-known inhabitant of them, extending the documented range of the exaerobic ecological strategy into the Cambrian Period. We consider it likely that some other monospecific trilobite assemblages consisting of abundant articulated individuals may also be related to extreme, low-oxygen conditions.

Keywords: Cambrian, exaerobic, trilobite, Wheeler Formation, *Elrathia*, oxygen, biofacies.

INTRODUCTION

Elrathia kingii (Meek, 1870) (Fig. 1A) is the most abundant complete nonagnostid trilobite found in North America. Museum and university collections contain thousands of specimens. In fact, *E. kingii* is so abundant that an entire industry has evolved around the fossil, which can be found on jewelry, greeting cards, and refrigerator magnets. Amazingly, its geographic range is limited to a handful of Middle Cambrian localities within a single paleotopographic basin in western Utah. *E. kingii* occurs in the Wheeler Formation, most commonly in monospecific communities with densities of as many as 500 complete individuals per square meter (this study). *E. kingii*, a ''ptychopariid,'' falls into the ''olenimorph'' ecomorphotype category of Fortey and Owens (1990), possessing many adaptations considered well suited for oxygen-deficient environments, including numerous thoracic segments and wide lateral extent of thoracic pleurae, both of which may have served to increase gill area (Hughes and Chapman, 1995). Additionally, *E. kingii* possessed a natant hypostome, indicative of a particle-feeding life habit (Fortey and Owens, 1999). However, in spite its unusual abundance and nature of occurrence, its paleoecology and the depositional environments it inhabited are essentially unknown.

The Wheeler Formation also contains many soft-bodied genera typical of the Burgess Shale (e.g., Robison, 1991) occurring in a facies that has been interpreted to be anoxic in origin, with allochthonous or pelagic fossils (Rees, 1986; Gaines et al., 2003). The facies bearing *E. kingii* occurs in close vertical association (on the centimeter scale) with the facies bearing soft-bodied fossils.

Recognition and paleoecological interpretation of oxygen-deficient environments have developed greatly since the pioneering studies of Rhoads and Morse (1971) and Byers (1977). Particularly significant is the recognition of the ''exaerobic zone'' (Savrda and Bottjer, 1987), a marine biofacies that occurs at the boundary between anoxic and dysoxic bottom waters, at the extreme low-oxygen end of the dysaerobic spectrum. The exaerobic zone is defined in the rock record by the presence of anomalous occurrences of shelly faunas in laminated strata at the transition from laminated to bioturbated horizons (Savrda and Bottjer, 1987). Exaerobic environments are readily recognizable in the rock record, as they are bounded by clear constraints on either side, whereas dysaerobic environments represent a continuum between aerobic and anaerobic environments, and thus are characterized by a broad range of levels of bioturbation (Rhoads and Morse, 1971; Byers, 1977).

Here we present results from microstratigraphic study of the Wheeler Formation in the House Range and Drum Mountains that demonstrate that *E. kingii* occupied a zone interpreted as exaerobic, at the margin of anoxic bottom waters (Savrda and Bottjer, 1987). This finding is significant because it represents the earliest-known example of this ecology and demonstrates the utility of fossils in delineating cryptic, yet profound differences in depositional environments.

GEOLOGIC SETTING

The Middle Cambrian Wheeler Formation accumulated in a localized fault-bounded trough termed the House Range embayment, which formed a prominent reentrant into a broad carbonate platform (Rees, 1986). Although lateral facies changes are conspicuous, the classic sections of the Wheeler Formation in the central House Range (39°15′N, 113°20′W) represent the deepest water facies of the embayment (Rees, 1986). Three selected intervals from this region and one interval of comparable facies from the adjacent Drum Mountains (39°30′N, 113°00′W) are included in this study. Mudstones of the Wheeler Formation in this region are composed exclusively of fine-grained mixed clay and carbonate mud, which accumulated below the influence of storm waves (Gaines et al., 2003). Workers previously noted that many features of the Wheeler Formation are consistent with anoxic conditions, notably the common absence of bioturbation and the presence of abundant Burgess Shale–type preservation (Rees, 1986; Gaines et al., 2003).

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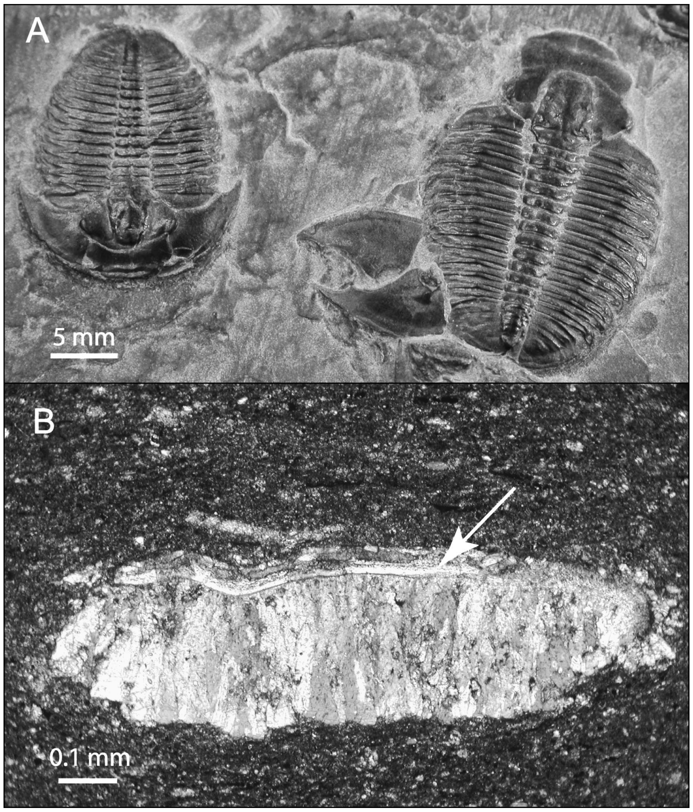

Figure 1. A: Typical bedding-plane association of *E. kingii*. Note association of molt and free cheeks in specimen on right. B: Photomicrograph of *E. kingii* in cross section, showing cone-in-cone calcite coating, radiating outward from ventral surface, below recrystallized exoskeleton (seen here as curved line indicated by arrow).

METHODS

An intensive microstratigraphic field and laboratory-based approach was used to investigate the paleoecology of *Elrathia kingii*. Hemipelagic to pelagic mudstone strata such as the Wheeler Formation are ideally suited for high-resolution paleoecological analysis because sedimentation was relatively constant, reworking by energetic events was rare to absent, and fossils are commonly preserved in situ (Savrda and Bottjer, 1991). As ichno-sedimentary attributes of mudstones are rarely visible in outcrop, intensive laboratory investigation of selected short, continuous stratigraphic intervals is necessary for paleoecological and environmental analysis. *E. kingii*–bearing intervals were identified in the field, and representative sections (15 cm to 2 m thick), chosen from four different localities, were sampled continuously. Samples were slabbed perpendicular to bedding. Sections were then reconstructed and logged on a millimeter scale, recording features of bedding, ichnofabric (additionally assessed with X-ray radiography) and abundance of *E. kingii* in cross section, later normalized to the width of each sample. *E. kingii* is conspicuous in cross section, owing to nearly ubiquitous cone-in-cone calcite encrustation (1–5 mm in length) of the ventral side of the carapace (Bright, 1959; Gaines et al., 2003), resulting in three-dimensional preservation (Fig. 1B). Agnostid trilobites also are preserved in this manner, but are distinguishable from *E. kingii* on the basis of size and morphologic criteria, except when ~2–4-mm-wide specimens (the range of overlap of small *E. kingii* and large agnostids) are cut exactly perpendicular to the long axis. Such instances, however, represent $<3\%$ of specimens, and they do not significantly bias the data. Other nonagnostid trilobites found in the Wheeler Formation are readily distinguishable from *E. kingii* in cross section on the basis of morphology and/or consistent lack of calcite coatings (Bright, 1959). Furthermore, these trilobites are absent from or occur only very rarely in the same beds as *E. kingii* (see discussion of results).

Relative paleo-oxygen levels were assessed by using ichnological criteria. Vertical successions of oxygen-deficient strata may encompass sedimentary rocks representing deposition under anaerobic, exaerobic (see discussion of results), and dysaerobic bottom waters, which are readily distinguished by using a trace fossil model (Savrda et al. (1984). Anaerobic conditions are characterized by an absence of all bioturbation, and increasing extent and depth of bioturbation are correlated with increasing oxygen availability. Ichnofabric was assessed on a bed-to-bed (millimeter-scale) basis. Sections examined contained intervals that are unbioturbated (i.i.1; see Table 1), weakly bioturbated (i.i.2), and weakly to moderately bioturbated (i.i.3). In addition to these three basic ichnofabric categories, we recognized within i.i.2 two types of ichnofabric: (1) i.i.2a beds are burrowed exclusively from above (postdepositional bioturbation) and (2) i.i.2b beds contain burrows originating within the bed (syndepositional bioturbation).

Orientation, taphonomy, and size of individuals of *E. kingii* found in bedding-plane assemblages were measured on slab samples recovered by commercial collectors, the best available material. One studied interval included the horizons from which the bedding-plane assemblages were removed. Each assemblage was treated as an individual data set, with an arbitrary north vector chosen for orientation measurements.

RESULTS

E. kingii occurs in fine-grained mixed clay and carbonate mudstones, which accumulated in a low-energy setting, below the influence of storm waves (Gaines et al., 2003). Independent sedimentologic and paleontologic data, including the total absence of bioturbation through meters of continuous section, absence of in situ fauna, and abundance of organic preservation of nonmineralized macrofossils (see following discussion), indicate prevalence of anoxic conditions throughout much of the Wheeler Formation. Wheeler mudstones consist of amalgamated gray to black couplets, which range from 1 to 20 mm in thickness (average 4 mm). In cross section, ichnofabric and body fossils are easily recognizable as conspicuous interruptions of the highly regular sedimentary fabric. *E. kingii* specimens typically occur in monospecific

TABLE 1. DISTRIBUTION OF *E. KINGII* WITH RESPECT TO BED TYPE

	WA	SS	SQ	DM	TOTAL
Total beds	449	215	103	32	799
i.i.1 beds	340	109	93	26	568
i.i.2 beds	98	76	10	6	190
i.i.3 beds	11	30	0	0	41
E. kingii–bearing beds	150	64	36	17	267
E. kingii i.i.2b beds	10 (6.7%)	5 (7.8%)	1 (2.8%)	1 (5.9%)	17 (6.4%)
E. kingii i.i.1/2a beds	140 (93.3%)	59 (92.1%)	35 (97.2%)	35 (97.2%)	250 (93.6%)

Note: Percentages given constitute percentage of beds within each category vs. the total number of *E. kingii*–bearing beds for each of four sections (WA, SS, SQ, DM) and in total.

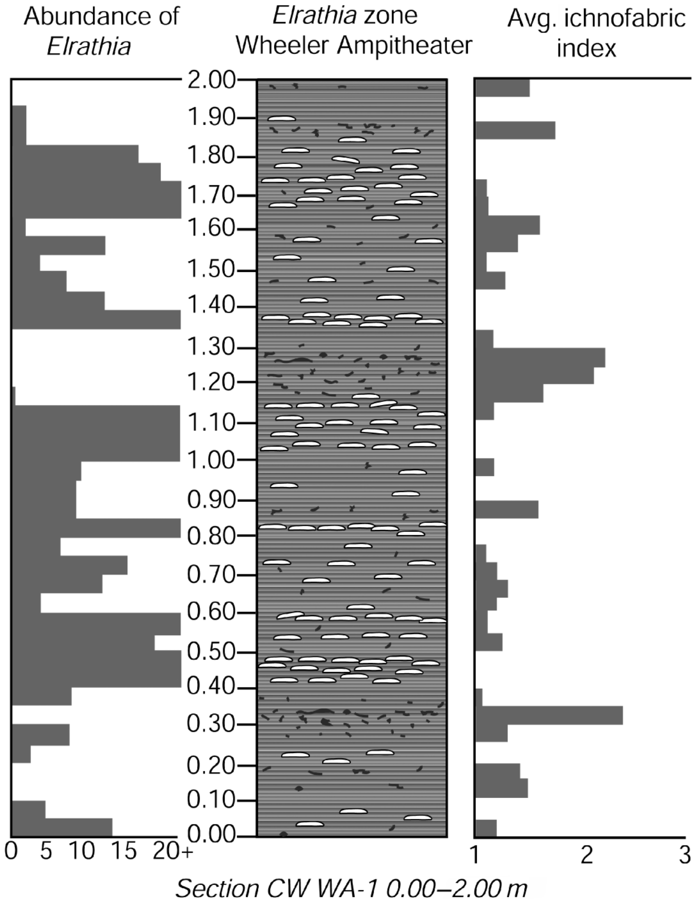

Figure 2. Stratigraphic section, 2 m thick, from Wheeler amphitheater, showing abundance of *Elrathia kingii* (normalized to 50 cm^2) and average ichnofabric index: 449 beds were examined in this section; schematic data shown represent bins spanning 5 cm of vertical section. Using 5 cm bins, abundance of *E. kingii* and ichnofabric index in this section are negatively correlated (correlation coefficient = −0.52).

associations, but rarely cooccur with the benthic trilobites *Bollaspidella* or *Asaphiscus*, with acrotretid brachiopods, or with various disarticulated nonmineralized alga, inferred to be allochthonous (Gaines et al., 2003). Agnostid trilobites occur on bedding planes with *E. kingii*, but were presumably pelagic in life habit (Robison, 1972).

E. kingii individuals occur dominantly in unbioturbated (i.i.1) beds (87.9%) and much less commonly in weakly bioturbated (i.i.2) beds (12.1%); they are not found in moderately bioturbated (i.i.3) beds. However, only 6.4% of the beds in which *E. kingii* occur are i.i.2b-type beds, showing evidence of contemporaneous bioturbation: 93.6% of beds bearing *E. kingii* show no evidence of contemporaneous infaunal activity. These results are highly consistent across the four studied intervals (Table 1). Horizons containing the highest abundances of *E. kingii* are exclusively unbioturbated, and *E. kingii* becomes progressively less common with increasing extent of bioturbation (Fig. 2). Typically, unbioturbated intervals lacking *E. kingii* are overlain by abundant blooms of the trilobite, which then become less common upward, coincident with increasing extent of bioturbation (Fig. 2). Unbioturbated intervals lacking *E. kingii* commonly contain abundant soft-bodied preservation (dominantly of algae), which is generally indicative of anoxic conditions (Allison, 1988; Gaines et al., 2003). Weakly to moderately bioturbated intervals lacking *E. kingii* typically host a more diverse benthic fauna dominated by the trilobite *Asaphiscus* with acrotretid brachiopods and other trilobites including *Bollaspidella*.

All available evidence indicates that *E. kingii* fossils occur in situ. Bedding-plane assemblages are dominated by complete, articulated specimens. Molts are commonly closely associated with molted sclerites (Fig. 1A), indicating that no transport has occurred. Additionally, sizes of complete individuals on single bedding planes vary over an order of magnitude (4–40 mm) and do not show a normal size-frequency distribution, providing no evidence of size sorting. Orientation data of individuals on single bedding planes show no strongly preferred orientation, although some influence of bottom-flowing currents may be inferred, as also suggested by the presence of common upside-down–oriented individuals.

DISCUSSION

Several aspects of *E. kingii* occurrences are unusual. (1) The trilobite occurs most commonly in monospecific benthic associations. (2) *E. kingii* associations are characterized by high density (to 500 complete individuals per square meter); other in situ benthic faunas of the Wheeler Formation are less dense by one to two orders of magnitude. (3) *E. kingii* associations are not transported, but clearly occur in situ. (4) *E. kingii* occur in maximum abundance, and with greatest frequency (93.6%), in unbioturbated or secondarily bioturbated strata, interpreted to represent deposition under bottom-water oxygen levels below those required to support an infauna. It occurs rarely in i.i.2 horizons and is absent from i.i.3 horizons (Table 1). Abundance of *E. kingii* is negatively correlated with extent of bioturbation. Along with independent sedimentologic data, these attributes of distribution provide strong evidence that *E. kingii* was adapted to very low oxygen conditions and suggest that *E. kingii* was specialized for conditions that were uninhabitable for contemporaneous benthic metazoans.

Relative bottom-water oxygen levels of early Paleozoic depositional environments cannot be assessed from the stratigraphic record with the same degree of accuracy possible in subsequent deposits. Trace fossils such as *Chondrites* and *Zoophycos*, which commonly mark the transition from anaerobic to dysaerobic environments (Savrda et al., 1984), were not yet present in basinal marine sediments, complicating interpretation of relative paleo-oxygen levels. Thus, the boundary between unbioturbated and bioturbated horizons in the Wheeler Formation may represent a higher concentration of dissolved oxygen in bottom waters than a comparable boundary found later in the Phanerozoic. However, exaerobic environments are readily recognizable, as they are marked by four important criteria not linked to specific trace fossils: exaerobic assemblages (1) are monotypic, (2) are abundant, (3) occur in unbioturbated strata, and (4) occur adjacent to laminated strata interpreted to represent deposition under anoxic conditions (Savrda and Bottjer, 1987). Furthermore, in the Wheeler Formation, independent proxies of anoxia exist in unbioturbated horizons that immediately underlie or overlie occurrences of *E. kingii*. These horizons contain abundant soft-bodied preservation along continuous bedding planes. In an investigation of conditions that led to soft-bodied preservation, Gaines et al. (2003) used the early-diagenetic mineral assemblages present as further support for anaerobic bottom waters during deposition of these horizons in the Wheeler Formation.

Although oxygen-deficient environments are stressful for most marine benthos, the exaerobic zone offers many advantages to the few organisms that can successfully adapt to low-oxygen conditions. As the habitat is only open to specialists, the ecological constraints of interspecific competition and predation are effectively lifted, allowing for blooms of an opportunistic species. Furthermore, the benefits of this habitat include the presence of an abundant food source, sulfur-oxidizing bacteria (Savrda and Bottjer, 1987, 1991). The anaerobic-dysaerobic boundary is a zone of significantly elevated microbial productivity and nutrient recycling, as both dissolved oxygen and free sulfides are present, providing ideal conditions for abundant benthic sulfur-oxidizing bacteria within this specific region of the seafloor (Savrda and Bottjer, 1987, 1991). In modern environments, colorless sulfur bacteria of the genera *Thioploca* and *Beggiatoa,* both facultative chemolithoautotrophs, thrive at this boundary (Schmaljohann et al., 2001). Sulfur-oxidizing bacteria also form symbiotic relationships with Metazoa found at hydrothermal vents and hydrocarbon cold seeps, where the bacteria are harbored within the gills of mollusks and worms and under the carapaces of arthropods (e.g., Felbeck et al., 1981; Cavanaugh, 1994; Nelson et al., 1995; Polz et al., 1998). Sulfur-oxidizing bacteria have been proposed as a primary food source for some metazoans in the Early Cambrian (Steiner et al., 2001).

Likely exaerobic fossil assemblages are recognized in strata as ancient as Silurian (Wignall and Simms, 1990); younger well-known examples include the Devonian brachiopod *Leiorhyncus* (Thompson and Newton, 1987) and the Miocene bivalve *Anadara montereyana* (Savrda and Bottjer, 1987), both occurring in high-density monospecific associations. Although all previously documented examples are either brachiopods or bivalves, Fortey (2000) proposed that the trilobite family Olenidae (Late Cambrian–Late Ordovician) was adapted for low-oxygen environments on the basis of morphology and occurrence in dark shales with high sulfide content. On this basis, Fortey (2000) proposed that olenid trilobites housed chemoautotrophic symbionts (i.e., sulfur-oxidizing bacteria) along the underside of the carapace, which was morphologically specialized for this purpose. It is also noteworthy that *E. kingii*, an olenimorph, shares morphological characteristics viewed specifically as adaptations for low-oxygen environments and microbial symbiosis (Fortey and Owens, 1990; Fortey, 2000).

All available evidence suggests that *E. kingii* was specifically adapted for life in exaerobic environments and represents the earliest-known example of this ecology. We suggest that *E. kingii* either grazed on benthic sulfur bacteria, which occur in great abundance below the oxygen levels required by most Metazoa, or had evolved a symbiosis with them, as Fortey (2000) proposed for the morphologically similar olenid trilobites. The genus *Elrathia* also occurs in association with a soft-bodied fauna and with the genus *Asaphiscus* in the Conasauga Formation of the Southern Appalachians (Schwimmer, 1989, 2000), indicating the possibility that the genus employed a similar lifestyle across a broad geographic range during the Middle Cambrian. These results suggest that a novel ecological strategy, likely decoupled from standard phototrophic-based food chains, was already in place to facilitate colonization of extreme environments by a newly evolved group during the Cambrian and is likely widespread in the geologic record. Dense, monospecific associations of articulated trilobites are common in the fossil record, and although some are clearly social associations (e.g., Speyer, 1987), we consider it likely that some of them may represent other examples of exaerobic biofacies.

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