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# Asynchronous trilobite extinctions at the early to middle Cambrian transition

F.A. Sundberg[1]*, K.E. Karlstrom[2], G. Geyer[3], J.R. Foster[4], J.W. Hagadorn[5], M.T. Mohr[6], M.D. Schmitz[6], C.M. Dehler[7] and L.J. Crossey[2]
[1]Museum of Northern Arizona, Flagstaff, Arizona 86001, USA
[2]Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, New Mexico 87131 USA
[3]Bayerische Julius-Maximilians-Universität Würzburg, 97074 Würzburg, Germany
[4]Utah Field House of Natural History State Park Museum, Vernal, Utah 84078, USA
[5]Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, Colorado 80205, USA
[6]Department of Geosciences, Boise State University, Boise, Idaho 83706, USA
[7]Department of Geosciences, Utah State University, Logan, Utah 84322, USA

## ABSTRACT

**Trilobites appeared and diversified rapidly in the Cambrian, but it is debated as to whether their radiations and extinctions were globally synchronous or geographically restricted and diachronous. The end of the early Cambrian is a classic example—it has traditionally been defined by the extinction of olenellid and redlichiid trilobites and the appearance of paradoxidid trilobites. Here we integrate the global biostratigraphy of these three trilobite groups with high-precision tuff and tandem detrital zircon U-Pb age constraints to falsify prior models for global synchronicity of these events. For the first time, we demonstrate that olenellid trilobites in Laurentia went extinct at least 3 Ma after the first appearance of paradoxidids in Avalonia and West Gondwana (ca. 509 Ma). They also disappeared before the extinction of redlichiids and prior to the base of the Miaolingian at ca. 506 Ma in South China. This indicates that these three trilobite groups (paradoxidids, olenellids, and redlichiids) and their associated biotas overlapped in time for nearly 40% of Cambrian Epoch 2, Age 4. Implications of this chronological overlap are: (1) trilobite transitions were progressive and geographically mediated rather than globally synchronous; and (2) paleontological databases underestimate the diversity of the early Cambrian. This ~3 Ma diachroneity, at a critical time in the early evolution of animals, also impacts chemostratigraphic and paleoclimatic data sets that are tied to trilobite biostratigraphy and that collectively underpin our understanding of the Cambrian Earth system.**

## INTRODUCTION

Cambrian rocks archive an unparalleled rise in disparity and diversity of animal life including the proliferation of biomineralized fossils such as trilobites. Understanding the Cambrian Earth system and the interactions between the rapidly evolving biosphere and physical and chemical changes in oceans hinges on accurate time-scale calibration. However, a major challenge has been the scarcity of Cambrian reference sections with coexisting cosmopolitan fossils and precisely dated volcanic layers where biological, environmental, and tectonic changes can be closely bracketed. For example, several geochronological dates are available for the traditional lower and upper Cambrian, but relatively few dates exist for the middle Cambrian (Peng et al., 2012; Geyer, 2019). Within this gap of geochronological data, two major groups of trilobites went extinct (olenellids and redlichiids) and another major group appeared (paradoxidids). These events are thought to have occurred at the Epoch 2–Miaolingian boundary. Unfortunately, the last appearance datum (LAD) of olenellids and redlichiids and the first appearance datum (FAD) of paradoxidids have notable discrepancies (e.g., Sundberg et al., 2016). Yet they are widely used for correlating the Series 2–Miaolingian boundary (e.g., Cohen et al., 2013; Zhao et al., 2019).

Recent detrital zircon maximum depositional ages (MDAs) from the Tapeats Sandstone, southwestern United States (Karlstrom et al., 2020), provide evidence for disparity in the origination and extinction of these three major trilobite groups and their associated biotas. This paper presents a novel integration of paleontological and geochronological advances of the type needed to calibrate the time scale, date key trilobite biozones, and foster improved understanding of the evolution of the early to middle Cambrian Earth system, such as the rate and timing of changes in biodiversity and ocean chemistry.

## THE TROUBLSOME LOWER TO MIDDLE CAMBRIAN BOUNDARY

The traditional lower to middle Cambrian boundary has been defined differently for several paleocontinents, in part for historical reasons, and in part because there are few abundant yet cosmopolitan trilobites available for correlation (Figs. 1 and 2; see reviews by Sundberg et al. [2016] and Lin et al. [2019]). In Baltica, Morocco, Spain, and Siberia, the FAD of paradoxidid trilobites has defined the boundary; in contrast, in Laurentia it has been defined by the LAD of olenellid trilobites, and in China it has been defined by the LAD of redlichiid trilobites. Explanations for the geographic differentiation of these early trilobite groups are still debated, as are their evolutionary trends (e.g., Dalziel, 2014).

These traditional definitions have been used by subsequent researchers in each region and are ingrained in the literature. Yet there are challenges in correlating these traditional

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*E-mail: freddeb85@cableone.net

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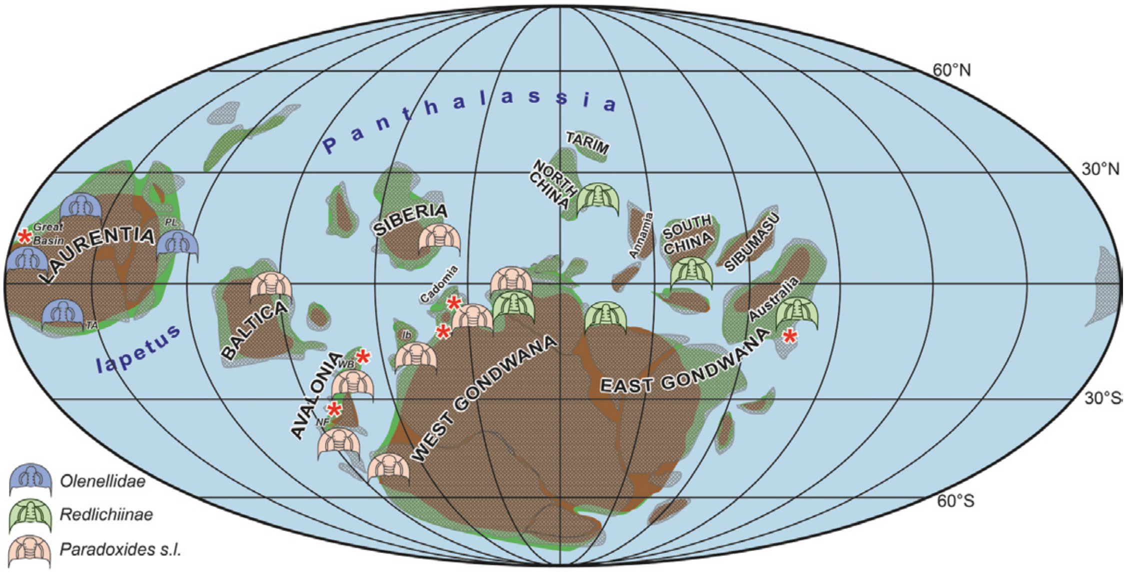

**Figure 1.** Paleogeographic reconstruction for lower to middle Cambrian boundary interval (ca. 508 Ma) showing locations of relevant dated Cambrian sections (red asterisks) and trilobite groups discussed herein (keyed to Fig. 2). Term "paradoxidids" refers to old collective genus *Paradoxides* in its broad sense (*s.l.*—*sensu lato*) and excludes early representatives of the family. Term "olenellids" includes families Olenellidae and Biceratopsidae. Term "redlichiids" includes Redlichiinae only. Continental plates and platelets are shown in dotted gray tone; highlands/landmasses without deposition are marked in brown; shelf areas, coastal regions, and lowlands with episodic deposition are in green; and full marine areas are in light blue. Map modified from Malinky and Geyer (2019). Key areas indicated by abbreviations: Atl—southern Moroccan Atlas ranges; Ib—Iberia; NF—southeastern Newfoundland, Canada; PL—Peary Land, North Greenland; TA—Taconic allochthon; WB—Welsh borderlands, UK.

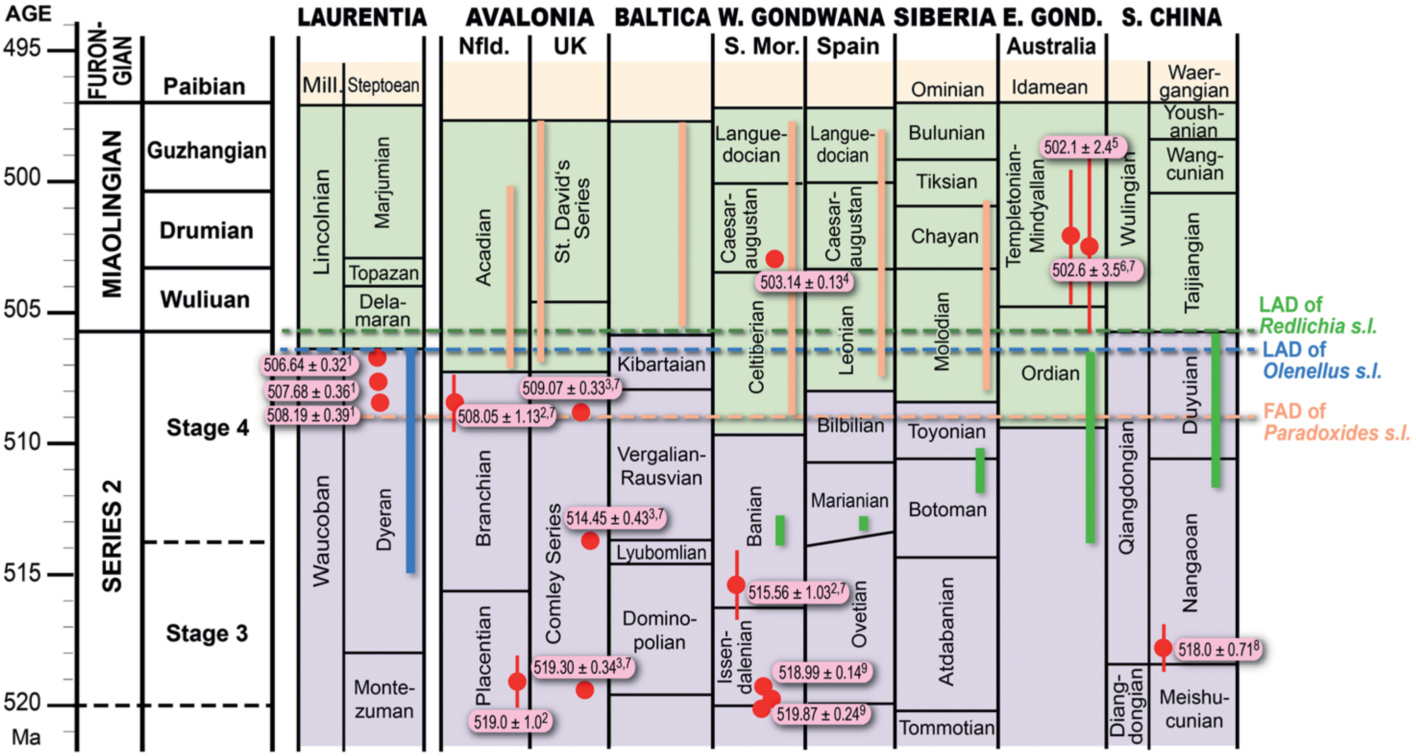

**Figure 2.** Chronostratigraphic correlation of portion of Cambrian (regional lower Cambrian in light purple, middle Cambrian in light green) illustrating differences in time between extinctions of olenellids (blue) and redlichiids (dark green) and first appearance of paradoxidids (peach). Relative thickness of series and stages of each region are based on correlations from Sundberg et al. (2016) and readjusted based on new radiometric dates from sources below. Radiometric dates (red dots; in Ma) and error bars (thin red lines = 2σ) are shown; simple dots are shown where error bars are smaller than dots. Radiometric date sources: 1—Karlstrom et al. (2020); 2—Landing et al. (1998, 2015) and Bowring and Schmitz (2003); 3—Harvey et al. (2011); 4—Landing et al. (2015) from Germany; 5—Encarnación et al. (1999) from Antarctica; 6—Perkins and Walshe (1993) from Tasmania; 7—dates modified by Schmitz (2012); 8—Yang et al. (2018); 9—Landing et al. (2017) (more precise dates from unpublished data by M. Schmitz, E. Landing, and G. Geyer). Abbreviations: Mill.—Millardian; Nfld.—southeastern Newfoundland; UK—United Kingdom; S. Mor.—southern Morocco; LAD—last appearance datum; FAD—first appearance datum; *s.l.*—*sensu lato*.

boundaries between paleocontinents (see summaries in Geyer [2005] and Fletcher [2007]). One major issue is the lack of a consistent co-occurrence of these groups of trilobites. Except for sporadic occurrences of redlichiids in West Gondwana, where paradoxidids have their maximum occurrence and earliest appearance, each trilobite group occurs in a different faunal realm (Peng et al., 2012; Álvaro et al., 2013; Fig. 1). This uncertainty can complicate tectonic- and basin-scale comparisons between continents—such as when rocks from Laurentia are assigned to the lower Cambrian while rocks from Morocco that bear coeval trilobites are assigned to the middle Cambrian (Geyer and Palmer, 1995; Sundberg et al., 2016).

Zhao et al. (2019) recently defined the global Miaolingian Series and Wuliuan Stage to replace the traditional lower to middle Cambrian boundary. The base of the series and stage are defined on the FAD of the corynexochid trilobite *Oryctocephalus indicus* in slope facies of South China, which is directly above the LAD of the redlichiids. However, this level lies two biozones above the extinction of olenellids in Laurentia (see Sundberg et al., 2016; Lin et al., 2019), and *O. indicus* is absent in West Gondwana, Avalonia, and Baltica—thus, its biostratigraphic relationship to paradoxidids is unknown.

## GEOCHRONOLOGY

To begin to resolve these challenges, we integrated new ages from Laurentia with previous geochronology in different regions to constrain the FADs, duration, and LADs of the three key lower to middle Cambrian trilobite groups. Some geochronologic constraints already exist for the paradoxidids (Fig. 2). All ages referred to in this paper were acquired by isotope dilution–thermal ionization mass spectrometry (ID-TIMS; see Karlstrom et al., 2020).

In Morocco, a 515.56 ± 1.03 Ma ash lies >50 m and two biozones below the earliest known onset of the paradoxidids (Landing et al., 1998). A 508.05 ± 1.13 Ma ash occurs below the local FAD of paradoxidids in New Brunswick (Canada) (Landing et al., 1998; see recalibration of Schmitz [2012]). Harvey et al. (2011) reported a 509.10 ± 0.33 Ma age for the Upper Comley Sandstone Formation of East Avalonia (southern UK), which lies below the local FAD of *Paradoxides*.

The only available radioisotope dates that provide an upper bracket for the extinction of olenellids are from the Drumian Stage of the Miaolingian Series (Fig. 2). Landing et al. (2015) reported a 503.14 ± 0.13 Ma age for a volcanic bed in the Triebenreuth Formation (Germany), which is overlain by a Drumian trilobite assemblage. Perkins and Walshe (1993) reported a 502.6 ± 3.5 Ma age for the Mount Read Volcanics (Tasmania), although there are difficulties in the precise faunal control of the samples (see Landing et al., 2015). Encarnación et al. (1999; recalculated by Schmitz, 2012) provided a 502.1 ± 2.4 Ma age for the lower Southwell Group (Antarctica), which corresponds to the Drumian Stage (Landing et al., 2015).

Detrital zircon MDAs (see Karlstrom et al., 2020) provide new constraints for the LAD of olenellids in the western United States. New chemical abrasion ID-TIMS dates of the youngest detrital zircons in the lower to middle Tapeats Sandstone from the Grand Canyon (northern Arizona), southern Nevada, and central Arizona (USA), yield MDAs of 508.19 ± 0.39 Ma, 507.68 ± 0.36 Ma, and 506.64 ± 0.32 Ma, respectively (Karlstrom et al., 2020). Zircons from the Tapeats Sandstone at Frenchman Mountain (Nevada) yield an MDA of 507.68 ± 0.36 Ma and occur ~45 m below the LAD of olenellids (Fig. 3).

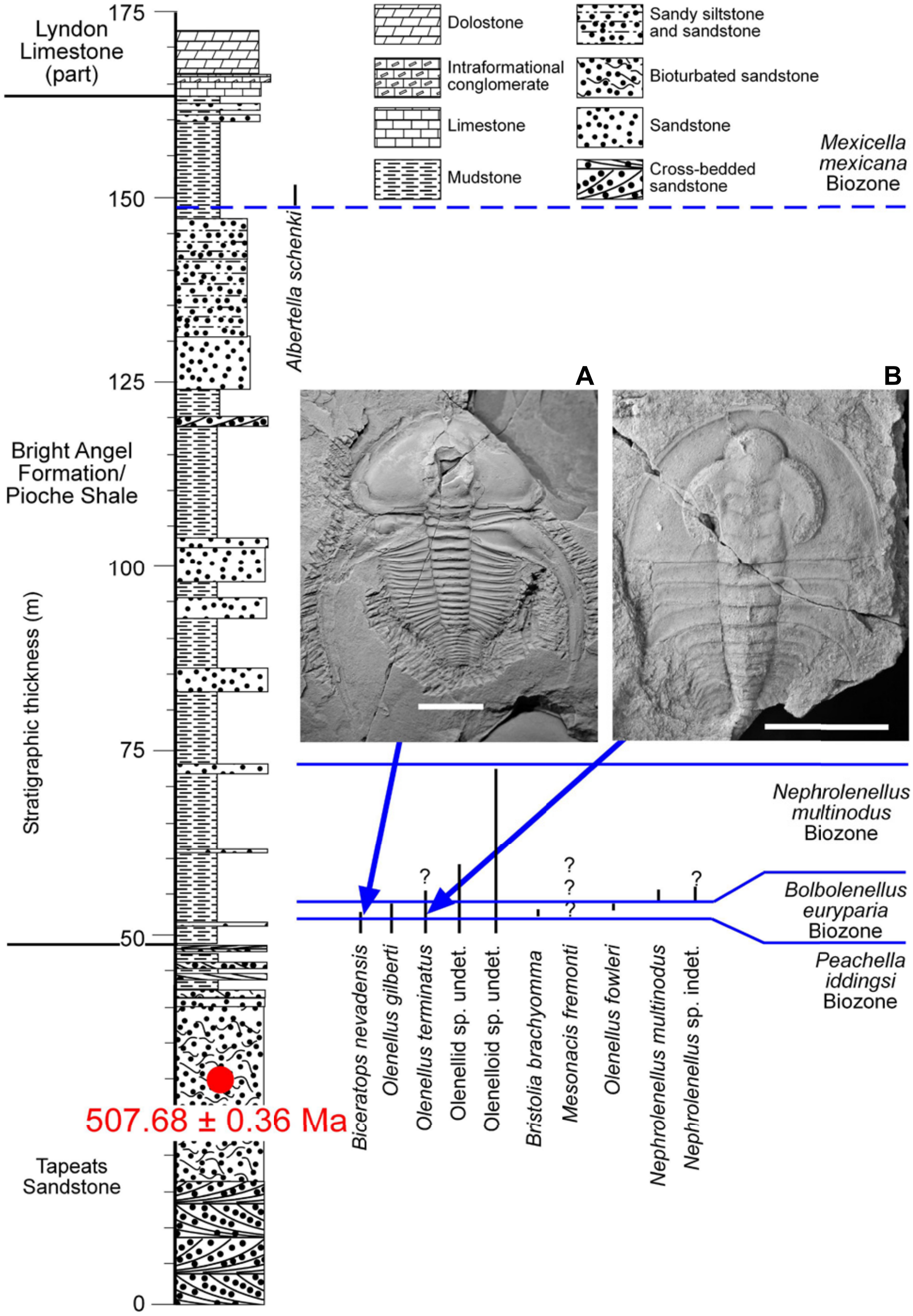

**Figure 3. Radiometric date of 507.68 ± 0.36 Ma from middle portion of Tapeats Sandstone and olenellid occurrences from Bright Angel Formation from Frenchman Mountain, Nevada, USA. Faunal ranges are from Webster (2011) and Pack and Gayle (1971); stratigraphic section is modified from Hardy (1986). Olenellid specimens from Frenchman Mountain section: (A) *Biceratops nevadensis* Pack and Gayle (1971; holotype U.S. National Museum [USNM] 168225); (B) *Olenellus terminatus* Palmer (1998; Institute for Cambrian Studies ICS-10143.11); white scale is 5 mm. Trilobite photos provided by Mark Webster.**

Thus, the maximum date for the extinction of olenellids and the traditional "lower to middle" Cambrian boundary of Laurentia is confidently <507.7 Ma and likely <506.6 Ma.

## IMPLICATIONS

The lower boundary of the Miaolingian Series was given an estimated date of 509.10 ± 0.22 Ma by Zhao et al. (2019, p. 178)—paradoxically, based on an age from British strata (Harvey et al., 2011). Harvey et al. (2011) placed this date near the Series 2–Series 3 boundary (Series 2–Miaolingian Series). Our new radioisotope data (Karlstrom et al., 2020) illustrate that the base of the Miaolingian Series is ≤506.5 Ma and the FAD of paradoxidids is older. We tentatively suggest that the base of the Miaolingian Series should be ca. 506 Ma (see Karlstrom et al., 2020) based on the 20–60 m of stratigraphic separation between the extinction of the olenellids and the base of the Miaolingian Series in Nevada (see Lin et al., 2019). Together, the mismatch of the extinction of olenellids (ca. 506.5 Ma) and redlichiids (ca. 506 Ma) relative to the appearance of paradoxidids (ca. 509 Ma; Fig. 2) yields an overlap that is >38% of the duration of Epoch 2, Age 4 of the Cambrian. This overlap will impact the way we interpret and correlate fossiliferous strata that were deposited during this interval, including some fossil Lagerstätten (e.g., Gámez Vintaned et al., 2011).

There are also implications for correlating global events and driving forces for biotic transitions. Babcock et al. (2015) suggested that most Cambrian faunal turnovers and diversifications are controlled by near-synchronous oceanic and geochemical events. Geyer (2019) pointed out that the base of the Drumian and the significant co-occurring $\delta^{13}$C excursion do not coincide with an extinction. The diachronous appearance of paradoxidids and the slightly staggered extinction of olenellids and redlichiids 3 Ma later suggest that these biotic changes are not the result of near-synchronous events. We suggest that the geographic separation of olenellids, redlichiids, and paradoxidids, combined with an ~3 Ma overlap in biotic transitions, indicates that asynchronous biotic changes occurred in the latter half of Epoch 2.

Studies exploring the dynamics of the Cambrian explosion, diversity, and extinction rates using paleontological databases (e.g., Sepkoski, 1979; Brasier, 1982; Bambach et al., 2004; Na and Kiessling, 2015) will also be impacted by this new geochronology. At present, biotas associated with the olenellid, redlichiid, and paradoxidid trilobite biozones have been misassigned to stages and series of the Cambrian. For example, Sepkoski's (2002) genus database (http://strata.geology.wisc.edu/jack) lists olenellids and redlichiids as ranging within the lower Cambrian and paradoxidids as middle Cambrian. The Paleobiology Database (https://paleobiodb.org/) lists olenellids as lower Cambrian, assigns redlichiid ages from the uppermost lower Cambrian (late Stage 3, Series 2) to late medial Cambrian (Miaolingian Series, Drumian Stage), and lists the paradoxidids as medial Cambrian (Miaolingian).

Errors in paleontological databases are to be expected (e.g., Adrain and Westrop, 2000). However, the time overlap reported here is a nonrandom bias. The redlichiid and olenellid faunal assemblages were assigned to the lower Cambrian, and the paradoxidid faunal assemblages were assigned to the middle Cambrian. Thus, diversity in Stage 4 has been significantly underestimated by the exclusion of the paradoxidids and associated biota (e.g., other trilobites, brachiopods, mollusks, small shelly fossils, trace fossils). As an example, in Siberia and West Gondwana, a minimum of 62 genera with 121 species could shift from the middle to the lower Cambrian as a result of our work (the *Enixus antiquus* and *Ovactoryctocara* biozones of the Siberian Platform [Varlamov et al., 2008; Shabanov et al., 2008]; the *Acadoparadoxides mureroensis* Biozone of Iberia [Liñán et al., 2008]; and the *Hupeolenus* and *Morocconus notabilis* biozones of the Atlas ranges, Morocco [Geyer and Landing, 2006]). Thus, a prediction of our work is that the addition of the paradoxidids should increase estimates of early Cambrian diversity.

## CONCLUSIONS

Tandem U-Pb detrital zircon MDAs from the Tapeats Sandstone in Arizona and Nevada indicate that the olenellid trilobites went extinct after 507.7 Ma, and likely ca. 506.5 Ma, prior to the onset of the Miaolingian (FAD of *O. indicus*). This new age constraint has first-order implications for understanding Cambrian Earth systems:

(1) Previously hypothesized synchrony of the extinction of olenellids and redlichiids with each other is unlikely, and both extinctions lagged, by ~3 Ma, the ca. 509 Ma or even slightly earlier appearance of paradoxidids.

(2) The hypothesis that globally synchronous trilobite extinctions and radiations occurred at the Epoch 2–Miaolingian boundary has been falsified.

(3) Paleobiological compilations have underestimated early Cambrian (Series 2) biotic diversity by considering olenellid and redlichiid assemblages as lower Cambrian and paradoxidids as strictly middle Cambrian.

Considered together, these conclusions signal opportunities to continue combining tandem detrital zircon geochronology and biostratigraphy to test hypothesized age models for other trilobite-based boundaries and for testing whether events from trilobite-keyed chemostratigraphies are global or local in nature (e.g., Lin et al., 2019).

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