



Volcanic ash, victims, and tsunami debris from the Late Bronze Age Thera eruption discovered at Çeşme-Bağlararası (Turkey)

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The Late Bronze Age Thera eruption was one of the largest natural disasters witnessed in human history. Its impact, consequences, and timing have dominated the discourse of ancient Mediterranean studies for nearly a century. Despite the eruption's high intensity (Volcanic Explosivity Index 7; Dense Rock Equivalent of 78 to 86 km) [T. H. Druitt, F. W. McCoy, G. E. Vougioukalakis, *Elements* 15, 185–190 (2019)] and tsunami-generating capabilities [K. Minoura *et al.*, *Geology* 28, 59–62 (2000)], few tsunami deposits are reported. In contrast, descriptions of pumice, ash, and tephra deposits are widely published. This mismatch may be an artifact of interpretive capabilities, given how rapidly tsunami sedimentology has advanced in recent years. A well-preserved volcanic ash layer and chaotic destruction horizon were identified in stratified deposits at Çeşme-Bağlararası, a western Anatolian/Aegean coastal archaeological site. To interpret these deposits, archaeological and sedimentological analysis (X-ray fluorescence spectroscopy instrumental neutron activation analysis, granulometry, micropaleontology, and radiocarbon dating) were performed. According to the results, the archaeological site was hit by a series of strong tsunamis that caused damage and erosion, leaving behind a thick layer of debris, distinguishable by its physical, biological, and chemical signature. An articulated human and dog skeleton discovered within the tsunami debris are in situ victims related to the Late Bronze Age Thera eruption event. Calibrated radiocarbon ages from well-constrained, short-lived organics from within the tsunami deposit constrain the event to no earlier than 1612 BCE. The deposit provides a time capsule that demonstrates the nature, enormity, and expansive geographic extent of this catastrophic event.

tsunami | volcanic ash | Minoan | geoarchaeology | Aegean

The Late Bronze Age (LBA) eruption of Thera on the Island of Santorini was a pivotal event for the Mediterranean and the world (1–3). Loss of life and property damage related to the eruption, including earthquakes, pyroclastic debris flow and ash, and tsunami landfall affected the entire region (4, 5) (Fig. 1). It has been proposed that climatic responses were felt for decades afterward (6). Polar archives (7) and distant tree-ring records (8, 9) also reflect the event. Debate exists regarding its role in the end of Minoan cultural dominance, particularly with regard to seafaring settlements (10). It is commonly used as a tephrochronological marker to interrelate stratigraphic sequences (11, 12).

Despite the massive size of the event, remains from human victims have never been reported, even in the heavily impacted near-field site of Akrotiri (13). Some scholars argue that initial, precursory volcanic activity drove residents

to evacuate the island, though many may have been incinerated at sea in pyroclastic density flows (14, 15). There were at least some surviving refugees, as is evident from the arrival of Thera-type architecture and cultural materials elsewhere postevent (16).

According to archaeological correlations, the event occurred during the Late Minoan IA Period (17, 18), which is contemporaneous with the 18th Egyptian Dynasty in the 16th century BCE (19). This range of dates is termed the “low chronology.” However, measurements from radiocarbon dating of olive wood from the ash layers at Santorini have produced older ages, primarily in the mid-late 17th century BCE, a range of dates referred to as the “high chronology” (20–22). This mismatch upsets the understanding of which people, what powers, and related events coexisted at that time (10, 23, 24).

Significance

The significance of this study is multi-faceted, touching upon methodological advances in multidisciplinary approaches (earth sciences/geology–archaeology) as well as contributing to the historical and chronological understanding of the Late Bronze Age Thera eruption impacts. Our study presents physical evidence that very large, damaging tsunamis arrived even in the northern Aegean, an area previously assumed to be affected only by ash fallout. The tsunami deposits at Çeşme-Bağlararası contain the first victims (human and dog) ever identified related to the eruption and its immediate consequences. The work also introduces nine radiocarbon ages directly from the event deposit that will be of great interest and cause significant discussion amongst scholars, particularly given their context within a well-constrained, undisturbed, stratigraphic archaeological sequence.

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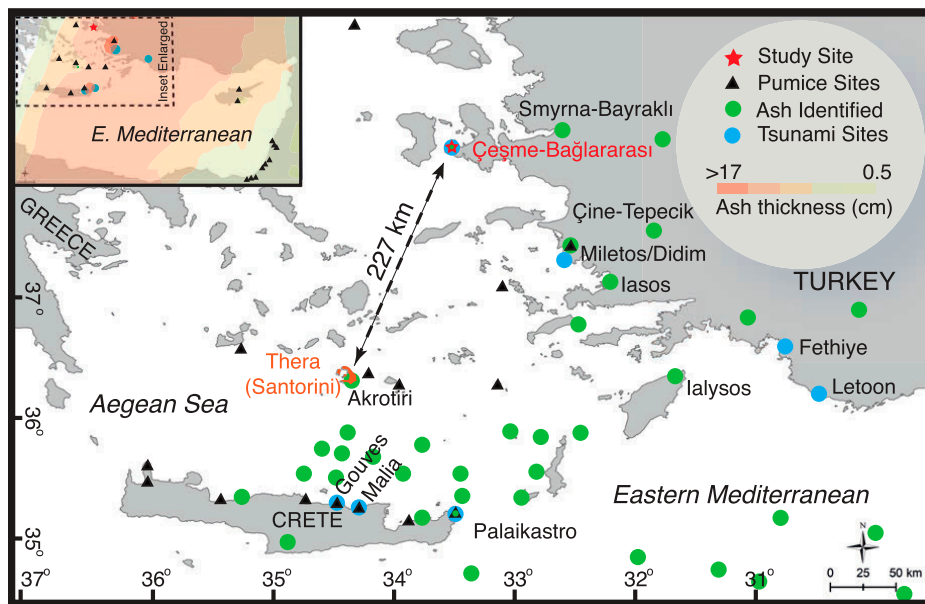


Fig. 1. Map of the Aegean and Eastern Mediterranean Seas, highlighting locations with evidence related to the LBA eruption of Thera (“Bo”) (11–15, 50, 57–59). The *Inset* map shows ash thickness contours (57).

Çeşme-Bağlararası (Fig. 1) was occupied near-continuously at least from the mid third millennium BCE until the 13th century BCE (25, 26). The site was a thriving western Anatolian coastal settlement with evidence for land and sea trade, including Minoan cultural elements during the first half of the second millennium BCE. Given its location and complexity, it would have been a central regional hub (26). Today, the site is located about 200 m from the modern Çeşme Bay coastline and marina. Paleogeographic reconstructions from the LBA place the waterline even closer (<100 m) and include east- and west-oriented rivers flanking the site (27). Estimates of relative sea level between 3,000 and 4,000 y ago are within a meter of modern values (including error) (28), and observations of the elevation relationship between architectural components of the site and the coastal water table (sweetwater) suggest similarity to today. Combined, this suggests that while relative sea level may be similar today, the coastal positioning has changed.

Beginning in 2009, excavations shifted to an area that was already deserted at the time of the Theran eruption. This area included massive fortification walls that were heavily disturbed with a laterally extensive layer of rubble and chaotic sediments, including a distinctive ash and a charred layer (Fig. 2 and *SI Appendix, Fig. S1*). A representative sedimentological section was analyzed using multiple proxy methodologies (*Materials and Methods*) to determine the source, age, transportation mechanisms, and taphonomic history of the sediments, which was then compared to the finds from the archaeological excavation.

Results

General Description of the Sedimentological Horizons. Three main sequences, H1, H2, and H3, were identified (Figs. 3 and 4), and the lowermost H1 subdivided into four subphases (H1a through d). The base of the sequence (H1a) contains framework-supported large rubble (~25 to 40 cm), pottery (CB Level 1, which includes Late Minoan IA [LM1A] Cretan and minoanizing pottery), shell, and bone. This is followed by similar but matrix-supported sediments without bedding, a fine, noncontinuous ash layer (<1 cm, top of H1a; Fig. 3), imbricated inclusions, and smaller rubble pieces. After the broken ash layer, another sequence (H1b) with the same chaotic characteristics repeats and are topped

by a thicker ash layer at an elevation of +0.62 msl (top of H1b; Fig. 3). Elemental values of the ash match tephra from the Santorini “Bo” eruption (*SI Appendix, Fig. S5*). The radiocarbon ages of two samples from above and two samples from below the layer are in the range of both low and high chronologies (Fig. 3 and *SI Appendix, Figs. S6–S8*). The lower contact of the H1b ash layer is sharp, and the upper contact has truncated flame-like structures. An approximately 8-cm-thick layer (H1c) above the ash contains similar sediments and inclusions as H1b; however, instead of another ash layer, it ends with a distinctive, charcoal-rich lens with charred remains. In H1d (Fig. 3), there is a repeat of similar sediments, inclusions, and pottery (CB Level 1, which includes LM1A Cretan and minoanizing pottery) but with the addition of larger rubble (~<15-cm diameter) capped by imbricated pebbles and a very fine (~1 cm) terminal silty layer lens (“mudcap,” Fig. 4).

Marine Markers and Elemental Values in the Sedimentological Horizons. The H1a through d sequence has an overall average foraminifera abundance of approximately five to nine

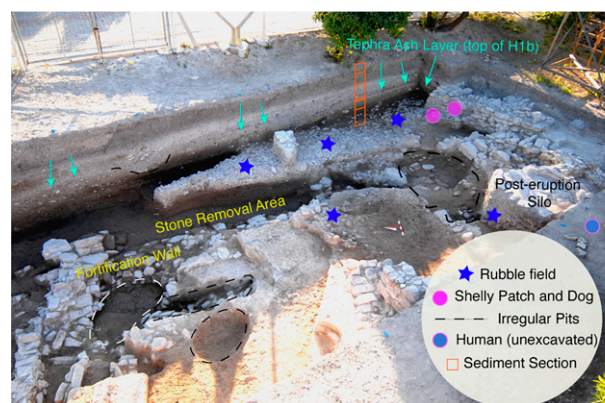


Fig. 2. Çeşme-Bağlararası Excavation. Photograph showing the site as it appeared in 2012. Features from the damaged and disrupted area as well as locations of sediment sampling are highlighted.

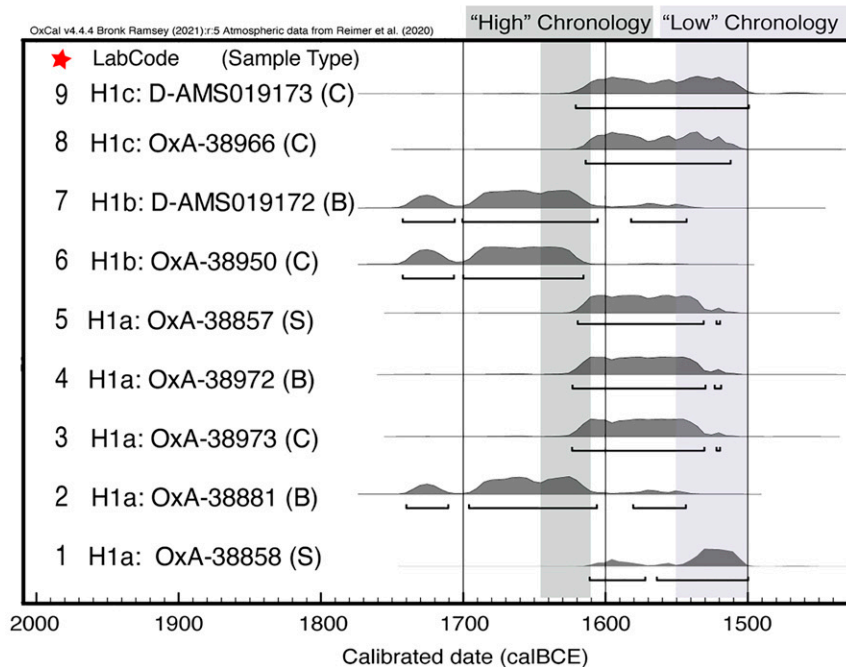
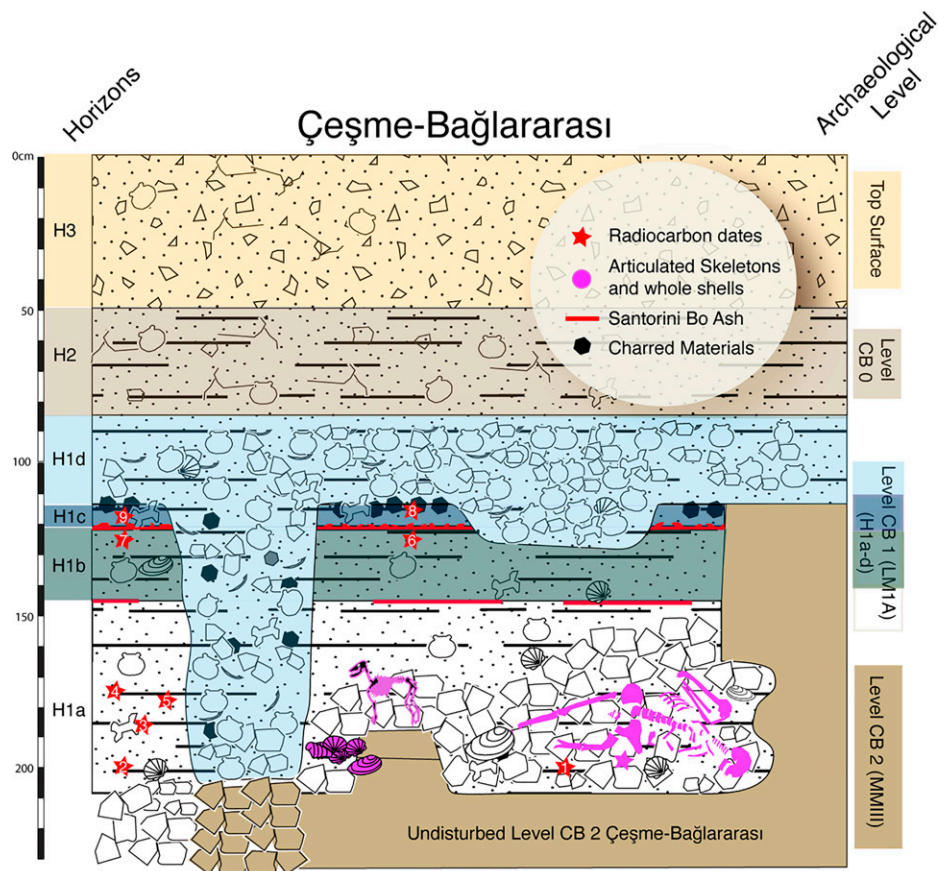


Fig. 3. Illustrated schematic of Çeşme-Bağlararası's stratigraphic sequence, highlighted features, and radiocarbon ages. C, S, and B are used to indicate charcoal, seed, or bone (SI Appendix, Table S1). The human and dog skeletons and shell-rich, muddy rip-clast bundle (H1a) are marked in purple. Horizons H1a through d all relate to the Thera eruption event but represent four consecutive but time-separated tsunami wave inundations. The intruding sediments from H1d were the result of the salvaging of building stones (deeper pit) and possibly rescue efforts (shallower pits) during a hiatus in tsunami arrivals. H2 is a later archaeological deposit that accumulated over time. H3 includes upper agricultural and top surface soils.

individuals/cm³ and 2.9 species/cm³ with a high proportion of staining (Fig. 4 and Dataset S1). All >500-µm samples included fragmented, whole-shell, and urchin spicula (combined total

average 12.2/cm³). Elemental values (X-ray fluorescence spectroscopy [XRF]; Dataset S1) in H1 relative to H2 and H3 are higher in Ca and lower in Al. The lower subhorizons H1a

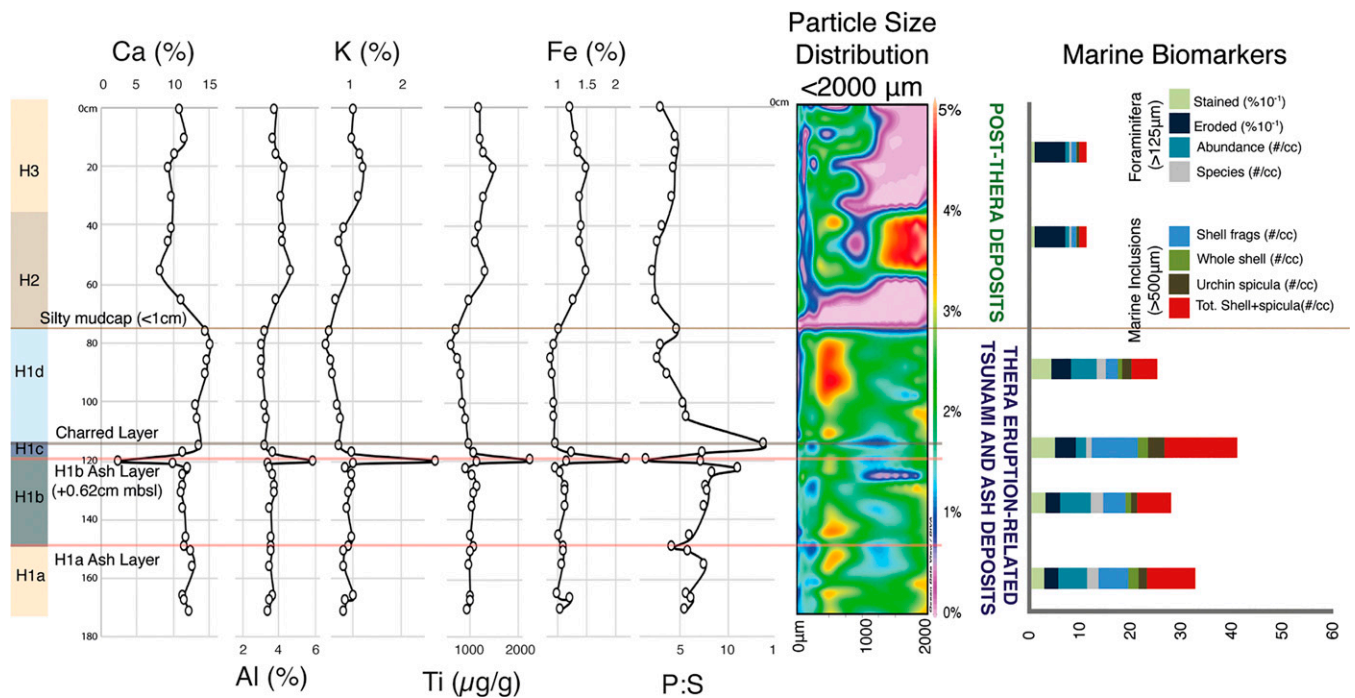


Fig. 4. Results of multiproxy analysis of sediment section outside of fortification walls. Elemental values (XRF), grain size distribution, and marine biomarkers from sedimentological section (Dataset S1) are shown with interpreted differentiation of layers. Ash layer is located at +0.62 cm mbsl. Contour grid of grain size data produced using Ocean Data View (60).

through c have slightly lower values of Ca and higher values of Al than H1d. The more prominent, ash layer at the top of H1b shows high peaks in Ti, Al, K, Fe, Si, and relatively lower values in Ca (Fig. 4 and Dataset S1). P:S values peak in the bone-rich charred layer (top of H1c) and fall in the ash layer (top of H1b). H1 includes Late Minoan IA pottery (CB Level 1).

H2 (Figs. 3 and 4) contains archaeologically rich deposits with CB Level 0 pottery including Mycenaean types (29) and root casts. Marine markers are lower than H1 (avg. 1.7/cm³). H3 contains living roots and mixed pottery from many phases including late Roman/Byzantine period. Some minor fluctuations are present in the uppermost exposed surface. The foraminifera abundance in layers H2 and H3 range from one to two individuals per cubic centimeter, all of which are eroded and lack signs of staining.

Archaeological Excavations. The lower rubble layer (H1a) was laterally extensive (30) (Fig. 2 and SI Appendix, Figs. S2–S4), abutted the fortification walls, and also intruded into the buildings. It included pottery, shell, bone, and charcoal and was dominated by stones similar to the adjacent structures. Late Minoan IA pottery, some of which was imbricated, and other archaeological artifact-rich sediments overlay the rubble. A patch (~40-m diameter) of *Cerastoderma glaucum* and *Patella* sp. shells within a muddy ripclast were wedged against a wall (Fig. 3 and SI Appendix, Fig. S1). Nearby, an articulated dog skeleton was found in an entryway beneath collapsed stones (Figs. 3 and 5). The corner of another room failed inward (SI Appendix, Figs. S2 and S3), and the incoming rubble spill was covered by a darker, silty sediment. Within a distance of a few meters from the collapsed and damaged area, structures were undamaged with intact pathways and walls. The contact between the disrupted area and the intact side was lenticular and abrupt with a scalloped shape (Fig. 3 and SI Appendix, Figs. S3 and S4).

An articulated young adult male human skeleton was found within the rubble in a prone, slightly curved position following

the curvature of this contact (Figs. 2, 3, and 5 and SI Appendix, Fig. S4). The skeleton did not have any signs of deliberate, culturally appropriate burial (e.g., positioning, grave goods, context, and treatment).

Pits were found throughout these ruins, some with the clear purpose of extracting building stones from underlying structures and others with no apparent function (Fig. 3 and SI Appendix, Figs. S2–S4).

Discussion

Signs of Tsunamis. The archaeological and sedimentological results from H1 horizon include ample indicators known from modern and paleotsunami deposits including allochthonous marine inclusions (31, 32) (Figs. 3–5), higher foraminifera abundance with staining (33), elemental trends skewed toward marine-like values, imbrication (34), collapsed structures (and related rubble layers), and nondeliberate burials.

C. glaucum, found in a patch at the excavation, are brackish water clams that live in highly concentrated beds (35). This muddy clast of shells was probably entrained, transported, and rafted until it was lodged against the building. *Patellae* sp. marine limpet mollusks were also identified among the rubble. This species attaches itself to hard surfaces, such as rocky coasts or marine structures (36), and similarly could have arrived during the tsunami. Whole, articulated domesticated animal skeletons in nonrefuse and nonburial context such as the dog found near the shelly patches is also a tsunami marker (37, 38).

There are signs of collapse and intrusion into the buildings that does not fit earthquake evidence, because the damage is unidirectional, and adjacent and nearby walls are unaffected (39). For example, in one of the houses connected to the fortification walls (40), a rubble layer intrudes from a collapsed portion of the wall and is blanketed by a darker soil that continues even further into the room (Fig. 3 and SI Appendix, Fig. S2). Such deposits would have required a very strong force to



Fig. 5. Tsunami rubble with articulated skeletal remains (Right). Articulated human skeleton (Top Left), articulated dog skeleton, and shell-rich muddy patch (Bottom Left) were present within the debris.

dismantle and redistribute the stones. The rubble at the base of the horizons (H1a) includes some very large clasts, in general ranging from ~25 to 40 cm, framework-supported with silty sediments in the cavities. The last of the tsunami-related horizons (H1d) is also rich with rubble, though the clasts are more similar to one another in size and do not exceed about 15 cm at their longest axis.

The articulated young male human skeleton exhibits classic signatures of deposition within debris flow. The location of the skeleton faces the most severely damaged portion of the fortification wall (SI Appendix, Fig. S4), suggesting the wall's failure point at the time of the event. A radiocarbon age measurement from a charred piece of *Hordeum vulgare* nearest to the skeleton within this same deposit gives the youngest range of age results among all of the measurements (Fig. 3 and SI Appendix, Figs. S6 and S7 and Table S1), fitting more with the "low" rather than "high" chronology.

Searching for the Injured and Missing. After a natural disaster such as a tsunami, survivors are tasked with the responsibility of rescuing victims, recovering the dead, caring for the injured, and post-event clean-up. At Çeşme-Bağlararası this effort is visible in the presence of misshapen pits, interpreted here as the preserved remains from their effort to retrieve victims from the tsunami debris. The human skeleton was located about a meter below such a pit, suggesting that it was too deep to be found and retrieved and therefore (probably unknowingly) left behind. It is also in the lowest part of the deposit, characterized throughout the debris field by the largest and heaviest stones (some larger than 40 cm in diameter; Figs. 3 and 5 and SI Appendix, Figs. S1 and S4), further complicating any retrieval effort.

In both the 2004 Indian Ocean Tsunami and the 2011 Tohoku Earthquake tsunami, missing persons accounted for over 10% of the dead even a decade after the events (41, 42). Victims that are swept up in the debris flow during a tsunami can get deeply buried within it or drown at sea, thereby making 100% victim recovery unrealistic. The Çeşme-Bağlararası young man is an ancient example of the same phenomenon.

The Age of the Eruption and Tsunamis. All radiocarbon ages have two sigma (95%) time ranges that coincide with both the high

and low chronologies for the LBA Thera eruption and tsunami events (H1a-d; Figs. 3 and 4 and SI Appendix, Figs. S6 and S7 and Table S1). However, the samples also group into two clusters, one which encompasses more of the "low" range and the other the "high" range, although this clustering has no association with stratigraphic position. The significance of this is that there is no age gradient by depth. H1a contains ages trending to both high and low chronologies, H1b (above H1a) contains high chronology trending ages, and H1c includes low chronology trending ages. This lack of chronological gradient associated to each tsunami horizon agrees with known tsunami sediment-related age mixing (38). We suggest that because all of the samples are from a well-sealed but heavily mixed (tsunami) context, the youngest ages are more relevant for determining the age that is closest to the event itself. Thus, a wide range of ages are expected and even diagnostic as evidence for tsunami deposition, due to their chaotic nature. According to this principle, the entire event deposit (H1a through d) cannot be older than the youngest measurement (terminus post quem) within it. The bimodal nature of the two clusters may reflect the mixing from the underlying archaeological settlement, which is an older, out-of-use portion of the site, with younger materials arriving from more recently active areas of the settlement. Accordingly, the two sigma (95%) radiocarbon age results of the sample closest to the human skeleton (OxA-38858; Cal BCE 1612 to 1573 [19.4%] and Cal BCE 1565 to 1501 [76.1%]) would be the most representative of the event's age. While these ages do not negate either chronology, it does limit the age to no older than 1612 BCE and includes ample support for the low chronology. The calibration within this time period is notoriously problematic and has long been the subject of extensive research (19, 21, 24, 43–45). While the dates presented here do not definitively resolve the issue, they do provide fresh radiocarbon data from a well-sealed, archaeologically associated, Thera eruption-related event horizon in the Aegean and will likely open discussion.

The Sequence of Events Related to the Eruption of Santorini, as Seen from Çeşme-Bağlararası. We propose that at the western Anatolian/Aegean site of Çeşme-Bağlararası, the eruption of Thera volcano produced a series of tsunami landfalls that

arrived at the semiclosed Bay of Çeşme (*SI Appendix, Fig. S8*). There are four discernible horizons identified, though more could be present. Here, we will address those that are clearly apparent. In the first tsunami (“H1a”), portions of the structures in the water’s path failed, and those stones were strewn across the area. In some cases, walls (perhaps sections which already exhibited weaker failure points) tumbled into building interiors, carrying debris and construction materials as well as unfortunate victims. “Çeşme Man,” the well-preserved articulated skeleton within this tsunami layer, represents the only preserved human remains identified in deposits associated with the LBA eruption of Thera.

After a short hiatus (a few hours), during which tephra accumulated, a second tsunami arrived (H1a/H1b contact), possibly associated to the same eruption phase. Following this second tsunami, a longer period of quiet occurred, allowing the ash to accumulate on top of the tsunami debris (H1b/H1c interface). Meanwhile, fires were actively burning throughout the Aegean (terrestrial and marine) as the ash fell, and burning materials floated at sea. After the hiatus following H1b, a third, smaller, tsunami incursion delivered a package of sediments and charred or still-burning materials (“H1c”). The flame-up structures present at the top of the ash layer between H1b and H1c occur at the interface of lower- and higher-density deposits, either due to liquefaction or water erosion, and has been reported in both modern and ancient tsunami deposits (46, 47). The truncation of the flame structures occurs as the sediment-dense water flow traverses the surface. The H1c tsunami deposit is similar to H1b but lacks the concentrated ash layer at its top and is instead capped with charred materials (e.g., bone and vegetation), a portion imbricated or laying horizontally.

After the third tsunami (H1c), we suspect that there was a longer (days to weeks) quiescence in event activity, during which people began to search for human remains and collect materials for repairs or new construction. Unfortunately for them, this period ended, as another tsunami arrived, of similar magnitude to the first tsunami, and left another thick deposit over the already damaged area, including filling the recently dug pits and stone-removal sections (Fig. 2). This entire sequence is presumed to have occurred in a matter of days or weeks.

The absence of ash at the surface of H1c might be explained by a few possibilities. One possibility is that ash fallout ended due to the exhaustion of its supply, indicating a time gap from the initial high, atmospheric, ash-extruding Plinian eruption (“Phase 1/Bo1”) or a shift in wind direction. A third possibility is that the layer was initially deposited but then did not preserve, because it was eroded away or otherwise disrupted, especially in the case of victim retrieval and reconstruction activities.

H1c is followed by another tsunami deposit (H1d). H1d has larger inclusions and is a thicker deposit (~35 cm versus ~6 cm), suggesting a stronger tsunami than H1c, though smaller than the lower tsunami sediment package (H1a and H1b >80 cm). The upper horizons (H2 and H3) fit typical near-coastal terrestrial values with regard to all proxies and lack the aforementioned tsunami-linked structural features (e.g., imbrication, erosional contacts, truncated flame structures, etc.).

The identification of multiple tsunami events at Çeşme-Bağlararası supports the proposed view that there were distinctive eruption phases, with varying hiatuses between them (5, 15, 48). While many tsunami scenarios concentrate attention toward the southern or southeastern directions (5) or near-field along the outskirts of the island itself (15), some simulations include as far north as Çeşme (49). This is evidence that supports that model.

Compound Disaster. Following the event, according to the archaeological remains, the thriving community at Çeşme-Bağlararası ceases to exist for at least a century. In addition to loss of life and property damage, any coastal features or harboring areas would

have been debris strewn and made unusable or highly compromised for a period, and the ash deposits would have altered the chemistry of the soils, impacted aquifers, and damaged crops (3).

Çeşme-Bağlararası is only one of many coastal settlements impacted by the eruption and related earthquakes, tsunamis, ash-fall, and fires and will provide a type site reference for identifying others. Despite this presumed regional impact, tsunami evidence has only been reported for a handful of sites; namely Malia (50), Letoon (51), Palaikastros (52), Gouves, Didim, and Fethiye (53) (Fig. 1). We argue that this dearth of reports is an artifact of methodological approach wherein 1) the ability to identify paleo-tsunami sediments has advanced in recent years, and 2) sites lacking tephra were usually not considered for tsunami waves. Although prevailing winds direct the ash cloud, the tsunami waves are propagated in a linear, concentric pattern to large distances, provided there is no obstacle (islands and peninsulas), in which case, the wave energy will bend, interfering and reflecting off of one another, resulting in either increased or decreased wave heights and coastal inundation (49). Tsunamis, unlike tephra fallout, are independent of wind patterns. Therefore, even in the absence of ash fallout, in areas such as the western Aegean coastlines, tsunami deposits may be present but not yet recognized.

Sea-borne trade at the time of the event was central to the vitality and power of societies, in particular the sea-dominating Minoans. The social fallout from the destruction of the system’s core infrastructure (ships, harbors, ports, and coastal settlements) cannot be understated. While many people survived the event, the dynamics of everyday life, political relationships, and economic structures would have shifted.

Disasters and the human reaction to them alter societies. In the case of the LBA eruption, it can be considered a compound disaster wherein multiple short-term (loss of life and property, settlement destruction, economic destabilization, and emigration) and long-term challenges (crop loss and demographic and trade network shifts) necessitated societal responses that would have had a multigenerational impact. While many people survived the event, their worlds would have changed. Çeşme Man is a representative of the many people who died or went missing on that tragic day and did not live to witness perhaps one of humanity’s most triumphant revivals.

Materials and Methods

Instrumental neutron activation analysis was conducted by Max Bichler and Johannes Sterba following protocols from (54, 55). Nearby samples from Chios were used for comparison as well as published data. An amount of 500 g of the ash band as provided was investigated for its chemical composition by neutron activation analysis. For the ash layer, contamination by sediments and organic material were visible. To separate a clean sample, the ash was treated twice with 500 mL of HNO₃ (1.4 M, suprapure) for acidic decarbonatization.

After filtering and washing, the sample was then fractionated by particle size by repeated suspension in distilled water. After 1 min of sedimentation time, the liquid was decanted and the process repeated until the liquid appeared clear. The remaining material was then, after drying with acetone, sieved to separate a fine fraction with a diameter of <0.5 mm.

Investigation of this fine fraction under a dual polarizing microscope showed an almost-pure glass fraction. Throughout the cleaning and sedimentation process, a total of eight single pieces of pumice (all less than 1 mm in diameter) were separated by flotation.

After sample processing, ~100 mg of the two separated fractions (fine and remainder) as well as all single pieces of pumice were weighed into Suprasil quartz glass vials and irradiated together with international certified reference materials CANMET reference soil SO1, NIST SRM 1633b Coal Fly Ash, BCR No. 142 light sandy soil, NIST SRM 2702 Inorganics in Marine Sediments, and the MC rhyolite GBW 07113 for 35 h in the TRIGA Mk II reactor of the TRIGA Center Atominstitut in Vienna at a neutron flux density of $1 \cdot 10^{13} \text{ cm}^{-2} \text{ s}^{-1}$. After irradiation, sample vials were decontaminated on the outside and measured twice after a cooling time of 5 d and 28 d, respectively. Measurement times on the high purity germanium radiation detector (1.78-keV resolution at the 1,332-keV ⁶⁰Co peak; 48.2% relative efficiency) were 1,800 s and 10,000 s. Gamma spectra were evaluated using the Genie 2000 software, and by

comparison with the reference materials, elemental concentrations for the elements Na, K, Sc, Cr, Fe, Co, Zn, As, Rb, Zr, Sb, Cs, Ba, La, Ce, Nd, Sm, Eu, Tb, Yb, Lu, Hf, Ta, Th, and U were calculated.

XRF methods followed Zirks et al., 2021 (56). Grain size measurement protocols followed Goodman-Tchernov et al., 2009 (4). Radiocarbon samples were measured at Direct AMS (Washington) and The Oxford Radiocarbon Accelerator Unit.

For marine bioindicators, 2.5 cm³ of each sediment section were sieved at 63-, 125-, and 500- μ m mesh-sized sieves. Each sample was assessed under a binocular microscope and described for general characteristics, mineral content, and inclusions. Foraminifera (125 μ m +) were counted and described with regard to taphonomic condition (33). Species were presumed based on morphological uniqueness and similarity, but not all were identified. Inclusions of urchin spines (bases), shell fragments, and whole shell in the 500+ μ m fraction of each sample were quantified by individual pieces.

Data Availability. All study data are included in the article and/or supporting information.

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