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Abstract (max 250 words)

Deep-sea corals are found on hard substrates on seamounts and continental margins world-wide at depths of 300 to ~3000 meters. Deep-sea coral communities are hotspots of deep ocean biomass and biodiversity, providing critical habitat for fish and invertebrates. Newly applied radiocarbon age date from the deep water proteinaceous corals *Gerardia sp.* and *Leiopathes glaberrima* show that radial growth rates are as low as 4 to 35 μm yr^{-1} and that individual colony longevities are on the order of thousands of years. The management and conservation of deep sea coral communities is challenged by their commercial harvest for the jewelry trade and damage caused by deep water fishing practices. In light of their unusual longevity, a better understanding of deep sea coral ecology and their interrelationships with associated benthic communities is needed to inform coherent international conservation strategies for these important deep-sea ecosystems.

Most of the interior of the global ocean remains unobserved. This leaves questions of trophic connectivity, longevity, and population dynamics of many deep-sea communities unanswered. Deep-sea macrofauna provide a complex, rich, and varied habitat that promotes high biodiversity and provides congregation points for juvenile and adult fish (*1-3*). Here we present results on Hawai'ian live pruned and sub-fossil specimens of the octocoral *Gerardia* sp. and live collected specimens of the deep-water black coral *Leiopathes glaberrima* (Antipatharia). Age and growth rates were determined using radiocarbon while trophic level and food source assessment was made using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$).

Gerardia sp. is a colonial zoanthid with a hard skeleton of hard proteinaceous matter that forms trees with heights of several meters and basal diameters up to 10s of cm. *L. glaberrima* also has a hard proteinaceous skeleton and grows to heights in excess of 2 m. In Hawai'ian waters these corals are found at depths of 300 to 500 m on hard substrates such as seamounts and ledges. *Gerardia* are also found in the Atlantic. *Leiopathes* is also ubiquitous and has been found south of Australia, and throughout the equatorial and northwest Pacific. Corals used in this study were collected at the Makapuu and Lanikai deep-sea coral (DSC) beds (Oahu, HI), Keahole Point DSC bed (Big Island, HI) and Cross Seamount (18°40'N, 158°10' W).

Previous radiocarbon studies have shown that individual *Gerardia* colonies from the Atlantic and Pacific Oceans have life spans of ~1800 ±300 (*4*) and 2740 ±15 years (*5*) respectively. These results contrast with a life span of 250 ±70 years calculated for the same Atlantic specimen using amino acid racemization (*6*) and a maximum life span of 70 years for Hawai'ian *Gerardia* specimens based on counts of what were assumed to be annual growth rings (*7*). The discrepancies between the radiocarbon, amino acid, and growth band age estimates were attributed to the incorporation of ^{14}C-free (*i.e.*, old) carbon into the *Gerardia* skeleton, thereby producing anomalously old ^{14}C ages (*6, 7*). ^{210}Pb measurements on two Atlantic *L. glaberrima* specimens suggested life spans of ~200 to ~500 years and radial growth rates of ~15 μm-yr^{-1}(*8*). A Hawai'ian *L. glaberrima* specimen from the Makapuu DSC bed had a ^{14}C-estimated lifespan of 2320 ±20 years (radial growth rate ~5 μm-yr^{-1}) (*5*). Resolution of the food (carbon) source and its impact, if any, on radiocarbon age estimates remains a contentious issue.

Results

Sources of Carbon. Carbon and nitrogen isotopic composition of living polyp tissue taken from specimens collected at the Lanikai DSC bed and Cross Seamount is compared with the isotopic ratios of surface water particulate organic matter (POM) (Fig. 1). $\delta^{13}C$ and $\delta^{15}N$ of Hawai'ian surface water POM varies from -20 to -23‰ (*9, 10*) and from -1 to +1‰ (*11*) respectively. $\delta^{13}C$ values of live polyp tissues from both *Gerardia* (10 specimens) and *L. glaberrima* (2 specimens) from two different locations are similar. The average values (1 std. dev.) for all *Gerardia* measurements are $\delta^{13}C$:-19.3‰ (±0.8 ‰), $\delta^{15}N$: +8.3±0.3 ‰, carbon to nitrogen (C:N) ratios are: 3.3 ±0.3 and the average values for all *L. glaberrima* are $\delta^{13}C$: -19.7±0.3 ‰, $\delta^{15}N$: +9.3±0.6 ‰, C:N 5.1±0.1. The slight difference in $\delta^{15}N$ that we observe is not statistically significant due to the small *Leiopathes* sample size. Assuming classic trophic level enrichments (12, 13) these results indicate *Gerardia* and *L. glaberrima* are low order consumers, primarily feeding upon freshly exported POM

To confirm the trophic level interpretation and acquire additional growth rate estimates, we determined the ^{14}C content at 100 μm resolution on the outer few mm of a live collected *Gerardia* branch from Cross Seamount, and the basal stalk of one live collected *L. glaberrima* from Lanikai, Hawai'i. Radiocarbon measurements were also done on living polyp tissue samples from both specimens. Polyp tissue $\Delta^{14}C$ values are similar to surface water dissolved inorganic carbon $\Delta^{14}C$ values and proteinaceous skeleton $\Delta^{14}C$ values over the outermost 3 mm of the *Gerardia* branch are indistinguishable from a reconstruction of the Hawai'ian surface water ^{14}C history (1950-1990) derived from a shallow water scleractinian coral (Fig. 2). Most significantly, the *Gerardia* skeleton captures the surface ocean uptake and redistribution of "bomb"-^{14}C with little to no amplitude attenuation (Fig. 2A). Two wafer-thin (~10 μm) flakes from the outermost skeleton of *L. glabberima* also contain "bomb"-^{14}C. When the sampling interval is increased to 100 μm, we recover an averaged value that is less than modern and does not exhibit ^{14}C enrichment. ^{14}C ages from 100μm increments over the outermost 0.9 mm of the *L. glaberrima* skeleton increase to ~700 cal years (1050 ±45 ^{14}C years) (Fig. 3). This equates to approximately 80 years of averaging in each 100μm increment. The *L. glaberrima* and *Gerardia* isotope results suggest that these organisms are acquiring their tissue and skeletal carbon from surface water organic matter after relatively rapid transport to depth. The radiocarbon results also imply little to no carbon turnover of the

proteinaceous skeleton and also demonstrate that ^{14}C-derived age estimates of *Gerardia* sp. and *L. glaberrima* are unaffected by the animals feeding upon "old" resuspended sedimentary carbon.

Ages and growth rate. Coral ages and growth rates are acquired by two different methods: 1) identification of the bomb-spike as a local radiocarbon inflection point that is assigned to the year 1957, and 2) conventional ^{14}C age based on radioactive decay. Radiocarbon analyses and conversion of ^{14}C-years to calendar years (14) of outer and inner samples from a suite of cross sections cut from sub-fossil *Gerardia* specimens allow us to calculate radial growth rates and longevity of a larger sample pool. The long-term radial growth rate of the live-collected *Gerardia* branch shown in Fig. 2A is 35 μm yr^{-1}, similar to the rate derived from the 1957-bomb ^{14}C inflection point at 2.1 mm (45 μm-yr^{-1}). This branch spans ~315 years (585 ±30 ^{14}C years). The average radial growth rate from the larger sample pool is 36 ±20 μm-yr^{-1} (1sd, n=17) with a range of 11-85 μm-yr^{-1} (Fig. 2B and Supplementary Table 1). The average life span of the analyzed specimens is 970 years and ranges from ~300 years for a small branch (radius = 11 mm) to ~2700 years (radius = 38 mm) (Fig. 4). These ages indicate a longevity that far exceeds previous estimates based on amino acid racemization and growth band counting (*6, 7*). We note that many of the sub-fossil samples that we have analyzed are branches and thus the ages may not document the maximum potential age of *Gerardia*.

Three live collected specimens of *L. glaberrima* were also radiocarbon dated along radial transects of inner to outer samples. The center age of the cross-sectional disk taken from the stalk of the specimen discussed above is 4200 ±70 calendar years BP (4105 ±40 ^{14}C years) (Fig. 3). The center of the basal attachment structure, some ~8 cm below the cross sectional disk on the stalk is 4265 ±44 calendar years (4150 ±35 ^{14}C years). The other two *L. glaberrima* colonies had ages of 350 calendar years BP (630 ±35 ^{14}C years) and 2370 calendar years (2600 ±35 ^{14}C years) (Fig 4 and Table S1). The radial growth rates of the three samples are <5 μm-$year^{-1}$.The 2370 year old specimen had a faster initial radial growth rate of ~13 μm-$year^{-1}$ over the inner most 5 mm of a 13 mm radial ^{14}C transect, supporting faster initial growth (Fig 5). Higher initial growth rates could be advantageous for a colony to establish itself. These results suggest that height may not be proportional to age for Leiopathes.

Discussion

Interest in conservation and protection of deep-sea corals, resulting from their potentially long life-spans, the recognition of their ecological importance as well as threats posed by fishing practices (1, 15, 16) has increased. The extremely long life-spans of *Gerardia* and *L. glaberrima* shown here reinforce the need for further protection of deep-sea corals and deep-sea coral beds. These results show that *L. glaberrima* is the oldest skeletal accreting marine organism known and perhaps the oldest colonial organism known. Based on ^{14}C the living polyps are only a few years old, or at least their carbon is, but they have been continuously replaced for centuries to millennia while accreting their underlying proteinaceous skeleton.

Emergent structure forming deep-sea megafauna increase the complexity of seafloor habitat, and provide shelter and feeding areas for commercial and non-commercial fish species and their prey (2, 17, 18). *Gerardia* and *L. glaberrima* are two of the largest megafauna in Hawai'ian deep-sea coral beds and have clear associations with a diverse assemblage of invertebrates and fish that in turn make these communities prime foraging targets for Hawai'ian monk seals (19). Activities that contact the seafloor, of which bottom trawling is the most significant, damage deep-sea coral beds (20-22). Hawai'ian deep-sea corals face direct threats via harvesting for jewelry (*7*) and from commercial fishing; as by-catch from trawling, and entanglement and damage associated with lines and gear. The extreme longevity of *Gerardia* and *L. glaberrima* challenges the concept that these species are 'renewable' in the context of fisheries management. In addition, damage to these coral species has far-reaching implications for biodiversity, ecosystem structure, and functional extinctions in the deep-sea (23).

Quantitative information regarding symbiosis between free-swimming fish, other invertebrates, and *Gerardia* and *Leiopathes* is lacking. During our own submersible dives and viewing dive tapes of other dives from nearby locations, we observe a increase in fish and invertebrate biomass and diversity within and adjacent to colonies of *Gerardia* and *Leiopathes*. Structure forming fauna such as *Gerardia* and *Leiopathes* in the deep-sea have a similar ecological functional purpose as their shallow water reef-building counterparts. We posit that the newly discovered longevity of poorly studied yet widely distributed deep-sea organisms such as proteinaceous corals provides an increased impetus for the development of a coherent

and effective international conservation strategy, particularly with regards to deep-sea trawling and activities that physically disturb the benthic environment.

In addition to direct and indirect threats of physical disturbance at depth, the tight coupling observed between deep-sea corals and surface ocean primary production implies that these communities can be influenced by natural and anthropogenic changes in surface ocean conditions. Predicted surface water impacts such as ocean acidification, warming, and altered stratification can all influence community structure and rates of primary production, both of which may influence the delivery of food to the deep sea. The potential effects of human activities not only transgress international and domestic boundaries but conventional management strategies. To be effective and successful, management and conservation policies require a trans-boundary ecosystem-based approach that considers impactsfrom the surface ocean to depth.

U.S. fisheries management law has established a legal trigger for fisheries management measures to protect seafloor habitats based on criteria of whether the effects of fishing are "more than minimal and not temporary" (24). Recruitment, growth rate, and longevity of these and other DSC ultimately determine the rate at which these habitats may recover from damage (25). Given that longevity is one of the most important factors in determining habitat recovery time, the loss of proteinaceous species such as those described here cannot be considered temporary on human time scales. Growth rates and longevity of DSC also indicate the extent to which they can be harvested. In the Hawai'ian precious coral fishery, growth rates for *Gerardia* suggest that current maximum sustainable yield limits are grossly overestimated (26).We suggest that any future harvesting be considered in the context of a non-renewable resource framework.

In the US economic zone, and as a result of recognizing their importance to deep-sea ecosystems and habitat, deep-sea coral beds were accorded greater protection during the 2006/2007 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act (MSA). Although they are considered by many of the nations Fisheries Management Councils to constitute "essential fish habitat" (EFH), the use of this designation has varied widely among councils and in some cases has been challenged because of the difficulty of proving this attribute. The

reauthorized MSA no longer requires a rigorous determination as an EFH as a trigger for protective measures. An increasing number of known deep sea coral localities are now being designated as "Habitat Areas of Particular Concern" (HAPC) by the Fisheries Management Councils. Our work establishing the heretofore unknown great longevity of keystone members of deep sea coral communities suggests an even more urgent need to accelerate the pace of governance and protection by the Fisheries Management Councils and local, state, and federal management authorities.

Stable isotope and radiocarbon analysis of living polyps (coral tissues) support the tenet that *Gerardia* and *L. glaberrima* feed primarily on labile and therefore ^{14}C-young, particulate organic carbon (POC). Analyses of living and subfossil *Gerardia* specimens indicate radial growth rates of 36 ±20 μm-yr^{-1} and lifespans of up to at least 2700 years. These results greatly expand on and support previous lifespan and radial growth rate estimates (*4, 5*). *L. glaberrima* has even slower growth rates (<5 μm-year^{-1}) and the longest known lifespan of any skeletal accreting marine organism. Longevity and slow growth are not unknown in deep-sea organisms. Our results suggest the need for new approaches and research directed towards a better understanding of deep-sea marine ecosystems that form in direct association with organisms of great longevity in the face of increased direct (physical habitat disturbance) and indirect (changes in ecosystem primary productivity, climate related changes, or ocean acidification) threats.

Materials and Methods

Sample Collection. Hawai'ian *Gerardia* sp. and *Leiopathes glaberrima* samples from 400-500 meters water depth were collected during the 2004 field season using the NOAA/HURL Pisces V submersible. *Gerardia* samples include pruned branches from living specimens, sub-fossil basal attachment stumps and fallen branches. The three *L. glaberrima* specimens were collected live. Upon recovery and for the few samples from live individuals the external polyps and tissue was removed and sub-samples were air dried prior to transfer to microcentrifuge vials. Upon removing the tissue layer the proteinaceous skeleton was washed with sea and fresh-water and allowed to air dry on deck.

Stumps and branches were cut into ~0.7 cm thick cross-section disks. *Gerardia* disks taken closest to the basal attachment often include a center carbonate

core from the *Isididae* (bamboo) coral that the *Gerardia* initially settled on and used as a preliminary attachment until it grew down and over it thereby attaching itself directly to the substrate. Cursory sampling of the skeleton was done by microdrilling center (inner), middle, and outer samples from across radial transects. In addition, we extracted a small ~ 2x2 mm rod from the basal cross-section from a live-collected *Gerardia* branch and from the stalk of a live collected *L. glaberrima* from the Lanikai DSC bed (Oahu, HI). The outer 1 to 3 mm of each rod was microtomed in 100 μm increments for ^{14}C analysis.

Analytical Methods Stable carbon and nitrogen isotopic analyses were completed at the Stanford University Stable Isotope Lab on dried and ground polyp/tissue using a Finnigan MAT Delta plus connected to a Carlo Erba NA1500 Series II elemental analyzer. Results are reported in conventional parts per mil notation versus V-PDB for δ^{13}C and air for δ^{15}N. Analytical error is ±0.10‰ and ±0.14 ‰ respectively. For *L. glaberrima* three repeat analyses were done on tissue samples from 2 specimens (n=6) and for *Gerardia* three repeat analyses were done on 10 specimens as well as three repeat analyses of tissues samples taken the tips and bases of one specimen (n=33). Repeat analyses of tissue samples from the tip (δ^{15}N 7.13 ±0.16‰; δ^{13}C -19.48 ±0.15‰; C:N 3.55 ±0.04; n=3) and tissue samples from the base (δ^{15}N 7.75 ±0.05‰; δ^{13}C -19.16 ±0.12‰; C:N 3.35 ±0.03; n=3) are within the uncertainty of all specimens measured. The S.D. is reported for the average of all the analyses; n=6 for *L. glaberrima* and n=33 for *Gerardia*.

For all radiocarbon samples, proteinaceous and tissue samples were treated with weak HCl, copiously rinsed with miliQ water, and dried. Samples were converted to CO_2 via sealed tube combustion, and upon cyrogenic purification the CO_2 was reduced to graphite in the presence of iron catalyst and a stoichiometric excess of hydrogen. Graphite targets were analyzed at the Center for Accelerator Mass Spectrometry. Radiocarbon results are presented as Δ^{14}C (‰) and conventional ages (27) and include a δ^{13}C correction and a blank subtraction based on analysis of ^{14}C -free coal. Analytical uncertainty for all but the smallest microtome sample (due to loss during handling: ≤19μg of carbon) was 3-4‰ or for Holocene samples or 30-40 ^{14}C years. Conventional ^{14}C ages are converted to calendar years using a reservoir age of 380 ^{14}C years (ΔR of -28 ± 4 ^{14}C years) (28) and Calib v5 (29, 30).

We compare our microtome ^{14}C "time-series" to a reconstruction of surface water $\Delta^{14}C$ derived from a *Porites* coral (drilled in 1990) from the west side of the Big Island (28, 31). The *Porites* age model utilizes the seasonal sea surface temperature cycle recorded in $\delta^{18}O$ coral and [Sr/Ca] coral.

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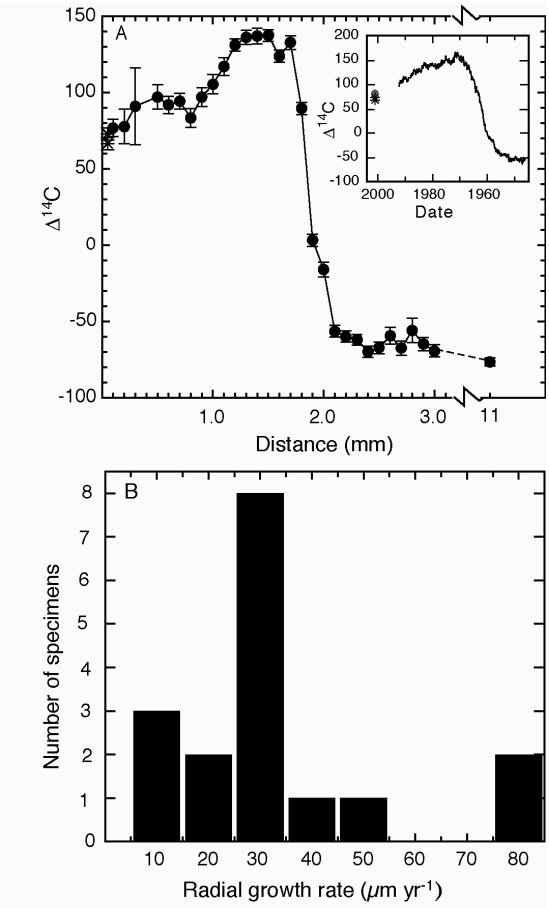
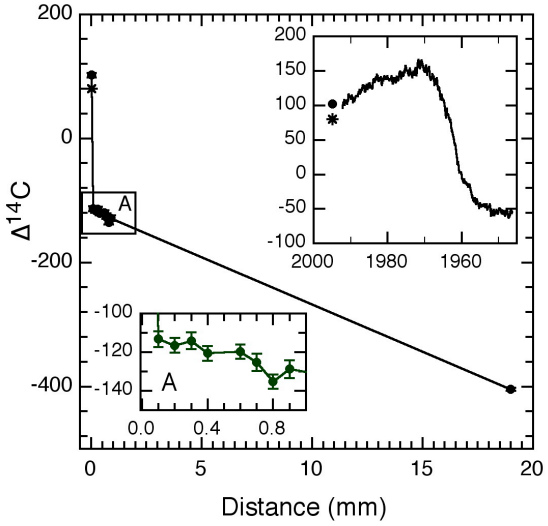
Figure 1. Carbon and nitrogen isotopic composition of outermost living polyp tissue (solid symbols) of *Gerardia*sp. (10 specimens) and *L. glaberrima*(2 specimens) from the Lanikai DSC bed and Cross Seamount. Average isotopic composition of proteinaceous skeleton (open symbols) of all specimens by species and location . The $\delta^{13}C$ and $\delta^{15}N$ range of Hawai'ian surface particulate organic matter (POM) is also shown (*9, 10*).



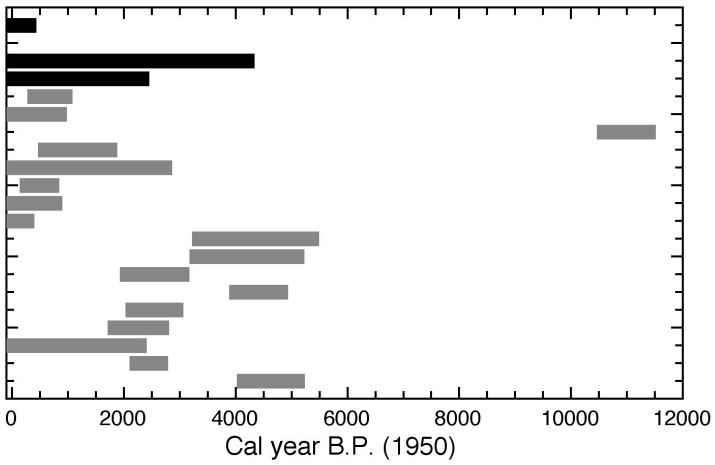
Roark Fig 1

Figure 2. *Gerardia* sp. ^{14}C results. a) Radiocarbon values of samples collected by microtome over the outermost 3 mm from a radial cross-section transect (solid symbols) and tissue (stars) from a pruned branch of a living *Gerardia*sp. The Gerardia^{14}C profile is indistinguishable from surface water $\Delta^{14}C$ history derived from a *Porites* coral (drilled in 1990, Guilderson and Schrag unpublished results) from the west side of the Big Island, HI (inset), and a discrete water sample collected at NEHLA, Keahole Point (Kona HI) in 2005 (Walker, McCarthy, and Guilderson unpublished results). Center age is 315 calendar years (585 ±30 ^{14}C years). Error bars are 1 S.D. b) Radial growth rate (μm-yr^{-1}) determined on 17 individuals. The average radial growth rate is 36 ±20 μm-yr^{-1} (1sd, n =17).



Roark Fig 2

Figure 3. *Leiopathesglaberrima*^{14}C results. Radiocarbon values of samples collected by microtome over the outermost 0.9 mm of a radial cross-section (solid symbols) and tissue (stars) from the stalk of a living *L. glaberrima.* Two outer most flakes (solid symbols) and tissue (stars) are indistinguishable from the expected surface water $\Delta^{14}C$ based on the extrapolation of the *Porites* coral $\Delta^{14}C$ record (inset, citation). The center age is 4200 ±70 calendar years BP (4105 ±40 ^{14}C years). Error bars are 1 S.D.



Roark Fig 3

Figure 4. "Life spans" of *Gerardia* sp. and *Leiopathes glaberrima* during the Holocene. Longevity estimates (age-range) as a function of calendar age (cal yr B.P.) for *Gerardia* sp. (gray) and *L. glaberrima* (black). The average life span of the *Gerardia* sp. specimens is 970 years and ranges from ~300 years to ~2700 years. Overlapping specimens in the same manner as tree ring studies will allow continuous records going back ~5000 years.

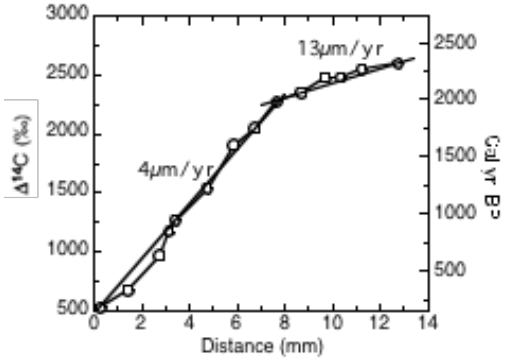


Figure 5. Radiocarbon radial transect of specimen BC-RD97-05 (5) showing a faster radial growth rate of 13μm yr^{-1} over the initial 400 years (inner most 5.1 mm) compared to the much slower growth rate of 4μm yr^{-1} over the last 1960 years (outer most 7.7 mm). The age of the center of the basal attachment structure of specimen (Lan04-Leio1), some ~15 cm below the cross sectional disk on the stalk is 4265 ±44 years (4150 ±35 ^{14}C years), within the error of the age established for the center of the stalk discussed in the main text (4200 ±70 years).

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