Pleistocene Extinction of *Genyornis newtoni*: Human Impact on Australian Megafauna

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More than 85 percent of Australian terrestrial genera with a body mass exceeding 44 kilograms became extinct in the Late Pleistocene. Although most were marsupials, the list includes the large, flightless mihirung *Genyornis newtoni*. More than 700 dates on *Genyornis* eggshells from three different climate regions document the continuous presence of *Genyornis* from more than 100,000 years ago until their sudden disappearance 50,000 years ago, about the same time that humans arrived in Australia. Simultaneous extinction of *Genyornis* at all sites during an interval of modest climate change implies that human impact, not climate, was responsible.

Australia suffered a major loss of its large- and medium-sized land mammals in the Late Pleistocene. All marsupials exceeding 100 kg (19 species) and 22 of 38 species between 10 and 100 kg became extinct (1), along with three large reptiles and the ostrich-sized *Genyornis newtoni* (2); two other large flightless birds, the emu (*Dromaius novaehollandiae*) and the cassowary (*Casuarius casuarius*), survived. Dwarfing and range restriction occurred in many other species (1). Collectively, the lost species are often referred to as the Australian megafauna, although most are of modest body mass.

For more than a century the cause of this exceptional extinction has been debated without a clear consensus, largely because of the difficulty in dating faunal remains close to the limit of radiocarbon dating (3). The cause of megafauna extinction initially focused on climate change (4) or human predation (5),

but more recently has included indirect consequences of human activity, particularly ecosystem change resulting from burning practices (6–8). Resolving the debate requires secure dates on the extinction events, on the arrival of humans in Australia, and on major climate and environmental changes. Here we present new dates that constrain the ages of these key events based on amino acid racemization, accelerator mass spectrometry (AMS), ^{14}C and thermal ionization mass spectometry (TIMS) U-series analyses on eggshells, and luminescence dates on associated sediment.

The abundance of fossil eggshell reflects, in order of importance, its preservation potential, subsequent exposure potential, and the number of nesting birds. To be preserved, mobile sediment, commonly eolian sand, must be available to bury the eggshell quickly. Eggshell is most frequently collected from natural exposures or deflation hollows. Without recent erosion, eggshell is rarely encountered because it survives only briefly at the surface. Bird populations are controlled primarily by climate, nutrient availability, and predator pressure (including humans).

Eggshells of large, flightless birds offer distinct advantages over bone for dating purposes. They are well preserved and surprisingly common across Australia, their dense calcite matrix is resistant to diagenesis, and, from a single fragment, ^{14}C activity, amino acid racemization (AAR), and stable isotope ratios can be measured. By dating eggshells of *Genyornis* and *Dromaius* collected from deposits formed during wetter and drier intervals, environmental change may be placed in a secure time frame, and the youngest *Genyornis* eggshells can hence provide a date

on the bird's extinction within each region. By dating the extinction event in several regions spanning a range of climates, continental extinction may be evaluated.

Most birds incorporate about 3% complex organic compounds in their eggshells as an intracrystalline organic web that is highly resistant to diffusional loss. Epimerization of the common protein amino acid isoleucine, preserved in the proteinaceous residues, follows first-order, reversible kinetics (9, 10). Expressed as the proportion of the non-protein D-alloisoleucine to its protein source, L-isoleucine, D/L increases from essentially zero in modern eggshell to an equilibrium ratio of 1.30 (11). The temperature dependence of isoleucine epimerization in *Dromaius* eggshell is well known (12). Eggshells of both *Genyornis* and *Dromaius* commonly occur together in all regions (13), suggesting that they coexisted and nested in close proximity, contrary to a recent assertion (14).

We measured D/L ratios in eggshells of both taxa from three regions (15): (i) an extensive series (1200 analyses) from dune and beach deposits within a 50-km radius of Madigan Gulf (MG) in Lake Eyre, the terminal playa of the Lake Eyre Basin; and modest collections (ii) from a 50-km radius centered on the north end of Lake Frome (LF) and (iii) from a 150-km radius centered on the confluence of the Darling and Murray rivers (DM) (Fig. 1). The MG region is currently arid [21°C, ~150 mm precipitation (16)]; LF is semiarid (19°C, ~400 mm precipitation) and has denser plant cover and thick riparian vegetation; and the DM region is semiarid (17°C, ~400 mm precipitation) with more reliable stream flow. The Darling River drains the summer-dominant precipitation regime of the north, whereas the Murray drains the winter-westerly–dominated precipitation regime of southern Australia. Consequently, the DM sites have one of the most dependable moisture supplies in the interior, and should have been a refugium for fauna during periods of climate stress. In all three regions, precipitation can occur in any season, but summer precipitation dominates in the MG region. Before European settlement, it supported mixed C_3 and C_4 vegetation. LF and DM support primarily C_3 plants.

In the MG region, the D/L record is calibrated by 90 paired AAR and calibrated AMS ^{14}C dates (17) on *Dromaius* eggshells, 8 luminescence dates between 40 and 120 thousand years ago (ka) on eolian sand from which eggshell has been collected, and 5 TIMS U-series dates on *Genyornis* eggshell. An age model developed from this calibration set allows calendar ages to be assigned to each D/L ratio for all samples <130,000 years old (Fig. 2).

Frequency histograms for the two taxa derived from the age model document the

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time dependence of the collection series over the past 130 thousand years (ky) (Fig. 3); the frequency distribution of the 90 ^{14}C-dated *Dromaius* eggshells (Fig. 3) mirrors that of the larger data set of model-derived ages. MG was continually occupied by breeding populations of *Dromaius* for at least the past 130 ky, even through the stage 2 arid phase. Intervals of greatest *Dromaius* eggshell abundance reflect peak sediment mobility (preservation) during early stage 5, early stage 3, and at about the stage 2/1 transition. Although the distribution of *Genyornis* eggshells is similar for the older part of the record, eggshells abruptly disappear about 50,000 years ago. The continuous presence of *Dromaius* eggshells confirms that the absence of younger *Genyornis* eggshell is not due to a lack of preservation or exposure potential, but must indicate the actual extinction of the birds in this area.

Insufficient age calibration is available for the other two regions to plot frequency distributions in the time domain, but we can evaluate them in the D/L domain (Fig. 4). D/L is a time-dependent quantity, but the epimerization rate exhibits a strong temperature dependency, and Pleistocene temperatures in central Australia were up to 9°C lower than in the Holocene (*12*); consequently, time is not linearly expressed. Furthermore, because the LF and DM regions are cooler than the MG region, the age for a specific D/L ratio is higher. Within these constraints, D/L histograms for all three regions exhibit similar trends. All three reveal near continuous occupation by *Dromaius*. The lack of old material at DM simply reflects the poor exposure there of older sediment. In sharp contrast to the continuity of *Dromaius* histograms, *Genyornis* displays a distinct termination in all three areas.
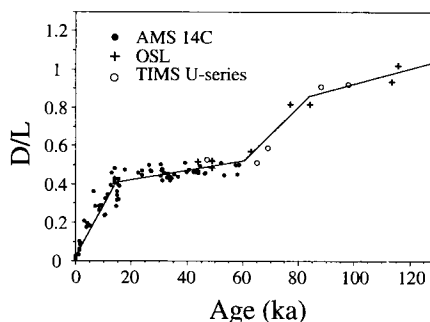
Because of the temperature differences, the age of the extinction event must be evaluated at each site. To do this, we radiocarbon dated fragments of both *Genyornis* and *Dromaius* that straddle the extinction event,
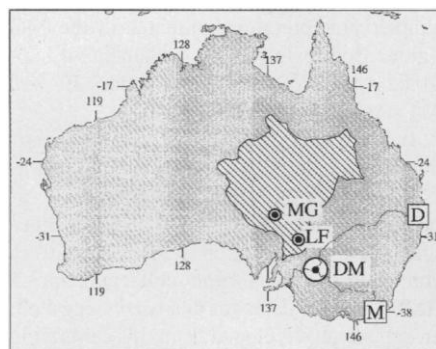
dated *Genyornis* eggshells directly by TIMS U-series (*18*), and dated sediment enclosing the youngest *Genyornis* eggshell by luminescence (*19*). At MG, *Genyornis* became extinct between D/L ratios of 0.46 and 0.50. AMS ^{14}C dates on 11 *Dromaius* eggshells within that range are all >38,700 ^{14}C years before the present (yr B.P.), essentially at the limit of the method. Five luminescence dates from the corresponding eolian unit are between 63 ± 5 ka and 44 ± 5 ka (*20*). U-series dates on terminal *Genyornis* eggshells from two different sites in MG are 47 and 65 ka. Radiocarbon ages of *Genyornis* eggshell that received only an acid-leaching pretreatment suggest that many of these eggshells are contaminated by younger carbon. For example, three fragments from levels stratigraphically below luminescence dates of 50 to 60 ka produced finite apparent radiocarbon ages between 36,700 and 39,500 ^{14}C yr B.P. Using a more rigorous pretreatment (90% acid leach; drilling out all pores), we obtained radiocarbon ages older than 42,000 ^{14}C yr B.P. for two fragments of *Genyornis* that gave the lowest D/L in the MG collections and that previously gave finite radiocarbon ages younger than 40,000 ^{14}C yr B.P. with less rigorous pretreatment. We conclude that the extinction event occurred at or beyond the limits of ^{14}C dating.

In the DM region *Genyornis* became extinct at a D/L ratio between 0.28 and 0.32, substantially lower than at MG because average temperatures at DM are 4°C less (*21*). One *Dromaius* eggshell slightly younger than the extinction event (D/L = 0.27) has a radiocarbon
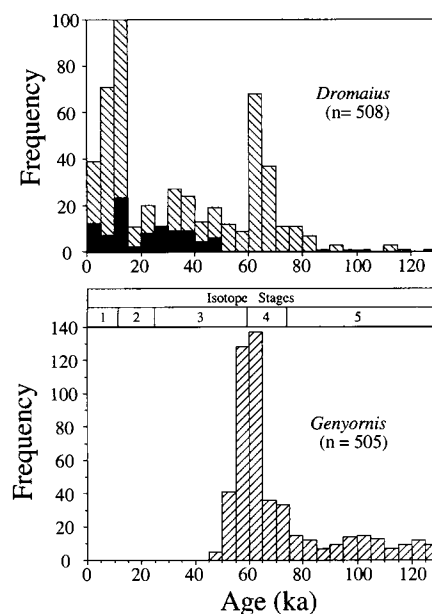
age of 37,600 ^{14}C yr B.P., and three eggshells from within the extinction window range between 38,100 and >45,100 ^{14}C yr B.P. Two *Genyornis* eggshells that slightly predate the extinction, based on their D/L ratios, yielded ages of 42,600 and >44,400 ^{14}C yr B.P., and five fragments from a single stratigraphic level, all with D/L ratios of 0.34 and therefore slightly older than the extinction, have an average TIMS U-series age of 53 ± 3 ka (*22*).

No independent dates are available from LF. The temperature averages 2°C lower there than at MG (*21*); consequently, the D/L ratio expected of a correlative extinction event is 0.40 ± 0.03, midway between those of extinction events at MG and LF. The D/L ratios of the youngest *Genyornis* at LF are higher (0.46 ± 0.02); hence, extinction may have occurred slightly earlier, although the small sample size may mean we failed to locate the youngest *Genyornis* there.

Our dates bracket the timing of *Genyornis* extinction. Luminescence and U-series dates demonstrate that *Genyornis* was common as recently as 60 to 50 ka. The radiocarbon evidence from eggshells of both taxa spanning the extinction event collectively demonstrate that it occurred at or beyond the effective limit of ^{14}C dating of carbonates (at least 42,000 ^{14}C yr B.P., corresponding to a calendar age of >46 ka). Thus, the extinction

Fig. 1. Locality map showing the Lake Eyre Basin (hatched area), Madigan Gulf sites (MG), Lake Frome sites (LF), and the Darling-Murray sites (DM) at the confluence of the Darling (D) and Murray (M) rivers.

Fig. 2. Age model used to convert D/L ratios to calendar ages based on 90 paired and calibrated (*17*) AMS ^{14}C dates and D/L ratios, 5 paired TIMS U-series dates and D/L ratios, and 8 luminescence dates on sediment from which eggshell D/L ratios were measured. The two initial linear segments are based on earlier assessments (*12*), whereas the older two linear segments are simple regressions fit through the data. Other configurations are plausible, but yield similar conclusions. LGM deposits in MG are thin, and the shallow burial, coupled with the low glacial-age temperature, results in poor age resolution for the interval between 16 and 60 ka, but the similar patterns for [14]C- and AAR-dated samples (Fig. 3) suggest that any biases in the histograms are minimal.

Fig. 3. Age-frequency histograms for *Dromaius* (above) and *Genyornis* (below) for the past 130 ky from the MG region, derived from D/L ratios on individual eggshell fragments collected from widely scattered sites that have been converted to calendar ages from the age model shown in Fig. 2. Solid bars in the upper panel represent the AMS ^{14}C-dated eggshells superimposed on the AAR-dated series. The sudden disappearance of *Genyornis* ~50 ka defines the extinction event in this region. Marine isotope stage boundaries are shown.

occurred 50 ± 5 ka. The similar pattern and timing of *Genyornis* extinction across three different regions, including the DM region that would be expected to serve as a refugium during times of drought, and the continuous occurrence of *Dromaius* through the extinction event and on to the present at all three sites suggest that extinction was taxonomically selective and on a continental scale.

To evaluate whether a change in climate may have led to the extinction, we examined paleoclimate reconstructions that extend through the extinction event in MG (past 150 ky) (*20*, *23*) and DM (past 70 ky) (*24*), concentrating on changes in available moisture, the limiting variable for vegetation across most of Australia.

During arid times, when precipitation is reduced over the Lake Eyre Basin, playa conditions dominate in MG, and groundwater salinity rises because of evaporative concentration. As the watertable is lowered, salts that crystallize at the groundwater capillary fringe within the sediment matrix disrupt the surface and promote deflation, removing sediment and salts from the basin. While disruption and deflation keep pace with watertable lowering, the playa floor is lowered, until 'the groundwater level reaches equilibrium with the evaporative conditions, and a halite crust develops. Thus, the maximum depth of deflation is a secure proxy for the intensity of an arid phase. Arid-phase deflation excavated the playa floor below its current level (15 m below sea level) about 140 ka, 60 to 50 ka, and between about 30 and 16 ka. Of these, the most extensive excavation occurred at 140 ka, when the playa was eroded to bedrock, as much as 19 m below sea level. Lake Eyre last carried a permanent waterbody ~60 ka; slow drying followed, but the extent of playa deflation, and by direct inference the intensity of aridity, was less

than at 140 ka, and probably less than the arid phase 30 to 16 ka. Eolian sands were deposited adjacent to the lake during the highstand 60 ka and as it subsequently dried. *Genyornis* eggshells occur throughout the eolian unit, but not in younger deposits, indicating that extinction occurred at the end of a modest drying event or during an immediately subsequent wetter interval.

The most complete record of moisture change in the DM region comes from the Willandra Lakes (*24*). A long period of aridity terminated about 60 ka, with increased moisture supporting abundant vegetation and filling the basin with permanent water. *Genyornis* and *Dromaius* eggshells are present in deposits of this age. Beginning at ~40 ka, the climate began to become drier; *Dromaius* was present, but no *Genyornis* have been reported in this or any younger units. After an interval of variable conditions, final desiccation occurred shortly after 20 ka, and Lake Mungo has remained dry since. In this region, *Genyornis* apparently became extinct before the onset of aridity.

It thus seems that *Genyornis* was able to survive through the range of natural environmental changes caused by Pleistocene climate oscillations. At the time of *Genyornis* extinction, 50 ± 5 ka, modest aridity (MG) to slightly wetter-than-present conditions (DM) prevailed. Consequently, climate change as an explanation for *Genyornis* extinction is unlikely. *Genyornis* is considered to be an element of the Australian megafauna (*1*), and its bones are associated with some of the youngest stratigraphic levels containing megafaunal remains. Thus, we argue that extinction of the Australian megafauna in general is likely to be coincident with *Genyornis* extinction, and that this occurred ~50 ka.

Dating the arrival of the first humans to Australia has proven difficult. The most reli-

able dates are luminescence ages of quartz grains enclosing human artifacts. The oldest widely accepted dates are 55 ± 5 ka (*25*, *26*), near the time of the extinction; older dates from northwest Australia (*27*) have been questioned (*28*, *29*), and indirect evidence that has been interpreted as humanly induced, such as changes in fire regime (*30*, *31*), remains tenuous.

Humans are known to have had an impact on large birds elsewhere. The extinction of all species of moa (*Dinornis* spp.) from New Zealand within a few centuries of human colonization is documented to have been a consequence of hunting and fires (*32*). *Genyornis* carried about twice the body mass of *Dromaius* and was presumably less agile. It is plausible that because it was less mobile, or possibly because of a more vulnerable breeding strategy, *Genyornis* was selectively predated by early hunters. However, evidence of direct predation on *Genyornis* by humans is limited to a single site (*33*), and kill sites for other elements of the megafauna are equally rare [for example, (*1*, *34–36*)]. Alternatively, ecosystem disruption as a consequence of early human activity may have impacted the fauna differentially, possibly on the basis of dietary preferences.

The gross feeding habits of *Genyornis* can be reconstructed from the isotopic composition of its eggshells, and its skeletal morphology. The $^{13}C/^{12}C$ ratio of carbon in a bird's food source is preserved in the calcite matrix of, and organic compounds within, its eggshells. In modern eggshell of *Dromaius*, *Struthio* (ostrich), and *Coturnix* (quail), the $\delta^{13}C$ of the organic fraction is enriched by 2 ± 1 per mil relative to the diet of the parent; the offset between the organic and inorganic fractions is 9 ± 1, 15 ± 1, and 14 ± 1 per mil, respectively (*37*, *38*). The organic-inorganic offsets are indistinguishable in Late Quaternary eggshell of *Dromaius* (10 ± 2 per mil; $n = 45$) and *Struthio* (14 ± 1 per mil; $n = 49$). The average isotopic offset between the two fractions for fossil *Genyornis* (14 ± 2 per mil; $n = 74$) is similar to that of *Struthio* and *Coturnix*. If we assume that the same 2 per mil enrichment of the eggshell organic fraction over dietary $\delta^{13}C$ measured in our modern controls applies to fossil samples, it is possible to reconstruct dietary $\delta^{13}C$ for the extinct *Genyornis*.

Dietary $\delta^{13}C$ reconstructed from 65 *Genyornis* and 49 *Dromaius* eggshells that were laid between 60 and 45 ka in MG averages −22 and −18 per mil, respectively. Twenty of 49 *Dromaius* eggshells are between −13 and −15 per mil, but some individuals have values as light as −26 and as heavy as −9 per mil. *Genyornis* group more tightly (54 of 65 are between −19 and −25 per mil; none are heavier than −14 per mil), suggesting that *Genyornis* ate primarily C_3 browse, whereas *Dromaius* had wider dietary tolerances including a signif-
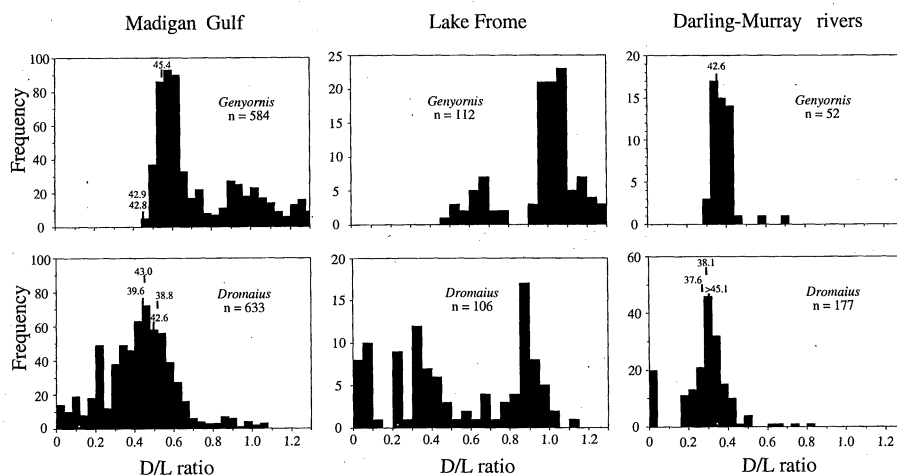
Fig. 4. D/L-frequency histograms for *Dromaius* and *Genyornis* from all three regions. *Dromaius* D/L ratios have been converted to equivalent *Genyornis* D/L ratios by dividing by 1.18, their average offset in paired collections of the two taxa, so that within each region the two taxa can be directly compared. Some key radiocarbon dates are indicated at their associated D/L ratio, showing that extinction occurred at or beyond the limit of ^{14}C dating of eggshell.

icant component of C_4 grasses. In contrast, 25 MG *Dromaius* eggshells from the last glacial maximum (AMS ^{14}C dates for each are between 28,000 and 14,000 yr B.P.) have a dietary $\delta^{13}C$ clustered between -19 and -22 per mil, indicating a shift to regional dominance by C_3 plants and a corresponding adjustment in the birds' diet. *Genyornis* from the DM region apparently ate exclusively C_3 plants ($\delta^{13}C = -26 \pm 1$ per mil; $n = 9$).

The isotopic data indicate that *Dromaius* had broader dietary tolerances than did *Genyornis* and was able to adapt its feeding strategies to a wider variety of ecological conditions. This ability may have contributed to its survival through the extinction event. The cranial morphology of the dromornithids, of which *Genyornis* is a member, indicates that the beak was used primarily in a shearing motion, a characteristic of browsing animals (*39*). Consequently, we conclude that *Genyornis* was primarily a browser and likely to be dependent on extensive shrubland.

Fire has exerted a major control on Australian vegetation throughout the Quaternary, but the adaptations to fire are to ignition during a restricted portion of the year and only after sufficient fuel loading had occurred. One possibility is that burning practices of the earliest human immigrants differed enough from that of the natural fire cycle to disrupt ecosystems across the semiarid zone. The ecosystem may have been particularly susceptible as a result of the continent's geological quiescence; soils in this low-relief landscape were depleted of most nutrients, resulting in a lack of ecosystem resiliency. We postulate that human burning at times of the year and at frequencies to which the vegetation was not pre-adapted resulted in a dramatic decrease in tree and shrub vegetation across the continental interior, which in turn placed unprecedented stress on the dependent fauna (*6, 7, 40*). This stress, possibly coupled with modest drying that occurred simultaneously and perhaps some direct human predation, led to megafauna extinction.

Most of the extinct megafauna were browsers (*1*). Vegetation over much of their former range is currently desert scrub and spinifex grassland, providing circumstantial evidence in support of major vegetation change. Those taxa with restricted dietary requirements, such as *Genyornis*, were at greatest risk, whereas more cosmopolitan, opportunistic feeders, such as *Dromaius*, were able to survive as a new equilibrium was established. Top-level predators were unable to sustain themselves in the face of reduced prey.

References and Notes

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11. Epimerization rates exhibit systematic offsets between taxa as a result of differences in the amino acid sequences in the protein each bird uses. D/L ratios measured in *Dromaius* and *Genyornis* eggshells from the same stratigraphic horizon indicate that isoleucine epimerizes 1.18 times faster in *Dromaius*; *Dromaius* D/L ratios have been adjusted by this amount to allow plots comparing the two taxa (Figs. 3 and 4) on a common scale.
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16. Climate data are mean annual temperature and mean annual precipitation calculated with programs described by McMahon et al. (*21*).
17. In Fig. 2 and in general discussions we have converted radiocarbon ages to calendar ages using the CALIB 3.0 Program (*45*) for samples <10,000 ^{14}C yr B.P., and the equation $CalibAge = -5.85 \times 10^{-6}(Conv^{14}CAge)^2 + 1.39(Conv^{14}CAge) - 1807$ (E. Bard, unpublished data based on paired U-series and ^{14}C dates). However, when citing specific dates, we leave these in radiocarbon years because most are at or beyond the limits of radiocarbon dating, for which there is no generally accepted terminology or calibration curve. All luminescence and U-series dates are given in calendar years; the U-series dates have 2σ uncertainties of about 2%, whereas the luminescence dates have 1σ uncertainties of 10 to 15%.
18. We evaluated the potential of TIMS U-series dating using 20 *Genyornis* eggshell fragments of known AAR. U-series dates are shown to be reproducible among different fragments from the same unit, despite a wide range in U concentrations, but some samples have enough common thorium (^{232}Th) to require correction for unsupported ^{230}Th. Eggshell has discrete pores that allow the developing embryo to exchange gases with the atmosphere, and in some fossil samples these have been infilled with clay, a carrier of thorium. We thus restrict our discussion to samples with $^{230}Th/^{232}Th$ activity ratios >30.
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