Bomb-curve radiocarbon measurement of recent biologic tissues and applications to wildlife forensics and stable isotope (paleo)ecology

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Above-ground thermonuclear weapons testing from 1952 through 1962 nearly doubled the concentration of radiocarbon (14C) in the atmosphere. As a result, organic material formed during or after this period may be radiocarbon-dated using the abrupt rise and steady fall of the atmospheric 14C concentration known as the bomb-curve. We test the accuracy of accelerator mass spectrometry radiocarbon dating of 29 herbivore and plant tissues collected on known dates between 1905 and 2008 in East Africa. Herbivore samples include teeth, tusks, soft tissue, hair, and horn. Tissues formed after 1955 are dated to within 0.3–1.3 y of formation, depending on the tissue type, whereas tissues older than ca. 1955 have high age uncertainties (~17 y) due to the loss of the bomb effect. 14C dating of tissues has applications to stable isotope (paleo)ecology and wildlife forensics. We use data from 41 additional samples to determine growth rates of tusks, molars, and hair, which improve interpretations of serial stable isotope data for (paleo)ecological studies. 14C dating can also be used to calculate the time interval represented in periodic histological structures in dental tissues (i.e., perikymata), which in turn may be used as chronometers in fossil teeth. Bomb-curve 14C dating of confiscated animal tissues (e.g., ivory, status) can be used to determine whether trade of the item is legal. We use a chronometric method to establish the age of death and determine the period (e.g., days or weeks) represented in growth increments in dental tissues, providing a basis for establishing a chronometer in fossil teeth. This approach is important in intratooth stable isotope and histological studies that aim to evaluate seasonal variability in past environments. We demonstrate that 14C dating can be used in forensic investigations to determine the age of confiscated animal tissues, which in many cases is equivalent to the date of death. For many animal parts, such as ivory and rhino horn, age often determines whether trade of the item is legally permitted.

Results

Fraction Modern Carbon and 14C-Calibrated Ages. 14C data are presented as fraction modern carbon (F14C), where 14C/13C0X = (A13C/13C0X × (0.975/0.981))2 × [(1 + δ14COX/1,000)/(1 + δ13COX/1,000)].


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The F\(^{14}\)C values plotted against the known age reveal that the F\(^{14}\)C in herbivore and plant samples tracks the F\(^{14}\)C of atmospheric CO\(_2\) during the period in which the tissue formed for samples collected after 1955 (Fig. L4). Pertinent sample information is provided in Dataset S1, Table S1, and all F\(^{14}\)C, \(\Delta^{14}\)C, and \(^{14}\)C-calibrated ages are given in Dataset S1, Table S2. The Northern Hemisphere 3 (NH3) and Southern Hemisphere 1 (SH1) calibration curves (1) are both plotted in Fig. L4 because we sampled animal tissues from both regions. The NH3 data set is appended with the Levin dataset (2, 16) (NH3+Levin) beginning at 1999.50 to permit \(^{14}\)C age calibration through 2006. The two curves, NH3+Levin and SH1, differ significantly before 1970 owing to bomb testing locations and atmospheric circulation, and subtle differences of 4–5‰ persist after 1970. Pre-1970 keratin and plant samples are confirmed (or in several cases presumed) to have been collected from the Southern Hemisphere and track the SH1 curve extremely well (Fig. L4).

Fig. LB shows the known age versus the calibrated \(^{14}\)C age for all samples (n = 22) collected from 1955 to 2006. Fig. LC includes four samples collected between 1905 and 1953 to illustrate the inaccuracy of calibrated \(^{14}\)C ages before 1955. The residual (r) between the \(^{14}\)C age (age\(_{14}\)) and known age (age\(_{\text{known}}\)) is given by \(r = \text{age}_{14} \pm \text{age}_{\text{known}}\) (Fig. S1 and Dataset S1, Table S2). The mean residual of 11 keratin samples collected after 1955 is ±1.3 ± 1.8 (16) years. For apatite samples (n = 5), the mean residual is ±0.8 ± 0.7 y; for grains (n = 3), it is 0.3 ± 0.6 y. For the soft tissue and collagen samples, the residuals are ±0.7 and ±1.2 y, respectively. Variation in mean residuals based on tissue type likely arises from differences in the total number of samples analyzed, in the amount of time integrated in different tissue types, and in the F\(^{14}\)C values (e.g., whether the samples fall on a steep or shallow part of the bomb-curve). Tissues formed during the steeper parts of the bomb-curve tend to have residuals less than 2 y (Fig. S1). The current slope of the bomb-curve is shallower than during the interval from 1955 to ca. 2005, increasing the uncertainty of \(^{14}\)C-calibrated ages in tissues formed from ca. 2005 forward (Fig. L4 and Dataset S1, Table S2).

A hair sample (L18830) from a Cercopithecus mitis (blue monkey) was reportedly collected in the Congo in 1962 but has a F\(^{14}\)C value of 0.9749 ± 0.0023 (this and all subsequent SDs are 2σ), which clearly indicates it formed before 1955. Nearly 70% of the blue monkey's diet is fruit and leaves, so significant dietary contribution from older plant material (more than several years old) is unlikely (17). Hair from other primates, including two other C. mitis, yield \(^{14}\)C ages consistent with known dates, further suggesting that diet is not the cause for the age discrepancy. The most likely explanation is that the date of museum accession, which we used as the known age of the sample, does not reflect the date of death.

**Tissue Growth Rates.** We use multiple \(^{14}\)C ages from elephant tusks, molar plates, and tail hair and hippo canines to calculate tissue growth rates (Table 1). A schematic of the general structure of tusks, molars, and canines is shown in Fig. S2. The period of growth for some canines and both tusks continued beyond 1997, when \(^{14}\)C data becomes sparse for both the NH3 and the SH1 data sets. Thus, we use the Levin dataset to calibrate \(^{14}\)C ages for samples more recent than 1960 with an F\(^{14}\)C ≤1.110.

**Elephant tusks.** Tusk growth rates for two female African elephants were determined from collagen-derived \(^{14}\)C ages. Growth rates are 4.13 ± 0.39 cm/y and 5.10 ± 0.74 cm/y for elephants R37 and Misha, respectively (Fig. 2A and Table 1). We use linear growth rates because they best fit the data from the two tusks, although a second-order polynomial also fits the tusk data from R37. Because there is no calibrated \(^{14}\)C age for the youngest data point for Misha, we use September 10, 2008, her known date of death.

Assuming an age at death of 53 ± 5 y for R37 based on molar wear (18, 19), the R37 tusk represents growth from 25 to 53 y of age, whereas Misha’s tusk represents growth from 13 to 28 y of age. Thus, the 20% difference in growth rate between the two tusks may be explained by ontogeny, but we may also relate to captive (Misha) versus wild (R37) diet or stress levels. Although linear growth rates are appropriate for the two tusks, our data suggest for tusks that record multiple ontogenetic stages (e.g., juvenile, adolescent, and adult), growth rates may not be linear.

Mastodon tusks show nonlinear growth rates based on measurements of annual incremental thicknesses and lengths over ~30 y (20, 21). Using the tusk lengths and growth rates for R37 and Misha, we calculate the time represented in the tusks to be 28.0 and 14.8 y, respectively (Table 1). Interestingly, this accounts for 54% and 53% of their total lifespans, respectively, suggesting similar overall rates of wear between the two female elephants. Additional \(^{14}\)C ages from tusks that formed between 1955 and 2005, particularly from male tusks and tusks that capture multiple ontogenetic stages, would elucidate variation in tusk growth rate as a function of sex and age.

**Hippo canines.** We calculate growth rates for five hippo canines using a total of 17 enamel \(^{14}\)C ages. Length measurements are made along the outer curve of the canine. Multiple \(^{14}\)C ages from a lower (n = 5) and an upper (n = 3) canine of an individual, presumed to be a juvenile or young adult based on canine shape

![Fig. 1](https://example.com/fig1.png)

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**Fig. 1.** (A) Fraction modern carbon (F\(^{14}\)C) vs. known age (year), where known age is determined by the known date of death or collection for post-1955 tissue and plant samples. The y-axis uncertainty is smaller than the symbols. Calibrated \(^{14}\)C age vs. known age for tissues and plants for (B) samples younger than 1955 (n = 23) and (C) all samples (n = 27). The y-axis uncertainty is 2σ; one-way x-axis uncertainty on some samples in A and B represents potential offset of up to 2 y between the actual date of death and date of collection or accession.
Table 1. Tissue growth rates determined from calibrated \textsuperscript{14}C ages

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Growth rate ± 2(\sigma)</th>
<th>Length, cm</th>
<th>Proximal \textsuperscript{14}C age</th>
<th>Distal \textsuperscript{14}C age</th>
<th>Time in tissue, y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail hair (keratin), mm/d</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TSV-171</td>
<td>0.81 ± 0.77</td>
<td>31.4</td>
<td>1996.7</td>
<td>1996.0</td>
<td>0.7</td>
</tr>
<tr>
<td>R37</td>
<td>NA</td>
<td></td>
<td></td>
<td>2001.9</td>
<td>2002.5</td>
</tr>
<tr>
<td>Hippo canines (bioapatite), cm/y</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>2KL (upper)</td>
<td>1.94 ± 0.31</td>
<td>17.0</td>
<td>1969.5</td>
<td>1964.2</td>
<td>8.8</td>
</tr>
<tr>
<td>KL</td>
<td>3.35 ± 0.25</td>
<td>37.2</td>
<td>1960.0</td>
<td>1970.6</td>
<td>11.1</td>
</tr>
<tr>
<td>K11-KF</td>
<td>4.51 ± 0.41</td>
<td>35.0</td>
<td>1979.0</td>
<td>1972.4</td>
<td>7.8</td>
</tr>
<tr>
<td>K08-201</td>
<td>4.87 ± 0.34</td>
<td>56.0</td>
<td>2006.5</td>
<td>1996.8</td>
<td>11.5</td>
</tr>
<tr>
<td>TSV-291</td>
<td>7.47 ± 0.88</td>
<td>60.0</td>
<td>1996.9</td>
<td>1989.6</td>
<td>8.0</td>
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<td>Elephant tusks (collagen), cm/y</td>
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<td></td>
<td></td>
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<tr>
<td>Misha</td>
<td>5.11 ± 0.75</td>
<td>73.0</td>
<td>2008.7</td>
<td>1993.9</td>
<td>14.8</td>
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<tr>
<td>R37</td>
<td>4.13 ± 0.39</td>
<td>115.6</td>
<td>2005.5</td>
<td>1978.1</td>
<td>28.0</td>
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<td>Elephant molar plates (bioapatite), cm/y</td>
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<tr>
<td>TE-95 Rm6.2</td>
<td>1.49 ± 0.54</td>
<td>10.1</td>
<td>1959.3</td>
<td>1955.0</td>
<td>6.8</td>
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<tr>
<td>TE-95 Rm6.4</td>
<td>1.46 ± 0.59</td>
<td>11.6</td>
<td>1959.7</td>
<td>1954.3</td>
<td>7.9</td>
</tr>
<tr>
<td>TE-95 Rm6.7</td>
<td>1.63 ± 0.14</td>
<td>12.3</td>
<td>1963.1</td>
<td>1957.1</td>
<td>7.5</td>
</tr>
<tr>
<td>TE-95 Rm6.9</td>
<td>1.62 ± 0.14</td>
<td>11.1</td>
<td>1963.9</td>
<td>1959.1</td>
<td>6.9</td>
</tr>
<tr>
<td>R37 Lm6.7</td>
<td>1.39 ± 0.27</td>
<td>7.8</td>
<td>1984.2</td>
<td>1979.6</td>
<td>5.6</td>
</tr>
<tr>
<td>R37 Lm6.10</td>
<td>1.61 ± 1.19</td>
<td>5.9</td>
<td>1988.4</td>
<td>1986.3</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Total time represented in tissue is based on growth rate and length.

and size, give linear growth rates of 3.35 ± 0.25 cm/y and 1.94 ± 0.31 cm/y, respectively (Fig. 2B). Growth rates from three other (lower) canines, presumably from males based on size, range from 4.51 ± 0.21 cm/y to 7.47 ± 0.88 cm/y (Table 1 and Fig. 2C). Passey et al. (22) measured lower canine growth rates in two female hippos from the Toledo Zoo by notching the tooth at the gum line and measuring the distance from the gum line the following year. Growth rates from the 48- and 8-y-old females were 1.35 cm/y and 1.94 cm/y, respectively (Fig. 2B). Growth rates from three other (upper) canines, presumably from males based on size, range from 1.39 ± 0.27 to 1.63 ± 0.14 cm/y (Table 1 and Fig. 3B and C). The rates fall within the range of those determined histologically for the extinct Columbian mammoth (Mammuthus columbi); 1.3–2.2 cm/y (23, 24). The \textsuperscript{14}C data do not reveal whether growth rates are linear; however, histological data from two extinct proboscidean species, M. columbi and Paleoloxodon cypriotes, indicate growth rates are highest near the initial occlusal surface and decrease toward the cervical margin (23).

A \textsuperscript{14}C age on collagen from the mesial root of TE-95 yields an age of 1964.2 ± 0.1, which is the best estimate for the date of death (Fig. 3A). Time represented in unworn molar plates from TE-95 is 7.3 ± 0.6 y, and time represented in an entire elephant molar is ca 0.10 y or more based on \textsuperscript{14}C ages from TE-95 and R37 (Table 1). The thick enamel and the long time intervals represented in a single plate or entire molar make fossil proboscidean teeth excellent candidates for intratooth stable isotope profiles in paleoecology (e.g., ref. 25).

Elephant tail hair. Only one of two tail hairs sampled provides a reasonable growth rate. Sample TSV-171, collected on July 17, 1998, from a female African elephant in Tsavo National Park,

![Fig. 2](https://www.pnas.org/cgi/doi/10.1073/pnas.1302266110)

Fig. 2. Calculated linear growth rates for (A) two tusks of female African elephants, (B) upper (U) and lower (L) hippo canines collected from an individual in Queen Elizabeth National Park, Uganda in 1971, and (C) lower canines from two hippos from Tsavo National Park, Kenya whose lives overlapped by ca. 1 y (shaded area). Growth rates (±2\(\sigma\)) are calculated from the slope of the regression lines. Calibrated \textsuperscript{14}C age uncertainty is 2\(\sigma\) and if not shown is smaller than the symbol.
yields a growth rate of 0.81 ± 0.07 mm/d (Table 1). Wittemyer et al. (26) used independent methods to calculate a growth rate of 0.81 ± 0.11 mm/d for female African elephants (n = 38). A second tail hair was collected from R37 within days of her death in September 2006. The proximal and distal ends of the 304-mm-long hair have nearly identical F14C values of 1.0820 and 1.0803, respectively, and the higher value in the proximal end precludes calculating a growth rate. Growth rates determined by independent methods from R37 tail hairs collected between 2001 and 2006 range from 0.56 to 0.62 mm/d.

**F14C variation based on tissue type and pretreatment.** Four tissue types were sampled at death from two elephants to test for variation in 14C based on tissue type. Collagen and apatite from tusk dentin sampled from the pulp cavity margin (e.g., the tissue forming at time of death) show indistinguishable F14C values (Dataset S1, Table S3). The F14C values can be used to calculate a 14C-calibrated age for R37, and the collagen and apatite ages fall within a range of less than 0.4 y. We tested whether treating tusk apatite with 3% NaOCl had any effect on Δ14C values. Treated and untreated apatite samples from Misha have nearly identical Δ14C values, whereas those from R37 differ by 5.6‰ but fall within the range of 2σ uncertainty (Dataset S1, Table S3). The data suggest treatment to oxidize organics before acid digestion is not necessary.

We also analyzed the proximal end of a tail hair (R37-prox-K) and soft tissue from R37’s tusk pulp cavity (R37-PC-tissue). The F14C value in the tail hair is anomalously high, resulting in an older age than the actual date of death (Dataset S1, Table S3). The soft tissue sample has a Δ14C value of 43.7‰ and a 14C-calibrated date of 2006.04, which is the closest to the actual date of death of all R37 tissues analyzed.

**Discussion**

**Application to Stable Isotope (Paleo)ecology.** 14C-correlated stable isotope profiles. Serial sampling or intratooth stable isotope profiles of enamel yield information about seasonal change in diet and water use, which relate to seasonality of precipitation and vegetation. This has been suggested as a method for (paleo)dietary and (paleo)ecological reconstruction in modern and fossil mammalian teeth (e.g., refs. 25, 27–31). In ungulate molars, tooth height and growth rate determine total formation time, which is generally no more than 2–3 y (32, 33). However, continuously growing teeth from large mammals (e.g., hippo canines and elephant tusks) and elephant molars form over years to decades and therefore can be used to evaluate long-term dietary and seasonality changes (28, 31, 34) and can capture ontogenetic transitions such as weaning (35).

We show that intratooth stable isotope profiles from two hippo canines overlap to provide a continuous 18-y isotope record. F14C values used as a tie point between the two canines are labeled with arrows indicating sample location. Based on the shape of the δ14C curves, the K08-201 profile has been shifted −0.3 y, which is within the 2σ range of uncertainty. Canine TSV-291 was collected in 1996 near the town of Mtito Andei, Kenya. The steep rise in δ18O that begins −200 d before death suggests physiological stress preceding death, a pattern observed in other serially sampled hippo canines. Canine K08-201 is from a hippo shot dead on October 10, 2007 as a (crop-raiding) nuisance animal near Mtito Andei.
indicating a switch to (C3) browsing beginning in the latter part of 1995, followed by a 4% increase in δ13C during last half year of the hippo’s life in 1996 (Fig. 4). The onset of the δ13C shift coincides with beginning of a prolonged drought that persisted until April of 1997. The 2008 canine dentin, which contained δ13C growth persisted among hippos in this region until the year 2000, when the diet returns to predominantly C4 grazing.

Overlapping isotope profiles from multiple teeth based on bomb-curve 14C ages can provide long-term ecological records. These records may be useful for tracking decadal (or longer) scale changes in land-use, climate, or life-history patterns and thus have potential application in wildlife ecology and conservation. Understanding how ecological change, such as periods of drought or seasonal precipitation, affects intratooth isotope profiles in extant taxa provides insight for interpreting profiles in fossil teeth.

Periodicity of incremental growth features. Periodic incremental growth features in tooth enamel and dentin (e.g., perikymata, striae of Retzius, and Andresen lines) can be used as accurate chronometers if the time interval represented by each increment is known (36). By establishing a chronometer, the teeth can provide information about the timing of tooth development and other aspects of life history. The chronometer is critical for interpreting intratooth stable isotope profiles in fossil teeth, where one of the primary goals is to determine the magnitude, duration, and periodicity of diet or environmental change in the past. Periodicities of some other hominin teeth, perikymata visible on the surface of a tooth represent a period of 7 or 8 d (37).

In proboscidean tusks, three hierarchical incremental growth features have been proposed: First-order increments have annual periodicity, second-order are weekly in elephants and mammoths (fortnightly in mastodons), and third-order are daily (38, 39).

We use 14C growth rates to determine the time interval represented in hippo canine perikymata and to confirm the weekly time interval represented in elephant tusk dentin. The distance between perikymata was measured along sections of canine K11-KF using a plugin (Inc Meas v.1.2) in ImageJ software (Fig. S3). Mean increment width is 1.26 ± 0.35 mm (n = 167), and given the growth rate of 45.1 mm/y, each increment represents 10.2 ± 2.9 (1σ) days (Dataset S1, Table S3). Other hippo canines for which 14C growth rates were determined either lacked visible perikymata or photos for making measurements.

In the R37 tusk, we measured the thickness of second-order increments on a transversely cut thin section located 2 mm from the horn of the pulp cavity using the same ImageJ plugin (Fig. S4). The average growth rate determined from histological measurements is 105 ± 11 μm/wk (Dataset S1, Table S4), which is 105 ± 11 μm/wk (Dataset S1, Tables S5 and S6). The 14C growth rate provides independent evidence for weekly periodicity of second-order growth increments in elephant tusk dentin.

The period recorded in growth increments in modern teeth and tusks can be applied with caution, because the period between increments may differ between modern and fossil teeth, to similar taxa in the fossil record that cannot be bomb-curve dated. Furthermore, tusks can be applied with caution, because the period be-

Conclusions

In this study, we show bomb-curve 14C can be used to accurately date keratin, collagen, apatite, and bulk plant tissue, and we provide examples of applications of the technique to stable isotope records in forensic science and wildlife forensics. Plant and animal tissues that formed between 1955 and 2008 have been accurately dated (−0.9 ± 1.4 yr, 1σ) for 21 samples of known age using bomb-curve 14C. Our results from all post-1955 tissues indicate their carbon was derived from recently photosynthesized CO2 (within ca. 1 y of sampling), regardless of tissue type and across a range of biological tissue enrichment factors.

We calculated growth rates of elephant tail hair, tusks, molar, and hippo canines from multiple 14C ages measured along tissue growth axes. 14C measurements from NaOCl-treated dentin, untreated dentin, enamel, and collagen are distinguishable, indicating both apatite and collagen are suitable for bomb-curve 14C dating, and that treatment of dentin apatite to remove organics is not necessary for 14C measurement.

Our results have the following immediate and unique applications to stable isotope (paleo)ecology and wildlife forensics. We concatenated intratooth δ13C and δ18O profiles from two hippo tusks using 14C ages to establish a tie point, resulting in an 18-y composite stable isotope record. Records such as these can be used to study long-term (i.e., multidecadal) population, climate, or ecosystem dynamics that would not be feasible from a single intratooth profile, exclusive of proboscidean tusks. Growth rates from bomb-curve 14C dating can be used to determine the time represented in periodic growth increments. Determining the time represented in periodic growth increments in teeth of extant taxa provides a potential chronometer in fossil teeth, where knowledge of growth rate is critical to interpretation of intratooth stable isotope profiles or histological data related to life history.

14C dating of raw or worked animal tissues can be used to establish sample age and in many cases date of death of an animal, which can determine whether trade is legal according to CITES or other regulations. Poaching for elephant tusks and rhino horn has increased significantly since 2006. Turnaround time and cost of AMS 14C measurements have decreased in the past decades, and therefore it is an accessible wildlife forensics tool. Combined with geolocation (e.g., DNA, stable isotope, and
histological) forensic techniques. 14C dating of animal parts can help budget-limited government agencies and nongovernmental organizations determine how and where to direct conservation and anti-poaching resources.

**Materials and Methods**

Sampling and analytical procedures are described in detail in *SI Text*. Briefly, inorganic tissues (bioapatite from dentin and enamel) were digested overnight in 10% (by density) phosphoric acid to generate CO2. Organic tissues (keratin, collagen, and bulk plant tissue) were combusted in sealed quartz tubes at 850 °C for 4 h in the presence of CuO and Ag foil to generate CO2. CO2 was cryogenically purified, graphitized, and measured for 14C by AMS at the University of Arizona. Stable carbon isotope ratios are reported as δ values relative to the Vienna Pee Dee Belemnite (VPDB) standard using permil (‰) notation, where δ13C = (Rsample - Rstandard) / Rstandard × 1000, and Rsample and Rstandard are the 13C/12C ratios in the sample and in the standard, respectively. The δ13C values are used for fractionation corrections of 14C.

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**Relevant Websites**

- <http://www.africawildlife.org/wildlife.html>
- <http://www.iucn.org/>
- <http://www.cites.org/eng/about/index.html>
- <http://www.ungg.org/>
- <http://www.nature.com/nature/journal/v180/180615a0/full/180615a0.html>
- <http://www.pnas.org/content/110/29/11741>