

peratures. Another observation in this connexion seems significant: the paper solution, even after filtering, was slightly cloudy owing to the suspension of a fine particulate matter. On standing, the latter slowly settled out as a precipitate, which became partly afloat and partly smudging the wall of the container. Coincident with this precipitation, the solution lost toxicity appreciably. These observations strongly suggest that the active causative agents here involved may be polycyclic aromatic hydrocarbons^{3,6}.

In conclusion, this work has shown mainstream smoke to be the most toxic of the cigarette components. This is true of all the brands tested (so are all other findings of this work, with a variability among the brands that is well expected). The fact that this finding is in agreement with the literature constitutes an endorsement of *Paramecium aurelia* as a useful assay organism. The ultimate realization of the significance of this fact comes from the consideration that mainstream smoke is what should directly concern the smoker. Within the past decade or so, evidence for deleterious effects of cigarette smoke on the epithelial cells of the respiratory tract has been fast accumulating from both *in vivo* and *in vitro* experiments⁷⁻¹³. *Paramecium* is a ciliated unicellular animal, and as such it is likely to bear certain physiological resemblance to human respiratory epithelium^{14,15}. On this ground alone the use of this organism in future research may be viewed as a desirable new approach to cigarette toxicity problems.

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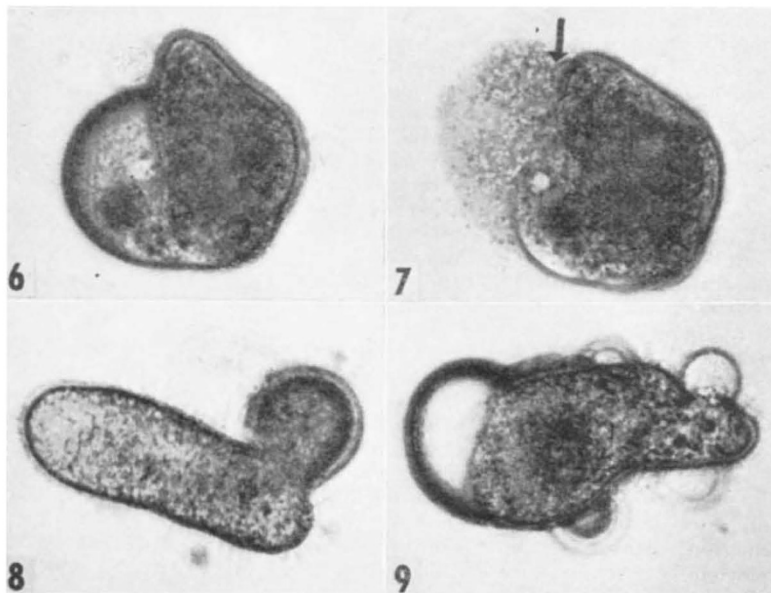


Fig. 6. A deformed *Paramecium* bearing an endoplasmic blister almost the size of body : in 1.0 concentration cigarette paper solution at 25° C 15 min after immersion

Fig. 7. The same organism in Fig. 6, 3 min. later showing the blister collapsing and releasing its contents following a break-through some distance above (arrow)

Fig. 8. Another deformed *Paramecium* with a typical sausage-shaped body with a round protrusion near one end; the latter is not a blister since it was filled with endoplasm from the start. Later, however, blisters may be formed anywhere along the body surface. Note deranged cilia. This organism was in 1.0 concentration cigarette paper solution at 25° C, 11 min after immersion

Fig. 9. A 'monster'-like *Paramecium* afflicted by 1.0 concentration cigarette paper solution at 31° C, showing a combination of body deformation and blistering. At this stage all its blisters were of ectoplasmic kind, although the one at top right-hand corner of this figure was just about to be converted into an endoplasmic blister. (× c. 330)

CORAL GROWTH AND GEOCHRONOMETRY

By PROF. JOHN W. WELLS

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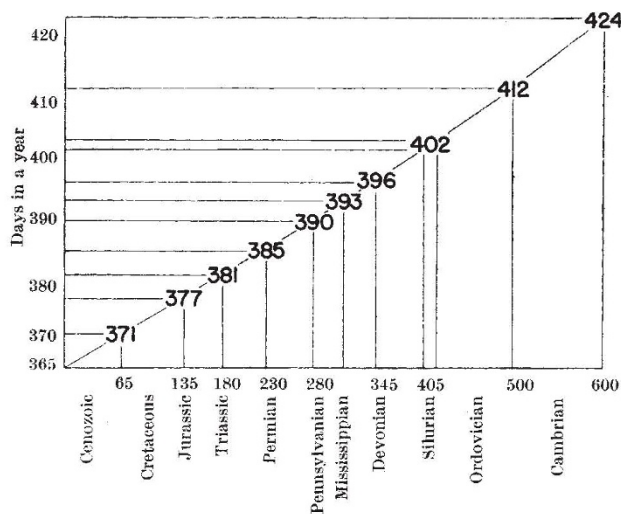
ABSOLUTE age determinations of points on the geological time-scale, based on radioactivity, are generally accepted as the best approximations now known, even though they rest on a series of assumptions, any one of which may be upset at any time. At present there is no means of confirming or denying the accuracy of these determinations by independent methods. Can palaeontology provide anything by way of verifying the pronouncements now emanating, at very considerable expense, from the black boxes? Can palaeontology give any support to the shaky chronometric creation of the geophysicists and astronomers?

Except for providing a relative geochronology, palaeontology has thus far offered no data on absolute geochronometry. Several geochronologists have noted that there is no fossil evidence concerning variations in the length of the day¹, the rotation of the Earth, or diurnal variations, in the geological past—variations that are

linked to the passage of time, whereas the changes of the seasons have left indelible records in such things as tree rings, fish scales, stalactites, anhydrite bands, and other kinds of varves, all of which have little or no bearing on the problem of age or position in geological time. Organic evolutionary rates provide no evidence for they are wholly dependent for their values in isotopic age estimates.

It seems not unlikely, however, that if we lower our sights on suitable units of time for expression of age from the generally used year to the humbler day, we might find data in palaeontological material for estimates of absolute age. How nice it would be if instead of paying a large sum for an isotopic analysis we could examine a fossil and estimate directly, with luck, not only its relative, but also its absolute age—every palaeontologist a geochronometrist; every fossil a geochronometer!

The two chief approaches to geochronometry are based on radioactive isotopes and on astronomical data. The



Geological time: millions of years (Kulp, 1961)
 Fig. 1. Relation between days in each year and geological time (radioactive age data from Kulp, 1961)

most recent estimates² of geological time based on the rates of radioactive decay give the Cenozoic a length of 65 million years, the Mesozoic 165 million years, and Palaeozoic 370 million years, and so on. The beginning of the Cambrian is placed about 600 million years ago. To accept these figures is an act of faith that few would have the temerity to refuse to make. The other approach, radically different, involves the astronomical record. Astronomers seem to be generally agreed that while the period of the Earth's revolution around the Sun has been constant, its period of rotation on its polar axis, at present 24 h, has not been constant throughout Earth's history, and that there has been a deceleration attributable to the dissipation of rotational energy by tidal forces on the surface and in the interior, a slow-down of about 2 sec per 100,000 years according to the most recent estimates. It thus appears that the length of the day has been increasing throughout geological time and that the number of days in the year has been decreasing. At the beginning of the Cambrian the length of the day would have been 21 h (ref. 1). After the first, a second act of faith is easy, and we can develop a simple relation between the geological time-scale and the number of days per year (Fig. 1).

Accepting this relation, in the absence of evidence to the contrary, it now follows that if we can find some means of determining the number of days per year for the different geological periods, we have a link between the results of geophysical and astronomical deductions. If we could determine, for example, that the number of days in the Cambrian year was of the order of 420, it would seem to confirm an indicated age of 600 million years based on tidal friction and in turn that since isotopic methods give the same result they too are in harmony. Is it possible to obtain estimates of the number of days per year from data preserved in recent and fossil organisms? I would like to think so.

Among the several groups of organisms which have an additive mode of skeletal formation, the corals—tabulates, rugosans and scleractinians—are fairly well known, and there is a good deal of empirical information on rates of growth of recent forms, and a very little on the factors governing growth.

The earliest notice of annual fluctuations in coral growth is fairly recent. In 1898, R. P. Whitfield³ described a large colony of the reef coral *Acropora palmata* from the Bahamas that showed regular undulations on the upper surface of the flat, spreading branches and suggested that these represented annual growth increments which he ascribed to seasonal temperature changes. The late T. Wayland Vaughan's experiments⁴ a few years later with the same species in the Bahamas gave virtually the same result: 40–100 mm per year compared with 50–100 mm one gets from measurements of the undulations shown in Whitfield's specimen.

It has since been speculated that the growth annulations so common on many Palaeozoic corals (Fig. 2) were the result of yearly fluctuations in growth produced by seasonal temperature change, variations in supplies of nutrients, or periodic reproductive activity. Beginning in 1934, T. Y. H. Ma⁵ undertook investigations of variation of annual growth increments in recent and fossil corals as a means of determining the temperatures and latitudes of

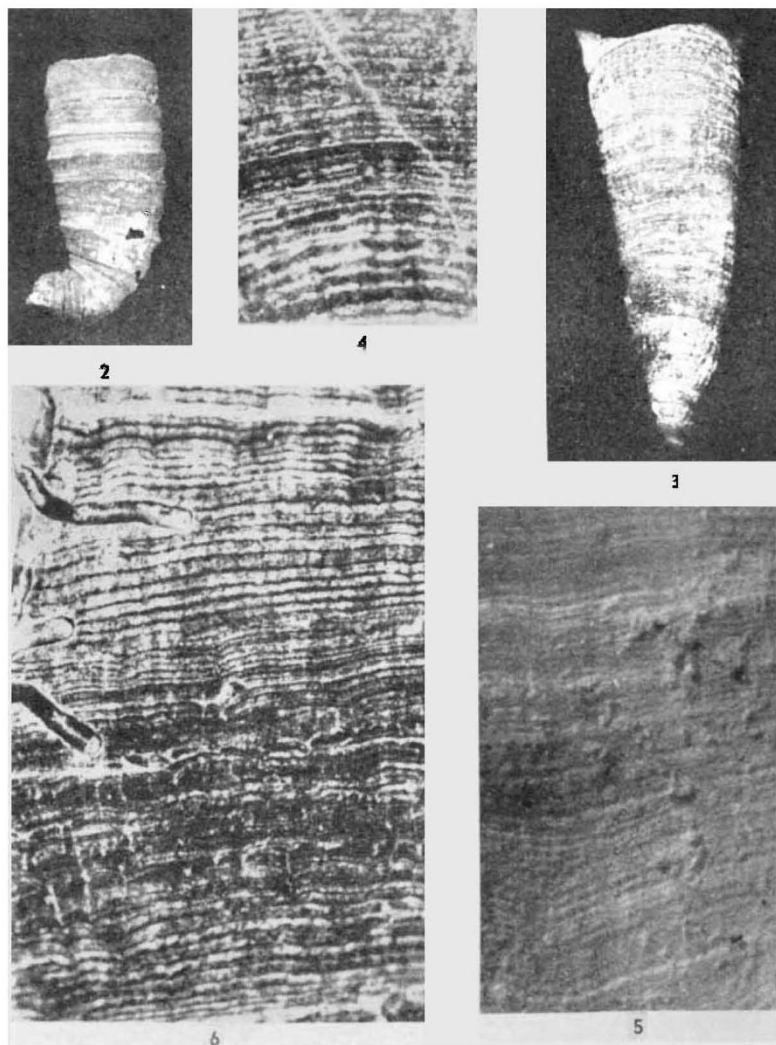


Fig. 2. *Heliophyllum halli*, Middle Devonian, western New York, showing 13 annual growth increments ($\times c. 0.5$). Figs. 3 and 4. *Holophragma calceoloides*, Lower Silurian, Gothland: (3) corallum about 240 days old, showing growth-lines on epitheca ($\times c. 2.7$); (4) growth-lines on epitheca ($\times c. 13$). Fig. 5. *Manicina areolata*, Recent, Dry Tortugas, Florida; growth-lines on epitheca ($\times c. 46$). Fig. 6. *Eridophyllum archiaci*, Middle Devonian, western New York; growth-lines on epitheca ($\times c. 21$)

the ancient seas, and assembled an appalling mass of very raw data on which he has leaped, with the agility of Raphael Pumpelly's mouflon, from assumption to assumption to heights of speculation where few would care to follow. But Ma's basic idea that annual growth-rates can be determined for many fossil corals appears to be sound.

Others have concluded that annulations or related internal variations in some Palaeozoic corals have an annual basis, but no experiments have been undertaken on living corals to determine directly whether or not there is a causal relation between such annulations and annual variations in temperature or other factors. I do not know why such an obvious and simple test has not yet been attempted. There are some experimental data on allometric and volumetric growth-rates but these have little bearing on the problem of annulations, nor do these data tell, or are likely to tell, much more than: (1) that reef corals grow more rapidly in warmer waters; (2) that some corals grow faster than others. There is some evidence that fluctuations in nutrient supplies and reproductive activity have little or no effect on the overall growth-rate of corals.

We must now make an act of faith and assume that the major annulations on corals represent annual growth increments or varves. This, however, is of no direct value in geochronometry, even though it can thereby be shown that some large fossil coral colonies endured for a couple of hundred years, and that some living colonies of reef corals have been growing for the past thousand years or so. There is nothing in these values to orient them in time. A closer look at certain coral structures is necessary.

A number of people have noticed the fine ridges (Figs. 3 and 4) on the surface of the coral epitheca, a fundamental skeletal structure in tabulates, rugosans, and scleractinians, the basic material not only of the exterior of the corallum but in various guises as septa and dissepiments. Whenever epitheca is present and unmodified these ridges are present, although in many fossil specimens they are obliterated by post-mortem wear. The ridges are parallel to the growing edge of the corallum and are tacitly accepted as growth increments variously termed striae, ridges and growth-lines. I cannot find, however, that anyone has concerned himself with their significance in growth-time. They clearly indicate regular variations in the rate of calcium carbonate secretion, but what is the relation of these to the passage of time? Hourly, daily, circadian, weekly, lunar monthly, periodic reproductive activity, yearly?

I submit that they indicate daily or circadian variation in skeletal deposition, and there is some slender evidence in this direction. Physiological studies on calcium carbonate secretion in recent corals, first made some years ago by Kawaguti and Sakumoto⁵, and recently and more elegantly by Goreau⁷, who used the isotope calcium-45, show that in reef corals the rate of calcium carbonate

uptake in coral tissues falls at night or in darkness and rises during the day, but the reflexion of this in the skeleton has not yet been investigated. A much less-sophisticated approach would be to compare the number of ridges with the annual growth-rate; but this has not been directly tried on living corals in the field. I have tested it indirectly on one or two recent corals the annual linear growth-rate of which is fairly well known, and to my gratification found that the number of ridges on the epitheca of the living West Indian scleractinian *Manicina areolata* (Fig. 5) hovers around 360 in the space of a year's growth. This strongly suggests, subject to experimental confirmation, that the growth-lines are diurnal or circadian in nature. It may be noted in passing that they may provide a much more sensitive caliper for measurement of annual growth-rates than the larger yearly annulations.

The next step, of course, is an attempt to determine the number of growth-lines per annum in fossil corals. Here, as is usually the case, hypothesis is easier than practice. Few fossil corals are sufficiently well preserved to show clearly the supposed diurnal growth-lines, and it is not easy to determine the annual rate. In epithecate recent corals the growth-lines are commonly abraded or corroded even before death of the polyp. The best of the limited fossil material I have examined so far is from the Middle Devonian of New York and Ontario, especially specimens of *Heliophyllum*, *Eridophyllum* (Fig. 6) and *Favosites*. Diurnal and annual growth-rates vary in the same individual, adding to the complexity, but in every instance there are more than 365 growth-lines per annum, usually about 400, ranging between extremes of 385 and 410. It is probably too much, considering the crudity of these data, to expect a narrower range of values for the number of days in a year in the Middle Devonian; many more measurements will be necessary to refine them.

A few more data may be mentioned: *Lophophyllidium* from the Pennsylvanian (Conemaugh) of western Pennsylvania gave 390 lines per annum, and *Caninia* from the Pennsylvanian of Texas, 385. These results imply that the number of days a year has decreased with the passage of time since the Devonian, as postulated by astronomers, and hence that values of the isotopic dates of the geophysicists agree well with the astronomical estimates of the age of the Earth. It is not claimed that coral growth proves that either is right; but it is suggested that palaeontology may well be able to supply a third stabilizing, and much cheaper, clue to the problem of geochronometry, and that further search for diurnal or circadian records in groups other than corals may result in strengthening this weak anthozoan prop.

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OBITUARIES

Prof. H. Graham Cannon, F.R.S.

HERBERT GRAHAM CANNON, Beyer professor of zoology in the University of Manchester, died in St. Bartholomew's Hospital on January 6 at the age of sixty-five. He had been in poor health for some time.

Born in London, Graham Cannon was educated at Wilson's Grammar School, Camberwell, and Christ's College, Cambridge. Having suffered compound fractures of his wrists during a fall in his youth, he was declared unfit for military service, and on graduation in 1918 became biologist to the then Board of Fisheries. A brief

period of research at Cambridge soon followed, and in 1920 he was appointed demonstrator, and later lecturer, in zoology in the Imperial College of Science and Technology. In 1926 he became professor of zoology in the University of Sheffield, and in 1931 Beyer professor of zoology in the University of Manchester. He was elected a Fellow of the Royal Society in 1935.

Graham Cannon's early zoological work, influenced by Doncaster, concerned the spermatogenesis of lice and the nature of the centrosomal force, but he soon turned to an active interest in the Crustacea, which was to last for the greater part of his life. At first his work consisted of