The Great Piltdown Hoax

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HEN Drs. J. S. Weiner, K. P. Oakley, and W. E. Le Gros Clark (1) recently announced that careful study had proven the famous Piltdown skull to be compounded of both recent and fossil bones, so that it is in part a deliberate fraud, one of the greatest of all anthropological controversies came to an end. Ever since its discovery, the skull of "Piltdown man" —termed by its enthusiastic supporters the "dawn man" and the "earliest Englishman"—has been a veritable bone of contention. To place this astounding and inexplicable hoax in its proper setting, some account of the facts surrounding the discovery of the skull and of the ensuing controversy seems in order.

Charles Dawson was a lawyer and an amateur antiquarian who lived in Lewes, Sussex. One day, in 1908, while walking along a farm road close to nearby Piltdown Common, he noticed that the road had been repaired with peculiar brown flints unusual to that region. These flints he subsequently learned had come from a gravel pit (that turned out to be of Pleistocene age) in a neighboring farm. Inquiring there for fossils, he enlisted the interest of the workmen, one of whom, some time later, handed Dawson a piece of an unusually thick human parietal bone. Continuing his search of the gravel pit, Dawson found, in the autumn of 1911, another and larger piece of the same skull, belonging to the frontal region. His discoveries aroused the interest of Sir Arthur Smith Woodward, the eminent paleontologist of the British Museum. Together, during the following spring (1912), the two men made a systematic search of the undisturbed gravel pit and the surrounding spoil heaps; their labors resulted in the discovery of additional pieces of bone, comprising-together with the fragments earlier recovered by Dawson-the larger part of a remarkably thick human cranium or brain-case and the right half of an apelike mandible or lower jaw with two molar teeth in situ (2). Continued search of the gravel pit yielded, during the summer of 1913, two human nasal bones and fragments of a turbinate bone (found by Dawson), and an apelike canine tooth (found by the distinguished archeologist, Father Teilhard de Chardin) (3). All these remains constitute the find that is known as Piltdown I.

Dawson died in 1916. Early in 1917, Smith Woodward announced the discovery of two pieces of a second human skull and a molar tooth (4). These form the so-called Piltdown II skull. The cranial fragments are a piece of thick frontal bone representing an area absent in the first specimen and a part of a somewhat thinner occipital bone that duplicates an area recovered in the first find. According to Smith Woodward's account, these fragments were discovered by Dawson early in 1915 in a field about two miles from the site of the original discovery.

The first description of the Piltdown remains, by Smith Woodward at a meeting of the Geological Society of London on December 18, 1912 (2), evoked a controversy that is probably without equal in the history of paleontological science and which raged, without promise of a satisfactory solution, until the studies of Weiner, Oakley, and Clark abruptly ended it. With the announcement of the discovery, scientists rapidly divided themselves into two main camps representing two distinctly different points of view (with variations that need not be discussed here) (5).

Smith Woodward regarded the cranium and jaw as belonging to one and the same individual, for which he created a new genus, *Eoanthropus*. In this monistic view toward the fragments he found ready and strong support. In addition to the close association within the same gravel pit of cranial fragments and jaw, there was advanced in support of this interpretation the evidence of the molar teeth in the jaw (which were flatly worn down in a manner said to be quite peculiar to man and quite unlike the type of wear ever found in apes) and, later, above all, the evidence of a second, similar individual in the second set of skull fragments and molar tooth (the latter similar to those imbedded in the jaw and worn away in the same unapelike manner). A few individuals (Dixon [6], Kleinschmidt [7], Weinert [8]), moreover, have even thought that proper reconstruction of the jaw would reveal it to be essentially human, rather than simian. Reconstructions of the skull by adherents to the monistic view produced a brain-case of relatively small cranial capacity, and certain workers even fancied that they had found evidences of primitive features in the brain from examination of the reconstructed endocranial cast (9, 10)—a notoriously unreliable procedure; but subsequent alterations of reconstruction raised the capacity upward to about 1400 cc-close to the approximate average for living men (10, p. 596).

A number of scientists, however, refused to accept the cranium and jaw as belonging to one and the same kind of individual. Instead, they regarded the brain-case as that of a fossil but modern type of man and the jaw (and canine tooth) as that of a fossil anthropoid ape which had come by chance to be associated in the same deposit. The supporters of the monistic view, however; stressed the improbability of

the presence of a hitherto unknown ape in England during the Pleistocene epoch, particularly since no remains of fossil apes had been found in Europe later than the Lower Pliocene. An anatomist, David Waterston, seems to have been the first to have recognized the extreme morphological incongruity between the cranium and the jaw. From the announcement of the discovery he voiced his disbelief in their anatomical association (11, p. 150). The following year (1913) he demonstrated that superimposed tracings taken from radiograms of the Piltdown mandible and the mandible of a chimpanzee were "practically identical"; at the same time he noted that the Piltdown molar teeth not only "approach the ape form, but in several respects are identical with them." He concluded that since "the cranial fragments of the Piltdown skull, on the other hand, are in practically all their details essentially human . . . it seems to me to be as inconsequent to refer the mandible and the cranium to the same individual as it would be to articulate a chimpanzee foot with the bones of an essentially human thigh and leg" (12).

In 1915, Gerrit Miller, curator of mammals at the United States National Museum, published the results of a more extensive and detailed study of casts of the Piltdown specimens in which he concluded that the jaw is actually that of a fossil chimpanzee (13). This view gradually gained strong support, e.g., from Boule (14) and Ramström (15). Miller, furthermore, denied that the manner of wear of the molar teeth was necessarily a peculiarly human one; he stated that it could be duplicated among chimpanzees. That some other workers (Friederichs [16]; Weidenreich [17]) have ascribed the jaw to a fossil ape resembling the orangutan, rather than to a chimpanzee, is unimportant. What is important, in the light of recent events, is that the proponents of the dualistic theory agreed in pronouncing the jaw as that of an anthropoid ape, and as unrelated to the cranial fragments. Piltdown II remained a problem; but there was some ambiguity about this discovery, which was announced after the death of Dawson "unaccompanied by any direct word from him" (5). Indeed, Hrdlička (18), who studied the original specimens, felt convinced that the isolated molar tooth of Piltdown II must have come from the original jaw and that there was probably some mistake in its published history.

A third and in a sense neutral point of view held that the whole business was so ambiguous that the Piltdown discovery had best be put on the shelf, so to speak, until further evidence, through new discoveries, might become available. I have not attempted anything resembling a thorough poll of the literature, but I have the distinct impression that this point of view has become increasingly common in recent years, as will be further discussed. Certainly, those best qualified to have an opinion, especially those possessing a sound knowledge of human and primate anatomy, have held largely—with a few notable exceptions either to a dualistic or to a neutral interpretation of the remains, and hence have rejected the monistic interpretation that led to the reconstruction of a "dawn man." Most assuredly, and contrary to the impression that has been generally spread by the popular press when reporting the hoax, "Eoanthropus" has remained far short of being universally accepted into polite anthropological society.

An important part of the Piltdown controversy related to the geological age of the "Eoanthropus" fossils. As we shall see, it was this aspect of the controversy that eventually proved to be the undoing of the synthetic Sussex "dawn man." Associated with the primate remains were those of various other mammals, including mastodon, elephant, horse, rhinoceros, hippopotamus, deer, and beaver (2). The Piltdown gravel, being stream-deposited material, could well contain fossils of different ages. The general opinion, however, seems to have been that it was of the Lower Pleistocene (some earlier opinions even allocated it to the Upper Pliocene), based on those of its fossils that could be definitely assigned such a date (2). The age of the remains of "Piltdown man" thus was generally regarded as Lower Pleistocene, variously estimated to be from 200,000 to 1,000,000 years (19). To the proponents of the monistic, "dawn-man" theory, this early dating sufficed to explain the apparent morphological incongruity between cranium and lower jaw.

In 1892, Carnot, a French mineralogist, reported that the amount of fluorine in fossil bones increases with their geological age-a report that seems to have received scant attention from paleontologists. Recently, K. P. Oakley, happening to come across Carnot's paper, recognized the possibilities of the fluorine test for establishing the relative ages of bones found within a single deposit. He realized, furthermore, that herein might lie the solution of the vexed Piltdown problem. Consequently, together with C. R. Hoskins, he applied the fluorine test to the "Eoanthropus" and other mammalian remains found at Piltdown (20). The results led to the conclusion that "all the remains of *Eoanthropus* ... are contemporaneous"; and that they are, "at the earliest, Middle Pleistocene." Howover, they were strongly indicated as being of late or Upper Pleistocene age, although "probably at least 50,000 years" old (19). Their fluorine content was the same as that of the beaver remains but significantly less than that of the geologically older, early Pleistocene mammals of the Piltdown fauna. This seemed to increase the probability that cranium and jaw belonged to one individual. But at the same time, it raised the enigma of the existence in the late Pleistocene of a human-skulled, large-brained individual possessed of apelike jaws and teeth-which would leave "Eoanthropus" an anomaly among Upper Pleistocene men. To complete the dilemma, if cranium and jaw were attributed to two different animals-one a man, the other an ape-the presence of an anthropoid ape in England near the end of the Pleistocene appeared equally incredible. Thus the abolition of a Lower Pleistocene dating did not solve the Piltdown problem. It merely produced a new problem that was even more disturbing.

As the solution of this dilemma, Dr. J. S. Weiner advanced the proposition to Drs. Oakley and Clark that the lower jaw and canine tooth are actually those of a modern anthropoid ape, deliberately altered so as to resemble fossil specimens. He demonstrated experimentally, moreover, that the teeth of a chimpanzee could be so altered by a combination of artificial abrasion and appropriate staining as to appear astonishingly similar to the molars and canine tooth ascribed to "Piltdown man." This led to a new study of all the "Eoanthropus" material that "demonstrated quite clearly that the mandible and canine are indeed deliberate fakes" (1). It was discovered that the "wear" of the teeth, both molar and canine, had been produced by an artificial planing down, resulting in occlusal surfaces unlike those developed by normal wear. Examination under a microscope revealed fine scratches such as would be caused by an abrasive. X-ray examination of the canine showed that there was no deposit of secondary dentine, as would be expected if the abrasion had been due to natural attrition before the death of the individual.

An improved method of fluorine analysis, of greater accuracy when applied to small samples, had been developed since Oakley and Hoskins made their report in 1950. This was applied to the Piltdown specimens. The results of these new estimations, based mainly on larger samples, are given in the first and second columns of the accompanying table. Little elaboration is necessary. The results clearly indicate that whereas the Piltdown I cranium is probably Upper Pleistocene in age, as claimed by Oakley and Hoskins, the attributed mandible and canine tooth are "quite modern." As for Piltdown II, the frontal fragment appears to be Upper Pleistocene (it probably belonged originally to Piltdown I cranium), but the occipital fragment and the isolated molar tooth are of recent or modern age. The foregoing conclusions are supported by evidence concerning the organic content of the specimens, as determined by analysis of their nitrogen content. This method is not as conclusive as fluorine analysis: but its results, given in the third column of the accompanying table, provide additional support for the conclusions arrived at by the fluorine-estimation method. In general, as would be expected, the nitrogen content decreases with age; the only specimen that falls out of line is the occipital of Piltdown II.

Weiner, Oakley, and Clark also discovered that the mandible and canine tooth of Piltdown I and the occipital bone and molar tooth of Piltdown II had been artificially stained to match the naturally colored Piltdown I cranium and Piltdown II frontal. Whereas these latter cranial bones are all deeply stained, the dark color of the faked pieces is quite superficial. The artificial color is due to chromate and iron. This aspect of the hoax is complicated by the fact that, as recorded by Smith Woodward (21), "the colour of the pieces which were first discovered was altered a little by Mr. Dawson when he dipped them in a solution of bichromate of potash in the mistaken idea that this would harden them." The details of the staining, which conTABLE 1. Fluorine content, ratio of fluorine to phosphorus pentoxide, and nitrogen content of the bones and teeth of the so-called Piltdown I and Piltdown II skulls, compared with those of various Upper Pleistocene and Recent bones and teeth. From Weiner, Oakley, and Clark (1), rearranged.

	% F	$\frac{\% \mathrm{F} \times 100}{\% \mathrm{P}_{2}\mathrm{O}_{5}}$	% N
Upper Pleistocene			
Bones (local) (minimum F			
content)	0.1	0.4	
Teeth, dentine (minimum			
F content)	0.1	0.4	
Bone (London)			0.7
Equine molar, dentine			
(Piltdown)			1.2
Human molar, dentine			
(Surrey)			0.3
Recent			
Neolithic bone (Kent)			1.9
Fresh bone			4.1
Chimpanzee molar,			
dentine	< 0.06	< 0.3	3.2
Piltdown I	•	-	
Cranium	0.1	0.8	1.4
Mandible, bone	< 0.03	< 0.2	3.9
Mandibular molar, dentine	$\gtrsim 0.04$	< 0.2	4.3
Canine	< 0.03	$\gtrsim 0.2$	5.1
Piltdown II	•	•	
Frontal bone	0.1	0.8	1.1
Occipital bone	0.03	0.2	0.6
Isolated molar, dentine	< 0.01	< 0.1	4.2

firm the conclusions arrived at by microscopy, fluorine analysis, and nitrogen estimation, need not be entered into here.

In conclusion, therefore, the disjecta membra of the Piltdown "dawn man" may now be allocated as follows: (1) the Piltdown I cranial fragments (to which should probably be added Piltdown II frontal) represent a modern type of human brain-case that is in no way remarkable save for its unusual thickness and which is, at most, late Pleistocene in age; (2) Piltdown I mandible and canine tooth and Piltdown II molar tooth are those of a modern anthropoid ape (either a chimpanzee or an orangutan) that have been artificially altered in structure and artificially colored so as to resemble the naturally colored cranial piecesmoreover, it is almost certain that the isolated molar of Piltdown II comes from the original mandible, thus confirming Hrdlička's (18) earlier suspicion; and (3) Piltdown II occipital is of recent human origin, with similar counterfeit coloration.

Weiner, Oakley, and Clark conclude that "the distinguished palaeontologists and archaeologists who took part in the excavations at Piltdown were the victims of a most elaborate and carefully prepared hoax" that was "so extraordinarily skilful" and which "appears to have been so entirely unscrupulous and inexplicable, as to find no parallel in the history of palaeentological discovery."

It may be wondered why forty years elapsed before

the hoax was discovered. Two factors enter here: first, there was no reason at all to suspect the perpetration of a fraud, at least, not until fluorine analysis indicated the relative recency of all the specimens, thus making the association of a human cranium and an anthropoid-ape jaw, either anatomically or geologically, hardly credible; and, second, methods for conclusively determining whether the specimens were actual fossils or faked ones, short of their wholesale destruction, were developed only in recent years (it will be recalled that even the fluorine-estimation method used by Oakley and Hoskins a few years ago was inadequate for detecting a significant difference between brain-case and jaw). It is of interest to note that Dawson, in his original report (2), stated: "A small fragment of the skull has been weighed and tested by Mr. S. A. Woodhead, M.Sc., F.I.C., Public Analyst for East Sussex & Hove, and Agricultural Analyst for East Sussex. He reports that the specific gravity of the bone (powdered) is 2.115 (water at 5° C. as standard). No gelatine or organic matter is present. There is a large proportion of phosphates (originally present in the bone) and a considerable proportion of iron. Silica is absent." This statement obviously refers to the brain-case alone; for, in both the title and text of the original report the authors spoke of "skull and mandible" (italics mine). One cannot help but wonder what might have come to pass if samples of the jaw and teeth had also been submitted to chemical analysis, even though the present, more refined methods were not then available.

The ready initial acceptance of the Piltdown discovery at its face value, at least by a majority of interested scientists, can probably be attributed to the philosophical climate that invested the problem of human evolution at that time. In September, 1912, before the announcement of the discovery of "Piltdown man," the distinguished anatomist, Elliot Smith, in an address before the Anthropological Section of the British Association for the Advancement of Science at Dundee (22), expressed a prevailing point of view when he developed the theory that the brain led the way in the evolution of man and that modification of other parts of the body followed. Thus the stage was set for the ready acceptance of the Piltdown fragments as constituting a single individual, a "dawn man" possessing a human cranium housing a human brain, but with phylogenetically laggard, hence simian. jaws and teeth. To quote the paleontologist, Sollas (23): "The surprise which was first excited by what appeared to be a monstrous combination disappears on further reflection. Such a combination had, indeed, been long previously anticipated as an almost necessary stage in the course of human development. . . . In Eoanthropus Dawsoni we seem to have realised precisely such a being ..., one, that is, which had already attained to human intelligence but had not yet wholly lost its ancestral jaws and fighting teeth." And, as Sir Arthur Keith, perhaps the most vocal champion of "Eoanthropus," argued in supporting this view: "... before the anthropoid characters would disappear from the body of primal man, the brain, the master organ of the human body, must first have come into its human estate. Under its dominion the parts of the body such as the mouth and hands, the particular servants of the brain, became adapted for higher uses. Looking at the problem from this point of view, we cannot reject the Piltdown mandible because as regards the mylo-hyoid ridge it is simian and not human in character" (10).

Recent finds of fossil men and other primates, however, indicate that it is the brain that was the evolutionary laggard in man's phylogeny; indeed, the studies of Tilly Edinger (24) of the phylogeny of the horse brain suggest that this may well be a general rule in mammalian evolution. It was such concepts as this, leading to a change in philosophical climate, that evoked an increasing skepticism toward the validity of the monistic interpretation of the Piltdown fragments and led in turn to what appears to have been the prevailing recent opinion, namely, that the fragments should, as expressed in 1949 by Le Gros Clark (25), "be laid aside without further comment until more evidence becomes available." This view, enhanced by the redating of the remains by Oakley and Hoskins. provided the proper psychological setting for the coup de grâce delivered by Weiner, Oakley, and Clark.

As the three latter point out, the solution of the Piltdown enigma greatly clarifies the problem of human evolution. For "Eoanthropus," both morphologically and geologically, just simply did not fit into the picture of human evolution that has gradually been unfolding as the result of paleontological discoveries throughout the world.

The Piltdown story is a significant one in the history of ideas, more particularly as it bears on the concept of the precise course of human evolution. For, if man's biological history be likened to a book, it is seen to be composed of both blank and written pages and, by those who note them carefully, many if not most of the written ones will be seen to be in the nature of palimpsests-pages that have been rewritten after their original writing has been rubbed out. Of this, the Piltdown affair is a striking demonstration. It is a demonstration, furthermore, that the palimpsest nature of the pages of man's history is not always due directly to new fossil discoveries but can also result from changes in the philosophical climate of the science. That this phenomenon is peculiar to anthropology, however, is seriously to be doubted.

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A Differential Ability of Strains of Tobacco Mosaic Virus to Bind Host-Cell Nucleoprotein¹

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NE OF THE PROBLEMS facing workers engaged in the purification of viruses and other proteins is the tendency for these large molecules to associate with other substances derived from the host tissue. It is recognized that a virus can form complexes with a wide range of substances (1, 2). Some of these complexes are rather stable whereas others are easily dissociable. Several examples of complexes between plant or animal viruses and host cell constituents have been cited by Pirie (2), who pointed out that such combinations are of limited interest unless they can be shown to be specific or related to some biological process or property. Tobacco mosaic virus (TMV) is particularly notorious in that different methods of purification yield preparations of varying degrees of color.

It is the purpose of this paper to report a selective ability of certain strains of TMV to form a stable complex with a nucleoprotein derived from the host cells, and to describe the conditions under which the complex may be dissociated.

It has been found possible to assign the strains of TMV being investigated in this laboratory into groups on the basis of biological, physical-chemical, and serological methods (3). Viruses of Group I are differentiated from each other by the symptoms they cause in Nicotiana tabacum and serologically, but the strains are indistinguishable with respect to the following characteristics: electrophoretic mobility, isoelectric point, ultraviolet absorption spectrum, and rate of inactivation by ultraviolet radiation. The strains within Group II are distinguishable also by symptoms and serology and are indistinguishable from each other by the above criteria, but the characteristics of the latter strains are sharply differentiated from the Group I viruses.

It is noteworthy that strains within Group I, of which common TMV is an example, are uniformly obtained as clear amber pellets on purification by ultracentrifugation in cacodylate buffer, whereas strains of Group II are colorless after the same treatment. The color remains associated with Group I viruses even after they are precipitated with acids or ammonium sulfate, or dialyzed at length against monovalent buffer salts in the range of pH 5-8 (e.g., acetate, cacodylate, and Veronal). The virus-color complex withstands freezing and thawing, and also precipitates as a complex when reacted with homologous antiserum. It cannot be dissociated by electrophoresis or by repeated ultracentrifugation. By these criteria the colored substance appears to be rather firmly bound to the virus molecule.

The virus-color complex can, however, be dissociated by exposure to various di- and polyvalent anions. The phenomenon was first noted in the course of attempts to remove the color enzymically. It was observed that virus in the control tubes, which was suspended in phosphate buffer during incubation, was obtained in nearly colorless pellets on centrifugation. Subsequent experiments showed that although the colored material after removal from the virus by phosphate treatment is readily separated by centrifugation, it cannot be separated by dialysis. Phosphate has been used in most of our investigations, although the effect is not limited to this ion.

After preliminary experiments indicated that the decolorization is not instantaneous at room temperature, the effect of temperature on the rate of the dissociation was studied. Clear amber pellets of strain

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