COMMENTARY

Hippocampus Minor and Man's Place in Nature: A Case Study in the Social Construction of Neuroanatomy

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ABSTRACT

In mid-19th century Britain the possibility of evolution and particularly the evolution of man from apes was vigorously contested. Among the leading antievolutionists was the celebrated anatomist and paleontologist Richard Owen and among the leading defenders of evolution was Thomas Henry Huxley. The central dispute between them on human evolution was whether or not man's brain was fundamentally unique in having a hippocampus minor (known today as the calcar avis), a posterior horn in the lateral ventricle, and a posterior lobe. The author considers the background of this controversy, the origin and fate of the term hippocampus minor, why this structure became central to the question of human evolution, and how Huxley used it to support both Darwinism and the political ascendancy of Darwinians. The use of ventricular structures to distinguish humans from other animals appears to reflect an importance given to the ventricles that stretches back to ancient Greek medicine. This account illustrates both the extraordinary persistence of ideas in biology and the role of the political and social matrix in the study of the brain.

Key words: history of neuroscience, evolution, Thomas Henry Huxley, calcar avis

EVOLUTION AND VICTORIAN POLITICS

For several decades before the publication of The Origin of Species in 1859, debate raged in Britain over the possibility of the transmutation of species and, especially, of an ape origin for man. J.-B. Lamarck (1809) elaborated the first coherent theory of evolution and unambiguously included man. He thought that evolution involved continuous upward progress, an inevitable transformation of lower into upper forms. This progressivism as well as his materialism and his belief in the inheritance of acquired characteristics made Lamarck very appealing to the London and Edinburgh radicals of the day. They took his idea that biological evolution implies progress and improvement and applied it to society to demand social evolution and social progress in the form of such transformations as the end of aristocratic and established church privilege, the introduction of universal suffrage, reform of medical care and medical education (many were physicians), education for women, and similar radical reformist notions. And correspondingly, the conservative Oxbridge scientist-clergy-men that dominated early Victorian science saw Lamarck as a direct threat to the established order of church and state (Desmond, 1989).

Evolutionary ideas and their radical political and theological implications became more widespread with the publication in 1844 of Vestiges of the Natural History of Creation by Robert Chambers, a scientific amateur who published anonymously because of the very real threats of blasphemy laws and economic and political persecution (Gruber, 1974). Vestiges argued for both cosmic and biological evolution and adopted Lamarck's idea that evolution implied improvement. Chambers' arguments for biological evolution included the location of simpler fossils in older strata, the fundamentally similar anatomical organization of all groups of animals, and the tendencies of embryos to go through stages similar to their putative ancestors. Vestiges was a sensational bestseller, with 24,000 copies sold in the next 10 years compared to 9,500 for the Origin over a similar period. That Chambers was a successful publisher, expert in marketing popular science, undoubtedly helped (Ruse, 1979; Mayr, 1982; Seacord, 1989).

The scientific establishment reacted rather violently to Vestiges. Adam Sedgwick, the professor of geology at Cambridge, president of the Geological Society, and a future president of the British Association for the Advancement of Science, wrote more than a 500 page review (Sedgwick, 1850) of this "beastly book" to place "an iron heel upon the head of the filthy abortion and put an end to its crawlings" in which he made clear that the problem with Vestiges was not merely scientific: "The world cannot bear to be turned
upside down . . . I can see nothing but ruin and confusion in such a creed . . . If current in society it will undermine the whole moral and social fabric and inevitably will bring discord and deal mischief in its train . . ." In a letter to Charles Lyell he went further, "if the book be true . . . religion is a lie; human law is a mass of folly, and a base injustice; morality is moonshine; our labours for the black people of Africa were the works of madmen . . ." (Young, 1970a).

In spite of the establishment attacks on it, Vestiges was a popular success, so much so that Disraeli (1847) parodied its fashion in middle class salons in his novel Tancred. Vestiges gave ammunition to the radicals and socialists who used its arguments of biological progress to demand social progress (Young, 1970a; 1973; Desmond, 1992). Chambers certainly made many factual errors and uncritical speculations in Vestiges, and yet, as Mayr (1982) wrote "it was he who saw the forest where all the great British scientists of his period (except Darwin) only saw the trees." Chambers’ book helped make both the scientific and lay world ready for the far more fashionable in middle class salons in his novel popular success, first heated argument that in turn implied materialism and social transformation, thereby threatening the established church and state. In the years before the publication of the Origin, Linnaeus had put men, apes, monkeys, and lemurs (and bats) into a single order, Primates. This grouping, minus bats, was subsequently accepted by most zoologists. Owen now rejected this dominant tradition and placed man apart from all other primates and indeed from all other mammals in a separate subclass, the Archontotheria (“ruling brain”). He did so on three anatomical criteria, all of them concerning the brain. Presumably, he chose brain structures because of the mental uniqueness and superiority of man. To strengthen his argument for the lack of continuity between man and animals, he argued that these three structures were actually found exclusively in humans, rather than merely being larger or different than in animals. He sought a truly qualitative difference between man and beast and he wanted it based on anatomical science.

The first fundamental difference between humans and animals claimed by Owen was that only in man does the "posterior lobe" (i.e., the posterior of the cerebral cortex) extend beyond the cerebellum. He supported this supposed uniqueness of man with illustrations contrasting the brain of a chimpanzee with that of a "Negro." (Comparisons of African to ape brains was common in the 19th and early 20th century because the prevailing opinion of zoologists and anthropologists was that they were the "lowest" race and therefore the most appropriate comparison to animals. The most often illustrated non-white brain was that of the famous "Hottentot Venus," who was exhibited in London and Paris and described in detail by many of the leading anatomists of the day, including Paul Broca and Georges Cuvier, both when she was alive and after her death and dissection [Tiedemann, 1836; Gould, 1981].)

The second difference proposed by Owen was that only humans have a posterior horn or cornu in their lateral ventricles. The third and most important difference was that only man has a hippocampus minor. These extraordinary claims were supported by no citations to the literature, no brain sections, and no illustrations other than those just mentioned. Near the end of the paper, just in case the reader overlooked the importance of the missing hippocampus minor and the other supposed deprivations of the animal brain, Owen wrote "Thus [man] fulfills his destiny as the supreme master of this earth and of the lower creation."

In the following section I describe what the hippocampus
HIPPOCAMPUS MINOR

The term "hippocampus minor" continues to be used interchangeably until the later part of the 19th century, when the latter term disappeared, having been officially expunged in the 1895 *Nomina Anatomica* (Lewis, 1923). This disappearance may have been related to the ridicule and controversy that swirled around the term in the debates I am about to relate. At this time "hippopotamus" returned for "hippocampus" but now in jest as in Charles Kingsley's (1863) *Water Babies*. The contrasting designation "hippocampus major" for what is now called the hippocampus lingered for a few more years, and then also fell out of use. Whereas the hippocampus minor was virtually absent from anatomy textbooks by the turn of the century, it survived in more conservative sources, dictionaries (e.g., *Webster's New International Dictionary*, 2nd ed., 1957) and encyclopedias (e.g., *Encyclopedia Britannica*, 13th ed., 1926).

Before returning to the fate of Owen's proposals for the hippocampus minor it may be helpful to summarize the state of contemporary knowledge of brain function. The year 1858 can be viewed as a period after the fertilization but before the birth of modern neuroscience. The phrenological movement initiated by Gall and Spurzheim at the turn of the century had popularized the idea of the cerebrum as a collection of organs...
with different psychological functions and focused attention on the functions of the cerebral cortex (Young, 1970b; Gross, 1987a). Gall’s errors of equating skull features with brain morphology had been realized in the scientific community, and the search for correlations between the size of cerebral damage and symptom had begun in man and animal. Flourens’ experimental work on pigeons and other animals in the 1820s had simultaneously demolished the extreme localization of phrenology and made the idea of more limited localization of function readily acceptable (Young, 1970b). At the time of Owen’s paper, there was no convincing evidence for the specific functions of any portion of the mammalian cerebrum; the hippocampus minor was no more a terra incognita than any other area.

In the years immediately after Owen’s paper, there were three crucial events in the development of understanding brain function. The first was Broca’s demonstration in 1861 of an area critical for speech in the left frontal lobe. It was the first generally accepted localization of psychological function in the human brain, and it was viewed at the time as a vindication of Gall. The second was Fritsch and Hitzig’s production of specific movements by electrical stimulation of discrete motor centers of the cortex in 1870. The third was the discovery of the sensory areas of the cortex that soon followed (Young, 1970b; Gross, 1987b).

T. H. HUXLEY AS YOUNG BULLDOG

Thomas Henry Huxley was 21 years Owen’s junior and was hostile to him almost from the beginning of his scientific career. In 1850, Huxley had just returned from a 4-year voyage aboard the HMS Rattlesnake. Unlike Darwin, on the Beagle as a gentleman naturalist, Huxley had been a lowly assistant surgeon and the research he did was on his own time. It was good enough, particularly that on coelenterates, that he was elected to the Royal Society in 1851. Yet, for several years after returning, he was without a job or research funds (and had a fiancée waiting in Australia) (Huxley L, 1900; Mitchell, 1901; Desmond, 1984).

In this period, Owen supported Huxley’s candidacy for the Royal Society and wrote several letters of recommendation for him for various teaching or research posts. At the end of 1852, Huxley wrote Owen for yet another letter of recommendation, this time to the navy. When Owen failed to answer in the next 10 days, Huxley wrote again, and still did not receive an answer. Four days later they happened to meet and Huxley described the meeting in a letter in a way that nicely epitomizes the personalities of the junior and senior scientist:

Of course I was in a considerable rage . . . I was going to walk past, but he stopped me, and in the bluest and most gracious manner said, ‘I have received your note. I shall grant it.’ The phrase and the implied condescension were quite ‘touching,’ so much that if I stopped for a moment longer I must knock him into the gutter. I therefore bowed and walked off. (Desmond, 1984, p. 26)

Owen sent the recommendation a few days later and the navy gave Huxley funds to complete publication of his research from the voyage. Yet in this period Huxley repeatedly attacked Owen, but only privately, writing, for example, that “Owen is both feared and hated” and that “he felt it necessary always to be on guard against him.” He even thought that Owen was blocking publication of his papers and taking his grant money, both charges were apparently without any justification. Huxley wrote to his sister in 1852, “Let him [Owen] beware. On my subjects I am his master and am quite ready to fight . . . And although he has a bitter pen . . . I can match him . . .” (Huxley L, 1900; Desmond, 1984).

In 1854, Huxley got a position teaching natural history at the Government School of Mines. (He kept it for another 30 years, eventually turning down chairs at Oxford and Harvard, among other places. By this time the Government School had become the Royal School of Science and would eventually become Imperial College (Bibby, 1959).) No longer needing job references from Owen, Huxley’s attacks on him became more public. Huxley’s scientific critiques of Owen in the late 1850s included ones on the subjects of parthenogenesis, on the presence of an anus in a group of brachiopods, on Owen’s classification of the Invertebrates, and on his comparative anatomy textbook (e.g., Huxley, 1851, 1855, 1856a, 1856b). With Owen in the chair, Huxley’s (1859) Croonian lecture to the Royal Society was a violent critique of Owen’s theory that the skull is composed of fused vertebrae. This was part of Owen’s (1848) theory of archetypes, the idea that there was a basic pattern to which all vertebrates conformed. This theory largely derived from the idealistic morphology of Naturphilosophie whose origin was the Platonic Romanticism of Goethe and Schiller (Nordenskiold, 1928; MacLeod, 1965). Contemporary skull nomenclature stems from this effort of Owen.

The final personal breach between Huxley and Owen came in 1857 when Owen gave a successful series of lectures on paleontology at the Government School of Mines. Owen listed himself as Professor of Comparative Anatomy and Paleontology in the School of Mines. Huxley was infuriated at this intrusion into his territory and complained, “Mr. Owen holds no appointment whatever at the Govt. School of Mines, and as I am the Professor of General Natural History (which includes Comparative Anatomy and Paleontology) in that Institution you will observe that the statement . . . is calculated to do me injury.” To a friend, Huxley wrote “I have now done with him, personally. I would as soon acknowledge a man who had attempted to obtain my money on false pretenses” (Desmond, 1984; DiGregorio, 1984).

Although scientific controversy tended to be much more openly nasty in Victorian England than today, the Owen and Huxley antagonism was extreme even by standards of the time and it had far from peaked at the time of this territorial dispute. Huxley’s youthful arrogance, hot temper, and anti-clericalism and Owen’s stubbornness, superciliousness, and religiosity served to exaggerate their scientific differences. The fact that both came from lower middle class backgrounds and that Owen eagerly sought and Huxley tended to resist social ascent probably further exacerbated their differences. Of course, in a few decades the amateur naturalist-clergymen Oxbridge establishment would give way to the professional scientist establishment with the Right Honorable Huxley at its very center (Desmond, 1984).

By the end of the 1850s, under Darwin’s tutorial, Huxley was gradually accepting the idea of transmutation and what
it implied about the origin of mankind; his prepublication reading of the Origin finally made him a total convert to the idea of evolution. Like most of Darwin’s contemporaries, Huxley never really accepted and probably never grasped Darwin’s core contribution, the concept of natural selection operating on random variation (Huxley L, 1900; Ruse, 1979; Mayr, 1982; Darwin, 1991).

OXFORD MEETING OF THE BRITISH ASSOCIATION, 1860

The 1860 meeting of the British Association for the Advancement of Science in Oxford was the first after the publication of the Origin of Species and, as a result, interest in it was high among the lay and scientific public. As had become his custom for virtually all public scientific meetings because of his chronic illness, Darwin did not attend, but eagerly awaited news, particularly from his closest colleagues, Huxley and the botanist J. D. Hooker (Darwin F, 1887).

On Thursday, June 28, the opening day of the meeting, after a paper “On the Final Causes of the Sexuality of Plants with Particular Reference to Mr. Darwin’s Work,” the chair called on Huxley for his comments. According to a report in The Athenaeum (July 7, 1860), the leading contemporary intellectual weekly, Huxley declined to comment because he “felt a general audience in which sentiment would unduly interfere with intellect, was not the public before which such a discussion should be carried out.” Owen then asked for the floor to present facts “by which the public could come to some conclusions . . . of the truth of Mr. Darwin’s theory.” He then repeated his argument that “the brain of the gorilla was more different from that of man than from that of the lowest primate particularly because only man had a posterior lobe, a posterior horn, and a hippocampus minor.” Hence the descent of man from the apes, a crucial implication of Darwin’s theory should be carried out.” Owen then asked for the floor to present facts “by which the public could come to some conclusions . . . of the truth of Mr. Darwin’s theory.” He then repeated his argument that “the brain of the gorilla was more different from that of man than from that of the lowest primate particularly because only man had a posterior lobe, a posterior horn, and a hippocampus minor.” Hence the descent of man from the apes, a crucial implication of Darwin’s ideas, was impossible. Huxley rose and “denied altogether that the difference between the brain of the gorilla and man was so great” making a “direct and unqualified contradiction” of Owen. In support of his position, Huxley cited previous studies and promised to support his arguments in detail elsewhere (Huxley L, 1900). He did so repeatedly over the next 3 years.

The next day Huxley was planning to leave the meeting because Samuel Wilberforce, Bishop of Oxford and a strong antievolutionist, was rumored to be planning to “smash Darwin” and Huxley was afraid that the “promised debate would be merely an appeal to prejudice in a mixed audience before which the scientific arguments of the Bishop’s opponents would be at the utmost disadvantage.” The Bishop had a first-class degree in mathematics and that supposedly made him an authority on science. Owen was staying with Wilberforce, prepping him for the debate, just as he had helped him with a very negative review of the Origin. That afternoon Huxley ran into Robert Chambers, who by now was generally believed to be the author of the revolutionary tract on evolution, Vestiges. Upon hearing that Huxley was planning to leave, Chambers “vehemently” urged him not to “desert them.” Huxley recalls replying “Oh! if you are going to take it that way I’ll come” (Huxley L, 1900).

The following day the lecture room was packed, and when Dr. Draper from New York finished his lecture on “The Intellectual Development of Europe considered with reference to the Views of Mr. Darwin and others that the Progression of Organisms is determined by Law,” the Bishop of Oxford rose and spoke for “full half an hour . . . ridiculing Darwin badly and Huxley savagely” and in general repeating his arguments from his review of the Origin of Species. Then turning to Huxley, and referring to the clash 2 days earlier between Owen and Huxley over brain anatomy and the relatedness of man and ape “he begged to know was it through his grandfather or his grandmother that he claimed descent from a monkey?”

Huxley rose, calmly, in his memory, but “white with anger” according to others, and defended Darwin’s theory as “the best explanation of the origin of species which had yet been offered.” He concluded with the most famous repartee in the history of science, that “he was not ashamed to have a monkey for his ancestor; but he would be ashamed to be connected with a man who used great gifts to obscure the truth.” According to some reports, “as the point became clear there was a great burst of applause,” “one lady fainted and had to be carried out,” “I for one jumped out of my seat,” “no one who was present can ever forget the impression it made.”

Other speakers followed, including FitzRoy, now admiral, formerly captain of the Beagle (regretting the publication of Darwin’s book) and John Lubbock, pioneering ethologist (accepting the Darwinian hypothesis as the best available). Speaking last and at length, J. D. Hooker, Darwin’s closest confidant, gave a detailed refutation of Wilberforce and defense of Darwin using his expertise as a botanist and biogeographer.

Years later, after accounts of these events were published by Huxley’s and Darwin’s sons, the exchange between Huxley and Wilberforce took on an exaggerated mythic existence as the “great battle in the war between science and religion,” the most famous 19th century battle after Waterloo (Moore, 1979), in which Huxley committed “forensic murder” and Wilberforce “involuntary martyrdom” (Irvine, 1955). At the time, however, both Wilberforce and Huxley believed himself the victor. Furthermore, Hooker thought he, rather than Huxley, had demolished Wilberforce. The audience seems to have been divided among these three views; The Athenaeum summarized it all as “uncommonly lively.” Jensen (1991) has critically reviewed the contemporary reports, the recollections of the participants, and the large and ever growing secondary literature on this so-called “debate.”

“DARWIN’S BULLDOG” ATTACKS

Huxley had been waiting and preparing for his attack on Owen at the British Association meeting for some time. As soon as he read Owen’s (1858) new classification scheme separating humans from other primates on the basis of brain structure, Huxley began to systematically dissect monkey brains. He soon realized the magnitude of Owen’s errors and saw his opportunity to “nail . . . [Owen] . . . that mendacious humbug . . . like a kite to the barn door.” He said nothing publicly until his contradiction of Owen in the opening session of the 1860 Oxford meeting previously described. Then, as promised, he attacked Owen’s claims in print and with a vengeance. Huxley used his new journal the Natural History Re-
view as a major platform. He had just founded it as a pro-
Darwin and anticlerical (“episcopophagous”) organ (Huxley, 1866; Huxley L, 1900; Desmond, 1984).

The opening of Huxley’s campaign came in 1861 in the first issue of the Natural History Review (Huxley, 1861a). There he attacked the three claims of Owen, that only man’s cerebrum covered the cerebellum (the posterior lobe), that only man had a posterior horn in his lateral ventricle, and that only man had a hippocampus minor. He did so with a barrage of citations, quotations, and personal communications from leading anatomists in Britain and abroad. Huxley was interested in doing more than proving Owen wrong. He wanted to prove him dishonest as well. Thus, Huxley put great emphasis on quoting three particular sources that Owen must have known about and that in failing to mention them was “guilty of wilful and deliberate falsehood” (Desmond, 1984).

The first of these sources was written by Owen (1835) himself in a monograph that was a major factor in establishing Owen’s anatomical reputation and that antedated Vestiges and Owen’s antipathy to transmutation. In it Owen briefly notes that the cerebral hemispheres of the baboon and chimpanzee extend beyond the cerebellum.

The second authority was F. Tiedemann, a distinguished German anatomist from whom Owen had copied, without attribution, the “Negro brain” drawing in his classification paper. Huxley was able to quote Tiedemann (1821, 1827) describing, in infrahuman primates, the cerebrum extending beyond the cerebellum and a posterior horn in the lateral ventricle. Huxley was being a little misleading here since in the paper from which Owen obtained the drawing of the Negro brain, viz. Tiedemann (1836), the illustrations of the orangutan and chimpanzee brains actually show the cerebrum not extending beyond the cerebellum. Huxley also quickly passed over Tiedemann’s (1821) earlier failure to find a hippocampus minor in any animal other than man. (The point of Tiedemann’s 1836 paper was to argue, rather iconoclastically, for the neuroanatomical, intellectual, and moral equality of whites and blacks.)

The third source used to impugn Owen’s integrity was a paper by the Dutch anatomists J. L. C. Schroeder van der Kolk and W. Vrolik (1849). Owen must have seen this paper since that is where he obtained, again without attribution, his illustration of a chimpanzee brain showing its cerebellum uncovered by the cerebrum. In this paper the authors clearly described a posterior horn and a hippocampus minor in the chimpanzee. As to their figure showing the exposed cerebellum, Huxley quotes Gratiolet, the leading brain anatomist of the day, that this specific chimpanzee figure is greatly distorted and misleading because of the way the brain was removed from the skull. Tiedemann’s (1836) drawings of both the orangutan and the chimpanzee showed this same distortion. This must have been a common error and not quite the absurdity Huxley claimed. Animals and certainly rare apes were not perfused with a fixative for anatomical purposes when they were still alive, as is done today, under anesthesia, for optimal histological fixation. Rather, when they died, usually in a zoo, their brains were removed, and then placed in a preservative. Under these conditions the kind of distortion that misled Owen and his sources must have been common indeed.

Owen’s Linnean (1858) and Rede (1859) lectures on classification of mammals were identical except for a footnote missing from the latter. In that footnote Owen says he is unable to shut his eyes to the “all-pervading similitude of structure which makes the determination of the differences between” man and chimpanzee “so difficult.” Presumably, he originally included this note to stress the importance of his three new cerebral criteria for distinguishing man and ape, but then may have omitted it in the republication because he realized it undercut his argument. In any case Huxley, here and many times again, reveled in quoting this footnote that he treated as the ultimate hoisting petard.

At the end of this paper Huxley readily admits that there are several differences between the human brain and that of the higher apes such as size, the relative proportions of different parts, and the complexity and number of convolutions. These he believes are “of no very great value” because they are the same as those between the brains of the “highest” and “lowest” human races “though more in degree.” He then takes exception to Tiedemann’s view that the Negro brain is no different from the European since this weakens his view of the continuity between man and apes, with the “lower” races of man intermediate. In any case, he concludes, the brains of monkeys “differ far more widely from the brain of an orang than the brain of an orang differs from that of man” and therefore, Owen’s dividing man from ape by cerebral characters is wrong.

As soon as this paper appeared, Huxley sent the Lord Bishop of Oxford a reprint of it with a short note to “draw attention” to it as a “full justification for contradicting Owen at the Oxford British Association meeting.” Wilberforce answered politely (Blinderman, 1957). When Darwin read Huxley’s paper he congratulated him and called the paper a “complete and awful smash... for Owen.” As to Owen, he called him a “humbug” for omitting the footnote on the similarity of man and apes in his Rede lecture to the “orthodox Cambridge dons” (Darwin F, 1903).

The second issue of the Natural History Review had an article on an orangutan brain by George Rolleston (1861), who won the Chair of Anatomy at Oxford, with Huxley’s help over Owen’s candidate. The article placed great emphasis on showing the cerebrum covering the cerebellum, a posterior horn, and hippocampus minor present in both orang and human. It was illustrated with an elegant three-dimensional engraving of a horizontal dissection of the orangutan brain showing a rather prominent hippocampus minor. (This same figure appeared again in this issue, whether by accident or design, attached to an article on the “crania of ancient races of man.” It is never cited in the article, which happens to contain another attack on Owen.) Rolleston noted that as he did not hold a materialist position, he believed these similarities of the brains of men and apes were irrelevant to their mental status. (Huxley L [1900] commented in a letter to Hooker that although Rolleston “had a great deal of Oxford slough [i.e., snake skin] to shed... his testimony on that very ground has been of especial service.”)

In the third issue, John Marshall (1861), another friend of Huxley’s, made essentially the same points about the falsity of Owen’s three distinctions, in this case for the chimpanzee and with a great flourish of detailed measurements. Presum-
between the myology of man and the apes than noted by others (such as Owen). Church's dissections suggested to him that the chimpanzee and the gorilla "are able to point with their finger in the same manner as man."

Owen answered Huxley at a Royal Institution lecture reported in The Athenaeum (March 23, 1861), with a circulation of about 15,000 as compared to the Natural History Review's circulation of about 1,000 (Ellegard, 1958). Owen repeated his claim of the three structures unique to man but hedged a little by saying that apes do not have a hippocampus minor "as defined in human anatomy." The accompanying brain illustrations were titled "section of a Negro's brain" and "section of animal's brain." Both were otherwise unlabeled and their details unrecognizable and inaccurate. The next week Huxley wrote in to ridicule the inaccurate and unlabeled figures and excoriate the reporter for failure to mention the many earlier scientists who reported that the three critical structures were found in animals, since "doubtless Prof. Owen, following the course which would be taken by most men of science . . . allowed full weight to the affirmations of these eminent persons . . . and pointed out how they had been so misled as to describe . . . and figure . . . structures which have no existence." In the following issue Owen blames "the Artist" for the poor figures but attests to the accuracy of the account otherwise and for a more accurate figure refers the reader to his original paper (i.e., to the distorted figure lifted from Schroeder van der Kolk and Vrolik).

Owen's next detailed answer came in the June (1861) issue of The Annals and Magazine of Natural History (circulation about 2,000). He republished the Dutch chimpanzee figure (in spite of Gratiolet, Marshall, and Huxley's comments on it) and Tiedemann's human brain figure that was in his original paper but added drawings of the lateral ventricle in both species. The chimp's ventricle had no hippocampus minor labeled on it and Owen failed to mention that its source indicated one existed in this species (Schroeder van der Kolk and Vrolik, 1849). This time Owen cited the sources of his figures and pointed out that neither the Dutch nor German workers could have been influenced by their views on evolution since both had published before the Origin and even before Vestiges. He ended the paper by simply restating his three original claims for a difference between the brains of man and all other creatures.

Later that year Huxley (1861b) weighed in with his own empirical paper "On the Brain of Ateles Paniscus," the South American spider monkey, in the Proceedings of the Zoological Society. As with the other primate anatomy papers spurred by the controversy, the emphasis was on refuting Owen's three points, particularly on the hippocampus minor. The paper included a set of carefully drawn human and simian coronal brain sections and a horizontal dissection of the lateral ventricle, all designed to show prominently the hippocampus minor. In the course of his detailed study of this structure, Huxley corrected a major error in his previous description of the human and other primate brains and effected a lasting change in sulcal terminology. Before Huxley, the major sulcus on the medial surface of the hemisphere was termed hippocampal fissure and was supposed to extend from the corpus callosum to almost the posterior pole. In the course of studying sections through the hippocampus minor, Huxley realized
that this hippocampal fissure consisted of two separate sulci, a posterior and anterior one. The indentation of the posterior one into the lateral ventricle formed the hippocampus minor, so he named it the calcarine sulcus after calcar avis, the original term for the hippocampus minor. He named the anterior part the dentate sulcus since it corresponded to the fascia dentate. Calcarine sulcus entered into the permanent canon but the term hippocampal fissure or sulcus was maintained for the anterior part (except by Huxley’s followers), perhaps because the term dentate gyrus was already widespread.

Huxley had only begun his campaign. In 1862 the onslaught against Owen spread to that most prestigious venue of them all, The Philosophical Transactions of the Royal Society. There another protégé of Huxley’s, William Henry Flower (later Sir), after stating that he had no views on transmutation or the origin of man proceeds to refute Owen’s three man-ape distinctions (Flower, 1862). First Flower provided a detailed review of the earlier literature and then carefully presented the results of his own new dissections of 16 different primate species including the orangutan, several species of old and new world monkeys, and several prosimians. Flower not only found a hippocampus minor in all these primates, but went on to claim that the hippocampus minor is largest in proportion to the mass of cerebral substance in the marmoset, next in monkeys, then apes, and least in man. Drawings of two of his dissections are shown in Figure 3; the hippocampus minor in both, particularly the marmoset, certainly appear prominent, if not exaggerated. In addition to his being a close friend of Flower, Huxley’s hand in the paper is shown explicitly in two ways. First, the nomenclature that Flower used included terms just introduced by Huxley (1861b). Second, Huxley was one of the anonymous reviewers for Flower’s paper and commented in his review “... both as regards manner and matter, Mr. Flower’s memoir appears to me to be eminently worthy of a place in the Philosophical Transactions.” (The other reviewer was John Marshall, another member of Huxley’s anti-Owen team of neuroanatomists. The reviews are available in the Archives of the Royal Society as RR.4.95-98.)

Huxley continued the campaign in his Natural History Review (1862) with a long unsigned review of the leading French zoologist Geoffroy St. Hillaire’s 1856 Histoire Naturelle Generale in which St. Hillaire is quoted at length on the similarities of the brains of humans and apes, particularly “for those of our readers who have followed the controversy respecting the brains of Apes and Man if that can be dignified by the name of a controversy where all the facts are on one side and mere empty assertion on the other.”

When the Dutch anatomists Schroeder van der Kolk and Vrolik discovered that Owen had repeatedly used the chimpanzee figure from their 1849 paper to justify his arguments they “resolved... to prevent the public from being misled” (Lyell, 1863). An orangutan had just died in the Amsterdam Zoo, so they dissected its brain and reported at an 1862 meeting of the Dutch Royal Academy of Science that this animal had an extensive posterior lobe covering the cerebellum and a posterior horn and a hippocampus minor. The attending audience, they wrote, had recognized all three structures. The authors admitted the inadequacy of their original figure due to the way they had removed the brain from the cranium, disavowed any position on transmutation but suggested that Owen had “gotten lost” and “fell into a trap” by his desire...
to combat Darwin. Huxley promptly reprinted the entire article, still in French, in his Review (Schroeder van der Kolk and Vrolik, 1862).

That year and the next, the confrontations between Owen and Huxley continued in person and in print. For example, when Owen defended his position at the 1862 British Association meeting in Cambridge, his talk was reported in detail in the Medical Times and Gazette (October 11, 1862) along with the objections by Huxley and his allies Rolleston and Flower, followed by Owen’s rebuttal. The next two issues contained further rounds between the combatants.

THE HIPPOCAMPUS MINOR GOES POP

While Owen and Huxley were fighting at meetings and in the scientific journals, the popular press was featuring and, usually, satirizing the hippocampus minor debate. One example is the anonymous poem from Punch (May 18, 1861) shown in Figure 4. It was written by Sir Philip Egerton, a paleontologist and member of parliament. After accurately epitomizing Vestiges, Darwin, and some recent archeological discoveries, Egerton focused in on Huxley and Owen’s debates over brain anatomy. Punch had about a half dozen satirical pieces about the debate or its participants that year.

Both Owen and Huxley were featured in the Charles Kingsley children’s fantasy Water Babies, originally published in 1863 and still a favorite in Britain. At one point its child protagonist is puzzled at the strange things that are said at British Association meetings. He thought that the difference between him and an ape was such things as “being able to speak, and make machines, and know right from wrong, and say your prayers” rather than having “a hippopotamus major in your brain.” He understands that “if a hippopotamus major is ever to combat Darwin. Huxley promptly reprinted the entire article, still in French, in his Review (Schroeder van der Kolk and Vrolik, 1862).

Then HUXLEY and OWEN,
With rivalry glowing,
With pen and ink rush to the scratch;
’Tis Brain versus Brain,
Till one of them’s slain;
By Jove! it will be a good match!

Says OWEN, you can see
The brain of Chimpanzee
Is always exceedingly small,
With the hindermost "horn."
Of extremity born,
And no "Hippocampus" at all.

The Professor then tells ’em
That man’s "cerebellum,"
From a vertical point you can’t see;
That each "convolution"
Contains a solution,
Of "Aphrencephalio" degree.

Then apes have no nose,
And thumbs for great toes;
And a pelvis both narrow and slight;
They can’t stand upright,
Unless to show fight,
With "Du Chalignu," that chivalrous knight!

Next HUXLEY replies,
That OWEN be lies,
And garbles his Latin quotation;
That his facts are not new,
His mistakes not a few,
Detrimental to his reputation,
"To twice slay the slain,"
By dint of the Brain,
(Thus HUXLEY concludes his review)
Is but labour in vain,
Unproductive of gain,
And so I shall bid you "Adieu!"

Then Darwin set forth,
In a book of much worth,
The importance of "Nature’s selection;"
How the struggle for life
Is a laudable strife,
And results in "specific distinction."

Fig. 4. Part of a page from the May 18, 1861 Punch. Several additional stanzas dealing with recent archaeological discoveries are not shown. “Gorilla” here is the pseudonym for Sir Philip Egerton.
discovered in one single ape’s brain, nothing will save your
great-great-great-great-great-great-great-greater-greatest-grandmother from having been an ape too.’’

In an anonymous (and very well-informed) 8-page squib, entitled “A Report of a Sad Case Recently Tried before the Lord Mayor, Owen versus Huxley . . . the Great Bone Case” (1863), Owen and Huxley are dragged into court for brawling in the streets and disturbing the peace (Blinderman, 1971). The fight continues in court with much shouting of “posterior cornu,” “hippocampus minor,” and so on, as

Huxley: Well, as I was saying, Owen and me is in the same
trade; and we both cut up monkeys, and I finds something in
the brains of them. Hallo! says I, here’s a hippocampus.
No, there ain’t says Owen. Look here says I. I can’t see it
he says and he sets to werriting and haggling about it, and
goes and tells everybody, as what I finds ain’t there, and what
he finds is” (Anonymous, 1863, p. 6)

Another anonymous pamphlet that year was entitled
“Speech of Lord Dundreary . . . on the great hippocampus
questions” and was also by Kingsley. The authors of these
parodies not only knew every detail of the controversy but the
personalities of the combatants and their friends intimately.

EVIDENCE AS TO MAN’S PLACE IN NATURE

The School of Mines, Huxley’s principal appointment for
most of his life, sponsored a series of evening lectures for
workmen (“vouched for by their employers,” although
Karl Marx managed to attend). Huxley participated with great
enthusiasm, writing that the workingmen “are as attentive
and intelligent as the best audience I ever lectured to. In fact
they are the best audience I ever had . . . I am sick of the
dilettante middle classes” (Bibby, 1959). In 1860, Huxley
began to devote these lectures to evolution and particularly
to the evolution of man, a topic that Darwin avoided in public
for another 20 years. On March 22, 1861 Huxley wrote to his
wife, “My working men stick by me wonderfully, the house
being fuller than ever last night. By next Friday evening they
will all be convinced that they are monkeys” (Huxley L, 1900).

Huxley soon expanded these lectures into a book telling
Sir Charles Lyell, “I mean to give the whole history of the
[Owen] business . . . so that the paraphrase of Sir Ph. Eger-
ton’s line “To which Huxley replies that Owen he lies,’ shall
be unmistakable” (Fig. 4; Huxley L, 1900). The book, de-
signed for a lay audience, was Evidence as to Man’s Place
in Nature (1863). Darwin loved it, exclaiming “Hurrah the
monkey book has come” (Desmond and Moore, 1992). It was
evertheless successful, selling out at once and quickly going
through several more printings.

The first part, “On the Natural History of the Man-like
Apes” is largely a review of travelers’ accounts of various
apes, stressing their human-like intelligence, emotions, and
social life. It lays the basis for Darwin’s (1871) and Romanes’
(1882) florid anthropomorphizing in defense of psychological
continuity between man and animals. When this tendency to
attribute high mental functions to animals was reduced by C.
Lloyd Morgan’s (1894) Law of Parsimony (i.e., Occam’s razor
for students of animal behavior), this continuity argument be-
came the basis of modern behavioristic psychology (Boring,
1950; Boakes, 1984).

The second part “On the Relations of Man to the Lower
Animals” is the heart of the book. It begins with arguments
from embryology and cell theory for the fundamental unity
of all animals, including humans. Then the bones, skull, and
teeth of humans and the apes are discussed with the conclu-
sion that “the lower Apes and the Gorilla differ more than
the Gorilla and the Man.” Next, and it almost seems like the
raison d’être for the whole book, is an account of the
fundamental similarity of the brain of apes and humans,
particularly the possession by both of a posterior lobe, a posterior
horn, and a hippocampus minor. The account is a long (12
pages), step-by-step argument; perhaps it needed to be since
the book’s audience had never heard of a brain ventricle,
let alone the hippocampus minor. At the end of the chapter,
Huxley points out that the close similarity of man and the apes
that he has just demonstrated proves the validity of Linnaeus’
original Primate order and ends by stating, in a rather offhand
manner, that Darwin’s theory provides an explanation of the
origin of man from ape.

Interposed between the second and third parts are six pages
of fine print providing, “a succinct History of the Controversy
respecting the Cerebral Structure of Man and the Apes,” that
is, how Owen “suppressed” and denied the truth about the
hippocampus minor, posterior horn, and posterior lobe and
how this was now a matter of “personal veracity.” The final
portion of Man’s Place, “On some fossil remains of man,”
outlines the evidence for a fossil link between ape and man,
which Huxley admitted was very meager indeed.

At the time, judging by a sample of the book reviews, Hux-
ley’s book was viewed chiefly as a polemic against Owen,
favorably so by Huxley’s partisans who were in the majority
by now and unfavorably by Owen’s allies (DiGregorio, 1984).
Darwin, natural selection, or even evolution, as distinct from
man’s systematic status, are not major issues in these reviews
and indeed they are not major concerns in the book. Probably
the most influential evaluation was that of Sir Charles Lyell,
Britain’s leading geologist and one of its most eminent scient-
ists. Through nine editions, his Principles of Geology had
rejected the idea of evolution. Now in his Antiquity of Man
(1863) he evenhandedly discussed the pros and cons of Dar-
win’s theory, disappointing Darwin, but actually moving a
very long way toward him. He also reviewed the hippocampus
minor debate in detail. Lyell came down totally and unambigu-
ously on Huxley’s side, which must have effectively ended
the debate in the scientific community.

Owen (1863a), not surprisingly, attempted to refute Lyell
and continued to defend his classification scheme against its
critics. He even found a new argument for the importance
of the hippocampus minor: that it was absent, or virtually so,
in an “idiot” (Owen, 1863b).

Owen’s final statements on the hippocampus minor con-
troversy are in On the Anatomy of Vertebrates (1866). There
his brain figures are accurate and in a long footnote, he finally
admits, citing himself and the earlier literature, that in apes
“all the homologous parts of the human cerebral organ exist.”
This admission, he believes, does not invalidate or even
threaten his classification of man in a separate subclass
because the critical structures, the posterior lobe, the pos-
terior horn, and the hippocampus minor, exist in apes only
“under modified form and low grades of development.’’ As
to Huxley and his neuroanatomical allies, their attacks on his classificatory scheme were "puerile," "ridiculous," and "disgraceful."

Owen's original aim was to define the uniqueness of human-kind: to find an objective way of differentiating humans from animals that was qualitative and not merely quantitative, solidly grounded in anatomical science rather than theology or speculation, and based on the brain, the origin of the most striking differences between man and animal. Owen's downfall was not this goal but his hubris in stubbornly defending his errors in trying to reach it. The tragedy was classical: Owen fell from the pinnacle of British science to be remembered, when at all, for his obstinate errors in this debate, rather than for his real contributions.

**SOURCES OF OWEN'S THREE CRITERIA**

Where did Owen get his three bench marks whose repudiation by Huxley destroyed Owen's credibility as a critic of Darwin and evolution? One source for his idea that the posterior extent of the cerebrum in man was a powerful indicator of his unique and elevated taxonomic status was probably a figure in Fletcher's (1835) *Rudiments of Physiology*. This figure shows a series of dorsal views of the brain, drawn to the same size, starting with cuttlefish, then eel, turtle, bird, marmot, and up through otter, and orangutan to man. A line is drawn at the posterior border of the cerebrum (or its supposed homolog) to show that moving upward in the animal scale the cerebrum moves posteriorly until, in man, it covers the rest of the brain, the cerebellum being the last structure to disappear from view. Fletcher's idea of systematic changes in the brain correlating with increasing complexity was used by Chambers as a major argument for evolution in *Vestiges* and therefore must have been well known to Owen, at least through this source. (Owen had originally been sympathetic to *Vestiges* [Owen, 1894; Richards, 1987].) This idea that the cerebrum was exposed even in the highest nonhuman primates was supported by published drawings of (distorted) ape brains (Tiedemann, 1836; Schroeder van der Kolk and Vrolik, 1849).

Owen's choice of structures in the lateral ventricles for his other two ways of distinguishing humans and animals presumably was a persistence of the importance Galen had given the ventricles centuries earlier. The ventricles played a central role in his physiological system, a set of theoretical views that dominated Western medicine for more than 1,400 years and was influential into the 19th century (Sarton, 1954; Gross, 1987b). Galen (1968) thought the ventricles were the primary site for production of psychic pneuma, which he believed was a critical mediator of cerebral function and the medium of transmission in sensory and motor nerves. Galen's description of the brain ventricles was quite accurate, although sometimes Vesalius and later anatomists thought they found errors because they did not realize Galen was describing an ox brain and not a human one, human brains being harder for Galen to obtain because of the Greek reverence for the body (Woolam, 1958). However, the early church fathers, particularly Nemesius, Bishop of Emesia (fourth century), radically altered Galen's conceptions of the structure and function of the ventricles (Pagel, 1958). They transformed the ventricles into three more perfect spheres. Galen had localized sensory and motor functions in the solid portions of the cerebrum, the former anteriorly and the latter posteriorly. The church fathers, however, were looking for a less mundane site for the interaction of the body and soul and chose for this purpose the empty spaces in the brain that Galen had described, the ventricles. They then took the Aristotelian faculties of the mind, sensation, cognition, and memory and located them in the anterior, middle, and posterior ventricles, respectively. Drawings of this ventricular localization of mental function hardly changed for over a thousand years except for the expression on the faces (Clarke and Dewhurst, 1972).

When systematic brain dissection began again in the Renaissance the brains were usually dissected from the top down, often in situ. The ventricles were carefully depicted and labeled because of their importance in Galenic theory. The most famous of these early horizontal dissections was that of Vesalius in his revolutionary work, *On the Fabric of the Human Body*, published in 1543 (Singer, 1952). Horizontal views in which the ventricular features are prominent continued to be a common way of depicting the internal structure of the human brain into the 19th century. Thus, ventricular structures were carefully depicted and named, whereas the cortex was often drawn in a schematic fashion, since until Gall and phrenology it was usually thought to be unimportant (Gross, 1987a). Presumably, the theoretical importance of the ventricles persisted because no better theory of brain function emerged, and better theories, not better facts, are required to overturn a theory. Given this tradition it is not all that surprising that Owen, looking for important and higher parts of the human brain, looked into the ventricles.

**MAN'S PLACE IN NATURE IN HISTORY**

A second edition of Huxley's *Man's Place in Nature* was published in 1896. A number of things had changed since the first edition. The general idea of evolution, including that of humans, was now accepted by most of the scientific community. Darwin's *The Descent of Man* (1871) had been published, offering detailed mechanisms for the evolution of man's body, mind, and morals. It included an appendix by Huxley on the similarities and differences between the brain of man and ape. The hippocampus minor is mentioned only in passing but never Owen. Sir Richard had died in 1892, and in the ultimate confirmation of the saying "history is written in the ultimate confirmation of the saying "history is written by the victors," Owen's son asked Huxley for an account of his father's "Position in the history of anatomical science" to include in his *Life* of his father (Owen, 1894). Huxley gave him 60 pages that did not refer to any of their bitter disputes and was full of phrases like "unabated industry," "wide knowledge," "great service," "splendid record," and "sagacious interpretations." By now Huxley was the Right Honorable (a privy counselor) and had been president of the Royal, Ethnological, Geological, and Palaeontographical Societies, the British Association, and the National Association of Science Teachers as well as university dean and president.

More generally, the social and political scene had changed. The Reform Act of 1867, giving the urban working class the vote, had eliminated the threat of revolution (or, perhaps, the decline of this threat made the Act possible), and the end of religious tests opened the doors of Oxford and Cambridge to dissenters and Jews as students and faculty. Both developments tended to reduce the political charge of evolutionary ideas. The dominance of the Oxbridge clergyman-naturalist
had given way to that of the professional scientist of which Huxley was the archetype (Desmond, 1984). As much as personality clashes or scientific differences, the conflict between Owen and Huxley represented this transfer of power. Although they came from similar middle class, nonuniversity backgrounds, Owen attached himself to the medical, religious, and political establishment of his time. By contrast, Huxley fought to professionalize science and free it from the dominance of clergy and gentry (although he carefully eschewed the political radicals of the time). In defeating Owen and his backers, Huxley and his friends became the scientific establishment (Jensen, 1991), and in doing so, the hippocampus minor was Huxley's most successful weapon.

The new edition of Man's Place reflected the changes in the status of evolutionary theory and of Huxley himself. The title became more assertive, dropping "Evidence as to" and becoming simply Man's Place in Nature. The section on the "Succinct History" of Owen's supposed perfidy was eliminated entirely and Owen was hardly mentioned.

In this century, Man's Place in Nature is usually viewed as a triumph of evolutionary thought rather than an attack on Owen or a defense of Linnaeus, and its relevance to the hippocampus minor has been totally lost. Huxley is admired for charging in where Darwin feared to tread for another 8 years. Homer Smith (1956), physiologist and historian of science, called it "the first [and still] definitive statement of the naturalistic interpretation [of man]." Sir Arthur Keith (1925), pioneering anthropologist, claimed it "laid the basis for a true science of anthropology and can only be compared to Harvey's Movement of the Heart and Blood." Ashley Montagu (1959), in an introduction to a paperback edition, called it a "great classic of science" and "among the most inspiring."

THE PLACE OF THE HIPPOCAMPUS MINOR IN MAN'S SEARCH FOR MEANING

Richard Owen chose the hippocampus minor and its associated structures as the touchstone of humanness. Other choices for this function from brain anatomy have included the size of the frontal lobes, brain laterality, and the position of the lunate sulcus. Perhaps the earliest was that of Herophilus, the Alexandrian anatomist in the second century BC, who attributed man's greater intelligence to his more complex cerebellum, or so Galen, in ridiculing this view, tells us (Galen second century, 1968).

Thomas Huxley chose language in Man's Place as the criterion of humanity and some of its contemporary reviewers pointed out that in doing so he played the same game he attacked when played by Owen (e.g., Antro Rev. 1863, 1: 107–117). Human language continues to be a popular candidate for a hippocampus minor although whether the uniqueness of language lies in its unbounded vocabulary, infinite set of sentences of arbitrary size and complexity, ability to code distant time and place, self-reference, or ability to lie is unclear.

For his ordering of organisms, Linnaeus preferred sexual characteristics, at least for plants, and when he could get them, for animals (e.g., mammalae). Perhaps inspired by him, variety of coital positions, desire for privacy during intercourse, and orgasm in females have all been offered as distinguishing features of Homo sapiens (and counterindicated) as has the ratio of the size of the erect penis and of the breasts to body weight (Diamond, 1992). DNA was a transient hope but the difference between man and the chimpanzee (about 1.6%) is rather anxiety provoking.

One basic human characteristic seems to be the need to establish differences between ourselves and our closest relatives; for that purpose, the hippocampus minor may be as good a criterion as any other.

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