DNA Hybridization: A Decade of Molecular Discourse in Hominoid Phylogeny

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Abstract: Biomolecular studies can provide an independent test of hominoid phylogeny from anatomical methods. One type of biomolecular approach to hominoid phylogeny will be discussed here, namely DNA hybridization. This paper presents the reader with a critical evaluation of the development of biomolecular research in hominoid phylogeny; consequently, both the internal and external problems that plague this research are discussed. The implications of accepting a human-chimpanzee phylogenetic connection are also considered critically. This paper argues that, due to the pivotal role that politics has played in DNA hybridization research, a more thorough understanding of the history of such political dynamics can engender a better appreciation for the role that DNA hybridization research plays in biomolecular studies of hominoid phylogeny. This unique approach of assessing research, argues for the importance of continued critical research.

Introduction

In 1984, two researchers, Charles Sibley and Jon Ahlquist, using the technique of DNA hybridization, surprised anthropologists and biomolecular researchers alike when they announced that they had resolved what had appeared to be an impossible task: how to split the trichotomy among humans, chimpanzees, and gorillas. According to these authors, humans and chimpanzees were each other's closest relatives, with gorillas having diverged from them at an earlier stage.

This paper is a critical evaluation of the technique of DNA hybridization. It is divided into four main sections. The first section, *Laying the Groundwork: What's Old, What's New in Hominoid Phylogeny*, is an important section because it allows the reader to appreciate the controversy and the wide-scale negative criticism that met Sibley and Ahlquist's (1984) study. The second section, *DNA hybridization: The Technique*, looks at the technical aspects of DNA hybridization and how it is used in hominoid phylogenetic research. The third section, *DNA hybridization in Perspective*, looks at the evolution of DNA hybridization studies and helps the reader to understand why Sibley and Ahlquist's work stood out above other studies conducted prior to it.

The fourth section, which is the discussion, is further divided into four sub-sections. The first is entitled *DNA hybridization: The Pros and Cons*. The second is *DNA hybridization: Methodological Questions*. The third section is *DNA hybridization: Its implications*, and the fourth is *The Sociology-of-Science: The Political discourse in DNA hybridization research*. This four-part discussion critically evaluates the technical, general, and sociological aspects of research in DNA hybridization. It is hoped that from this section, the reader will be exposed to the enormous controversy

that plagues DNA hybridization research, and concur with the author that, because of the internal and external conflicts facing research in this area, it will be very difficult to accept any conclusions from DNA hybridization research pertaining to hominoid phylogeny.

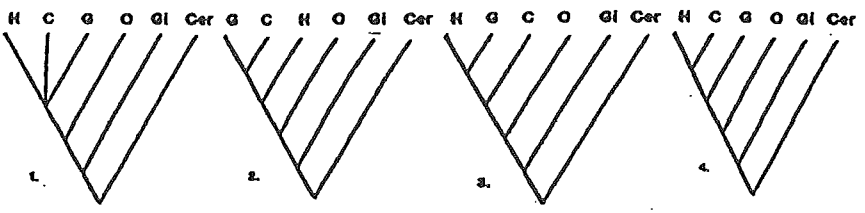
Laying the Ground Work: What's old, What's new in Hominoid Phylogeny?

There are two common methods used to reconstruct hominoid phylogeny: the classical anatomical methods, and the biomolecular or genetic methods. The anatomical method focuses on the implications of individual homologies. This method uses deductive-analytical procedures in order to make inferences that are themselves the basis for reconstructing history (Mishler 1994). The second method, the biomolecular method, tends to treat phylogenetic inference as a statistical estimation problem (Cavalli-Sforza and Edward 1967). According to Mishler, "because of the modern synthesis emphasis on genetics and the gradual divergence of lineages, overall genetic distance measures [the way the bimolecular data is expressed] are often used to indicate 'relationship'" (1994:45). DNA hybridization is just one of the many approaches that constitute the bimolecular tradition. However, to give the reader an appreciation for the controversy that surrounds DNA hybridization studies, this brief discussion will look at the reconstruction of hominoid phylogeny without the contribution of DNA hybridization studies.

The living hominoids are human (*Homo sapiens*), common chimpanzee (*Pan troglodytes*), pygmy chimpanzee (*Pan paniscus*), gorilla (*Gorilla gorilla*), orangutan (*Pongo pygmaeus*), and nine species of gibbons (*Hylobates spp*) (Fleagle 1988). Among researchers of hominoid phylogeny the composition of these groups and the branching sequence of the gibbons and orangutan are not in dispute. However, a great deal of controversy exists in the methods of reconstructing the relationships among the gorilla, chimpanzee, and human lineages, as well as with the dating of the divergence of these groups. For a more detailed discussion, see Fleagle (1988) and Ciochon and Fleagle (1985). This controversy results from the fact that different researchers, along with their respective methods for reconstructing hominoid phylogeny, consistently produce one of the four topologies for the gorilla, chimpanzee, and human branches of hominoid tree: (1) a trichotomy; (2) gorilla-chimpanzee, human; (3) gorilla-human, chimpanzee; and (4) chimpanzee-human, gorilla (Sibley *et al.* 1990; Sibley and Ahlquist 1984, 1987) (See Figure 1).

Cladogram 1, which includes the trichotomy among humans, chimpanzee and gorillas, has proven difficult brake because these three lineages branch closely together in time, and the resolving power of most techniques cannot separate the nodes. This trichotomy was proposed by Andrews (1987), Bruce and Ayala (1979), Benveniste and Todaro (1976), and Koop *et al.* (1986), to name only four studies.

Cladogram 2 has received a great deal of support, and is the pattern most often suggested by morphological studies (e.g., Delson 1977; Oxnard 1981). Support for this branching pattern also comes from bimolecular studies, such as that by Hixson and Brown (1986).



H=human C=chimpanzee O=orangutan Gi=Gibbons Cer=ceropithecoids

Figure 1: Four possible topologies indicated by current research in hominid phylogeny. (Source: Sibley and Ahlquist 1987)

Cladogram 3 was suggested by Miller (1977) on the basis of chromosome banding patterns but, according to Sibley and Ahlquist (1984), recent technical advances in karyology make this and other chromosome banding studies obsolete.

The chimpanzee-human pattern, seen in Cladogram 4, is one that was proposed as early as the mid-1970s by King and Wilson (1975). Since then there has been a steady increase in the number of advocates for this pattern of branching (morphological studies: Stern and Susman 1981; and biomolecular studies: Yunis and Prakash 1982; Goodman and Cronin. 1982 *cf.* Sibley and Ahlquist 1984). There have been over twelve other biomolecular studies that have been published since 1984 which, for reasons that will be made clear later on in this paper, will not be discussed here.

As is apparent from the above discussion, the results from research in hominoid phylogeny are by no means concordant. Indeed, many biomolecular researchers still find that the most acceptable pattern of phylogeny is the trichotomy. Such a view was expressed by Goodman and Cronin in their review of molecular anthropology:

> One may not be able to detect certain lineages at the molecular level. This may be the case for the trichotomy of *Homo-Pan-Gorilla*. Twenty years of intensive data collection have not yet resolved this important sequence of speciations (*1982:139*).

Thus, it was no surprise that Sibley and Ahlquist (two researchers who are ornithologists by training) shocked anthropologists and biomolecular researchers alike when, in 1984, they announced that they had resolved what had appeared to be an intractable issue in hominoid phylogenetic research using DNA hybridization.

DNA Hybridization: The Technique

DNA is a two-stranded molecule whose hereditary information is encoded in a sequence of nucleotide pairs. These nucleotide pairs are the building blocks of DNA and are held together by hydrogen bonds, two linking the A-T pair and three linking the G-C pair (Figure 2).

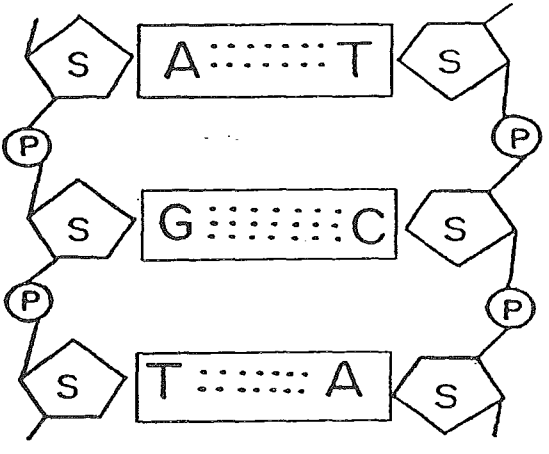


Figure 2

The two DNA strands are held together by weak bonds (dotted) joining the nucleotide pairs. S and P indicate the sugar and phosphate aspects respectively, of the DNA molecule.
Adenine (A) and Thymine (T) are joined by two bonds; Guanine (G) and Cytosine (C) are joined by three bonds. Heating breaks these bonds and leaves the DNA as two single strands.
Source: Tattersall et al. 1988:151

Adding energy in the form of heat breaks these bonds and dissociates the two strands from one another. This is called *denaturing* the DNA (Tattersall *et al.* 1988; Marks *et al.* 1988). Poorly-paired DNA strands will dissociate at much lower temperatures than well-paired DNA strands. Thus, the thermal stability of duplex DNA is proportional to the integrity of the base pairing (Weiss 1987; Marks *et al.* 1988). According to Marks *et al.* (1988:29), if the process of evolution can be reduced to the progressive accumulation of point mutations in DNA, then the melting temperature of DNA that is composed of two strands from different species will be an indication of the amount of genetic difference which has accumulated between those two species.

The typical hybridization experiment involves preparing sheared fragments (approximately 500 base-pairs) of DNA (Sibley and Ahlquist 1984, 1987; Sibley *et al.* 1990). A unique-sequence DNA is, in turn, taken from one species (the *tracer*) and denatured. It is then mixed with a great excess of denatured DNA from a different species (*the driver*). Instead of finding its own complementary strand, the tracer will bind imperfectly to the more abundant, nearly-complementary strand from the other species (Tattersall *et al.* 1988; Watson *et al.* 1992).

This *heteroduplex* DNA is then isolated and denatured again. However, there are now fewer bonds that holding the DNA molecule together. Thus, less energy is required to break the two strands apart. This means that this heteroduplex DNA will

dissociate at a slightly lower temperature than the homoduplex DNA (Tattersall *et al.* 1988). The critical temperature is generally given as that at which 50 percent of the DNA being studied is single-stranded, and is statistically represented as *T50H*. However, as will be discussed later on in this paper, there is debate among different researchers about the approximate statistics that should be used. Two other statistics have been proposed: *Tm* and *Tmode*. Essentially, the difference among the three is the amount of DNA that is accounted for by each of the statistics (Marks 1991; Sarich *et al.* 1989; Marks *et al.* 1988; Sibley *et al.* 1990; Lewin 1988; Caccone and Powell 1989). The difference in dissociation temperature between homoduplex and heteroduplex DNA is proportional to the amount of genetic mutation that has accumulated between the two species. The difference in temperature then, is used as a measure of the *genetic distance* between the two species being studied (Tattersall *et al.* 1988:152).

DNA Hybridization in Perspective

The main goal of the discussion thus far is two-fold. First, it is hoped that the reader has gained an appreciation of the research in hominoid phylogeny, prior to the introduction of DNA hybridization. Second, the reader should now have a clear understanding of DNA hybridization. Not only are these points essential for an understanding of any discussion on the contribution of DNA hybridization to hominoid phylogeny, but also an awareness of the above two points enables one to appreciate the controversy that plagues this area of research. As mentioned before, Sibley and Ahlquist's 1984 paper in took many researchers in this area by surprise. It is precisely the nature of this reaction by researchers that led me to investigate this subject more thoroughly.

A review of the literature on this subject revealed that there were only four different studies of hominoid DNA hybridization on record (Hoyer *et al.* 1972; Benveniste and Todaro 1976; Sibley and Ahlquist 1994; Caccone and Powell, 1989). At this point, the reader should note the 1972 and 1976 studies, since I have explained that most of the controversy came as a result of Sibley and Ahlquist's 1984 study.

The study by Hoyer *et al.* (1972) used *Homo* and *Pongo* single-copy DNAs as tracers, and compared them with the DNAs of *Homo*, *Pan*, and *Gorilla*, among others. However, they only used one comparison between the tracer DNAs and the driver DNAs, and as a result, they had to conclude that their data could not indicate with any certainty whether the chimpanzee and gorilla are closer to each other than to humans, or if either of them might be closer to humans than to each other.

This takes us to Benveniste and Todaro's (1976) study. They also made only one DNA-DNA hybrid for each pairwise comparison, but their data did not resolve the *Homo-Pan-Gorilla* trichotomy. So, when Goodman and Cronin concluded in 1982 that over twenty years of intensive data collection had not resolved the trichotomy of *Homo-Pan-Gorilla*, they obviously were also talking about these two DNA hybridization studies. Not only should this shed light on the reaction of researchers to Sibley and Ahlquist's (1984) paper, but it should also provide at least one reason why the last

decade of molecular phylogenetics has been described in this paper as a decade of molecular discourse. The remainder of this paper deals with the nature of this discourse.

In 1984, the third publication of hominoid DNA hybridization was published by Sibley and Ahlquist (hereafter referred to as "S/A"). It was the first study using DNA hybridization that presented a complete matrix of distance values based on the average of five or more comparisons for each node, and it was also the first to present molecular evidence for a Pan-Homo clade. Based on the 183 DNA hybrids that were formed, the researchers interpreted the evidence to mean that the branching order, from oldest to most recent, was gibbons, orangutan, gorilla, chimpanzees, and human, as illustrated in Figure 1.1 (Sibley and Ahlquist 1984).

However, because of pressure generated from the criticism of other researchers in this field (e.g., Templeton 1985; Lewin 1984), S/A were forced to substantiate their results with an expanded data set, which was published in 1987. In this paper, they presented values for an additional 331 delta *T50H* values,plus the 183 values from their 1984 paper, for a total of 514. The authors state that, "as in 1984, we conclude that the phylogeny depicted [here] is supported by the data, and that it is highly probable that it represents the correct reconstruction of the phylogeny of the hominoid primates" (Sibley and Ahlquist 1987:108-109).

With this additional data set, the debate became an issue of discordance among mainly molecular anthropologists. And, more importantly, there was an irony: rather than resolving or alleviating the controversy, this expanded data set did quite the opposite. Apart from the debate about the ability of DNA hybridization to split the trichotomy, S/A were now facing more serious challenges. First, a major problem involved the unavailability of primary data and controls, which would permit the critical evaluation of the robusticity of S/A's conclusions. Second was the notion that S/A used an inappropriate method of analysis of their data, thus giving misleading results. Third, and most serious, were suggestions that as much as 40 percent of the authors data concerning humans and apes had been subjected to manipulations that were intended to make their data look better (Lewin 1988a, 1988b; Sarich *et al.* 1989; Marks *et al.* 1988, 1989; Marks 1988, 1991, 1994).

Sibley and Ahlquist did concede to manipulating their data:

> It did not seem to be very important at the time, because errors seemed to be clear and it was easy to see in which direction they were. Yes, of course we should have indicated that we'd corrected them. And yes, it is very embarrassing. (*Lewin 1988b:1758*)

So again, S/A were forced to reanalyze their data, and in 1990, in a paper titled, DNA hybridization evidence of hominoid phylogeny:a reanalysis of the data, they stated: "from this reanalysis of the data we conclude that the chimp-human clade is real and that the phylogeny proposed by Sibley and Ahlquist's (1984, 1987) was justified" (Sibley *et al.* 1990:235). Exhausted by six years of intense scrutiny and

"bashing" (as some researchers described some of the criticisms against Sibley and Ahlquist's work), S/A stated that they "will not respond to further critiques because [they] wish to proceed with the production of new, and better, data pertaining to the phylogenies of birds and mammals" (p.236).

The fourth[1] study of hominoid DNA hybridization resulted from the controversy of S/A's paper. It took over a year of intense pressure for S/A to finally make primary data and controls available to the scientific community. It was then that Caccone and Powell (1989) (researchers who had only done DNA hybridization on *Drosophila*) set out to have an independent repetition of S/A's work. However, these researchers used a different method than that used by S/A (1984, 1987) to determine the thermal stability. Caccone and Powell (1989) used the so-called TEACL (tetraethylammonium chloride) method, instead of the hydroxyapatite (HAP) method used by S/A. According to these authors, the TEACL method allows them to control for two factors other than the base-pairs mismatch that determine the thermal stability of DNA duplexes: these are the base composition and the length of the duplexes (Caccone and Powell 1989). In this way, Caccone and Powell's study did not replicate the S/A (1984, 1987) experiments but, instead, tested whether independent measurement of the same parameter (the thermal stability of DNA molecules) yields the same results (1989:926). These authors conclude that:

> The problems of the relative genetic relatedness of the hominoids have been largely solved. Humans and chimpanzees are genetically most close, followed in order by gorillas, orangutans, gibbons, and the Old World monkeys. (*Caccone and Powell 1989:938*)

So, then, what is the role of DNA hybridization in reconstructing hominoid phylogeny? How effective is this method in reconstructing hominoid phylogeny? And are humans, in fact, more closely related to chimps, as the above studies suggest? All these important questions plague research in this area Before they can be answered, a more detailed discussion of some of the technical aspects of DNA hybridization, along with a more in-depth discussion of the studies mentioned above is required. Further, I would argue that a critical analysis of the implications of these studies is also important if we are to answer these questions. The discussion that follows is intended to provide answers to the above questions and elucidate these issues.

Discussion

DNA Hybridization: The Pros and Cons

The technique of DNA hybridization has been available for over twenty years and has been hailed by some as representing the most powerful approach for comparison of genomic information (Brunk and Olson 1990; Sibley and Ahlquist 1984, 1987, 1990; Diamond 1984), mainly because the technique of DNA hybridization drastically increases the scale of genetic comparison. That is, DNA hybridization remains unique in its ability to compare virtually the entire genome of

different organisms. By involving every piece of homologous single-copy DNA between two species, Diamond (1984, 1990) argues that the technique automatically addresses one of the strongest criticisms of molecular clocks in general: that is, the notion that a biological unit will tick clocklike and uninterrupted for very long periods of time. But Sibley and Ahlquist (1984) argue that this is no problem for the technique of DNA hybridization, because the large number of nucleotides involved in the comparison ensures that fluctuations away from the average in one direction, will be matched by fluctuations in the opposite direction.

Besides these two points, most other arguments for the technique seem less clear-cut. For example, most cladists claim that because distance data cannot be partitioned into primitive and derived traits, they cannot be used to reconstruct phylogeny. Advocates of DNA hybridization argue that this notion is false, since cladists fail to offer proof that the phylogenies produced by DNA hybridization data are wrong (Sibley and Ahlquist 1987).

Another criticism against DNA hybridization (or DNA-DNA hybridization) data is that it is the same as any distance statistic, in that it is not possible to isolate the changes that are being measured, and therefore it is inherently untestable (Andrews 1987). Those who support the DNA hybridization method argue that the ultimate test is congruence with DNA sequences, and that there have already been examples for this congruence (Sibley and Ahlquist 1987, 1990; Caccone and Powell 1989).

Finally, Andrews claims that DNA hybridization "produces a distance statistic which fails to distinguish character homology, and this must raise questions about the reliability of the DNA-DNA hybridization results" (1987:45). According to Sibley and Ahlquist, this is another false criticism that is based on the assumption that all distance data are incompetent, and that only character data can "distinguish character homology" (1987:106).

DNA Hybridization: Methodological questions

To add further complication to the already existing problem (of the constant attacks by those who do not support DNA hybridization), the field itself is plagued by internal conflict among its own supporters. This takes us back to the issue of the appropriate method of analysis or statistic to describe the results. As mentioned previously, there are three options for interpreting DNA hybridization data: *T50H* (used by Sibley and Ahlquist 1984, 1987, 1990), *Tm* (used by Caccone and Powell 1989) and *Tmode* (supporters include Sarich *et al.* 1989; Marks *et al.* 1988). The difference between each is in the amount of DNA involved in the comparison.

Plotting the denaturation of the hybrid DNA into single strands against temperature, yields a bell-shaped curve which can be transformed into a cumulative sigmoid curve (See Figure 3). This analysis allows the researcher to document and track shifts in the DNA peak, which represent the differences in the thermal stability of different hybrid DNA samples (Marks 1991:208).

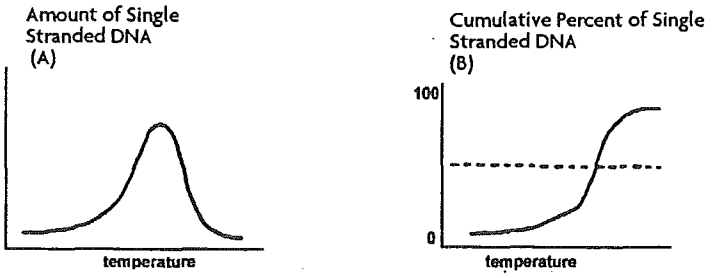


Figure 3

Hypothetical melting profile for determining the thermal stability of a sample of hybrid DNA, assuming complete hybridization. (A) the DNA remains double-stranded at low temperatures, denatures into single strands at high temperatures, until the sample is fully denatured. (B) The same data presented as a cumulative or integrated curve. The 50% point can be taken as the melting temperature.

Source: Marks 1991:209

T50H measures 50 percent of the DNA which could conceivably have formed hybrids that is, including the amount of unhybridizated DNA as part of the total. *Tm*, on the other hand, is a median measurement and measures 50 percent of the DNA that has been hybridized. Thus, unhybridized DNA is excluded from any analysis using this statistic. The third statistic, *Tmode*, measures the modal temperature of melting, and thus corresponds to the highest point on the curve. For a more detailed discussion on the above statistics, the interested reader is directed to Marks (1991), Marks *et al.* (1989), Caccone and Powell (1989), Sarich *et al.* (1989), Schmid and Marks (1990), and Britten (1990).

Marks (1991) argues that *T50H* and *Tm* are both sensitive to variations or anomalies in the shape of the curve, while *Tmode* is insensitive to such variations or anomalies, as it only takes the highest point on the curve. Figure 4 clearly illustrates this point, as it diagrammatically shows differences among the three statistics based on the kinds of phenomena encountered in S/A's data.

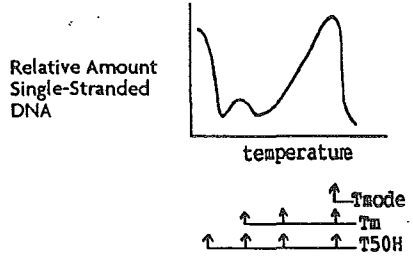


Figure 4

Differences among the three statistics, based on the kinds of phenomena encountered in the Sibley-Ahlquist data. Arrows represent the position on the curve measured by each statistic.

Source: Marks 1991:211

Another area of discordance among advocates of the DNA hybridization technique involves methods that measure the reassociation of the strands. There are two different techniques that accomplishes this: *HAP* and *TEACL*. Caccone *et al.* (1988) have shown that, for the same taxa, these two methods give somewhat different results. They show that the percentage reassociation is consistently smaller using the TEACL technique, and they argue that this occurs because the TEACL technique trims up overhanging ends and cuts out insertion/deletion differences.

Due to space limitations, I have only touched on the major methodological limitations that have caused internal conflict among those who support DNA hybridization. However, there are many other problems, and for those who wish to pursue these in greater depth, the following papers are extremely useful: Caccone and Powell (1989); Marks *et al.* (1988, 1989); Schmid and Marks (1990); Brunk and Olson (1990); and Britten (1989, 1990).

DNA Hybridization: Its Implications

Two main issues that will be discussed in this section. The first involves the plight of morphological or classical studies of anatomy; that is, does DNA (or DNA-DNA) hybridization sound the death knell for classical anatomical studies? Second, what does demonstrating a phylogenetic connection between humans and chimpanzees imply for the discipline of physical anthropology?

With respect to the former question, one only has to recall the quote by S/A (1987) to understand the possible implications of DNA hybridization studies, or any molecular study for that matter, on research in classical anatomical studies. The criticisms against anatomical studies by molecular researchers are often twofold. First, they argue that ancestral relationships are hard to establish, and second, that anatomical characters have to be involved in order to determine relationships and to study evolutionary change (e.g., Diamond 1990). The advocates of DNA hybridization then argue that their technique now permits phylogenies to be reconstructed with confidence, without having to rely on anatomical characters (Diamond 1990:799). While this may be true, one cannot negate the controversy stemming from both the internal and external conflicts described above that plagues this research technique. Thus, I would argue that morphologists need not react as though molecular systematics will put them out of jobs (Pilbeam 1986; and Diamond 1990). And I will further argue that, instead of bullying each other, both molecular and comparative anatomical data can be brought together to minimize the apparent conflict between various kinds of evidence (Goodman and Cronin 1982; Mishler 1994; Cronin 1986; Pilbeam 1986; Diamond 1990). After all, the bodies of data can be concordant. We should not forget, as Goodman and Cronin (1982) point out, that there can only be one true phylogeny.

What about the second question regarding the phylogenetic connection between humans and chimpanzees? If this is in fact true, Marks (1991) claims that this could be one of the most significant revisions to physical anthropological theory in the twentieth century. As Marks (1991:27) notes, this would mean modelling the evolution of humans (from chimp-like or non-chimp-like ancestor), and modelling the evolution of

bipedalism (from a knuckle-walking or non-knuckle-walking ancestor). In thinking about this point, I decided to investigate whether any morphologist had made this claim prior to it being made by DNA hybridization studies in 1984. Indeed, it was suggested as early as 1978 by Zihlman *et al.* (see also Stern and Susman 1981). Such a find obviously weakens any claims or criticisms made by molecular researchers intended to demean classical studies. However, one cannot help but acknowledge the magnitude of Marks' statement above. Such a finding indeed would have major implications in the field of physical anthropology.

The Sociology-of-Science: The Political Discourse in DNA Hybridization Research

While conducting research for this paper, I found that one of the issues that most intrigued me was what appeared to be a personal conflict among researchers, and how this manifest itself in their academic publications. The reader will recall, that one of the problems that S/A faced was the accusation of having manipulated their data, to which they later conceded. As should be clear by now, it was a trio of researchers (Jon Marks, Vincent Sarich, and Carl Schmid) who were responsible for exposing S/A. In 1988, Jon Marks wrote to Zuckerkandl the editor of the *Journal of Molecular Evolution* (which published S/A's paper), and demanded that the papers be retracted. But Zuckerkandl declined (Lewin 1988).

It appears that, from this point onwards, what had begun as an ostensibly objective examination (conducted by Sarich and his colleagues) of the power of the technique of DNA hybridization in general, and also of S/A's work, "had quickly degenerated into a rather personal conflict; with big egos on both sides" (Lewin 1988a:1598). Roy Britten of the California Institute of Technology later explained that "those manuscripts [by the trio] are not scientific articles, they are weapons with political purposes" (Lewin 1988a:1598). Due to space restrictions what follows is a summary of a number of events that elucidate the political warfare in this academic research:

1. Marks' own thesis work on chromosome banding supported the more conventional chimp/gorilla association. In the fall, of 1987, he made an unsubstantial attack on the significance of some DNA sequences by Goodman (1987), which supported S/A's conclusion.

2. In 1988, a manuscript by the trio, describing the extent of the manipulation by S/A, was rejected by Zuckerkandl, the editor of the *Journal of Molecular Evolution* (*JME*) which was also the Journal that published S/A's work. (Note: the manuscript had passed through several revisions for more than one year).

3. In early 1988, Allan Wilson of the University of California, Berkeley, included a copy of the rejected *JME* manuscript as part of an assessment of a research grant proposal submitted by Sibley to the National Science Foundation (NSF). The proposal was rejected. Most researchers consider Wilson to have acted improperly. (Note: Wilson is a long-time associate of Sarich, one of the trio).

4. In another manuscript by Sarich and his colleagues, arguing that the Tmode statistic is the superior measure over the T50H measure used by S/A, five referees were invited to review this manuscript. Britten, although not invited to act as a referee, nevertheless obtained a copy of the manuscript and offered comments directly to the editor, Zuckerkandl. "The finest possible analytical job," replied one referee. "An important contribution to the field of molecular evolution," said another. However, Britten deplored the manuscript. (Note: Britten is the codeveloper of the T50H method).

5. In January 1988, Marks persuaded his Yale colleague, Powell, to produce an independent repetition of S/A's work. Caccone and Powell's (1989) conclusion supported S/A. Marks (1991) denounces Caccone and Powell's work. (Lewin 1988a; 1988b).

6. In 1989, a conference on DNA-DNA hybridization and Evolution was held to resolve the conflicts and to clear the air, so that all concerned could proceed with their work.

Everyone thought this was an end to almost a decade of S/A bashing. However, in 1993, in a book review for *Scientific Misconduct: Where 'Just Say No' Fails*, Marks wrote:

> Indeed the next generation of books on this topic will probably feature the story of Charles Sibley, a researcher in molecular evolution who was arrested in the 1970s for smuggling the eggs of endangered bird species out of England and into his starch-gel apparatus... In the 1980s he resurfaced with a technique called DNA hybridization which solved the problems of avian and primate phylogeny with fanfare enough for election into the National Academy. (*Marks 1993a:382*)

Marks went on to condemn Sibley again for data manipulation. This condemnation in turn outraged the scientific community and, in an issue of the *American Scientist* (1993), the following researchers deplored Marks' behaviour: Sibley and Ahlquist, Britten, Powell, Czelusniak and Goodman, Kirsch and Krajewski , and Brunk. Marks (1993b:410-411) replied with an apology: "I extend my apologies to *American Scientist* and stand duly chastised".

This episode has certainly shed some new light on academic research. These episodes should help the reader be more aware of research criticism, as it has for me.

Conclusion

I have presented a critical analysis of both the technical and general aspects of DNA hybridization research. I have also given the reader an appreciation of the current atmosphere of research in this area. It was my intention to share with the reader the enormous discordance that exists both internally and externally, with DNA hybridization research. It is my position that, when all these factors are taken into consideration, it is very difficult to accept the human-chimpanzee connection suggested by DNA hybridization research. This is not to say that the technique should be made obsolete, but rather that, if DNA hybridization is to stand its ground, it first needs to be purged of its problems both external and internal. Also, its advocates need to work

towards complementarity, rather than conflict, with classical anatomical studies. After all, most of the information that we are now getting from molecular studies for more than a century has been provided to us by anatomical studies.

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Notes

1. Note that all three papers by S/A (1984, 1987, 1990) have been taken to represent one study of hominoid DNA hybridization since each paper was simply a follow-up of the previous one.

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