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Testing hominoid phylogeny with the PHYLIP programs

Computer assisted cladistic analyses were undertaken in order to test the utility of the PHYLIP program and 2. rev to resolve the problem of hominoid phylogeny as approached from comparative morphological computer programs are of great assistance, as long as some idea of ancestral status is possible, but different parsimony assumptions are about equally plausible. But there is no substitute for careful selection of characters, depending on different methods of selection: a *Pan-Homo* clade and a *Pan-Australopithecus* clade can both be supported.

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Computer programs for cladistic analysis

One of the major advances and advantages recently associated with cladistic analysis is the availability of computer programs able to handle the onerous activity of cladogram generation and validation. The two most popular and broadly available are PHYLIP (PHYLogeny Inference Package) by Joseph Felsenstein of the Department of Genetics, University of Washington, Seattle, Washington, U.S.A. and PCLIP (Phylogenetic Analysis Using Parsimony) by David Swafford of the State Natural History Survey, Champaign, Illinois, U.S.A. Both programs are available for a broad range of personal computers, operating under both Macintosh and MS-DOS systems, as well as mini and mainframe computers. A third program which is available to Macintosh users is MacClade by Wayne Maddison, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. The analyses reported here were carried out using Felsenstein's PHYLIP programs.

The PHYLIP program set

PHYLIP is a co-ordinated package containing a number of programs for "phylogenetic inference". PHYLIP is able to generate phylogenetic inferences from discrete state data, gene frequency data, distance matrix data, and molecular sequence data. It also includes a program to amalgamate cladograms from different programs into a final "consensus" tree. The set of programs has been widely disseminated, and is available for virtually any computer system having a Pascal compiler. The currently available Macintosh set is Version 3.1, and has been provided to us by Willem Ellis of the Department of Entomology, Institute of Taxonomic Zoology, University of Amsterdam. Felsenstein uses the term "phylogenetic tree" for the output from the PHYLIP programs throughout the documentation, but we prefer to follow the use as dictated by Eldredge (1979), and call these products "cladograms", reserving the use of phylogenetic tree for the activity of ancestry reconstruction.

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For the purposes of this analysis series, only 12 of the 30 programs in PHYLLIP are employed; the set relevant to discrete characters. These include programs named:

MIX, which uses either Wagner or Camin-Sokal parsimony rules, and allows a specified mixed parsimony criteria set (see Parsimony Table below) to construct character state trees;

METRO, which uses the Metropolis *et al.* (1953) simulated annealing algorithm for similar mixed parsimony models;

PENNY, which is a program to find all of the most parsimonious trees through the use of the "branch and bound" search algorithm (Hendy & Penny, 1982); and

BOOT, a bootstrapped method of repeating sampling with replacement from a data set to determine confidence intervals on mixed method parsimony.

Each of these has an equivalent using the Dollo and Polymorphism parsimony rules below in the form of the programs:

DOLLOP, the equivalent of MIX;

DOLMETRO, using the Metropolis *et al.* algorithm;

DOLPENNY, using the "branch and bound"; and

DOLBOOT for the bootstrapped sampling.

The other relevant program is CONTEM, for the handling of continuous data derived from gene frequency or from measurement sets. These nine programs form the core of the PHYLLIP system as utilized for analysis of discrete state characters. There are three other programs with specific functions which serve as tools to aid the processes of analysis. Two of these are useful before the generation of phylogenies:

FACTOR is a program which expands or "factors" a data set which contains multistate characters (i.e., where a character is scored as having more than just a plesiomorphic and an apomorphic state, such as O, A, B, C, D or 0, 1, 2). FACTOR reduces these to binary form with only ancestral and derived states present, and increases the number of characters in the set. It also writes a control line for other programs to keep track of these multistate character sets, and can generate a hypothetical "ANCESTOR" line from the data set containing the known or calculated ancestral conditions (0 or 1) or a "???" if the plesiomorphic condition cannot be decided by the program. The second is:

CLIQUE, a compatibility program which is used to identify sets of two state characters which change together and hence may represent parts of linked functional complexes. The final program is:

CONSENS, which is used to test the output of the other programs for consensus in the phylogenetic trees produced. This program can be instructed to use either a strict consensus or a majority rule to reach its conclusion.

This subset of PHYLLIP programs uses a standard data format. The format is a matrix of character states recorded, for discrete data, as "zero" or "one", 0 or 1. The data for the continuous data programs are input as "real" numbers with decimal points. The basic file structure starts with a first line containing the number of species and the number of characters in the file, and any options or instructions for the particular program. Each of the following lines allocates the first ten spaces to a taxon identification label or species

name, followed by the character states or real numbers. The data may be separated by spaces between each character, though that is required only for the continuous data programs; in the others it is optional.

The output from each of the programs is either a single most parsimonious cladogram or a set of equally parsimonious cladograms. The programs MIX and DOLLOP also produce two sets of ancillary data: a count of the number of character changes in the associated clade, with a table showing the number of transitions for each character in the whole clade; and a second table showing the steps between each node of the cladogram, and the character changes associated with the two nodes. These tables can then be used to evaluate the results of the program.

Parsimony methods

Each of the parsimony methods applied to cladogram and phylogenetic analysis has slightly varying assumptions underlying it, as well as certain specific allowances for polarity changes. Each method may yield variant cladograms and the resultant phylogenetic trees. All of the accepted parsimony methods can be specified in PHYLLIP, and it is valuable to note the underlying assumptions for each.

Camin-Sokal parsimony derives from the work of Camin & Sokal (1965), and is entirely unidirectional. Camin-Sokal parsimony only allows changes from plesiomorphic to apomorphic states, and of necessity assumes knowledge of the ancestral state. Reversals of polarity are not permitted, as they are considered to be highly improbable occurrences. The Wagner parsimony method was established in the work of Erik & Dahlhoff (1969), and Kluge & Farris (1969). This version of parsimony allows the reversal change from apomorphic to plesiomorphic to occur within a cladogram, and makes no assumption of knowledge concerning the plesiomorphic condition. These two methods differ primarily in the matter of polarity reversals; the assumptions behind them being otherwise essentially the same according to Felsenstein (1988):

- (1) Ancestral states are known (Camin-Sokal) or unknown (Wagner).
- (2) Different characters evolve independently.
- (3) Different lineages evolve independently.
- (4) Changes from plesiomorphic to apomorphic states are much more probable than changes from apomorphic to plesiomorphic (Camin-Sokal), or are equally probable (Wagner).
- (5) Both of these kinds of changes are *a priori* improbable over the evolutionary time spans involved in the differentiation of the group in question.
- (6) Other kinds of evolutionary event such as retention of plesiomorphism are far less probable than plesiomorphic-apomorphic changes.
- (7) Rates of evolution in different lineages are sufficiently low that two changes in a line segment of the tree are far less probable than one change in a short segment (modified from Felsenstein, 1988).

The Dollo parsimony method has no relationship to Dollo's Law (irreversibility as a general characteristic of evolution), but instead derives from work by LeQuesne (1974) and Farris (1977). It is named after the 19th century biologist Louis Dollo since he was one of the first to assert that it is more difficult to evolve a complex feature than it is to lose it. Some of the assumptions (nos 1, 2, 3 and 6) are the same as those of the Camin-Sokal and Wagner methods; others are different:

- (4) The probability of a plesiomorphic to apomorphic change is small over the evolutionary times involved.

- (3) The probability of a polarity reversal is also small, but still far larger than the probability of a plesiomorphic—apomorphic change, so that many reversions are easier to envisage than even one extra apomorphic change.
- (7) The lengths of segments of the true tree are not so unequal that two changes in a long segment are as probable as one in a short segment. (modified from Felsenstein, 1988)

The Polymorphic parsimony method is claimed by Felsenstein as being first used by him, though an example of the results of such an analysis was published by Liger in 1967. Felsenstein published his version of the method in 1979 without knowledge of a contribution by Farris in 1978. This method explains the pattern of state distribution through the mechanism of a single plesiomorphic—apomorphic transformation followed by a pattern of retention of polymorphism for the character; i.e., the plesiomorphic and apomorphic conditions exist side by side. This may be followed by a loss of one or the other state in different lineages to produce the final pattern of states. Felsenstein's assumptions 1, 2, 3 and 4 are the same as those of the Dollo method; the others are as follows:

- (5) Retention of polymorphism is highly improbable, but far more probable than plesiomorphic to apomorphic change, so that we can more easily envisage more polymorphism than even one additional derived change.
- (6) Once the apomorphic state is reached, reoccurrence of the plesiomorphic condition is very improbable, much less probable than multiple retentions of polymorphism.
- (7) The lengths of segments of the true tree are not so unequal that we can more easily envisage retention events occurring in both of two segments than one retention in a short segment (modified from Felsenstein, 1988).

The selection of an appropriate parsimony method for use depends upon the biological realities of the particular case under study, as well as the theoretical perspectives of the researcher. Logically, several parsimony methods should be tried and then a secondary effort made to understand and resolve differences produced in the results. Our hope is that as the popularity of computerized phylogenetic analysis spreads, and the plausibility of the results under the different parsimony methods is assessed, important conclusions on the nature of the evolutionary process itself will emerge.

One of us (Groves, 1986) listed 120 morphological characters which vary among the five extant genera of the Hominoidea (*Hylodotus*, *Pongo*, *Gorilla*, *Par. Homo*), and analysed them cladistically using both Old and New World Monkeys as outgroups. The analysis was performed by hand; inevitably, a few errors recurred, and only the most parsimonious cladogram was fully analysed, with no confidence estimates. The polarity of some of the characters is questionable, and a few are clearly incorrect. Apposite comments on this analysis are by Groves (1987) and Andrews (1988). In view of continuing controversies over the details of hominoid phylogeny (Schwartz, 1986; Marks *et al.*, 1988), it seemed to us that this would be an appropriate case on which to test the comparative qualities of the different methods in the PHYTLP program.

The problem of hominoid phylogeny

The problem of whether the *Homo/Par Gorilla* separation is a genuine three-way split, or can be resolved into two successive dichotomies, is discussed by Groves (1986, 1989). If the trifurcation is to be resolved, then only *Par. Homo* vs. *Gorilla* and *Par. Gorilla* vs. *Homo* are in serious question; there seems to be little or no support for the proposition that *Gorilla* might be the sister taxon to *Homo*.

An alternative, that *Pongo* might actually be the sister taxon to *Homo*, was put forward by

Table 1 Parsimony assumptions for Wagner, Camon-Sokal (C-S), Dollo and Polymorphic parsimony types

Assumption	Wagner	C-S	Dollo	Polymorphic
Universal states are known	No	✓	✓	✓
Different characters evolve independently	✓	✓	✓	✓
Different lineages evolve independently	✓	✓	✓	✓
Probability of changes plesiomorphic to apomorphic	Equal	Small	Small	Small
Probability of changes apomorphic to plesiomorphic	Equal	Very small	Small	Small
Both kinds of changes are a priori improbable	✓	✓	✓	✓
Retention of polymorphism far less probable than plesiomorphic	✓	✓	✓	✓
Retention of polymorphism far less probable than plesiomorphic	✓	✓	✓	✓
Rates of evolution in different lineages are sufficiently low that two changes in a long segment of the tree are less probable than one change in a short segment	✓	✓	✓	✓
Probability of a polarity reversal is small, but far larger than the probability of a plesiomorphic—apomorphic change	✓	✓	✓	✓
Reversions easier to envisage than extra apomorphic change	✓	✓	✓	✓
Retention of polymorphism is highly improbable, but more probable than plesiomorphic to apomorphic change	✓	✓	✓	✓
Retention of polymorphism for both plesiomorphic and apomorphic states is highly improbable	✓	✓	✓	✓
Retention of the plesiomorphic condition is much less probable than multiple retentions of polymorphism	✓	✓	✓	✓

Schwartz (1984, 1986). This hypothesis was quickly shown to be without substantial evidence, but was highly productive in terms of research, and resulted in the publication of an excellent book (Schwartz, 1988). The "Red Ape Hypothesis" therefore joins the ranks of some of the more worthy ideas which history deems wrong but fruitful.

The criticisms of Groves's (1986) cladogram by Andrews (1988) form the starting point for this analysis. Andrew's remarks (1988: 299), that in *Comparative Primate Biology*, "There is not a single computer-assisted phylogeny in any of the chapters, although the data for the hominoids and Ford for the platyrrhine monkeys present their data in a form that makes them available for such an analysis". He states further on that he has investigated the characters listed in Groves's (1986, Table 2a), and would accept 20 of the original 120, further reduction from the 27 in the revised list of Groves (1987). Again, he would reduce the human/chimpanzee synapomorphies from 25 in Groves (1986, Table 2a) to only eight, and would increase the chimpanzee/gorilla list by the addition of knuckle-walking characters (Andrews, 1987) and dental enamel characters (Marin, 1983).

Andrews (1987, Table 2, 3) lists ten "knuckle-walking adaptations" which are included in his states, surely derived characters of a clade which includes gorilla and chimpanzee, as he shows in his 1988 paper, their inclusion (and that of the dental enamel characters) as characteristic of a clade restricted to chimpanzee and gorilla would render such a character human/chimpanzee one about equally supported. There are two problems with this. First is the question of whether most of the knuckle-walking characters, a closely related functional complex as Andrews indeed notes, are really different characters, rather than manifestations of the same character. The question "what is a character?" is a real problem which has all too rarely been asked by cladists (Groves, 1989). For this reason, we should

still be cautious about including them here. The second problem is that they are closely associated with a locomotor complex which *Homo* does not have, but might have had in the past; the throating locomotor specializations of human anatomy are so pervasive that one may doubt whether any knuckle-walking characters would be detectable even if they were part of the human heritage.

The problem associated with the important dental enamel data (Martin, 1985) is similar. Andrews (1987) treats these data as three characters: enamel thickness; pattern 1:3 proportion; and enamel accretion rate. The problem of "how many characters?" is acute; the proportions of patterns 1 and 3 are not independent of enamel thickness nor of accretion rate, because pattern 3 forms at a much higher rate than pattern 1 and so, over a given time, builds to a greater thickness. Clearly there are several characters there, because there are clear differences between gibbon, orang-utan, and chimpanzee/gorilla; but it is not so far possible to discriminate clearly which they are, nor their polarity. Delson (1985) has in fact queried the polarity inference as far as the fossil hominoids *Kenyapithecus* and *Dryopithecus* are concerned, and this is why we feel that, like the knuckle-walking complex, the dental enamel complex needs to be laid to one side and interpreted *a posteriori*—that is to say, only after the most parsimonious cladogram has been constructed using clear-cut characters. Such a plan might, in turn, help to illuminate the polarity of the changes, and indeed the distribution of the characters, in the locomotor and enamel complexes.

The data sets for this analysis series

Five data sets have been utilized in this analysis series. The first set is derived (by JDP) from Groves (1986: Tables 2a, 2b, 3a, 3b, 3c, 4a, 4b, 4c), with the deletion of some characters as per Groves (1987), and the addition of Schwartz's (1986) data for *Pongo* and *Homo* synapomorphies. This set contains 103 characters. The second set was constructed by CPG as an update, involving the further removal of dubious characters, and the addition of multistate forms to 11 of the original characters. This set contained 89 characters, which after running through FACTOR yielded 100 characters for use. Set three consists of the subset of characters from Groves (1986) which were approved by Andrews (1988) and extracted from set one, although (for reasons explained in Groves, 1986) it does not contain the knuckle-walking specializations which Andrews would prefer to add. It contains only 27 characters. The fourth set was extracted from Andrews (1987) and contains 48 characters. The final set, number five, consists of set two with the addition of the ten knuckle-walking characters from Andrews (1987) and two dental enamel originals. The data sets numbers four and five are listed as the appendices; data set two consists of the first 100 items of set five.

Analysis procedures

Data set number one was generated initially for the purposes of testing the PHYLLIP 3.1 (Ellis compiled) programs by one of us (JDP) and discussion of the results led to a decision to proceed with further analyses. Modifications on data set One yielded data set Two, and for comparison purposes sets Three, Four, and Five were generated. Analyses were performed on a 2.5 Megabyte Macintosh Plus under Systems 6.0.2.

Each data set was run through MIN, with both Wagner and Camin-Sokal parsimony regimes, and through DOLLOP for Dollo parsimony. Since no polymorphic characters were included in the data sets, no runs under Polymorphic parsimony were performed.

Initial runs were also performed on data set One with METRO and PENNY. These produced the same results, but at the expense of much longer processing times. Secondary analyses for confidence limits were performed using BOOT, again for Wagner and Camin-Sokal parsimony, and DOLBOOT for Dollo parsimony. It is worth noting that the use of Wagner parsimony produces an unrooted tree, while both Camin-Sokal and Dollo yield rooted trees.

Results

Data set One, 103 characters, consistently resulted in the trees illustrated below. The unrooted version from MIN (Wagner parsimony), METRO, PENNY, Wagner, and BOOT (Wagner), the rooted version produced by MIN (Camin-Sokal), DOLLOP, and DOLBOOT (Camin-Sokal), and DOLBOOT. The confidence level of these trees under each of the repeated sampling procedures is 100%. This is, in a way, not too surprising, as data set One is largely that of Groves (1986), but the modifications adding the data of Schwartz (1986) and the pruning by Groves (1987) did have open the possibility of a different result.

Data set Two resulted from processing by FACTOR which, as noted above, has the ability to generate a hypothetical "ancestor", and to write a line which links the characters derived from the multistate characters together. Both of these capabilities were utilized. Since all of the characters of the original set have both plesiomorphic and apomorphic states across the four species, the program, operating without specific directions, was unable to assign the "ancestor" a known set of plesiomorphic states. The resultant line contained a large number of "?" marks to indicate that the ancestor's state for the character was indeterminate. A set of bootstrapped analyses were run with the indeterminate ancestor, and a second set with the "ancestor" set to a completely plesiomorphic character set.

Initial runs through MIN (both Wagner and Camin-Sokal) and DOLLOP yielded the same trees as data set One (Cladogram 1 and 2). A set of runs through the bootstrapped programs without the "ancestor", but with the "factors" line, yielded the same trees, but with differing confidence in the *Homo*—*Pan* clade. Confidence levels were 60%, 112 of 20 replications) under Wagner, 100% (20 of 20) under Camin-Sokal, and 70% (14 of 20) under Dollo. The triplet of *Homo*—*Pan*—*Gorilla* occurs at 100% in all runs, leaving *Pongo* as the outgroup.

The bootstrapped runs with the "indeterminate ancestor" and the "factors" resulted in three distinct trees each related to the type of parsimony in control. Wagner parsimony confidence levels of 35% (7 of 20), 30% (10 of 20), and 100% (Camin-Sokal parsimony resulted in *Pan*—*Gorilla* clade, joined with *Homo* and *Pongo* as the outgroup (Cladogram 1, again with confidence levels of 30%, 30% and 100%). The Dollo parsimony yielded a pattern identical to Cladogram 2, but with the *Homo*—*Pan* clade at the 30% level and the *Homo*—*Pan*—*Gorilla* clade at 70%. It is obvious that resultant trees produced by the program are heavily dependent upon the form of parsimony chosen when an "indeterminate ancestor" is part of the analysis. In general, however, it is clear that there is a wide measure of agreement over the ancestral state of many of the characters, so that use of an "indeterminate ancestor" may be considered the least appropriate situation for this set of analyses.

The final series of runs on data set Two utilized a "plesiomorphic ancestor" in which

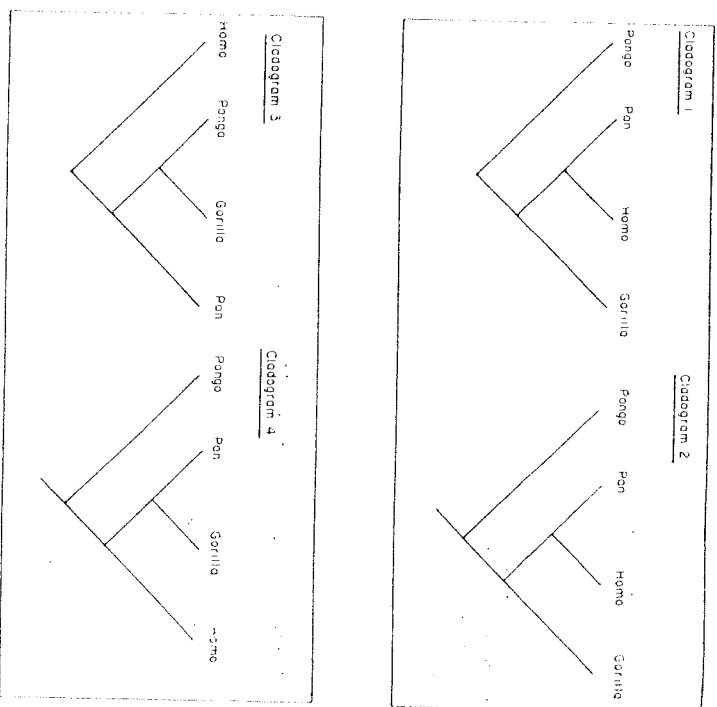


Figure 1

every character is set to the primitive condition, and the "factors" line controls the evaluation of the data derived from the multistate characters. The result is a cladogram identical to Cladograms 1 and 2 for the appropriate parsimony modes. The levels of confidence, do however, differ between the three types. These are presented as Table 2.

Data set Three consists of the 27 characters which Andrews (1988) views as the acceptable few from Groves (1986). In all runs, MIN (Wagner; Camin-Sokal), DOLLOP, BOOT (Wagner; Camin-Sokal), and DOLBOOT yielded trees identical to Cladograms 1 and 2. The levels of confidence for all segments of the bootstrapped cladograms was uniformly at 100%.

Data set Four, the 48 characters derived from Andrews (1987), provides a distinctive cladogram, one which is also produced by data set Five. Both runs of MIN (Wagner & Camin-Sokal) and that of DOLLOP provided the same relationships, presented as Cladogram 5 (unrooted—Wagner) and Cladogram 6 (rooted—Camin-Sokal and Dollo). In interpreting these cladograms, the data from the two MIN runs and the DOLLOP

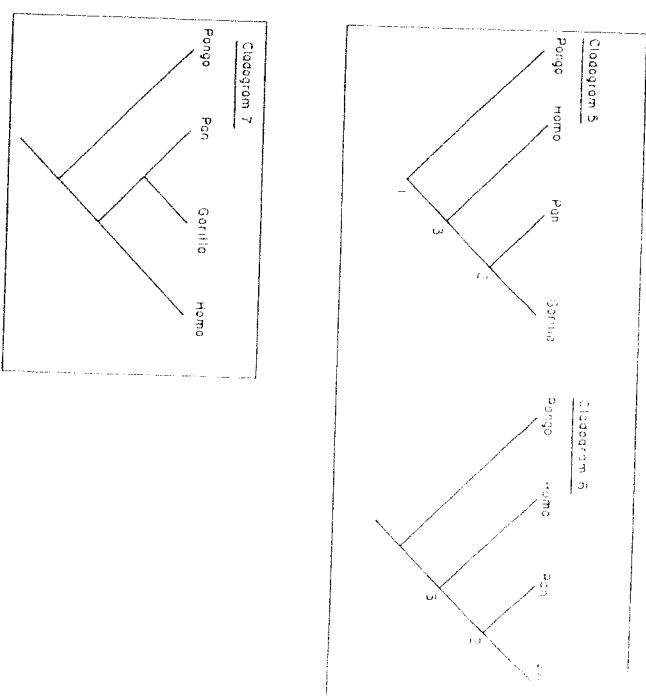


Figure 2

run indicate that there are no changes from the node numbered as 3 to node *Homo* and further that there are no changes from node 2 to either of node *Pan* or node *Gorilla*. Superficially this data set indicates that the two latter genera are inseparable, and that the African apes are derived from a *Homo*! Perhaps this is support for Kurtén's (1972) view that the African apes are derived from a *Homo*-like ancestral form. The results from the bootstrapped runs are uniformly as Cladogram 7 (rooted and unrooted versions are the same) and are all of 100% confidence level (20 of 20).

Data set Five, 114 characters, consistently yielded cladograms identical to the illustrated 5, 6, and 7 versions, that is they were identical in form to those produced from Andrews (1987) data. This was consistent throughout all runs, and seems to indicate the extreme importance of the set of knuckle-walking characters to this analysis. Throughout *Pongo* the outgroup sample with the *Homo*, *Pan*, and *Gorilla* clade consistently grouped together, as is the *Pan*—*Gorilla* pairing.

All bootstrapped runs, both with the "indeterminate ancestor" and the "plesiomorphic ancestor", irrespective of the parsimony mode employed, produced the equivalent Cladogram 7, although with variances in the levels of confidence in the clades. The presented in Table 3.

Table 2

Clade	Levels of confidence for 3 modes of parsimony, plesiomorphic ancestor, 99 characters (100 derived characters)		
	Wagner	Camino-Sokal	Dollo
<i>Pan-Homo</i>	85% 17 of 20)	60% 12 of 20)	85% 17 of 20)
<i>Pan-Homo-Gorilla</i>	100% 20 of 20)	95% 19 of 20)	100% 20 of 20)

Discussion

From our exploratory application of PHYLLIP to the problem of hominoid phylogeny, it is obvious that computerized processing is a valuable addition to the compendium of techniques available to the taxonomist. However, the general rule about the use of computers, the infamous "Garbage In—Garbage Out" or GIGO principle, persists in the way of cladograms and phylogenetic tree construction, they only constitute pictographic representation of the data set. If the selection of characters and estimation of their polarity falls short in any way, the validity of the cladogram becomes suspect, and the resultant phylogenetic tree becomes, at least potentially, unusable.

Part of the original data set (data set One, the characters listed in Groves, 1986; has been criticized by Andrews (1988) and corrected by Groves (1987). In the form used for the initial analyses, it contained a number of characters which demonstrated substantial overlap in ranges. The effect of these characters under PHYLLIP appears to have been the generation of clearer dichotomies between the four genera. Each character was treated as a binary state rather than a continuous variable. The partitioning of the character into just two discrete forms thus reinforced the differences in the data, and led to a higher confidence level. Purging the data of these false dichotomies and a reconsideration of some further characters which reflected progressive or sequential changes led to data set Two. The 89 features which we would prefer to use for the generation of cladograms.

The differences between sets Three and Four are instructive. The 48 characters of data set Four are those in Tables 2.1, 2.2, and 2.3 (Andrews, 1987). They consist of 20 synapomorphies of the Orang clade, the opposite state of which can be taken as apes and humans linked with presumed plesiomorphy in the Orang clade; and finally 16 synapomorphies between *Pan* and *Gorilla* which thus can be related to plesiomorphic conditions in *Pongo* and *Homo*. On inspection of the data set (in the Appendices) it can be seen that *Pan* and *Gorilla* are identical in all character states. This is the mechanism which generates the 100% confidence level in a *Pan-Gorilla* clade for Andrews data set.

Data set Five and the results from it were a surprise to us. We had not expected the addition of the knuckle-walking characters to make such a strong and consistent difference in the cladograms. In particular it was expected for Dollo parsimony, that the higher probabilities for reversion to a less specialized hand structure, a neotomous process, could confirm a *Pan-Homo* clade. It can, however, be noted in Table 3 that, for the plesiomorphic ancestor, Dollo produced a 100% level of confidence. While it would appear that the knuckle-walking specializations—ten characters—and the enamel features are

Table 3

Clade	Levels of confidence for 3 modes of parsimony in data set Five, 101 characters (114 derived characters)		
	Wagner	Camino-Sokal	Dollo
Bootstrapped, no ancestor			
<i>Pan-Gorilla</i>	100% 20 of 20)	100% 20 of 20)	100% 20 of 20)
<i>Pan-Gorilla-Homo</i>	90% 18 of 20)	73% 15 of 20)	84% 17 of 20)
Bootstrapped, indeterminate ancestor			
<i>Pan-Gorilla</i>	100% 20 of 20)	100% 20 of 20)	100% 20 of 20)
<i>Pan-Gorilla-Homo</i>	95% 17 of 20)	100% 20 of 20)	70% 14 of 20)
Bootstrapped, plesiomorphic ancestor			
<i>Pan-Gorilla</i>	100% 20 of 20)	100% 20 of 20)	100% 20 of 20)
<i>Pan-Gorilla-Homo</i>	50% 10 of 20)	70% 14 of 20)	100% 20 of 20)

very important to the distinction of the *Pan-Gorilla* clade, we still express a degree of reservation about the validity of these characters.

Conclusions

(1) *The PHYLLIP package* appears to be a valuable resource for the analysis of taxonomic relationships. The programs are relatively simple to operate, but one aspect of their design is irritating to one of us (JDP) in that variations in parsimony, and the number of replications, must be specified within the data file, not set as program options at run time. This results in a proliferation of data files, each slightly different, and this can rapidly become burdensome when performing extended series of analyses. The Macintosh version also misbehaves somewhat in that it does not properly "clean-up" after itself and restore the system to its original condition. This is most obvious in the compression of the menu characters and window titles. These are all minor problems which are likely to be cleared up in future releases. An aspect which is unlikely to change is the relative slowness of many of the programs, especially where either larger numbers of taxa or characters are being used. The MIX and DOLLOP programs ran in two to three minutes during our tests, but the BOOT and DOLBOOT programs, due to the repeated sampling, took 20 to 40 minutes to complete their operations. At this point the only option to speed up processing is to use a faster computer (BOOT and DOLBOOT run in 6 minutes on a Macintosh IIx). In spite of these minor flaws, our conclusion is that PHYLLIP is a worthwhile addition to any taxonomist's toolkit.

As to the various parsimony options in the package, we are unable to draw definitive conclusions, except to note that if consistency is any guide, the Wagner, Camino-Sokal and Dollo methods score about equally highly. But considering the results from data set Two,

we urge that at least some ancestral states be available if at all possible, as the potentiality for nonsense results under an "indeterminate ancestor" regime is considerable.

(2) *The phylogeny of the Hominoidea*

In the matter of hominoid phylogeny, we conclude (in response to one of Andrews' 1988 criticisms of the Swindler & Erwin volume) that the use of a computer program to generate cladograms is no substitute for careful attention to character selection, and examination of the character states. The first order of attention must be to the data and, in that respect, we feel that our Data set Two, representing 89 hominoid characters, is to be preferred. After testing it in a number of ways we conclude that it is more extensive than Andrews' 1987 data. While data set Five should undoubtedly be favoured due to its inclusion of the knuckle-walking complex and the dental characters, we retain some reservations about their validity as useful characters. While it is still possible that a "trichotomy" may exist between *Homo*—*Pan*—*Gorilla* (and we accept that the levels of confidence in our preferred cladograms do not reject this possibility), we do feel that our Cladograms 1 and 2 and the set of Cladograms 5, 6 and 7 represent the most acceptable alternative patterns at present. These result in the nested patterns of:

((((Homo, Pan) Gorilla) Pongo) for data set Two, and
 (((Gorilla, Pan) Homo) Pongo) for data set Five as the preferred cladograms.

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Appendix
Data Set Four

#	Character	Homo	Par	Coriida	Pingu
1	Orbits higher than broad	0	0	0	1
2	Interorbital pillar narrow	0	0	0	1
3	Reduced glabella	0	0	0	1
4	Mouth zygomatic foramina, above inf. marg. of orbit	0	0	0	1
5	Palatine foramen small, slit-like	0	0	0	1
6	No incisive fossa	0	0	0	1
7	Nasal floor unstepped	0	0	0	1
8	Ulnar styloid process does not contact scaphoid	0	0	0	1
9	Inteross. 11 > 12 (130-200%)	0	0	0	1
10	Molars with low dentine horns	0	0	0	1
11	Enamel partly pattern 1, intermediate, slow formed	0	0	0	1
12	Molars with deep secondary wrinkling	0	0	0	1
13	Proessus vaginatus persists	0	0	0	1
14	Large parts intermedia of adenohypophysis	0	0	0	1
15	Proessus infundibul present	0	0	0	1
16	Small axillary organ	0	0	0	1
17	Scalp hair on scalp: 160 cm ⁻³	0	0	0	1
18	Fliform tongue papillae restricted to middle region	0	0	0	1
19	Furiform tongue papillae few	0	0	0	1
20	Small gall bladder, lacking bend	0	0	0	1
21	Frontal sinus present	0	0	0	1
22	Supraorbital tori developed, continuous	1	1	1	0
23	Postorbital sulcus developed	1	1	1	0
24	Greater middle ear depth (8.5-12.5 mm)	1	1	1	0
25	Fusion of os centrale to scaphoid	1	1	1	0
26	Subdivision of the prostate	1	1	1	0
27	Large uterus	1	1	1	0
28	Apocrine glands sparsely distributed over body	1	1	1	0
29	Ecrine glands abundant over body	1	1	1	0
30	Large axillary organ	1	1	1	0
31	Small single larynx tuberculum cuneiforme	1	1	1	0
32	Low proportion (3-21%) type 1 aorta	1	1	1	0
33	Six sacral vertebrae	1	1	1	0
34	Short ethmoid-lacrimal contact (40-90%)	0	0	0	1
35	Fronto-maxillary contact in orbits (30-50%)	0	0	0	1
36	Thin enamel	0	0	0	1
37	40% pattern 1 enamel	0	0	0	1
38	Enamel accretion rate < 1.5 μ m/day	0	0	0	1
39	Dorsal transverse ridges on metacarpal heads	0	0	0	1
40	Dorsal extension of articular surface of metacarpals	0	0	0	1
41	Dorsal ridges on distal radius and scaphoid	0	0	0	1
42	Volar and ulnar inclination of dist. art. surf. of radius	0	0	0	1
43	Well developed trochlear ridge of humerus	0	0	0	1
44	Very deep olecranon fossa of humerus	0	0	0	1
45	Thumb short relative to body weight	0	0	0	1
46	Flexor digitorum superficialis strongly developed	0	0	0	1
47	Shortened flexor tendons	0	0	0	1
48	Knauckle pads over middle digits	0	0	0	1

Note: Data binary coded 0 = plesiomorphic condition, 1 = apomorphic condition.

Appendix
Data Set Five (Data Set Two consists of items 1-100)

#	Character	Homo	Par	Coriida	Pingu
1	Palmar pattern intensity not greater than plantar	1	1	1	0
2	Relative lower limb length above 120	1	1	1	0
3	Dental eruption delayed	1	1	1	0
4	Palatine ridges to p ² or M ¹	1	1	1	0
5	Ileocecal valve compressed	1	1	1	0
6	Proessus vaginatus obliterated in adult	1	1	1	0
7	Uterus broad > 37 mm (Mullisate 1a)	1	1	1	0
8	Uterus broad > 37 mm (Mullisate 1b)	0	0	0	1
9	Anterior papillary muscle of heart single	1	1	1	0
10	A. recurrens ulnaris splits anterior-posterior	1	1	1	0
11	Few or no apocrine glands over body surface	1	1	1	0
12	Large elaborated axillary organ	1	1	1	0
13	Scalp more densely haired than dorsum (Mullisate 2a)	1	1	1	0
14	Scalp more densely haired than dorsum (Mullisate 2b)	1	1	1	0
15	No embryonic parts intermedia of adenohypophysis	1	1	1	0
16	Gut length > 91 times head and body length	1	1	1	0
17	Small intestine > 8 times head and body length	1	1	1	0
18	Middle ear depth > 6.3 mm	1	1	1	0
19	Can. orifice submandibular & greater sublingual gland	1	1	1	0
20	Inner ear area > 60 mm ²	1	1	1	0
21	Eardrums present	1	1	1	0
22	Frontomaxillary suture in orbit	1	1	1	0
23	Hamate vert. align. spiral facet, conjunct rotation	1	1	1	0
24	Os centrale fused to scaphoid earlier than ulnare	1	1	1	0
25	Frontal sinuses present	1	1	1	0
26	Pyritorn aperture broad, squared interior margin	1	1	1	0
27	Relative upper facial height < 80	1	1	1	0
28	Plasma testosterone < 1000 ng/100 ml	1	1	1	0
29	Posterior cervical spines lengthened (Mullisate 3a)	0	0	0	1
30	Posterior cervical spines lengthened (Mullisate 3b)	0	0	0	1
31	Humerus longer than femur (Mullisate 4a)	0	0	0	1
32	Humerus longer than femur (Mullisate 4b)	0	0	0	1
33	Relative upper limb length > 170	0	0	0	1
34	Relative hand length > 40 (Mullisate 5a)	0	0	0	1
35	Relative hand length > 40 (Mullisate 5b)	0	0	0	1
36	M. flexor pollicis longus rudimentary/absent (Mullisate 6a)	0	0	0	1
37	M. flexor pollicis longus rudimentary/absent (Mullisate 6b)	0	0	0	1
38	Patrotid gland orifice opposite p ²	0	0	0	1
39	Tubia magna absent in adult	0	0	0	1
40	Facial index > 70	0	0	0	1
41	A. recurrens radialis from A. brachialis	0	0	0	1
42	Appendix > twice length of cecum	0	0	0	1
43	Clans penis lacking corona	0	0	0	1
44	Relative chest girth > 180	0	0	0	1
45	Foliate papillae mostly dorsal in location	0	0	0	1
46	Throat sack enlargement, lobated (Mullisate 7a)	0	0	0	1
47	Throat sack enlargement, lobated (Mullisate 7b)	0	0	0	1
48	Kidney large > 0.4% of body weight	0	0	0	1
49	Metacardial of P ₁ enlarged	0	0	0	1
50	Upper ear height 40% of ear length	0	0	0	1

#	Character	Homo	Pan	Canis	Range
31	Gall bladder with very slight or no bend	1	0	0	1
32	Parotid glands with small accessory lobes	1	0	0	1
33	No sexual swelling	1	0	0	1
34	Fused incisor foramina	1	0	0	1
35	Scapula short, deep, with nearly horizontal spine	1	0	0	1
36	Retardation of shoulder & wrist ossification	1	0	0	1
37	Reduced talar tubercle	1	0	0	1
38	Development of cerebral asymmetry	1	0	0	1
39	Hand preference	1	0	0	1
40	High oestral levels in late pregnancy	1	0	0	1
41	1 st similar in size and shape to 1 st	1	0	0	1
42	Basal keel of lower canine absent	1	1	0	0
43	Sulcus obliquus of lower molars reduced	0	0	1	1
44	Ankle epiphyses fuses at same time as hip & elbow	1	1	0	1
45	Liver with only two lobes	1	1	0	1
46	Puberty delayed to >7 years	1	1	0	1
47	Pendulous scrotum	1	1	0	1
48	Uterine fundus flattened sagittally	1	1	0	1
49	Baculum reduced <60 mm or absent	1	1	0	1
50	Erect penis large >80 mm in length	1	1	0	1
51	Prominent labia minora	1	1	0	1
52	Ejaculate volume of >1 ml	1	1	0	1
53	Cranial end of heart opposite 2nd rib (Multistate 8a)	1	1	1	0
54	Cranial end of heart opposite 2nd rib (Multistate 8b)	1	1	0	0
55	Thoracalis suprema artery present	1	1	1	0
56	Hair on dorsum reduced <100 cm ² (Multistate 9a)	1	1	1	0
57	Hair on dorsum reduced <100 cm ² (Multistate 9b)	1	1	0	0
58	Only three lobes on right lung	1	1	0	1
59	Throat sac reduced, few or no recesses	1	1	0	1
60	Parotid gland free from M. sternocleidomastoidus	1	1	0	1
61	Molar protoconid grooves reduced (Multistate 10a)	1	1	0	1
62	Molar protoconid grooves reduced (Multistate 10b)	0	1	1	1
63	Axis of ear bones over 90°	1	1	0	0
64	Spine of Axis (C2) <150% of body height	1	1	0	0
65	No thorax luteinization in second half of cycle	1	1	0	0
66	Deep head of M. flexor pollicis brevis absent	0	1	1	1
67	Parotid gland small	0	1	1	1
68	White pygal pit in infant, at least	0	1	1	1
69	Trigonid basin enlarged	0	1	1	1
70	Brachial index <80	1	0	1	1
71	Power arm of foot >35% of lever (Multistate 11a)	1	1	1	0
72	Power arm of foot >35% of lever (Multistate 11b)	1	0	1	0
73	Fluorescent booties in sperm	1	0	1	1
74	Chest hair sparse <5/cm ²	1	0	1	1
75	Ear breadth <70% of length	1	0	1	1
76	Valvulae conniventes well developed in adult	1	0	1	0
77	Gestation length more than 200 days	1	0	1	0
78	Testes less than 0-1% of body weight	1	0	1	1
79	Ovaries >40 mm long	1	0	1	1
80	Interstitial tissue abundant in pregnant state	1	0	1	0
81	Dorsal transverse ridges on metacarpal heads	0	1	1	0
82	Dorsal extension of articular surface of metacarpals	0	1	1	0
83	Dorsal ridges on distal radius and scaphoid	0	1	1	0

#	Character	Homo	Pan	Canis
104	Valvar and ulnar incination of dist. art. surf. of radius	0	1	1
105	Well developed trochlear ridge of humerus	0	1	1
106	Very deep olecranon fossa of humerus	0	1	1
107	Thumb short relative to body weight	0	1	1
108	Flexor digitorum superficialis strongly developed	0	1	1
109	Shortened flexor tendons	0	1	1
110	Knuckle pads over middle digits	0	1	1
111	Enamel thickness (Multistate 12a)	1	0	0
112	Enamel thickness (Multistate 12b)	1	0	0
113	Proportion Pattern 1 Enamel (Multistate 13a)	0	1	1
114	Proportion Pattern 1 Enamel (Multistate 13b)	0	1	1

Note: Data binary coded 0 = plesiomorphic condition, 1 = apomorphic condition