Current events

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The significance of *Otavipithecus namibiensis* to interpretations of hominoid evolution

Journal of Human Evolution (1994) **27**, 385–394

Nothing else is nearly so important in systematics as a carefully assembled set of characters for which ranges and pattern of variation (age, sexual dimorphism, pathology, interspecific, etc.) are well established. Glenn Conroy (1994) presents a different view of methodological rigor in systematics. There are so many different perspectives on methodology in systematics that a debate on these points in this context would not be fruitful. Neither is it particularly enlightening to characterize previous research as plagued with *a priori* and *post hoc* assumptions, as Conroy does, without specific references to these fatal flaws.

Conroy's analysis of phylogenetic relations among Miocene hominoids is based on a very small data set derived from a single anatomical complex, to use his term, the mandible and lower dentition. Compared to all other Miocene hominoid genera *Otavipithecus* is the least well known, and is represented only by a structure that has proven very difficult to assess from a phylogenetic perspective. When the sample consisted mostly of mandibles or fragmentary maxilla, the affinities of *Sivapithecus, Ramapithecus, Kenyapithecus, Dryopithecus* and *Proconsul* were thought to be very different from current interpretations based on much more complete material. Though it is theoretically possible that analysis of the mandible and postcanine dentition alone could provide an accurate reconstruction of hominoid phyletic relations, this is much more likely to result from analyses that include more data from a diversity of anatomical regions. The more restricted a character set is, the less likely the character tree generated from it will be an accurate reflection of a phylogenetic tree derived from more numerous anatomical complexes. Nevertheless, *Otavipithecus* does potentially represent a new outgroup, and a careful analysis may reveal new insight into hominoid relations. However, the incongruities in Conroy (1994) compared to other work on Miocene hominoid systematics, and the restricted nature of the data base, suggest that there is a problem with this analysis, either in terms of the phylogenetic relevance of the included characters or the manner in which they were coded for each taxon. In this paper I will detail specific problematic areas of Conroy's argument and suggest an alternative interpretation.

There is no necessary association in systematics between rigorous, competent analysis and numerical methods applying one computer algorithm or another (*contra* Conroy, 1994). There is a recognition among scientists generally that, *in the absence of a reason to believe otherwise*, the simplest explanation is the best, a point of logic often attributed to the 14th century philosopher William of Ockham and usually referred to in systematics as parsimony (Tassy, 1991). This, however, is hardly an advocacy in evolutionary biology of cladistic *versus* phenetic *versus* evolutionary approaches, nor does it have much to do with software. There is nothing bad about the use of software to perform the *clustering* portion of phylogenetic analysis. This can be quite useful in testing hypotheses generated by non-computer means. Unfortunately, software cannot replace common sense, awareness of variation, and attention to detail.

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Conroy (1994) suggests that it is unlikely that *Otavipithecus* is closely related to *Afropithecus leakeyi* because they are separated in space and time. Despite his claims of pure scientific objectivity, it is in fact an *a priori* assumption to rule out phylogenetic relationship based solely on temporal or spatial separation. Even conspecificity or congenerity, a taxonomic as opposed to a phylogenetic question, is not impossible, as evidenced by such taxa as *Papio, Macaca, Pliopithecus, Aotus, Sivapithecus, Dryopithecus* and others, widespread in space and time. Ultimately the only relevant criterion in determining phylogenetic relations is morphology.

The results of the cladistic analysis of catarrhine mandibles in Conroy (1994) are surprising at first glance. To my knowledge this is the first suggestion of a sister group relation between a *Pliopithecus/Dendropithecus* clade and large bodied hominoids excluding *Proconsul.* Most of the evidence argues for a closer relationship among large bodied forms (Fleagle, 1983; Fleagle & Kay, 1983; Andrews, 1978, 1985; Harrison, 1987; Martin, 1986; Andrews & Martin, 1987; Szalay & Delson, 1979; Walker & Teaford, 1989). Based on much larger data sets, the positions of *Afropithecus, Dryopithecus,* and *Kenyapithecus* proposed by Conroy are also highly unlikely (Andrews, 1985; Martin, 1986; Andrews & Martin, 1987; Pickford, 1985; Begun, 1992*a,b*; Leakey *et al.*, 1988; McCrossin & Benefit, 1993).

Character choice, polarity determination, and taxon coding are the parts of any phylogenetic analysis that require the highest level of analytical rigor. As it turns out, a few of Conroy's characters need to be dropped, a number added, and most modified, at least in terms of the way they are defined and distributed among the taxa included in his analysis (see below). Conroy's analysis of the *Otavipithecus* mandible is restricted to characters that come from some previously published lists (Martin, 1986; Andrews, 1985), though additional features could have been included. His 13 characters are a selection of traits from these lists. Curious by their presence are several characters not preserved on the specimen. Examination of the original specimen, a good cast (I am grateful to Glenn Conroy for providing this to me), and published photographs (Conroy *et al.*, 1992*a,b*), indicate that the canine is represented only by an obliquely broken root lodged deep in its alveolus, and the P_3 is preserved only distolingually. Is this what Conroy means by being "creative in seeking synapomorphic features", (Conroy, 1994)? It is useless to speculate on the details of the morphology of these teeth. Curious by their absence from his list, despite being apparent on the specimen, are several characters from the lists of Andrews (1985), Martin (1986), and other citations provided by Conroy. These include P_4 talonid height, symphysis robusticity, and M_1 size relative to M_2.

In order to compare *Otavipithecus* more completely and more rigorously to previously analysed hominoid taxa, Conroy's characters 1–3 must be dropped, while three additional mandibular characters known to vary among hominoid taxa can be added (Table 1). In addition, Conroy's character 6 is actually two separate characters, since tapering and reduction of M_3 occur separately (de-coupling) among various hominoids. Character 7, enamel thickness, has to my knowledge only been measured indirectly on *Otavipithecus* and in a manner not directly comparable to the measurements provided by Martin (1985). In addition, there is some question as to ranges of variation in enamel thickness among hominoids, particularly among those within the thin and intermediate categories (Martin, 1993). For these reasons, character 7 is removed from this analysis as well. Conroy's character 13 is a mixture of several characters that vary independently among Miocene and extant hominoids, as is the case for character 6. It can be divided into at least two separate characters (Table 1). This leaves a total of 14 characters. A more detailed analysis of this specimen would undoubtedly uncover still more attributes, but 14 should be sufficient to test Conroy's conclusions in the manner he suggests.

Table 1 Characters included in this analysis and their polarities (outgroup=*Propliopithecus*)

Character	States		
1	0=strong cingulum	1=moderate cingulum	2=weak cingulum
2	0=square M_1-M_2 (<1·09)	1=rectangular M_1-M_2 (>1·10)	
3	0=long M_3 (>1·16)	1=shorter M_3 (<1·14)	
4	0=tapered M_3	1=non-tapered M_3 (<1·08)	
5	0=gracile mandible (<60)	1=robust mandible (63–67)	2=very robust (>74)
6	0=tooth rows divergent	1=tooth rows more parallel	
7	0=ITT[1] weak	1=ITT≥STT[2]	
8	0=narrow incisor region	1=wider incisor region	
9	0=P_4 (0·92–0·95)	1=longer P_4 (>100)	2=shorter P_4 (<91)
10	0=low P_4 talonid	1=high P_4 talonid	
11	0=centralized cusps	1=peripheralized cusps (broader basins)	
12	0=gracile symphysis	1=robust symphysis	
13	0=M_1 <75% of M_2	1=M_1 >79% of M_2	
14	0=tall molar cusps	1=lower, more rounded cusps	

1. ITT-Inferior transverse torus.
2. STT-Superior transverse torus.

The next step is to determine the distribution of characters among the taxa included in the analysis and to identify an outgroup. Conroy (1994) does not specifically identify an outgroup, though this presumably consists of *Propliopithecus, Pliopithecus* and *Dendropithecus*. *Propliopithecus* is the most primitive, according to Conroy's data matrix and to numerous previous analyses, and is defined here as the outgroup taxon. Specifying *Propliopithecus* as the outgroup means that the character states in *Propliopithecus* are initially taken to be primitive, unless they can be shown to be autapomorphic (see below). This results in changes in the polarity of a number of characters compared to Conroy's assessment. P_4 length is intermediate in *Propliopithecus* compared to some other catarrhines (Table 2), so P_4 of intermediate length is considered primitive, while shorter and longer P_4 are derived states for the taxa included in this analysis, which differs from Conroy's polarity assignment. The same is true for molar length, which is short in *Propliopithecus*.

A number of the characters included in this analysis can be quantified (Table 2), which allows for a more reproducible determination of character state for each taxon. When this is done, in addition to the changes in polarity noted above, many of the character state determinations for individual taxa listed by Conroy are shown to be incorrect. For example, *Dryopithecus* is said by Conroy to have deeper mandibles, and a longer P_4 than *Otavipithecus* when in fact it has a shorter P_4 and mandibles of the same thickness relative to depth (Table 2). *Proconsul* also has a shorter P_4 than *Otavipithecus*, and not the reverse. Metric data were converted to non-metric scores for character state coding by defining states where the largest differences among means occurred. Although defining character states by ranking means can be criticized (e.g., Trinkaus, 1990), means are merely statistical approximations of a central tendency toward a morphological difference and are no different from widely used qualitative assessments of morphological differences among taxa for which some overlap in traits is documented. The method of scoring used for these seven traits is arbitrary but has the advantage of being an explicit metric criterion as opposed to a subjective non-metrical assessment. Ranges for each measurement are provided where they are available in order to more completely evaluate the differences among taxa in these characters.

Table 2 Means, ranges and sample sizes of metric attributes included in Conroy's character list

Taxon	Mand. T/D	M1	M2	M1-M2	M3	M3 taper	P4
Propliopithecus[1]	46	1·07 (17) (0·98–1·18)	1·02 (16) (0·91–1·10)	73·6 (14) (57–96·9)	1·25 (14) (1·10–1·33)	strong	0·92 (14) (0·80–1·08)
Pliopithecus	53	115 (12) (1·03–1·24)	1·13 (11) (1·05–1·24)	84·9 (7) (79·6–89·4)	1·27 (6) (1·15–1·41)	strong	1·02 (9) (0·94–1·12)
Dendropithecus	50 (9) (42·2–58·2)	1·25 (14) (1·15–1·33)	1·20 (16) (1·12–1·32)	73·3 (4) (72·4–74·4)	1·25 (13) (1·17–1·36)	1·09 (12) (1·03–1·14)	1·10 (10) (0·88–1·27)
Otavipithecus	64·8	1·12	1·09	70·2	1·23	1·04	1·02
Afropithecus	56·8 (est.)	—	1·12 (4) (1·07–1·12)	—	1·28 (3) (1·26–1·30)	strong	0·93 (3) (0·86–1·03)
Proconsul	55·9 (11) (43·3–65·6)	1·15 (29) (1·06–1·22)	1·15 (19) (1·03–1·33)	70·2 (12) (58–80)	1·26 (21) (1·14–1·47)	1·08 (21) (1·00–1·17)	0·94 (29) (0·83–1·16)
Kenyapithecus	89·6	1·14 (8) (1·07–1·23)	1·10 (3) (1·07–1·16)	62·5 (2) (61·0–64·0)	1·17 (5) (1·10–1·23)	strong	0·94 (6) (0·84–1·15)
Griphopithecus	—	1·10	1·11	75·0	1·22	strong	0·90
Çandir	84·4	1·06	1·06	78·9	1·21	1·24	0·79
Sivapithecus	64·2 (11) (57–83)	1·12 (15) (1·06–1·28)	1·16 (19) (1·03–1·28)	74·6 (14) (58·7–86·7)	1·20 (29) (1·00–1·28)	1·08 (19) (0·92–1·28)	0·86 (21) (0·74–1·00)
Pongo	53 (20) (44–65)	1·10 (125) (1·03–1·23)	1·07 (110) (0·94–1·33)	84·8 (20) (76–100)	1·12 (113) (0·98–1·25)	weak	0·94 (13) (0·83–1·00)
Dryopithecus	63·8 (7) (56·4–74·6)	1·15 (21) (1·01–1·28)	1·14 (21) (1·04–1·26)	79·4 (11) (75·1–90)	1·20 (11) (1·10–1·32)	1·09 (13) (1·05–1·19)	0·95 (12) (0·85–1·12)
Ouranopithecus	66·4 (3) (46·8–80·2)	1·14 (3) (1·11–1·16)	1·12 (4) (1·08–1·19)	81·8 (3) (78·0–86·9)	1·21 (2) (1·19–1·24)	1·16 (2) (1·12–1·20)	0·84 (2) (0·80–0·88)
Gorilla	59 (40) 65 (20)♀ 54 (20)♂ (55–83) (45–71)	1·15 (370) (1·00–1·23)	1·14 (370) (0·98–1·27)	80·0 (20) (73–87)	1·13 (335) (0·98–1·27)	1·12 (40) (1·01–1·25)	0·89 (50) (0·71–1·06)
A. afarensis	74·7 (7) (66·7–91·2)	1·04 (11) (0·97–1·13)	1·04 (15) (0·93–1·18)	83·6 (7) (79·2–94·6)	1·10 (7) (0·99–1·21)	strong	0·87 (4) (0·78–0·93)
Pan	58 (40) (45–74)	1·11 (231) (1·00–1·28)	1·06 (231) (0·92–1·27)	98·2 (20) (84–115)	1·07 (218) (0·77–1·29)	weak	0·89 (11) (0·80–0·96)

Measurements as defined in Pilbeam (1969) and Andrews (1978). Mand. T/D=mandibular corpus thickness relative to depth @ M_2 (100); P4, M1, M2 and M3=ln/bd; M1-M2=ln × bd/ln × bd (100); M_3 taper=trigonid bd/talonid bd. Values for *Otavipithecus* from Conroy *et al.* (1992*a*). Mand. T/D in *Otavipithecus* calculated from measurements in Conroy *et al.* (1992*a*) appears high compared to measurements on the cast and high quality photos in Conroy *et al.* (1992*b*). The measurements may have been taken differently than in the other specimens reported here, and the ratio could be closer to *Afropithecus*, *Gorilla*, and *Pan*.

Mandibular shape in *Gorilla* given for males and females, illustrating the typical pattern of robusticity in male *vs.* female hominoids. Values for *Griphopithecus* are based on ratios of the Paşalar sample means in Alpagut *et al.* (1990). Data on the Çandir mandible, which is usually attributed to the same taxon as Paşalar, were collected by the author. In a few instances where measurements are not available a qualitative assessment is given. Measurements are from the author's data and many additional sources (McCrossin & Benefit, 1993; Leakey *et al.*, 1988; Kelley, 1988; Greenfield, 1974, 1975, 1979, 1980; Kay, 1982; Pilbeam *et al.*, 1977, 1980; Gregory & Hellman, 1926; Gregory *et al.*, 1938; Frayer, 1974; Prasad, 1962, 1964, 1969; Conroy *et al.* 1992; Tekkaya, 1974; Pickford, 1985; Pilbeam, 1969; Andrews, 1978; White & Johanson, 1982; Johanson *et al.*, 1982).

See text for discussion.

1. Includes data from *Aegyptopithecus* and *Propliopithecus* from Kay *et al.* (1980).

The measurements in Table 2 also illustrate the problem of combined sex samples in phylogenetic analysis. *Otavipithecus* mandibular robusticity is very close to female *Gorilla* whereas *Afropithecus* is close to male *Gorilla*, though *Otavipithecus* is coded as robust and *Afropithecus* and *Gorilla* as gracile. The *Afropithecus* specimen (KNM-WK 16840) is probably a male (Leakey *et al.*, 1988) and the *Otavipithecus* specimen possibly a female, based on the relative canine alveolus size. The same is true for symphyseal robusticity, with female

Table 3 Character state distribution in selected catarrhines (outgroup=*Propliopithecus*)

Taxon	Characters and character states													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Propliopithecus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pliopithecus	0	1	0	0	0	0	0	0	1	0	0	0	1	0
Dendropithecus	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Otavipithecus	2	1	0	1	1	0	1	0	1	0	0	1	0	0
Afropithecus	1	1	0	0	0	0	0	0	0	1	0	0	—	1
Proconsul	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Kenyapithecus	1	1	0	0	2	0	1	0	0	1	0	1	0	1
Griphopithecus	1	1	0	0	2	0	1	0	0	1	0	1	0	1
Sivapithecus	2	1	0	0	1	0	1	1	2	1	1	0	0	1
Pongo	2	0	1	1	0	1	1	1	0	1	1	0	1	1
Dryopithecus	2	1	0	0	1	0	1	0	0	1	1	1	1	0
Ouranopithecus	2	1	0	0	1	0	1	0	2	1	1	0	1	1
Gorilla	2	1	1	0	0	1	1	1	2	1	1	0	1	0
Pan	2	0	1	1	0	1	1	1	2	1	1	0	1	0
A. afarensis	2	0	1	0	2	0	1	1	2	1	1	1	1	1

See text for discussion.

gorillas having more robust symphyses than males, though not enough data are currently available to me to compare them metrically (scores based on Andrews, 1978). More specimens, including males and females of each fossil taxon, may change the scoring of *Otavipithecus* and *Afropithecus* for these traits, and thus the interpretation of *Otavipithecus-Afropithecus* relations (see below).

Non-metric traits are also miscoded in Conroy's data matrix. For example, there is no difference in the development of molar cingula between *Dryopithecus* and *Otavipithecus*. The only *Dryopithecus* teeth with sizeable molar cingula are the M_2's of the type. This represents a frequency of 2 in 95 for *Dryopithecus* molars, like the frequency of well developed cingula in fossil and modern hominids (great apes and humans, author's data). In contrast to Conroy's coding, *Kenyapithecus*, in particular the sample from Maboko, has a high incidence of well developed molar cingula. In addition, the tooth rows of many specimens of *Proconsul* are no more divergent posteriorly than in taxa for which Conroy assigns the parallel-sided tooth row state. In fact, all the taxa included in this analysis have somewhat divergent tooth rows, except living great apes. Finally, Conroy's group "hominids" (African apes and humans) differ among themselves in a number of characters included in this analysis and so must be treated separately, as was *Pongo*. In order to make the analysis more complete, other Miocene hominoid genera [*Ouranopithecus* (Bonis & Melentis, 1977) and *Griphopithecus* (Alpagut *et al.*, 1990)] were added as well. In sum, when the entire sample of *Dryopithecus* and larger samples of other taxa are considered, many of the differences among taxa cited by Conroy disappear or need to be modified. With even larger samples of other taxa, such as *Afropithecus* and *Kenyapithecus*, the coding for these taxa are likely to change as well. Cladistics is often criticized for its supposed failure to account for ranges of variation among taxa (Trinkaus, 1990). It is apparent, however, that attention to ranges of variation as well as other factors said to be neglected by cladists (e.g., trait identification) can and should be as much a part of a cladistic analysis as they are a part of any other phylogenetic methodology.

The data in Table 3 were input into the phylogenetic analysis program Hennig 86 (Farris, 1988). As in Conroy (1994), characters were unweighted and unordered, and all trees of

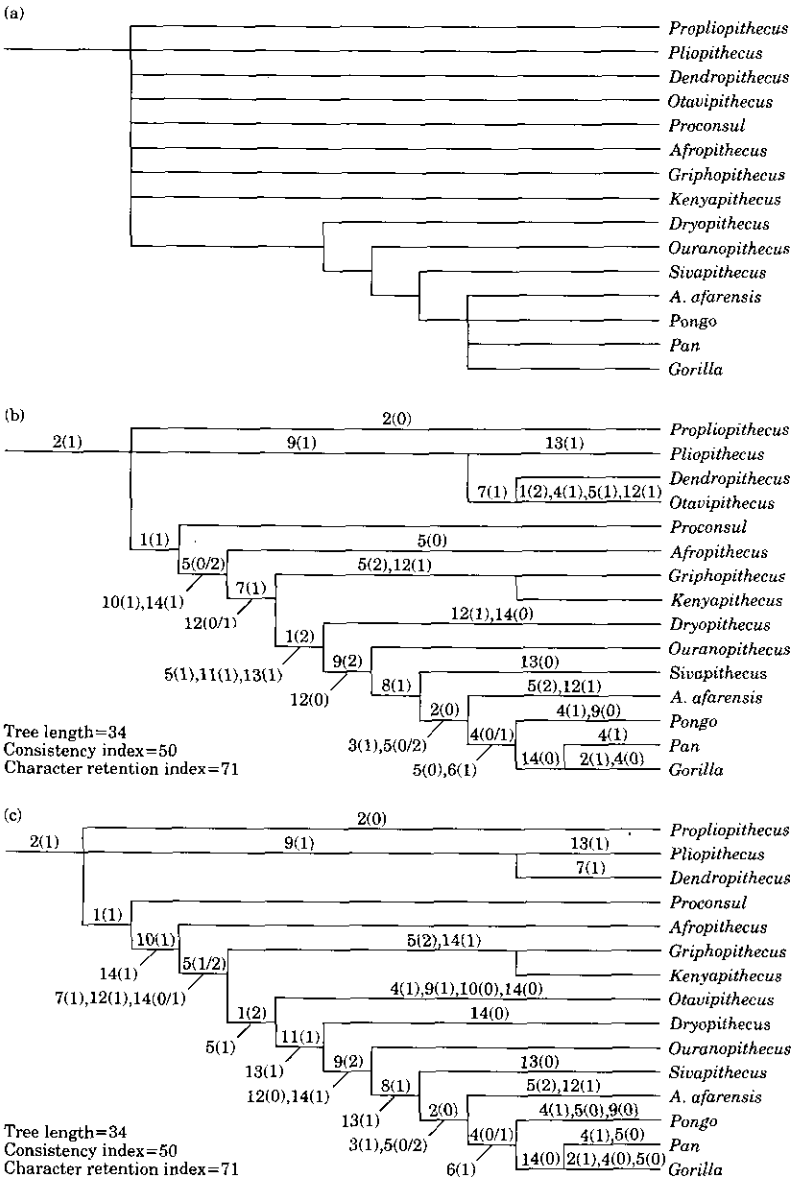

Figure 1. Cladograms generated from the data matrix reproduced in Table 3. These represent a character tree for mandibular data and not a definitive statement of phylogenetic relations. See text for discussion.

minimal length were analysed and diagnosed for length and fit statistics. The strict consensus tree was also calculated. The results are represented in Figure 1. Without elaborating in detail on the implications of Figure 1, several aspects are noteworthy. The strict consensus tree (Figure 1a) is derived from 18 most parsimonious cladograms. This cladogram is not particularly informative, as is predictable from data of this sort, with relatively low consistency and fewer characters than taxa. It does show a major subdivision (supported by five derived character states) between two groups, with *Otavipithecus* nestled in a polychotomy of primitive catarrhines and early to middle Miocene East African hominoids. This is dramatically different from the strict consensus tree in Conroy (1994). More informative because they represent the actual most parsimonious hypotheses are the 18 equally parsimonious trees. Two of these are reproduced here with the character state changes labeled. Most of the 18 cladograms place *Otavipithecus* and the *Kenyapithecus/Griphopithecus* clade in the great apes and human clade, to the exclusion of *Afropithecus*, and *Proconsul* (Figure 1c), and this is in basic agreement with Conroy's tree. However, as can be seen in the consensus tree (Figure 1a), *Otavipithecus* is never linked specifically with "hominids", as he suggests it is. The cladogram in Conroy (1994) was generated with demonstrably incorrect data (see above). Figure 1 here was generated with more data incorporating more fossils and more information on ranges of variation, more explicitly defined traits, *and* is more in line with previous analysis based on still larger data sets (Andrews & Martin, 1987; Begun, 1992*a,b*; Kelley, 1992; Harrison, 1987). It is based on these factors that the two hypotheses must be compared.

Different from most previous analyses is the placement of *Sivapithecus* relative to *Pongo* and the relations among African apes and humans. Interestingly, the separation of great apes of *Australopithecus* and other fossil forms is reminiscent of older interpretations of the fossil record of hominoid evolution, based in large part on the evidence of the mandible, before more complete cranial material were available for analysis (at least for *Dryopithecus* and *Sivapithecus*). This suggests that cladistic and "evolutionary" approaches to phylogeny reconstruction are relatively congruent for these data, and that the problem is not so much the methods, when properly employed, but the data themselves. In the final analysis, evidence of the mandibles and postcanine dentition of Miocene hominoids, even when rigorously analysed, is relatively inconsistent with regard to phylogeny reconstruction, and should be supplemented with additional data from other anatomical regions. For data such as these, from very limited data sets, it would probably be more appropriate to constrain the generation of phylogenetic trees in Hennig 86, PAUP, MacClade or other programs. Clades such as *Sivapithecus-Pongo* and African ape-human, supported by much larger data sets, would be imposed, so that new data could be integrated with previous research. This would only apply to clades that are not being tested by the analysis of the restricted data set.

The cladograms in Figure 1 should be taken as representative of the evidence of the mandible (a character tree for mandibular data) *and not as a definitive statement on Miocene hominoid relations*. These are more likely to be more accurately represented in any of the differing cladograms of Andrews & Martin (1987), Andrews (1992); Begun (1992*a,b*), Harrison (1987) and Kelley (1992), based on much larger and more anatomically diverse data.

Conroy's second data matrix is from Begun (1992*b*). His premise in "reanalysing" these results stems from his analysis of the mandibular data, which he claims casts doubt on the relevance of *Dryopithecus* to an analysis of great ape-human relations. Of course, the position of *Dryopithecus* among Miocene hominoids does not affect its usefulness as an outgroup to test hypotheses of relations among hominids as long as it is not in the ingroup. Thus, even if they were reproducible, Conroy's results are completely irrelevant to the results presented in Begun (1992*b*). Outgroup taxa do not have to be resolved among themselves to serve as outgroups. The unresolved outgroups in Conroy's cladogram did not seem to influence his view of the relations between *Otavipithecus* and "hominids", nor should they, as long as the ingroup relations are consistently the same. His sarcasm aside, Conroy's concern about the number of characters related to the incisive canal may not be serious, in view of his use of a number of very closely interrelated characters of unclear functional significance in his data set and in view of the restricted anatomical coverage of his analysis *versus* the one in Begun (1992*b*). His implied dismissal of the significance of palatal characters because of uncertainty about function is a classic case of *a priori* character weighting, and confuses the issues of evolutionary process (function, selection, adaptation, stochastic change) and evolutionary pattern (relations among taxa, the outcomes of these processes).

Regardless of the reasons for doubting a proposed phylogeny, it is obviously legitimate to test hypotheses using different appropriate methodologies. However, Conroy's exercise does not constitute a test of the conclusions presented in Begun (1992*b*). The character list from Begun (1992*b*) is not a comprehensive list of traits that vary among the hominoids analysed, but the tabulated results of a cladistic analysis. Most autapomorphies were excluded from the list to save space, as were characters not known in *Dryopithecus*. Thus, this is not a data matrix to be analysed but a list of characters defining nodes revealed by an analysis, as in Conroy (1994, figures 1 and 2), and Figure 1 here. Using these characters to generate a new cladogram with PAUP does *not* constitute a test of the data or the methods used so much as a test of PAUP. In fact, Conroy's strict consensus and majority rule cladograms are basically the same as the cladogram in Begun (1992*b*) with the exception that *Gorilla* is not placed in a clade with chimps and humans. Again, Conroy's concern about resolving relations among outgroup taxa is misplaced and inconsistent. As noted in Begun (1992*b*), the most significant result of the comparison of modern hominids to *Dryopithecus* was the recognition that *Gorilla* retains a large number of characters that are primitive for the African ape-human clade, because they are shared by the outgroup, in this case, *Dryopithecus*. Since gorillas are primitive in most of the features for which the character state was known in *Dryopithecus*, it would not be possible to resolve relations to other hominids using only these characters. Since the main point of the paper was to discuss Miocene hominoids and their relevance to the chimp-human clade, additional characters not available for analysis in the Miocene hominoid sample and necessary to resolve these additional relations were not included in the character list, though some were noted in the text (e.g., knuckle-walking) and were used to resolve the position of *Gorilla* represented in the cladogram. These characters have been described extensively elsewhere (Groves, 1986; Andrews & Martin, 1987; Szalay & Delson, 1979; Andrews & Cronin, 1982; Kelley & Pilbeam, 1986; Ward & Kimbel, 1983; Kordos & Begun, submitted).

Conroy's analysis of these data is hardly more rigorous than the analyses of Begun (1992*b*), Andrews & Martin (1987), Harrison (1987) or others that did not employ cladistics software. In view of the problems with Conroy's character state analysis (see above), his analysis can be characterized as less rigorous. It is just more automated. It does attempt to represent a different approach. If anything, it reaffirms the results presented in Begun (1992*b*). However, it appears that Conroy's results themselves are not supported when the data are subjected to a more rigorous analytical protocol. Conroy *et al.* (1992*a*) hedged on the phylogenetic position of *Otavipithecus*, and the results of this analysis suggest that they were justified in doing so. Mandibles are poor indicators of phylogenetic relations among hominoids. It would be preferable to await the discovery of more than one fragmentary specimen of a new taxon before attempting to overhaul hominoid systematics.

If there is something "sobering and disconcerting", to quote Conroy (1994), in these results, it must be in the message they convey about the uses and potential abuses of cladistic software. Labelling the results of a poorly constituted data matrix analysed by a computer program as a "rigorous taxonomic interpretation" is a clear abuse of the power of this technology. PAUP, MacClade, Hennig 86 and others are extremely useful and offer tremendous advantages in terms of speed of clustering analysis, in the ability to find all equally parsimonious cladograms, and in the ability to test alternative hypotheses. Common sense dictates, however, that the results of their use can only be as reliable as the data input.

Acknowledgements

I am grateful to Clark Howell, Tim White, Susan Anton, Gary Richards and Bill Kimbel for helpful discussions, and to Glenn Conroy for access to the fossils in his care. This work was carried out at the University of California at Berkeley and supported by the resources of that University and the Laboratory for Human Evolutionary Studies.

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