Evolution of P$_3$ Morphology in *Australopithecus afarensis*

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ABSTRACT   The *Australopithecus afarensis* dental sample exhibits a wide range of variation, which is most notable in the morphology of the lower third premolar (P$_3$). P$_3$ morphology in the *A. afarensis* sample ranges from the primitive sectorial extreme in AL 128-23 to the derived, bicuspid (molarized) extreme in AL 333w-1. In this paper, the degree and patterning of variation of the 20 known *A. afarensis* P$_3$s are examined and the evolutionary implications are discussed.

Initially, a series of dental and mandibular metric criteria are evaluated to determine whether this sample may be analyzed as a single species. From the metrics, it is clear that the single species hypothesis cannot be rejected. Next, a series of morphological criteria is devised to measure P$_3$ molarization. Taken as a whole, the *A. afarensis* P$_3$ sample displays more variation than a sample of modern hominoids (*Pan troglodytes*) and shows a slight trend toward increased molarization through time. When separated by sex, the *A. afarensis* sample still displays greater variation than the chimpanzee sample; however, only the male *A. afarensis* specimens show a trend toward increased molarization. Additionally, the male *A. afarensis* P$_3$s are more molarized than the female, a pattern that is seen as well (though less markedly) in the chimpanzee sample.

The trend toward increased molarization over time indicates selection for grinding in *A. afarensis.* The sexual differences parallel those seen in the postcrania (cf. Stern and Susman: *Am. J. Phys. Anthropol. 60:*279–318, 1983), as the females tend to retain the primitive condition, while the males display the derived morphology. Consequently, a model of sexual differences in niche exploitation, with the females exploiting a more arboreal environment, would seem to be supported by both the dental and postcranial evidence.

The canine/premolar complex has changed significantly over the course of hominoid evolution. Many theories of hominid origins have stressed changes in the function of this complex from shearing to grinding. Reduction of projecting canines and development of bicuspid lower third premolars (P$_3$s) have been associated with early hominids' development of tools (Dart, 1957; Darwin, 1871; Washburn and Lancaster, 1968). Other theories of hominid origins have emphasized a shift in dietary regime that resulted in the evolution of a grinding masticatory complex characterized by molarized P$_3$s with thick enamel and by reduced canines that would not impede movement of the jaw (Jolly, 1970, 1973; Simons and Pilbeam, 1971; Wolpoff, 1979, 1980; Wolpoff and Russell, 1981; *contra* Kay, 1981). However, it is now known from the dental remains of *Australopithecus afarensis* that at least some of the earliest hominids possessed a pongidlike canine/P$_3$ complex, as indicated by the presence of single-cusped P$_3$s, large, projecting maxillary and mandibular canines, and characteristic shearing wear on at least one of the mandibular canines (BMNH-18773) (White, 1981a; Wolpoff, 1980) and possibly some of the P$_3$s (i.e., AL 288-1 and AL 128-23). Consequently, it now appears that fully reduced canines and molarized P$_3$s were not part of the initial hominid adaptation.

Critical changes in the morphology of the P_3 took place during the period between the Miocene hominoids (i.e., *Ramapithecus* and *Sivapithecus* sps.) and the emergence of *A. africanus* in the Pliocene. These two forms represent the ends of a continuum; the Miocene hominoids exhibit primarily and almost universally the unicuspid, sectorial P_3 morphology, and *A. africanus* displays the molarized, bicuspid morphology. Specimens of *A. afarensis* are intermediate in time and morphology and therefore offer the information needed to examine the evolution of the hominid canine/P_3 complex from the presumed ancestral pongid condition. Moreover, the great variation in P_3 morphology, plus the fact that these specimens range between two morphological extremes (the primitive, sectorial P_3, and the derived bicuspid P_3) provide the opportunity to ascertain whether there are evolutionary trends within *A. afarensis*.

The purpose of this paper is to analyze the variation in the P_3 forms of the *A. afarensis* sample, examine the morphological changes that occurred in the canine/P_3 complex over time, and use this evidence to evaluate the roles of dental cutting and grinding in hominid evolution. In order to assess the variation, relative age and sex of the specimens are first determined. Criteria for evaluating P_3 morphology are then established, allowing for assessment of the variation in the *A. afarensis* sample and comparison of this variation to that found in a sample of P_3s from a modern hominoid group.

Three hypotheses about variation in *A. afarensis* are tested in this study: (1) The sample represents a single species; (2) there was evolutionary change in the P_3 morphology within *A. afarensis*; and (3) there are sexual differences in the morphology of the P_3s in this sample. The first hypothesis is tested by comparing the range of variation in the *A. afarensis* sample and samples of modern hominoid species for several dental and mandibular characteristics. If the variability in the *A. afarensis* sample is consistently greater than that found in the modern hominoid species, the null hypothesis of a single species must be rejected. A series of tests is required to address the second hypothesis fully. Initially, the degree of variation in P_3 morphology in the *A. afarensis* sample is established. Next, the evidence for a temporal trend in the P_3 morphology of *A. afarensis* is assessed. Finally, apparent temporal trends are critically evaluated to determine whether these trends represent evolutionary changes in masticatory adaptations or merely reflect changes in tooth and/or body size. Tests of the third hypothesis require determination of whether differences in P_3 morphology can be discerned between the presumed males and females of the *A. afarensis* sample. The patterns are then compared to those observed in another hominoid species.

Finally, in light of the results of these analyses, ecological correlates of the evolution of the hominid P_3 are considered. The results are considered in the context of models previously derived from analyses of the postcranial anatomy (Stern and Susman, 1983).

MATERIALS AND METHODS
The sample

The species designation of *A. afarensis* was initially made by Johanson et al. (1978) to distinguish the Laetoli and Hadar hominid specimens taxonomically from the later South and East African australopithecine specimens. The Laetoli sample, generally regarded as the earlier, has been dated to 3.6–3.8 mya, while the Hadar specimens were found over several different stratigraphic levels, with the youngest dating about 2.9 mya (White et al., 1984) to 3.1 mya (Hall et al., 1985). In addition, a few other hominid specimens with geological ages between about 2.8 and 4 million years are known from other East African sites. Specifically, specimens from the Tulu Bor levels at East Turkana and the earliest levels at the Omo have been attributed to *A. afarensis* on the basis of morphology and chronology (Johanson and Edey, 1981; Kimbel et al., 1984).

The *A. afarensis* specimens of principal interest in this study are those bearing P_3s. The sample analyzed in this study consists of 20 specimens: five from Laetoli, 13 from Hadar, and one each from the Tulu Bor level at East Turkana (KNM-ER 5431), and the white sands of the Omo (W-978) (see Table 1 for a list of the specimens). Morphological data on these and other non-P_3-bearing *A. afarensis* specimens were obtained from observation of primary casts at the Cleveland Museum of Natural History as well as from published (Coppens, 1973; Howell, 1969; Johanson and White, 1979; Johanson et al., 1978, 1982a–c; Kimbel et al., 1982; Leakey and Walker, 1985; White, 1977, 1980, 1981a,b; White and Johanson, 1982; White et al., 1981; Wolpoff, 1979) and unpublished (Wolpoff, n.d.) descriptions of the material. Dental metrics

TABLE 1. A. afarensis *specimens used in this study*

Specimens with P_3 present			Specimens with no P_3 present		
Specimen	Site	Reference[1]	Specimen	Site	Reference[1]
LH-2	Laetoli	E,F	LH-23	Laetoli	F
LH-3	Laetoli	E,F	AL 145-35	Hadar	D,H
LH-4	Laetoli	E	AL 188-1	Hadar	D,H
LH-14	Laetoli	E,F	AL 241-14	Hadar	D
LH-24	Laetoli	F	AL 333-90	Hadar	D
AL 128-23	Hadar	D,H	AL 333-103	Hadar	H
AL 198-1	Hadar	D,H	AL 333w-10	Hadar	D
AL 207-13	Hadar	D,H	AL 333w-12	Hadar	D,H
AL 266-1	Hadar	D,H	AL 333w-27	Hadar	D
AL 277-1	Hadar	D,H	AL 333w-48	Hadar	D
AL 288-1	Hadar	C,D	L 333w-57	Hadar	D,H
AL 311-1	Hadar	D,H	AL 333w-59	Hadar	D,H
AL 333-10	Hadar	D,H	W-508	Omo	A
AL 333w-1	Hadar	D,H	BMNH 18773	Laetoli (Garusi)	F,G
AL 333w-46	Hadar	D,H			
AL 333w-58	Hadar	D,H			
AL 333w-60	Hadar	D,H			
AL 400-1	Hadar	D,H			
KNM-ER 5431	Koobi Fora	B			
W-978	Omo	I			

[1]A—Howell (1969); B—Leakey and Walker (1985); C—Johanson et al. (1982a); D—Johanson et al. (1982c); E—White (1977); F—White (1980); G—White (1981a); H—White and Johanson (1982); I—Coppens, (1973).

were provided by M.H. Wolpoff, mandibular measurements are from published sources, and all the data are available in the sources listed in Table 1.

There is no clear consensus regarding the taxonomic status of this sample. Some have disputed the separation of the Laetoli and Hadar hominids from those of *A. africanus.*, arguing that the morphological differences are not great enough to warrant taxonomic distinction (Brace, 1979; Tobias, 1980a,b). Conversely, others have argued, on the basis of basicranial, dental, and postcranial data, that the specimens assigned to *A. afarensis* actually represent more than one species (Coppens, 1981, 1983; Olson, 1981, 1985; Read, 1984; Senut and Tardieu, 1985; Tardieu, 1983; Zihlman, 1985a,b). Consequently, the question of whether this sample represents a single species will be specifically addressed before the variation in P_3 morphology is analyzed (see *Sex Determination* section).

Age determination

As individuals age, the wear on their teeth becomes more pronounced and the dental morphology and function may change. Therefore, before evaluating morphological and functional patterns in relation to sexual differences or evolutionary changes in the *A. afarensis* P_3s, it was necessary to account for the variation that is related to the age of the individuals. Assessing the age of individuals was also important for determining patterns

and possible changes in how dental morphology and function change during life.

Relative ages were estimated according to eruption sequences established for the *A. afarensis* specimens and seriation of the older individuals according to wear on the molars. In two specimens, LH-2 and LH-3, the deciduous dentition is still present, and the P_3s are unerupted, though free of the damaged mandibles. Consequently, the ages of these individuals were bracketed between 3 and 6 years (see Smith, 1986; Lewin, 1987; Mann, 1975 for discussion of different interpretations of Australopithecine dental development). All other specimens have their permanent teeth and therefore were aged on the basis of relative amounts of wear. The specimens, seriated according to relative amounts of wear, are listed in order and grouped into categories below.

Juvenile: LH-2, LH-3, W-978.
I (little wear): AL 128-23, KNM-ER 5431, AL 333w-1.
II (moderate wear): AL 266-1, AL 400-1, AL288-1[1], AL 333w-60, AL 333w-46, AL 207-13, LH-14.
III (heavy wear): AL 277-1, AL 311-1, LH-4, AL 198-1, LH-24.
Uncertain: AL 333-10, AL 333w-58.

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[1]The M_3 wear on AL 288-1 is minimal and may be due to malocclusion (Kimbel, personal communication). Therefore, M_3 wear was not used to assess age as it might have resulted in underestimation.

Sex determination

Currently, there is great debate as to whether the *A. afarensis* dental sample represents one or two species (see Kimble et al., 1985; White, 1985; White et al., 1981; Olson, 1981, 1985; Read, 1984, for opposing views). Therefore, before the specimens are ultimately assigned sexes, the null hypothesis that the dental sample represents a single species is tested. To test this hypothesis, several criteria will be examined in order to establish ranges of dental and mandibular metric variation and to assign tentative sexes to the specimens. For each criterion assessed, the amount of variation and proposed degree of sexual dimorphism in the sample are compared to the variation and degree of sexual dimorphism observed in samples of modern hominoid species (Table 2). If the variation and/or proposed degree of sexual dimorphism is comparable to that of the modern analogs, it is not appropriate to taxonomically partition the sample. The criteria used in sexing this sample are (1) the mandibular canine (breadth and morphology), (2) M_2 breadth, (3) mandibular corpus height at P_3/P_4 and M_1/M_2, and (4) P_3 breadth.

Canine breadth and morphology: Canine size is a useful indicator of sex in primate species since its distribution is often a bimodal one that clearly discriminates males from females (Gingerich and Schoeninger, 1979; Mahler, 1973; Pilbeam and Zwell, 1972; Wolpoff, 1976). Breadth is the preferable measurement of size, as it is not affected by interproximal wear. The distribution of canine breadths is shown in Figure 1. Contrary to expectations, the distribution appears unimodal. Consequently, aspects of canine morphology must also be used to help determine the sex of the specimens.

In modern hominoids, male canines are usually projecting, with massive roots that are often curved. Females, on the other hand, tend to have less projecting canines with roots that are less robust. The four specimens that are the smallest (AL 128-23, 198-1, 188-1, and 400-1) are female in morphology (nonprojecting and/or small, uncurved roots; see Ward, et al., 1982, for radiographs), and therefore were sexed as females. All four specimens (LH-4, LH-14, AL 277-1, 333-90) in the modal range (10.5–11.0 mm) have the male morphology. Hence, these specimens, and those with greater canine breadths (including LH-3, AL 311-1, 333w-58, and 333w-60) were all sexed as males. The two speci-

mens between the male and female ranges do not have associated P_3s.

From the tentative sexing above, there appears to be a male bias in the mandibular canines (11 males, five females), a fact that has been noted by other authors (White, 1985; Frayer and Wolpoff, 1985). This bias explains why the canine breadths do not distribute bimodally, as the oversampling of the males appears to be obscuring the true distribution. When the percent sexual dimorphism is calculated for the *A. afarensis* mandibular canine sample, the value falls in the range for modern hominoid species (male/female ratio: *A. afarensis*, 128%; Table 2).

Furthermore, the coefficient of variation (CV) also indicates that we should not reject the single species hypothesis on the basis of canine size. The CV ([mean × 100]/SD) is a measure that can be used to compare the degree of variation in two samples which have different means (Sokal and Rohlf, 1981.)[2] Table 2 shows that the degree of variability for the *A. afarensis* sample is generally less than that seen in modern hominoids. Therefore, the variation in canine breadths is very much consistent with the expectations for a single species.

M_2 breadth: A second dental measurement useful in determining sex in the later australopithecines is M_2 breadth (Wolpoff, 1976). As seen in Figure 2, and as noted previously by Read (1984), the M_2 breadths of the *A. afarensis* sample appears to distribute bimodally. This interpretation is confirmed by a chi-square goodness-of-fit test, as the distribution is significantly different from normal ($\chi^2 = 22.1$; $P \leqslant .01$).

Of the four specimens that retain P_3s and that have M_2 breadths in the lower mode (12.0–12.5 mm), three (AL 128-23, 198-1, 288-1) were sexed as females on the basis of their canines as well; the fourth (AL 207-13) does not have a canine but was sexed as a female on the basis of this distribution. Similarly, two of the four P_3-bearing specimens with M_2 breadths at or above the higher mode (greater than 14.0 mm) were also sexed as males on the basis of their canines (AL 277-1

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[2]Vitzthum (1986) discusses the limitations of the use of CVs in delimiting species. She demonstrates that among cercopithecoid species, CVs do not vary in any systematic way with regard to taxonomic level. These results indicate that it is inappropriate to use CVs as "taxonomic thresholds" for separating fossil samples. Rather, they should be used to tell us whether the variation in a fossil sample and a modern analog are broadly comparable.

TABLE 2. Variation and sexual dimorphism in A. afarensis and modern hominoid dental and mandibular samples

Sample	Canine breadth[1]				M2 breadth[1]				P3 breadth[1]				Mandibular height[2] at M_1/M_2		
	N	Mean	CV	% Sex. dimorph.	N	Mean	CV	% Sex. dimorph.	N	Mean	CV	% Sex. dimorph.	N	Mean	% Sex. dimorph.
A. afarensis															
Male	11	11.35	10.2	—	7	14.37	5.7	—	11	12.21	8.6	—	4	34.20	—
Female	5	8.90	10.2	—	10	12.78	7.3	—	8	10.60	6.9	—	5	29.02	—
Total	16	10.58	14.2	128	20	13.51	8.2	112	20	11.51	10.4	115	9	31.32	118
Pan troglodytes															
Males	76	11.57	13.7	—	111	10.51	7.2	—	112	8.22	11.8	—	38	—	—
Females	85	9.55	13.7	—	120	10.21	7.1	—	121	7.57	7.5	—	58	—	—
Total	161	10.50	16.8	121	231	10.35	7.2	103	233	7.88	10.8	109	96	—	109
Gorilla gorilla															
Males	214	14.48	9.0	—	243	15.62	6.2	—	238	11.99	8.0	—	85	—	—
Females	110	10.28	7.6	—	127	14.49	5.8	—	124	10.49	7.4	—	54	—	—
Total	324	13.05	17.6	141	370	15.23	7.0	108	362	11.48	10.0	114	138	—	124
Pongo pygmaeus															
Males	46	12.77	8.3	—	64	13.58	6.1	—	65	10.50	8.9	—	12	—	—
Females	55	9.07	10.6	—	69	12.15	6.7	—	64	9.15	8.5	—	16	—	—
Total	101	10.75	19.6	141	133	12.84	9.6	112	129	9.83	11.0	115	28	—	117

[1] *A. afarensis* data from this study; modern hominoid data from Mahler (1973).
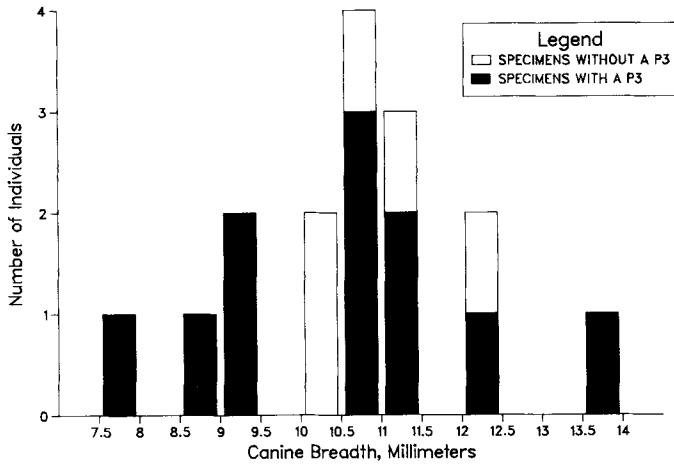[2] Data from this study and Frayer and Wolpoff (1985).

Fig. 1. Distribution of *A. afarensis* mandibular canine breadths used in sexing. Specimens with P3s: AL 128-23, 198-1, 277-1, 288-1, 311-1, 333w-58, 333w-60, 400-1; LH-3, 4, 14. Specimens without P3s: AL 145-35, 333-90, 333-103, 333w-10; BMNH 18773.
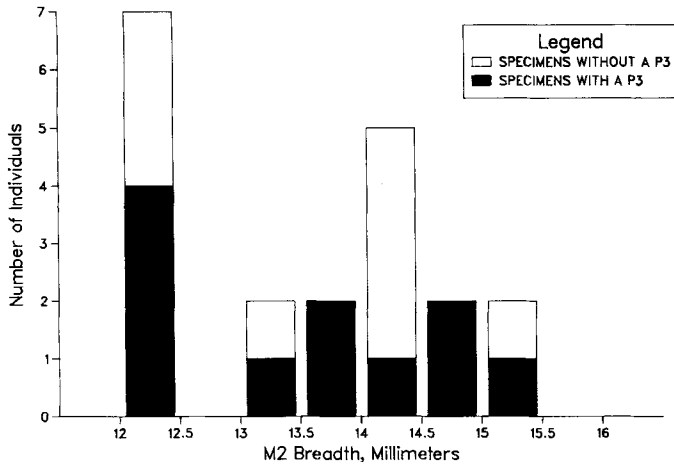

Fig. 2. Distribution of *A. afarensis* M_2 breadths used in sexing. Specimens with P3s: AL 128-23, 198-1, 207-13, 266-1, 277-1, 288-1, 333w-1, 333w-60, 400-1; LH-4; ER 5431. Specimens without P3s: AL 145-35, 188-1, 241-14, 333w-27, 333w-48, 333w-57, 333w-59; LH-23; W-508.

and 333w-60); a third (KNM-ER 5431) does not have a canine but its M_2 is among the largest (15.0–15.5 mm) and could therefore be considered male. However, the fourth P3-bearing specimen with an M_2 breadth at or above the higher mode is AL 400-1, which was sexed as a female on the basis of its canine breadth. Consequently, this distribution of M_2 breadths sheds some uncertainty on the sex assigned to AL 400-1. However, because the canine is generally a better discriminator of sex in higher primates, the ca-

nine has priority as a sexing criterion, and thus AL 400-1 is still considered a female.

The bimodality in the distribution of M_2 breadths might be used to argue for two species in this sample (Pilbeam and Zwell, 1972). Given the extreme degree of body size dimorphism known to exist from the postcranial remains, it is not unreasonable to expect great variation in molar tooth size. As seen in Table 2, however, the CV for this sample (8.2) is within the range seen in the modern hominoid species. Moreover, the degree of
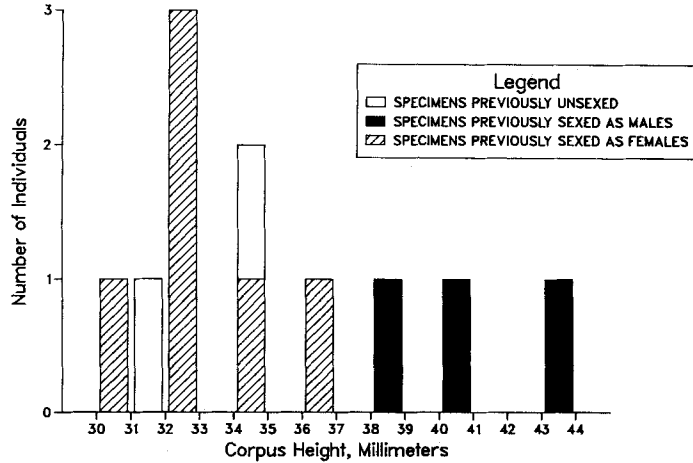
Fig. 3. Distribution of *A. afarensis* mandibular corpus heights at P_3/P_4 used in sexing. Specimens with P_3s: AL 128-23, 198-1, 266-1, 277-1, 288-1, 333w-46, 333w-60, 400-1; LH-4. Specimens without P_3s: AL 145-35, 333w-12.

dimorphism between the proposed males and females of this sample is comparable to that of *Pongo* (see Table 2). Therefore, although there is great variability in M_2 breadth, the hypothesis that the sample represents a single species cannot be rejected.

Mandibular height: Height of the mandibular corpus was also used in this analysis to assign sexes. Wolpoff (1976) noted that the height of the mandibular corpus (especially at M_1/M_2) was useful in separating sexes in the later australopithecines. Distributions of corpus height at P_3/P_4 and M_1/M_2 for the *A. afarensis* sample are shown in Figures 3 and 4, with the sex assignments from the previous criteria indicated.

The distribution for corpus height at P_3/P_4 is consistent with the other criteria in distinguishing specimens (Fig. 3). All three specimens that fall at the highest end of the range (greater than 38 mm) were sexed as males on other criteria (AL 277-1, 333w-60, LH-4). Of those seven specimens having a corpus depth of less than 35 mm, four were sexed as females on other criteria (AL 288-1, 198-1, 128-23, and 145-35). The other three were previously unsexed and include two specimens with P_3s, AL 333w-46 and 266-1. Since they clearly sort with the other proposed females on the basis of this criterion, AL 333w-46 and 266-1 were designated as females. The height of the AL 400-1 mandible is at the middle of this distribution, (36–37 mm), so its sex could not be better resolved.

Measurements of corpus height at M_1/M_2 produce a distribution similar to that of the P_3P_4 corpus height (Fig. 4). Five of the six specimens which fall at the lower end of the range (less than 32 mm) were previously sexed as females (AL 145-35, 207-13, 288-1, 266-1, 198-1). LH-4, which was sexed as a male on the basis of both its canine and its corpus height at P_3/P_4, was the only specimen which did not sort consistently with the previous criteria. However, multiple criteria, including the canine, have priority, so LH-4 continued to be sexed as a male. The only previously unsexed specimen in the distribution of M_1/M_2 mandibular corpus height is the early adolescent AL 333w-1. Its mandibular height is in the lower part of the male range, and with age its jaw probably would have grown larger and into the upper part of the male range; therefore, AL 333w-1 was sexed as a male.

Additionally, when percent dimorphism is calculated for the mandibular corpus height in this sample, the values are comparable to those obtained from samples of modern hominoid species. In this study, the proposed percent dimorphism for corpus height is 123% at P_3/P_4 and 118% at M_1/M_2, as compared to values ranging from 109 to 124% in the hominoids (see Table 2).

P_3 Breadth: Finally, P_3 breadth is investigated as a sexing criterion. The use of P_3 breadth as a sexing criterion in this study of P_3 evolution is justified for three reasons: (1)
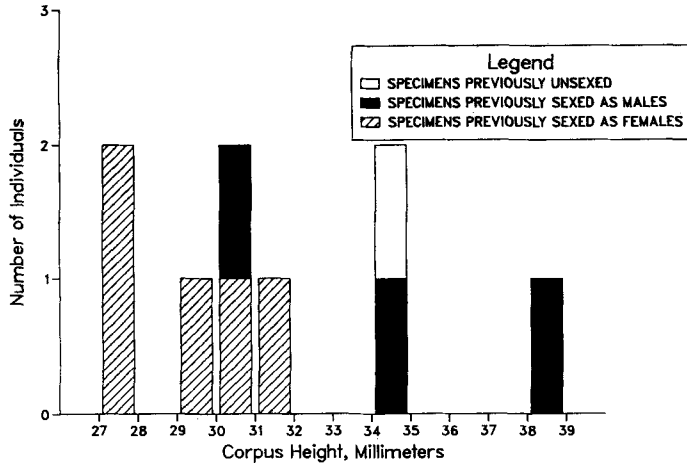
Fig. 4. Distribution of A. afarensis mandibular corpus heights at M_1/M_2 used in sexing. Specimens with P_3s: AL 198-1, 207-13, 266-1, 288-1, 333w-1, 333w-60; LH-4. Specimens without P_3s: AL 145-35, 188-1.
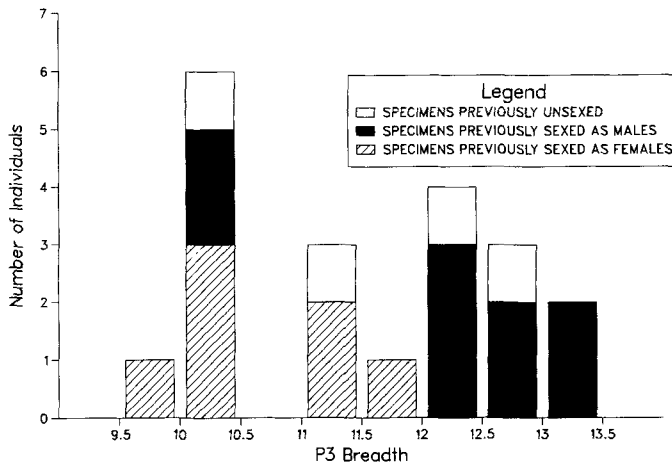

Fig. 5. Distribution of A. afarensis P_3 breadths used in sexing.

This study focuses on P_3 morphology, not size; (2) the distribution of P_3 breadths is examined in light of sex assignments based on other criteria for many specimens; and (3) P_3 size is the only criteria that can be used to assign the sex of some specimens, particularly isolated teeth. The distribution of P_3 breadths is shown in Figure 5. It appears bimodal, with most of the males in the higher mode and most of the females in the lower. However, two males (AL 333w-1 and 311-1) are also in the lower mode. The problematic AL 400-1, sexed as a female on the basis of its canine, is intermediate in this distribution of P_3 breadth, so its sex cannot be determined more definitively. Still, this distri-

bution provides a criteria for sexing three of the four specimens of previously undetermined sex. LH-24 falls in the upper part of the male range (12.5–13.0) and AL 333-10 falls in the lower part of the male range (12.0–12.5 mm), so both were sexed as males. LH-2 falls in the intermediate range (11.0–11.5 mm) so its sex could not be determined. The fourth unsexed specimen, W-978, falls in the female range (10–10.5 mm) and was therefore sexed as a female, since no tooth previously sexed as a male was smaller than it.

The variation in the sample is comparable to that seen in modern hominoids (CV=10.4; hominoid range=10.0–11.0; Table 2). Based

on the sexing for the P$_3$s, there is 115% sexual dimorphism in the size of this tooth. Once again, this value is no more extreme than those obtained from other hominoid species. Therefore, as with the previous criteria, there is nothing about the degree of variation or dimorphism in P$_3$ breadth that indicates that the sample represents more than one species.

In summary, the range of variation and degree of dimorphism for the dental metrics analyzed here are quite consistent with the hypothesis that this sample represents a single species. These results are similar to those obtained by the more extensive studies of White (1985) and Kimbel et al. (1984, 1985), and are in marked contrast to those of Olson (1981). We are in agreement with Kimbel et al. (1985) in their critique of Olson's arguments for two species. It clearly seems that for the *A. afarensis* dental and mandibular sample there is great evidence to support the claim of a single species. Therefore, for the subsequent analyses in this study, the sample will be considered as one species, with a sex composition as determined above.

Of the 20 *A. afarensis* specimens bearing P$_3$s, sexes were assigned to 19, based on dental and mandibular characteristics. Eleven of the specimens were sexed as males, and eight of the specimens were sexed as females, one tentatively. The specimens with their assigned sexes and the criteria used in determination are listed in Table 3.

Evaluation of P$_3$ morphology

In order to evaluate the variation in the *A. afarensis* P$_3$ sample, several criteria were established for judging morphological states, given differences in preservation and wear. The morphological criteria were divided into two sets, with the first reflecting molarization of the P$_3$ directly, and the second reflecting P$_3$ placement (rotation) and mandibular morphology. The latter criterion is important, as it determines the capacity of the maxillary canine to shear against the premolar.

Criteria of molarization: The extent to which a tooth can function as a molar in grinding foods is basically a function of the occlusal area, other factors remaining constant. Thus, in considering the molarization of the P$_3$ directly, differences in the development of the metaconid, which increase the occlusal area, were a primary concern. However, the degree of metaconid development is difficult to discern on even moderately worn teeth; therefore, using relatively unworn specimens as a guide, a number of criteria indicative of molarization were devised. These criteria, which distinguish the unicuspid and bicuspid extremes (represented by relatively unworn AL 128-23 and AL 333w-1, respectively), can also be evaluated on worn and middle-range teeth. The criteria evaluate molarization on the basis of (1) direct observation of metaconid development, (2) metaconid development as judged by slope of the transverse ridge, and (3) closure of the anterior fovea (criteria I-III, respectively). The final criterion, IV, evaluates the cutting capacity of the tooth as reflected by the prominence of the transverse ridge (see Wolpoff, 1979; Wolpoff and Russell, 1981; and White, 1981b, for various interpretations).

The scales of the four criteria used to assess P$_3$ molarization are listed in Table 4. In order to facilitate comparison, numerical indices were assigned to each criteria, with higher values indicating greater molarization. Additional variables that may affect judgment of the criteria but do not directly indicate degree of metaconid development are noted with capital letters. The indices of development assigned to the specimens are listed in Table 5.

Assessing P$_3$ morphology on the basis of these criteria allowed the specimens to be rank ordered on the basis of degree of molarization. Where more than one specimen fit a single category, specimens were differentiated within the category in order to partition the rank order more finely. Anterior fovea closure was evaluated by only one criterion (Table 4,III), so the ranking of the specimens according to anterior fovea closure was based only on the five categories of criterion III. Metaconid development was evaluated by both criteria I and II; however, both criteria could not be evaluated for each tooth. Consequently, the rank order of metaconid development was based on a combination of criteria I and II:

$$\text{RANK ORDER} = \frac{(I_{observed}/I_{max}) + (II_{observed}/II_{max})}{X}$$

where:

$I_{max} = 5$
$II_{max} = 4$
X = number of criteria judged.

TABLE 3. *Final sex determination and supporting criteria for specimens used in this study*

Specimens with P₃ present			Specimens with no P₃ present		
Specimen	Sex	Supporting criteria[1]	Specimen	Sex	Supporting criteria[1]
LH-2	?		LH-23	?	
LH-3	Male	1,5	AL 145-35	Female	3,4
LH-4	Male	1,2,3,5	Al 188-1	Male	2,4
LH-14	Male	1,5	AL 241-14	?	
LH-24	Male	5	AL 333-103	Male	1
AL 128-23	Female	1,2,5	AL 333w-103	Male	1
AL 198-1	Female	1,2,3,5	AL 333w-10	Male	3
AL 207-13	Female	2,4,5	AL 333w-12	Female	2
AL 266-1	Female	2,3,4	AL 333w-27	Male	2
AL 277-1	Male	1,2,3,5	AL 333w-48	Female	2
AL 288-1	Female	1-6	AL 333w-57	Female	
AL 311-1	Male	1	AL 333w-59	?	
AL 333-10	Male	5	W-508	Female	2
AL 333w-1	Male	4	BMNH 18773	Male	1
AL 333w-46	Female	3			
AL 333w-58	Male	1,5			
AL 333w-60	Male	1-5			
AL 400-1	Female?	1			
KNM-ER 5431	Male	2,5			
W-978	Female	5			

[1]—canine breadth; 2—M_2 breadth; 3—mandibular height at P3/P4; 4—mandibular height at M1/M2; 5—P_3 breadth; 6—postcranial remains.

TABLE 4. Morphological criteria

I. Development of the metaconid as it can be judged on relatively unworn specimens

  A) worn or damaged, but generally discernable

    1) no metaconid present

    2) transverse ridge swells at the lingual margin, but metaconid not distinct

    3) metaconid small but distinct

    4) metaconid prominent, but smaller than the protoconid

    5) metaconid and protoconid of approximately equal size

II. Development of the metaconid as judged by the transverse ridge profile

  B) definite step present, indicative of metaconid

  C) definite step was probably present, but has been obscured by wear

  D) ridge deteriorated between the cusps

    1) ridge slopes directly down from the protoconid (approx. equiv. to I-1)

    2) ridge slopes directly down from the protoconid, but with slight step indicative of metaconid development (approx. equiv. to I-2 or -3

    3) ridge slopes only slightly from the protoconid (approx. equiv. to I-3 or -4)

    4) ridge runs approximately horizontally

III. Closure of the anterior fovea

  E) "pitlike"

  F) elongate

    1) fovea open and defined by only the mesial-distal and transverse ridges

    2) fovea partially closed by small mesial marginal ridge extending from the mesial-distal ridge

    3) fovea partially closed by a small mesial marginal ridge extending from the mesial-distal ridge and a small mesial marginal ridge extending from the transverse ridge

    4) fovea completely closed

    5) fovea completely closed and well defined

IV. Transverse ridge development

    1) ridge slightly present or absent

    2) substantial ridge slopes from protoconid to lingual edge

    3) substantial ridge slopes from protoconid to metaconid

    4) substantial ridge runs from protoconid to metaconid, sloping slightly

    5) ridge deteriorated between the two cusps

Of the molarization criteria, transverse ridge development (criterion IV) is the least variable, and consequently, it was felt that specimens could not be more finely seriated than the basic 1–5 ranking noted in Table 4.

Finally, overall molarization was obtained by a mean rank for all four criteria. Since not all four criteria could be evaluated on each specimen, a simple mean could not be used. Therefore, the mean rank (I–IV) was calculated:

$$\text{MEAN} = \frac{\underset{i=1,4}{\Sigma} \text{ rank(criterion i)}}{\underset{i=1,4}{\Sigma} \text{ rank}_{max}\text{(criterion i)}}$$

For example, LH-4 could be evaluated on only three criteria. Therefore:

$$\text{MEAN} = (2 + 5 + 3)/(4 + 5 + 5) = 0.71.$$

Obviously, since the fractions were derived from rank-order, categorical variables, they have no arithmetic meaning; however, their relative values can be used to seriate the specimens.

The ranks assigned to the specimens for criteria of metaconid development (criterion I/II), anterior fovea closure (criterion III), and mean molarization (mean criteria I–IV) are listed in Table 6.

Criteria of P₃ rotation and mandible shape: The capacity for canine/P₃ shearing is also directly related to the amount of buccal surface area afforded by the P₃. The exposure of the buccal shearing surface is affected by the shape of the jaw (Molnar and Ward, 1977) and by the orientation of the P₃ in the tooth row. Therefore, in order to quantify the amount of buccal face exposure of the tooth, a measure sensitive to both mandibular shape and P₃ rotation was needed.

Angulation of the mandible was taken to be the angle of intersection (α) between the occlusal line (line between midpoints of post-canine teeth) and the midline (see Fig. 6). This angle was determined in two ways: (1) by direct measurement from published diagrams, and (2) by calculation, using measurements taken directly from casts of the specimens (methods shown in Fig. 6A and B, respectively). Mandibular angulation values used in this study were the averages of those obtained by each method. These are listed by specimen in Table 5.

Orientation of the P₃ was determined by measurement of the angle between the major axis of the tooth and the occlusal line of the tooth row (best straight line through the midpoints of the postcanine teeth). Considering the shape of the P₃ as an oval, the major axis of the tooth is defined as the line of maximal buccal-lingual distance running through the

TABLE 5. Morphological criteria, specimens ordered chronologically

Specimen	Sex	Criteria				Angulation	
		I	II	III	IV	α	γ
LH-2	?	3	2	3	3	—	—
LH-3	M	3	2	3	3	—	—
LH-4	M	—	2A	5E	3	18°	39°
LH-14	M	3	2	3	3	—	—
LH-24	M	—	2A	4E	—	—	—
ER 5431	M	3	2	3	5	—	—
W-978	F	4	4D	3	5	—	—
AL 198-1	F	—	—	2	—	—	33°
AL 128-1	F	1	1	1	2	15°	33°
AL 400-1	F?	—	4C	3	4	16°	39°
AL 277-1	M	—	—	2	2	—	60°
AL311-1	M	—	2A	3	—	—	—
AL 207-13	F	2A	2	2	3	7°	34°
AL 266-1	F	4A	3B	4E	4	12°	42°
AL 333w-1	M	5	4BD	5E	5	—	85°
AL 333w-46	F	—	3C	5AE	4	—	—
AL 333w-58	M	5A	4A	5E	4	—	—
AL 333w-60	M	5A	4B	4F	5	10°	71°
AL 333-10	M	—	4C	5F	4	—	—
AL 288-1	F	1	1	2	2	16°	44°

TABLE 6. Rankings of A. afarensis specimens

Specimen	Sex	Chron. rank	Ranking according to morphological criteria			
			Criteria I & II	Criterion III	Mean criteria (I–IV)	Angulation
LH-2	?	3	8.5	7	8	—
LH-3	M	3	8.5	8	8	—
LH-4	M	3	5	16	12	4.5
LH-14	M	3	8.5	6	8	—
LH-24	M	3	5	13	10	—
KNM ER-5431	M	6.5	8.5	11	11	—
W-978	F	6.5	13	9	15	—
AL 198-1	F	8	—	3	3.5	1.5
AL 128-23	F	9	1.5	1	1	1.5
AL 400-1	F?	10.5	14.5	10	13.5	4.5
AL 277-1	M	10.5	—	5	3.5	8
AL 311-1	M	12	5	12	6	—
AL 266-1	F	13	12	14	13.5	3
AL 207-13	F	14	3	4	5	6
AL 333w-1	M	17	17	20	20	10
AL 333w-46	F	17	11	19	16	—
AL 333w-58	M	17	17	18	18.5	—
AL 333w-60	M	17	17	15	18.5	9
AL 333-10	M	17	14.5	17	17	—
AL 288-1	F	20	1.5	2	2	7

midpoint of the tooth, with the corresponding minor axis being the mesial-distal line running through the midpoint and perpendicular to the major axis. The angle between the major axis and the occlusal line is minimized as the major axis approaches a mesial-distal orientation and maximized when the major axis is perpendicular to the occlusal line. The first orientation is denoted as rotated, the latter as unrotated.
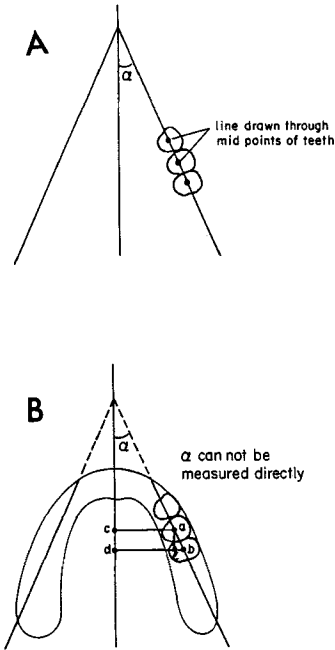
Fig. 6. Methods for determining the angulation of the mandibles: A): Method applied to illustrations: Best line connecting midpoints of postcanine teeth was drawn. The angle between this line and the midline was then measured with a protractor. B): Method applied to actual specimens: This method requires measurement of the distance between the midpoints of two postcanine teeth (AB) and the perpendicular distances between the midpoints of each of these teeth to the midline (AC and BD). From these measurements, trapezoid ABCD is established. The trapezoid is then subdivided into a rectangle (ACDE) and a right triangle (ABE) by dropping a perpendicular from point A (the midpoint of the more anterior tooth) to BD. Next, the length of BE is determined, as it is known that BE = BD − AC. Given the lengths of two sides of triangle ABE, θ (angle ABE) could be determined by: $\cos(\theta)$ = BE/AB. From this information the angulation of the mandible was obtained: $\alpha = 90° - \theta$.

On the basis of these two criteria, four ideal categories of mandibles were developed (Fig. 7: (A) mandibles with divergent tooth rows (V-shaped) and rotated P$_3$s; (B) those with divergent tooth rows and unrotated P$_3$s; (C) those with parallel tooth rows (U-shaped) and rotated P$_3$s; and (D) those with parallel tooth rows and unrotated P$_3$s. Type A is the best suited for shearing, since it provides the maximum surface area on the buccal face of the P$_3$ for shearing against the maxillary canine. Type D is least suited for shearing, and is associated with molarization of the P$_3$, while types B and C represent intermediate forms. The *A. afarensis* sample contains the
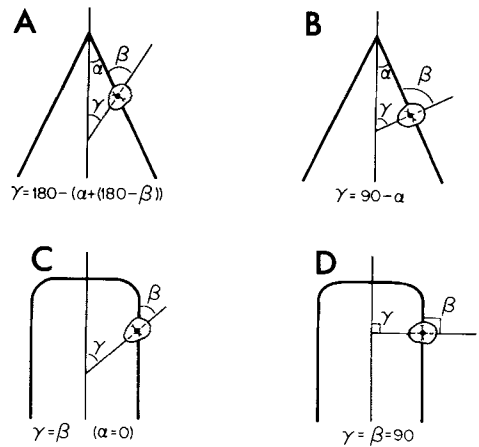

Fig. 7. Ideal types of mandibular angulation and P$_3$ rotation: A: Type 1: V-shaped mandible, rotated P$_3$. γ is minimized. B: Type 2: V-shaped mandible, unrotated P$_3$. C: Type 3: U-shaped mandible, rotated P$_3$. D: Type 4: U-shaped mandible, unrotated P$_3$. γ is maximized.

entire range of variation expressed by these four categories; specimens such AL 288-1 and many ramapithecines (i.e., RPL-54, 55) fit the type A morphology while AL 333w-60 represents the type D morphology of later australopithecines (i.e., MLD-2).

A measure which is sensitive to both the angulation of the mandible and the rotation of the P$_3$ is the angle between the major axis of the P$_3$ and the midline (γ). This angle is minimized in the primitive type A specimens and maximized in type D (grinding) specimens (Fig. 7). Therefore, it was used as an index of overall shearing capacity of the P$_3$. The three measures of angulation and rotation (angle of the mandible, rotation of the P$_3$, and angle between the major axis and the midline) were judged on the ten most complete *A. afarensis* specimens. Mandibular angulation (α) and P$_3$ rotation (γ) for these specimens are listed in Table 5 and ranked according to γ in Table 6.

Comparative sample

The dental morphology of a comparative sample (*Pan troglodytes*)was also analyzed in this study. Comparisons were made in order to gain insight into the possible ecological and evolutionary significance of the variation in the P$_3$ morphology of *A. afarensis*. The chimpanzee sample consists of 60 mandibles (30 male and 30 female) from the Hamann-Todd Collection of the Cleveland

Museum of Natural History. The morphology of all the P_3s in this sample was scored on the same criteria used for the *A. afarensis* sample. Rotation of the P_3 was obtained by direct measurement.[3]

Analytical methods

In assessing the morphological criteria of the *A. afarensis* and chimpanzee samples, ranks were assigned to each of the specimens for each of the four morphological criteria. Similarly, for the *A. afarensis* sample, a chronological ranking was given to each of the 20 specimens. Additionally, P_3 and M_1 breadth measurements for the *A. afarensis* specimens were also converted into rank orders to make them comparable to the morphological data (Table 6).

For the *A. afarensis* sample, the chronological ranking given is based on the geological dating and chronological sequences established for Laetoli, Hadar, the Tulu Bor tuff at Koobi Fora, and the white sands at the Omo. It has generally been held that the Laetoli (3.6–3.8 mya) *A. afarensis* remains are older than any of the Hadar hominids (Boas et al., 1982; Brown, 1982, 1983; Brown et al., 1985). However, Aronson et al. (1983) and White et al. (1984) have suggested that the earliest hominids at Hadar may be as old as 3.7 mya, and therefore that the basal levels at Hadar may overlap in time with Laetoli. For the purposes of this analysis, we will consider Laetoli as older than all of the Hadar levels. We feel that the bulk of the evidence still indicates that the Laetoli is older than Hadar, and secondly, that even if the basal member at Hadar is 3.7 my, it does not preclude Laetoli from being older, given that estimates for Laetoli have been as great as 3.8 my. This is in agreement with White (1985:149) that "it is appropriate to assess any differences between the Hadar and Laetoli site samples for possible evidence of evolutionary change." Therefore, Laetoli will be ranked older than Hadar, and within the Hadar sequence, the specimens will be chronologically seriated according to their stratigraphic placement (cf. Johanson et al., 1982b; Fig. 3).

The two other specimens, ER 5431 from the Tulu Bor levels at Koobi Fora and W-978 from the Omo white sands, are chronologically ranked according to data from Brown et al. (1985) and Harris (1985). Brown and colleagues have associated the earliest Omo and Tulu Bor levels with the same eruptive event, and this event has been noted to be older than the basal member at Hadar. Additionally, Harris (1985:77) notes that the Laetoli beds appear to be older than the early levels at Koobi Fora.

Analyses required the use of parametric and nonparametric statistical tests. Chisquared Fischer's exact test and t-tests were used to determine the significance of differences between samples, particularly between males and females. To determine the relationship between variables, Spearman's rank correlation (Dixon and Massey, 1967:349–351; Snedecor and Cochran, 1967:193–195) was used to test hypotheses of independence between P_3 size, body size (as judged by M_1 size), the molarization criteria (metaconid development and fovea closure), and relative chronological order. This procedure makes no assumptions about the distributions of the ranks and provides a measure of similarity in rankings equivalent to a correlation coefficient. Such tests were used to discern morphological trends in the *A. afarensis* P_3 sample.

RESULTS
Variation of A. afarensis *P_3s*

Variation in P_3 morphology is evident in both the modern and fossil samples. Great variation, ranging from sectorial to bicuspid morphologies, is evident in the *A. afarensis* sample. Modern apes, on the other hand, tend to have sectorial P_3s, though the development of a metaconid is not uncommon (Huag, 1977; Johanson and Edey, 1981), and the orientation of the P_3 is variable as well.

Comparison of the *A. afarensis* and chimpanzee samples indicates that variation in *A. afarensis* is generally greater than that of the chimpanzees. As is shown in Table 7 and Figures 8A–C and 9A–C, for three of the five molarization criteria the range of variation seen in *A. afarensis* is greater than that seen in the chimpanzees, and in no case is the variation in *A. afarensis* less than that in the chimpanzees. Moreover, as shown by chisquare analysis (Table 7), for each molarization criterion there are significant differences between *A. afarensis* and *Pan*. In combination, these two factors indicate that the range of variation in P_3 morphology is significantly greater in *A. afarensis* than in *Pan*.

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[3]For each mandible, data were obtained for both P_3s, if present. In cases of differences in the morphological criteria I-IV between the left and right P_3s rotation, averages of the left and right were used when both were present.

TABLE 7. Range of morphological variation: A. afarensis vs. P. troglodytes

Sample	No.	Crit. I		Crit. II		Crit. III		Crit. IV		Angulation range
		Range	χ^2	Range	χ^2	Range	χ^2	Range	χ^2	
Total samples										
A. afarensis	20	1–5		1–4		1–5		2–5		33–85°
P. troglodytes	60	1–4	28.7**	1–3	22.8**	1–3	33.1**	1–4	31.7**	28–79°
Male samples										
A. afarensis	11	3–5		2–4		3–5		3–5		39–85°
P. troglodytes	30	1–4		1–3		1–3		2–4		39–79°
Female samples										
A. afarensis	8	1–4		1–4		1–5		2–4		33–42°
P. troglodytes	30	1–4		1–3		1–3		1–3		28–57°

**P ⩽ .01.

The demonstration that the variation in P_3 morphology is greater in A. afarensis than in a modern hominoid analog is interesting in light of the results obtained from the dental metric data. Two possible explanations for this high degree of variation are (1)The sample represents *more* than one species (Olson, 1981; Read, 1984; Zihlman, 1985a,b), and (2) the morphology of the A. afarensis P_3 was changing over time. Since the previous analyses indicate that the metric variation is consistent with a single-species hypothesis (see also Kimbel et al., 1985; White, 1985), we shall focus on the latter hypothesis.

Temporal trends

The next question considered in these analyses is whether there is evidence for evolutionary change in the P_3 morphology of A. afarensis. Given that one of the Miocene apes gave rise to hominids (see Ciochon, 1983; Greenfield, 1972, 1979, 1980, 1983; Kay, 1982a,b; Kay and Simons, 1983; Pilbeam, 1979; Simons, 1981; Simons and Pilbeam, 1971; Wolpoff, 1982, 1983c, for various interpretations), we hypothesize that the earliest hominids, A. afarensis, exhibit evolutionary change in their P_3 morphology from the primitive unmolarized condition seen in most of the Miocene hominoids to the derived bicuspid condition, seen in later australopithecines and *Homo*. The proposition that such an evolutionary trend occurred in A. afarensis is supported by the results shown in Table 8. When the sample is considered as a whole, all of the morphological criteria are positively correlated with chronological rank— although none of them significantly so (criterion I/II: r_s=0.334; criterion III: r_s=0.306; mean criteria I–IV: r_s=0.327; P_3 angulation: r_s=0.616, p=.09).

However, when the males and females are considered separately, different patterns emerge. All molarization criteria are significantly correlated with chronological rank in the males (lingual cusp development [criterion I/II]: r_s=0.786; closure of the anterior fovea [criterion III]: r_s=0.610; mean criteria I–IV: r_s=0.599) and angulation is highly correlated (r_s=0.949), though not statistically significant because of the small sample size. Conversely, for the sample of female P_3s, criterion I/II is negatively correlated with chronological rank, while criterion III and mean criteria I–IV have very low, non-significant positive correlations with chronological rank. Angulation of the females' P_3s on the other hand shows a higher positive correlation (r_s=0.638).

These results indicate that both sexes of A. afarensis developed changes in the angulation of the mandibles and P_3s over time, such that the position of the P_3s became less well suited for shearing. However, parallel changes are not detected in the morphology of male and female P_3s. Specifically, in the males there appears to be a temporal trend toward the development of equal meta- and protoconids. The earliest males tend to have the least molarized P_3s. There are no male P_3s that are distinctly sectorial (i.e., like AL 128-23); however, chronologically early male specimens such as LH-14 and AL 277-1 show evidence of only slight metaconid development. The latest males, represented by specimens from site 333 (most notably 333w-60 and 333w-1a), show clear development of the metaconid to a level near or equal to that of the protoconid.

A similar trend is *not* discerned for the females, as shown in Table 8 by the lack of significant positive correlations between
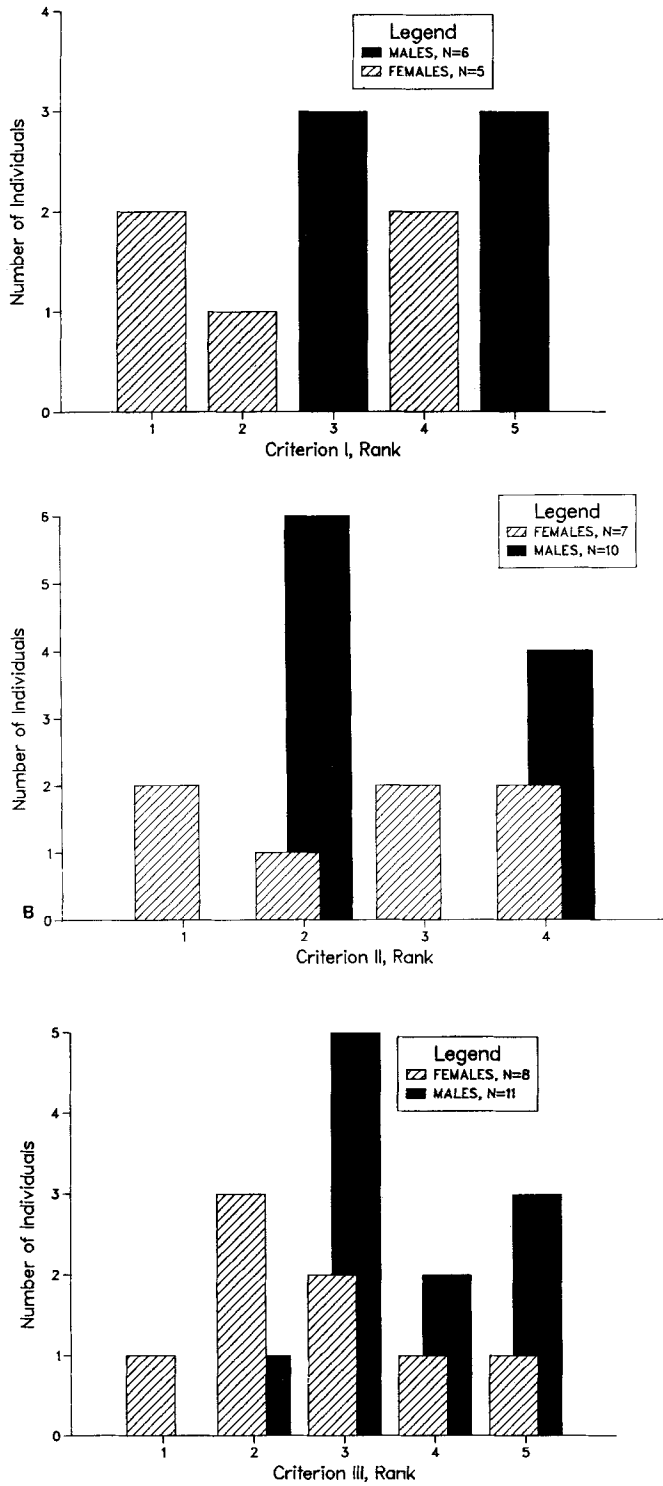
Fig. 8. Sexual differences in the molarization and angulation of *A. afarensis* P_3s: Criterion I—lingual cusp development observed directly; criterion II—transverse ridge development as an indication of lingual cusp development; criterion III—closure of the anterior fovea.
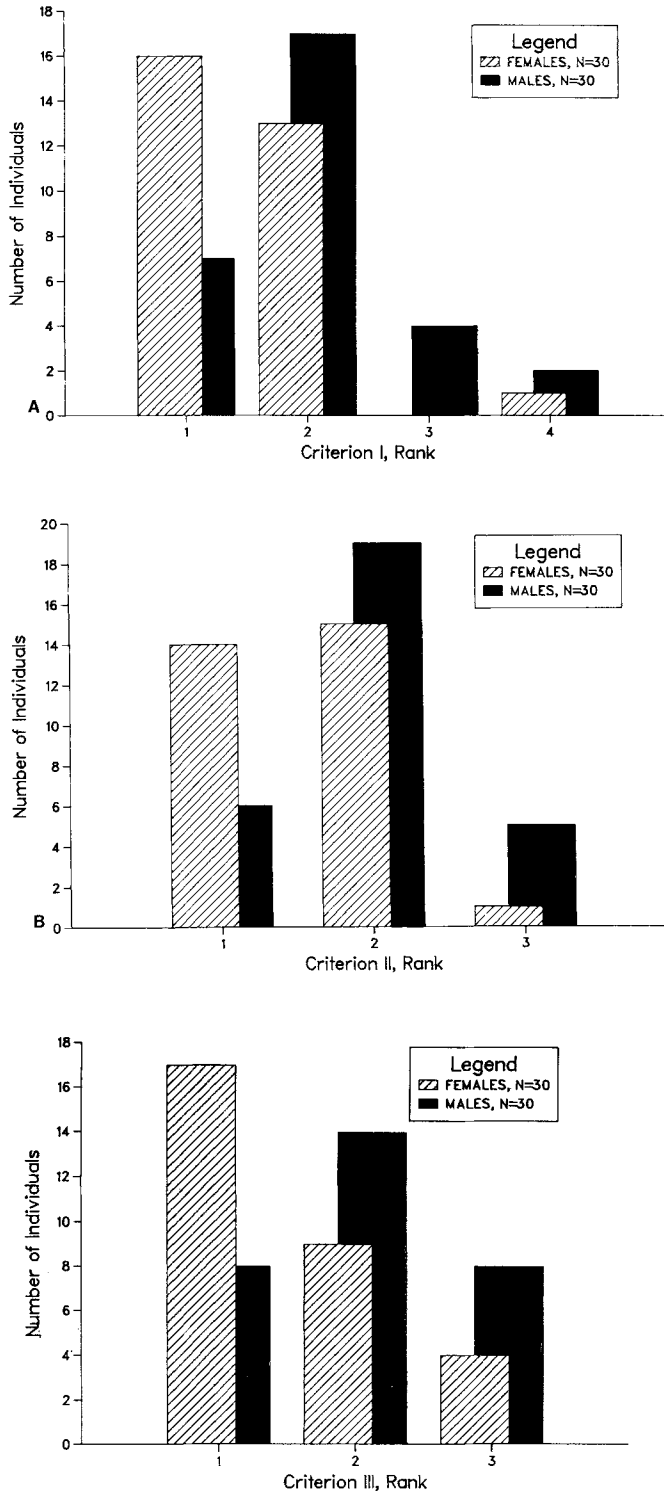
Fig. 9.   Sexual differences in the molarization and angulation of chimpanzee P$_3$s: Criterion I—lingual cusp development observed directly; criterion II—transverse ridge development as an indication of lingual cusp development; criterion III—closure of the anterior fovea.

TABLE 8. Rank correlations: Morphological change vs. chronological rank

Sample	Criteria I/II vs. chronological rank	Criterion III vs. chronological rank	Mean criteria (I–IV) vs. chronological rank	Angulation vs. chronological rank
Males				
r_s	0.786**	0.610*	0.599*	0.949
N	10	11	11	4
Females				
r_s	−0.451	0.167	0.024	0.638
N	7	8	8	6
Total sample				
r_s	0.334	0.306	0.327	0.616
N	18	20	20	10

*$P \leqslant .05$.
**$P \leqslant .01$.

morphology and chronological rankings. Two of the most unicuspid females are early in the sequence (AL 128-23 and AL 198-1) and several of the more bicuspid specimens are late (AL 207-13, AL 266-1 and AL 333w-46).

However, the P_3 of the late specimen, "Lucy" (AL 288-1), contradicts this trend, since it is a small, single-cusped tooth from the latest of the Hadar localities. The P_3 of AL 288-1, therefore, indicates that the single cusp morphology was maintained (although possibly at a low frequency) in the A. afarensis females throughout the time period spanned by the Hadar remains.

The influence of size on the morphological trends

To evaluate fully the apparent molarization trend in the male A. afarensis P_3s, it is necessary to determine whether this trend is an artifact of size. Larger animals with greater nutritional requirements are expected to exhibit larger occlusal areas as an adaptation for processing larger amounts of food. Consequently, since the development of a second cusp would tend to increase the occlusal surface area and size of the P_3, patterns of molarization could be merely a reflection of the interrelationship between body size and P_3 size. In order to analyze the relationship between size and morphology, various correlations were determined for (1) P_3 size and molarization criteria, (2) P_3 size and angulation, (3) P_3 size and chronological rank, (4) M_1 size and P_3 molarization criteria, (5) M_1 size and P_3 angulation, and (6)P_3 size and M_1 size. M_1 breadth was used as an indicator of body size, since it is a conservative tooth with relatively low intraspecific variation (Gingerich and Schoeninger, 1979; Gingerich, 1982).

The correlations are listed in Table 9. Two general relationships provide background for further interpretation. First, the breadths of M_1s and P_3s are significantly correlated with each other, a predictable result since concordance in tooth size is expected within individuals. Second, tooth breadths are negatively correlated with chronological rank for the males. The negative correlation is statistically significant only for the total sample of M_1s, but these results indicate that these teeth did not increase significantly in size over time.

The earlier analysis indicated that changes in A. afarensis P_3 morphology were different for males and females. The relationship of P_3 morphology to P_3 breadth and to body size as indicated by M_1 breadth is also different for males and females (Table 9). For the total sample, all four morphological criteria are positively correlated with both M_1 and P_3 breadths. The female tooth breadths, taken separately, also are positively correlated with the morphological criteria (with the exception of angulation and M_1 breadth). However, the male tooth breadths are negatively correlated with the morphological criteria.

The statistical significances of the correlations between tooth breadths and P_3 morphology for the separate male and female samples are limited because of the small sample sizes. However, the consistent negative correlation for the males and positive correlation for the females suggest some important differences. Female A. afarensis P_3s do not become increasingly molarized over time, judged by lingual cusp development (criterion I/II) and by anterior fovea development (criterion III) or mean molarization (mean criteria on I/IV) (Table 8). All three of these criteria are positively correlated with

TABLE 9. Rank correlations of tooth morphology and size

Correlated variables	Males		Females		Total sample	
	11	r_S	N	r_S	N	r_S
P_3 breadth and chron. rank	11	−0.459	8	0.287	20	−0.276
P_3 breadth and crit. I/II	10	−0.006	7	0.613	18	0.313
P_3 breadth and crit. III	11	−0.346	8	0.754*	20	0.333
P_3 breadth and mean crit. (I–IV)	11	0.098	8	0.416	20	0.315
P_3 breadth and angulation	4	−0.200	6	0.216	10	0.531
P_3 breadth and M_1 breadth	6	0.812*	5	0.800*	12	0.886**
M_1 breadth and chron. rank	6	−0.204	5	−0.500	12	−0.580*
M_1 breadth and crit. I/II	6	−0.047	4	0.949	11	0.305
M_1 breadth and crit. III	6	−0.638	5	0.600	12	0.301
M_1 breadth and mean crit. (I–IV)	6	−0.147	5	0.800*	12	0.564*
M_1 breadth and angulation	3	−0.500	5	−0.410	8	0.072

*$P \leqslant .05$.
**$P \leqslant .01$.

tooth breadth (significantly so for criterion III vs. P_3 breadth and mean criteria I–IV vs. M_1 breadth; see Table 9), suggesting that since there is no significant shift in female P_3 morphology, the morphological variation over time remains associated with tooth and/or body size. In contrast, male P_3s became increasingly molarized over time (Table 8), and the molarization is not positively correlated with tooth breadths (Table 9). These trends indicate that among the males, the P_3s became increasingly molarized over time regardless of tooth and body size. In other words, there appears to be an association between body/tooth size and P_3 molarization in the females, while this association seems to have been uncoupled in the males, which show a trend toward molarization.

Sexual differences in morphology

We have shown that the P_3s of *A. afarensis* males and females exhibit different morphological trends over time and that these differences are not merely size related. Thus, it is not surprising that there are overall differences in morphology between the sexes. The values for the morphological criteria are listed and ranked in Tables 5 and 6, and the distributions of the ranks, divided by sex, are illustrated in Figure 8. Fisher's exact test was used to evaluate male and female differences in the molarization criteria. This test was used to accommodate the small sample sizes. [4] As shown in Table 10, the P_3s of *A. afarensis* males are significantly more molar-

ized than those of the females (criterion I, p=.06; criterion III, p=.07; see also Fig. 8A–C). Additionally, the mean angulation of the P_3 in males of *A. afarensis* is significantly greater (68° versus 39°, p $\leqslant$ .05) than that of the females. Females, on average, show less rotation of the premolar than males. This pattern is consistent with the molarization patterns, as less molarized P_3s are generally less rotated.

It is important to note that when male and female differences in P_3 molarization are considered for the chimpanzee sample, the *same pattern emerges* (Table 11, Fig. 9). The range of variation in the male P_3s tends more toward the molarized end of the spectrum for all three criteria, with significant differences (p $\leqslant$ .05) for all three criteria (Fig. 9A–C), and as in *A. afarensis*, the rotation of the P_3 was significantly greater (50° versus 39° p $\leqslant$ .01) in the males (Fig. 9D).

This comparison of *A. afarensis* and chimpanzees shows that the pattern of sexual differences is the same in both species. In both cases the male P_3s are significantly more molarized than the female P_3s, according to a number of criteria. Additionally, this similarity is interesting in light of previous studies which have used P_3 morphology to

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[4]Male/female differences for each criterion were evaluated as a 2 × 2 table in order to maximize the number of individuals per cell, Blalock (1972). Fisher's exact test is the preferred method of analysis when sample sizes are too small for a chi-square test (Tenhave, personnal communication).

TABLE 10. A. afarensis P_3 differences in male and females[1]

Criteria	No. of males	No. of females	P
I-rank	6	5	.06
II-rank	10	7	NS
III-rank	11	8	.07

[1]Fisher's exact test.

TABLE 11. P. troglodytes P_3s: Chi-square analyses of difference in male and female

Criteria	No. of males	No. of females	Test result
I-rank	30	30	8.39*
II-rank	30	30	6.34*
III-rank	30	30	5.66*

*P ≤ .05.

support a claim of two species at Hadar and Laetoli. Specifically, Olson (1981) has argued that the *Paranthropus* specimens at Hadar and Laetoli display a variable lingual cusp while the *Homo* specimens do not. As should be clear from the data presented here, however, molarization of the P_3 is a continuous rather than a discrete (e.g., "present" vs. "absent") trait. Moreover, several of the specimens which Olson attributes to *Paranthropus* (i.e., AL 207-13 and 277-1) are, according to our criteria, among the *least molarized* of the *A. afarensis* P_3s. We would agree that in general, the smaller, more gracile specimens from Hadar and Laetoli have less molarized P_3s; however, as has been clearly demonstrated above, this pattern is seen in male and female chimpanzees and does not lend support to the hypothesis that there are two species at Laetoli and Hadar.

DISCUSSION

Patterning and temporal trends in morphology have been discerned within the P_3 sample of *A. afarensis*. It has been demonstrated that the variation in the P_3 morphology of the *A. afarensis* sample is greater than that found in modern chimpanzees. However, the general patterning of the variability appears to be very similar. Specifically, the males in both groups tend to have P_3s which display greater development of the metaconid, degeneration of the transverse ridge, closure of the anterior fovea, and most notably, increased rotation with respect to the midline. The similarity in the *patterns* of sexual differences in P_3 morphology support the contention that the variation is that of a single species, rather than several. The fact that the *overall variation* in *A. afarensis* P_3 morphology is greater than in a modern species may then be a reflection of temporal trends in the *A. afarensis* P_3s.

With respect to change over time, there appears to be a trend toward increased molarization in the male specimens of the sample. Moreover, this trend *cannot* be accounted

for simply by changes in P_3 or body size. The general progression apparent in the morphology of the male P_3s is development of the metaconid, degeneration of the transverse ridge, closure of the anterior fovea by a developing mesial marginal ridge, and increased rotation of the P_3 with respect to the midline.

Increasing molarization of the P_3 over time in the *A. afarensis* sample therefore may reflect increased selection for a grinding adaptation. The data then indicate that the females of the sample retain the primitive condition (sectorial P_3), while the males show the derived condition which characterizes the later hominids. It should be noted as well that aspects of the postcranial morphology indicate the same type of sexual differences, with the proposed females retaining such primitive features as curved pedal phalanges (Jungers, 1982, 1983; Latimer, 1983, 1984; Stern and Susman, 1983; Stern et al., 1984; Susman et al., 1985; Wolpoff, 1983a,b).

Several different interpretations have been put forth to explain the variation in the *A. afarensis* postcranial remains. Stern and Susman (1983; Susman et al., 1985; Stern et al., 1984) have argued that the variation may be explained in terms of "sexual dinichism," with the smaller females exploiting a more arboreal habitat, while the males exploited a more terrestrial one. Others such as Zihlman (1985a,b) have claimed that there are two species, maintaining that the postcranial differences are too great to be accounted for by sexual dimorphism. We have previously noted that the dental data support a single-species interpretation; additionally, we find Zihlman's conclusions from the postcranial evidence to be unsupported, as her analyses (1) compare the ratios of *largest/smallest A. afarensis* postcrania to ratios of *mean male/ mean female* hominoid postcrania and (2) are based on extremely small sample sizes. Moreover, a recent study by McHenry (1986) indicates that the degree of dimorphism in the *A. afarensis* postcrania is not, in fact, greater than that seen in some hominoid species. It would seem, then, that both the dental and postcranial variation should be considered within a single species context.

On the other hand, Stern and Susman's "sexual dinichism" model appears to be a plausible one which is consistent with the dental as well as the postcranial data. Their model suggests the Bornean orangutan as a useful modern analogy. Highly dispersed resources in Borneo dictate independent exploi-

tation patterns and are reflected by differences in the diets and environmental ranges between the males and females (Rijksen, 1974; MacKinnon, 1974; Rodman, 1977, 1984; Galdikas, 1979). Males tend to exploit the ground and lower levels of the canopy more heavily than the females, and consume larger amounts of low-quality food such as bark (Rodman, 1977). The smaller, more arboreal females, on the other hand, have a higher proportion of fruit in their diet.

For the early hominids, it has been hypothesized that dependent, altricial young may have led to selection for male provisioning and a reduction in the range of the females (Lovejoy, 1981; Tanner, 1981). Accordingly, it would seem that for the females, a restricted, partially arboreal habitat would have been favorable, as it would have afforded protection against predators and provided a more stable source of high-quality resources which are critical during periods of pregnancy and lactation. The males, however, not being constrained by such factors, could have exploited a larger, less arboreal range. Additionally, male provisioning, a feature often associated with the emergence of hominids (Lovejoy, 1981; Tanner, 1981), would have selected for larger ranges in males.

Such a model provides an explanation for the observed differences in body size, postcranial anatomy, and tooth morphology between the proposed males and females of *A. afarensis*. In the females, there would have been selection for smaller body size and the limb proportions suited to retention to a partially arboreal lifestyle. For the males, selective pressures would have favored large body size and increased molarization of the dentition as an adaptation to a more terrestrial habitat with a high proportion of low-quality foods in the diet.

Therefore, the postcranial as well as the dental differences may reflect differences in the ranges of males and females of *A. afarensis*. This model does not imply that females were strictly or even primarily arboreal, and therefore incapable of efficient bipedal locomotion. Rather, it posits that there was not a complete overlap of the ranges, and consequently, there were different selective pressures acting on the males and females of *A. afarensis*. We do not maintain the dental evidence alone provides definitive support for this model; however, it does seem to corroborate the postcranial evidence very well. Clearly, further analyses of *A. afarensis* would benefit from comparison of sex differences in morphology to those seen in modern primate species.

In sum, the results of this study indicate (1) the morphological variation in *A. afarensis* P$_3$s is greater than in a modern hominoid analog; (2) there is a trend toward increased molarization of the P$_3$ for the proposed males of the *A. afarensis* sample; and (3) the differences in molarization between the proposed males and females of the *A. afarensis* sample parallel the differences between male and female chimpanzees. Consequently, the explanation for the great variation in the *A. afarensis* P$_3$s appears to be twofold. First, an evolutionary trend toward increased molarization of the P$_3$ in the *A. afarensis* males would be expected to produce greater variation than in a temporally limited analog. Additionally, the Stern and Susman model of males and females exploiting different ranges would imply that the extreme variation is also associated with different selective pressures acting on the two sexes.

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