

The Uto-Aztecan Premolar Among North and South Amerindians: Geographic Variation and Genetics

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ABSTRACT The Uto-Aztecan premolar (UAP) is a dental polymorphism characterized by an exaggerated distobuccal rotation of the paracone in combination with the presence of a fossa at the intersection of the distal occlusal ridge and distal marginal ridge of upper first premolars. This trait is important because, unlike other dental variants, it has been found exclusively in Native American populations. However, the trait's temporal and geographic variation has never been fully documented. The discovery of a Uto-Aztecan premolar in a prehistoric skeletal series from northern South America calls into question the presumed linguistic and geographic limits of this trait. We examined published and unpublished data for this rare but highly distinctive trait in samples representing over 5,000 Native Americans from North and South America. Our findings in living Southwest Amerindian populations

corroborate the notion that the variable goes beyond the bounds of the Uto-Aztecan language family. It is found in prehistoric Native Americans from South America, eastern North America, Northern and Central Mexico, and in living and prehistoric populations in the American Southwest that are not members of the Uto-Aztecan language stock. The chronology of samples, its geographic distribution, and trait frequencies suggests a North American origin (Southwest) for UAP perhaps between 15,000 BP and 4,000 BP and a rapid and widespread dispersal into South America during the late Holocene. Family data indicate that it may represent an autosomal recessive mutation that occurred after the peopling of the Americas as its geographic range appears to be limited to North and South Amerindian populations. *Am J Phys Anthropol* 143:570–578, 2010. © 2010 Wiley-Liss, Inc.

Dental morphological traits have long been used to assess population-genetic affinities and microevolutionary trends among recent human populations (Irish, 1997; Scott and Turner, 1997; Coppa et al., 2007; Delgado-Burbano, 2007). Most crown and root traits are polymorphic in populations throughout the world, with some attaining frequencies that are low (5–20%), moderate (20–70%), or high (70–100%) in any given group. Shovel-shaped incisors and Carabelli's trait are classic examples that exhibit this type of frequency variation. Less attention has been paid to dental traits that are in very low frequency (<5%) or are totally absent in some worldwide populations. This pattern applies to the highly distinctive but exceedingly rare dental variant expressed on the first maxillary premolars referred to as the Uto-Aztecan premolar (UAP) (Morris et al., 1978) or distosagittal ridge (Turner et al., 1991).

Morris (1967) found three cases of a distinctive first premolar variant in a sample of 200 living Papago Amerindians from southern Arizona. As the variant shared a common set of characteristics in the three individuals and was expressed bilaterally, he considered it a distinct dental trait rather than a developmental anomaly. He suggested that it could serve as a marker to help trace genetic affinities among human populations, but he did not coin a specific term for the trait.

During the 1970s, premolars similar to those described by Morris (1967) were found in several Amerindian populations from the American Southwest. Decades earlier, Hrdlička (1921) observed and illustrated the same trait in a Bannock Amerindian from Idaho, but he did not appreciate the fact that it was more than an isolated finding. Morris (1967) included a photo of the Bannock premolar along

with a first premolar variant illustrated by Brabant et al. (1958). The provenance of the latter premolar is unknown but Morris (1967) notes the specimen lacks the distinctive distobuccal fossa and is probably not homologous to the premolar variant he described for the Papago.

After amassing a large amount of data on the geographic variation of this premolar variant, Morris et al. (1978) found it was largely if not entirely limited to Uto-Aztecan speakers. It was at that point the term UAP was adopted and applied to this unusual premolar phenotype. These authors hypothesized that the trait was geographically restricted to the North American Southwest and limited to members of the Uto-Aztecan language family. They noted that 2,800 non-Amerindian individuals with very different ancestries did not express the trait. For Native Americans, they report data for the variant in prehistoric sites in Arizona (Pueblo Amerindian area, including Sinagua), New Mexico (Gran Quivira),

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and Mexico (Casas Grandes, Chihuahua). The highest frequency for contemporary samples was found among the Papago of southern Arizona (1.6%). For archaeological samples, the Sinagua from northern Arizona (sites NA 10806 and NA 405) had frequencies ranging from 5.0 to 7.1%. Kabori et al. (1980) reported a frequency of 9.5% for the Hopi site of Awatovi in northern Arizona. In living populations, the trait is present in both the Shoshonean (Hopi and Bannock) and Sonoran (Papago) branches of the Uto-Aztecan language family. Although establishing linguistic affiliation among prehistoric samples is difficult, the presence of this trait in Gran Quivira (New Mexico) suggested that it might also be found in Tanoan speaking groups (Morris et al., 1978).

Kabori et al. (1980) tested the possible distribution of UAP among samples from the Great Basin region, specifically in prehistoric skeletal collections of California, Nevada, and Utah, which fall within the geographic boundaries of the Numic branch of Uto-Aztecan. However, due to small sample sizes and the very low frequency of the trait, they did not find a single occurrence in Great Basin samples.

To date, it has only been possible to make rudimentary observations on the genetics of the UAP. Morris et al. (1978: 70) noted that "In one Papago family all four siblings of the propositus had one maxillary first premolar missing although the remaining teeth were unaffected." Another affected individual had two siblings and both of them failed to express the trait. In the Papago sample, there were no instances where observations could be made on the parents or children of affected individuals. Despite their inability to demonstrate a simple mode of inheritance using limited family data, Morris et al. (1978: 75) tentatively concluded that "plausibly the trait appeared as a mutation in a member of a small band of hunter-gatherers in the American West."

In this collaborative effort, we consider both the distributional and genetic aspects of the UAP, including its presence in South America, far beyond the realm of Uto-Aztecan speakers, and the genetic inferences that can be made from Pima Indian families (casts collected by Albert and Thelma Dahlberg, observations by GRS). Additionally, GRS and CGT have amassed extensive data on this trait in living and prehistoric New World populations, much of which has never been reported until now.

MATERIALS AND METHODS

A standard upper first premolar has two cusps, a buccal cusp (paracone) and a lingual cusp (protocone). In contrast to the upper second premolar (UP2) where the main axes of the buccal and lingual cusps run almost parallel, the distal border of the buccal cusp of the upper first premolar (UP1) diverges toward the cheek away from the central sulcus. The effect of this divergence is to produce a UP1 that is more triangular in shape than UP2, which is somewhat square (Hillson, 1996).

The Uto-Aztecan premolar involves an even more pronounced distobuccal divergence of the paracone than the typical UP1. It is so dramatic that a sagittal ridge running parallel to the central sulcus is separated from the paracone by a deep fossa. Morris et al. (1978) note the following characteristics of the Uto-Aztecan premolar: (1) it is expressed only on UP1, never UP2; (2) it involves a marked buccolingual expansion of the paracone; (3) the paracone is broadened distally with the distal portion exhibiting a large distinctive fossa; (4) a lobular ridge, at times equal in size to the paracone's distal occlusal border, intersects the border at the distal terminus of the



Fig. 1. A symmetrical case of the Uto-Aztecan premolar in a male individual from the Portalegre site (Muisca Period) in northern South America. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

sagittal sulcus; and (5) the fossa lies between the ridge and the true distal occlusal border of the paracone. Although the trait does show a modest amount of variation in expression, it is always scored as present or absent and can be manifested either unilaterally or bilaterally.

In a dental morphological study of 432 Northern Andean skeletons spanning the range from late Pleistocene to recent times, the first author (MEDB) found a distinctive and symmetrical Uto-Aztecan premolar in a sample from the Portalegre site (915 ± 115 BP– 720 ± 110 BP) in Colombia (see Fig. 1).¹ The series belongs to the Muisca period (~2550–450 BP) in the East Andes Cordillera (Therrien and Enciso, 1991). To put this find in a broader geographic context, unpublished observations on 2,400 Pima Indians and 1,022 Southwest Amerindians representing Uto-Aztecan, Athapaskan, Yuman, and Zunian populations are provided by GRS. Also included are the observations of CGT on 2,101 North and South American Indians and Eskimo-Aleuts. The greatest part of the dental data presented in this study were collected during the past four decades and come from unpublished and/or partially described materials (Scott, 1973; Turner, 1984). The new dental data reported from the Northern Andes samples are part of another project. Additional comparative data were gathered from the literature for samples from the American Southwest (LeBlanc et al., 2008) and Northeastern South America (Reyes et al., 2008), respectively. The total sample exceeds 5,000 individuals, an important consideration when a rare trait is examined.

A chi-square analysis was performed to test statistical significance ($P = 0.05$ and 1 df) in UAP frequencies between pooled North and South American Indian samples. The individual count method was used to derive trait frequencies. This method assumes that an individual has only one genotype for any specific trait and should therefore be classified in only one phenotypic category (Scott, 1980). Additionally, it assumes that when asymmetric expression is evident, the antimere showing the greatest degree of trait expression is considered the best reflection of the underlying genotype. Consequently, when there is asymmetry for UAP, it is scored as present. Detailed information on the samples can be found in Scott (1973), Scott et al. (1983), Turner (1984), Scott and Turner (1997), Turner and Scott (2007), and Delgado-

¹Additional graphic material on UAP morphology can be found in Morris (1967), Morris et al. (1978), Kabori et al. (1980) and Scott and Turner (1997). Also the ASUDAS system provides a plaster plaque for this trait (Turner et al., 1991).

TABLE 1. *Uto-Aztecan premolar occurrence in living Pima Indians*

| Sex | N | 0-0 | -0/0- | 1-1 | 1-0 | 0-1 | 1- | -1 | A/N | % |
|--------|-------|------|-------|-----|-----|-----|----|----|----------|------|
| Male | 1,133 | 1015 | 110 | 0 | 3 | 3 | 0 | 2 | 8/1,133 | 0.71 |
| Female | 1,267 | 1142 | 115 | 1 | 3 | 5 | 1 | 0 | 10/1,267 | 0.79 |
| Total | 2,400 | 2157 | 225 | 1 | 6 | 8 | 1 | 2 | 18/2,400 | 0.75 |

0-0, absent on both right and left antimeres; -0/0-, absent on left or right antimere, one antimere not observable; 1-1, present on both antimeres; 1-0, present on left, absent on right; 0-1, present on right, absent on left; 1-, present on left, right unobservable; -1, present on right, left unobservable.

TABLE 2. *Uto-Aztecan premolar frequencies among contemporary Native American populations from the American Southwest*

| Sample | Sex | Affected | N | % |
|---------------------------|-------|----------|-------|------|
| Papago | M | 2 | 92 | 2.18 |
| | F | 0 | 88 | 0.00 |
| | Total | 2 | 180 | 1.11 |
| Hopi (ASU) | M | 2 | 55 | 3.64 |
| | F | 0 | 111 | 0.00 |
| | Total | 2 | 166 | 1.20 |
| Hopi (Chicago) | M | 0 | 56 | 0.00 |
| | F | 0 | 68 | 0.00 |
| | Total | 0 | 124 | 0.00 |
| UTO-AZTECAN | M | 4 | 203 | 1.97 |
| | F | 0 | 267 | 0.00 |
| | Total | 4 | 470 | 0.85 |
| Navajo (Keam's Canyon) | M | 0 | 40 | 0.00 |
| | F | 3 | 119 | 2.52 |
| | Total | 3 | 159 | 1.89 |
| Navajo (Tuba City) | M | 3 | 80 | 3.75 |
| | F | 3 | 78 | 3.85 |
| | Total | 6 | 158 | 3.80 |
| Navajo (Ramah) | M | 1 | 45 | 2.22 |
| | F | 0 | 49 | 0.00 |
| | Total | 1 | 94 | 1.06 |
| San Carlos Apache (M + F) | Total | 0 | 26 | 0.00 |
| | M | 4 | 165 | 2.42 |
| | F | 6 | 246 | 2.43 |
| ATHAPASKAN | Total | 10 | 437 | 2.29 |
| | M | 1 | 26 | 3.85 |
| | F | 1 | 30 | 3.33 |
| Yuma | Total | 2 | 56 | 3.57 |
| | M | 0 | 19 | 0.00 |
| | F | 0 | 13 | 0.00 |
| Mohave | Total | 0 | 32 | 0.00 |
| | M | 0 | 5 | 0.00 |
| | F | 0 | 7 | 0.00 |
| Havasupai | Total | 0 | 12 | 0.00 |
| | M | 1 | 50 | 2.00 |
| | F | 1 | 50 | 2.00 |
| Yuman | Total | 2 | 100 | 2.00 |
| | M | 0 | 17 | 0.00 |
| | F | 0 | 24 | 0.00 |
| Zuni | Total | 0 | 41 | 0.00 |
| | M | 9 | 435 | 2.07 |
| | F | 7 | 587 | 1.19 |
| Total Southwest | Total | 16 | 1,048 | 1.53 |

Burbano (2010). Additional data will be provided to interested authors upon request.

RESULTS

Geographic variation

Morris et al. (1978) opine that the Uto-Aztecan premolar is not present in Navajo or Pima Amerindians, but data reported here show those observations were premature. It is not surprising that A.A. Dahlberg did not remember any instances of the UAP in his large Pima Indian collection. The trait is extremely rare. One of the

authors (GRS) observed 1,440 Pima dental casts initially (cf. Scott et al., 1983) and then reexamined those casts and 1,000 more and found 18 total UAP expressions out of 2,400 individuals (Table 1). In the Pima, the trait is equally frequent in males (0.71%) and females (0.79%), with an overall frequency of less than 1% (i.e., 0.75%). In only one instance was the trait expressed bilaterally. There were 14 individuals who expressed the trait on one side but not the other, with no significant side preference. In three cases of trait presence, only one first premolar could be scored.

Earlier, GRS scored the trait in over 1,000 Papago, Hopi, Navajo, Apache, Zuni, Yuma, Mohave, and Havasupai dental casts as part of a larger analysis of dental variation among living Southwest Native Americans (Scott, 1973). The Uto-Aztecan premolar was not included in the final biological distance analysis because of its rarity. When the original tabulations were examined, an additional 16 cases were found in 1,048 individuals (Table 2). For these samples, the trait is present in two Uto-Aztecan samples, the Papago and Hopi, in a frequency similar to that of the Pima (4 of 470; 0.85%). However, contrary to Morris et al. (1978), the trait is not only present in Athapaskan samples, but also is in higher frequency in this language family (10 of 437; 2.29%). The frequency in Yuman samples is similar (2 of 100; 2.0%). The trait was not found among the Zuni (0 of 41), but the sample is so small, we cannot draw a conclusion about its presence or absence in this population.

The distribution of UAP in South America is presented in Table 3. The main finding is its presence in divergent and widely dispersed South American samples from Colombia, Venezuela, Ecuador, Chile, and Brazil (see Fig. 2). Low frequencies are also registered in the subcontinent with only six cases (seven teeth) out of 950 South Amerindians (0.62%). Although this trait is characterized by low frequencies throughout the Americas, the South American samples have the lowest frequencies of all. According to the chronology of the samples with UAP, this trait is only present during the late Holocene (but see below). It is not present in early Holocene samples from Colombia, Peru, Brazil, and Chile. These data suggest a north to south dispersal pattern for UAP during the late Holocene, albeit with a wide distribution across South America (see Fig. 2).

Table 4 shows the frequency of UAP in North and Central American prehistoric samples. The frequency for the pooled North-Central American sample of 1.63% (54 of 3,299) is more than twice as high as that for South America. Although the trait is most common in the American Southwest, it is not limited to that region. It is also present in the northeastern (i.e. Ohio valley) and southeastern (Arkansas and Alabama) regions of North America. Additional cases were found in northeast and south-central Mexico (Coahuila and Cuicuilco-Tehuacan). Despite its relatively widespread distribution in North America, many of

TABLE 3. Frequency of the Uto-Aztecan premolar polymorphism in South American prehistoric samples

| Location | Site/group | Chronology ^a | Affected | N | % | A.T ^b | Observer/reference | |
|-------------|--|-------------------------|----------------|-----|------|------------------|--------------------|---------------------|
| Panama | Cerro Mangote-Venado Beach | M.H | 0 | 43 | 0.0 | – | CGT | |
| Colombia | Costa Caribe | F.L.H | 0 | 20 | 0.0 | – | MEDB | |
| | Guane | F.L.H | 0 | 26 | 0.0 | – | MEDB | |
| | Lache | F.L.H | 0 | 26 | 0.0 | – | MEDB | |
| | Nariño | 2,000–230 BP | 0 | 26 | 0.0 | – | MEDB | |
| | Porce | 7,080–3,910 BP | 0 | 10 | 0.0 | – | MEDB | |
| | Sabana de Bogotá early Holocene | 10,090–7,090 BP | 0 | 7 | 0.0 | – | MEDB | |
| | Sabana de Bogotá middle Holocene | 6,830–5,025 BP | 0 | 30 | 0.0 | – | MEDB | |
| | Sabana de Bogotá initial late Holocene | 3,410–3,200 BP | 0 | 16 | 0.0 | – | MEDB | |
| | Muisca–Marín | 700–600 BP | 0 | 20 | 0.0 | – | MEDB | |
| | Muisca–Soacha | F.L.H | 0 | 30 | 0.0 | – | MEDB | |
| | Muisca–Bogotá | 1,180–700 BP | 0 | 27 | 0.0 | – | MEDB | |
| | Muisca–Portalegre | 915–720 BP | 1 | 37 | 2.7 | 2 | MEDB | |
| | Coronado | 2,150–1,750 BP | 0 | 31 | 0.0 | – | MEDB | |
| | Estadio | 2,950 BP | 0 | 20 | 0.0 | – | MEDB | |
| | Guacarí | 1,160–730 BP | 0 | 20 | 0.0 | – | MEDB | |
| | CSBM ^c | 2,950–1,510 BP | 0 | 22 | 0.0 | – | MEDB | |
| | Venezuela | Las Locas | 2,350–2,150 BP | 1 | 25 | 4.0 | 1 | Reyes et al. (2008) |
| | Ecuador | Ayalan | 2,450–220 BP | 1 | 74 | 1.3 | 1 | CGT |
| | | Chanduy Valley | 5,250–3,450 BP | 0 | 12 | 0.0 | – | CGT |
| | | Cotocollao | 3,750–2,350 BP | 1 | 27 | 3.7 | 1 | CGT |
| Santa Elena | | 8,000–6,700 | 0 | 25 | 0.0 | – | CGT | |
| Peru | Paloma | 7,800–4,700 BP | 0 | 29 | 0.0 | – | CGT | |
| | Chicama valley Huaca Prieta | ~5,450–3,750 BP | 0 | 118 | 0.0 | – | CGT | |
| Chile | Cuchipuy, La Herradura, Punta Teatinos | ~8,070–1,320 BP | 1 | 79 | 1.2 | 1 | CGT | |
| Brazil | Corondó–Minas Gerais | 4,000–3,000 BP | 1 | 34 | 2.9 | 1 | CGT | |
| | Lagoa Santa | 11,500–7,000 BP | 0 | 56 | 0.0 | – | CGT | |
| | North and South Sambaqui | 4,000–2,000 BP | 0 | 74 | 0.0 | – | CGT | |
| Total | | | 6 | 964 | 0.62 | 7 | | |

^a M.H: Middle Holocene (6000–4000 BP); F.L.H: Final Late Holocene (1000 BP-recent).

^b Affected teeth.

^c Pooled sample from Cauca river Valley region (Cerrito, Santa Bárbara and Malagana).

the samples with UAP are located in the American Southwest and northern Mexico. This suggests a Southwest origin for the trait in agreement with earlier observations (Morris, 1967; Morris et al., 1978). Although more samples are needed, this assumption is supported by the statistically significant difference between North and South American frequencies ($\chi^2 = 5.23$, 1 d.f., $P = 0.02$), and because only in the North American Southwest has the trait been observed in living individuals.

In a broad context, Tables 3 and 4 show the limited presence of UAP in the Americas. These data exemplify the rarity of this trait with an overall hemispheric frequency of 1.4% (60 of 4,263). The absence of this trait in other regions of the globe, its very low frequency in the New World, and its presumed relatively late appearance and dispersion suggest a dental trait with a short evolutionary history that may be a private dental marker for Native Americans.

Genetics

Morris et al. (1978) had only two affected individuals with but a few siblings in a Papago sample to address the issue of UAP genetics. Here, we have access to a much larger set of family data. Eighteen individuals expressed the trait in the Pima sample, and most affected individuals could be placed in a genealogical context (see Appendix 1 for Pima family data). Although it is not possible to do a classic mating type analysis, we can make an informed opinion on the mode of inheritance of the UAP.

1. The trait is not X-linked. Morris et al. (1978) note that the trait is present in both males and females

and the Pima data support this entirely. Eight males (0.71%) and 10 females (0.79%) expressed the trait, making it highly unlikely that X-linkage is involved in trait expression.

2. The trait is not an autosomal dominant. There were two families where both parents exhibited trait absence but one offspring expressed the trait (families 6053 and F6289). This could only happen with autosomal dominance if you invoked incomplete gene penetrance in one of the parents or brought paternity into question. Also, there were three families where one parent expressed the trait but the combined eight offspring all exhibited trait absence (families 6053, F6289b; 6448). Assuming the three parents were UAP/uap, you would expect four presence and four absence phenotypes among eight offspring. Assuming autosomal dominance, the probability of finding no affected individuals out of eight offspring from mating types including one affected parent is 0.0039, making this mode of inheritance unlikely.

3. The trait is potentially a rare autosomal recessive. For autosomal recessive traits, (1) both males and females should be equally affected; (2) the trait should be found in siblings but not in parents of affected nor children of affected; (3) it may be isolated or sporadic in small sibships; and (4) the recurrence risk in siblings of a affected individual is 25%. Males and females expressed the trait with very similar frequencies, supporting criterion 1. There were two families where one offspring expressed the trait, but it was absent in both parents (6063 and 6076). In another family (6053), an unaffected father and affected mother produced three offspring who were unaffected.



Fig. 2. Geographical distribution of Uto-Aztecan premolars in the Americas based on approximate locations of samples (Tables 1–4). Black circles, prehistoric sites. Gray circles, contemporary Amerindian populations. North America. Northeast HO: Hopewell; PR: Proctorville; BU: Buffalo. Southeast- ARK: Arkansas; ALB: Alabama. West CA: California. Southwest: BA: Bannock; NAV: Navajo Area; HO: Hopi; YU: Yuma; PAP: Papago; PI: Pima. NA 405 and 10809 Wupatki Pueblo; GQ: Gran Quivira; NM: New Mexico; DSS: Different Southwest sites (Pt. Pimes, Canyon Chelly and Kayenta, Chavez Pass, Grasshooper). Central America. CG: Casas Grandes; COA: Coahuila; CUI: Cuicuilco; THE: Tehuacan. South America. Colombia PA: Portalegre. Venezuela LC: Las Locas. Ecuador CO: Cotacollao; AY: Ayalan. Brazil MG: Minas Gerais. Chile. CP: Cuchipuy.

In another instance, an affected father and unaffected mother had two children that lacked the trait (family 6448). These two examples are consistent with criterion 2. There were 12 sibships that included one affected individual (sibship size including affected: 2, 2, 3, 3, 3, 4, 5, 5, 5, 5, 6, and 7). This fits the third criterion of sporadic presence in small sibships as 12 affected of 50 total sibs (24%) approximates the expectation of a rare recessive allele (25%). However, if the calculation of recurrence risk in the sibs of affected individuals is 25%, then the probably of finding zero affected sibs is very low ($P = 0.00032$).

4. The Uto-Aztecan premolar is heritable and possibly polygenic. There is no evidence to support a model of simple X-linked inheritance or autosomal dominant inheritance. Despite the absence of sib and parent-child linkages, there are genealogical ties in the Pima pedigrees: (1) an aunt (2111) and a nephew (3355)

express the trait and (2) male (1733) and female (2231) first cousins, twice removed, manifest the UAP. In a third case, a female (4139) exhibits a distinct expression of UAP while a female first cousin (3427) exhibits what was noted as a threshold trait expression. The remaining Pima Amerindians who had UAP had no other first degree ($n = 53$) or second/third degree relatives ($n = 37$) with the trait. The overall pattern of UAP in the genealogies is consistent with the expectations of a quasicontinuous variant with a polygenic mode of inheritance (Scott, 1973; Harris, 1977; Scott and Turner, 1997). At this point, we do not have enough information to posit strongly either autosomal recessive or polygenic inheritance. We are more confident in ruling out X-linked inheritance and autosomal dominance.

DISCUSSION AND CONCLUSIONS

Morris et al. (1978) place the origin of the Uto-Aztecan premolar sometime before 3,200 BP in the American West and suggest that it possibly appeared as a mutation in a member of a small band of desert-dwelling hunter-gatherers. Because the feature does not affect occlusion or make a tooth more caries susceptible, the authors believed that it was maintained in low frequencies in subsequent generations, ultimately being dispersed over a wide geographic area. A relatively late emergence for UAP in the above-mentioned region and a pattern of North to South dispersal are supported by several lines of evidence: (a) the chronology of the North and South American samples never go beyond 3,500–4,000 BP; (b) an exhaustive review in several late Pleistocene/early Holocene skeletal samples from North and South America did not reveal the presence of the trait before 4,000 BP; (c) only in the American Southwest do living populations exhibit the trait; and (d) North American samples have the highest frequencies and present a more structured pattern of geographic variation, whereas in South America, the trait's greater dispersal and unclear geographic pattern is the norm.

We should acknowledge that there may be some bias affecting our inferences on the spatial and temporal distribution of the Uto-Aztecan premolar. Because this feature is so rare, its absence in some populations may be primarily a function of sample size. This is especially true for more ancient human remains that are typically represented by very small samples. Substantial sample sizes per population are needed to establish definitive trait presence or absence. In addition, the temporal frame of the UAP pattern of variation is still unclear, because the dating of several samples in North and South America is not well known. These aspects allow us to conclude that a date of 4,000 BP is reasonably the upper temporal limit according to the available evidence, but its origins may be earlier, perhaps between 15,000 and 4,000 BP.

In addressing the evolutionary mechanisms that influence human dental morphology, Scott and Turner (1997: 254) note "Given the phylogenetic history of most crown and root traits, mutations likely contribute little if anything to normal dental variation, excepting perhaps rare traits with no fossil history such as the Uto-Aztecan premolar." The Pima family data provide some support for a possible autosomal recessive mutation, but this will have to be tested through further family studies. The possibility remains that the UAP is a quasicontinuous variant with a polygenic mode of inheritance, the hereditary pat-

TABLE 4. Frequency of the Uto-Aztec premolar polymorphism in North and Central American prehistoric samples

| Region/location | Sample/group | Chronology ^a | Affected | N | % | Observer/reference | |
|-----------------|---------------------------|-------------------------|----------------|-------|------|------------------------------|------------------------------|
| Canada | Archaic Canada | I. L. H. | 0 | 34 | 0.0 | CGT | |
| | Iroquois Canada | F. L. H. | 0 | 116 | 0.0 | CGT | |
| United States | Maryland | F. L. H. | 0 | 54 | 0.0 | CGT | |
| | California | M. L. H. | 1 | 91 | 1.1 | CGT | |
| | Grand Gulch, Utah | M. L. H. | 0 | 33 | 0.0 | CGT | |
| | Chelly and Kayenta | F. L. H. | 1 | 59 | 1.7 | CGT | |
| | Chavez Pass | F. L. H. | 1 | 24 | 4.7 | CGT | |
| | New Mexico | F. L. H. | 1 | 128 | 0.8 | CGT | |
| | Grasshopper | F. L. H. | 5 | 124 | 4.0 | CGT | |
| | Pt. Pines early | I. L. H. | 1 | 38 | 2.6 | CGT | |
| | Pt. Pines late | F. L. H. | 0 | 44 | 0.0 | CGT | |
| | Arkansas | F. L. H. | 4 | 97 | 4.1 | CGT | |
| | Alabama | F. L. H. | 3 | 159 | 1.9 | CGT | |
| | Ohio valley | Hopewell | ~ 2100–1500 BP | 1 | 41 | 2.4 | Johnston and Sciuilli (1996) |
| | | Proctorville | ~ 500–400 BP | 1 | 35 | 2.9 | Johnston and Sciuilli (1996) |
| Buffalo | | ~ 350–300 BP | 3 | 176 | 1.7 | Johnston and Sciuilli (1996) | |
| Southwest | Awatovi | 370 ± 95 BP | 2 | 21 | 9.5 | Morris et al. (1978) | |
| | N.A. 10806 (Arizona) | ~ 890–550 BP? | 1 | 14 | 7.1 | Morris et al. (1978) | |
| | Wupatki Pueblo | ~ 870–725 BP | 2 | 40 | 5.0 | Morris et al. (1978) | |
| | Gran Quivira (New Mexico) | ~ 1150–278 BP | 2 | 71 | 2.8 | Morris et al. (1978) | |
| | Basketmaker II–III | ~ 2450–950 BP | 0 | 117 | 0.0 | LeBlanc et al. (2008) | |
| | Mimbres | ~ 1750–820 BP | 2 | 241 | 0.8 | LeBlanc et al. (2008) | |
| | Comparative ^b | Various periods | 19 | 1,273 | 1.5 | LeBlanc et al. (2008) | |
| Mexico | Casas Grandes Chihuahua | ~ 700–600 BP | 1 | 94 | 1.1 | Morris et al. (1978) | |
| | Coahuila | F. L. H. | 2 | 31 | 6.5 | CGT | |
| | Cuicuilco and Tehuacan | M. L. H. | 1 | 59 | 1.7 | CGT | |
| | Tlatelolco | F. L. H. | 0 | 85 | 0.0 | CGT | |
| Total | | | 54 | 3,299 | 1.63 | | |

^a L.H. Late Holocene (4,000–400 BP); I.L.H.: Initial Late Holocene (4,000–3,000 BP); M.L. H.: Middle Late Holocene (3,000–1,000 BP); Final Late Holocene (1,000 BP-recent).

^b For samples and dates see LeBlanc et al. (2008: p. 113).

tern consistent with most common tooth crown and root traits. Molecular analysis in living individuals with UAP presence will clarify its genetic basis like recent research has shown for other dental traits (Kimura et al., 2009).

The geographic range of variation of the Uto-Aztec premolar is broader than Morris et al. (1978) supposed, extending even outside North America (see Fig. 2). It has now been observed in one male Chibcha speaking individual from the Portalegre site (915 ± 115 BP–720 ± 110 BP) belonging to the Muisca period in the East Andes Cordillera from Colombia (Table 3 and Fig. 2). Although the geographic origin of the Chibcha linguistic stock is in Central America, a possible relation with Uto-Aztec and Tanoan languages is unlikely even in the context of Amerindian language macro-phyla. Additionally, Turner (1984) reported the trait in linguistically and bioculturally distinct samples from South America—Ecuador (Ayalan, Cotacollao), Chile (Cuchipuy), and Brazil (Minas Gerais)—but with very low frequencies (see Table 3). A recent finding in a late Holocene sample from Venezuela (Las Locas site) expands its geographic range to Northeast South America (Reyes et al., 2008). The relatively late chronology of samples, their geographic distribution, and sample frequencies suggest a wide and rapid dispersal of this dental variant into the South American continent. This possibly reflects the highly complex intracontinental population dynamics in the New World.

Johnston and Sciuilli (1996) report five cases of the UAP among prehistoric Native Americans from the Ohio Valley region. These authors conclude the trait possibly represents a primitive feature among Native Americans that is not limited to Uto-Aztec-Tanoan speaking populations. LeBlanc et al. (2007) observed the trait in several Basketmaker, Mimbres, and other prehistoric Southwest Amerin-

dian samples. Although the trait was not observed in 117 Basketmaker skeletons, other prehistoric Southwest samples had UAP frequencies similar to those reported for living Southwest Amerindians (i.e., 0.8–1.5%). Although the American Southwest/North Mexico region has the highest frequencies of the UAP trait, recent research has shown that it is practically nonexistent in ~2,500 individuals from neighboring areas (central and southern Mexico) (Scherer, 2005; Aubry, 2009). However, this contrasts our findings (Table 4 and elsewhere) that show frequencies from 1.1% to 6.7% in samples from northeast and south-central Mexico.

At this point, a preliminary hypothesis is that the gene or genes involved in UAP trait expression only appeared in Native Americans following colonization of the New World. It does not, however, appear in all New World populations. Turner (1984) did not observe UAP in over 400 Eskimo-Aleuts and North Asians. One of the authors (GRS) has never seen the trait in over 500 Alaskan Eskimo skeletons from Kodiak Island, St. Lawrence Island, Nunivak Island, and Golovin Bay. Morris et al. (1978) also failed to report the trait in a small Eskimo sample. The trait is, however, present in southern Athapaskans (i.e., Navajo). If Athapaskans and Amerinds diverged at an early date (Turner, 1983; Scott and Turner, 2008), this presents a conundrum. UAP potentially appeared before the divergence of Athapaskans and Amerindians, making its origin older than we presume. An alternative is that the trait appeared in the Navajo following gene flow with neighboring Puebloan groups who had the gene(s) for the trait. The rare genetic variants Al*Naskapi and Al*Mexico provide clear evidence that gene flow occurred between Athapaskan and non-Athapaskan groups in the Southwest (Smith

et al., 2000), and so this might also explain the presence of UAP in the Navajo.

The pattern of geographic variation of the Uto-Aztecan premolar and its very low frequency suggest that it possibly represents a distinctive Amerindian dental marker that emerged and evolved in the Americas similar to private molecular markers (certain mtDNA and Y-chromosome haplogroups and autosomal traits) found in North and/or South Amerindians (Santos et al., 1994; Merriwether et al., 1995; Rikards et al., 1998; Bortolini et al., 2003; Wang et al., 2007; Malhi et al., 2010). Recent modern humans share a common set of morphological dental traits (e.g., Carabelli's tubercle in upper molars, shovel-shaped incisors in upper and lower incisors, Y groove pattern in lower molars, etc) with frequencies highly variable between and within populations. By contrast, the UAP is only present in some Amerindian groups, suggesting a highly restricted variant in a geographic sense with potential for addressing future research about Amerindian population history, affinities and microevolution. Despite this claim, a Japanese dental anthropologist (T. Hanihara, personal communication) noted recently that UAP may be present, albeit rare, in Japanese populations. We encourage researchers around the world to publish their findings on the presence of UAP in their samples, so we can establish accurately the temporal and spatial bounds of this uncommon variant.

Although the term "Uto-Aztecan premolar" may not be technically accurate given the presence of this trait in many populations outside of the Uto-Aztecan language family, it does have historical precedent. Although Turner et al. (1991) and Johnston and Sciulli (1996) suggest the

distosagittal ridge is more appropriate than a linguistically and geographically delimited name, this terminological suggestion has not been widely adopted. LeBlanc et al. (2007) and Turner and Scott (2007) continue using the term Uto-Aztecan premolar for this variant. Like "Carabelli's" cusp and "Bolk's" paramolar tubercle, the Uto-Aztecan appellation has had staying power and is generally used in article titles when authors address the subject. Despite the presence of the Uto-Aztecan premolar well beyond its originally described bounds, the term has gained a descriptive power that transcends alternatives. For now, it also retains its unique status as the potential product of a New World mutation.

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APPENDIX A1

Pima family data for Uto-Aztecan premolar

| No. family ^a | No. father | No. mother | No. son | No. daughter |
|-------------------------|--------------|--------------|-------------------------|---|
| 4305a | 3018 | Unobservable | 1089 | 2588 2111 2104 2112 |
| 4305b-related family | 1089 | Unobservable | 3355^b | 4113 |
| 5035 | Unobservable | Unobservable | – | 4370 4375 4390 |
| 6011 | Unobservable | 2460 | – | 2456 2457 2458 2459 2633 2794 2805 |
| 6053 | 3277 | 2049 | 31671 3134 1941 | – |
| 6063 | 3282 | 1923 | 1643 3132 | 2163 2221 2886 2902 |
| 6076 | 3001 | 4002 | 1292 | 2882 2264 |
| F6289a | Unobservable | Unobservable | 1733 1095 | 2781 |
| F6289b-related family | 1733 | Unobservable | 1720 1722 | 2390 |
| 6351a | Unobservable | 4406 | – | 2967 2947 2615 2621 4139 |

Appendix A1. (Continued)

| No. family ^a | No. father | No. mother | No. son | No. daughter |
|-------------------------|--------------|---------------------------|-------------------------|-------------------------|
| 6351b-related family | Unobservable | Sibship ^c 4406 | 3096 | – |
| 6448 | 1413 | Sibship 2335 | 3427^d | |
| 6449 | Unobservable | 2446 | 1412 | 4123 |
| | | Unobservable | 1490 | 2944 |
| | | | | 2231^e |
| 6476 | Unobservable | 4329 | 1870 | 4170 |
| | | | | 4172 |
| | | | | 4175 |
| | | | | 4189 |
| | | | | 4554 |
| 6602 | Unobservable | Unobservable | 1485 | 2627 |
| | | | 3110 | 2361 |
| | | | | 4165 |

^a Affected individuals boldfaced.

^b Nephew of 2111.

^c For sibships only observable phenotypes noted.

^d First cousin of 4139.

^e First cousin of 1733.

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