

What are the Lothagam and Tabarin Mandibles?

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ABSTRACT

The mandibular fragments from Lothagam (KNM-LT 329) and Tabarin (KNM-TH 13150) were once considered plausible candidates for status as the earliest hominin (e.g., Kramer 1986; Ward and Hill 1987). Recent fieldwork, though, has lessened the relevance of these fossils by recovering samples from horizons more than two million years earlier. Yet despite the increase of comparative samples, these two mandibular fragments remain difficult to diagnose. Here we consider the morphology and dental metrics of these two specimens in comparison to the larger samples of Miocene and early Pliocene hominins recovered during the last fifteen years. We show, based on molar size, that KNM-TH 13150 is consistent with the hypodigm of *Ardipithecus*, while the Lothagam mandible is not consistent with *Ardipithecus* in its molar dimensions. These results have important biogeographic implications and hint at a more complex Early Pliocene hominin phylogeny than previously appreciated.

INTRODUCTION

The first few years of this century saw the description of Late Miocene genera including *Sahelanthropus tchadensis* (M Brunet et al. 2002), *Orrorin tugenensis* (Senut et al. 2001), and *Ardipithecus kadamba* (Haile-Selassie 2001), all of which may represent early hominins. Before this time, the mandibular fragment from Lothagam, Kenya (KNM-LT 329), was often cited as the earliest known specimen that could be attributed to the hominins. A second mandible from Tabarin, Kenya (KNM-TH 13150), with nearly the same antiquity, was also cited as a possible early hominin. Although these two fragments themselves present relatively little information about human origins, their status remains an interesting question (Figure 1). KNM-LT 329 in particular gave rise to substantial debate about the adaptations of the first hominins. We approached their taxonomic attribution as a forensic problem with broad historical interest for paleoanthropology.

Some scholars have described one or both mandibles as closely aligned to early australopithecines (Hill et al. 1992; Kramer 1986; Leakey and Walker 2003; Ward and Hill 1987). More recently, others have emphasized the morphological similarity of the Tabarin mandible to *Ardipithecus* (Haile-Selassie et al. 2009). Because of their geological age, we propose that the null hypothesis for both mandibles is an assignment to *Ardipithecus*. We then consider the morphology and dental dimensions of both mandibles to test this hypothesis.

The Lothagam mandible (KNM-LT-329), found 15km west of Lake Turkana in northern Kenya, is a portion of the right mandibular body, with M_1 still intact (Patterson et

al. 1970). The corpus extends from a section anterior to the mental foramen and is broken off at the ramus. The roots of M_2 and part of the M_3 roots have been preserved, along with much of the body below the molars. While originally dated to 5.5 mya, this mandible is now of uncertain age (McDougall and Feibel 2003). The mandible was found in the Apak Member of the Nachukui Formation. A tuffaceous horizon within this formation has been dated to 4.22 mya, and the Nachukui Formation itself is capped by the Lothagam Basalt at 4.20 mya based on Ar-Ar dating, suggesting the fossil is no younger than 4.2 mya. The preceding Nawata Formation may have extended up to 5.0 mya, based on dating of the Purple Marker, and paleomagnetic analysis suggests this marker is 5.2 mya, lending support to the argon date of 5 mya. Based on these data, it seems that the older date of 5.5 mya is erroneous and a better estimated age of the fossil is between 5.2 and 4.2 mya. However, there is some suggestion of a hiatus across the boundary between the two formations, which would indicate 5.2 mya is too old. McDougall and Feibel (2003) suggested that a good age bracket for Lothagam is 4.9–4.2 mya. Leakey and Walker (2003) argued that as the fossil was found near the Purple Marker, it is closer in age to 5 mya than to 4.2 mya. A date older than 4.4 million years ago would place the specimen outside of the time range of the earliest species of *Australopithecus*, *Au. anamensis*, which is evidenced from both the Turkana Basin and Afar (Ward et al. 2001).

The Tabarin fossil (KNM-TH 13150) from the Tugen Hills in Kenya, located northwest of Lake Baringo, is also a right mandibular corpus, with both the first and second molars present (Ward and Hill 1987). The third molar,

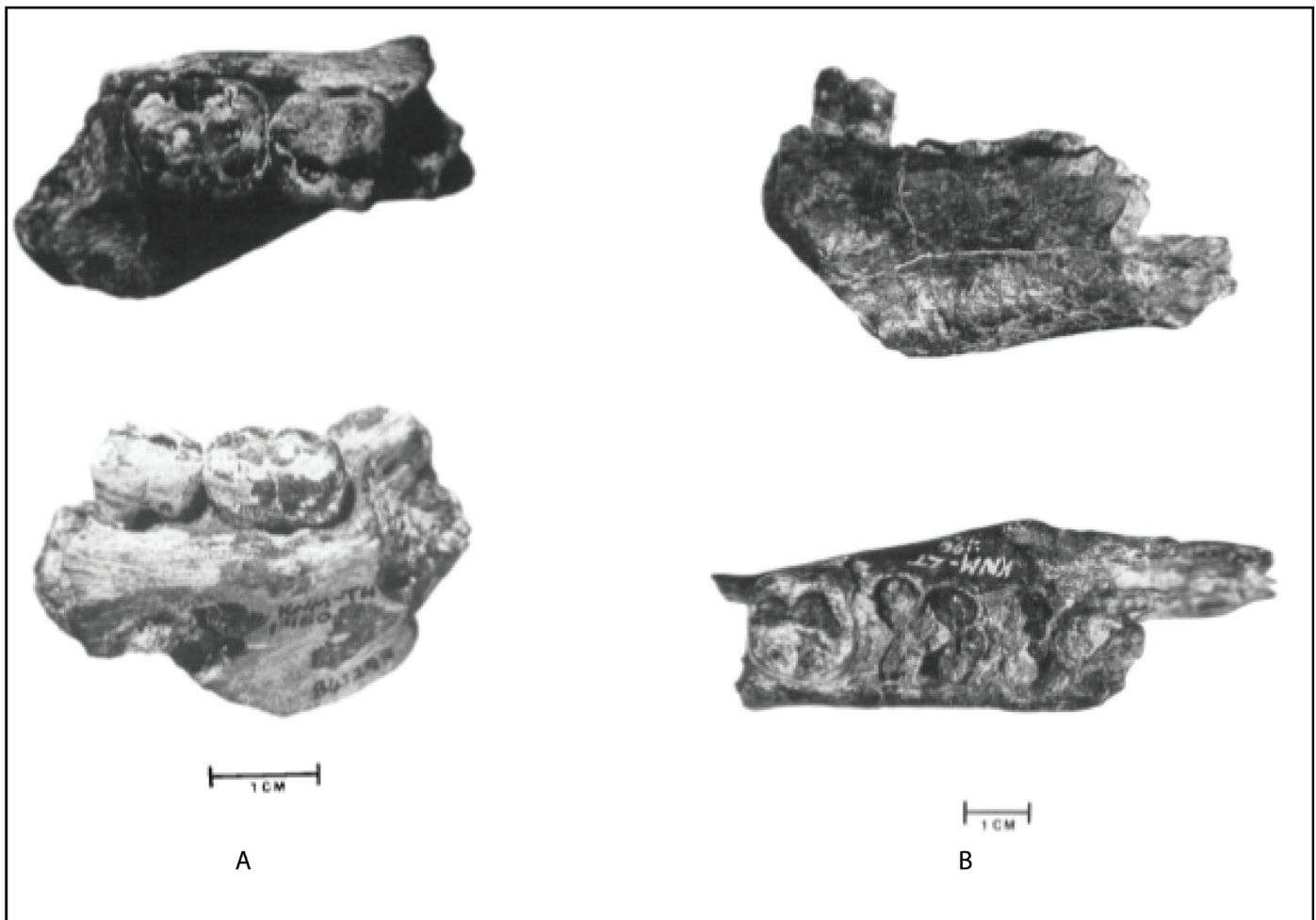


Figure 1. Mandibular fragments discussed in this text. Tabarin mandible (KNM-TH 13150) in occlusal and medial view and Lothagam mandible (KNM-LT 329) in medial and occlusal view. Image after Hill and Ward (1998).

though not found, was located behind the edge of the ramus. Reanalysis of the site by Deino et al. (2002) suggested that the fossil is bound at a maximum age of 4.428 (dated with K-Ar), and based on inferred sedimentation rate they consider the fossil itself to date to 4.42 MYA, with an absolute youngest age at 4.3 MYA.

MOLAR METRICS

The phylogenetic relevance of molar shape and size in hominins is limited. Within early *Homo*, there is extensive overlap in the size and shape of molars, and some varieties (e.g., “*Homo rudolfensis*”) are not well distinguished from late *Australopithecus* by molar dimensions (Figures 2 and 3). Yet, some hominin taxa are well differentiated by molar dimensions, making them important aspects of taxonomic diagnosis. The differences in molar size between *Ardipithecus* and early *Australopithecus* are stark. Both *Ar. ramidus* and *Ar. kadabba* samples have M_1 dimensions at the bottom of the range of *Au. afarensis* and *Au. anamensis* samples. The M_2 dimensions of *Ardipithecus* are even smaller, beyond the presently-known range of either *Au. afarensis* or *Au. africanus*. Molar dimensions have the potential to test the assignment of dental remains to one or another of these taxa, particularly if other observations are consistent with the

assignment.

The first molar of KNM-LT 329 is relatively large—it exceeds the *Ardipithecus* mean by three standard deviations. This comparison may be accentuated by the relatively small variation within the *Ardipithecus* samples, which is only around half the standard deviation of *Au. afarensis* or *Au. anamensis* despite a similar sample size in the latter species. Considering the length and breadth of the crown, KNM-LT 329 is in the range of overlap of many australopithecine species, including *Au. afarensis*, *Au. anamensis*, *Au. africanus*, and the mesiodistal length is nearly identical to *Kenyanthropus*. Taken together, these dimensions place the Lothagam mandible far from the two *Ardipithecus* species. Although the buccolingual breadth of KNM-LT 329 exceeds the *Ar. kadabba* sample only slightly, its mesiodistal dimension is much longer than the *Ar. kadabba* molars.

KNM-TH 13150 preserves both the first and second molars. Both teeth measure mesiodistally at the high end of the range for *Ardipithecus ramidus*, but buccolingually at the low end of the *Ar. ramidus* range (see Figures 2 and 3). As a result, the overall area of the crowns is within the variation seen for this species. Interestingly, the second molar is quite close in size to that of the smallest-known *Au. afarensis* second molar, from the A.L. 12823 mandible, but KNM-

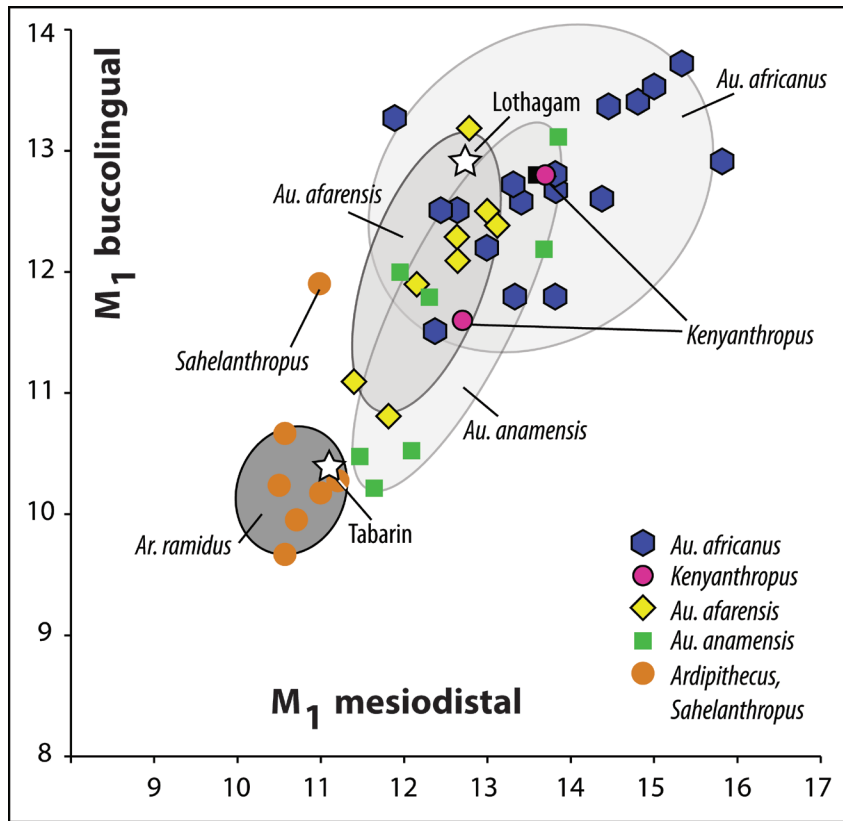


Figure 2. Mesiodistal vs. buccolingual measurements for M₁.

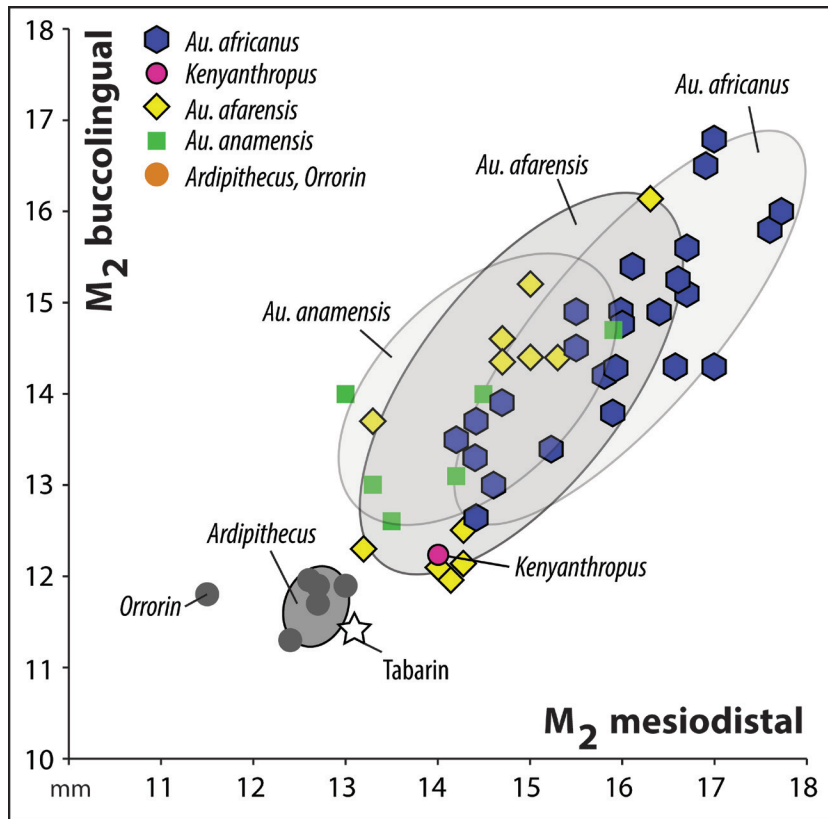


Figure 3. Mesiodistal vs. buccolingual measurements for M₂.

TH 13150 has a somewhat different shape, elongated in the mesiodistal dimension. The other hominin species with M_2 area equal or less than KNM-TH 13150 is *Orrorin tugenensis*. The *Orrorin* M_2 is compressed mesiodistally compared to the Tabarin tooth, but is the only other early hominin with an equivalently small crown area.

DENTAL NON-METRICS

Subocclusally, the pulp chambers of the two Tabarin molars are low and vertically compressed. The pulp chamber of KNM-LT 329 is low and constricted, appearing very similar to KNM-TH 13150 (Ward and Hill 1987). Interestingly, the roots of the first and second molars, as well of the distal premolar root and the mesial root of M_3 , are of equivalent length. There is a slight difference in the root length of the KNM-LT 329 M_1 and the preserved roots of the second and third molar, but this may reflect differential preservation. The orientation of the roots in both specimens is in the 'serrate' pattern, with two roots, one mesial and one distal (Ward and Hill 1987). This 'serrate' pattern has also been described in *Ardipithecus ramidus* (White et al. 1994), as well in *Au. anamensis*, but is absent in more recent hominins (Kimbel and Deleuzene 2009).

Ward and Hill (1987) emphasized the similarities between these two fossils and the Hadar mandibles, as the latter have low, vertically constricted pulp cavities, roots of equal-length throughout the molar series, and a serrate root morphology. Such a pattern can be seen in LH 4 as well. However, Wood et al. (1998) note that all *Au. afarensis* mandibular molars from Hadar have mesial and distal roots that are subequal in length, with the mesial root being more compressed mesiodistally (Wood et al. 1988), which may complicate using such descriptions for taxonomic purposes.

Both fossils show a similar cusp size pattern, with the metaconid the largest, followed by the protoconid, hypoconid, entoconid, and hypoconulid (Kramer 1986; Ward and Hill 1987). The hypoconulids of these molars are reduced in size, producing a somewhat rounded square shape, as is seen in many australopithecine molars. In Lothagam, Tabarin, and *Au. Afarensis*, molar attrition is concentration on the buccal portion of the crown to a greater degree than is seen in *Au. africanus*, in which, after some buccal attrition, wear is even across the crowns.

The first molar of Tabarin exhibits buccal molar flare (Ward and Hill 1987), another similarity to *Au. afarensis*. Such flare is also seen in the Lukeino molar (KNM-LU 335), a M_1 from Tugen Hills in Kenya, which some scholars have suggested to be a member of *Orrorin tugenensis* (Senut et al. 2001). Molar flare is also known from *Otaviipithecus*, a Miocene hominoid (Singleton 2000). Singleton (2003) has argued that molar flare is a result of the interaction between both functional and phylogenetic aspects, and that it may be a condition for the basal catarrhine, with a reduction among early hominoids and a secondary increase in hominins. This observation reduces the phylogenetic relevance of buccal molar flare in diagnosing these fossil specimens.

MANDIBULAR NON-METRICS

As earlier studies of these mandibles focused on whether either mandible was a hominin or a hominoid, the comparison of extant and Miocene apes has dominated the description of these fossils. Before 1994, only *Australopithecus* was available as an exemplar of early hominin morphology; the Hadar and Laetoli samples being most relevant. Some characteristics were described as similar to *Au. afarensis*, others as being more primitive. These assessments do not necessarily inform us about the taxonomic placement of the fossils *within* the hominins. Following prior workers (Ward and Hill 1987) we accept that both mandibles are hominin and focus our consideration of the morphology on the mandibles' phylogenetic position relative to fossil taxa. From this perspective, many of the observed characters of the mandibles are uninformative, because they are present in both *Ardipithecus* and *Australopithecus*.

Much work has been based on the mental foramen's placement and orientation on the mandible. In KNM-LT 329 the mental foramen is placed below the mesial edge of the M_1 , is positioned high on the body (above the mid-point), and opens anterior-superiorly. This configuration is present in specimens of both *Ardipithecus* and *Australopithecus*. The ARA-VP-1/401 and ARA-VP6/500 mandibles of *Ar. ramidus* appear to have their mental foramina placed more mesial (Suwa et al. 2009). The mental foramen of the Alayla mandible is also located below P_4 , around midcorpus, and opens anterior-superiorly (Haile-Selassie et al. 2009). Leakey and Walker (2003) noted some similarities to the Kanapoi mandibles (Ward et al. 2001) especially in their superior and inferior tori, where the inferior torus is low in all three mandibles (KNM-LT-329, KNM-KP 2981, and KNM-KP 31713). As with KNM-LT 329, both of these mandibles have an anteriorly-opened mental foramen, though unlike the Lothagam specimen, the foramina are placed lower on the corpus. The DIK-1-1 mandible (Alemseged et al. 2006) opens anterior-superiorly as well, matching the pattern seen in other juvenile australopithecines such as AL 333-43b (White and Johanson 1982). Given the pattern of variability in *Australopithecus* and *Ardipithecus*, the position and direction of the mental foramen does not contradict any assignment for KNM-LT 329.

PREVIOUS ASSESSMENTS

Kramer (1986) suggested KNM-LT 329 is most similar to *Au. afarensis*, specifically due to the position of the mental foramen, the breadth of the alveolar margin, the origin of the ascending ramus, the reduction of the hypoconulid, and the size of the first molar. White (1977) noted that the Lothagam mandible differs from the other fossils he analyzed and recognized several pongid-like characteristics, such as the clear anterior opening of the foramen, its flattened lateral corpus contours, strong subalveolar hollowing, and the suggestive occurrence of a simian shelf, leading him to assign it as indeterminate hominoid. Later, White (1986) demonstrated that the molar dimensions of KNM-LT 329 lie inside the range of *Au. afarensis*, but emphasized that the other morphological characters shared by the mandible

TABLE 1. SUMMARY STATISTICS OF LOWER FIRST MOLAR AREA FOR THE TWO SPECIMENS UNDER STUDY HERE AND COMPARATIVE DATA FROM LATE MIOCENE AND EARLY PLIOCENE SAMPLES*.

Species	M ₁ area (mean)	SD	N
KNM-LT 329	163.83	.	1
KNM-TH 13150	115.44	.	1
<i>Sahelanthropus</i>	130.90	.	1
<i>Ardipithecus ramidus</i>	109.74	4.71	6
<i>Australopithecus anamensis</i>	147.16	24.50	8
Woranso Mille	143.99	.	1
<i>Australopithecus afarensis</i>	154.93	16.31	13
<i>Australopithecus africanus</i>	181.71	23.99	22
<i>Kenyanthropus platyops</i>	161.34	19.83	2
<i>Australopithecus sediba</i>	137.99	9.91	2

*Data gathered from the literature. Species distinctions and molar dimensions based on original descriptions in Brunet et al. (2005), de Ruiter et al. (2013), Haile-Selassie et al. (2010), Hill et al. (1992), Kimbel and Deleuzene (2009), Leakey et al. (2001), Ward and Hill (1987), Ward et al. (2001), and White and Johanson (1982).

with the known *Au. afarensis* sample are primitive characters that might have been shared by “several different taxa” of hominins.

Leakey and Walker (2003) noted some similarities between the Lothagam and Kanapoi mandibles (Ward et al. 2001), especially in their superior and inferior tori. As with KNM-LT 329, both of these mandibles have an anteriorly-opened mental foramen, though unlike the Lothagam specimen, the foramina are placed lower on the corpus. There is also an outward swing in the mandibles. The only indication, according to Leakey and Walker, that Lothagam is not in the same group is the enamel thickness. They note that due to the limited fossils of *Ar. ramidus* available at the time, they were unable to conclude which species it belongs to but rather place it in “Hominidea indeterminate.”

The recent discovery/publication of both species of *Ardipithecus* has caused some scholars to reexamine both fossils in light of this new data. Haile-Selassie and colleagues (Haile-Selassie et al. 2009) compared the ALA-VP-2/10 mandible, assigned to *Ar. kadabba*, to mandibles from *Sahelanthropus*, Lothagam, Tabarin, *Au. anamensis*, and *Au. afarensis*. They noted that the mental foramen of ALA-VP-2/10 is placed about mid-corpus, slightly below the position in Lothagam. In general, they noted that the mandibular specimens of *Sahelanthropus*, *Ar. ramidus*, Lothagam, and Tabarin are similar in morphological features to the *Ar. kadabba* mandible. These differ from *Au. anamensis* and *Au. afarensis*

in that they are smaller, thinner and have a weaker lateral flare of the ramus root. While they asserted no species distinction for either mandible, the overall morphology of the two mandibles appears more similar to *Ardipithecus* than to *Australopithecus*.

Most of the work that has been done on these two fossil fragments has been concentrated on mandibular characteristics. In our study, we concentrate instead on an often overlooked aspect of their morphology—the size of the first and second molars. After collecting data on all pre-*Au. afarensis* molars from the published literature (see Table 1 for references), we compare specimens with well-established species identification to the molar dimensions of both of these enigmatic fossils. These data are presented in Figures 2 and 3, and the summary statistics are in Tables 1 and 2.

RESULTS AND CONCLUSIONS

The dental metrics of KNM-TH 13150 support its inclusion in the hypodigm of *Ardipithecus*. None of the other morphological characters of the mandible, nor its date at around 4.4 million years ago, contradict this hypothesis. We suggest that the mandible be provisionally attributed to cf. *Ardipithecus* cf. *ramidus*. Recognizing Tabarin as a field locality for *Ar. ramidus* would substantially extend the known geographic range of both the species and genus. Alternatively, although the date of the specimen is a closer fit to *Ar. ramidus*, its anatomy does not preclude assignment to *Orrorin*.

TABLE 2. SUMMARY STATISTICS OF LOWER SECOND MOLAR AREA FOR TABARIN AND COMPARATIVE DATA FROM LATE MIOCENE AND EARLY PIOCENE SAMPLES*.

Species	M ₂ area (mean)	SD	N
KNM-TH 13150 (Tabarin)	149.34	.	1
<i>Ardipithecus ramidus</i>	147.80	7.32	3
<i>Australopithecus anamensis</i>	191.29	23.83	6
Woronso Mille	205.95	51.81	3
<i>Ardipithecus kadabba</i>	149.86	.	2
<i>Orrorin</i>	135.70	.	1
<i>Australopithecus afarensis</i>	190.08	23.36	19
<i>Australopithecus africanus</i>	245.20	42.46	10
<i>Kenyanthropus platyops</i>	169.58	.	1
<i>Australopithecus sediba</i>	178.89	9.72	2

*Data gathered from the literature. Species distinctions and molar dimensions based on original descriptions in Brunet et al. (2005), de Ruiter et al. (2013), Haile-Selassie et al. (2010), Hill et al. (1992), Kimbel and Deleuzene (2009), Leakey et al. (2001), Ward and Hill (1987), Ward et al. (2001), and White and Johanson (1982).

Too little is currently known about mandibular variation to be confident in the assertion that Tabarin is *Ar. ramidus*, but no observations at present contradict that diagnosis.

The Lothagam mandible, KNM-LT 329, is a poor fit to *Ardipithecus*. Its molar dimensions, as seen in Figure 2, are well outside the known range for that genus. Both *Au. afarensis* and *Au. anamensis* ranges encompass the molar dimensions of the specimen, and none of the other mandibular features exclude it from these samples. We suggest that the attribution of the mandible to *Australopithecus* sp. is consistent with its overall morphology.

An attribution to *Australopithecus* may pose a problem considering the date of the specimen. If KNM-LT 329 is as old as five million years, its morphology suggests that an *Australopithecus*-like species co-existed with *Ardipithecus* (and possibly other hominoids) in the latest Miocene. *Ardipithecus* exhibits relative locomotor and dental conservatism relative to *Au. anamensis*, the earliest species of obligate bipeds (Suwa et al. 2009). If KNM-LT 329 represents a 5 mya australopithecine, it may better represent the ancestral form of *Au. afarensis* and *Au. anamensis* than *Ardipithecus* does. However, if the true date of the specimen were as recent as 4.2 million years ago, an attribution to *Australopithecus* would not necessitate any adjustment to the origin of that genus. Further work to resolve the chronology of the site might answer these questions and clarify the placement of this mandibular specimen in early hominin evolution.

The species designation of these admittedly fragmentary (and often over-looked) fossils may pale in compari-

son to other recent finds. Yet, the recognition that the first lower molar of Lothagam is simply too large to be considered part of the *Ardipithecus* genera is an important one. Depending on the age of the fossil, it may indicate australopithecines flourished alongside Ardi's species. As for Tabarin, we suggest that it should be tentatively considered *Ar. ramidus*, which would increase the biogeographic range of the species. Thus, this short report illustrates the variability of late Miocene hominoids and hominins. Future work at the Tabarin and Lothagam field sites may help to resolve these important issues.

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