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SOCIAL SCIENCES

Ledi-Geraru strikes again: Morphological affinities of the LD 350-1 mandible with early *Homo*

WALTER NEVES, MARIA H. SENGER, GABRIEL ROCHA, LINCOLN SUESDEK & MARK HUBBE

Abstract: The origins of the genus *Homo* have been a focus of much debate in the paleoanthropological literature due to its importance in understanding the evolutionary trajectories that led to the appearance of archaic humans and our species. On the level of taxonomic classification, the controversies surrounding the origins of *Homo* are the result of lack of clear classification criteria that separate our genus from australopiths, given the general similarities observed between fossils ascribed to late australopiths and early *Homo*. The challenge in finding clear autapomorphies for *Homo* has even led to debates about the classification of *Homo habilis* and *Homo rudolfensis* as part of our genus. These debates are further complicated by the scarcity of fossils in the timeframe of appearance of our genus, making any fossils dated to between 3.0 and 2.5 Ma of particular relevance in the context of this discussion. The Ledi-Geraru mandible is one such fossils, which has called the attention of researchers due to its combination of primitive traits seen in *Australopithecus* and derived traits observed in later *Homo*. Despite being fragmented and poorly preserved, it is one of the key fossil specimens available from the period mentioned above.

Key words: *Australopithecus afarensis*, *Homo* sp., Plio-Pleistocene hominins, Principal Component analysis.

INTRODUCTION

The LD 350-1 mandible (Figure 1) was excavated in 2013 by Chalachew Seyoum in the Lee Adota region of the Ledi-Geraru research area, Afar Regional State, in Ethiopia. It was recovered 10 meters above the Gurumaha Tuff, which was radiometrically dated to 2.822 ± 0.006 Ma (Villmoare et al. 2015a), consistent with the date obtained by DiMaggio et al. (2015) of 2.8 - 2.75 Ma using the laser single-crystal incremental heating dating method. The specimen consists of a well-preserved left mandibular corpus with dental roots and crowns from C to M3. Its symphyseal region, the root of the ascending ramus and the inferior margin of the corpus are intact. However, its buccal alveolar margin is damaged between P3 and M1 (Villmoare et al. 2015a).

Due to its age and location, it has been suggested that the mandible might represent a young specimen of *Australopithecus afarensis*. However, despite its primitive traits shared with australopithecines, Villmoare et al. (2015a) discarded this interpretation based on the presence of a set of derived features shared with *Homo*. Furthermore, the LD 350-1 mandible is at least 0.2 Ma younger than the most recent known *A. afarensis* specimen. Therefore, Villmoare et al. (2015a) assigned the LD 350-1 to the genus

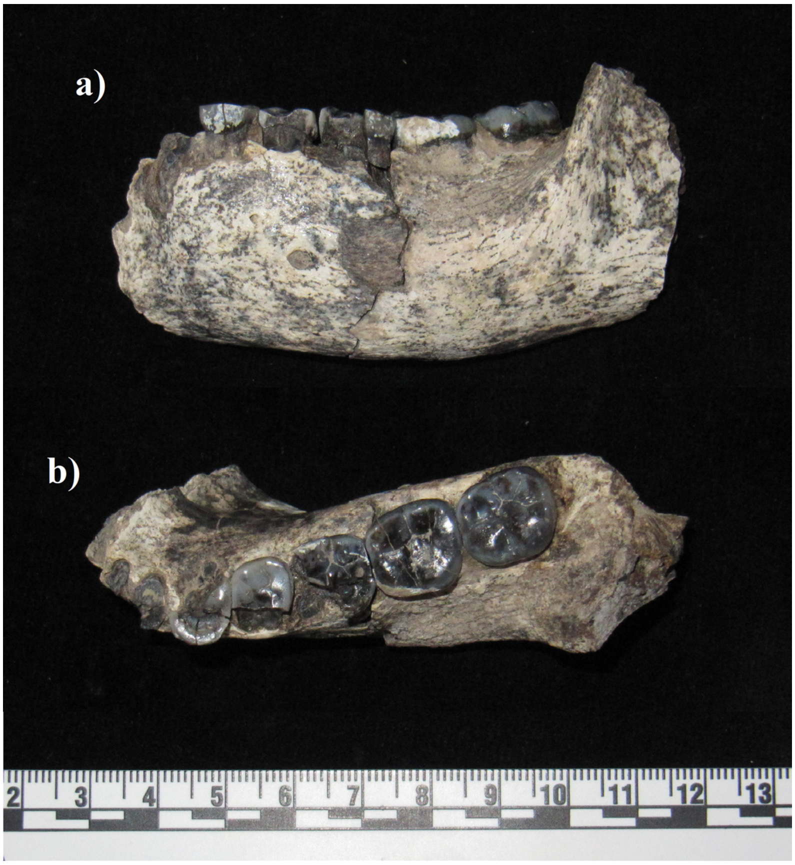

Figure 1. The LD 350-1 mandible. **a)** Lateral view. **b)** Occlusal view. Photo by Brian Villmoare.

Homo, suggesting that this clade emerged ca. 0.4 Ma earlier than previously thought.

A subsequent study led by Hawks et al. (2015) contested the *Homo* assignation and drew attention to the fact that the Ledi-Geraru mandible also presents significant similarities with *A. afarensis, A. africanus,* and *A. sediba*. They emphasized that LD 350-1 is an isolated and partial remain, making a genus assignation unwise. This interpretation, however, was rejected by Villmoare et al. (2015b), who maintained their original position.

Since the original analysis was based on a limited number of comparative specimens and dental measurements and only on bivariate analyses, in this study we contribute to the debate about the classification of LD 350-1 by exploring its morphological affinities through multivariate statistical comparison based on an extended database of comparative Plio-Pleistocene mandibular corpuses. We aim to test the hypothesis that the Ledi-Geraru mandible shows significant morphological affinities with early *Homo* species, as initially suggested by Villmoare et al. (2015a).

MATERIALS AND METHODS

To evaluate the biological affinities of the Ledi-Geraru mandible, we compiled metric data for 135 hominin mandibles, including the LD 350-1, containing 8 linear mandibular corpus measurements used in Wood (1991). This dataset was constructed from data published in Weidenreich (1936), Rightmire (1990), Wood (1991), Kimbel et al. (2004), Berger et al. (2010), Villmoare et al. (2015a) and Laird et al. (2017), after ensuring that the reference points used by these authors were homologous.

Our database comprises 9 different Plio-Pleistocene species: *Paranthropus boisei* (N=24), *P. robustus* (N=9), *A. afarensis* (N=32), *A. sediba* (N=1), *A. africanus* (N=11), *H. erectus* (N=38), *H. rudolfensis* (N=7), *H. habilis* (N=7); and *H. naledi* (N=5), plus the Ledi-Geraru specimen (Table I). Although Villmoare et al. (2015a) used 7 of these species in their original study, they used a much more restricted number of specimens to represent each taxa.

The Ledi-Geraru specimen was compared to other hominin mandibles based on eight linear metric variables of the corpus measured in the Ledi-Geraru specimen (Table SI – Supplementary Material). The data from LD 350-1 were compared to the centroids of the comparative species, which was defined as the average values of each variable considering only data present in comparative fossils. The comparisons with centroids allow to contextualize the morphology of LD 350-1 inside the morphological variability

Table I. Species and specimens included in this study.

Species	N	Specimens	Source
Ledi-Geraru	1	LD 350-1	Villmoare et al. (2015a)
Paranthropus boisei	24	KNM-ER 403 R, KNM-ER 726 L, KNM-ER 727 R, KNM-ER 728 R, KNM-ER 733 R, KNM-ER 805A L, KNM-ER 818 L, KNM-ER 1469 L, KNM-ER 1803 R, KNM-ER 1806 L, KNM-ER 3229 L, KNM-ER 3230 L, KNM-ER 3729 L, KNM-ER 3731 L, KNM-ER 3889 R, KNM-ER 3954 L, KNM-ER 5429 L, KNM-ER 5877 R, KNM-ER 15930 L, KNM-ER 16841 R, OMO L74A-21 R, OMO L7A-125 L, Peninj 1 L, SK 23 L.	Wood (1991)
Paranthropus robustus	9	KNM-ER 404 R, KNM-ER 725 L, KNM-ER 729 L, KNM-ER 801A R, KNM-ER 810A L, SK 12 L, SK 34 L, SK 6 L, TM 1517 R.	Wood (1991)
Australopithecus afarensis	32	A.L. 128-23, A.L. 145-35, A.L. 188-1, A.L. 198-1, A.L. 198-22, A.L. 207-13, A.L. 225-8, A.L. 228-2, A.L. 266-1, A.L. 277-1, A.L. 288-1I, A.L. 311-1, A.L. 315-22, A.L. 330-5, A.L. 333W-12, A.L. 333W-1A,B, A.L. 333W-32+60, A.L. 400-1A, A.L. 417-1A, A.L. 418-1, A.L. 432-1, A.L. 433-1A,B, A.L. 436-1, A.L. 437-1, A.L. 437-2, A.L. 438-1, A.L. 444-2, A.L. 582-1, A.L. 620-1, L.H. 4, MAK 1/12, MAK 1/2.	Kimbel et al. (2004)
Australopithecus africanus	11	MLD 2, MLD 18 R, MLD 29, MLD 34 R, MLD 40 L, STS 7 L, STS 36 L, STS 52 L, STW 84, STW 404, STW 498.	Wood (1991), Laird et al. (2017)
Australopithecus sediba	1	MH2	Laird et al. (2017)
Homo erectus	38	D211, D2600, D2735, KGA 10-1, KNM-BK 67, KNM-BK 8518, KNM-ER 730 L, KNM-ER 731 L, KNM-ER 817 L, KNM-ER 992 L, KNM-ER 1506A R, KNM-ER 1812 R, KNM-ER 3734 L, KNM-ER 3950 L, KNM-WT 15000, OH 22 R, OH 23 L, OH 51, SA 1B R, SA 8 L, SA 9 R, SA 21, SA 22, SA Bk 7905, SA Bk 8606, SA Ng 8503, SA Sb 8103, Sidi, SK 15, SK 847/45, TG 1 L, TG 2 L, TG 3 L, TQ., ZH-AII, ZH-GI, ZH-HI, ZH-K1.	Weidenreich (1936), Wood (1991), Rightmire (1990), Laird et al. (2017)
Homo habilis	7	KNM-ER 1501, KNM-ER 1502, KNM-ER 1805, KNM-ER 1811 L, OH 7 L, OH 13 L, OH 37 L.	Wood (1991), Laird et al. (2017)
Homo naledi	5	DH 1, DH 3, UW 101-001, UW 101-010, UW 101-1142.	Laird et al. (2017)
Homo rudolfensis	7	KNM-ER 819 L, KNM-ER 1482 L, KNM-ER 1483 L, KNM-ER 1801, KNM-ER 1802, KNM-ER 60000, UR 501.	Wood (1991), Laird et al. (2017)

of early hominins, without the need to estimate missing values in the fossils from the comparative data.

The morphological affinities between LD 350-1 and the comparative species were explored using Principal Component Analyses based on the covariances among the metric variables. Principal Components (PCs) were calculated from the original measurements (size and shape) and from measurements corrected for the effect of size (shape alone). To eliminate size effect, each variable was divided by the geometric mean of all variables of the species and of the specimen LD 350-1 (Darroch & Mosimann 1985). The morphological affinities among the cases were represented through scatterplots of their positions according to the first two PCs. All analyses were done in R (R Core Team 2022), including functions from packages MASS (Venables & Ripley 2002), and ggplot2 (Wickham 2016).

RESULTS

The analysis of morphological affinities of LD 350-1 and the comparative series based on size and shape information is shown in Figure 2. In this analysis, PC1 explains 91.97% of the variance and is highly correlated with all variables (as a result of size of the specimens; Table SII), resulting in larger mandibles having small PC values and vice-versa. The second component explains only 3.14% of the original variance, and shows only weak correlations with the original variables (Table SII). Consequently any interpretation of the position of the cases along this PC would be unwise. The robust australopiths (*P. boisei* and *P. robustus*) appear as outliers on this analysis, due to their size, and LD 350-1 shows high affinities with *A. afarensis, H. erectus* and *A. sediba*. *H. rudolfensis* occupies a position not very far from this cluster.

The analysis that considers only shape is shown in Figure 3. The first PC explains 44.96% of the variance, and shows strong negative correlations (r<-0.8) with Corpus height at M1 and Corpus height at M2, and strong positive

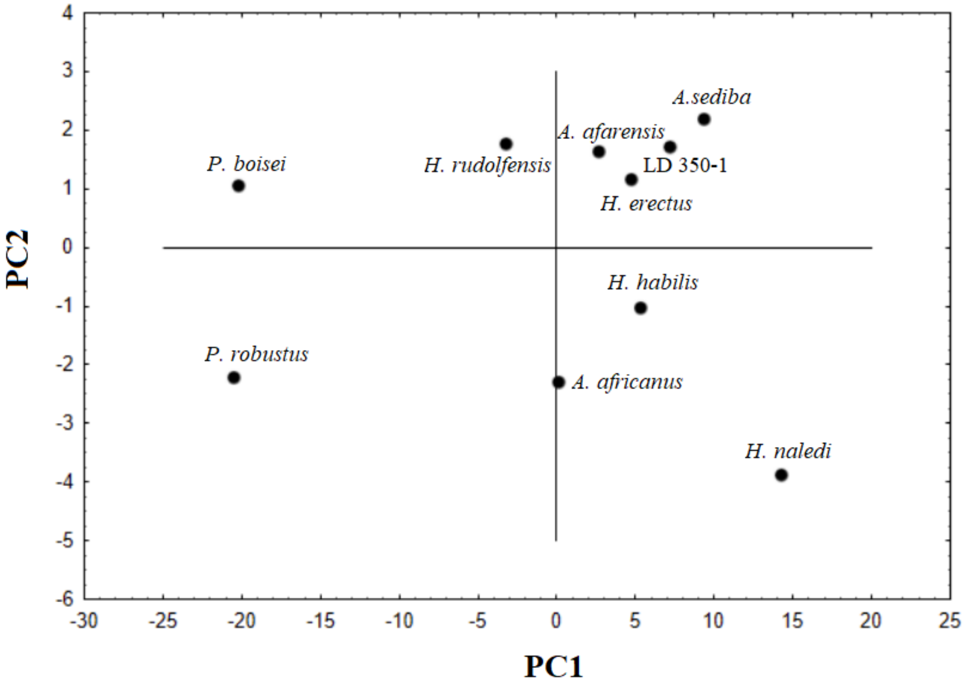

Figure 2. Morphological affinities of hominin species based on the coordinates of the first two Principal Components (PC).

correlation (r>0.7) with Corpus width at M2 (Table SIII). As such, high values in PC1 are associated with relatively tall and thick corpuses, and vice-versa. The second PC explains 20.60% of the variance, and shows strong negative correlation with Corpus width at P4 (r=-0.72; Table SIII), and strong positive correlation with Height of Mental Foramen (r=0.72). In this size-corrected analysis, the Ledi-Geraru mandible shows a tight affinity with *H. erectus*, since they both present low corpuses at P4 and M1, narrow corpuses at M1, median wide corpuses at P4 and median high mental foramina. Notably, *Homo habilis* still appears very distant from Ledi-Geraru, and the robust australopiths are more integrated in the morphospace, associated with *H. habilis* and *A. africanus*.

In summary, our results show a strong morphological affinity of LD 350-1 with *A. afarensis, H. erectus,* and *A. sediba,* when size and shape are considered. However, when only shape is taken into account, there is a remarkable association between LD 350-1 and *Homo erectus*. One striking result is that in both analyses *Homo habilis* appears in the morphospace very far from Ledi-Geraru.

DISCUSSION AND CONCLUSIONS

Our analyses of the morphological affinities of mandibles in australopiths and early *Homo* show that the challenge of discriminating between early *Homo* and earlier hominins is not restricted only to the fossil of Ledi-Geraru. None of our analyses demonstrate a clear pattern of association among species of the same genus. The Ledi-Geraru mandible exemplifies this scenario well, as it presents a morphology that is closer to the morphology of earlier *Australopithecus afarensis* and later *Homo erectus,* but not to early *Homo habilis*.

Within this context of ambiguous morphological affinities, our analyses agree only partially with Villmoare et al. (2015a). Our results and those presented originally by Villmoare found strong morphological affinities of LD 350-1 with *A. afarensis*. However, the original study reported a closer affinity of the Ledi-Geraru

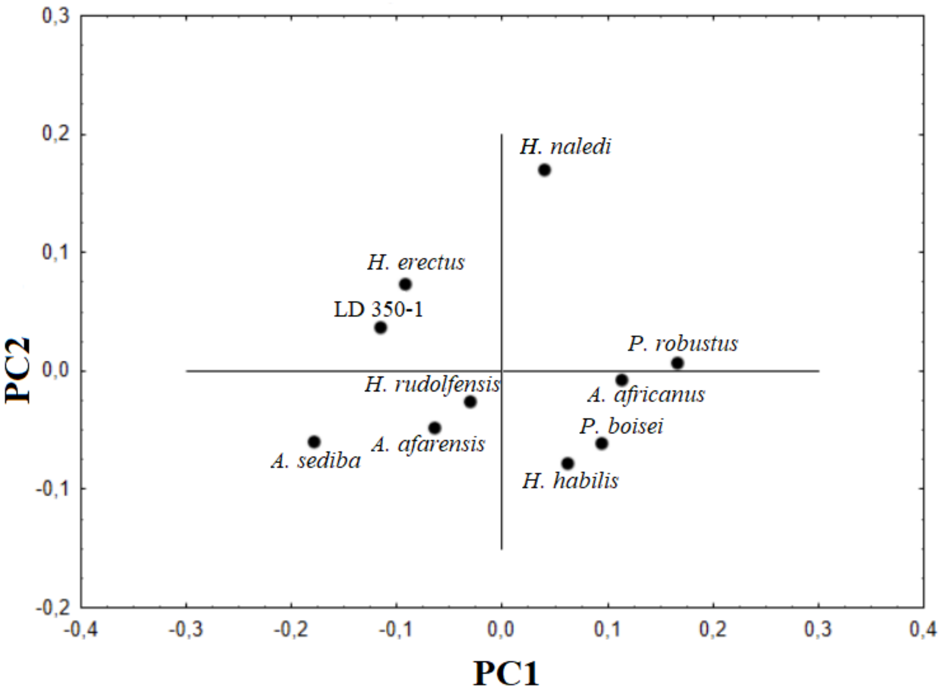

Figure 3. Morphological affinities of hominin species based on the coordinates of the first two Principal Components (PC).

mandible with non-erectus early *Homo*. Our analyses, based on a much larger sample, points towards a closer similarity between LD 350-1 and *H. erectus*, rather than between the former and non-erectus early *Homo*.

It is important to note that, as can be seen in Figures S1, S2 and S3, adapted from the original graphics of Villmoare et al. (2015a), the Ledi-Geraru specimen appears closer to *H. erectus* than to non-erectus early *Homo* in their study as well, even though this closer proximity was not emphasized by the authors. Although it seems contradictory that such an early specimen aligns with a "late" species of the genus *Homo*, the closer proximity of the Ledi-Geraru mandible with *H. erectus* cannot be denied. As with many previous studies on the morphological characteristics of hominins, this association illustrates how complex the ancestral relationships of hominins are, especially during the period explored here, when multiple species of hominins coexisted in time.

In summary, our results consistently evidence a close morphological affinity between LD 350-1, *Homo erectus*, *Australopithecus afarensis*, and *Australopithecus sediba*, when size and shape are considered. However, since size is much influenced by immediate external factors, we prefer to rely our conclusions on the analysis that took into account only shape information. When this is done, there is an unquestionable tight proximity between LD 350-1 and *Homo*, favoring the initial conclusion of Villmoare et al. (2015a). This would extend back the *Homo* fossil record by ca. 0.4 Ma. A cautionary note is however necessary at this point. Our analyses failed to integrate *Homo habilis* as part of the transition between australopiths and *Homo erectus*. More fossil material between 3.0 and 2.0 Ma will be of paramount importance to clarify this possibility.

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SUPPLEMENTARY MATERIAL

Figures S1-S3
Tables SI-SIII

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