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Short Communications

Relationship between interproximal and occlusal wear in *Australopithecus africanus* and Neanderthal molars

Luca Fiorenza [a, *, 1], Waseem Habashi [b, 1], Jacopo Moggi-Cecchi [c], Stefano Benazzi [d], Rachel Sarig [b, e]

[a] *Monash Biomedicine Discovery Institute, Department of Anatomy and Developmental Biology, Monash University, 3800 Melbourne, VIC, Australia*
[b] *Department of Oral Biology, The Goldschleger School of Dental Medicine, Sackler Faculty of Medicine, Tel Aviv University, 39040 Tel Aviv, Israel*
[c] *Department of Biology, University of Florence, 50121 Florence, Italy*
[d] *Department of Cultural Heritage, University of Bologna, 48121 Ravenna, Italy*
[e] *Dan David Center for Human Evolution and Biohistory Research, Sackler Faculty of Medicine, Tel-Aviv University, 39040 Tel Aviv, Israel*

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1. Introduction

The analysis of dental wear is a valuable tool to obtain information about diet, ecology, and daily-task activities in past human populations and in extinct hominin species (Molnar, 1972; Smith, 1984; Kaifu et al., 2003). Interproximal wear is found along the mesial and distal aspects of tooth crowns between adjacent teeth. Similar to occlusal wear, the contact between neighboring teeth promotes the formation of interproximal wear facets (Whittaker et al., 1987; Benazzi et al., 2011; Sarig et al., 2013, 2015). However, the formation of interproximal wear is complex and is caused by a combination of several factors, not necessarily directly related to diet. The newly erupted posterior teeth push forward toward a common center by the action of the mesial drift, a complex mechanism involving the migration of teeth by bone remodeling and dental resorption (Moss and Picton, 1970).

It has been observed that prehistoric human populations and recent hunter–gatherer groups displayed greater levels of interproximal wear than contemporary human populations Moss and Picton, 1967; Wolpoff, 1971). Based on these observations, Hinton (1982) examined the interproximal wear facet breadth in Native North Americans from different chronological times finding interpopulation variation in the amount of interproximal wear. Corruccini (1990) analyzed the dentition of modern Australian Aborigines finding a considerable reduction in the amount of interproximal wear when compared to more traditional hunter–gatherer groups. Similarly, Sarig et al. (2016) measured the amount of interproximal wear areas of Pleistocene human remains from Qesem Cave (400–200 ka) and compared them with those of recent modern humans finding lower levels of interproximal wear in the latter group.

These studies suggested that the observed difference in interproximal wear depended on the type of food consumed by these populations and on the way they prepared their meals (Hinton, 1982; Corruccini, 1990). Hinton (1982) further suggested that interproximal wear is influenced by the magnitude and frequency of applied occlusal forces, which are indirectly related to diet. However, while interproximal wear is directly related to the magnitude of the masticatory force, the rates of occlusal wear depend upon both masticatory force and physical properties of the ingested food. It is therefore possible that occlusal and interproximal wear may not be closely related as has been assumed (Wolpoff, 1971). A few studies investigated the relationship between interproximal and occlusal wear, leading, however, to conflicting results (Hinton, 1982; Whittaker et al., 1987; Lukacs and Pastor, 1988; Deter, 2012; Sarig et al., 2015). While previous studies found a positive association between the two wear variables (Hinton, 1982; Whittaker et al., 1987; Lukacs and Pastor, 1988), more recent analyses found a weak (Sarig et al., 2015, 2016) or negative relationship between occlusal and interproximal wear, especially in more heavily worn molars (Deter, 2012).

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* Corresponding author.
E-mail address: luca.fiorenza@monash.edu (L. Fiorenza).
[1] These authors contributed equally to this work.

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The aim of this study is to answer this question by using the occlusal fingerprint analysis (OFA) method (Kullmer et al., 2009), a three-dimensional (3D) digital approach based on quantitative analyses that measure macrowear variables and links them with dental function, masticatory movements, culture, and diets (Fiorenza et al., 2018, 2019). The advantage of OFA is the use of high-resolution 3D digital models of teeth that allows to accurately measure different occlusal wear variables (Kullmer et al., 2009). The analysis of these parameters allows to describe the major occlusal movements responsible for the formation of wear facets, information that can be used to track changes in dental function, jaw movements, and diet (Fiorenza et al., 2011, 2015, 2022; Kullmer et al., 2020; Harty et al., 2022).

Moreover, while previous studies only measured the breadth of interproximal wear using calipers (Hinton, 1982; Deter, 2012), here we quantify the surface area of the entire interproximal wear facets using metrology software and 3D digital models of teeth. Sarig et al. (2013, 2015, 2016) have measured the size of interproximal wear facets instead of buccolingual distances, which proved to be a more reliable approach to accurately evaluate the amount of interproximal wear considering that the shape of these facets can be considerably variable, ranging from ovoid to subrectangular types (Fig. 1).

In this study, we investigate the correlation between occlusal and interproximal wear by examining the molars of *Australopithecus africanus* and Neanderthals. We test two main hypotheses: hypothesis 1) we expect to find a positive correlation between interproximal and occlusal wear. Specifically, the size of interproximal wear facets should increase in those molars characterized by larger occlusal wear, as suggested by Hinton (1982) and hypothesis 2) the interproximal wear should be inversely related to wear plane angles since in more advanced wear stages, the occlusal crowns flatten because of cusp removal (Smith, 1984; Fiorenza et al., 2018, 2020). Therefore, we should find larger interproximal wear facets in flatter molars (i.e., lower inclination values).

2. Materials and methods

2.1. Materials

The surface area of interproximal wear facets can be measured only in teeth where either (or both) mesial and distal aspect of the crown is visible. Consequently, we specifically selected isolated molars and molars from tooth rows where the mesial or the distal interproximal facet could be measured. The sample consists of 69 molars, evenly split between Neanderthals ($n = 36$) and *A. africanus* ($n = 33$; Table 1; Supplementary Online Material [SOM] Table S1). We focused on molars characterized by a slight to a moderate degree of wear (between wear stages 1 and 4; Smith, 1984).

Positive replicas of teeth were created using a specialized dental die stone material (GC Fujirock® EP) that has smooth and non-reflective properties, ideal for surface scanning (Fiorenza et al., 2009). Polygonal digital models were generated via a fully automated 3D scanning system based on blue light emitting diode technology and with a 3D resolution up to 29 μm (Artec Micro, Artec 3D). Postprocessing and alignment of the scanned data was carried out with Artec Studio Professional v. 15 (Artec 3D, Luxembourg) and with the IMEdit module of Polyworks v. 12 (InnovMetric, Québec).

2.2. Occlusal and interproximal wear

Occlusal wear facets and mesial (MIP) and distal (DIP) interproximal wear facets were manually outlined onto the polygonal model using the polyline tool available in Polyworks (Fig. 2A). We measured the surface areas (in mm^2) of interproximal and occlusal wear facets. We sum the surface areas of all occlusal facets and tip crush areas to obtain the total occlusal wear area (TOWA). In addition, we also calculated the facet inclination, which is obtained by measuring the angle between the reference plane with the facet plane. The reference plane is created by using the least squares best-fit method selecting the vertices along the molar cervical line, which is then rotated to the original coordinate system (Fiorenza et al., 2018). Similarly, to create the plane of each facet, we selected all triangles included within the facet perimeter and used the best-fit tool available in Polyworks. For each tooth, we calculated the average inclination by summing the plane angle of all occlusal facets and tip crush areas and dividing this value for the number of facets and tip crush areas. Finally, we also calculated the 3D occlusal area (3DOA) by selecting al triangles of the polygonal models above the occlusal plane (Harty et al., 2022). The occlusal plane is obtained by translating the cervical plane along the *z* axis until it reaches the deepest point of the occlusal surface or central fossa.

2.3. Statistical analysis

We used summary statistical analysis (median and standard deviation) for each variable considered in this study. In addition, we evaluated the relationship between occlusal and interproximal wear using bivariate analysis based on ordinary least squares regression, Pearson's r correlation, and coefficient of determination r^2 (Warton et al., 2006) for each tooth type and for each species with a minimum sample size of six. The statistical analysis was performed using the software PAST v. 4.04 (Hammer et al., 2001).

3. Results

We observed larger interproximal wear facet areas in those molars characterized by greater occlusal wear areas (SOM Table S2). This pattern is found in *A. africanus* (SOM Fig. S1) and Neanderthals (SOM Fig. S2), and it affects both MIP and DIP. In *A. africanus*, maxillary molars MIP values show high levels of correlation with TOWA (SOM Fig. S3; Table 2), whereas this relationship is less

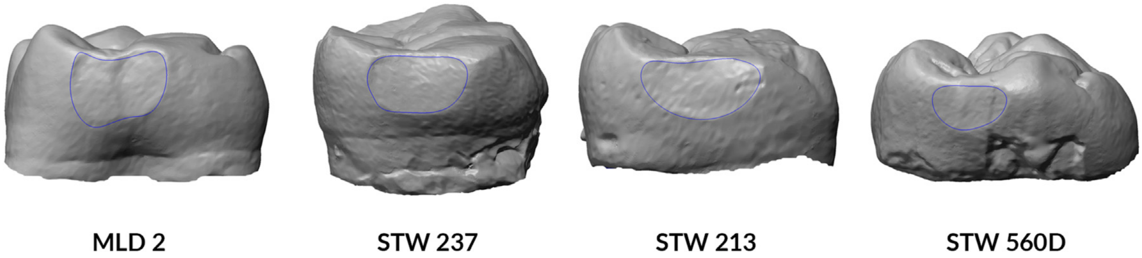

Figure 1. Shapes of mesial interproximal facets outlined onto digital polygonal models of *Australopithecus africanus* molars.

Table 1
List of *Australopithecus africanus* and Neanderthal specimens used in this study. Dating of the *Australopithecus africanus* specimens from Sterkfontein follows Pickering et al. (2019). Individual tooth identification of *A. africanus* molars follows Moggi-Cecchi et al. (2006) while individual tooth identification of Neanderthal isolated molars from Krapina follow Wolpoff (1979) and Radovčić et al. (1988).

Group	*n*	Specimens	Country	Dating
Australopithecus africanus	33	MLD 2, 6, and 19	South Africa	2.5 Ma
		STS 8, 12, and 37	South Africa	2.8–2.0 Ma
		STW 19b, 106, 120, 131, 151 (156), 151 (157), 179, 183, and 188	South Africa	2.8–2.0 Ma
		STW 213, 234, 237, 246, 291, 295, 309, 353, and 364	South Africa	2.8–2.0 Ma
		STW 421, 520, 529, 560d and 560e	South Africa	2.8–2.0 Ma
		TM 1512 and 1518	South Africa	2.8–2.0 Ma
Neanderthals	36	Krapina 1, 4, 6, 7, 9, 10, 66, 77, 79, 80, 81, 85, and 86	Croatia	130 ± 10 ka
		Krapina 107, 134, 135, 136, 165, 166, 167, and 169	Croatia	130 ± 10 ka
		Krapina 171, 175, 177	Croatia	130 ± 10 ka
		Monsempron 2 and 3	France	120–100 ka
		Kulna 1	Czech Republic	44–38 ka
		Le Moustier 1	France	41 ka
		Petit Puy 2	France	60–40 ka
		Tabun 1	Israel	122 ± 16 ka
		Shanidar 2 and 6	Iraq	~44 ka
		Vindija V259	Croatia	42–32 ka
		Spy 2	Belgium	36 ka
		La Quina 20	France	71–57 ka
		Guattari 2	Italy	50–60 ka

evident in Neanderthals (SOM Fig. S4; Table 2). The relationship between DIP and TOWA is less clear in Neanderthal maxillary molars (SOM Fig. S5). MIP and DIP areas of *A. africanus* and Neanderthal mandibular molars increase in those specimens characterized by greater levels of occlusal wear.

Neanderthal molars are characterized by slightly higher inclination values than in *A. africanus*, although we observe a higher degree of variability in the latter group (SOM Table S2). This is particularly evident in molars characterized by wear stage 3, whereas the inverse situation is found in less worn molars (wear stages 1 and 2), where wear facet planes are steeper in *A. africanus* (SOM Table S3).

Inclination is generally inversely related with the MIP values of *A. africanus* (SOM Fig. S6) and Neanderthal maxillary molars (SOM Fig. S7). This relationship is also observed with DIP values in Neanderthal maxillary molars (SOM Fig. S8). In *A. africanus* mandibular molars, MIP areas tend to increase in flatter molars with the exception of M_2s, where there is a slight but positive relationship between the two variables (SOM Fig. S6). In Neanderthals, we found smaller MIP areas in flatter molars (SOM Fig. S7).

Interproximal wear areas are greater in *A. africanus* maxillary molars characterized by larger 3DOA (SOM Fig. S9). This pattern is not observed in Neanderthal maxillary molars, where the relationship between MIP and 3DOA (SOM Fig. S10) and that between DIP and 3DOA (SOM Fig. S11) are generally inverted. The situation is more variable when we look at the relationship between 3DOA and MIP in *A. africanus* and Neanderthal mandibular molars, finding both positive and negative correlations (SOM Figs. S9 and S10).

Mesial interproximal wear facets seem to be correlated with occlusal wear areas in *A. africanus* and Neanderthal molars following similar patterns. More specifically, while MIP is positively correlated to TOWA in *A. africanus* and in Neanderthals, it is inversely correlated with facet inclination in both groups (SOM Table S3).

The Pearson correlation coefficients show a high to moderate degree of association between these variables, and this is also confirmed by the significant *p*-values in some molars (<0.01; Table 2). However, we do not find any strong association between the 3D occlusal area and the mesial interproximal wear. The Pearson correlation coefficient and coefficient of determination values

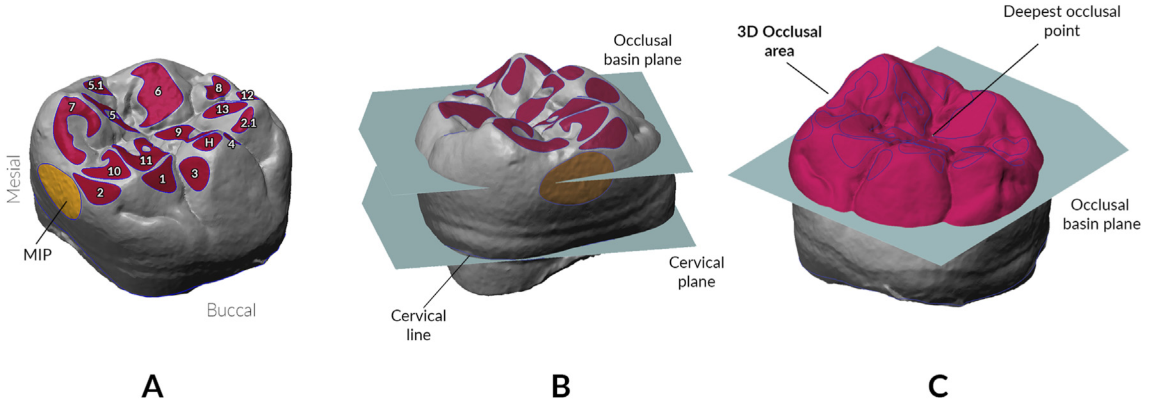

Figure 2. Occlusal fingerprint analysis method. Three-dimensional digital model (A) of *Australopithecus africanus* left M_1 (STW 364) showing interproximal (in yellow) and occlusal wear facets (in magenta). The occlusal wear facets are numbered according to the Maier and Schneck's (1981) labeling system. We also identify flat worn areas on the tip of the molar cusps, known as tip crush areas, which are created during puncture-crushing (Gordon, 1984; Janis, 1990). The occlusal plane (B) is obtained by translating the reference (or cervical) plane along the *z* axis until it reaches the deepest point of the occlusal surface. The three-dimensional occlusal area (C) is measured by selecting all the triangles of the polygonal model above the occlusal basin plane. Abbreviation: H = hypoconid. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Ordinary least square regressions, divided by molar type, between different tooth wear variables in *Australopithecus africanus* and in Neanderthals including the Pearson's r correlation, the coefficient of determination r^2, and the *p*-values obtained from the permutation test (1999 replicates).[a]

Correlation	Tooth	*Australopithecus africanus*			Neanderthals		
		r	r^2	*p*	r	r^2	*p*
TOWA-MIP	M^1	0.9297	0.8644	**0.0020**	0.1970	0.0388	0.5828
	M^2	–	–	–	0.5249	0.2755	0.1201
	M_1	0.7138	0.5095	0.0978	–	–	–
	M_2	0.1345	0.0181	0.7707	0.7748	0.6002	**0.0307**
	M_3	0.6565	0.4309	0.1572	–	–	–
Inclination-MIP	M^1	−0.8339	0.6953	**0.0156**	−0.3727	0.1389	0.2941
	M^2	–	–	–	−0.7569	0.5729	**0.0084**
	M_1	−0.9216	0.8494	**0.0226**	–	–	–
	M_2	0.1458	0.0213	0.7638	−0.8121	0.6596	**0.0179**
	M_3	−0.3703	0.1371	0.4695	–	–	–
3DOA-MIP	M^1	0.5529	0.3057	0.1535	−0.0171	0.0003	0.9634
	M^2	–	–	–	−0.4382	0.1920	0.2074
	M_1	−0.5397	0.2913	0.2448	–	–	–
	M_2	−0.6696	0.4484	0.1060	−0.7610	0.5791	0.0596
	M_3	0.5813	0.3379	0.2354	–	–	–
TOWA-DIP	M^1	–	–	–	0.4794	0.2298	0.2803
	M^2	–	–	–	0.5900	0.3481	0.1256
Inclination-DIP	M^1	–	–	–	−0.54349	0.29538	0.21200
	M^2	–	–	–	−0.73135	0.53487	**0.03770**
3DOA-DIP	M^1	–	–	–	−0.10459	0.01094	0.86550
	M^2	–	–	–	−0.65568	0.42992	0.08480

Abbreviations: DIP: distal interproximal wear; 3DOA: three-dimensional occlusal area; MIP: mesial interproximal wear; TOWA: total occlusal wear area.

[a] Significant *p*-values (<0.05) are highlighted in bold.

are generally very moderate in *A. africanus* showing both positive and negative relationships (Table 2). In Neanderthals, the correlation between MIP and 3DOA is slightly higher, especially in mandibular molars. The *p*-values of the correlation between the 3D occlusal area and the mesial interproximal wear are not statistically significant (Table 2).

4. Discussion

Our results seem to indicate that mesial interproximal wear is positively correlated to occlusal wear (hypothesis 1). Although the association is not always strong, it is statistically significant in several molar types and in agreement with previous studies based on modern human populations (Hinton, 1982; Sarig et al., 2015). We found larger mesial interproximal wear facets in molars characterized by larger occlusal wear areas. This relationship is observed in both Neanderthals and *A. africanus* molars, and it follows similar levels of correlation. The relationship between mesial interproximal wear and occlusal wear does not seem to be influenced by molar size. In fact, we did not find any statistically significant correlation between 3D occlusal area and mesial interproximal wear facet size in Neanderthal and *A. africanus* molars.

In general, we observe that the occlusal and interproximal wear facet areas in *A. africanus* mandibular molars increase distally (M1 < M2 < M3), whereas in the maxillary molars, the two wear types follow different patterns: M1 < M2 > M3 for occlusal wear, and M1 > M2 > M3 for interproximal wear. In Neanderthals, these patterns are less clear. Occlusal wear areas are larger in M1s, followed by M2s and M3s. However, we found that the largest mesial interproximal wear in Neanderthal is visible in M_3s and M^2s. Such results would suggest that most of the chewing in *A. africanus* occurs distally, between M2 and M3, whereas in Neanderthals, it occurs more mesially, between M1 and M2. This probably reflects molar size differences between these two species and the amount of occlusal surface available (Hunt and Vitzthum, 1986; Evans et al., 2016).

The positive correlation found between occlusal and interproximal wear areas in Neanderthals and *A. africanus* could partially indicate that the mechanisms behind the formation of these two types of dental wear are similar or somehow related to each other. It is however difficult to identify the main mechanisms that drive the formation of interproximal dental wear. There are many independent confounding factors, each with varying intensity and duration, which can determine the formation of a multitude of different wear patterns (Kaidonis, 2008). Nevertheless, it is still interesting to note that similar levels of correlation between occlusal and interproximal wear have been observed in modern human populations as well (Hinton, 1982; Whittaker et al., 1987; Lukacs and Pastor, 1988; Deter, 2012; Sarig et al., 2015). However, this positive and linear correlation between interproximal and occlusal wear is less clear in more heavily worn teeth (Deter, 2012; Sarig et al., 2015). Unfortunately, due to limitations in the OFA method, which requires the use of moderately worn teeth for the identification of occlusal wear facets, we could not include in the study more heavily worn molars. It would be interesting to see if this change in correlation between the two wear types would also be observed in *A. africanus* and Neanderthals.

In Neanderthals, the level of correlation between DIP and occlusal wear follow the same trends observed between MIP and TOWA. However, in *A. africanus* molars, the areas of the DIP facets follow different and more variable patterns. Unfortunately, due to sample size limitations, we could not test if distal interproximal wear in *A. africanus* molars is correlated with the other wear and dental variables. Differences in mesial and distal interproximal wear have been found also in modern humans, where concave facets were more common on mesial surfaces, whereas convex facets were more frequent on the distal side (Whittaker et al., 1987). The authors of this study suggested that complex rotatory movements between adjacent teeth would result in concave facets mesially and convex faceting distally. Pokhojaev et al. (2018) tested this hypothesis with surface texture analysis suggesting that fretting, a wear process occurring as a result of small-amplitude cyclic motion of two solid contacting surfaces, represents the major mechanism in the formation of interproximal wear facets.

The results of this study also seem to confirm our second hypothesis, generally finding a negative correlation between occlusal wear plane inclination and the size of mesial interproximal facets in both groups. We observed large mesial interproximal wear surfaces in those molars characterized by flatter occlusal surfaces and smaller interproximal facets in molars exhibiting higher facet plane values. However, the correlation between inclination and DIP in Neanderthal molars was weak. This different result could be affected by the smaller number of molars displaying distal interproximal wear examined in this study. It is also interesting to note that *A. africanus* molars generally display higher inclination values than those of Neanderthals in the initial stages of wear (wear scores 1 and 2), followed by a rapid decrease at wear stage 3 (SOM Table S2). On the other hand, in Neanderthals, the inclination difference between consecutive wear stages is less pronounced. This would suggest a faster rate of occlusal wear in *A. africanus* teeth than those of Neanderthals. Dental histological data suggest a more rapid dental maturation in early African hominins than in later *Homo* (Moggi-Cecchi, 2001; Macchiarelli et al., 2006; Smith et al., 2007, 2010; Guatelli-Steinberg, 2009; Mahoney et al., 2021). This more rapid molar development in *A. africanus* would be consistent with a faster occlusal wear rate observed in this study. However, we cannot exclude the possibility that other causes, such as diet and environmental abrasiveness (Fiorenza et al., 2018, 2020), may have played a significant role in this variation. Further studies are needed to accurately measure occlusal wear rates in these two taxa.

The results of our study seem to confirm that interproximal and occlusal wear are somehow related to each other. However, due to the reduced sample size and methodological limitations, we are unable to draw clear conclusions on this relationship. Future studies could investigate in more details the relationship between occlusal and interproximal wear in other hominin species and past human populations. Moreover, shape and surface texture analyses could provide further insights for better understanding the mechanisms behind the formation of interproximal wear as highlighted in previous studies (Sarig et al., 2015; 2016; Pokhojaev et al., 2018). Our current analysis was limited by the use of a relatively small sample size and focused only on molars characterized by a moderate degree of wear. Moreover, the sample used in this study mostly consists of isolated tooth crowns with no information about the individual age and with roots missing. It has been suggested that the rate of interproximal wear is strongly associated with the mesial tilting of tooth crowns relative to the roots (Wolpoff, 1971; Sarig et al., 2016). The use of micro computed tomography data could overcome these limitations because it would allow to study teeth included in tooth rows, and it would permit to measure root angulation as well.

Declaration of competing interest

There are no conflicts of interest.

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Supplementary Online Material

Supplementary Online Material to this article can be found online at https://doi.org/10.1016/j.jhevol.2023.103423.

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