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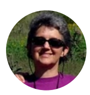

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A New Model for Calculating the Lumbar Lordosis Angle in Early Hominids and in the Spine of the Neanderthal From Kebara

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ABSTRACT

The debate over the posture of early hominids is longstanding, perhaps because the absence of a reliable method for reconstructing the lumbar lordosis angle (LA) in early hominid spines has made it difficult to determine whether their posture resembled or differed from that of modern humans. We have developed a new model for predicting the lordotic curvature of the lumbar spine of early hominids based on the relationship between the lordotic curvature and the orientation of the articular processes in the lumbar spines of living primates (modern humans and nonhuman primates). The orientation of the inferior articular processes explains 89% of the variation in lordotic curvature among living primates and, thus, should be a reliable predictor of the lumbar LA in disarticulated hominid spines. Based on this model, we calculated a LA of 25–26 degree angle for the Kebara 2 Neanderthal. The calculated value for Kebara 2 is below the normal range of lordosis for modern humans (30–79 degree angle). Anat Rec, 293:1140–1145, 2010. © 2010 Wiley-Liss, Inc.

Key words: articular process; vertebral spine; spinal curvature; hominids; primates

The lordotic curvature of the lumbar spine (lumbar lordosis) stabilizes the upper body over the lower limbs in humans and allows the loads applied to the vertebral column to be efficiently absorbed (Gracovetsky and Iacono, 1987; Farfan, 1995; Whitcome et al., 2007). The lumbar lordosis of humans is formed by the wedging of both the lumbar vertebral bodies and the intervertebral disks (Harrison et al., 2001; Kimura et al., 2001; Vaz et al., 2002; Roussouly et al., 2005). This curvature influences the morphology of the anterior pillar (formed by the vertebral body and intervertebral disks) and the posterior pillar (formed by the articular processes and the laminae) of the spine (Sanders 1998). The orientation of the inferior articular processes in humans explains 62% of the variation in lordosis angle (LA) (Been et al., 2007).

LA, however, can only be measured reliably on intact spines, because it is effected by both osseous and soft tissue (e.g., the intervertebral disk). Articular process angles, however, can be measured on both articulated and disarticulated vertebra, because their measurement

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relies on elements contained within a single vertebra. Thus, a relationship between articular process angles and LA would be useful in reconstructing fossil LAs, because it would tie together what is knowable for fossils (articular process angles) to a functionally important, but unknowable attribute (LA).

The LA in modern human spines can be calculated by examining the orientation of the inferior articular processes, whether or not the relationship between the LA and the orientation of the inferior articular processes in the lumbar spines of nonhuman primates is like as in humans is not known. If such a relationship exists—that is, if the lumbar spines of nonhuman primates that lack lumbar lordosis have low inferior articular process angles—we will be able generalize the relationship to all primates, which would enable us to reconstruct the lumbar LAs in early hominid spines.

The aim of this study is, then, twofold. First, we investigate the relationship between the LA, the vertebral body wedge angle, and the orientation of the inferior articular processes in the lumbar spines of nonhuman primates. Second, we combine these results with those of Been et al., (2007) to devise a tool for calculating the LA of early hominid spines.

MATERIALS AND METHODS

Radiographs

Lateral radiographs of the lumbar spines of 123 nonhuman primates were examined. All radiographs were taken with a standard film to tube distance of 3 feet and the beam centered on L_1. The radiographs come from the collection of the University of Washington, Seattle and from a number of zoos and veterinary hospitals in Israel. The radiographs from the University of Washington are part of a research collection and the radiographs from the hospitals and zoos in Israel were taken to detect health problems in the nonhuman primates. Out of the 123 radiographs, 74 were selected based on the following criteria: (1) Adult subjects with no radiographic abnormalities (e.g., degeneration or reduced disk height) detected and (2) high quality radiographs with clear view of the lumbar spine. The nonhuman primates included the spinal (lumbar) radiographs of *Macaca* (52), *Lemur* (8), *Saimiri* (4), *Saguinus* (3), and a single representative from each of the following genera: *Pan*, *Pongo*, *Hylobates*, *Mandrillus, Alouatta, Colobus*, and *Loris*.

In all cases, standard lateral lumbar radiographs were obtained with subjects lying on their sides with flexed shoulders, hips, and knees in a position as relaxed and as close to a natural posture as possible (Fig. 1). Preuschoft et al., (1988) demonstrated that lateral spinal radiographs of anesthetized monkeys (*Macaca fuscata*) exhibit similar spinal curvatures to the lateral radiographs of naturally standing (quadrupedal) monkeys. Our natural position, which is similar to the position described by Preuschoft et al., (1988), was chosen as the standard for the University of Washington collection after examination of a pilot sample of radiographs of the same monkeys in natural and (unnaturally) extended (arms pulled above the head, legs fully extended at hip and knee) position. Recently, we re-examined these pilot radiographs to measure LA and found that full extension increases LAs on average 2 degree angle from the natural position.

Fig. 1. A lateral radiograph of macaque monkey.

Measurements

The typical number of lumbar vertebrae varies among primate genera. For example, the lumbar spine of *Loris* consists of eight lumbar vertebrae, *Lemur* and *Macaca* have seven lumbar vertebrae, and *Pan* has only four lumbar vertebrae (Schultz, 1961). Because LA is dependent on the number of vertebrae included in the calculation (Harrison et al., 2001; Vialle et al., 2005), comparison of results among different primate genera requires standardization. Most of the early hominid lumbar spines have five lumbar vertebrae (Trinkaus, 1983; Arensburg, 1991; Haeusler et al., 2002). Thus, we chose to compare the lordosis formed by five segments. To facilitate comparison among the different primate groups, we numbered the vertebrae in relation to the sacrum, as others have compared the lumbar vertebrae of nonhuman primates, early hominids, and modern humans (Latimer and Ward, 1993; Abitbol, 1995). The vertebra just above the sacrum is called PS_1 (first presacral) in all of the spines; the vertebra above it is called PS_2, and so forth.

For each of the five vertebrae (PS_1–PS_5), three lines were drawn (Figs. 2,3): along the cranial endplate of the vertebral body (including the first sacral vertebra); along the caudal endplate of the vertebral body; and along the ventral border of the inferior articular process. These lines were used to measure four angles:

1. The LA between the cranial endplate of PS_5 and the cranial endplate of S_1.

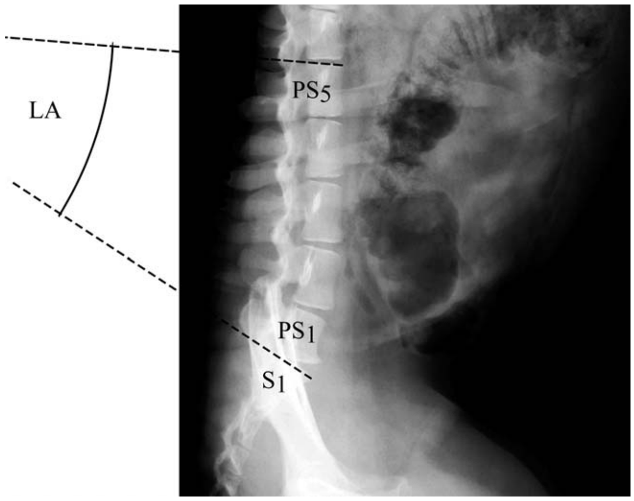

Fig. 2. Lumbar LA shown on a lateral radiograph of macaque monkey.

2. The total segmental angle (T) between the cranial endplate of one vertebra and the cranial endplate of the next vertebra.
3. The vertebral body wedge angle (B) between the cranial and caudal end plates of the vertebral body.
4. The inferior articular process angle (AP) between the cranial endplate and the ventral border of the inferior articular process of the same vertebra, as seen in the lateral radiograph in the facet joint space.

Measurements T, B, and AP were taken for each of the five segments. The LA is shown in Fig. 2 and the other angles in Fig. 3. All measurements were taken by the same investigator (EB) using a 25 cm Jamar goniometer with a 360 degree angle scale in 1 degree angle increments. Summations of measurements B and AP were also calculated: Σ**B** equals the sum of the body wedge angles of vertebrae PS_1–PS_5; and Σ**AP** equals the sum of the inferior articular process angles of this vertebrae.[1]

Descriptive statistics and Pearson correlation analysis were performed using SPSS (SPSS, Chicago) for the nonhuman primates and for the combined primate group (nonhuman primates from this study and humans from Been et al., 2007). On the basis of these correlations, simple linear regression models were developed to predict the lumbar LA. An ANCOVA test was conducted to determine whether or not the slope and intercept of the regression lines for humans and nonhuman primates differed. The significance value was set at $\alpha = 0.05$.

Fossil Hominids

To demonstrate this methodology on a disarticulated fossil specimen, we obtained lateral spinal radiographs of the lumbar spinal vertebrae of Kebara 2, an adult Neanderthal (*Homo neanderthalensis*) male, which lived 60,000 years ago on the southern slopes of Mount Carmel, Israel (Arensburg et al., 1985; Valladas et al., 1987; Arensburg, 1991). We measured the articular process angles of the presacral vertebrae as described above.

[1]Reproducibility test: 65 measurements were recorded twice, 3 weeks apart. Intraclass correlation coefficient was >0.88 ($P < 0.01$).

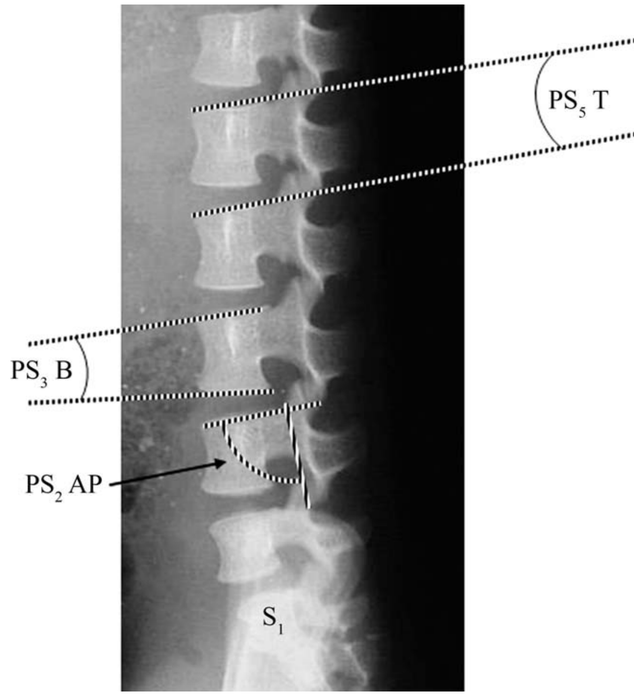

Fig. 3. Segmental measurements shown on a lateral radiograph of *colobus* monkey. PS5 T, total segmental angle of the fifth presacral vertebra; PS3 B, vertebral body angle of the third presacral vertebra; PS2 AP, inferior articular process angle of the second presacral vertebra.

RESULTS

The nonhuman primates exhibit LAs that range from 12 degree angle of kyphosis (*Loris*) to 25 degree angle of lordosis (*Hylobates and Pan*). The segmental angles of the nonhuman primates (T) change gradually, ranging from 6 degree angle of kyphosis (*Pan*) to 6 degree angle of lordosis (*Pongo*) at the fifth presacral vertebra (PS_5); up to 6 degree angle of kyphosis (*Loris*) to 14 degree angle of lordosis (*Pan*) at the first presacral vertebra (PS_1).

The sum of vertebral body wedge angles (Σ**B**) of the nonhuman primates is kyphotic, ranges from 32 degree angle of kyphosis (*Mandrillus*) to 8 degree angle of kyphosis (*Hylobates*). In all of the nonhuman primates (except for the *Loris*) the bodies of the PS_5–PS_3, show more kyphotic wedging than the bodies of PS_2 and PS_1. For example the wedging of upper three vertebral bodies (PS_5–PS_3) of macaques is -7 ± 4, and the wedging of the last vertebral body (PS_1) is -2 ± 5.

The average Σ**AP**—the sum of the inferior articular process angles of PS_1–PS_5 in the nonhuman primates—ranges from 478 (*Pongo*) to 427 (*Loris*). The angular values of the inferior articular process (AP) of the nonhuman primates vary little along the spine, for example the inferior articular process (AP) of macaques ranges from 87 ± 4 degree angle at PS_5 to 88 ± 5 degree angle

TABLE 1. Lumbar spinal angles of nonhuman primates

	Macaca	Lemur	Saimiri	Saguinus	Pan	Pongo	Hylobates	Mandrillus	Alouatta	Colobus	Loris
N	52	8	4	3	1	1	1	1	1	1	1
LA	14 ± 10	8 ± 8	23 ± 5	9 ± 17	25	22	25	13	4	13	−12
ΣB	−28 ± 13	−16 ± 5	−9 ± 8	−21 ± 8	−16	−15	−8	−32	−19	−18	−18
ΣAP	440 ± 15	430 ± 10	456 ± 23	440 ± 28	470	478	465	418	452	455	427
PS_5 B	−7 ± 4	−4 ± 2	−3 ± 1	−4 ± 1	−8	−6	−4	−4	−4	−4	−1
PS_5 T	−1 ± 4	−2 ± 3	0 ± 3	1 ± 3	−6	6	0	−2	−3	2	2
PS_5 AP	87 ± 4	83 ± 3	91 ± 3	83 ± 6	91	103	94	82	86	90	85
PS_4 B	−7 ± 3	−3 ± 2	−3 ± 2	−6 ± 0	−6	−4	−5	−11	−4	−4	−4
PS_4 T	0 ± 4	−1 ± 3	2 ± 2	−1 ± 3	3	1	−2	−2	0	1	−4
PS_4 AP	87 ± 5	85 ± 3	90 ± 4	88 ± 7	98	94	97	86	92	91	88
PS_3 B	−7 ± 4	−3 ± 2	−2 ± 2	−5 ± 2	−1	−5	−4	−8	−4	−6	−5
PS_3 T	1 ± 4	2 ± 2	6 ± 2	1 ± 2	5	1	0	2	0	3	0
PS_3 AP	89 ± 5	86 ± 2	89 ± 6	85 ± 4	94	95	92	84	90	90	85
PS_2 B	−5 ± 4	−3 ± 2	−1 ± 2	−3 ± 2	−4	0	2	−5	−4	−4	−5
PS_2 T	4 ± 4	4 ± 2	9 ± 3	5 ± 3	9	7	11	5	0	4	−3
PS_2 AP	89 ± 4	87 ± 2	93 ± 3	89 ± 2	95	92	93	82	94	88	83
PS_1 B	−2 ± 5	−2 ± 2	−1 ± 1	−3 ± 4	3	0	3	−4	−3	0	−4
PS_1 T	9 ± 6	5 ± 7	8 ± 4	5 ± 5	14	3	11	10	1	2	−6
PS_1 AP	88 ± 5	88 ± 3	94 ± 10	95 ± 11	92	94	89	84	90	96	86

Note: Positive values indicate lordotic wedging; negative values indicate kyphotic wedging. LA, lordosis angle; ΣB, sum of the body wedge angles; ΣAP, sum of the inferior articular process angles; B, body wedge angle; AP, inferior articular process angle; T, segmental angle.

TABLE 2. Linear correlations between the lordosis angle and the sum of the inferior articular process angles (ΣAP) and prediction for Kebara 2

	Linear regression	r	R^2	SE	Kebara 2 (in degree angle)
Combined (nonhuman primates and humans)	LA = 0.53 · ΣAP–221	0.942	0.89	7.2	25
Nonhuman primates	LA = 0.43 · ΣAP–176	0.709	0.50	7.3	
Humans[a]	LA = 0.565 · ΣAP–237	0.787	0.62	6.8	26

[a]From Been et al. (2007).
Note: For an explanation of the abbreviations, see Table 1.

at PS_1. All of the angular measurements are summarized on Table 1.

The LA of the nonhuman primates is correlated with the sum of the inferior articular process angles (ΣAP) ($r = 0.71$, $P < 0.01$), allowing us to develop a predictive linear regression model (Table 2, Fig. 4). Only weak correlation is found between the sum of vertebral body wedge angles (ΣB) and the LA ($r = 0.29$, $P < 0.05$).

To devise a tool for predicting the LAs of early hominids, we used lateral radiographs of the spines of nonhuman primates and humans (combined primate group), as the lumbar LAs of nonhuman primates and of modern humans were found to be highly correlated with the sum of the AP angles (ΣAP), and the ANCOVA test revealed that the regression lines of the two groups are not significantly different ($P = 0.226$). When the measurements of the LA and the sum of the inferior articular process angles (ΣAP) from this study are combined with those from Been et al., (2007), the resulting linear regression model explains 89% of the variability in the lumbar LA among primates ($r^2 = 0.89$, Table 2, Fig. 5), with a standard error of 7.2 degree angle ($S_E = 7.2$).

We calculated the lordosis for the Neanderthal from Kebara (Kebara 2) based on two models—the modern human model and the entire primate model—as one might argue that Neanderthals are close relatives of modern humans and therefore their posture should be predicted based on the modern human sample, whereas another would argue that as the posture of an extinct hominid is unknown it should be predicted based on the entire sample of primates. The ΣAP for Kebara 2 is 465; the calculated lordosis based on the modern human model is 26 degree angle of lordosis and based on the entire primate group is 25 degree angle of lordosis (Table 2).

DISCUSSION

This study demonstrates a linear relationship between the LA and the orientation of the inferior articular process in nonhuman primates and modern humans. We use this relationship to devise a new linear regression model, which is suitable for calculating the lumbar LA of disarticulated early hominid spines. This new model is based on the correlation between the morphology of the posterior pillar of the lumbar spine (which is composed of the laminae and articular processes) and the amount of lordotic curvature exhibited by the anterior pillar (which is formed by the vertebral bodies and intervertebral disks).

The kinematics of primate lumbar spine is variable, dependent on habitual posture, and positional behavior. For instance, compared with the great apes, cercopithecoids (old world monkeys) have a relatively long lumbar region

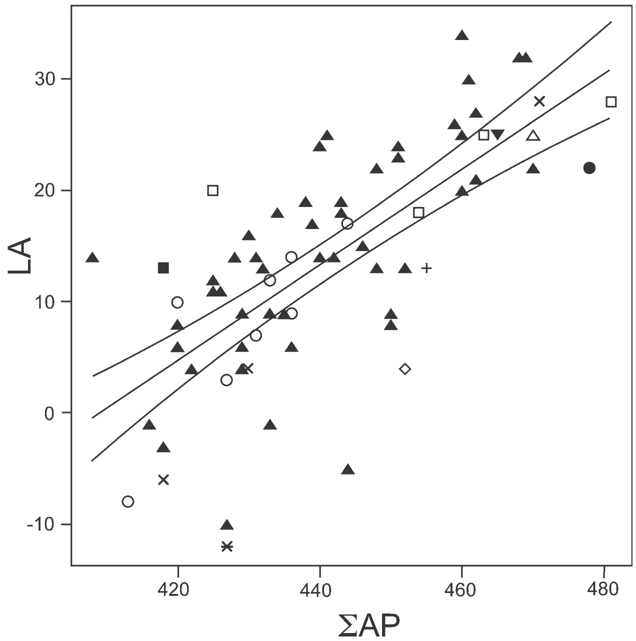

Fig. 4. Correlation between ΣAP and the lumbar LA of nonhuman primates; r = .709, $P < 0.01$. Linear regression with 95% mean prediction interval. ▲ = *Macaca*; ○ = *Lemur*; □ = *Saimiri*; × = *Saguinus*; △ = *Pan*; ▼ = *Hylobates*; ● = *Pongo*; ■ = *Mandrillus*; ◇ = *Alouatta*; + = *Colobus*; * = *Loris*.

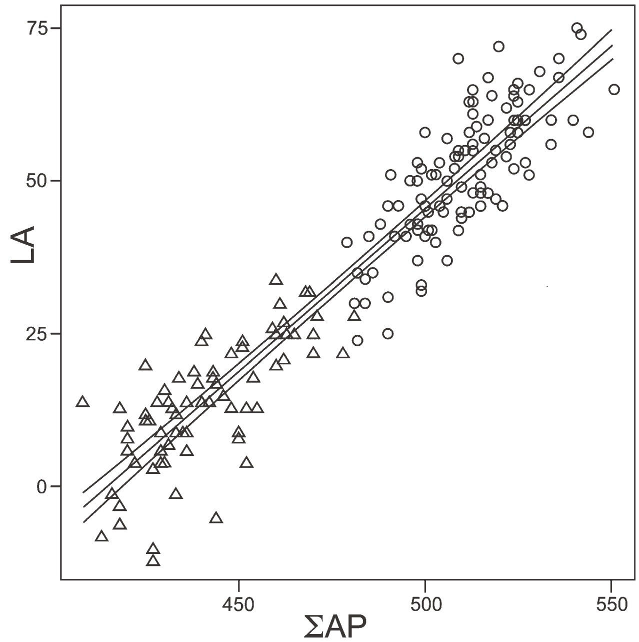

Fig. 5. Correlation between ΣAP and the lumbar LA of the entire primate group (modern humans and nonhuman primates); r = 942, $P < 0.01$. Linear regression with 95% mean prediction interval. ○ = Modern humans; △ = Nonhuman primates.

TABLE 3. Lumbar lordosis angle of primates

	Shultz (1961)	Preuschoft (1988)	Abitbol (1995)	Current study
Method	Ventral profile of the lumbar and sacral region	Cobb angle PS_5–S_1	Cobb angle PS_3–S_1	Cobb angle PS_5–S_1
Position (measured in degree angle)		Side lying	Side lying	Side lying
Apes	24–35 (5)[a]		22 ± 2.1 (7)[a]	24 ± 2.5 (3)[a]
Macaca	11	12 ± 10 (7)[a]	14 ± 0.8 (16)[a]	14 ± 10 (52)[a]

[a]Number of animals included.

that facilitates leaping or running by increasing vertebral mobility in the sagittal plane (Jungers, 1984; Ward, 1991; Shapiro, 1993), whereas lateral bending of the lumbar spine varies among strepsirhines because of the differences in the magnitude and effect of velocity (Shapiro et al., 2001). The primate species that our sample includes have varied habitual postures and forms of locomotion, which presumably put varied functional demands on their spines. Nonetheless, the regression model explains 89% of the variability found in the lumbar LA of the entire group (humans and nonhuman primates) (R^2 = 89) and has standard error of 7.2 degree angle.

The radiographs of the nonhuman primates were taken, when the animals were anesthetized. Consequently, they were not in their habitual posture but were lying on their sides in a position as relaxed as possible and close to the natural stance posture, similar to the position described by Preuschoft et al., (1988). The LA of reclining nonhuman primates may not reflect the LA of these primates in their natural stance posture, but some evidence suggests that it does: *Macaca* that were trained to walk bipedally and developed pronounced lordosis demonstrated similar LAs in orthograde and pronograde posture (Hayama, 1986; Preuschoft et al., 1988; Hayama et al., 1992). The same has been shown in humans: the LA of modern humans does not differ between upright and supine position (Andreasen et al., 2003) and the LA of supine humans is not influenced by differences (5–10 degree angle) in the position of the legs (Murrie et al., 2002). Finally, the LAs measured in the current study closely resemble previously published data (Table 3) of nonhuman primates (Schultz, 1961; Preuschoft et al., 1988; Abitbol, 1995).

The debate over the lumbar LA of Kebara 2 is ongoing. Most researchers agree that the lumbar spine of Kebara 2 exhibited a LA similar to that of modern humans (Arensburg, 1991; Cleuvenot, 1999; Hilton and Nuger, 2004), whereas others claim that the lumbar spine of Kebara 2 showed natural kyphosis (Weber and Pusch, 2008). Normal LA in modern humans ranges from 30 to 79 degree angle (Korovessis et al., 1998; Harrison et al., 2001; Vialle et al., 2005; Been et al., 2007;

Hart et al., 2007), so the predicted value for Kebara 2 of 25–26 degree angle is below the range of modern humans, but it is clearly not kyphotic.

Future work will address lumbar lordosis in other fossil hominids, whose LA should be predicted using an appropriate regression model. For early nonhominid primate (like *Morotopithecus*), the LA should be predicted based on the nonhuman primate model (Table 2). For incomplete lumbar spines such as those of the Nariokotome *H. erectus*, the Stw −431 *Australopithecus*, and the La Chapelle-aux-Saints Neanderthal (Boule, 1911–1913; Walker and Leakey, 1993; Sanders, 1998), specific models need to be developed to allow the use of all the intact vertebrae available for each specimen.

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