Narrative Review Article

The Factors Leading to Reduced Sexual Dimorphism in *H. floresiensis* and *H. naledi*

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ABSTRACT

Homo naledi (*H. naledi*) and Homo floresiensis (*H. floresiensis*) are hominin species that both display reduced sexual dimorphism. The factors that cause this reduction are debated. For *H. naledi,* two factors are debated as the primary causes. Those factors include the emergence of new tools, which make hunting easier, and pair bonding, which reduces male competition, leading to postponed adolescence and smaller canines and body size in males. Their mix of ancient and derived anatomical traits also makes it difficult for researchers to differentiate between the sexes. As for *H. floresiensis*, the island rule suggests that fewer resources result in a smaller overall body size for the species. The smaller overall body size increases pair bonding to fend off predators, which means less male competition, making things like larger canines and bigger body size a waste of energy. This review finds that while there is evidence supporting the theories of pair bonding, insular evolution, and reduced male competition, the current framework used for sex determination requires additional evidence to draw a definitive conclusion, and the available data remain too limited to distinguish whether these reductions reflect adaptive social strategies or developmental constraints.

Keywords: Sexual dimorphism; Homo floresiensis; Homo naledi; hominin; insular evolution

INTRODUCTION

H. floresiensis is a small-bodied hominin with a striking morphology (1). The cranial and postcranial remains exhibited a unique combination of primitive traits, such as a low cranial vault and short stature, and derived traits, including bipedal locomotion, suggesting a distinct evolutionary path (2). Subsequent findings supported the interpretation of *H. floresiensis* as a valid species rather than a pathologically modern human. Analyses of wrist bones, for instance, have revealed similarities to australopiths rather than *Homo sapiens (H. sapiens)*, thereby undermining hypotheses that attribute the morphology to disorders such as microcephaly (3). The shoulder and upper limb morphology also resembled that of earlier hominins, indicating a mosaic anatomy that defied simple classification within established hominin lineages (2, 4). Some scholars argue for descent from an early *Homo erectus* population that underwent extreme insular dwarfism (5), while others propose an earlier dispersal of a more primitive hominin. The skeletal evidence, particularly from cranial and lower limb morphology, suggests a complex evolutionary history characterized by isolation and adaptation to local environments (6).

Flores Island's isolation likely subjected its fauna, including *H. floresiensis*, to the "island rule"—a pattern

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of dwarfism in large mammals and gigantism in small ones (7). The island's community, including dwarf elephants (*Stegodon*) and giant rats, conforms to this biogeographic trend (7, 8). The lack of large predators and limited resources likely exerted strong selective pressure favoring small body size and efficient energy use among resident hominins (9). The phenomenon of insular dwarfism, well-documented in vertebrate populations, has been proposed as the driving mechanism behind the reduced stature and brain size of *H. floresiensis* (10). According to this model, reduced caloric availability and ecological simplicity favored the evolution of a smaller-bodied hominin adapted to constrained energy budgets. Morphological changes in limb proportions and brain scaling are consistent with patterns seen in other dwarf mammals (10). The absence of advanced tool technology and relatively simple lithic artifacts, in comparison to other *Homo erectus,* further supports the idea of cultural stasis, potentially linked to reduced cognitive capacity or limited social complexity (5, 11, 12).

As outlined beforehand, the island rule provides a compelling explanation for the overall smaller body plan of *H. floresiensis* (13, 14). The developmental biology of small-bodied hominins also informs hypotheses about dwarfism. Studies indicate that energy constraints during growth can result in truncated development and a reemergence of ancestral traits, a phenomenon known as heterochrony (14). In *H. floresiensis*, this could explain the combination of modern postcranial traits with primitive cranial morphology. The patterns observed in the wrist and shoulder bones further suggest a developmental regression to earlier morphotypes (2, 3).

The absence of definitive transitional fossils limits evolutionary resolution; however, the dwarfism hypothesis remains one of the most plausible explanations, grounded in comparative anatomy and ecological theory (8). *H. floresiensis* is represented by fewer than a dozen individuals, limiting statistical power for traditional sex estimation. Metric variability in cranial and limb elements falls within a narrow range relative to body size, suggesting intrinsically low sexual dimorphism; however, this finding should be viewed with skepticism due to the small sample size currently available (15, 16). When contrasted with similarly small-bodied primates, the Flores sample clusters tightly, reinforcing the inference that size differences between males and females were minimal, perhaps an energy-saving adaptation to Flores' resource-poor setting (8). Attempts to assign sex using pelvic fragments or overall robusticity have produced equivocal results. Tooth-enamel peptide analysis, a method increasingly used in Pleistocene *Homo*, has not yet yielded definitive chromosomal sex markers for the Flores specimens, leaving morphological criteria as the sole line of evidence (3, 17). Yet those criteria are confounded by dwarfism, which compresses sexual size dimorphism and alters growth trajectories in ways that mimic juvenile or female traits in modern humans (14). Consequently, most authors treat *H. floresiensis* as exhibiting "ambiguous" or "reduced" dimorphism rather than attempting binary sex allocations (6). This ambiguity may not be a methodological failure, but rather a signal of evolutionary novelty: insular dwarfism alters the developmental schedule, blurring ancestral patterns of male–female differentiation; however, more specimens would be needed to confirm this conclusion (18).

Building on this, the present review examines how processes such as insular dwarfism, developmental plasticity, and population history might have contributed to the reduced or ambiguous sexual dimorphism observed in *H. floresiensis* and *H. naledi*, to clarify the evolutionary mechanisms behind these patterns (14, 19). Overall, the interplay between ecological limitation and developmental plasticity provides a plausible framework for the reduced sexual dimorphism observed in *H. floresiensis;* however, the limited sample size makes it challenging to determine whether these patterns represent adaptive convergence or a demographic artifact (8, 16).

HOMO NALEDI: DISCOVERY, ANATOMY AND ECOLOGICAL SETTING

Discovery and defining mosaic features

H. naledi samples were excavated in the Dinaledi Chamber of South Africa's Rising Star cave (4, 17). The cranial vault is small, with a mean volume of around 560cc, similar for both sexes. However, the frontal and parietal bones of the brain exhibit more modern morphology, such as an expanded frontal lobe and well-developed parasagittal eminences, typically found in larger-brained hominins, including *Homo neanderthalensis* (18, 19).

Detailed analyses of the hand reveal a human-like carpal complex that facilitates precision grips, contrasting with ape-like finger curvature suited for arboreal behavior (20, 21). Similarly, the foot combines an arched mid-foot and adducted hallux with a robust calcaneus, supporting efficient bipedalism despite the small stature (22). These mosaics complicate phylogenetic placement: *H. naledi* branches deep within

Homo yet retains primitive traits potentially linked to niche specializations such as climbing or subterranean habitation (17).

Given these complexities, this review also considers how such mosaic features, along with demographic and ecological pressures, may have contributed to the reduced or ambiguous sexual dimorphism in *H. naledi*, paralleling questions raised for *H. floresiensis* (14, 24).

Environmental context and potential adaptive pressures

Geological evidence situates the Dinaledi Chamber assemblage between 236 ka and 335 ka, a period of climatic fluctuation in southern Africa (23). Stable-isotope studies of surrounding sediments indicate a patchwork landscape of woodlands and grasslands, providing both arboreal and terrestrial foraging zones (23).

The physical barrier of narrow cave passages implies that bodies were deposited deliberately, suggesting cultural behavior that could buffer environmental stressors by fostering group cohesion (17). Social buffering, in turn, may select against pronounced sexual dimorphism if cooperative breeding and shared provisioning dilute male–male competition (14, 24).

Energetically, the combination of a small brain and human-like limb proportions may represent an optimized compromise, where reduced metabolic cost of neural tissue is balanced against locomotor efficiency in a heterogeneous habitat (19). Such trade-offs could parallel insular dwarfism, albeit driven by niche complexity rather than island isolation.

Hypotheses of reduced dimorphism

Metric analyses show a limited size spread in the Dinaledi sample; femoral head diameters vary by <10%, narrower than those in most extant hominoids (19). This homogeneity suggests either a small breeding population or selection for size convergence, both of which attenuate sex-linked variance (21).

Developmental plasticity offers another explanation: growth trajectories in energetically constrained settings favor postponed sexual maturation and smaller adult stature across sexes (14). Such heterochronic shifts dampen dimorphism and generate mosaic traits as modular regions of the skeleton respond differently to growth suppression.

Comparative work further indicates that pelvic dimorphism scaled down more steeply than cranial dimorphism, paralleling modern human high-latitude populations where obstetric demands are met via shape rather than size (18). In *H. naledi*, a similar decoupling could accommodate childbirth despite the overall small body size.

Limitations of current fossil evidence

Although *H. naledi* is known from hundreds of elements, key sexual markers, specially complete pelvises, remain fragmentary, impeding definitive sex allocation (23). Moreover, the assemblage may represent a time-averaged burial horizon, conflating individuals from different generations and obscuring ontogenetic signals (17).

Post-depositional processes such as water flow and sediment compaction distort fragile features like pubic bones, leading to under-representation of diagnostically sexual regions (23). Without a balanced sample of mature pelves and crania, quantitative dimorphism indices risk being biased downward.

Finally, the absence of DNA or peptide-based sexing prevents cross-validation against morphological inference. Until biomolecular methods succeed—or new, better-preserved specimens emerge—interpretations of dimorphism in *H. naledi* will remain provisional (3).

COMPARATIVE MORPHOLOGICAL ANALYSIS

Morphological Comparison

The hands of *H. naledi* are quite interesting. The hand morphology is characterized by robust metacarpals and strongly curved proximal phalanges, anatomical traits commonly associated with forceful grasping and possibly arboreal locomotion (9). While this suggests arborality, it may also lend credibility to the theory of rock climbing while retaining bipedality (21). In contrast, *H. floresiensis* has more gracile hands, combined with a more human-like carpal configuration, which supports fine motor precision and dexterity, consistent with advanced tool-related behaviors (2).

Brain size differentials, although small in absolute terms, illuminate developmental trajectories (Figure 1). *H. floresiensis* has a brain size of 417–450cc, corresponding to its dwarfed body size, whereas *H. naledi* has brain sizes ranging from 465 to 615cc, again corresponding with a more robust body and following the usual trajectory of hominid brain case evolution (17, 25). Pelvic fragments tell a complementary story: *H. floresiensis* pelves scale predictably with overall dwarfism, whereas preserved *H. naledi* ilia are mediolaterally broad, hinting at obstetric adaptations uncoupled from stature (Figure 1) (18).

Mechanisms Shaping Dimorphism

Environmental constraints provide the first explanation. On Flores, limited calories and the absence of major predators favored selection for universally smaller bodies, thus reducing the need for large body size as it pertains to male competition and relaxing sexual selection (7). By contrast, the closed-habitat niche of *H. naledi* may have prioritized cooperative foraging and social cohesion, both of which are known to diminish dimorphism in extant primates (14).

Developmental plasticity constitutes a second explanation. Experimental work in nutritional ecology reveals that energy scarcity during growth delays puberty and reduces adult size differences (25). Such heterochrony can be adaptive, permitting survival under constraints, or merely a developmental by-product. In both fossil species, skeletal evidence of slowed growth plates supports life-history shifts toward delayed maturity (19).

A third explanation concerns the evolutionary process. Insular dwarfism blurs the line between sexual dimorphism and species-wide size reduction, whereas in small, isolated populations, genetic drift can fix alleles that tend to reduce dimorphism (10,26). For *H. naledi*, drift in a founding population, reinforced by cultural buffering, may have converged on a low-dimorphism phenotype; for *H. floresiensis*, selection for reduced body size overwhelmed any sexually selected size divergence (6).

EVOLUTIONARY MECHANISMS UNDERLYING REDUCED SEXUAL DIMORPHISM

Dwarfism vs. sexual dimorphism: where lines blur

Insular dwarfism results in a species-wide reduction in body size, which can obscure sexual dimorphism patterns observed in larger populations (10, 7). Systematic downsizing complicates the identification of sex based solely on size, as traits traditionally used to distinguish males from females become less pronounced (6, 27). Moreover, developmental plasticity associated with dwarfism may affect growth rates and timing, further masking dimorphic signals by altering adult morphology in ways that do not neatly map onto

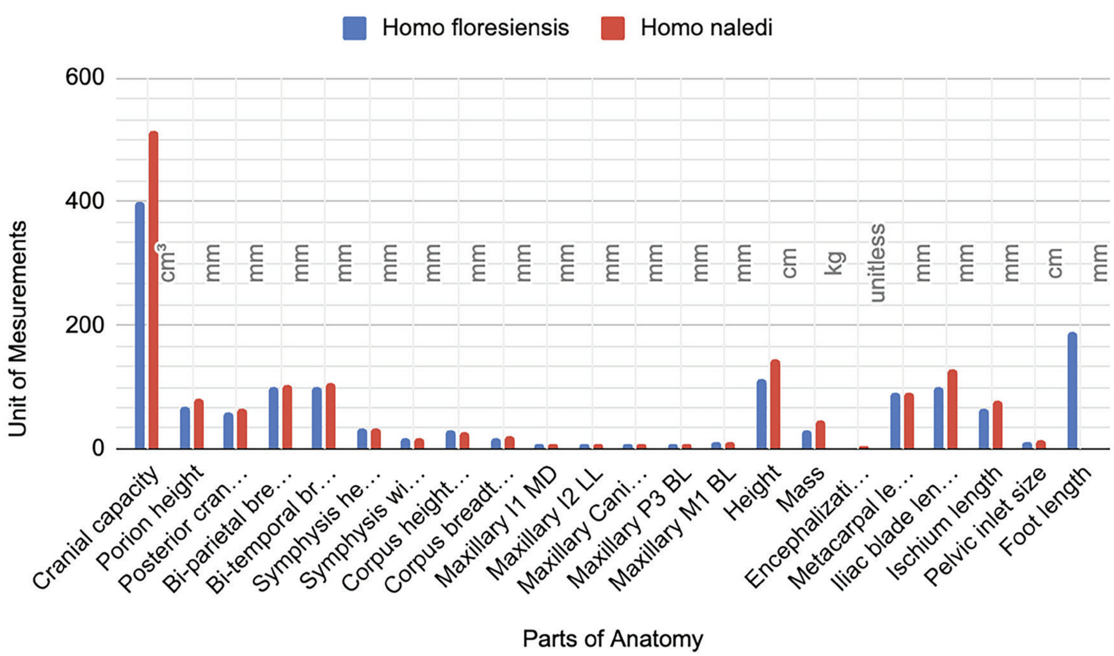

Figure 1. The graph illustrates the morphological measurements of *H. naledi* (red) and *H. floresiensis* (blue). Most notable differences between the two species are found in height, cranial capacity, iliac blade length, and foot length, with *H. naledi* being larger in all cases, as expected. Data taken from publicly available papers (1, 15,28, 33-42).

sex differences (18). As a result, dwarfism and sexual dimorphism may overlap or blur, making it challenging for paleoanthropologists to disentangle these processes when interpreting fossil variation (14).

Role of Natural Selection vs. Genetic Drift on Isolated Populations

In isolated or small populations, such as those hypothesized for *H. floresiensis* and *H. naledi*, natural selection and genetic drift both influence morphological traits, but they operate through distinct mechanisms (7, 14). Natural selection acts on traits that improve survival or reproductive success in specific environmental contexts, such as reduced body size in resource-limited island habitats, which enhances energy efficiency (14). Genetic drift, however, is a stochastic process that can randomly fix or eliminate alleles, particularly in small populations with limited gene flow, leading to changes in traits that are independent of their adaptive value (6). For *H. naledi*, genetic drift may have randomly altered allele frequencies, affecting size variance between sexes and potentially amplifying or reducing dimorphism, independent of selection pressures, especially given the evidence for a small, adequate population size (14). This randomness means drift does not inherently reduce or increase dimorphism but can influence its expression in small, isolated populations. Furthermore, these evolutionary forces may act in concert or opposition, with drift sometimes overriding weak selective pressures in small populations, resulting in unique morphological outcomes that complicate evolutionary interpretations (28).

COMPARATIVE DISCUSSION OF DIMORPHISM AMBIGUITY

A direct comparison highlights the parallel ambiguity arising from distinct evolutionary pathways. *H. floresiensis* displays extreme ambiguity rooted in systemic dwarfism, whereas *H. naledi* shows high ambiguity linked to mosaic adaptation and population history (16, 19). Both cases deviate substantially from modern human patterns, demonstrating that sexual dimorphism is neither uniform nor linear within *Homo* (18). Synthesizing multiple skeletal indices reveals a hierarchy of ambiguity, with pelvic metrics being the most equivocal in *H. floresiensis*. At the same time, cranial traits are most ambiguous in *H. naledi*, reflecting differing developmental constraints (Figure 1) (14). This contrast highlights the need for trait-specific, species-specific models of dimorphism, rather than blanket assumptions derived from *Homo sapiens*.

H. floresiensis presents extreme ambiguity due to insular dwarfism, which significantly disrupts expected hominin body scaling and challenges phylogenetic placement (10, 15). Its unusually small brain and body size raise debates about whether these traits reflect a distinct lineage or the result of evolutionary pressures such as island isolation and resource scarcity (Figure 1) (7, 28). These morphological anomalies complicate interpretations of tool use, cognitive ability, and developmental pathways in early *Homo* (12, 16).

H. naledi displays high ambiguity due to its low degree of sexual dimorphism, which contrasts with the pronounced differences seen in many other hominin species (18,29). The species exhibits a unique mosaic of primitive and derived features—such as australopith-like shoulders with modern foot structure—making its evolutionary timeline difficult to define (9, 17). This anatomical patchwork blurs traditional taxonomic lines, forcing a reconsideration of behavioral and cognitive expectations based on morphology (19, 30).

Interpretive challenges remain formidable. Small sample sizes can inflate confidence intervals, and fragmentary preservation can bias the representation of traits (24). Nonetheless, convergence on low dimorphism across two ecologically distinct species strengthens the inference that hominin sexual dimorphism was more labile than often assumed (10). Recognizing ambiguity as an evolutionary signal, rather than an analytical flaw, fosters a more nuanced and pluralistic view of hominin diversity (14). Recognizing these patterns as evolutionary signals reframes morphological ambiguity as evidence of adaptive flexibility within *Homo*.

Challenges and Limits of Interpretation

Fragmentary fossils, taphonomic distortion, and excavation bias impede robust statistical assessment. In both sites, weight-bearing bones are over-represented, whereas delicate pelvic and cranial features crucial for sexing are rarer (11, 24, 30). Such sampling asymmetry limits multivariate analyses that assume random preservation.

Distinguishing ontogeny, pathology, and sexual traits further complicates matters. Growth disruption from nutritional stress can mimic sex-linked gracility, and localized pathology can exaggerate robusticity (3, 31). Without histological or molecular corroboration, attribution of variation to sex remains tentative (18).

Projecting modern sexual dimorphism templates onto early hominins risks circular reasoning. Human pelvic sexual dimorphism evolved under obstetric, climatic, and cultural pressures absent or altered in earlier taxa (6). These interpretive limitations underscore the need to develop more refined methods, rather than treating fossil ambiguity as mere analytical noise. (14).

CONCLUSION

H. floresiensis and *H. naledi* both manifest pronounced ambiguity in sexually dimorphic traits, but for different ecological and developmental reasons: extreme insular dwarfism versus mosaic adaptation and demographic constraints (10, 17). These cases underscore the evolutionary plasticity of dimorphism within the genus *Homo*. Three primary frameworks emerge from the comparative data: insular dwarfism, developmental plasticity, and reduced male competition.

Insular Dwarfism

Insular dwarfism is one of the strongest explanations for sexual dimorphism and overall ambiguity found in *H. floresiensis.* As previously stated, the island rule means larger-bodied species tend towards smaller body plans due to a lack of predators and limited resources (7, 10, 14). The small brain and body size of *H. floresiensis,* coupled with other evidence of endemic fauna on the island of Flores, suggests environmental pressures that produced smaller body sizes in typically larger-bodied species. (8, 28). However, because insular dwarfism is thought to reduce allometric variation across traits, this process obscures distinctions between male and female morphologies, leading to the appearance of low dimorphism (14). The evidence presented here is substantial and consistent across independent studies; however, it is limited by the small number of specimens available, which constrains statistical validation (16, 18). Additionally, this explanation does not apply to *H.naledi* as the environment near the Dinaledi caves was more spatially constrained rather than subject to the forces of the island rule. (7, 22, 23)

Developmental Plasticity

Developmental plasticity provides a broader explanation applicable to both species. In energetically constrained environments, such as near the Dinaledi caves and the Island of Flores, growth trajectories often shift toward delayed maturity and smaller adult size across both sexes (14, 25). These heterochronic changes can dampen sexual dimorphism by affecting separate bones, such as phalanges, skull shape, or the pelvic inlet, thereby producing mosaic morphologies that are independent of one another. For *H. floresiensis*, this mechanism complements the insular model, as nutritional and ecological pressures on growth may have reinforced dwarfism and further minimized sexual divergence (14, 15). For *H. naledi*, plasticity likely played a central role in its evolution. Morphological evidence of small body size combined with modern limb proportions suggests life-history shifts driven by energy efficiency rather than ecological isolation (19,24). Although direct developmental evidence (e.g., histological or ontogenetic markers) is lacking, plasticity remains a plausible integrative framework uniting both taxa.

Reduced Male Competition and Pair Bonding

Reduced sexual dimorphism is often linked to social structures characterized by low inter-male competition and greater cooperation. The hypothesis that pair bonding and shared provisioning reduce selective pressure for large male size and weaponry, as such traits are unneeded in Pair-bonded groups that would otherwise require significant energy investment, is well supported in primate comparative data (14). For *H. naledi*, the combination of a small yet adequate population size, possible cooperative burial behavior (although still debated), and evidence of social cohesion supports the idea that social buffering mechanisms may have reduced sexual competition (17, 23, 32). This interpretation aligns with the observed convergence in body size and the reduced variance in femoral and cranial dimensions (19, 21).

For *H. floresiensis*, the evidence for pair bonding or cooperative behavior is weaker. Archaeological data suggest simple tool use and limited cultural complexity (5, 12), providing little basis for inferring sustained social monogamy or male provisioning. While reduced dimorphism may superficially appear consistent with this model, the evidence is more parsimoniously explained by ecological constraints rather than social restructuring.

These hypotheses are not mutually exclusive and can operate with each other. Not all proposed hypotheses apply to each species. As previously stated, the hypotheses of insular evolution and developmental plasticity jointly provide the most consistent explanation for the observed dimorphism, with little support for behavioral hypotheses. In contrast, *H. naledi* has developmental and social explanations, while ecological isolation plays a minimal role. Across both taxa, the convergence toward low dimorphism underscores the flexibility of sexual differentiation in hominin species, indicating that the reduction of dimorphism can arise through multiple evolutionary pathways, contingent upon environmental and demographic contexts.

Further research should integrate morphometric, developmental, and social-behavioral data rather than treating dimorphism as a single-variable trait. Expanding peptide- and DNA-based sexing methods and applying quantitative models of growth and energy use may clarify whether these reductions reflect adaptive strategies or stochastic demographic effects, or whether the current theories are due to the fragmentary nature of current data. Future analyses should explicitly test these frameworks by integrating morphometric, developmental, and behavioral indicators rather than treating dimorphism as a singular metric.

Limitations

Due to the understudied nature of this field, a wealth of different perspectives is not currently available. Many of the fossils found, even if they are diagnostic, are warped or crushed by the taphonomic process of burial. Even subtle warping may artificially inflate or reduce apparent differences between individuals. Sample sizes, especially for *H. floresiensis*, are extremely small, with fewer than fifteen specimens, making it impossible to establish population-level patterns of sexual dimorphism with confidence. The small sample size can also exaggerate or underestimate the degree of sexual dimorphism, primarily when relying on small fragments.

Furthermore, while current biomolecular sexing methods have advanced, they operate on the assumption that males of the species are larger than females. Although this is usually the case, such a presumption can lead to biases in the work, as not all species exhibit male-favored dimorphism. Drawing from extant primates for these comparative models, though it allows us to make hypothesis, relies on the assumption that the social and environmental pressure for these ancient hominins were the same as for us, imposing what is a hard to prove external factor, that may not be true causing the research to miss nuances that may have produced different patterns in the species sexual dimorphism. Together, these limitations suggest that estimates of sexual dimorphism in fossil hominins, especially *H. naledi* and *H. floresiensis*, should be treated with caution, as they may reflect methodological shortcomings rather than biological reality.

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CONFLICT OF INTERESTS

The author declares that there are no conflicts of interest regarding the publication of this paper.

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