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Decagonal and Quasi-Crystalline Tilings in Medieval Islamic Architecture

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Decagonal and Quasi-Crystalline Tilings in Medieval Islamic Architecture

Peter J. Lu[1]* and Paul J. Steinhardt[2]

The conventional view holds that girih (geometric star-and-polygon, or strapwork) patterns in medieval Islamic architecture were conceived by their designers as a network of zigzagging lines, where the lines were drafted directly with a straightedge and a compass. We show that by 1200 C.E. a conceptual breakthrough occurred in which girih patterns were reconceived as tessellations of a special set of equilateral polygons ("girih tiles") decorated with lines. These tiles enabled the creation of increasingly complex periodic girih patterns, and by the 15th century, the tessellation approach was combined with self-similar transformations to construct nearly perfect quasi-crystalline Penrose patterns, five centuries before their discovery in the West.

Girih patterns constitute a wide-ranging decorative idiom throughout Islamic art and architecture (*1*–*6*). Previous studies of medieval Islamic documents describing applications of mathematics in architecture suggest that these girih patterns were constructed by drafting directly a network of zigzagging lines (sometimes called strapwork) with the use of a compass and straightedge (*3*, *7*). The visual impact of these girih patterns is typically enhanced by rotational symmetry. However, periodic patterns created by the repetition of a single "unit cell" motif can have only a limited set of rotational symmetries, which western mathematicians first proved rigorously in the 19th century C.E.: Only two-fold, three-fold, four-fold, and six-fold rotational symmetries are allowed. In particular, five-fold and 10-fold symmetries are expressly forbidden (*8*). Thus, although pentagonal and decagonal motifs appear frequently in Islamic architectural tilings, they typically adorn a unit cell repeated in a pattern with crystallographically allowed symmetry (*3*–*6*).

Although simple periodic girih patterns incorporating decagonal motifs can be constructed using a "direct strapwork method" with a straightedge and a compass (as illustrated in Fig. 1, A to D), far more complex decagonal patterns also occur in medieval Islamic architecture. These complex patterns can have unit cells containing hundreds of decagons and may repeat the same decagonal motifs on several length scales. Individually placing and drafting hundreds of such decagons with straightedge and compass would have been both exceedingly cumbersome and likely to accumulate geometric distortions, which are not observed.

On the basis of our examination of a large number of girih patterns decorating medieval Islamic buildings, architectural scrolls, and other forms of medieval Islamic art, we suggest that by 1200 C.E. there was an important breakthrough in Islamic mathematics and design: the discovery of an entirely new way to conceptualize and construct girih line patterns as decorated tessellations using a set of five tile types, which we call "girih tiles." Each girih tile is decorated with lines and is sufficiently simple to be drawn using only mathematical tools documented in medieval Islamic sources. By laying the tiles edge-to-edge, the decorating lines connect to form a continuous network across the entire tiling. We further show how the girih-tile approach opened the path to creating new types of extraordinarily complex patterns, including a nearly perfect quasi-crystalline Penrose pattern on the Darb-i Imam shrine (Isfahan, Iran, 1453 C.E.), whose underlying mathematics were not understood for another five centuries in the West.

As an illustration of the two approaches, consider the pattern in Fig. 1E from the shrine of Khwaja Abdullah Ansari at Gazargah in Herat, Afghanistan (1425 to 1429 C.E.) (*3*, *9*), based on a periodic array of unit cells containing a common decagonal motif in medieval Islamic architecture, the 10/3 star shown in Fig. 1A (see fig. S1 for additional examples) (*1*, *3*–*5*, *10*). Using techniques documented by medieval Islamic mathematicians (*3*, *7*), each motif can be drawn using the direct strapwork method (Fig. 1, A to D). However, an alternative geometric construction can generate the same pattern (Fig. 1E, right). At the intersections between all pairs of line segments not within a 10/3 star, bisecting the larger 108° angle yields line segments (dotted red in the figure) that, when extended until they intersect, form three distinct polygons: the decagon decorated with a 10/3 star line pattern, an elongated hexagon decorated with a bat-shaped line pattern, and a bowtie decorated by two opposite-facing quadrilaterals. Applying the same procedure to a ~15th-century pattern from the Great Mosque of Nayriz, Iran (fig. S2) (*11*) yields two additional polygons, a pentagon with a pentagonal star pattern, and a rhombus with a bowtie line pattern. These five polygons (Fig. 1F), which we term "girih tiles," were used to construct a wide range of patterns with decagonal motifs (fig. S3) (*12*). The outlines of the five girih tiles were also drawn in ink by medieval Islamic architects in scrolls drafted to transmit architectural practices, such as a 15th-century Timurid-Turkmen scroll now held by the Topkapi Palace Museum in Istanbul (Fig. 1G and fig. S4) (*2*, *13*), providing direct historical documentation of their use.

The five girih tiles in Fig. 1F share several geometric features. Every edge of each polygon has the same length, and two decorating lines intersect the midpoint of every edge at 72° and 108° angles. This ensures that when the edges of two tiles are aligned in a tessellation, decorating lines will continue across the common boundary without changing direction (*14*). Because both line intersections and tiles only contain angles that are multiples of 36°, all line segments in the final girih strapwork pattern formed by girih-tile decorating lines will be parallel to the sides of the regular pentagon; decagonal geometry is thus enforced in a girih pattern formed by the tessellation of any combination of girih tiles. The tile decorations have different internal rotational symmetries: the decagon, 10-fold symmetry; the pentagon, five-fold; and the hexagon, bowtie, and rhombus, two-fold.

Tessellating these girih tiles provides several practical advantages over the direct strapwork method, allowing simpler, faster, and more accurate execution by artisans unfamiliar with their mathematical properties. A few full-size girih tiles could serve as templates to help position decorating lines on a building surface, allowing rapid, exact pattern generation. More-

[1]Department of Physics, Harvard University, Cambridge, MA 02138, USA. [2]Department of Physics and Princeton Center for Theoretical Physics, Princeton University, Princeton, NJ 08544, USA.

*To whom correspondence should be addressed. E-mail: plu@fas.harvard.edu

over, girih tiles minimize the accumulation of angular distortions expected in the manual drafting of individual 10/3 stars, with concomitant errors in sizing, position, and orientation.

Girih tiles further enable the construction of periodic decagonal-motif patterns that do not arise naturally from the direct strapwork method. One class of such patterns repeats pentagonal motifs but entirely lacks the 10/3 stars that establish the initial decagonal angles needed for direct drafting with straightedge and compass. Patterns of this type appear around 1200 C.E. on Seljuk buildings, such as the Mama Hatun Mausoleum in Tercan, Turkey (1200 C.E.; Fig. 2A) (*5*, *15*, *16*), and can be created easily by tessellating bowtie and hexagon girih tiles to create perfect pentagonal motifs, even in the absence of a decagon star (i.e., lacking decagon girih tiles; see fig. S5). Even more compelling evidence for the use of girih tiles occurs on the walls of the Gunbad-i Kabud in Maragha, Iran (1197 C.E.) (*11*, *17*, *18*), where seven of eight exterior wall panels on the octagonal tomb tower are filled with a tiling of decagons, hexagons, bowties, and rhombuses (Fig. 2, B and C). Within each wall panel, the decagonal pattern does not repeat; rather, the unit cell of this periodic tiling spans the length of two complete panels (fig. S6). The main decorative raised brick pattern follows the girih-tile decorating lines of Fig. 1F. However, a second set of smaller decorative lines conforms to the internal rotational symmetry of each individual girih tile without adhering to pentagonal angles (Fig. 2, C and D): Within each region occupied by a hexagon, bowtie, or rhombus, the smaller line decoration has a two-fold, not five-fold, rotational symmetry, and therefore could not have been generated using the direct strapwork method. By contrast, constructing both patterns is straightforward with girih tiles. Two sets of line decoration were applied to each girih tile: the standard line decoration of Fig. 1F, and a second, nonpentagonal set of motifs with an overall two-fold symmetry (Fig. 2, C and D). The girih tiles were then tessellated, with the regular line pattern expressed in large raised brick on the tower and the second set of lines expressed in smaller bricks. The dual-layer nature of line patterns on the Maragha tower thus adds strong evidence that the pattern was generated by tessellating with the girih tiles in Fig. 1F.

Perhaps the most striking innovation arising from the application of girih tiles was the use of self-similarity transformation (the subdivision of large girih tiles into smaller ones) to create overlapping patterns at two different length scales, in which each pattern is generated by the same girih tile shapes. Examples of subdivision can be found in the Topkapi scroll (e.g., Fig. 1G; see also fig. S4A) and on the Friday Mosque (*17*) and Darb-i Imam shrine (1453 C.E.) (*2*, *9*, *19*) in Isfahan, Iran. A spandrel from the Darb-i Imam shrine is shown in Fig. 3A. The large, thick, black line pattern consisting of a handful of decagons and bowties (Fig. 3C) is subdivided into the smaller pattern, which can also be perfectly generated by a tessellation of 231 girih tiles (Fig. 3B; line decoration of Fig. 1F filled in with solid color here). We have identified the subdivision rule used to generate the Darb-i Imam spandrel pattern (Fig. 3, D and E), which was also used on other patterns on the Darb-i Imam shrine and Isfahan Friday Mosque (fig. S7).

A subdivision rule, combined with decagonal symmetry, is sufficient to construct perfect quasi-crystalline tilings—patterns with infinite perfect quasi-periodic translational order and crystallographically forbidden rotational symmetries, such as pentagonal or decagonal—which mathematicians and physicists have come to understand only in the past 30 years (*20*, *21*). Quasi-periodic order means that distinct tile shapes repeat with frequencies that are incommensurate; that is, the ratio of the frequencies cannot be expressed as a ratio of integers. By having quasi-periodicity rather than periodicity, the symmetry constraints of conventional crystallography can be violated, and it is possible to have pentagonal motifs that join together in a pattern with overall pentagonal and decagonal symmetry (*21*).

The most famous example of a quasi-crystalline tiling is the Penrose tiling (*20*, *22*), a two-tile tessellation with long-range quasi-periodic translational order and five-fold symmetry. The Penrose tiles can have various shapes. A convenient choice for comparison with medieval Islamic architectural decoration is the kite and dart shown on the left side of Fig. 4, A and B. As originally conceived by Penrose in the 1970s, the tilings can be constructed either by "matching rules" or by self-similar subdivisions. For the matching rules, the kite and dart can each be decorated with red and blue stripes (Fig. 4, A and B); when tiles are placed so that

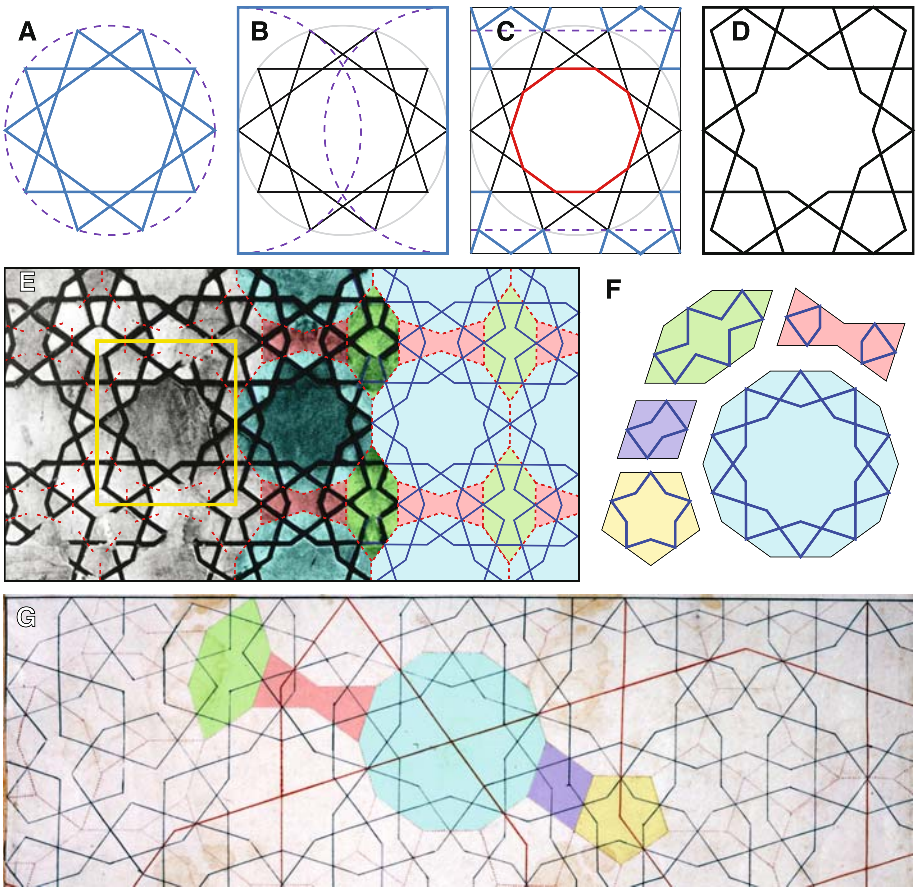

Fig. 1. Direct strapwork and girih-tile construction of 10/3 decagonal patterns. (**A** to **D**) Generation of a common 10/3 star pattern by the direct strapwork method. (A) A circle is divided equally into 10, and every third vertex is connected by a straight line to create the 10/3 star that (B) is centered in a rectangle whose width is the circle's diameter. In each step, new lines drafted are indicated in blue, lines to be deleted are in red, and purple construction lines not in the final pattern are in dashed purple. (**E**) Periodic pattern at the Timurid shrine of Khwaja Abdullah Ansari at Gazargah in Herat, Afghanistan (1425 to 1429 C.E.), where the unit cell pattern (D) is indicated by the yellow rectangle. The same pattern can be obtained by tessellating girih tiles (overlaid at right). (**F**) The complete set of girih tiles: decagon, pentagon, hexagon, bowtie, and rhombus. (**G**) Ink outlines for these five girih tiles appear in panel 28 of the Topkapi scroll, where we have colored one of each girih tile according to the color scheme in (F).

the stripes continue uninterrupted, the only possible close-packed arrangement is a five-fold symmetric quasi-crystalline pattern in which the kites and darts repeat with frequencies whose ratio is irrational, namely, the golden ratio $\tau \equiv (1 + \sqrt{5})/2 \approx 1.618$. We see no evidence that Islamic designers used the matching-rule approach. The second approach is to repeatedly subdivide kites and darts into smaller kites and darts, according to the rules shown in Fig. 4, A and B. This self-similar subdivision of large tiles into small tiles can be expressed in terms of a transformation matrix whose eigenvalues are irrational, a signature of quasi-periodicity; the eigenvalues represent the ratio of tile frequencies in the limit of an infinite tiling (*23*).

Our analysis indicates that Islamic designers had all the conceptual elements necessary to produce quasi-crystalline girih patterns using the self-similar transformation method: girih tiles, decagonal symmetry, and subdivision. The pattern on the Darb-i Imam shrine is a remarkable example of how these principles were applied. Using the self-similar subdivision of large girih tiles into small ones shown in Fig. 3, D and E, an arbitrarily large Darb-i Imam pattern can be constructed. The asymptotic ratio of hexagons to bowties approaches the golden ratio τ (the same ratio as kites to darts in a Penrose tiling), an irrational ratio that shows explicitly that the pattern is quasi-periodic.

Moreover, the Darb-i Imam tile pattern can be mapped directly into Penrose tiles following the prescription for the hexagon, bowtie (*22*), and decagon given in Fig. 4, C to E. Using these substitutions, both the large (Fig. 3C) and small (Fig. 3B) girih-tile patterns on the Darb-i Imam can be mapped completely into Penrose tiles (fig. S8). Note that the mapping shown in Fig. 4, C to E, breaks the bilateral symmetries of the girih tiles; as a result, for an individual tile, there is a discrete number of choices for the mapping: 10 for the decagon, two each for hexagon and bowtie. Therefore, the mapping is completed by using this freedom to eliminate Penrose tile edge mismatches to the maximum degree possible. Note that, unlike previous comparisons in the literature between Islamic designs with decagonal motifs and Penrose tiles (*18*, *24*), the Darb-i Imam tessellation is not embedded in a periodic framework and can, in principle, be extended into an infinite quasi-periodic pattern.

Although the Darb-i Imam pattern illustrates that Islamic designers had all the elements needed to construct perfect quasi-crystalline patterns, we nonetheless find indications that the designers had an incomplete understanding of these elements. First, we have no evidence that they ever developed the alternative matching-rule approach. Second, there are a small number of tile mismatches, local imperfections in the Darb-i Imam tiling. These can be visualized by mapping the tiling into the Penrose tiles and identifying the mismatches. However, there are only a few of them—11 mismatches out of 3700 Penrose tiles—and every mismatch is point-like, removable with a local rearrangement of a few tiles without affecting the rest of the pattern (Fig. 4F and fig. S8). This is the kind of defect that an artisan could have made inadvertently in constructing or repairing a complex pattern. Third, the designers did not begin with a single girih tile, but rather with a small arrangement of large tiles that does not appear in the subdivided pattern. This arbitrary and unnecessary choice means that, strictly speaking, the tiling is not self-similar, although repeated application of the subdivision rule would nonetheless lead to the same irrational τ ratio of hexagons to bowties.

Our work suggests several avenues for further investigation. Although the examples we have studied thus far fall just short of being perfect quasi-crystals, there may be more interesting examples yet to be discovered, including perfectly quasi-periodic decagonal patterns. The subdivision analysis outlined above establishes a procedure for identifying quasi-periodic patterns

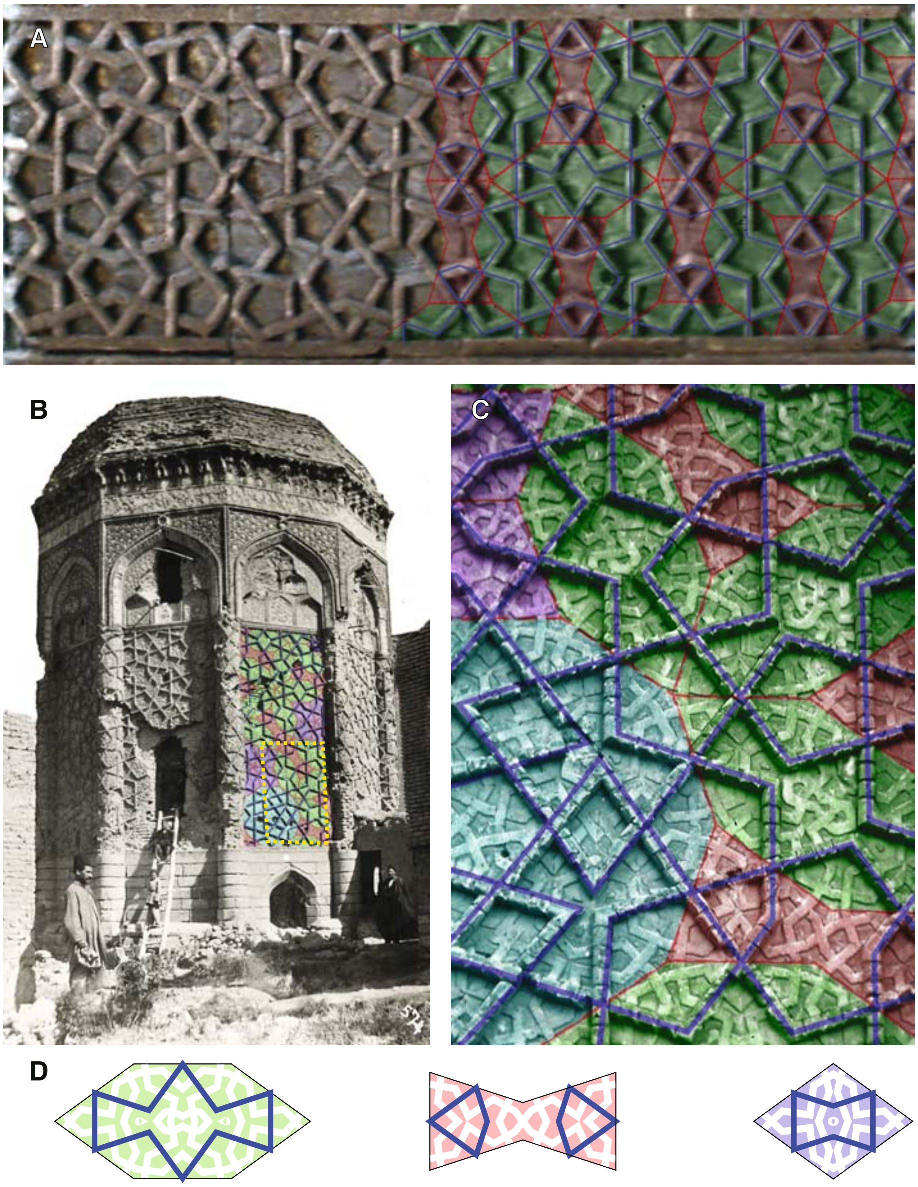

Fig. 2. (**A**) Periodic girih pattern from the Seljuk Mama Hatun Mausoleum in Tercan, Turkey (~1200 C.E.), where all lines are parallel to the sides of a regular pentagon, even though no decagon star is present; reconstruction overlaid at right with the hexagon and bowtie girih tiles of Fig. 1F. (**B**) Photograph by A. Sevruguin (~1870s) of the octagonal Gunbad-i Kabud tomb tower in Maragha, Iran (1197 C.E.), with the girih-tile reconstruction of one panel overlaid. (**C**) Close-up of the area marked by the dotted yellow rectangle in (B). (**D**) Hexagon, bowtie, and rhombus girih tiles with additional small-brick pattern reconstruction (indicated in white) that conforms not to the pentagonal geometry of the overall pattern, but to the internal two-fold rotational symmetry of the individual girih tiles.

and measuring their degree of perfection. Also, analogous girih tiles may exist for other noncrystallographic symmetries, and similar dotted tile outlines for nondecagonal patterns appear in the Topkapi scroll. Finally, although our analysis shows that complex decagonal tilings were being made by 1200 C.E., exactly when the shift from the direct strapwork to the girih-tile paradigm first occurred is an open question, as is the identity of the designers of these complex Islamic patterns, whose geometrical sophistication led the medieval world.

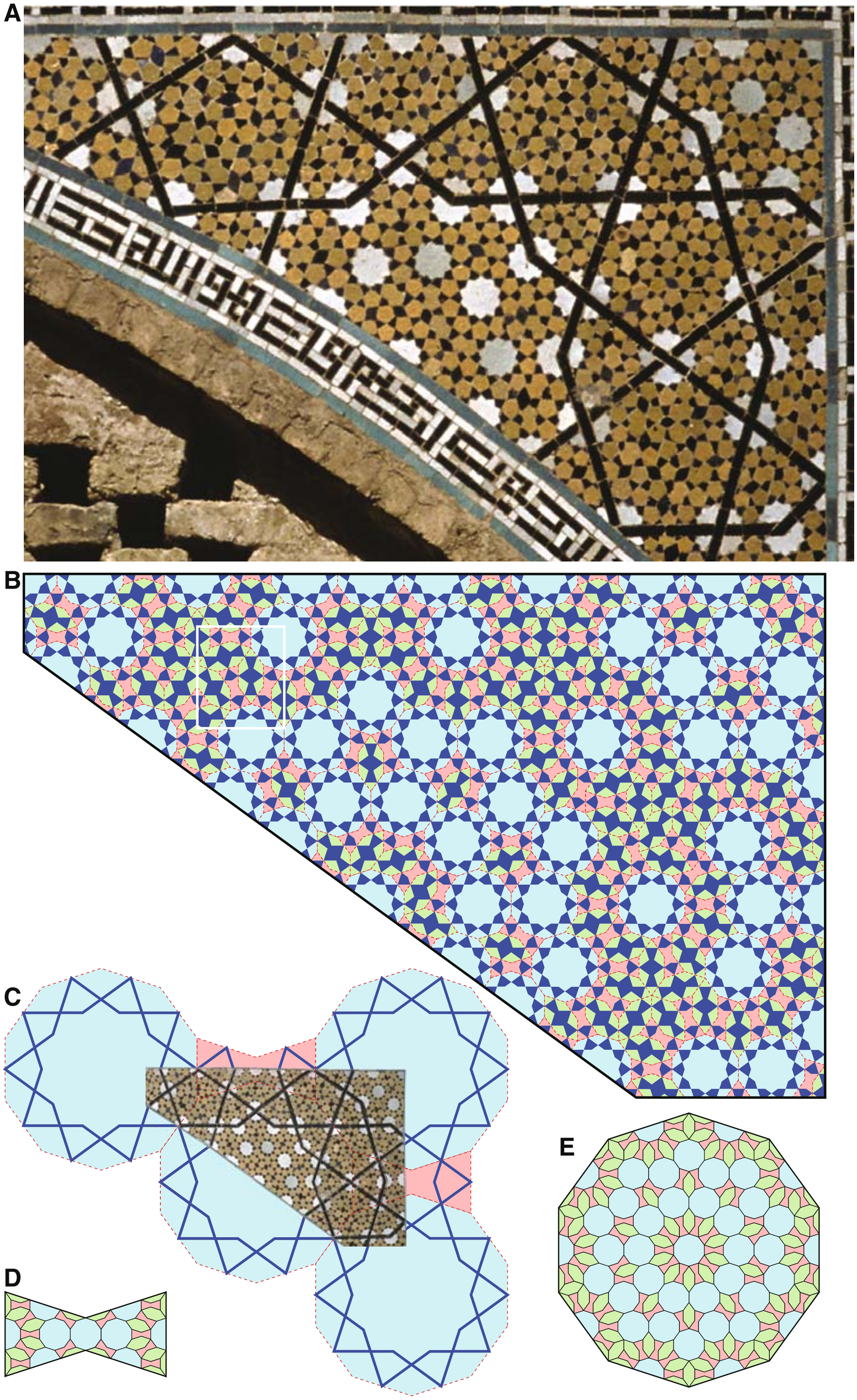

Fig. 3. Girih-tile subdivision found in the decagonal girih pattern on a spandrel from the Darb-i Imam shrine, Isfahan, Iran (1453 C.E.). (**A**) Photograph of the right half of the spandrel. (**B**) Reconstruction of the smaller-scale pattern using girih tiles where the blue-line decoration in Fig. 1F has been filled in with solid color. (**C**) Reconstruction of the larger-scale thick line pattern with larger girih tiles, overlaid on the building photograph. (**D** and **E**) Graphical depiction of the subdivision rules transforming the large bowtie (D) and decagon (E) girih-tile pattern into the small girih-tile pattern on tilings from the Darb-i Imam shrine and Friday Mosque of Isfahan.

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10. Additional examples of this particular 10/3 decagonal pattern, shown in fig. S1: the Seljuk Congregational Mosque in Ardistan, Iran (~1160 C.E.) (*16*); the Timurid Tuman Aqa Mausoleum in the Shah-i Zinda complex in Samarkand, Uzbekistan (1405 C.E.) (*9*, *16*); the Darb-i Kushk shrine in Isfahan, Iran (1496 C.E.) (*2*, *9*, *17*); and the Mughal I'timad al-Daula Mausoleum in Agra, India (~1622 C.E.) (*28*).
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12. Additional architectural examples of patterns that can be reconstructed with girih tiles, shown in fig. S3: the Abbasid Al-Mustansiriyya Madrasa in Baghdad, Iraq (1227 to 1234 C.E.) (*26*); the Ilkhanid Uljaytu Mausoleum in Sultaniya, Iran (1304 C.E.) (*17*); the Ottoman Green Mosque in Bursa, Turkey (1424 C.E.) (*27*); and the Mughal I'timad al-Daula Mausoleum in Agra, India (~1622 C.E.) (*28*). Similar patterns also appear in the Mamluk Qurans of Sandal (1306 to 1315 C.E.) and of Aydughdi ibn Abdallah al-Badri (1313 C.E.) (*29*). Note that the girih-tile paradigm can make pattern design structure more clear. For example, all of the spandrels with decagonal girih patterns we have thus far examined (including Fig. 3C and figs. S2 and S3A) follow the same prescription to place decagons: Partial decagons are centered at the four external corners and on the top edge directly above the apex of the arch.
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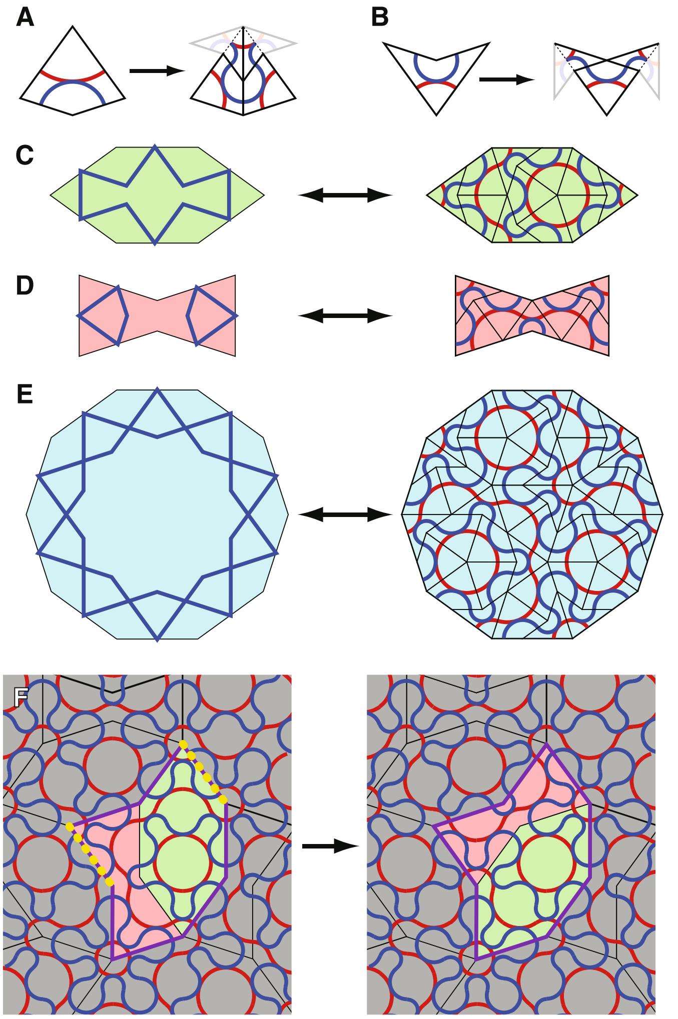

Fig. 4. (**A** and **B**) The kite (A) and dart (B) Penrose tile shapes are shown at the left of the arrows with red and blue ribbons that match continuously across the edges in a perfect Penrose tiling. Given a finite tiling fragment, each tile can be subdivided according to the "inflation rules" into smaller kites and darts (at the right of the arrows) that join together to form a perfect fragment with more tiles. (**C** to **E**) Mappings between girih tiles and Penrose tiles for elongated hexagon (C), bowtie (D), and decagon (E). (**F**) Mapping of a region of small girih tiles to Penrose tiles, corresponding to the area marked by the white rectangle in Fig. 3B, from the Darb-i Imam shrine. At the left is a region mapped to Penrose tiles following the rules in (C) to (E). The pair of colored tiles outlined in purple have a point defect (the Penrose edge mismatches are indicated with yellow dotted lines) that can be removed by flipping positions of the bowtie and hexagon, as shown on the right, yielding a perfect, defect-free Penrose tiling.

Zuzan, Iran (1219 C.E.) (*30*) (fig. S5), as well as on a carved wooden double door from a Seljuk building in Konya (~13th century C.E.), in the Museum of Islamic Art in Berlin (Inv. Nr. 1.2672).
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32. We thank G. Necipoglu and J. Spurr, without whose multifaceted assistance this paper would not have been possible. We also thank R. Holod and K. Dudley/M. Eniff for permission to reproduce their photographs in Figs. 2C and 3A, respectively; C. Tam and E. Simon-Brown for logistical assistance in Uzbekistan; S. Siavoshi and A. Tafvizi for motivating the exploration of Isfahan's sights; and S. Blair, J. Bloom, C. Eisenmann, T. Lentz, and I. Winter for manuscript comments. Photographs in Fig. 2, A and B, and in the online figures courtesy of the Fine Arts Library, Harvard College Library. Supported by C. and F. Lu and by the Aga Khan Program for Islamic Architecture at Harvard University.

Supporting Online Material
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Figs. S1 to S8

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Ex Situ NMR in Highly Homogeneous Fields: ^{1}H Spectroscopy

Juan Perlo, Federico Casanova, Bernhard Blümich*

Portable single-sided nuclear magnetic resonance (NMR) magnets used for nondestructive studies of large samples are believed to generate inherently inhomogeneous magnetic fields. We demonstrated experimentally that the field of an open magnet can be shimmed to high homogeneity in a large volume external to the sensor. This technique allowed us to measure localized high-resolution proton spectra outside a portable open magnet with a spectral resolution of 0.25 part per million. The generation of these experimental conditions also simplifies the implementation of such powerful methodologies as multidimensional NMR spectroscopy and imaging.

Single-sided nuclear magnetic resonance (NMR) sensors have been used for over two decades to characterize arbitrarily large samples (*1*). In contrast to conventional NMR apparatus, where the sample must be adapted to fit into the bore of large superconducting magnets, single-sided NMR experiments use portable open magnets placed on one side of an object to detect NMR signals ex situ. This configuration is convenient for the nondestructive inspection of valuable objects from which fragmentary samples cannot be drawn, but it does not allow generation of the high and homogeneous magnetic fields that afford spectral resolution in conventional NMR studies. Given these detrimental conditions, the standard techniques of conventional NMR do not work, and new strategies need to be developed in order to extract valuable information from the NMR signal (*2*–*8*).

Starting from simple relaxation-time measurements, more sophisticated methods of ex situ NMR have been developed, such as Fourier imaging (*5*), velocity imaging (*6*), and multi-

Institut für Technische Chemie und Makromolekulare Chemie, Rheinisch-Westfälische Technische Hochschule–Aachen, D-52056, Germany.

*To whom correspondence should be addressed. E-mail: bluemich@mc.rwth-aachen.de

LETTERS

edited by Etta Kavanagh

When the Oil Supply Runs Out

THE ARTICLE "THE LOOMING OIL CRISIS COULD ARRIVE UNCOMFORTABLY SOON" (R. A. KERR, News of the Week, 20 Apr., p. 351) is far too equivocal in its discussion of such a vital topic, noting first that the most likely scenario is a resource-constrained peak by 2020, then that political factors must be taken into account in a discussion of peak oil production, and finally concluding that there is so much uncertainty that "predicting the peak may not be worthwhile."

Much, but not all, of the political uncertainty regarding production rates can be captured by partitioning conventional oil extraction into OPEC and non-OPEC components. This has been done by ExxonMobil and others (*1*–*4*); ExxonMobil has concluded that non-OPEC production will peak by 2010. On the basis of this forecast, ExxonMobil has publicly stated that it will build no new refineries, presumably because the crude supplies needed may not be available from OPEC producers. The high and rapidly fluctuating U.S. gasoline prices currently being experienced are due in large part to a shortage of domestic refinery capacity, so that we are in fact already feeling the effects of an imminent non-OPEC peak.

Recently, Ecuador rejoined OPEC, and Angola has also become a member. Over the next two or three years, it will become clear that crude oil is indeed a finite resource, and we will be forced to adapt to much higher petroleum prices as India and China continue to expand their automobile and airline fleets. Fortunately, there are many ways to cope with this new state of affairs, first and foremost by embracing energy efficiency and conservation not as virtues for the elite, but as urgent and universal national goals.

ALFRED CAVALLO

Energy Consultant, Princeton, NJ, USA.

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Testosterone and Male Fertility in Red Deer

IN "MALE FERTILITY AND SEX RATIO AT BIRTH IN red deer" (Reports, 1 Dec. 2006, p. 1445), M. Gomendio *et al.* discovered that the proportion of males born to red deer was correlated with the degree of fertility of the fathers. These observations support the hypothesis that the strongly beneficial trait of male fertility favors the production of more sons that can then perpetuate this trait. This study provides insight into possible extragenetic contributions to sex ratios among offspring that likely have implications in other mammalian species, including humans.

The proportion of male births has been steadily declining in some human populations from North America and Europe (*1*). The reason for this decline is unknown, but the phenomenon has been associated with exposure to chemical pollutants (*2*–*5*). Among the Aamjiwnaang First Nation community (Ontario, Canada), not only is the proportion of male live births decreasing, but the magnitude of this disproportion has increased over time (*6*). Investigators have suggested that this localized disruption in sex ratio is a consequence of the abundant chemical industry in the vicinity (*6*).

A decrease in the proportion of male offspring has been associated with reduced testosterone levels or decreased testosterone/gonadotropin ratios in fathers (*7*, *8*). Gomendio *et al.* did not report testosterone levels among fathers in the studied red deer population. However, they associate fertility—the trait linked to altered sex ratio—with antler size. Testosterone is a major determinant of antler growth (*9*). Thus, it can be hypothesized that androgen status of fathers influences the proportion of males sired and that the decreasing proportion of male births documented in many human populations is due to declining testosterone levels among the fathers. A possible role for testosterone in regulating sex ratios of offspring has been debated for some time, but the issue remains unresolved. The study by Gomendio *et al.* provides new insight into a potential role for hormones in determining offspring sex in mammals, including humans.

GERALD A. LEBLANC

Department of Environmental and Molecular Toxicology, North Carolina State University, Box 7633, Raleigh, NC 27695–7633, USA.

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IN "MALE FERTILITY AND SEX RATIO AT BIRTH IN red deer" (Reports, 1 Dec. 2006, p. 1445), M. Gomendio *et al.* reported that in red deer, (i) male fertility is significantly and positively correlated with offspring sex ratio (OSR) (proportion of males), and (ii) the percentage of morphologically normal sperm correlates positively with OSR.

A decade of animal cloning

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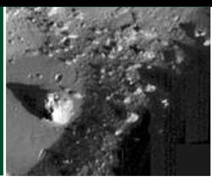

Gravel piles in space

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These authors interpreted their results as supporting adaptive theory, but were uncertain of the identity of the proximate cause(s) of variation in OSR. They also noted that although much work has been done by adaptive theorists on OSRs of female mammals, little has been done by them on OSRs of male mammals. However, there are prodigious quantities of data relating the variation of men's OSRs to selected environmental factors. For instance, men's OSRs are affected by nine different adverse chemical exposures, five different pathological conditions, and four types of occupational exposure (*1*). In all 18 of these conditions, the OSRs correlated positively and significantly with men's testosterone concentrations. Indeed, there is strong evidence that the sexes of offspring of mammals (including humans) are partially controlled by the hormone levels of both parents around the time of conception (*2*, *3*). This would suggest that high levels of testosterone around the time of conception are associated with the subsequent births of sons.

WILLIAM H. JAMES

The Galton Laboratory, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK.

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Response

WE REPORTED THAT MORE FERTILE RED DEER males, with a higher proportion of morphologically normal spermatozoa, produce a greater proportion of male offspring, who are likely to inherit enhanced fertility. Le Blanc and James suggest that testosterone may mediate the relationship between male fertility and offspring sex ratio (OSR) in this and other species, including humans. LeBlanc notes that, in our study population, male fertility is associated with antler size (*1*) and, on the basis of his premise that testosterone is a major determinant of antler growth, concludes that differences in OSR may be due to differences in testosterone levels between males. LeBlanc and James propose a role for testosterone by extrapolating from studies in humans where indirect evidence suggests that biases in OSR linked to environmental factors could be caused by changes in testosterone levels.

Although the idea has been around for some time, the hypothesis that testosterone influences OSR has not been properly tested. We do not have testosterone data from our OSR experiment, but we do have data on testosterone levels for a captive red deer population throughout the year ($N = 18$) and for a large sample of males from natural populations during the breeding season ($N = 77$), which we have used to test the relationships proposed.

Red deer are seasonal breeders and cast and regrow their antlers every year. In our captive population, testosterone levels remained low during antler growth, increased during antler mineralization, reached a peak just before the breeding season started, and decreased thereafter, similar to previous reports (*2*, *3*). Thus, although testosterone may control the timing of key events in the antler cycle, the observation that testosterone levels are low during antler growth supports the current view that the presumed positive link between testosterone levels and antler size is mistaken (*4*, *5*). In fact, the opposite may be true, at least in red deer, because males treated with anti-androgens grow larger antlers than controls, and testosterone reduces antler growth by influencing IGF-1 binding, the latter having an important role in antler growth (*5*).

Further evidence against the presumed link between testosterone levels and antler size comes from natural populations, where we found no relationship between males' testosterone levels during the breeding season and antler size. It should be noted that both variables are uncoupled in time, i.e., antlers grow in spring, when testosterone levels are minimal, and remain unchanged during the breeding season, when testosterone levels increase. Thus, the idea that testosterone levels during the breeding season are associated both with antler size and OSR would imply that males with higher testosterone levels during spring have increased antler growth rates, and that differences between males in testosterone levels remain consistent during the breeding season when absolute values increase. Further studies are needed to test these possibilities.

The annual cycle in testosterone levels is mirrored by changes in testes size, and, in natural populations, males with higher testosterone levels have larger testes and produce more sperm. However, the potential links between testosterone and other aspects of semen quality remain to be demonstrated.

The close relationship between testosterone and sperm production justifies the use of sperm numbers as an indirect measure of testosterone levels for each male. This allows us to test the presumed relationship between testosterone and OSR for the males used in our OSR experiment. In our study sample, there was no relationship between numbers of spermatozoa and OSR. Thus, it seems unlikely that differences in testosterone levels between males during the breeding season explain the biases in OSR observed.

MONTSERRAT GOMENDIO,[1] AURELIO F. MALO,[1,2] ANA J. SOLER,[3] JULIAN GARDE,[3] EDUARDO R. S. ROLDAN[1]

[1]Reproductive Ecology and Biology Group, Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales (CSIC), 28006 Madrid, Spain. [2]Department of Conservation Biology, National Zoological Park, Smithsonian Institution, Washington, DC 20008, USA. [3]Instituto de Investigación en Recursos Cinegéticos (CSIC-Universidad de Castilla-La Mancha-Junta de Comunidades de Castilla-La Mancha), 02071 Albacete, Spain.

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Further Notes on Quasi-Crystal Tilings

WE APPRECIATE THAT *SCIENCE* HAS CLARIFIED its news article ("Quasi-crystal conundrum opens a tiling can of worms," News of the Week, J. Bohannon, 23 Feb., p. 1066; see Corrections and Clarifications on page 982 in this issue) regarding our paper "Decagonal and quasi-crystalline tilings in medieval Islamic architecture" (Reports, 23 Feb., p. 1106). We certainly recognized that our study builds on earlier work, as acknowledged in our references (*3*–*6*, *14*, *18*–*19*), and citations therein, although more can be said. Many authors from Hankin in 1925 [(*14*) in our Report] to Wade

CORRECTIONS AND CLARIFICATIONS

News of the Week: "Quasi-crystal conundrum opens a tiling can of worms" by J. Bohannon (23 Feb., p. 1066). The article presented opinions of Dov Levine of the Israel Institute of Technology and Joshua Socolar of Duke University in a way that has led to misperceptions. The article discussed a paper by Peter Lu and Paul Steinhardt (*Science*, 23 Feb., p. 1106) on the use of tiling designs by medieval Islamic architects that form the basis of nonrepeating patterns called quasi-crystals. It went on to report that Levine and Socolar "doubt that the architects truly understood quasi-crystals." That comment—the only outside comment in the article on the paper's conclusions—is consistent with what was concluded in the Lu-Steinhardt paper itself; it does not, and was not meant to, contradict the central claim that the architects used a method capable of creating a perfect quasi-crystal tiling. The article also included a quote from Emil Makovicky of the University of Copenhagen that his earlier publication on Islamic tiling patterns was cited by Lu and Steinhardt "…in a way that [the ideas] look like their own." Immediately following, Levine and Socolar were quoted regarding Makovicky's contributions to the field. The context of their quotes implied that they agreed with Makovicky's characterization, but neither of them did so.

Special Section: Sustainability and Energy: Perspectives: "Biomass recalcitrance: engineering plants and enzymes for biofuels production" by M. E. Himmel *et al.* (9 Feb., p. 804): The legend describing panels B and C of Fig. 1 was reversed in the online version of the paper. Panel B shows the atomic force micrograph, and panel C shows the scanning electron micrograph. The legend was correct in print. The correct text was posted online on 13 February.

TECHNICAL COMMENT ABSTRACTS

Comment on "A Centrosome-Independent Role for γ-TuRC Proteins in the Spindle Assembly Checkpoint"

Stephen S. Taylor, Kevin G. Hardwick, Kenneth E. Sawin, Sue Biggins, Simonetta Piatti, Alexey Khodjakov, Conly L. Rieder, Edward D. Salmon, Andrea Musacchio

Müller *et al*. (Reports, 27 October 2006, p. 654) showed that inhibition of the γ-tubulin ring complex (γ-TuRC) activates the spindle assembly checkpoint (SAC), which led them to suggest that γ-TuRC proteins play molecular roles in SAC activation. Because γ-TuRC inhibition leads to pleiotropic spindle defects, which are well known to activate kinetochore-derived checkpoint signaling, we believe that this conclusion is premature.

Full text at www.sciencemag.org/cgi/content/full/316/5827/982b

Comment on "A Centrosome-Independent Role for γ-TuRC Proteins in the Spindle Assembly Checkpoint"

Beth A. A. Weaver and Don W. Cleveland

Müller *et al*. (Reports, 27 October 2006, p. 654) proposed a role for microtubule nucleation in mitotic checkpoint signaling. However, their observations of spindle defects and mitotic delay after depletion of γ-tubulin ring complex (γ-TuRC) components are fully consistent with activation of the established pathway of checkpoint signaling in response to incomplete or unstable interactions between kinetochores of mitotic chromosomes and spindle microtubule.

Full text at www.sciencemag.org/cgi/content/full/316/5827/982c

Response to Comments on "A Centrosome-Independent Role for γ-TuRC Proteins in the Spindle Assembly Checkpoint"

Hannah Müller, Marie-Laure Fogeron, Verena Lehmann, Hans Lehrach, Bodo M. H. Lange

Weaver and Cleveland and Taylor *et al*. contend that our data on the involvement of γ-tubulin ring complex (γ-TuRC) in the spindle assembly checkpoint (SAC) can be fully explained by kinetochore-derived checkpoint signaling. We maintain that (i) the interactions of γ-TuRC with Cdc20 and BubR1 and (ii) the activation of SAC by γ-TuRC depletion, in addition to the abrogation of kinetochore microtubule interactions, argue for a more complex mechanism of SAC signaling.

Full text at www.sciencemag.org/cgi/content/full/316/5827/982d

(*1*), Critchlow (*2*), and Kaplan (*3*) have related Islamic geometric patterns to configurations of polygons, including some with the same outlines as the decorated girih tiles introduced in our paper. Bonner [(*19*) in our Report] has applied these ideas to self-similar geometric patterns with five-fold and other symmetries. Makovicky [(*18*) in our Report], and previously Zaslavsky *et al.* (*4*) and Chorbachi [(*31*) in our Report], suggested relations between certain historic Islamic tilings and Penrose tilings based on studies of small isolated motifs or fragments embedded within manifestly periodic patterns.

We gladly acknowledge all these contributions, which complement our own. However, we wish to emphasize a few distinctions here. First, our approach was founded on the historical record, particularly the Topkapi scroll first understood and published by Gulru Necipoglu (Harvard University), who guided us. Insisting on exact reconstructions of historical monuments resulted in some differences from previous work; for example, our analysis of the Gunbad-i Kabud tomb tower (Figs. 2 and S6), based directly on archival photographs, differs systematically from the transcription used in reference (*18*) and reveals plainly the intentional periodicity and regular deviations from a true Penrose tiling. Second, our explanation of these patterns clearly differs from earlier ideas: We propose that historical designers constructed a wide range of patterns by tessellating with the same five units ("girih tiles") described in our paper, not merely polygons but shapes with specific interior line decorations that form the pattern when the tiles are joined together. Constructing patterns by laying these girih tiles edge to edge this way is simpler than other proposed methods; we have observed young children successfully applying it in the classroom. Moreover, other methods generate many patterns that do not appear historically; by contrast, we presented a series of patterns from historically significant buildings, scrolls, and Qurans throughout the medieval Islamic world that can all be constructed from the same five girih tiles (including their decorations). Third, our analysis of the Darb-i Imam shrine revealed two other novel elements—the explicit subdivision of these girih tiles into smaller girih tiles of the same shape, and a large fragment based on decagonal symmetry that is not embedded in a periodic matrix, properties sufficient to transform the Darb-i Imam shrine pattern into an infinite quasi-crystalline tiling. Our conclusions were guarded, concurring with the remarks by Socolar and Levine in the accompanying news article, suggesting that evidence beyond a single large fragment is needed to prove that the designers understood this possibility. We hope our small contribution, combined with the earlier works, will lead to further explorations of these impressive works of art and mathematics.

PETER J. LU[1] AND PAUL J. STEINHARDT[2]

[1]Department of Physics, Harvard University, Cambridge, MA 02138, USA. [2]Department of Physics and Princeton Center for Theoretical Physics, Princeton University, Princeton, NJ 08544, USA.

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