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Phylogenetic Analysis Shows That Neolithic Slate Plaques from the Southwestern Iberian Peninsula Are Not Genealogical Recording Systems

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Abstract

Prehistoric material culture proposed to be symbolic in nature has been the object of considerable archaeological work from diverse theoretical perspectives, yet rarely are methodological tools used to test the interpretations. The lack of testing is often justified by invoking the opinion that the slippery nature of past human symbolism cannot easily be tackled by the scientific method. One such case, from the southwestern Iberian Peninsula, involves engraved stone plaques from megalithic funerary monuments dating ca. 3,500–2,750 B.C. (calibrated age). One widely accepted proposal is that the plaques are ancient mnemonic devices that record genealogies. The analysis reported here demonstrates that this is not the case, even when the most supportive data and techniques are used. Rather, we suspect there was a common ideological background to the use of plaques that overlay the southwestern Iberian Peninsula, with little or no geographic patterning. This would entail a cultural system in which plaque design was based on a fundamental core idea, with a number of mutable and variable elements surrounding it.

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Introduction

Prehistoric engraved plaques dating ca. 3,500–2,750 B.C. (calibrated age) (Table 1) are found in archaeological sites across the southwestern Iberian Peninsula. The plaques are thin slabs, usually of slate or schist but in some cases of sandstone, that vary in shape from rectangular to trapezoidal. Size is highly variable, but most specimens range in length from 10 cm to 20 cm and have maximum widths in the 5–10-cm range (Fig. 1). In addition to geometric, anthropomorphic, or zoomorphic designs engraved on one face, most specimens have one or two drilled holes at one end, through which, it has been proposed [1], [2], strings were passed so they could be worn. The majority of plaques have come from burial sites (~200), in some cases resting directly on or to the side of human skeletons [2]. Plaques are usually associated with undecorated pottery, flint blades, and other chipped and polished stone tools with no clear evidence of wear [2].

Interpretations of the intended function(s) of the stone plaques extend back to the last quarter of the nineteenth century and include:

- a kind of ideographic writing system [3];
- prestige objects [1], [4], [5];
- symbolic items used by groups within a social hierarchy [6], [7];
- heraldic objects [8], [9];
- amulets or cult objects [10], [11], perhaps used in superstitious activities [12];
- apotropaic images of the deceased to ward off evil [13];
- idols [14]–[16], perhaps related to the devotion of specific divine figures [17]–[21]; and
- symbolic expressions related to different specific geographical regions and units of cultural identity [22], [23].

More recently, Katina Lillios combined two of those functions—ideographic writing and heraldic items—hypothesizing that the majority of the plaques codify genealogical information [2], [24]–[27], whereas others perhaps were relics or specific expressions of several individuals [28], [29]. She proposed that decorative motifs on the lower portion of the plaque—the end opposite the hole (Fig. 2)—identify individual descent groups and that the number of decorative “registers”—the horizontal rows of triangles shown on the specimen in Fig. 2—indicates the generational distance between the deceased and the founding ancestor of his or her lineage. For example, a plaque containing two rows of triangles would connote “a person two generations removed from a founding ancestor” [2]—the triangle lineage]…. The increase in register [row] numbers suggests gradual demic diffusion away from a core ‘ancestral area over time’” ([2], p. 149). Thus plaques with a higher number of rows should be later that those with fewer rows. And, just as with the concentric circles that radiate out from a pebble thrown in a pond, the number of rows should increase with distance from the original center of plaque development, as groups moved outward, carrying the plaque-making tradition with them.
Lillios created a sequence of types based on expected chronological changes in various features of the plaques, with emphasis on decorative motifs on the lower portion of the plaque. She anchored the sequence with plaques containing vertical bands, herringbone designs, or checkerboard patterning (Fig. 1), followed by plaques with zigzag decoration, followed by plaques with chevrons and triangles. Her reasoning was that many of the examples with vertical bands, herringbone designs, and checkerboard patterning appeared to come from the Évora district of southern Portugal, which many Iberian archaeologists consider to be the original heartland of Late Neolithic peoples responsible for the megalithic tombs in which many of the plaques have been found [10], [30], [31]. So her reasoning went, as those peoples moved out from Évora, the plaques they made became increasingly younger in age, ending with triangle designs.

Lillios ([2], pp. 157–158) states that she used both the “proxy method of ordering the plaques” as well as phyletic seriation [32] to “propose a tentative chronological sequencing” of plaques, but she presents no data that would allow us to examine the strength of her hypothesis. Despite these problems, Lillios’s hypothesis has gained considerable weight among archaeologists working on the Iberian Peninsula ([33], [34]; but see [21]). To test her hypothesis, we turned to an evolutionary model—cladogenetic, or branching, evolution—that reflects the nature of evolutionary change, whether in organisms or material culture [35]–[37]. Instead of collapsing all change into a single line of ancestry, as in the model underlying phyletic seriation, the cladogenetic model recognizes that ancestry is bushy, or tree-like. As we detail below, we designed a series of phylogenetic exercises—similar to protocols used on other archaeological materials [36], [38], [39]—to maximize the expectations of Lillios’s hypothesis. This meant that we weighted every experimental protocol and analytical decision in favor of her hypothesis, our rationale being that if we tried every way possible to meet the expectations but could not, then the hypothesis should be rethought.

In summary, our analysis did not support Lillios’s hypothesis that the plaques are genealogical mnemonic recording systems. We should say that her hypothesis is not supported in its current form, meaning that it is her proposed sequence of plaque designs that is unsupported. Our analysis does not negate the possibility that the plaques served as mnemonic devices or some other function tied to “external symbolic storage” [40], [41]. Whatever their purpose, it appears there was a common ideological background to the use of plaques that overlay the southwestern Iberian Peninsula—a cultural system in which plaque design was based on a fundamental core tradition, similar to Swadesh’s [42] “morphological kernel” of a language [43], [44], with a number of mutable and variable elements surrounding it.

Table 1. Available radiocarbon dates directly associated with plaques.

| Site and District1 | Sample       | Date RCYBP      | Date BC     | Cal Date BC2(1 sigma) | Plaque (Espírit Number) | Reference |
|-------------------|--------------|-----------------|-------------|-----------------------|-------------------------|-----------|
| Gruta da Lapa do Fumo (Set) | ICEN-240     | 4420±45 BP      | 2470±45 BC  | 3101–3000 BC          | 658                     | [82]      |
| Covas das Lapas I (Lei) | ICEN-463     | 4550±60 BP      | 2600±60 BC  | 3238–3108 BC          | 1103                    | [20]      |
| Gruta da Marmota (San) | Ox-a-5535    | 4605±55 BP      | 2655±55 BC  | 3509–3426 BC          | Unknown                 | [82]      |
| Gruta da Lapa do Bugio (Set) | Ox-a-5507   | 4420±110 BP     | 2470±110 BC | 3119–2919 BC          | Unknown                 | [82]      |
| Anta da Bola da Cera (Port) | ICEN-66     | 4360±50 BP      | 2410±50 BC  | 3023–2909 BC          | Unknown                 | [81]      |
| Sala n’ 1 (Bej) | ICEN-448     | 4140±110 BP     | 2190±110 BC | 2876–2618 BC          | Unknown                 | [82]      |
| Anta de STAM-3 (Evo) | Beta-166422 | 4270±40 BP      | 2320±40 BC  | 2917–2877 BC          | 650                     | [82]      |
| Olival da Pega 2b (Evo) | ICEN-957    | 4130±60 BP      | 2180±60 BC  | 2763–2620 BC          | 137, 492, and 515       | [82]      |
| Olival da Pega 2b (Evo) | ICEN-955    | 4290±100 BP     | 2340±100 BC | 3034–2856 BC          | 137, 492, and 515       | [82]      |
| Olival da Pega 2b (Evo) | ICEN-956    | 4180±80 BP      | 2230±80 BC  | 2817–2664 BC          | 137, 492, and 515       | [82]      |
| Anta 4 de Coureleiros (Port) | ICEN-976   | 4240±150 BP     | 2290±150 BC | 3022–2617 BC          | Unknown                 | [81]      |
| Pê da Erra (San) | ICEN-587     | 4220±45 BP      | 2270±45 BC  | 2808–2755 BC          | Unknown                 | [82]      |
| Anta da Horta (Port) | Beta-194313 | 4480±40 BP      | 2530±40 BC  | 3332–3214 BC          | [81] Figs. 138 (above) and 147 (below) | [81] |
| Anta da Horta (Port) | Beta-194312 | 4270±50 BP      | 2320±50 BC  | 2928–2866 BC          | [81] Figs. 136–149      | [81]      |
| Gruta Praia das Maçãs (Lis) | Ox-a-5509   | 4410±75 BP      | 2460±75 BC  | 3107–2916 BC          | Unknown                 | [82]      |
| Gruta Praia das Maçãs (Lis) | Ox-a-5510   | 4395±60 BP      | 2445±60 BC  | 3096–2916 BC          | Unknown                 | [82]      |

1See Fig. 4 for district locations.
2Calibrations are made in software Calib 7.0 based on IntCal 13 data sets.

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Figure 1. Engraved plaques from the Iberian Peninsula. a, Valencina de la Concepción, Sevilla, Spain (Museo Arqueológico de Sevilla [MAS]); b, S. Geraldo, Montemor-o-Novo, Évora, Portugal (Museo Nacional de Arqueología de Portugal [MNAP]); c, Monsaraz, Reguengos de Monsaraz, Évora (MNAP); d, Mora, Évora (MNAP); e, Jabugo, Aracena, Huelva, Spain (MAS); f, Ciborro, Monte-o-Novo, Évora (MNAP); g, Marvão, Portalegre, Portugal (MNAP); h, Estremoz, Évora (MNAP); and i, Pavia, Mora, Évora (MNAP).

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Materials

Our data were derived from the online Esprit (Engraved Stone Plaque Registry and Inquiry Tool) database (http://research2.its.uiowa.edu/iberian/index.php) created by Lillios and collaborators [45]. It contains information on over 1400 plaques. Although some archaeologists [46] have claimed that the data set does not contain the total number of excavated plaques, which is likely, we have no reason to think that it is not representative of the variation in decoration that existed across the southwestern Iberian Peninsula.

Because of inconsistencies in how plaque types have been created by the authors of and contributors to Esprit—not an unusual occurrence in archaeology—we used paradigmatic classification to define analytical classes [35], [47]. In paradigmatic classification, the investigator specifies a priori the characters and character states that are of analytical interest, and each specimen is then classified by linking the state of each character. Any character state can combine with any of the states of the other characters to create a class (taxon). Key to Lillios’s hypothesis is the character “base decorative motif” (DM), but five other characters are also proposed to have chronological significance: “structure (ST),” “tattoo straps (TT),” “necklace (NK),” “head motif (H),” and “number of registers (rows).” We excluded the last character because, if we use Lillios’s reasoning, it is not an independent variable. As we mentioned above, to her, rows of engraved lines tell us about the use life of a plaque, not its chronological age. To use our earlier example, a plaque with two rows signifies two generations, whereas a plaque with five rows signifies five generations. The first plaque could have been made many centuries before the second one but did not record as many generations before it was placed in the ground. Fig. 3 shows the possible discrete states of each of the five characters used.

By excluding specimens that were broken, showed evidence of re-engraving, or were not illustrated in the online database, we ended up with a population of 735 plaques. We judged the population to be too large to analyze because of the number of unique classes involved (see below), so we reduced it to 349 specimens using a 5% error and a 99% confidence interval (http://www.med.unne.edu.ar/biblioteca/calculos/calculadora.htm). Those 349 specimens were spread across 81 classes. Table 2 lists the number of specimens by class and Esprit database identification number [45]. For the latter we used the first specimen listed in the database as the class representative. For example, class 1 contains 15 specimens that are identical in terms of character states. We list only one specimen identification number for that class instead of all 15. Table 3 reorders the data in Table 2 to show the number of duplicate cases across the sample. For example, the first row of the table shows that 36 classes contain only one specimen (there are zero duplicate specimens in those 36 classes). The second-to-last row shows that there is one class that contains 27 specimens (one plus 26 duplicates). We can see from Table 2 that that 27-specimen class is class 3.

Because the tree-building computer program we used—PAUP* 4.0 [40] (see below)—could not accommodate that number of classes, we took a weighted random sample (with replacement [SPSS v. 20]) from the 81-class sample to create 4 samples of 20 classes each. (The weight of each class was determined by the number of specimens in it.) Table 3 reorders the classes each sample. For example, class 1 contains 15 specimens that are identical in terms of character states; Table 3 reorders the data in Table 2 to show the number of duplicate cases across the sample. For example, the first row of the table shows that 36 classes contain only one specimen (there are zero duplicate specimens in those 36 classes). The second-to-last row shows that there is one class that contains 27 specimens (one plus 26 duplicates). We can see from Table 2 that that 27-specimen class is class 3.

Because the tree-building computer program we used—PAUP* 4.0 [40] (see below)—could not accommodate that number of classes, we took a weighted random sample (with replacement [SPSS v. 20]) from the 81-class sample to create 4 samples of 20 classes each. (The weight of each class was determined by the number of specimens in it.) Table 3 reorders the classes in each sample and their character states; Fig. 4 shows the distribution of classes geographically.

Method

Phylogenetic reconstruction is the main method used in biology to construct testable hypotheses of ancestor–descendant relationships [49]–[52]. It has also begun to see wide usage in archaeology [37–39], [53–58] and other studies of material culture [59]–[67]. As Riede ([58] p. 799) points, cultural phylogenetics has advantages over traditional typological approaches in that a given phylogeny constitutes a quantitative hypothesis of the historical relatedness among the chosen units of analysis…. Such hypotheses can then be evaluated statistically and in relation to external datasets, such as stratigraphic, geographical or radiocarbon dating information. While a phylogenetic quantification of material culture relations alone can reveal important new insights in its own right, phylogenies can also be used in additional comparative analyses.
Phylogenetics is based on a model of descent with modification in which new taxa arise from the bifurcation of existing ones. Phylogenetic relationships are defined in terms of relative recency of common ancestry: Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon. The evidence for exclusive common ancestry is the sharing of evolutionarily novel, or derived, character states, termed synapomorphies.

Various methods have been used for phylogenetic inference, each based on different models and each having its own strengths and weaknesses [68]–[72]. The one we used, maximum parsimony, is based on a model that seeks to identify the least number of evolutionary steps required to arrange the taxonomic units under study. In simplest form, the method consists of four steps:

1. Generation of a data matrix that shows the states of the characters exhibited by each taxon.
2. Establishment of direction (polarity) of evolutionary change among the states of each character. One method for doing this is outgroup analysis [73], which entails examining a close relative of the study group. When a character occurs in two states among the study group, but only one of the states is found in the outgroup, the principle of parsimony is invoked (see above), and the state found only in the study group is deemed to be evolutionarily novel with respect to the outgroup state.
3. Construction of a branching diagram of relationships for each character by joining the two most derived taxa—those at the branch tips of a tree—and then successively connecting each of the other taxa according to how derived they are. Ideally, the distribution of character states among the taxa will be such that all the character trees imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character trees will suggest relationships that are incompatible—a phenomenon known as homoplasy. This problem is overcome through the fourth step:
4. Construction of an ensemble tree that is consistent with the largest number of characters and therefore requires the smallest number of homoplasies to account for the distribution of character states among the taxa. We refer to such a tree as the “most parsimonious” solution. Parsimony trees are evaluated on the basis of the minimum number of character-state changes required to create them, without assuming a priori a specific distribution of trait changes. This compensates for the process pathways, biases, and random variation that characterize “cultural transmission” [74]–[76]. It is worth underscoring that trees are hypothetical statements of relatedness, “given the model and parameters used” ([68] p. 189), not irrefutable statements of precise phylogenetic relationships.

Numerous techniques are available for measuring the goodness of fit between a data set and a given tree, with the consistency index (CI), the retention index (RI), and the rescaled consistency index (RC) being the most commonly used. The CI measures the relative amount of homoplasy in a data set but is dependent on the...
The number of taxa. Thus, the expected CI for a given tree must be assessed relative to the number of taxa used in the analysis [77]. The RI measures the number of similarities in a data set that are retained as homologies in relation to a given tree. It is insensitive to both the presence of derived character states that are present in only a single taxon and the number of characters or taxa employed. Thus, it can be compared among studies. The rescaled consistency index (RC) is the product of the consistency index and the retention index. Indices range from zero, which indicates a lack of fit between a tree and the data set used to generate it, to 1.0, which represents a perfect fit.

Our phylogenetic analysis consisted of four exercises (Table 5), each of which was carried out on each of the four samples listed in Table 4. Each exercise searched for the best-supported tree using the same tree-building methods and character/character-state parameters (Table 4). We used the “parsimony heuristic search” in PAUP*. All searches were carried out using the stepwise-addition strategy for the addition of classes, with a simple addition sequence and keeping only one tree at every step; the tree bisection and reconnection method, with the branch-swapping algorithm in relation to the tree rearrangements; and a maximum set of 100 for the initial trees. The following scores were extracted from all searches: number of trees, length of trees, consistency index (CI), retention index (RI), and rescaled consistency index (RC). We generated three kinds of consensus trees—strict, semi-strict, and majority-rule—to reconcile different outcomes. We also generated bootstrap trees using the following parameters: 100 bootstrap replicates; simple weighting; randomly starting seed; parsimony

Figure 3. Character states used in the analysis.
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optimality criterion; and 500 saved trees in each bootstrap replicate step.

Certain characters can be hypothesized as being more important than others in determining phylogenetic relationships, and thus more analytical weight can be placed on them. As mentioned, our goal was to stack the deck in favor of Lillios's hypothesis, in which character DM plays a crucial role, so for exercises 2 and 4 (Table 5), we assigned it a weight of 2, whereas characters ST, TT, NK and H were each assigned a weight of 1.

Character states can also be ordered, which means there are defined pathways that a character transformation can take [78]. Thus, for example, it may be the case that evolutionary “laws” dictate that an organism can lose or gain only one toe at a time. It could move from five toes to four toes, or vice versa, but never from five to three or from two to four. The character “number of toes,” then, is said to have ordered character states. In reality, an

**Table 2.** Distribution of specimens across the 81 classes.

| Class | Esprit Identification | Number of Specimens |
|-------|-----------------------|---------------------|
| 1     | 1                     | 15                  |
| 2     | 2                     | 1                   |
| 3     | 3                     | 27                  |
| 4     | 8                     | 5                   |
| 5     | 12                    | 2                   |
| 6     | 13                    | 6                   |
| 7     | 14                    | 23                  |
| 8     | 15                    | 3                   |
| 11    | 18                    | 4                   |
| 12    | 19                    | 1                   |
| 13    | 23                    | 17                  |
| 14    | 29                    | 22                  |
| 15    | 30                    | 5                   |
| 16    | 31                    | 3                   |
| 18    | 33                    | 2                   |
| 20    | 35                    | 1                   |
| 21    | 36                    | 10                  |
| 24    | 44                    | 6                   |
| 25    | 45                    | 1                   |
| 26    | 46                    | 8                   |
| 32    | 53                    | 24                  |
| 39    | 61                    | 2                   |
| 41    | 63                    | 5                   |
| 42    | 64                    | 6                   |
| 44    | 66                    | 7                   |
| 45    | 68                    | 9                   |
| 50    | 75                    | 5                   |
| 56    | 85                    | 3                   |
| 59    | 89                    | 4                   |
| 91    | 157                   | 10                  |
| 94    | 160                   | 18                  |
| 96    | 163                   | 4                   |
| 97    | 164                   | 3                   |
| 107   | 175                   | 5                   |
| 111   | 180                   | 1                   |
| 114   | 183                   | 3                   |
| 138   | 226                   | 4                   |
| 146   | 236                   | 4                   |
| 150   | 241                   | 11                  |
| 151   | 243                   | 3                   |
| 155   | 253                   | 2                   |
| 161   | 259                   | 2                   |
| 169   | 268                   | 1                   |
| 174   | 275                   | 5                   |
| 177   | 279                   | 1                   |
| 180   | 282                   | 1                   |
| 189   | 296                   | 1                   |
| 211   | 321                   | 1                   |
| 219   | 332                   | 2                   |

**Table 2.** Cont.

| Class | Esprit Identification | Number of Specimens |
|-------|-----------------------|---------------------|
| 222   | 335                   | 1                   |
| 225   | 340                   | 2                   |
| 244   | 365                   | 1                   |
| 249   | 370                   | 3                   |
| 271   | 405                   | 1                   |
| 304   | 466                   | 2                   |
| 313   | 479                   | 2                   |
| 321   | 489                   | 1                   |
| 328   | 499                   | 1                   |
| 330   | 501                   | 1                   |
| 342   | 513                   | 3                   |
| 344   | 515                   | 1                   |
| 355   | 536                   | 1                   |
| 361   | 544                   | 1                   |
| 401   | 612                   | 1                   |
| 415   | 637                   | 1                   |
| 420   | 650                   | 2                   |
| 432   | 676                   | 1                   |
| 438   | 700                   | 1                   |
| 442   | 709                   | 1                   |
| 478   | 836                   | 1                   |
| 483   | 844                   | 1                   |
| 497   | 861                   | 1                   |
| 498   | 862                   | 1                   |
| 616   | 1074                  | 1                   |
| 618   | 1076                  | 1                   |
| 623   | 1084                  | 1                   |
| 638   | 1109                  | 1                   |
| 660   | 1165                  | 1                   |
| 670   | 1178                  | 1                   |
| 681   | 1191                  | 1                   |
| 690   | 1221                  | 1                   |

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ordered transformation series is a hypothesis about a particular pathway because rarely will we know absolutely what is possible in nature. Lillios’s hypothesis assumes that the lower portion of the plaques, containing character DM, represents lineage affiliations, whereas the number of rows represents the generations back to the founding ancestor of the lineage [2], [24], [25]. With respect to character DM, Lillios suggests that plaques with checkerboard (DM4) and herringbone (DM6) designs are ancestral to plaques with other decorative designs, given that the former are more limited to her suspected core area of plaque manufacture and use (the Évora district of southern Portugal).

For exercises 3 and 4 (Table 5), we assigned costs to changes that violated the order of character states indicated by Lillios’s hypothesis. As shown in Fig. 5, transformations from supposed ancestral character states to derived states—say, from herringbone (DM4) to zigzag (DM5)—have the lowest cost (1), meaning that they have evolved in the manner Lillios suggested. At the other end of the spectrum, a transformation from a derived state to the original ancestral state—say, from triangle (DM2) to herringbone (DM6) or from unipartite (ST0) to bipartite (ST2)—has a cost of 3. Any transformation between a derived state and one immediately preceding it (an intermediate state)—say, from triangles (DM2) to zigzag (DM4)—has a cost of 2 [79]. If anything, this move stacked the deck even further in favor of Lillios’s hypothesis, given that the best two trees (see below) both contained ordered character states. We did not order characters TT and NK because Lillios’s hypothesis is unclear as to their chronological ordering.

Two exercises were carried out with outgroups (ROOT in Table 5) and two without outgroups (UNRT in Table 5). We used classes 21, 59, 146, and 618 as outgroups because they display all or most of the presumed ancestral states in Lillios’s hypothesis—again, a deliberate decision to maximize polarity in favor of the hypothesis. In summary, exercise 1 used unweighted characters, unordered character states, and unrooted trees; exercise 2 used weighted characters, unordered character states, and unrooted trees; exercise 3 used unweighted characters, ordered character states, and rooted trees; and exercise 4 used weighted characters, ordered character states, and rooted trees (Table 5).

Results

Table 6 presents the following scores for each heuristic search: number of most-parsimonious trees returned, branch length of trees, consistency index (CI), retention index (RI), and rescaled consistency index (RC). The number of most-parsimonious trees obtained in the exercises is high, running into the tens of thousands. The CI, RI, and RC show strong differences among the exercises. In particular, the CI decreases dramatically between exercises 1 and 2, with a mean of 0.56, and exercises 3 and 4, with a mean of 0.16. The RI, however, decreases from 0.65 to only 0.52. The RC indicates the same trend as the CI: Exercises 1 and 2 have a mean of 0.36, whereas exercises 3 and 4 have a mean of 0.08.

### Table 3. Frequency and percentage of classes that have multiple specimens.

| Number of Multiple Specimens | Frequency | Percentage of 349 Specimens | Cumulative Percentage of 349 Specimens |
|------------------------------|-----------|-----------------------------|---------------------------------------|
| 0                            | 36        | 10.3                        | 10.3                                  |
| 1                            | 10        | 5.7                         | 16.0                                  |
| 2                            | 8         | 6.9                         | 22.9                                  |
| 3                            | 5         | 5.7                         | 28.6                                  |
| 4                            | 6         | 8.6                         | 37.2                                  |
| 5                            | 3         | 5.1                         | 42.3                                  |
| 6                            | 1         | 2.0                         | 44.3                                  |
| 7                            | 1         | 2.3                         | 46.6                                  |
| 8                            | 1         | 2.6                         | 49.2                                  |
| 9                            | 2         | 5.7                         | 54.9                                  |
| 10                           | 1         | 3.1                         | 58.0                                  |
| 14                           | 1         | 4.3                         | 62.3                                  |
| 16                           | 1         | 4.9                         | 67.2                                  |
| 17                           | 1         | 5.1                         | 72.3                                  |
| 21                           | 1         | 6.3                         | 78.6                                  |
| 22                           | 1         | 6.6                         | 85.2                                  |
| 23                           | 1         | 6.9                         | 92.1                                  |
| 26                           | 1         | 7.7                         | 99.8                                  |
| Total                        | 81        | 99.8                        |                                        |

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The RI scores from all the exercises indicate that the data set has some consistency and phylogenetic structure. The sharp contrast observed for CI and RC values between the first two and the last two exercises indicates a significant difference related to the methodological parameters applied, specifically the switch from parameter US (unordered states) to parameter OS (ordered-states). In contrast, parameter WC, which implements different weights for a couple of characters, has no influence on the values.

| Class | ID | DM | ST | TT | NK | H |
|-------|----|----|----|----|----|---|
| Sample 1 |     |    |    |    |    |   |
| 2 Evo⁷ 2 | 1 2 1 | 1 | | | | |
| 6 Evo 13 | 3 2 0 | 1 | | | | |
| 12 Evo 19 | 2 2 0 | 1 2 | | | | |
| 13 Evo 23 | 2 2 1 | 1 | | | | |
| 14 Evo 29 | 3 2 1 | 1 | | | | |
| 15 Evo 30 | 5 2 0 | 2 1 | | | | |
| 18 Evo 33 | 3 0 0 | 0 2 | | | | |
| 26 Evo 46 | 5 0 0 | 0 0 | | | | |
| 32 Evo 53 | 2 2 1 | 0 1 | | | | |
| 59 Evo 89 | 4 2 1 | 0 1 | | | | |
| 94 Lis 160 | 2 2 0 | 0 1 | | | | |
| 96 Far 163 | 2 2 0 | 1 1 | | | | |
| 107 Lis 175 | 5 2 0 | 0 1 | | | | |
| 169 Port 268 | 5 2 0 | 1 2 | | | | |
| 222 Port 335 | 2 1 3 | 0 1 | | | | |
| 342 Set 513 | 1 2 1 | 1 1 | | | | |
| 415 Port 637 | 6 0 0 | 1 1 | | | | |
| 420 Evo 650 | 2 0 0 | 0 2 | | | | |
| 478 Cac 836 | 1 0 0 | 0 3 | | | | |
| 497 Evo 861 | 3 1 4 | 0 1 | | | | |
| Sample 2 |     |    |    |    |    |   |
| 4 Evo⁷ 8 | 3 2 4 | 0 1 | | | | |
| 8 Evo 15 | 1 2 2 | 0 1 | | | | |
| 12 Evo 19 | 2 2 0 | 1 2 | | | | |
| 21 Evo 36 | 4 2 2 | 0 1 | | | | |
| 26 Evo 46 | 5 0 0 | 0 0 | | | | |
| 32 Evo 53 | 2 2 1 | 0 1 | | | | |
| 39 Evo 61 | 2 2 3 | 0 1 | | | | |
| 114 Lis 183 | 3 1 2 | 0 1 | | | | |
| 138 Lis 226 | 3 2 0 | 0 0 | | | | |
| 177 Port 279 | 2 1 0 | 0 0 | | | | |
| 222 Port 335 | 2 1 3 | 0 1 | | | | |
| 321 Bad 489 | 3 2 2 | 0 0 | | | | |
| 401 Evo 612 | 5 1 1 | 1 1 | | | | |
| 415 Port 637 | 6 0 0 | 1 1 | | | | |
| 442 Port 709 | 2 1 0 | 1 2 | | | | |
| 483 Set 844 | 3 2 0 | 0 1 | | | | |
| 616 Evo 1074 | 3 2 0 | 0 1 | | | | |
| 618 Evo 1076 | 6 2 1 | 0 1 | | | | |
| 660 Set 1165 | 3 1 1 | 1 1 | | | | |
| 681 Bad 1191 | 2 2 2 | 1 1 | | | | |
| Sample 3 |     |    |    |    |    |   |
| 1 Evo⁷ 1 | 3 2 1 | 0 1 | | | | |
| 12 Evo 19 | 2 2 0 | 1 2 | | | | |
| 14 Evo 29 | 3 2 1 | 1 1 | | | | |
| 15 Evo 30 | 5 2 2 | 0 1 | | | | |
| 16 Evo 31 | 3 0 0 | 1 1 | | | | |
| 21 Evo 36 | 4 2 2 | 0 1 | | | | |

Table 4. Data matrix for the four samples.

| Class | ID | DM | ST | TT | NK | H |
|-------|----|----|----|----|----|---|
| 24 Evo 44 | 2 2 0 | 0 2 | | | | |
| 25 Evo 45 | 6 1 0 | 0 1 | | | | |
| 32 Evo 53 | 2 2 1 | 0 1 | | | | |
| 45 Evo 68 | 5 2 1 | 0 1 | | | | |
| 138 Lis 226 | 3 2 0 | 0 0 | | | | |
| 146 Evo 236 | 6 2 1 | 1 1 | | | | |
| 177 Port 279 | 2 1 0 | 0 0 | | | | |
| 189 Evo 296 | 2 1 0 | 1 1 | | | | |
| 304 San 466 | 5 2 0 | 0 2 | | | | |
| 321 Bad 489 | 3 2 0 | 2 0 | | | | |
| 344 Evo 515 | 1 2 3 | 0 1 | | | | |
| 361 Evo 544 | 3 2 0 | 2 2 | | | | |
| 438 Cac 700 | 2 2 1 | 0 0 | | | | |
| 442 Port 709 | 2 1 0 | 1 2 | | | | |
| Sample 4 |     |    |    |    |    |   |
| 3 Evo⁷ 3 | 2 2 0 | 1 1 | | | | |
| 4 Evo 8 | 3 2 4 | 0 1 | | | | |
| 11 Evo 18 | 2 0 0 | 0 1 | | | | |
| 13 Evo 23 | 2 2 1 | 1 1 | | | | |
| 14 Evo 29 | 3 2 1 | 1 1 | | | | |
| 16 Evo 31 | 3 0 0 | 1 1 | | | | |
| 24 Evo 44 | 2 2 0 | 0 2 | | | | |
| 32 Evo 53 | 2 2 1 | 0 1 | | | | |
| 96 Far 163 | 2 2 0 | 1 1 | | | | |
| 146 Evo 236 | 6 2 1 | 1 1 | | | | |
| 151 Bej 243 | 3 0 0 | 0 0 | | | | |
| 174 Port 275 | 5 2 0 | 0 0 | | | | |
| 177 Port 279 | 2 1 0 | 0 0 | | | | |
| 249 Evo 370 | 1 0 0 | 0 0 | | | | |
| 342 Set 513 | 1 2 1 | 1 1 | | | | |
| 415 Port 637 | 6 0 0 | 1 1 | | | | |
| 432 Lei 676 | 3 1 2 | 1 1 | | | | |
| 438 Cac 700 | 2 2 1 | 0 0 | | | | |
| 498 Evo 862 | 1 2 0 | 1 1 | | | | |
| 618 Evo 1076 | 6 2 1 | 0 1 | | | | |

¹ID = specimen number in the ESPRIT database [45].
²DM = decorative motif.
³ST = structure.
⁴TT = tattoo straps.
⁵NK = neck.
⁶H = head.
⁷Abbreviations to the right of the class numbers refer to the geographic provinces shown in Fig. 5.
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The RI scores from all the exercises indicate that the data set has some consistency and phylogenetic structure. The sharp contrast observed for CI and RC values between the first two and the last two exercises indicates a significant difference related to the methodological parameters applied, specifically the switch from parameter US (unordered states) to parameter OS (ordered-states). In contrast, parameter WC, which implements different weights for a couple of characters, has no influence on the values.
This indicates that the suspected order of character states in the hypothesis is inaccurate.

We next created four trees per exercise and sample—three consensus trees (strict, semistrict, and 50% majority rule) and a bootstrap tree (Table 5). The result was 64 trees (16 × 4). We then reduced the number of trees to two in order to focus on those that best fit the expectations of Lillios’s hypothesis (Table 6). Those two trees come from exercise 2 (sample 3)—termed the “2/3 tree” (Fig. 6)—and exercise 4 (sample 2)—the “4/2 tree” (Fig. 7). Both are 50% majority-rule trees [80]; the 2/3 tree was unrooted, and the 4/2 tree was rooted. When PAUP* creates rooted trees, it sets polarity—the direction of character-state change—using outgroups selected by the analyst. The 4/2 tree (Fig. 7) was rooted using class 21 (Table 5), the class in the sample that displayed the highest number of presumed ancestral states in Lillios’s hypothesis. When PAUP* creates unrooted trees, its default is to start with the first taxon in the input list and build from there. PAUP* constructed the 2/3 tree using class 1 as a starting point. After examining the tree, however, we went a step further in favoring the hypothesis. We swapped class 146 for class 1 because it is another class that displays all or most of the presumed ancestral states in Lillios’s hypothesis. The CI, RI, and CR remained unaffected.

In general, the two trees have large sections that exhibit poor structural and topological resolution. Both have some large polytomies (unresolved branches) close to their roots. In the 2/3 tree (Fig. 6), the basal branching episode creates class 25, but it also creates nine unresolved branches (class 1 through class 361). The 4/2 tree (Fig. 7) has a basal polytomy, five branches of which (class 4 through class 8) are completely unresolved. Both trees also exhibit sections where relationships are more resolved. The 2/3 tree (Fig. 6), for example, contains a seven-class clade, shown in red, with considerable branching structure. The 4/2 tree (Fig. 7) also contains a seven-class clade, shown in green, that contains two smaller, multiclass clades.

Given the overall lack of deep structure, it is not surprising that no character is free of homoplasy. In the 2/3 tree (Fig. 6), only 9 of the 32 character-state changes are nonhomoplastic, and only 4 of

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Figure 4. Distribution map of the four data sets. Sample 1: red; sample 2: green; sample 3: blue; and sample 4: pink. Gray numbers reference plaques that belong to more than one sample. The names of Portuguese districts are Leiria (Lei), Lisboa (Lis), Setúbal (Set), Beja (Bej), Faro (Far), Évora (Evo), and Portalegre (Port), and the Spanish provinces are Cáceres (Cac) and Badajoz (Bad).

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those are synapomorphic (TT1→0 and NK1→0 at the base of the tree; DM6→5 at the next node up; and DM3→2 in the seven-class red clade). The character with a balance between nonhomoplasmatic (not necessarily synapomorphic) and homoplasmatic change is DM, which has four instances of the former and three of the latter. There are several reversals to ancestral states as a result of convergence. In the 4/2 tree (Fig. 7), only six changes are nonhomoplastic. Of these, four are synapomorphies (DM6→5, TT2→0 at the base; DM3→2 in the seven-class green clade; and H1→2 in the clade comprising classes 12 and 442). All characters exhibit at least one instance of homoplasy.

Discussion

Synapomorphies help resolve trees, but here our interest is primarily in the polarity of specific character states: How well does polarity meet the expectations of Lillios’s hypothesis? We identified the following expectations:

1. With respect to DM, states other than DM4 and DM6—the presumed ancestral states (Fig. 5)—should be located nearer to the branch tips;
2. ST2 (bipartite structure) is ancestral to ST1 (transitional) and ST0 (unipartite); and
3. H1 (inverted triangles) is presumed to be ancestral to H0 (no head), H2 (triangles and appendages), and H3 (appendages and figurative features).

To assess how well the expectations are met, we created the trees shown in Figs. 8 and 9. With two exceptions, the character-state transformations are the same as in Figs. 6 and 7, but they have been converted to binary states in which character-state changes either meet or do not meet expectations. The two exceptions are character states for NK and TT because, although Lillios [2] believes they have chronological significance, her hypothesis is silent as to their polarity. Based on its location on trees 2/3 and 4/2 (Figs. 6 and 7), character NK has no clear nonrandom patterning in the former, and it has the direction NK0→1 in the latter (three instances of convergence). With respect to character TT, there is no clear, nonrandom patterning.

How do the expectations fare in the 2/3 tree, which has weighted characters and unordered character states (Fig. 8)? In general, the majority of changes appear in the direction Lillios [2] suggested. Of the 19 changes, only 3 show an unexpected polarity, indicated by black boxes. Nevertheless, 13 are homoplasmatic changes, which are indicated by asterisks. Specific expectations are considered below:

1. Only one of the seven changes in character DM has an unexpected direction (three are homoplasmatic changes), the transition DM6→5 (zigzags→checkerboard) in class 21. The majority of the changes (five out of seven) are located on terminal branches and thus contribute nothing to the tree structure. Only two synapomorphies are consistent with the expected polarity: DM6→5 (herringbone→zigzags) in the large polytomy and then DM3→2 (zigzags→triangles), which creates the clad of seven classes.

2. Character ST has four changes that fit the expected polarity (three are homoplasmatic), and none is a synapomorphy. The ancestral state (ST2) is highly conserved, appearing in 15 of the 20 classes.

3. Character H exhibits eight changes (all involve homoplasy), four of them in the hypothesized direction and another four in the opposite direction, with repeated transitions H2→1 (triangle & appendage→absence) and H2→1 (triangle & appendage→triangle). In addition, the two H2→1 reversals are located in unexpected places along the tree. Instead of appearing close to the basal node (H1 is the ancestral state), they are at the branch tips of classes 32 and 189. Also, the ancestral trait (H1) is highly conserved, appearing in 15 of the 20 classes.

How do the expectations fare in the 4/2 tree, which has weighted characters and ordered character states (Fig. 9)? At first glance, portions of this tree also seem consistent with expected polarity. Only two of the 15 character-state changes are unexpected, although only four are nonhomoplasmatic. Specific expectations are considered below:

1. Five of the seven changes in character DM exhibit the expected polarity, but two of those are homoplasmatic. The only two synapomorphies that are consistent with the expected polarity are DM6→5 (checkerboard→zigzags) in the basal node and DM3→2 (zigzags→triangles), which creates the green clade.

2. All seven changes in character ST have the expected polarity, but all of them are homoplasmatic. Also, the ancestral state (ST2) is very conserved, remaining in 12 of the 20 classes.

3. The three changes in character H meet the expected polarity, but two are homoplasmatic. The one synapomorphy—H2→1 (triangle→triangle & appendage)—sorts only classes 12 and 442. The ancestral state (H1) is also highly conserved, remaining in 13 of the 20 classes.

What does the combined topology of two trees tell us about Lillios’s hypothesis, especially in combination with radiocarbon dates and stratigraphic information? With respect to character

| Exercise | Sample | Methods | Parameters | Outgroup |
|----------|--------|---------|------------|----------|
| 1        | 1      | PH5/ACT/BT | UC/US | UNRT |
| 1        | 2      | PH5/ACT/BT | UC/US | UNRT |
| 1        | 3      | PH5/ACT/BT | UC/US | UNRT |
| 1        | 4      | PH5/ACT/BT | UC/US | UNRT |
| 2        | 1      | PH5/ACT/BT | WC/US | UNRT |
| 2        | 2      | PH5/ACT/BT | WC/US | UNRT |
| 2        | 3      | PH5/ACT/BT | WC/US | UNRT |
| 2        | 4      | PH5/ACT/BT | WC/US | UNRT |

1. Parsimony Heuristic Search.
2. All Consensus Trees (strict, semistrict, and 50% majority rule).
3. BooTstrap.
4. Unweighted Characters.
5. Unordered States.
6. UNRooTed trees (no predefined outgroup).
7. Weighted Characters.
8. Ordered States.
9. ROOTed trees (predefined outgroup).

Table 5. Conditions of the four phylogenetic exercises.
DM, the data might appear at first glance to support Lillios’s prediction that plaques with herringbone and checkerboard decoration at the bottom may be the oldest forms. However, there are several reversals (DM3 → R4 [zigzags → checkerboard] and DM3 → R6 [zigzags → herringbone]) in both trees, which undermine the suspected relative late position of plaques containing zigzag decoration. Also, most changes in character DM occur at the branch tips in both trees, which reduces the consistency of this presumptive positive result (recall that DM was weighted in the heuristic searches).

Radiocarbon dates and stratigraphic information also call into serious question the proposed sequence, with several of the oldest dated plaques exhibiting the triangle motif at their base (DM2), as, for example, at Cova das Lapas I, in the district of Leiria, with a radiocarbon date of 4550±60 B.P. (3238–3108 B.C. [1 sigma]) [20], and the oldest level of Anta da Horta, in the Portalegre district of Portugal [81], with a radiocarbon date of 4480±40 B.P. (3332–3214 B.C. [1 sigma]) [81] (Table 1). According to Lillios’s hypothesis, triangles should be the most derived character state. Conversely, the checkerboard motif (DM4), supposedly the most ancestral in the suggested sequence of character states, is a late occurrence at Olival da Pega 2b, in the district of Évora, with three calibrated dates [82] that average 2830 B.C. (Table 1). With respect to stratigraphic positioning, plaques from the earliest levels at Anta da Horta exhibit the triangle motif (DM2) but so do those from later levels. There also are late plaques that exhibit zigzag motif (DM3), when, according to the hypothesis, they should be older than plaques with triangles.
With respect to character ST, character state ST₂ (bipartite) appears to be ancestral to ST₁ (transitional) and ST₀ (unipartite)—in line with predictions. In fact, the bipartite structure (ST₂) is highly conserved. The few relevant dates and available stratigraphic evidence support the conservatism in ST₂ as well as the derived nature of ST₀. Whereas dated bipartite (ST₂) plaques occur (in Cova das Lapas I, and Sala n° 1) at least throughout the period 4550 ± 60 B.P. to 4140 ± 60 B.P. (3238–3108 B.C., and 2876–2618 B.C. [1 sigma]), dated unipartite (ST₀) plaques occur only in the early part of the third millennium (from 4270 ± 40 B.P. [2917–2877] B.C. 1 sigma) in Anta de STAM-3. At Anta da Horta, all of the plaques in the oldest level are bipartite (ST₂), and the majority of plaques in the later levels are unipartite (ST₀).

Recall that predictions relative to character H are not well met in the 2/3 tree (Fig. 8), but they are, broadly, in the 4/2 tree (Fig. 9). There, the inverted-triangle head (H₁) is the ancestral character state, and appendages (H₂) and plain (H₀) are the derived states. H₁ is highly conserved in the 4/2 tree, and radiocarbon and stratigraphic data bear this out. At Anta da Horta [81], one of the two earliest plaques displays character-state H₁ and the other H₂. Plaques from the latest levels exhibit states H₀ and H₂. At Olival da Pega 2b [82], H₂ lasts throughout the sequence, becoming associated with other character states in the later levels.

Conclusions

The overall implications of Lillios’s hypothesis with respect to the evolutionary history of stone plaques on the Iberian Peninsula are not met by a phylogenetic model, even when the two best trees—one with weighted characters (the 2/3 tree) and the other with weighted characters and ordered character states (the 4/2 tree)—are considered. There are at least three possible causes for the poor and arbitrary topology of large sections of both trees, with numerous polytomies and instances of homoplasy:

1. The people who created the plaques were free to use any of the possible states in the design palette at any time and any place. If this were the case, however, we would expect to see unlimited and totally random character-state reversals, which is not the case.

2. There was a high rate of cultural borrowing or horizontal transfer of information among populations scattered across the southwestern Iberian Peninsula, which tended to swamp most of the phylogenetic signal. This would mean that different genealogical and heraldic clans (according to Lillios) shared and transferred much of the information reflected in this material culture, an assumption that would run counter to the hypothesis that the plaques were linked to specific lineages and/or clans.

3. There was a common ideological background (whether religious, apotropaic, and the like) to the use of plaques that overlay the southwestern Iberian Peninsula. This would entail a cultural system in which plaque design was based on a fundamental core idea, with a number of mutable and variable elements surrounding it.

We suspect number 3 was the case, at least in part. It seems reasonable to conclude that most cultures have a conservative “core tradition”—similar to Swadesh’s [42] “morphological kernel” of a language [43], [44]. The question is whether we can identify it [59]. We might start by examining how archaeologists have long viewed traditions, going back to Willey’s [83] definition: a line or related lines of development through time within the confines of a certain technique or constant. A tradition includes broad categories of such things as plaque designs that undoubtedly have value in expressing historical relationships when the relationships are confined to the geographic boundaries of cultures. We thus should not be surprised that some of the phylogenetic trees derived from the plaque data exhibit internal branching because cultural evolution is, after all, a process that produces cladogenesis [56].

Table 6. Parsimony heuristic search scores.

| Exercise | Sample | Number of Trees | Length of Trees | Consistency Index | Retention Index | Rescaled Consistency Index |
|----------|--------|-----------------|-----------------|-------------------|----------------|---------------------------|
| 1        | 1      | 69800           | 25              | 0.600             | 0.655          | 0.393                     |
| 1        | 2      | 54368           | 26              | 0.538             | 0.636          | 0.343                     |
| 1        | 3      | 21545           | 24              | 0.583             | 0.667          | 0.389                     |
| 1        | 4      | 73400           | 24              | 0.500             | 0.625          | 0.312                     |
| 2        | 1      | 73400           | 33              | 0.606             | 0.649          | 0.393                     |
| 2        | 2      | 71100           | 33              | 0.576             | 0.659          | 0.379                     |
| 2        | 3      | 71600           | 32              | 0.594             | 0.658          | 0.391                     |
| 2        | 4      | 69100           | 31              | 0.516             | 0.625          | 0.323                     |
| 3        | 1      | 72900           | 29              | 0.172             | 0.467          | 0.080                     |
| 3        | 2      | 72100           | 27              | 0.185             | 0.532          | 0.099                     |
| 3        | 3      | 71600           | 27              | 0.185             | 0.500          | 0.093                     |
| 3        | 4      | 71600           | 26              | 0.154             | 0.511          | 0.079                     |
| 4        | 1      | 70900           | 36              | 0.139             | 0.516          | 0.072                     |
| 4        | 2      | 72100           | 34              | 0.147             | 0.554          | 0.081                     |
| 4        | 3      | 72100           | 34              | 0.147             | 0.532          | 0.078                     |
| 4        | 4      | 72900           | 31              | 0.129             | 0.565          | 0.073                     |

Bold indicates samples with the best general scores for every exercise.

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Nor should we be surprised that within the broad trees comprising classes of Neolithic slate plaques from the southwestern Iberian Peninsula, several character-state polarities suggested by Lillios seem broadly successful. After all, people learn from those with whom they are culturally related and/or with those with whom they are in contact, and ideas as well as people move across the landscape. Thus we should expect some structure in the data. In fact, given the manner in which we stacked the analysis in favor of Lillios’s hypothesis, one might have expected more structure in the plaques from the southwestern Iberian Peninsula, irrespective of

Figure 6. Fifty-percent majority-rule consensus tree from exercise 2, sample 3. The tree, which uses weighted characters but unordered character states, has a CI of 0.594, an RI of 0.658, and an RC of 0.391. When generated by PAUP, the tree was unrooted, but it subsequently was rooted with class 146 to resolve the topology in favor of Lillios’s hypothesis. Numbers at nodes are bootstrap values. doi:10.1371/journal.pone.0088296.g006
Figure 7. Fifty-percent majority-rule consensus tree from exercise 4, sample 2. The tree, which uses weighted characters and ordered character states, has a CI of 0.147, an RI of 0.554, and an RC of 0.081. Numbers at nodes are bootstrap values.
doi:10.1371/journal.pone.0088296.g007
Figure 8. Fifty-percent majority-rule consensus tree from exercise 2, sample 3 (the 2/3 tree) showing character-state changes states according to the assumed polarities for characters DM, ST, and H. Changes of states for characters TT and NK do not appear here because Lillios’s hypothesis makes no assumptions about polarity. Numbers at nodes are bootstrap values.

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Figure 9. Fifty-percent majority-rule consensus tree from exercise 4, sample 2 (the 4/2 tree) showing character-state changes states according to the assumed polarities for characters DM, ST, and H. Changes of states for characters TT and NK do not appear here because Lillios’s hypothesis makes no assumptions about polarity. Numbers at nodes are bootstrap values.
doi:10.1371/journal.pone.0088296.g009
whether they served the purpose(s) assigned to them. Certainly the available stratigraphic evidence and radiocarbon dates do not impart clear chronological structure to the plaques, which is yet another strike against Lillios’s hypothesis that they served as genealogical mnemonic recording systems.

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Author Contributions

Conceived and designed the experiments: DGR MJO. Performed the experiments: DGR MJO. Analyzed the data: DGR MJO. Contributed reagents/materials/analysis tools: DGR MJO. Wrote the paper: MJO DGR.

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