Cave art, art and geometric morphometrics: Shape changes and the babirusa of Sulawesi

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Keywords
art, sulawesi, geometric, morphometrics:, shape, changes, cave, babirusa, art

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Abstract

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Keywords: cave art, Maros, Sulawesi, babirusa, geometric morphometrics

Introduction

Within the Maros cave site of Leang Timpuseng (Leang = ‘cave’; Timpuseng = ‘tapering’) in the southwestern peninsula of Sulawesi, a profile illustration of an animal has recently been dated using the uranium-thorium (UTh) method. The results show that this animal was depicted ~35,400 years ago, and is therefore one of the oldest naturalistic representations in the world (Aubert et al. 2014). The authors of this paper provisionally interpret the animal to be a representation of a female babirusa (see Figure 5.1), but allow the possibility that it could also
be an illustration of the Sulawesi warth pig, both of which are endemic suids of Sulawesi and both are present in the Late Pleistocene fossil record of this Indonesian island. Frantz et al. (2016), however, in their review of the evolution of Suidae, state that the Leang Timpuseng cave art is ‘clearly picturing a Babyrousa female’ (n.p., text box insert ‘The Enigmatic Babyrousa’).

Traditional morphometrics has been applied to analyse human hand and crocodile claw stencils (e.g. Galeta et al. 2014; Honoré et al. 2016) and naturalistic cave art depictions of horses and bison (Cheyne et al. 2009). The advantage of using geometric morphometrics over traditional morphometrics is that more complex patterns of 3D and 2D shape variance can be measured and their statistical values expressed (O’Higgins and Jones 2006; Rohlf 2015), though because of the number of ‘measures’ used in geometric morphometrics, studies that are limited in sample sizes are of necessity exploratory rather than conclusive (Cardini and Elton 2007). We appear to be the first to apply geometric morphometrics to cave art depictions, and the first to compare cave art depictions with historical and contemporary illustrations. Our inclusion of artistic illustrations as well as photographs is justifiable as it results in an exploratory analysis that compares like with like. The Leang Timpuseng representation is an artistic rendering, and therefore some of the ways that it may differ from photographs may be due to those features that are characteristic of how humans tend to depict real world objects. These include the influence of the materials and the medium in shaping a depiction (Gombrich 1977), as well as the role of human visual perception, memory, recall and recognition (e.g. Arnheim 1974; Gombrich 1977; Ramachandran and Hirstein 1999; Cavanagh 2005; Vogt and Magnussen 2007).

The babirousa of Sulawesi and its neighbouring oceanic islands have fascinated Europeans for centuries, and continue to do so today, primarily because of the adult male babirousa upper and lower canines, which take the shape of distinctive upward and posteriorly curved tusks (see Figure 5.2). It is for this reason that the animals have the Malay name of babirousa, or deer-pig (babi = ‘pig’, rusa = ‘deer’, with the Malay syntax noun + adjective). The size and curvature of these tusks varies between the known species of babirousa. The largest and most notably curved canines belong to the male Sulawesi babirousa (Babyrousa celebensis), which is thought to be currently extinct in the southwest peninsula of Sulawesi (Meijaard and Groves 2002) where the Leang Timpuseng cave art is located. This animal is also distinctive in that both the males and females display sparse or absent body hair, and both have a nearly hairless tail tuft. Comparatively little is known about the extinct B. bolabatensis, though its Late Pleistocene fossil remains are noted to be similar in tooth size to that of the extant Moluccan hairy/golden babirousa (B. babyrussa) from the Sula Islands and Buru (Hooijer 1950; Groves 1980). Although there are no fossil remains that have been identified as being hairy/golden babirousa in Sulawesi, it is possible that its past habitat included the southwestern peninsula (Meijaard and Groves 2002). The extant hairy/golden babirousa differs from the Sulawesi babirousa in that it is smaller, the males have shorter tusks, both sexes have a coat of long, relatively thick body hair, and both display a tail tuft that is well developed.
Compared to the babirusa, the Sulawesi warty pig (*Sus celebensis*) appears to have attracted very little European interest. This animal has a short mane, a coat of body hair that is often dark with a dark dorsal stripe, and its tail is long and simply tufted (Groves 1980, 1981). Where the Sulawesi warty pig differs from the babirusa is that while the adult males have similarly large canine-tusks, these are only weakly curved and the upper canines project laterally and occlude with the lower canines, and male warty pigs also possess three pairs of facial warts (Groves and Grubb 2011). The females of both the babirusa and the Sulawesi warty pig have small canines, which do not have the appearance of tusks, and it is likely for this reason that the females of both species are minimally represented in both photographs and illustrations.

Animals described variously as babirusa, babirussa, babiroussa, babyrous, babiroussa and babiruza have appeared in English texts since 1673 (Scott 1896). Internet image searches conducted between 2013–2016 indicate that historical illustrations (c. 1740–1860) depict both the hairy/golden babirusa (e.g. Beilby et al. 1790) (see Figure 5.3) and the Sulawesi babirusa (e.g. Werner 1835, 1830) (see Figure 5.4). The Sulawesi babirusa appears to predominate after about 1820, which is following the first living pair to be housed in a European zoo (*Jardin des Plantes*, Paris) (Renshaw 1907). No illustrations of the female hairy/golden babirusa, and just one historical profile illustration of the female Sulawesi babirusa, could be found during our internet searches (2013–2016). Only one contemporary image of a hairy/golden babirusa could be sourced (Naish 2010), and this is a stuffed exhibit housed in the Raffles Museum of Biodiversity Research (Singapore). Similarly, only one artistic illustration of the Sulawesi warty pig was able to be found, which is a scientific illustration dated to the mid-1800s (Reichenbach 1845), and while there are very few photographs of this animal published on the internet, we were able to source profile photographs of one male and one female.
As with the historical illustrations, there are not many contemporary illustrations (c. 1950 to present day) of the female babirusa. Furthermore, contemporary illustrations appear to only depict the Sulawesi babirusa, which include 3D sculptures accomplished in a variety of media (e.g. clay, cloth, metal, paper, wool), as well as 2D drawings and paintings. Where both the photographs and contemporary illustrations differ from historical illustrations is that the contemporary images show the babirusa in a wide variety of body orientations and from a range of different perspectives. Nearly all of the pre-photography illustrations, however, show the hairy/golden babirusa, Sulawesi babirusa and Sulawesi warty pig in a profile view, a characteristic that is also a global feature of Late Pleistocene cave art.

The Late Pleistocene preference for profile views may suggest this is evidence of an ancient pattern of global cultural exchange that has been sustained well into the late Holocene. This preference, however, is thought to be far more likely the result of how anatomically modern humans have evolved to visually process animals (e.g. Hodgson 2008, 2013, 2014; Dobrez and Dobrez 2013; Hodgson and Watson 2015). Profiles can more easily show the visually diagnostic characteristics of a particular animal (i.e. body shape, body proportions and salient anatomical features), and as a consequence profile depictions are more rapidly recognised (Dobrez and Dobrez 2013; Hodgson 2013). A further characteristic of artistic depiction is a tendency for exaggeration of what are perceived to be salient features. This occurs across all artistic media and regardless of the degree of abstraction or verisimilitude, though what is considered salient will vary according to time, place, what animal is being depicted and by whom (Bedaux 1996; Ramachandran and Hirstein 1999). In cave art, the more salient features are understood to be those that are more attended to during actual human–animal interactions, and are therefore recalled with greater clarity. Studies suggest that the sequence and extent of detail in the drawing process follows this order of salience: neck and body, head, legs, and tail (Cheyne et al. 2009; Hodgson 2008).

To summarise, there are four possible candidates for which animal was selected for depiction in Leang Timpuseng some 35,400 years ago. These are the Sulawesi babirusa, the hairy/golden babirusa, the extinct Babyrussa bolabatuensis and the Sulawesi warty pig. Only the extant candidates are able to be tested, and we include illustrations as well as photographs to carry out our analyses. This is because, due to human visual processing regarding how an animal is perceived, recalled and represented, no artistic illustrations, including naturalistic cave art depictions and scientific illustrations, are likely to be anatomically accurate renderings of an animal in profile. Instead, the illustrations will likely contain elements of emphasis and exaggeration, which are related to both what are perceived to be the diagnostic characteristics of an animal, and which aspects of the animal are seen to have the greater salience. Our 2D geometric morphometric exploratory analysis of the Leang Timpuseng cave art is therefore an estimation of:

(i) the extent to which the illustration accords with the body morphology of extant babirusa and the Sulawesi warty pig as depicted in profile photographs

(ii) how this Late Pleistocene cave art compares to historical and contemporary illustrations of the hairy/golden babirusa, Sulawesi babirusa and Sulawesi warty pig.
Materials and methods

Image data
All images (n=36) used in this analysis are profile depictions selected from over 200 images sourced from the internet over three periods (September 2013; August–September 2015; January 2016). As is discussed above, the Sulawesi warty pig, hairy/golden babirusa and females generally are unavoidably under-represented in the database. The image types and references to the image sources are as follows:

(i) photograph of the Leang Timpuseng cave art (Aubert et al. 2014)
(ii) photographs of male (n=5) and female (n=4) Sulawesi babirusa (see References, under Babirusa Photographs c. 2000)
(iii) photograph of a stuffed hairy/golden babirusa Museum exhibit (n=1) (Naish 2010), which for this analysis is taken to be equivalent to both a photograph of a living animal and an artistic illustration
(iv) photographs of male (n=1) and female (n=1) Sulawesi warty pig (see References, under Warty Pig Photographs c. 2000)
(v) historical and contemporary illustrations of male (n=18) and female (n=3) babirusa (see References, under Babirusa Art ~300 BP to present) and a historical illustration (n=1) of the Sulawesi warty pig (Reichenbach 1845). The selected historical representations are those that have an associated date of publication, which in most cases is likely later than the actual date of artistic production.

Landmark coordinates
Those images displaying a right profile were mirrored to the left and, using Adobe Photoshop CS2, all were rotated to best fit with the body orientation of the Leang Timpuseng cave art, referencing the hindquarters and start of the hind limbs. Because the Leang Timpuseng cave art can be interpreted as displaying a mane, two versions were entered into the analyses—one without and one with a mane. The landmarks (x, y coordinates) were digitised using tpsDig2, v.2.17, 2013 (Rohlf 2008). Anchor points consisting of 17 homologous landmarks were first identified following the anatomical features able to be identified in the Leang Timpuseng cave art. Because the cave art depicts the limbs as narrow ‘sticks’, which is a common feature of cave art animal profiles and possibly due to being low in the order of salience (Cheyne et al. 2009; Hodgson 2008), we do not include the shape of the fore or hind limbs, but only where the left lateral limbs intersect with the hindquarters, abdomen, trunk and chest. The anchor points were subsequently referenced to calculate 10 semi-landmark curves by length. Initial analyses indicated that variance in tail length and curvature exceeded all other variance, and because this was a significant difference between animals of the same genus, species and sex, only the anchor points for the base of the tail were included in the analyses.

The resulting 38 landmarks (16 homologous anchor landmarks and 9 curves comprising 22 semi-landmarks) are shown in Figure 5.5 and defined in Table 5.1. The lighter wireframe in Figure 5.5 shows the Leang Timpuseng cave art with a mane. In all other respects, the landmark sets (with and without a mane) are identical. Dark circles are the homologous landmarks, while the lighter, unnumbered circles are the semi-landmarks.
Figure 5.5: Landmarks used in the geometric morphometric analyses.
Source: Authors’ adaptation of Figure 5.1.

Table 5.1: Homologous landmark definitions.

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Anterior top of nose</td>
</tr>
<tr>
<td>2</td>
<td>Posterior end of the nose disc/posterior edge of the rhinarium</td>
</tr>
<tr>
<td>3</td>
<td>Proximal termination of the muzzle, at the point where the frontal starts to rise</td>
</tr>
<tr>
<td>4</td>
<td>Back of the head at the point where the occipital crest merges into the neck</td>
</tr>
<tr>
<td>5</td>
<td>Proximal onset of the neck, showing as a depression in front of the spine of the first thoracic vertebra or dorsal tip of the shoulder blade.</td>
</tr>
<tr>
<td>6</td>
<td>Most superior point of the back. Depending on sex, species and medium of depiction, this point can be at the rump, the loin or the anterior back region</td>
</tr>
<tr>
<td>7</td>
<td>Superior onset of the tail</td>
</tr>
<tr>
<td>8</td>
<td>Inferior onset of the tail</td>
</tr>
<tr>
<td>9</td>
<td>Posterior projected intersection of the left hind leg and hindquarter. This is the receding point where the biceps femoris crosses the gastrocnemius muscle</td>
</tr>
<tr>
<td>10</td>
<td>Anterior projected intersection of the left hind leg and the abdomen</td>
</tr>
<tr>
<td>11</td>
<td>Midway point between landmarks 10 and 12</td>
</tr>
<tr>
<td>12</td>
<td>Posterior projected intersection of the left front limb with the chest</td>
</tr>
<tr>
<td>13</td>
<td>Anterior projected intersection of the left front limb with the chest</td>
</tr>
<tr>
<td>14</td>
<td>Angle of neck where the neck merges into the lower jaw</td>
</tr>
<tr>
<td>15</td>
<td>Most anterior and inferior projecting point of the lower lip</td>
</tr>
<tr>
<td>16</td>
<td>Base of nose/upper lip</td>
</tr>
</tbody>
</table>

1 Although Babyrousa differs from Sus in the lack of a bony nose disc, the posterior dorsal termination of the rhinarium (wet snout in most mammals) can be clearly distinguished in the pictures of members of both genera.
Source: Authors’ analysis.

Geometric morphometric analyses

The landmark and semi-landmark coordinate data were uploaded into the statistical shape analysis software morphologika2, v.2.5 (O’Higgins and Jones 2006), which outputs the statistical variance arising from multivariate regression and Principle Components (PC) analyses as dynamic wireframes and Thin Plate Spline (TPS) deformation grids. In order to overcome the confounding variable of differences in size due to image type and resolution, all images were first Procrustes registered, which rotates and scales the landmark coordinates to best overall comparable fit. This also enables calculation of the Procrustes Distances (PD), which is the degree of overall morphological similarity between each of the images. The morphologika2 Procrustes registered coordinate data were also analysed using the palaeontological statistics software PAST, v.3.11, 2016 (Hammer et al. 2001). The PAST principle components analysis (relative warps) (PCA) replicates the PC results of morphologika2 and, in addition to the output being of
a higher image resolution than morphologika2 in the PC scatter plots, PAST includes minimal spanning trees (morphological distances between the shapes within individual PC pairings) and 95% confidence ellipses (a bootstrap value of 100 was used for all analyses).

The image datasets with which the two versions (with and without the appearance of a mane) of the Leang Timpuseng cave art were compared are listed below, together with the independent variables applied for the morphologika2 multivariate regression analyses:

(i) photographs of the babirusa and the Sulawesi warty pig (independent variables = image type; sex)
(ii) historical and contemporary illustrations of the hairy/golden babirusa, Sulawesi babirusa and the Sulawesi warty pig (1740–1860; c. 2000) (independent variables = year, sex)
(iii) all representations of the babirusa and the Sulawesi warty pig (photographs, historical illustrations, contemporary illustrations) (independent variable = image type).

**Results**

Because the number of landmarks (n=38) is greater than the total number of images (n=36) and exceeds the number of individuals in all of the multivariate regression analyses, the results are constrained to the significant correlation coefficients that include the largest variance (i.e. PC1 and PC2), and in these instances only the adjusted $r^2$ results are reported ($r^2$ expresses the size of the variance under the assumption that every independent variable explains the variance, whereas adjusted $r^2$ expresses only the variables that affect the dependent variables). However, the statistical significance of all of the results, regardless of size and power, need to be interpreted as indicative of trends that may, or may not, sustain with a larger and more representative database of images.

(i) **Photographs of babirusa and the Sulawesi warty pig (n=14)**

A multivariate regression by image type (cave art 1, photograph 3) accounts for 30% of the overall variance, which is significant ($p = 0.02$) and there are two significant partial regression coefficients, PC1 (adjusted $r^2 = 0.39$, $p = 0.01$) and PC2 (adjusted $r^2 = 0.23$, $p = 0.046$). The wireframe and TPS deformation grids resulting from this multivariate regression are shown in Figure 5.6, and indicate that the Leang Timpuseng cave art differs from the photographs in displaying a smaller and narrower head and neck, and a larger and more rounded shape to the hindquarters. When the photographs of the babirusa and Sulawesi warty pigs and the Leang Timpuseng cave art are analysed by sex, sexual dimorphism is insignificant. Sexual dimorphism accounts for 9.7% of the overall variance when the cave art is coded as indeterminate sex (the wireframes and TPS deformation grid arising from the multivariate regression analysis is shown in Figure 5.8). When the cave art is coded as female, the overall sexual dimorphism increases to 17.2%, but the multivariate regression remains statistically insignificant ($p = 0.08$).
Figure 5.6: Leang Timpuseng cave art compared to photographs.

Wireframes and Thin Plate Spline deformation grids of how the cave art differs from the photographs (left), and how the photographs differ from the Leang Timpuseng cave art (right) following a multivariate regression with image type (cave art, photograph) as the independent variable.

Source: Authors’ adaptations of Figure 5.5.

PCA (relative warps) of the Procrustes registered landmark coordinates in PAST shows the Leang Timpuseng cave art falls well within the 95% confidence ellipsis, and the minimal spanning tree indicates the cave art is most similar to a photograph depicting a young adult female Sulawesi babirusa. Within morphologika2, the PD between the Leang Timpuseng cave art and the photographs (range 0.011–0.226) replicates the results of the PAST minimal spanning tree, with the Leang Timpuseng cave art having greatest morphological similarity to (lowest PD from) the same young adult female Sulawesi babirusa (PD = 0.128). This is followed by a photograph of a mid-adult female Sulawesi babirusa (PD = 0.142) and, third, the male hairy/golden babirusa Museum exhibit (PD = 0.158).

Overall, these results indicate that the Sulawesi babirusa, which dominate the group, may have a low level of sexual dimorphism in body shape. The morphology of the Leang Timpuseng cave art, however, is most similar to that of a young Sulawesi babirusa female, and given that coding of the cave art as female nearly doubles the variance due to sexual dimorphism, it is possible that the Leang Timpuseng cave art may be depicting a female body morphology in a more exaggerated form.

(ii) Artistic depictions of babirusa and the Sulawesi warty pig (n=28)

The multivariate regression analysis by chronology shows there is a significant shape variance according to when the artistic depictions were published (overall variance 20.7%, \( p = 0.001 \)). This analysis results in the first two PCs being significant correlation coefficients (PC1 adjusted \( r^2 = 0.48, p = 0.0001 \); PC2 adjusted \( r^2 = 0.24, p = 0.008 \)), which are shown in Figure 5.7. The scatter plot of PC1 (horizontal x axis) and PC2 (vertical y axis) shows the clustering of the Leang Timpuseng cave art (black dots: LTCA, LTCAm, where m = with mane), historical illustrations (numbers are year of publication) and contemporary illustrations (Mod, ModF, where F = female). The hairy/golden babirusa illustrations are enclosed in a rectangle in the negative values of PC1; the filled square (HGB) is the photograph of the hairy/golden babirusa museum exhibit. Historical illustrations of the Sulawesi babirusa and warty pig (the warty pig is shown as a triangle) are nearly all enclosed in the adjacent rectangle. Modern illustrations are nearly all enclosed in the largest rectangle within the high positive values of PC1. The wireframes show the statistical trend of each PC axis and are taken from the maximum values for individuals on each axis. See the Legend for more detail regarding coding of the symbols.
Figure 5.7: Changes to babirusa illustrations over time.
Source: Authors’ data.

As can be seen, PC1 is separating the depictions by species as well as by chronology. The Leang Timpuseng cave art has the most negative values on PC1, followed by the historical illustrations of the male hairy/golden babirusa. The historical illustrations of the Sulawesi babirusa tend to have close to the mean and positive values, while the contemporary artistic illustrations of the Sulawesi babirusa have the highest positive values on PC1 because they display a larger neck and body shape. The hairy/golden babirusa museum exhibit clusters with the historical illustrations of this species, while the historical illustration of the Sulawesi warty pig is located between the historical illustrations of the hairy/golden babirusa and the historical illustrations of the Sulawesi babirusa.
Although female babirusa and the Sulawesi warty pig are under-represented in the historical and contemporary illustrations, when sexual dimorphism is examined the multivariate regression attains significance, and this significance is sustained whether the Leang Timpuseng cave art is coded male (7.1% overall variance, \( p = 0.03 \)), indeterminate (6.9% overall variance, \( p = 0.03 \)) or female (9.3% overall variance, \( p = 0.02 \)). For all analyses, the sexual dimorphism manifests as the females displaying a smaller head, narrower neck, broader mid-section and larger, higher and more rounded hindquarters, which is similar to how the Leang Timpuseng cave art is morphologically differentiated from the dataset of photographs (see Figure 5.6). How these sexually dimorphic features are more exaggerated in the artistic depictions than the statistically insignificant sexual dimorphism of the photographs is shown in Figure 5.8 (for both of these multivariate regressions the sex of the Leang Timpuseng cave art is coded as indeterminate).

**Figure 5.8: Sexual dimorphism in illustrations and photographs.**

Wireframes showing how male (far left) and female (centre) depictions differ following a multivariate regression with sex as the independent variable. The upper row is the degree of sexual dimorphism in the illustrations (historical and contemporary) and the lower row is the sexual dimorphism as displayed in the photographs. The Thin Plate Spline deformation grids indicate how the females differ in morphology from the males.

Source: Authors’ adaptations of Figure 5.5.

PCA (relative warps) of the Procrustes registered landmark coordinate data in PAST shows the Leang Timpuseng cave art pairs fall outside the 95% confidence ellipsis for the artistic illustrations. Within the minimal spanning tree for PC1/PC2, the closest individual to the Leang Timpuseng cave art is a male hairy/golden babirusa illustration that was published in 1835. When the PD output of morphologika2 is examined (range 0.011–0.232), a historical depiction of the hairy/golden babirusa illustration published in 1856 is closest in overall morphology to the cave art (PD = 0.133 to the version with a mane, PD = 0.135 to the version without a mane), followed by the same 1835 hairy/golden babirusa illustration that was linked to the cave art within the PCA (relative warps) minimal spanning tree.

What this analysis of the artistic illustrations shows is that sexual dimorphism tends to be exaggerated in the historical and contemporary illustrations, with this sexual dimorphism increasing only slightly when the Leang Timpuseng cave art is coded as female. However, despite the Leang Timpuseng cave art displaying a more female body morphology, within the group of illustrations the cave art is most similar, morphologically, to the historical illustrations of the hairy/golden babirusa—all of which are depicted bearing distinctively curved tusks and therefore all of which can be assumed to be male.
(iii) Photographs and artistic depictions of babirusa and the Sulawesi warty pig (n=36)

Figure 5.9 is a scatter plot of PC1 (horizontal x axis) and PC2 (vertical y axis) showing the Leang Timpuseng cave art (black dots), illustrations (open shapes), the hairy/golden babirusa museum exhibit (filled orange square), and photographs (other filled shapes). Most of the photographs and contemporary illustrations are in the positive values of PC1 and enclosed in an ellipse. The historical illustrations are enclosed in an ellipsis within the negative values of PC1. The wireframes show the statistical trend of each PC axis, and are taken from the maximum values for individuals on each axis. Thus, when the photographs and illustrations of the babirusa and Sulawesi warty pigs are analysed together, it can be seen that they cluster together, and are morphologically distinct from both the Leang Timpuseng cave art and the historical illustrations of the hairy/golden babirusa, Sulawesi babirusa and Sulawesi warty pig. Also, the dynamic wireframes extracted from PC1 and PC2 indicate that both the photographs and the contemporary illustrations of the Sulawesi babirusa display an animal with a more downwards head orientation and a fatter neck and body than the historical illustrations and the Leang Timpuseng cave art.

Figure 5.9: Babirusa illustrations compared to photographs.
Source: Authors’ data.
The overall variance of the photographs and illustrations is sexually dimorphic when the Leang Timpuseng cave art is coded as being of indeterminate sex (overall variance due to sex 6.7%, \( p = 0.01 \)). This overall dimorphism rises slightly (8%, \( p = 0.001 \)) and PC2 is a significant correlation coefficient for sexual dimorphism when the Leang Timpuseng cave art is coded as female (PC2 adjusted \( r^2 = 0.154, p = 0.01 \)). It is the negative values that are associated with female body morphology on PC2 and, as can be seen in Figure 5.9, the Leang Timpuseng cave art is located with the photograph of a female Sulawesi warty pig at the extreme of the negative PC2 values (< −0.10).

Within the PCA (relative warps) minimal spanning tree for PC1/PC2, the Leang Timpuseng cave art is closest to a hairy/golden babirusa with a publication date of 1749. The morphologika2 PD pattern (range 0.011–0.232) repeats the previous analyses and shows the Leang Timpuseng cave art to be closest in overall morphology to the same photograph of a young adult female Sulawesi babirusa (PD = 0.128). This is followed by the same two historical images of hairy/golden babirusa (illustration from 1856, PD = 0.135; illustration from 1835, PD = 0.137), with the Leang Timpuseng cave art 'with mane' version being closest to the 1856 hairy/golden babirusa illustration (PD = 0.133).

To summarise, what these analyses of the complete dataset (Leang Timpuseng cave art, historical illustrations, contemporary illustrations and photographs) suggest is that the Leang Timpuseng cave art is most similar, morphologically, to the golden/hairy babirusa (all of which are illustrations of males), but shares morphological affinity with the female form, at least in so far as this is represented in a photograph of a young adult female Sulawesi babirusa. The Leang Timpuseng is not, however, morphologically similar to either the relatively slender historical illustrations of male and female Sulawesi babirusa, or the somewhat fatter contemporary illustrations of these animals.

**Discussion**

The geometric morphometric analyses, while not conclusive due to the ratio of landmarks to images, do suggest that the Leang Timpuseng cave art is morphologically similar to young adult female Sulawesi babirusa, and that the sexual dimorphism of the dataset is more evident in the illustrations than the photographs. However, despite the Leang Timpuseng cave art displaying female characteristics that include (in addition to the lack of clearly visible tusks) a comparatively small head, narrow neck, rounded and higher hindquarters and a wider mid-section, the Leang Timpuseng cave art does not cluster with any of the historical or contemporary illustrations of male and female Sulawesi babirusa. Instead the Leang Timpuseng cave art shows a closer morphological affinity to historical illustrations of the male hairy/golden babirusa.

A summary of the findings indicated by these analyses are that:

(i) Both the photographs and the contemporary illustrations depict an animal that is fatter and displays a more downwards head pose than the historical illustrations. This is possibly because the contemporary photographs are predominantly of grazing zoo babirusa, which may tend towards obesity. It is also likely that many, if not all, of the contemporary illustrations are sourced from photographs of zoo babirusa and/or living zoo babirusa. In contrast, nearly all of the historical illustrations depict an animal with an upright head pose and a relatively slender body. A noted exception to this trend is the downwards head pose of the only historical illustration that was able to be sourced of a female babirusa.
Photographed Sulawesi babirusa tend to display a limited level of sexual dimorphism. This, however, may be in part due to the obesity levels displayed by most of the babirusa photographed. Two notable exceptions are the photographs of a young adult female Sulawesi babirusa and a female warty pig, both of which were photographed in the wild. It is the young adult female Sulawesi babirusa that, when it is included in the analyses, bears the highest morphological similarity (lowest PD) to the Leang Timpuseng cave art.

Allowing for the compounding variable of zoo babirusa obesity, both the contemporary and historical illustrations of the babirusa appear to exaggerate sexual dimorphism, and this characteristic may also be a feature of the Leang Timpuseng cave art. However, the cave art does not cluster with any of the illustrations of female Sulawesi babirusa. This may be because two depict the female babirusa with a more downwards head orientation—in one (c. 1835) the female babirusa is nurturing an infant, while in the other (c. 1950) the female is shown with a lower head orientation than the male that accompanies her. Somewhat in contrast, although comparatively slender and displaying an upwards head pose, the third illustration of a female babirusa (c. 2000) is similar in head size and hindquarter morphology to the males. In effect, this illustration has the head and body of a male babirusa lacking tusks, and this may explain why this artwork clusters with the male historical illustrations in all of the analyses that include it. Therefore, the Leang Timpuseng cave art would appear to be the only illustration of a morphologically female suid displaying a comparatively active body pose.

On balance, the evidence, limited as it is, suggests the Leang Timpuseng cave art does depict a female suid. This is not just because of the absence of canine-tusks in the image, which could have been depicted using a less resilient material and therefore may have disappeared with the passage of time, but because the body morphology is more clearly female than male. The evidence is also that the Leang Timpuseng cave art may depict a babirusa, but not necessarily a Sulawesi babirusa. The analyses repeatedly link the cave art's overall morphology to historical illustrations of the hairy/golden babirusa, and never to any illustrations of the Sulawesi babirusa (females and males) or the illustration of the Sulawesi warty pig (sex indeterminate).

Two features of the Leang Timpuseng cave art that were not captured by the geometric morphometric analyses, but that also suggest the cave art may not be of the Sulawesi babirusa, are (i) the inscription of what appear to be relatively horizontal lines within the body of the animal, and (ii) the shape of the tail tuft. As noted, the Sulawesi babirusa has scarce body hair and is distinctive in displaying vertical skin folds, which are described by Renshaw (1907:171) as 'wrinkled transversely [sic] like a maggot's'. The golden/hairy babirusa is, as its name suggests, hairy and, as with the Leang Timpuseng cave art, in all of the historical illustrations of this animal the coat is depicted with short lines running horizontally across the body and converging beneath the tail. The Leang Timpuseng cave art, however, differs from both the Sulawesi babirusa and the hairy/golden babirusa in the depiction of the tail. The hairy/golden babirusa has a distinctive tail tuft, and an early description is that the tail is both long and twisted (Beilby et al. 1790), while the Sulawesi babirusa has a relatively straight and minimally tufted tail. The tail of the Leang Timpuseng cave art is not long, does not appear to be tufted, but it is twisted. This may be due to the depicted animal not having a tail tuft, having this detail lost through weathering and time, and/or this aspect of the animal having, like the legs, less salience for the artist. Another possibility that cannot be ruled out given the composition of the images in this analysis is that the Leang Timpuseng cave art is a depiction of a Sulawesi warty pig. The Sulawesi warty pig is also hairy, has a long and simply tufted tail, and has a mane, which may or may not be present.
in the Leang Timpuseng cave art (and thus two versions were used for the analyses). However, while Aubert et al. (2014) allow for this possibility, Frantz et al. (2016) state that it is clear that the Leang Timpuseng cave art depicts a female babirusa, and not a warty pig.

Overall, this study suggests that the Leang Timpuseng cave art is a depiction of a female hairy/golden babirusa, which to date does not appear in the published fossil record of Sulawesi. The fossil record of the southwestern peninsula does, however, contain the remains of an extinct babirusa, *Babyrousa bolabatuensis*, which is similar in tooth size to the hairy/golden babirusa (Hooijer 1950; Groves 1980), and it is possible that the hairy/golden babirusa once inhabited this part of Sulawesi. However, until more images of the Sulawesi warty pig, the hairy/golden babirusa and females of both animals can be sourced, the only relative certainty is that this analysis shows that:

(a) geometric morphometrics can be used to meaningfully analyse the anatomical characteristics of cave art depictions

(b) sexual dimorphism is more apparent or exaggerated in both the Leang Timpuseng cave art and the illustrations than photographic depictions

(c) the Leang Timpuseng cave art differs from both historical and contemporary European depictions in that it shows a morphologically female suid in an active pose.

**Conclusion**

Due to the limitations of the sample size, the limited representation of the Sulawesi warty pig in both photography and art, the absence of hairy/golden babirusa in photographs and the absence of any photographs or illustrations depicting a female hairy/golden babirusa, the results of the analyses conducted here are at best indicative. What the results do seem to suggest is that the Leang Timpuseng cave art is most likely female, and is most similar to later, historical depictions of the hairy/golden babirusa. If this is the case, then the Leang Timpuseng cave art would appear to be not just the oldest, or amongst the oldest, naturalistic cave art depiction (Aubert et al. 2014), but is possibly also a depiction of a female hairy/golden babirusa (which is not currently known to occur on the island of Sulawesi) or a female of the extinct *Babyrousa bolabatuensis*, whose fossilised remains have been noted as being somewhat similar to that of the hairy/golden babirusa (Hooijer 1950; Groves 1980).

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