

# Scutes for Sturgeon Size Reconstruction: Traditional and Geometric Morphometric Techniques Applied to *Acipenser sturio* and *A. oxyrinchus*

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**RESUMEN:** Se exploran alternativas tradicionales y de morfometría geométrica en la inferencia de la talla del esturión europeo (*Acipenser sturio*) y Atlántico (*A. oxyrinchus*) a partir de placas dérmicas. La correlación existente entre la longitud del pez y diferentes medidas de las placas dérmicas fue evaluada a través de regresiones lineales utilizando 58 esturiones en colecciones de museos. Dado que la precisión de tal técnica era limitada se exploró la posibilidad de determinar la posición de placas dérmicas aisladas dentro de la serie corporales en función de su forma y dimensiones. Aunque en las filas laterales y dorsales la forma y tamaño de las placas cambia a lo largo del eje antero-posterior, las diferencias son demasiado graduales para poder establecer la posición original de una placa dentro de la serie. También se constataron las diferencias de talla y forma en placas procedentes de esturiones de distinto tamaño, pero estas tampoco eran suficientemente marcadas como para realizar una estimación precisa de la talla corporal. Se concluye por ello que las placas dérmicas aisladas no pueden proporcionar estimaciones precisas de la talla corporal. No obstante, los modelos de regresión que presentamos permiten verificar si tanto las placas dérmicas laterales como las dorsales pertenecieron a esturiones de más de un metro de longitud. En caso afirmativo, las placas pueden ser identificadas a nivel de la especie a través de su ornamentación al tratarse ésta de un carácter dependiente de la talla.

**PALABRAS CLAVE:** RECONSTRUCCIÓN DE LA TALLA, MORFOMETRÍA GEOMÉTRICA, MORFOMETRÍA TRADICIONAL, PLACA DÉRMICA, *ACIPENSER STURIO*, *ACIPENSER OXYRINCHUS*

**ABSTRACT:** Different traditional and geometric morphometric approaches are explored for the size reconstruction of European (*Acipenser sturio*) and Atlantic sturgeon (*A. oxyrinchus*) on the basis of isolated bony scutes. The relationship between fish length and different scute measurements was tested with linear regressions using 58 modern sturgeons from museum collections. As the accuracy of this approach was limited, we explored the possibility of determining the position of an isolated scute within its row on the basis of its shape or dimension. In the dorsal and lateral rows, the shape and dimension of the scutes change along the antero-posterior axis, but this difference is too gradual to allow establishing the original position of an isolated scute within the row. No consistent changes in the shape or dimensions of ventral scutes were observed according to their place within the row. Differences in scute shape or dimensions between large and small animals have been documented as well, but these differences were not sufficiently pronounced for an accurate estimation of size. We conclude that isolated scutes cannot provide very accurate fish length reconstructions. However, the regression models presented in this study,

allow verifying whether individual lateral and dorsal scutes belonged to sturgeons larger than 1 m total length. In that case they can be identified to species level on the basis of their surface ornamentation, which is size dependent.

KEYWORDS: SIZE RECONSTRUCTION, GEOMETRIC MORPHOMETRICS, TRADITIONAL MORPHOMETRICS, SCUTE, *ACIPENSER STURIO*, *ACIPENSER OXYRINCHUS*

## INTRODUCTION

Relationships between fish size and measurements taken on isolated skeletal elements are provided in the literature for numerous fish species (e.g. Leach *et al.*, 1996; Harvey *et al.*, 2000; Thieren *et al.*, 2012). These equations are used for the back-calculation of fish lengths of archaeological remains, which provide information on former fishing methods, exploited fishing grounds, selective consumer behavior and human impact on fish populations through time (Greenspan, 1998; Leach & Davidson, 2001). When dealing with sturgeon remains from Western European sites, it is essential to first reconstruct fish size of the skeletal elements that need to be identified to species. The distinction between archaeological dermal bones of the two European sturgeon species, *Acipenser oxyrinchus* Mitchell 1815 and *A. sturio* Linnaeus 1758, can be made by the difference in the bone's surface structure, with *A. sturio* having a 'tubercular' surface pattern and *A. oxyrinchus* an 'alveolar' pattern (Magnin, 1964; Desse-Berset, 2009). However, this pattern is to some extent size dependent (Wuertz *et al.*, 2011; Thieren *et al.*, in press). Large *A. oxyrinchus* display the alveolar ornamentation type in most cases, but the ornamentation of small *A. oxyrinchus*, less than 1m total length (TL), is similar to that of *A. sturio*, and this on the scutes as well as on the bones of the head and pectoral girdle (Thieren *et al.*, in press). Therefore, it is important to establish the size of archaeological remains with a tubercular ornamentation pattern before assigning them to species. Skeletal elements of the head and the pectoral girdle allow a rather accurate size estimation (Thieren & Van Neer, 2014). These bones are frequently retrieved from archaeological excavations, and often sufficiently preserved to allow size reconstruction. However, since scutes are more numerous in archaeo-ichthyological assem-

blages it is worth investigating their potential for fish length reconstruction.

Dermal scutes are found in all acipenserids and occur in 5 rows alongside the body (Figure 1). Besides one median dorsal row, there is a lateral and ventral row on each side of the body, with the number of scutes depending on row and species. *A. oxyrinchus* has 7 to 16 dorsal scutes, 24 to 35 lateral and 6 to 14 ventral scutes, while *A. sturio* has 9 to 16 dorsal, 24 to 40 lateral and 8 to 15 ventral scutes (Jordan, 1910; Vladykov & Beaulieu, 1946; Mohr, 1952; Magnin, 1964; Vasil'eva, 1999; Vecsei *et al.*, 2001; Desse-Berset, 2011; Wuertz *et al.*, 2011). The number of scutes varies between individuals, and, in the case of the paired rows, sometimes even between the left and right row of the same individual (Vladykov & Beaulieu, 1946). Both *A. oxyrinchus* and *A. sturio* keep their scutes throughout their lives with size and thickness increasing during growth (Magnin, 1963). Resorption of scutes observed in other sturgeon species, e.g. *A. fulvescens* (Peterson *et al.*, 2007), has not been reported in *A. sturio* and *A. oxyrinchus*.

Scutes vary considerably in shape and size between rows and also within each row. However, determining the row from which an isolated scute is derived, is straightforward if the element is sufficiently well preserved. Dorsal scutes are symmetrical and dihedral, and they have a distinctive median crest (Magnin, 1963). An unornamented articulation area can be seen in their anterior part (Figure 1c). The dorsal scute row starts from the median nuchal plate which is fully incorporated in the skull roof and ends with the last large scute before the dorsal fin basal fulcrum. Although the fulcrum has a different shape compared to the dorsal scutes, some authors (e.g. Brinkhuizen, 1986; Desse-Berset, 2011) consider this element as the last dorsal scute. Sometimes one or two pairs of smaller bony plates are situated between the last

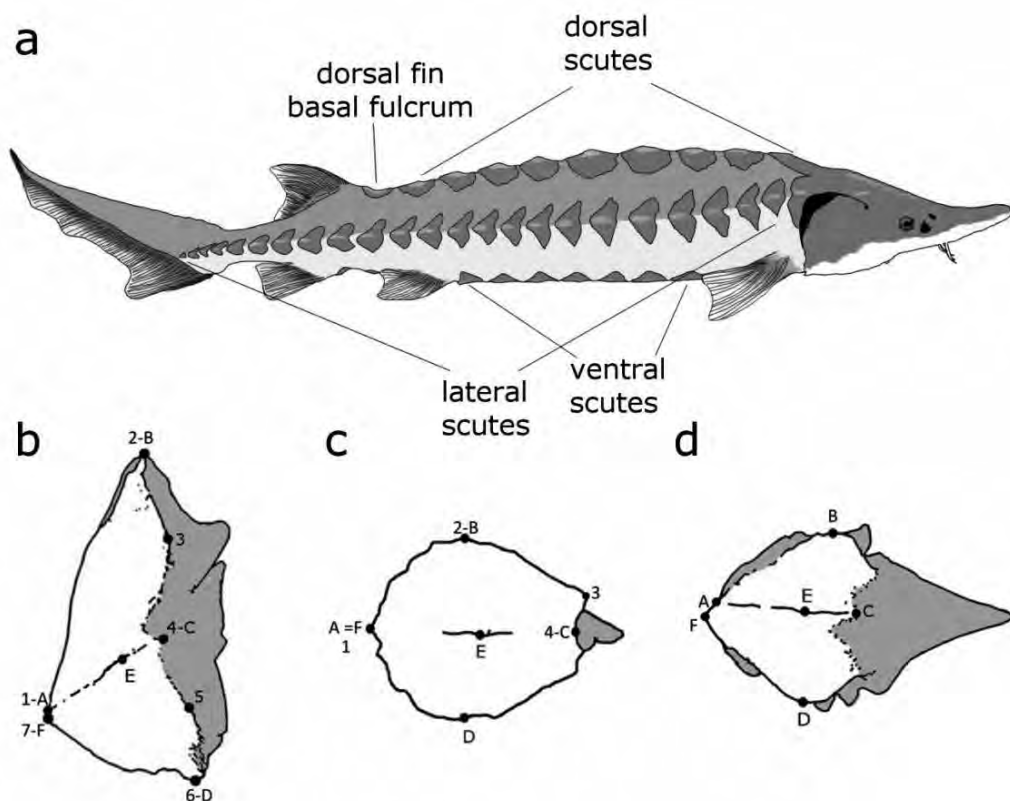


FIGURE 1

Overview of the scutes. a. Complete individual with the dorsal, lateral and ventral scutes; b. Isolated right lateral scute; c. Isolated dorsal scute; d. Isolated right ventral scute. The unornamented articulation area is indicated in grey. Following measurements were defined: M1: B-D; M2: A-C; M3: F-E; M4: B-E; M5: B-C; M6: B-F; M7: D-E; M8: D-C; M9: D-F. Landmarks on lateral scutes (b) are labelled 1 to 7: 1. The point where the keel ends caudally; 2. The dorsal point of the scute 3. Curve point in the upper scute wing, 4. The anteriormost point of the keel in the ornamented part of the scute; 5. The curve point in the lower scute wing; 6. The ventral point of the scute; 7. The posterior point of the scute. Landmarks on the dorsal scute (c) are labelled 1 to 4: 1. The posterior point of the scute; 2. The left lateral point of the scute; 3. Curve point; 4. The anteriormost point of the keel in the ornamented part of the scute.

‘regular’ dorsal scute and the dorsal fin fulcrum, but these are not considered dorsal scutes. These additional scutes are rounded, they are without the longitudinal crest and do not have the characteristic anterior articulation area.

The lateral scutes are situated on the right and left side of the body at the level of the lateral line. The shape of the lateral scutes is more or less rhomboid, with the crest of the scute usually coinciding with the short diagonal of the rhomboid (Sewertzoff, 1926; Brinkhuizen, 1986) (Figure 1b). Magnin (1963) describes the shape of lateral scutes as triangular, wider than their length and pointing backwards, with the articulation area situated at the base of the scutes. This area does not display any surface structure and lies underneath the previous

scute in small animals. The lateral row starts directly behind the supracleithrum, although some authors (e.g. Vladykov & Beaulieu, 1946) consider that bone as the first lateral scute. The last scute with a ridge or crest along its short axis is considered as the last scute.

The ventral scutes occur medio-caudally of the clavicles between the pectoral and pelvic fins. They are also paired and resemble the dorsal scutes but are asymmetrically shaped (Figure 1d). The last scute, and sometimes also the first one, have an aberrant shape, with the last one being more rounded and the first one irregularly shaped.

In addition to the aforementioned scutes, smaller bony plates are situated between the pelvic and anal fin (pre-anal scutes), next to the anal fin base

and behind the anal fin (post-anal scutes). These scutes are not further considered in this study. Their shape is very similar to that of the dorsal pairs of smaller scutes mentioned above: they are rounded and without the distinctive crest and characteristic unornamented articulation area.

Attempts have been made before to reconstruct the length of sturgeons from their scutes. For example, van Maren (1971) back-calculated the total length of sturgeon remains from the Neolithic site of Vlaardingen (the Netherlands) by comparing the archaeological scutes with a single modern museum specimen of known size. However, it is unclear how the original position of an archaeological scute within the row was determined in that study. Since the dimensions of scutes vary considerably within one row, this method may have been somewhat inaccurate and the results of van Maren (1971) should therefore be interpreted with caution. Brennan & Cailliet (1989) described a linear relationship between the TL of white sturgeon (*A. transmontanus*) and the width of the median nuchal plate, and between TL and dorsal scute length. It is not mentioned explicitly which dorsal scutes were considered for these relationships. Benecke (1986) calculated total lengths of up to 5 m for archaeological sturgeons from Ralswiek (Germany) by comparing the dorso-ventral and postero-anterior lengths of archaeological scutes to those of the scutes from one recent specimen of known size. Debus (1999) recalculated the total lengths of the same remains, using a linear regression of TL on the dorso-ventral length of the largest lateral scute from 33 Baltic sturgeons (then assumed to be *A. sturio*) and obtained a maximum length of 2.75 m. This method will result to some extent in an underestimation of the TL since it is based on the dimensions of the largest lateral scute of modern sturgeons, and because evidently not all archaeological scutes used for size reconstruction will have been the largest of the sturgeon from which it is derived.

Brinkhuizen (1989: 254-255) used an alternative approach and took into account the size variation along the lateral scute row by providing a minimum and maximum TL estimation for each measurable archaeological scute (assumed to be *A. sturio*). Using 4 museum specimens as a reference, he calculated two least square regressions between the greatest height of the lateral scute and TL of the sturgeon, namely one for the smallest and one for the largest scute of each modern individual. These two regression equations were then used

to establish the minimum and maximum length corresponding to 6 lateral archaeological scutes from the Roman site of Velsen (the Netherlands), all assumed to come from the same animal. The size reconstruction ranged between 96 cm - based on the largest archaeological scute assumed to be the largest within the original scute row - and 126 cm, based on the smallest archaeological scute assumed to be the smallest scute within the row.

Finally, using 9 reference specimens, Desse-Berset (2011) constructed a regression model to calculate the TL of *A. oxyrinchus* from the width of the dorsal scute. The model was based on the mean of the widths of the dorsal scutes, excluding both the first scute (the so-called nuchal plate) and the dorsal fin basal fulcrum. The author stipulates that the estimation of the TL would be more precise if the place of the scute within the row could be determined more precisely.

In the present paper, we further explore the possible value of scutes for size reconstruction using three different approaches. The first one is a direct back-calculation of TL based on the regression of TL on different scute measurements. Secondly, we tried to improve the former approach by estimating the position of an individual scute within its row through measurements or through its shape. As a third approach, measurements and shape of individual scutes were used to define size classes.

## MATERIAL & METHODS

In this study, 58 dry mounted or liquid preserved *A. sturio* and *A. oxyrinchus* specimens from different European museum collections were used as reference material (Table 1). These include 19 *A. sturio*, 27 *A. oxyrinchus*, 5 hybrids and 7 *A. oxyrinchus/A. sturio* (indet.) (for species identifications, see Thieren *et al.*, in press) with sizes ranging between 17.7 and 276 cm TL. For 32 of these specimens, the morphological species identification was confirmed through genetic analysis, either through our own analysis (Thieren *et al.*, in press) or published data (Ludwig *et al.*, 2002; Chassaing *et al.*, 2013). Sixteen of them were identified as *A. oxyrinchus*, 11 as *A. sturio* and 5 as hybrid. The examined specimens were more or less complete, with the scutes still embedded in the animal, for this reason only the visible part of the scute, the part with surface structure, could be examined.

Nr	Specimen	Species
1	AML 8797	<i>A. oxyrinchus</i>
2	BAI 1884	<i>A. sturio</i>
3	DCB 721	<i>A. sturio</i>
4	KUL MD N/A	<i>A. oxyrinchus</i>
5	MHNN Z19398	<i>A. sturio</i> *
6	MHNN Z19558	<i>A. oxyrinchus</i> *
7	MHNN Z58274	<i>A. sturio</i> *
8	MHNN Z58275	<i>A. sturio</i> *
9	MNHN-IC-0000-3108	<i>A. oxyrinchus</i> *
10	MNHN-IC-0000-3110	<i>A. oxyrinchus</i> *
11	MNHN-IC-0000-3113	<i>A. oxyrinchus</i> *
12	MNHN-IC-0000-3115	Hybrid*
13	MNHN-IC-0000-3119	<i>A. sturio</i> *
14	MNHN-IC-0000-3574	Indet.
15	MNHN-IC-0000-4843	<i>A. oxyrinchus</i>
16	MNHN-IC-0000-9114	<i>A. oxyrinchus</i>
17	MNHN-IC-1969-0172	<i>A. oxyrinchus</i> *
18	MNHN-IC-B-2598	<i>A. oxyrinchus</i> *
19	MRSN N/A	<i>A. oxyrinchus</i>
20	NHM 1859.3.51.1	<i>A. oxyrinchus</i>
21	NHM 1865.5.23.3	<i>A. oxyrinchus</i>
22	NHM 1886.8.24.1	Indet.
23	NHM 1931.12.7.1	<i>A. sturio</i>
24	NHM 1986.5.21.1	Indet.
25	NHM 2005.6.22.6	<i>A. oxyrinchus</i>
26	NHM 2015.2.18.1	<i>A. sturio</i>
27	NRM 94	Indet.
28	NRM 1709	<i>A. oxyrinchus</i> *
29	NRM 8948	<i>A. sturio</i>
30	NRM 13336	<i>A. sturio</i> *
31	NRM 18265	<i>A. sturio</i>
32	NRM 21705	<i>A. oxyrinchus</i>
33	NRM 21707	<i>A. oxyrinchus</i> *
34	NRM 21708	<i>A. sturio</i> *
35	NRM 21710	<i>A. sturio</i> *
36	NRM 21712 (Large)	Hybrid*
37	NRM 21712 (Middle)	Hybrid*
38	NRM 21712 (Small)	Hybrid*
39	NRM 35435	<i>A. sturio</i> *
40	NRM 35438	<i>A. oxyrinchus</i> *

41	NRM 35439	<i>A. sturio</i> *
42	NRM 35442	<i>A. sturio</i>
43	NRM 36002	Indet.
44	NRM 36074	<i>A. oxyrinchus</i>
45	NRM 49317	<i>A. oxyrinchus</i> *
46	NRM 55538	<i>A. oxyrinchus</i>
47	NRM 60292	<i>A. oxyrinchus</i> *
48	NRM 60821	<i>A. oxyrinchus</i>
49	NRM 61784	<i>A. oxyrinchus</i>
50	RBINS 1528	<i>A. oxyrinchus</i> *
51	RBINS 24792	<i>A. oxyrinchus</i> *
52	RBINS 4449	<i>A. sturio</i>
53	RBINS N/A (1)	<i>A. sturio</i> *
54	RBINS N/A (2)	Hybrid*
55	RBINS N/A (5)	<i>A. sturio</i>
56	SML N/A	<i>A. oxyrinchus</i> *
57	UUZM UPSZTY 170	Indet.
58	UUZM UPSZTY N/A	Indet.

TABLE 1

List of the examined specimens. Genetic identifications are indicated with \*

### *Traditional morphometrics*

Traditional morphometry often uses distances between landmarks, angles and ratios to study the shape of objects. For our study we measured the TL of the sturgeons and took nine measurements on dorsal, lateral and ventral scutes (Figure 1b-d). These nine measurements (M1 to M9) were made on scutes with an uneven rank. Only measurements M1 and M2 were recorded for scutes with an even rank due to time constraints. Measurements were made only on the right side of the specimen for the paired scutes of the lateral and ventral row. When this proved to be impossible due to the preservation state or accessibility of the animal, left-sided scutes were measured. Measurements on bones were taken with digital callipers to the nearest 0.1mm.

### *Landmark-based geometric morphometrics*

In order to explore the differences in scute shape in relation to their place within the scute row or

to the TL of the animal, landmark-based geometric morphometric techniques were used, in which shape is described by landmark configurations on biological forms or images.

Using tpsDig v.2.16 (Rohlf, 2010a), landmarks were digitized on images of dorsal and lateral scutes only. Ventral scutes are unsuitable for 2D geometric morphometrics because they are strongly angulated, with one half on the scute faced sideways and the other half downwards. Therefore, no coplanar landmarks can be defined. The images of the scutes were taken in an as standardized way as possible, which was not always easy because the reference sturgeon specimens are often large and difficult to access. Only the lateral scutes on the right side of the animal were considered, except when this was impossible due to the preservation state or accessibility of the specimen. In that case, landmarks were digitised on mirrored images of the scutes on the left side of the body. In total, 7 landmarks were digitised on the lateral scutes; on the left part of the dorsal scute 4 landmarks were digitized (Figure 1b-c).

### Statistical analysis

#### Shape analysis

To remove effects of translation, scale and rotation, landmark coordinates were submitted to a General Procrustes Analysis (GPA) in tpsRelw v.1.49 (Rohlf, 2010b). The centroid size, i.e. the square root of the summed squared distances of each landmark to the centroid of the landmark configuration, and the weight matrix (W matrix), containing partial warps and uniform components, were generated for further statistical analysis. TpsSmall v. 1.20 (Rohlf, 2003) was used to test whether the tangent space approximation is sufficient to use the landmark coordinates for statistical analysis. Procrustes distances between specimens in Procrustes alignment were plotted against the Euclidean distances in the tangent space. If slope and correlation were more or less equal to one, the approximation was sufficient and statistical analysis could thus proceed.

#### General statistical analysis

Scute measurements as ratios to TL and W matrices were subjected to Principal Component

Analysis (PCA) to explore the pattern of variation among the different specimens and the different positions within the scute rows. To test for potential species-specific differences in scute dimensions and shape, Analysis of Variance (ANOVA) was used. Pearson correlation coefficients ( $r$ ) and coefficients of determination ( $R^2$ ) were determined to evaluate the potential of scute measurements for the estimation of TL. The relationships between TL and the different measurements were modelled using simple linear regression.

Canonical Variates Analysis (CVA) was performed to assess whether the original place within the dorsal, lateral or ventral row of an isolated scute can be estimated with scute measurements or the W matrix and to assess whether an isolated scute can be assigned to a certain size class. CVA on data which is not independent leads to the overestimation of the potential to discriminate between the different classes and to an increased probability of erroneously rejecting the null hypothesis, i.e. that there is no discrimination between groups (type I error). Therefore, in case the percentage of classification was deemed significantly high, results were cross validated by subsequently repeating the CVA with all scutes from one individual used as test-dataset.

Since the number of variables exceeded the number of observations in some groups, which can lead to increased chances of overfitting, CVA was conducted on the original dataset and repeated after the reduction of dimensionality with PCA.

Statistical analysis was performed with STATISTICA (StatSoft Inc., 2013) and R (R Core Team, 2014).

## RESULTS AND DISCUSSION

### *Differences in scute size between species*

Differences in scute size between *A. sturio* and *A. oxyrinchus* have been reported in the literature, with scutes of *A. oxyrinchus* being larger than those of *A. sturio* (Magnin, 1964; Desse-Berset, 2011; Wuertz *et al.*, 2011). Our own morphometric analysis on dorsal and lateral scutes from the 32 genetically identified sturgeon specimens confirmed this. Statistically significant differences between species were found for measurements M1/TL and M2/TL

on the lateral scutes (ANOVA, M1:  $F_{(2,941)}=3.48$ ,  $p<0.05$ ; M2:  $F_{(1,796)}=21.56$ ,  $p<0.001$ ) and dorsal scutes (ANOVA, M1:  $F_{(2,341)}=27.02$ ,  $p<0.001$ ; M2:  $F_{(2,339)}=22.59$ ,  $p<0.001$ ). For the ventral scutes, only a statistically significant difference for M1/TL was observed (ANOVA,  $F_{(2,267)}=2.802$ ,  $p<0.05$ ).

Similar species specific differences were found with geometric morphometric analysis of the scutes. As mentioned above, 2D geometric morphometrics techniques cannot be applied on ventral scutes since they are strongly angulated and no coplanar landmarks could be defined. Seven landmarks were digitized on a total of 605 lateral scutes and 4 landmarks were digitized on a total of 239 dorsal scutes from 10 *A. sturio*, 13 *A. oxyrinchus* and 5 hybrids (for species identification, see Thieren *et al.*, in press). Landmarks were superimposed twice: once for all scutes from the same rank and once for all ranks pooled together. In both cases, the tangent space approximation was considered sufficient for further statistical analysis (slope and correlation coefficient almost equal to 1). Although no species-specific differences in centroid size per rank were detected (ANOVA,  $p>0.05$ ), when data from all scute ranks were pooled, the centroid size of lateral and dorsal scutes differed significantly between species (ANOVA, lateral:  $F_{(2,602)}=37.3$ ,  $p<0.00001$ ; dorsal:  $F_{(2,236)}=5.6$ ,  $p<0.005$ ), with the scutes of *A. oxyrinchus* and hybrids being larger than those of *A. sturio*. This difference in scute size between *A. sturio* and *A. oxyrinchus* is most likely related to the larger number of scutes in *A. sturio*. Because this species has a larger number of scutes, they are smaller compared to those of *A. oxyrinchus* of the same length.

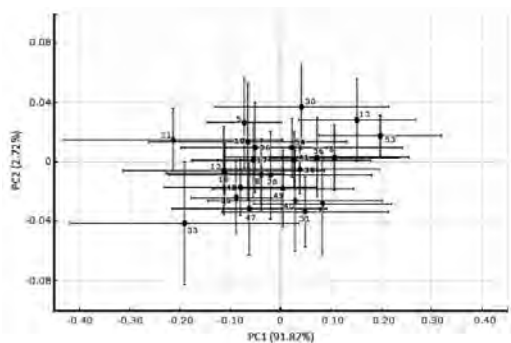


FIGURE 2

Scatterplot of PC2 against PC1, based on lateral scute measurements/TL on genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean  $\pm$  standard deviation of the PC scores are shown per individual, with specimens numbered as in Table 1.

This means that size reconstruction would be more accurate if separate models would be constructed for each species. However, this is not possible because the reconstructed length is needed before a species identification can be carried out (Thieren *et al.*, in press). Archaeological remains from small *A. oxyrinchus* have a tubercular surface pattern similar to that of *A. sturio*, which makes species identification of remains with the tubercular ornamentation difficult when the size of the animal is not known (Thieren *et al.*, in press).

#### *Differences in scute shape and dimensions between different individuals*

Another limiting factor for the modelling of the length based on scute dimensions or scute shape is the resemblance of scutes within the individual rows of one specimen. Scute dimensions and shapes of scutes within the rows from one individual are not independent, and it is likely that scutes from the same individual show some resemblance. The difference in scute dimensions between individual specimens was assessed with a PCA on the measurements/TL of all genetically identified specimens. The plot of the first two PC's, which explained in total 94.54% of the observed variation, indicates some clustering per specimen for the lateral scutes (Figure 2). Some clustering is also evident for the dorsal and ventral scute rows (Figure 3 and Figure 4). The interindividual difference in lateral and dorsal scute shape was assessed with PCA of the W matrix. The plot of the first two

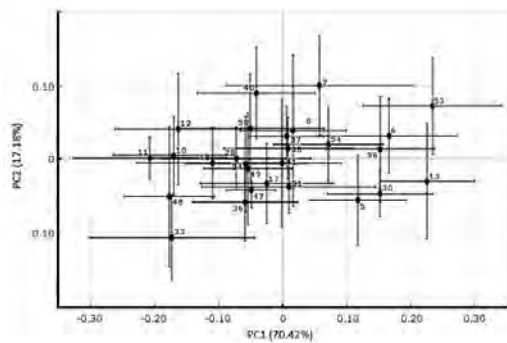


FIGURE 3

Scatterplot of PC2 against PC1, based on dorsal scute measurements/TL on genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean  $\pm$  standard deviation of the PC scores are shown per individual, with specimens numbered as in Table 1.

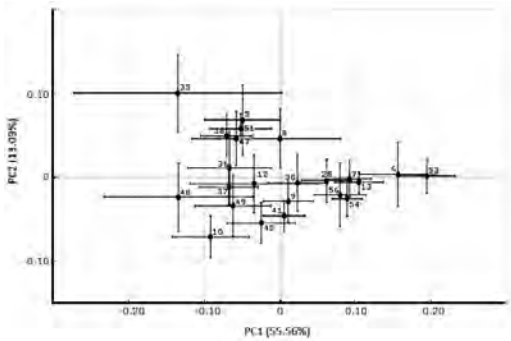


FIGURE 4

Scatterplot of PC2 against PC1, based on ventral scute measurements/TL on genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores shown per individual, with specimens numbered as in Table 1.

PC's of the PCA on the W matrix of the lateral and dorsal scute rows of all morphologically and genetically identified sturgeons revealed some clustering per specimen, comparable to the traditional morphometric data (Figure 5a and Figure 6a). This confirms that the data is pseudoreplicated, i.e. not independent, which might influence results. As said earlier, dependent data leads to an increased probability of erroneously rejecting the null hypothesis during CVA.

*Scute dimensions as indicator of total length*

A positive correlation between TL and the different scute measurements for dorsal, lateral and ventral scutes (all ranks pooled together) is observed. Correlation coefficients are all significant (Tables 2-4), indicating some potential for size estimation.

Lateral scutes

Positive correlations between M1 of the largest ( $M1_{max}$ ) and/or smallest ( $M1_{min}$ ) lateral scute of sturgeon specimens and TL have been described by Brinkhuizen (1989) ( $TL_{min} = -0.16 + 2.18 M1_{max}$ ,  $R^2 = 0.99$  and  $TL_{max} = 12.59 + 4.89 M1_{min}$ ,  $R^2 = 0.98$ ) and Debus (1999) ( $TL_{min} = -0.70 + 2.34 M1_{max}$ ,  $R^2 = 0.93$ ). These models were applied with M1 of the lateral scutes from the 58 museum specimens. In addition, new regression models were fitted with TL on  $M1_{max}$  ( $TL_{min} = 7.82 + 2.10 M1_{max}$ ,  $R^2 = 0.91$ ) and TL on  $M1_{min}$  ( $TL_{max} = 58.69 + 6.65 M1_{min}$ ,

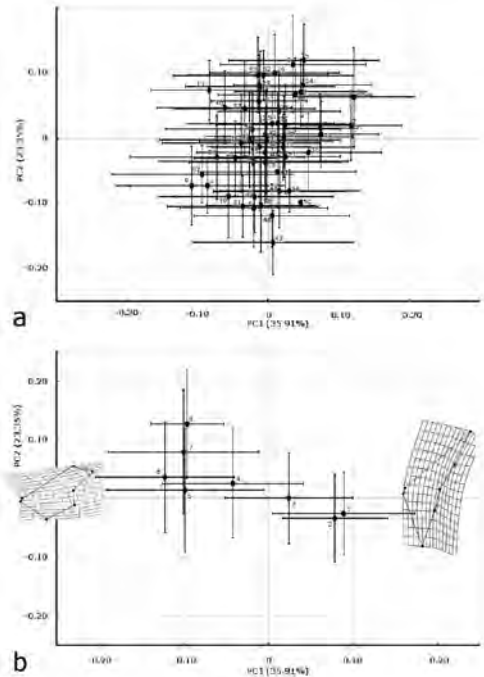


FIGURE 5

Scatterplot of PC2 against PC1, based on the lateral scutes from morphologically and genetically identified museum specimens' W matrix. Mean ± standard deviation of the PC scores shown (a) per individual, with specimens numbered as in Table 1; and (b) per rank. 1: Scutes 1-5; 2: Scutes 6-10; 3: Scutes 11-15; 4: Scutes 16-20; 5: Scutes 21-25; 6: Scutes 26-30; 7: Scutes 31-35; 8: Scutes > 35. Deformations of the reference configurations corresponding to the extremes of PC1 are shown (generated with tpsRelw v. 1.49 (Rohlf, 2010b)).

$R^2 = 0.29$ ) of those museum specimens (Figure 7). The models of Brinkhuizen (1989) were based on 4 specimens (with total lengths of 39, 94, 140 and 225 cm) and Debus (1999) only used specimens from the Baltic Sea, which might influence the accuracy of those models. Our data indicate that, although there is a strong positive correlation between  $M1_{max}$  and TL ( $r = 0.95$ ,  $p < 0.0001$ ) this is not the case for  $M1_{min}$  and TL ( $r = 0.55$ ,  $p < 0.0001$ ).

The models of Brinkhuizen (1989), Debus (1999) and our own model based on  $M1_{max}$  were very similar. Consequently, the Standard Errors of Estimate (SEE) for these three models are comparable, between 56.6 and 60.4 cm. Our equation based on  $M1_{min}$  and the one from Brinkhuizen (1989) differed considerably, which is reflected in a large difference in SEE of 106 cm. This is probably due to the fact that Brinkhuizen's model was based



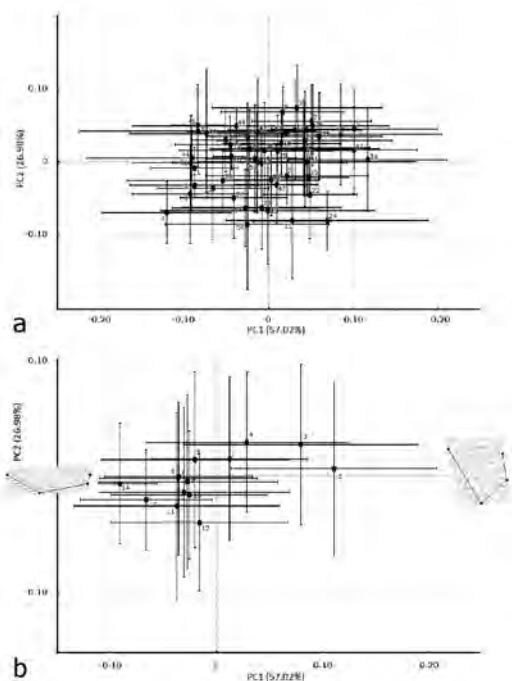


FIGURE 6

Scatterplot of PC2 against PC1, based on the dorsal scutes from morphologically and genetically identified museum specimens' W matrix. Mean  $\pm$  standard deviation of the PC scores are shown (a) per individual, with specimens numbered as in Table 1; and (b) per rank. Numbers indicate the scute rank. Deformations of the reference configurations corresponding to the extremes of PC1 are shown (generated with tpsRelw v. 1.49 (Rohlf, 2010b)).

on only 4 specimens, which might underestimate the actual existing variation in smallest scute sizes. The size range calculated through the combined use of  $M1_{\min}$  and  $M1_{\max}$  is quite large, especially for the larger scutes (Figure 7). However, to identify *A. sturio* and *A. oxyrinchus* to species based on the dermal bone surface morphology, the exact TL does not have to be known. It is sufficient to determine if a sturgeon with a tubercular bone surface morphology is larger or smaller than  $\sim 1$  m TL (Thieren *et al.*, in press). Therefore, the maximal possible TL, calculated with  $M1_{\min}$ , is not relevant for species identification. Only the minimum size ( $TL_{\min}$ ) has to be determined, which should be possible with the models with  $M1_{\max}$ . To evaluate the accuracy of the  $M1_{\max}$ -based models in indicating whether individual scutes belong to specimens smaller or larger than 1 m TL, they were applied with M1 of each individual scute of each museum specimen. The percentage of scutes from sturgeon < 1 m TL

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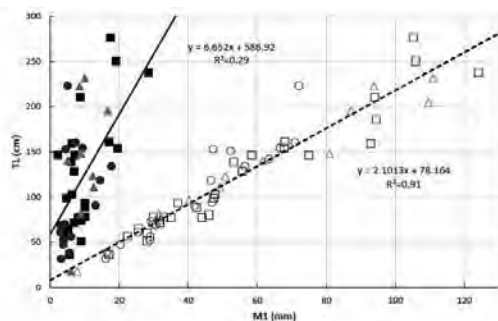


FIGURE 7

Plot of TL on the M1 from the smallest (filled markers) and largest (white markers) lateral scute of *A. sturio* and *A. oxyrinchus* museum specimens, with linear regression lines. Square: *A. oxyrinchus*; Circle: *A. sturio*; Triangle: hybrids or *A. oxyrinchus/A. sturio*.

with a back-calculated  $TL_{\min} > 1$  m is small, varying from 0.1% for Brinkhuizen (1989), 2.4% for Debus (1999) and 2% for our own calculation (Table 6). The percentage of scutes from sturgeons > 1 m TL which gave a back-calculated  $TL_{\min} < 1$  m is considerably higher, ranging between 35 and 51%. Since the other measurements ( $M2$  to  $M9$ ) also showed potential for size reconstruction, with high correlation coefficients (Table 2), the relationship between these measurements  $M_{\max}$  and TL were also modelled. Table 5 gives an overview of the retained models. These models gave similar results as the model with  $M1_{\max}$  (Table 6).

However, since the scutes of *A. sturio* are smaller than those of *A. oxyrinchus*, regression models based on both species will systematically underestimate TL when applied on *A. sturio* scutes, and overestimate TL when applied on *A. oxyrinchus* scutes. When calculated for each species separately, the percentages of specimens < 1 m TL with a back-calculated length > 1 m TL is quite similar for both species, and vary between 0 and 4.5%, depending on which measurement is used. However, the percentages of *A. oxyrinchus* > 1 m TL with a back-calculated length < 1 m TL vary between 25 and 47%, while those of *A. sturio* vary between 48 and 76%.

The tubercular scute ornamentation of sturgeons smaller than 1 m cannot be confidently used as an identification criterion because it can occur in both *A. sturio* and small *A. oxyrinchus*. As shown above, scutes from sturgeons less than 1 m TL will rarely have a back-calculated size larger than 1 m. Hence, when scutes with a tubercular surface pattern with

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>
All	<b>0.72</b>	0.52	<b>0.79</b>	0.62	<b>0.75</b>	0.56	<b>0.74</b>	0.55	<b>0.69</b>	0.48	<b>0.76</b>	0.58	<b>0.70</b>	0.49	<b>0.74</b>	0.55	<b>0.71</b>	0.50
1	<b>0.90</b>	0.81	<b>0.93</b>	0.87	<b>0.79</b>	0.62	<b>0.87</b>	0.75	<b>0.87</b>	0.75	<b>0.90</b>	0.81	<b>0.87</b>	0.76	<b>0.88</b>	0.77	<b>0.87</b>	0.79
2	<b>0.93</b>	0.86	<b>0.91</b>	0.84	<b>0.86</b>	0.74	<b>0.86</b>	0.74	<b>0.87</b>	0.75	<b>0.92</b>	0.85	<b>0.86</b>	0.85	<b>0.85</b>	0.73	<b>0.90</b>	0.83
3	<b>0.94</b>	0.89	<b>0.86</b>	0.75	<b>0.78</b>	0.60	<b>0.93</b>	0.86	<b>0.91</b>	0.82	<b>0.93</b>	0.86	<b>0.89</b>	0.79	<b>0.92</b>	0.84	<b>0.92</b>	0.84
4	<b>0.95</b>	0.91	<b>0.93</b>	0.86	<b>0.91</b>	0.83	<b>0.92</b>	0.84	<b>0.91</b>	0.83	<b>0.93</b>	0.86	<b>0.92</b>	0.84	<b>0.92</b>	0.85	<b>0.90</b>	0.81
5	<b>0.95</b>	0.90	<b>0.90</b>	0.81	<b>0.84</b>	0.70	<b>0.94</b>	0.88	<b>0.91</b>	0.84	<b>0.94</b>	0.88	<b>0.94</b>	0.89	<b>0.95</b>	0.91	<b>0.92</b>	0.84
6	<b>0.95</b>	0.91	<b>0.88</b>	0.77	<b>0.82</b>	0.67	<b>0.92</b>	0.86	<b>0.91</b>	0.83	<b>0.94</b>	0.88	<b>0.92</b>	0.85	<b>0.93</b>	0.87	<b>0.89</b>	0.80
7	<b>0.95</b>	0.89	<b>0.89</b>	0.80	<b>0.89</b>	0.80	<b>0.94</b>	0.88	<b>0.91</b>	0.83	<b>0.94</b>	0.88	<b>0.93</b>	0.87	<b>0.94</b>	0.89	<b>0.92</b>	0.85
8	<b>0.94</b>	0.89	<b>0.91</b>	0.83	<b>0.91</b>	0.83	<b>0.91</b>	0.83	<b>0.88</b>	0.77	<b>0.94</b>	0.88	<b>0.92</b>	0.85	<b>0.94</b>	0.87	<b>0.91</b>	0.83
9	<b>0.94</b>	0.89	<b>0.88</b>	0.77	<b>0.81</b>	0.66	<b>0.94</b>	0.88	<b>0.91</b>	0.82	<b>0.93</b>	0.86	<b>0.91</b>	0.82	<b>0.90</b>	0.81	<b>0.91</b>	0.83
10	<b>0.93</b>	0.87	<b>0.90</b>	0.81	<b>0.91</b>	0.83	<b>0.91</b>	0.83	<b>0.88</b>	0.77	<b>0.91</b>	0.83	<b>0.87</b>	0.76	<b>0.87</b>	0.76	<b>0.86</b>	0.75
11	<b>0.94</b>	0.88	<b>0.93</b>	0.86	<b>0.88</b>	0.77	<b>0.92</b>	0.85	<b>0.87</b>	0.76	<b>0.94</b>	0.88	<b>0.92</b>	0.85	<b>0.92</b>	0.86	<b>0.92</b>	0.85
12	<b>0.92</b>	0.85	<b>0.93</b>	0.87	<b>0.88</b>	0.78	<b>0.92</b>	0.84	<b>0.86</b>	0.75	<b>0.92</b>	0.85	<b>0.88</b>	0.78	<b>0.90</b>	0.81	<b>0.89</b>	0.80
13	<b>0.92</b>	0.85	<b>0.92</b>	0.85	<b>0.87</b>	0.75	<b>0.91</b>	0.83	<b>0.90</b>	0.81	<b>0.93</b>	0.86	<b>0.89</b>	0.79	<b>0.90</b>	0.81	<b>0.91</b>	0.82
14	<b>0.92</b>	0.85	<b>0.92</b>	0.84	<b>0.85</b>	0.72	<b>0.90</b>	0.81	<b>0.88</b>	0.78	<b>0.92</b>	0.84	<b>0.85</b>	0.72	<b>0.88</b>	0.78	<b>0.87</b>	0.76
15	<b>0.91</b>	0.82	<b>0.91</b>	0.83	<b>0.85</b>	0.72	<b>0.92</b>	0.84	<b>0.85</b>	0.73	<b>0.92</b>	0.84	<b>0.86</b>	0.75	<b>0.88</b>	0.77	<b>0.90</b>	0.82
16	<b>0.92</b>	0.85	<b>0.87</b>	0.76	<b>0.82</b>	0.67	<b>0.90</b>	0.81	<b>0.90</b>	0.81	<b>0.93</b>	0.86	<b>0.84</b>	0.70	<b>0.87</b>	0.76	<b>0.83</b>	0.69
17	<b>0.92</b>	0.85	<b>0.89</b>	0.79	<b>0.82</b>	0.67	<b>0.91</b>	0.84	<b>0.87</b>	0.77	<b>0.94</b>	0.88	<b>0.85</b>	0.73	<b>0.87</b>	0.75	<b>0.90</b>	0.80
18	<b>0.93</b>	0.86	<b>0.90</b>	0.81	<b>0.83</b>	0.69	<b>0.92</b>	0.86	<b>0.86</b>	0.74	<b>0.86</b>	0.75	<b>0.87</b>	0.76	<b>0.88</b>	0.78	<b>0.86</b>	0.74
19	<b>0.90</b>	0.81	<b>0.91</b>	0.83	<b>0.79</b>	0.63	<b>0.88</b>	0.78	<b>0.82</b>	0.67	<b>0.90</b>	0.80	<b>0.85</b>	0.72	<b>0.86</b>	0.74	<b>0.87</b>	0.75
20	<b>0.91</b>	0.82	<b>0.91</b>	0.83	<b>0.82</b>	0.67	<b>0.89</b>	0.81	<b>0.87</b>	0.75	<b>0.94</b>	0.89	<b>0.82</b>	0.68	<b>0.87</b>	0.76	<b>0.87</b>	0.75
21	<b>0.88</b>	0.78	<b>0.89</b>	0.79	<b>0.77</b>	0.59	<b>0.87</b>	0.76	<b>0.81</b>	0.66	<b>0.89</b>	0.79	<b>0.83</b>	0.68	<b>0.87</b>	0.75	<b>0.86</b>	0.75
22	<b>0.87</b>	0.75	<b>0.89</b>	0.80	<b>0.72</b>	0.51	<b>0.77</b>	0.59	<b>0.70</b>	0.50	<b>0.82</b>	0.68	<b>0.77</b>	0.59	<b>0.79</b>	0.62	<b>0.81</b>	0.65
23	<b>0.84</b>	0.70	<b>0.84</b>	0.70	<b>0.81</b>	0.65	<b>0.82</b>	0.67	<b>0.76</b>	0.57	<b>0.84</b>	0.70	<b>0.79</b>	0.62	<b>0.79</b>	0.62	<b>0.84</b>	0.70
24	<b>0.82</b>	0.68	<b>0.88</b>	0.77	<b>0.80</b>	0.63	<b>0.75</b>	0.56	<b>0.68</b>	0.47	<b>0.80</b>	0.65	<b>0.63</b>	0.40	<b>0.69</b>	0.47	<b>0.78</b>	0.62
25	<b>0.82</b>	0.68	<b>0.86</b>	0.73	<b>0.78</b>	0.61	<b>0.86</b>	0.74	<b>0.74</b>	0.55	<b>0.85</b>	0.73	<b>0.66</b>	0.44	<b>0.68</b>	0.47	<b>0.76</b>	0.58
26	<b>0.74</b>	0.55	<b>0.86</b>	0.75	<b>0.62</b>	0.39	<b>0.71</b>	0.50	<b>0.66</b>	0.43	<b>0.73</b>	0.53	<b>0.49</b>	0.24	<b>0.61</b>	0.37	<b>0.61</b>	0.37
27	<b>0.66</b>	0.45	<b>0.81</b>	0.65	<b>0.75</b>	0.57	<b>0.78</b>	0.61	<b>0.70</b>	0.49	<b>0.76</b>	0.58	<b>0.52</b>	0.27	<b>0.62</b>	0.39	<b>0.60</b>	0.36
28	<b>0.86</b>	0.74	<b>0.90</b>	0.82	<b>0.81</b>	0.66	<b>0.83</b>	0.69	<b>0.75</b>	0.56	<b>0.83</b>	0.69	<b>0.60</b>	0.36	<b>0.63</b>	0.39	<b>0.70</b>	0.48
29	<b>0.86</b>	0.75	<b>0.87</b>	0.76	<b>0.75</b>	0.56	<b>0.87</b>	0.77	<b>0.83</b>	0.69	<b>0.89</b>	0.80	<b>0.73</b>	0.54	<b>0.75</b>	0.56	<b>0.79</b>	0.64
30	<b>0.71</b>	0.51	<b>0.88</b>	0.78	<b>0.61</b>	0.37	<b>0.83</b>	0.69	<b>0.35</b>	0.12	<b>0.86</b>	0.74	<b>0.31</b>	0.10	<b>0.56</b>	0.31	<b>0.64</b>	0.41

TABLE 2

Pearson correlation coefficient (r) and R<sup>2</sup> values between TL and different lateral scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified *A. sturio* and *A. oxyrinchus*. Significant values are in bold (p<0.05) or bold underlined (p<0.002).

back-calculated lengths of less than 1m are excluded, chances are reduced that small *A. oxyrinchus* would be erroneously identified as *A. sturio*. This means that despite these seemingly disappointing results regarding accurate size reconstruction on the basis of lateral scutes, these bones can be

confidently used for species identification when back-calculated total lengths are larger than 1 m. The application of the regression models to sturgeons over 1m TL erroneously yields back-calculated lengths smaller than 1m in about 50% of the cases and hence significantly reduces the number

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>
All	<b>0.87</b>	0.77	<b>0.90</b>	0.80	<b>0.88</b>	0.77	<b>0.80</b>	0.64	<b>0.85</b>	0.73	<b>0.87</b>	0.76	<b>0.79</b>	0.62	<b>0.87</b>	0.75	<b>0.88</b>	0.77
1	<b>0.95</b>	0.91	<b>0.83</b>	0.66	<b>0.87</b>	0.75	<b>0.92</b>	0.85	<b>0.88</b>	0.78	<b>0.91</b>	0.83	<b>0.87</b>	0.75	<b>0.89</b>	0.79	<b>0.92</b>	0.86
2	<b>0.93</b>	0.86	<b>0.89</b>	0.80	<b>0.91</b>	0.83	<b>0.90</b>	0.80	<b>0.86</b>	0.73	<b>0.91</b>	0.83	<b>0.88</b>	0.78	<b>0.90</b>	0.82	<b>0.88</b>	0.77
3	<b>0.93</b>	0.86	<b>0.88</b>	0.78	<b>0.86</b>	0.75	<b>0.88</b>	0.77	<b>0.85</b>	0.73	<b>0.90</b>	0.82	<b>0.87</b>	0.76	<b>0.81</b>	0.66	<b>0.92</b>	0.84
4	<b>0.93</b>	0.86	<b>0.89</b>	0.78	<b>0.92</b>	0.84	<b>0.88</b>	0.77	<b>0.86</b>	0.85	<b>0.90</b>	0.81	<b>0.87</b>	0.75	<b>0.89</b>	0.79	<b>0.91</b>	0.83
5	<b>0.93</b>	0.87	<b>0.88</b>	0.78	<b>0.91</b>	0.83	<b>0.88</b>	0.77	<b>0.89</b>	0.80	<b>0.92</b>	0.84	<b>0.86</b>	0.74	<b>0.91</b>	0.84	<b>0.91</b>	0.83
6	<b>0.92</b>	0.84	<b>0.96</b>	0.92	<b>0.92</b>	0.85	<b>0.88</b>	0.78	<b>0.94</b>	0.88	<b>0.91</b>	0.82	<b>0.86</b>	0.74	<b>0.93</b>	0.87	<b>0.93</b>	0.86
7	<b>0.91</b>	0.83	<b>0.96</b>	0.93	<b>0.90</b>	0.80	<b>0.88</b>	0.78	<b>0.89</b>	0.79	<b>0.93</b>	0.87	<b>0.83</b>	0.69	<b>0.94</b>	0.88	<b>0.92</b>	0.86
8	<b>0.89</b>	0.79	<b>0.94</b>	0.88	<b>0.93</b>	0.87	<b>0.83</b>	0.69	<b>0.92</b>	0.84	<b>0.90</b>	0.81	<b>0.85</b>	0.72	<b>0.92</b>	0.85	<b>0.93</b>	0.87
9	<b>0.87</b>	0.76	<b>0.94</b>	0.88	<b>0.90</b>	0.81	<b>0.81</b>	0.65	<b>0.88</b>	0.77	<b>0.86</b>	0.74	<b>0.82</b>	0.68	<b>0.89</b>	0.79	<b>0.89</b>	0.80
10	<b>0.85</b>	0.72	<b>0.88</b>	0.78	<b>0.90</b>	0.80	<b>0.79</b>	0.62	<b>0.87</b>	0.76	<b>0.83</b>	0.68	<b>0.78</b>	0.61	<b>0.88</b>	0.78	<b>0.84</b>	0.71
11	<b>0.89</b>	0.80	<b>0.94</b>	0.88	<b>0.90</b>	0.82	<b>0.76</b>	0.58	<b>0.92</b>	0.85	<b>0.92</b>	0.84	<b>0.79</b>	0.62	<b>0.91</b>	0.83	<b>0.90</b>	0.81
12	<b>0.84</b>	0.71	<b>0.84</b>	0.71	<b>0.87</b>	0.75	<b>0.68</b>	0.46	<b>0.87</b>	0.76	<b>0.75</b>	0.57	<b>0.77</b>	0.59	<b>0.86</b>	0.73	<b>0.79</b>	0.62
13	<b>0.86</b>	0.74	<b>0.91</b>	0.83	<b>0.83</b>	0.69	<b>0.46</b>	0.21	<b>0.86</b>	0.75	<b>0.92</b>	0.86	<b>0.54</b>	0.29	<b>0.88</b>	0.77	<b>0.81</b>	0.66
14	<b>0.92</b>	0.85	<b>0.88</b>	0.78	<b>0.97</b>	0.95	<b>0.85</b>	0.72	<b>0.85</b>	0.97	<b>0.97</b>	0.94	<b>0.59</b>	0.35	<b>0.89</b>	0.79	<b>0.98</b>	0.96

TABLE 3

Pearson correlation coefficient (r) and R<sup>2</sup> values between TL and different dorsal scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified *A. sturio* and *A. oxyrinchus*. Significant values are in bold (p<0.05) or bold underlined (p<0.002).

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>	r	R <sup>2</sup>
All	<b>0.88</b>	0.77	<b>0.84</b>	0.71	<b>0.80</b>	0.64	<b>0.73</b>	0.54	<b>0.72</b>	0.51	<b>0.80</b>	0.65	<b>0.73</b>	0.53	<b>0.72</b>	0.51	<b>0.83</b>	0.69
1	<b>0.88</b>	0.78	<b>0.88</b>	0.78	<b>0.91</b>	0.82	<b>0.89</b>	0.79	<b>0.87</b>	0.76	<b>0.88</b>	0.78	<b>0.82</b>	0.67	<b>0.85</b>	0.74	<b>0.89</b>	0.79
2	<b>0.86</b>	0.74	<b>0.84</b>	0.70	<b>0.83</b>	0.68	<b>0.80</b>	0.63	<b>0.73</b>	0.53	<b>0.76</b>	0.58	<b>0.79</b>	0.62	<b>0.69</b>	0.48	<b>0.84</b>	0.70
3	<b>0.87</b>	0.77	<b>0.86</b>	0.74	<b>0.86</b>	0.74	<b>0.78</b>	0.60	<b>0.87</b>	0.76	<b>0.83</b>	0.69	<b>0.82</b>	0.68	<b>0.76</b>	0.58	<b>0.87</b>	0.76
4	<b>0.90</b>	0.81	<b>0.85</b>	0.79	<b>0.82</b>	0.75	<b>0.81</b>	0.62	<b>0.58</b>	0.34	<b>0.81</b>	0.66	<b>0.79</b>	0.62	<b>0.68</b>	0.46	<b>0.84</b>	0.70
5	<b>0.90</b>	0.80	<b>0.85</b>	0.73	<b>0.83</b>	0.68	<b>0.81</b>	0.66	<b>0.80</b>	0.64	<b>0.84</b>	0.71	<b>0.83</b>	0.69	<b>0.78</b>	0.61	<b>0.87</b>	0.76
6	<b>0.91</b>	0.83	<b>0.83</b>	0.69	<b>0.81</b>	0.65	<b>0.79</b>	0.62	<b>0.53</b>	0.28	<b>0.85</b>	0.72	<b>0.84</b>	0.71	<b>0.71</b>	0.60	<b>0.87</b>	0.76
7	<b>0.90</b>	0.82	<b>0.80</b>	0.64	<b>0.79</b>	0.62	<b>0.81</b>	0.66	<b>0.76</b>	0.57	<b>0.88</b>	0.78	<b>0.79</b>	0.62	<b>0.77</b>	0.60	<b>0.80</b>	0.64
8	<b>0.88</b>	0.78	<b>0.81</b>	0.65	<b>0.78</b>	0.60	<b>0.78</b>	0.60	<b>0.65</b>	0.42	<b>0.88</b>	0.78	<b>0.63</b>	0.40	<b>0.67</b>	0.44	<b>0.88</b>	0.77
9	<b>0.86</b>	0.73	<b>0.84</b>	0.71	<b>0.68</b>	0.46	<b>0.66</b>	0.43	<b>0.74</b>	0.54	<b>0.75</b>	0.56	<b>0.70</b>	0.49	<b>0.78</b>	0.62	<b>0.84</b>	0.70
10	<b>0.86</b>	0.73	<b>0.88</b>	0.77	<b>0.90</b>	0.80	<b>0.64</b>	0.41	<b>0.62</b>	0.39	<b>0.89</b>	0.79	<b>0.53</b>	0.28	<b>0.59</b>	0.35	<b>0.83</b>	0.69
11	<b>0.81</b>	0.66	<b>0.89</b>	0.78	<b>0.79</b>	0.63	<b>0.56</b>	0.32	<b>0.54</b>	0.29	<b>0.72</b>	0.52	<b>0.57</b>	0.32	<b>0.63</b>	0.40	<b>0.60</b>	0.36
12	<b>0.95</b>	0.91	<b>0.92</b>	0.84	<b>0.77</b>	0.59	<b>0.44</b>	0.19	<b>0.84</b>	0.71	<b>0.81</b>	0.65	<b>0.84</b>	0.71	<b>0.70</b>	0.48	<b>0.97</b>	0.94

TABLE 4

Pearson correlation coefficient (r) and R<sup>2</sup> values between TL and different ventral scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified *A. sturio* and *A. oxyrinchus*. Significant values are in bold (p<0.05) or bold underlined (p<0.002).

of larger specimens for which a species identification can be obtained. Nevertheless, the remaining

specimens that yield size reconstructions above 1m will allow accurate species identification. Table 5

	Lateral			Dorsal						Ventral		
	All scutes			Excluding first scute			All scutes			Excluding last scute		
	Equation	R <sup>2</sup>	Min	Equation	R <sup>2</sup>	Min	Equation	R <sup>2</sup>	Min	Equation	R <sup>2</sup>	
<b>M1</b>	7.816+2.10 M1max	0.91	43.9	4.593+2.54 M1MaxExclD1	0.86	37.6	1.937+2.45 M1max	0.91	40.0	-8.939+4.21 M1MaxExclVlast	0.82	
<b>M2</b>	0.935+4.78 M2max	0.89	20.7	6.722+2.09 M2MaxExclD1	0.92	44.6	10.324+1.97 M2max	0.90	45.5	-1.797+3.74 M2MaxExclVlast	0.86	
<b>M3</b>	7.865+8.51 M3max	0.87	10.8	11.241+3.86 M3MaxExclD1	0.89	23.0	10.006+3.89 M3max	0.90	23.1	19.252+5.77 M3MaxExclVlast	0.81	
<b>M4</b>	5.182+3.47 M4max	0.88	27.3	-1.325+3.88 M4MaxExclD1	0.82	26.1	-5.935+3.95 M4max	0.81	26.8	11.906+5.74 M4MaxExclVlast	0.62	
<b>M5</b>	14.847+3.70 M5max	0.83	23.0	8.031+2.82 M5MaxExclD1	0.81	32.6	11.756+2.64 M5max	0.81	33.4	14.316+4.73 M5MaxExclVlast	0.75	
<b>M6</b>	6.181+2.82 M6max	0.91	33.3	7.584+3.01 M6MaxExclD1	0.85	30.7	5.759+2.99 M6max	0.88	31.5	-12.104+4.86 M6MaxExclVlast	0.83	
<b>M7</b>	8.459+4.08 M7max	0.87	22.4	0.852+3.84 M7MaxExclD1	0.73	25.8	-2.421+3.89 M7max	0.77	26.3	-35.184+8.06 M7MaxExclVlast	0.74	
<b>M8</b>	6.404+4.00 M8max	0.90	23.4	-3.978+3.12 M8MaxExclD1	0.87	33.3	3.688+2.84 M8max	0.84	33.9	-10.607+5.76 M8MaxExclVlast	0.78	
<b>M9</b>	14.325+3.66 M9max	0.86	23.4	2.877+3.12 M9MaxExclD1	0.86	31.1	0.949+3.11 M9max	0.88	31.8	-4.427+4.77 M9MaxExclVlast	0.81	

TABLE 5

Equations and R<sup>2</sup> for the equation of TL (cm) based on the maximum value of different scute measurements (mm). The minimum value for each measurement (Min) to attain a back-calculated length of > 1 m TL is also given for the lateral and dorsal scutes

includes the minimum values needed for each measurement to attain back-calculated lengths larger than 1 m TL. Scutes with measurements equal to or larger than this minimum value can be identified to species on the basis of their ornamentation pattern. However, it should be kept in mind that lengths of *A. sturio* are systematically underestimated using these models, while those of *A. oxyrinchus* will be overestimated. This means that the ratio *A. sturio*/*A. oxyrinchus* in an archaeological assemblage cannot be determined with this method.

#### Dorsal scutes

Desse-Berset (2011) constructed a model ( $TL = 2.52 M1_{\text{mean excl. D1}} - 15.54$ ,  $R^2 = 0.96$ ) for dorsal scutes, based on the mean width of the dorsal scutes from 9 *A. oxyrinchus* specimens, excluding the first scute and the basal dorsal fin fulcrum.

According to Desse-Berset (2011), M1 does not vary considerably within the dorsal row and is therefore the best measure for TL reconstructions. Our own measurements on museum specimens indicate that M1 (excluding the first dorsal scute) can vary up to 2.3% of the TL of an individual. We tested Desse-Berset's (2011) model on the museum specimens, also without taking into account the basal dorsal fin fulcrum. Using this model, about 3.5% of the back-calculated TL from sturgeons < 1m TL was larger than 1m, and 40% of

the back-calculated TL from sturgeons > 1m TL was smaller than 1m (Table 6). This means that, similar to the lateral scutes, the dorsal scutes with a back-calculated length larger than 1m can be confidently used for species identification. It also appears that a large percentage of scutes from sturgeons larger than 1m would mistakenly be excluded for species identification.

Similar to the lateral scutes, least squares linear regression models were developed for the dorsal scutes, based on TL and on the maximal measurements ( $M1_{\text{max}} - M9_{\text{max}}$ ), both with and without the first dorsal scute (Table 5). With these, the percentages of back-calculated  $TL_{\text{min}} > 1\text{m}$  based on scutes from sturgeons < 1m TL (ranging from 0.9 to 8.4% vs 3.5%, Table 6) were comparable to the results with Desse-Berset's (2011) equation. The percentage of back-calculated  $TL_{\text{min}} < 1\text{m}$  based on scutes from sturgeons > 1m TL ranges from 19.6% to 30.0% for the model without the first dorsal scute and from 22.5% to 31.6% for the model including that scute. In both cases, this is a slight decrease compared to the 39.7% attained with Desse-Berset's (2011) model. As with the lateral scutes, these regression models would wrongfully indicate that many scutes from sturgeons > 1m TL came from sturgeons < 1m, but only few scutes from sturgeons < 1m TL would be back-calculated as > 1m, which is important for correct species assignment, as explained above for the lateral scutes. As for the later-

	Dorsal scutes			Ventral scutes			Lateral scutes		
	25 cm	50 cm	1m	25 cm	50 cm	1 m	25 cm	50 cm	1 m
<b>W matrix + CS</b>	48.4	59.9	78.7				51.8	59.7	80.0
<b>PC1&amp;PC2 (W matrix) + CS</b>	46.3	58.4	78.5				33.7	43.9	68.0
<b>Measurements</b>	61.7	68.3	81.3	55.7	53.2	73.7	42.7	56.2	71.4
<b>PC1&amp;PC2 (measurements)</b>	54.8	59.6	79.0	44.3	50.4	71.7	38.6	45.9	67.4

TABLE 6

Percentage of correct classification based on measurements, the weight matrix (and centroid size (CS)) and the first two principle components (and CS) from a PCA on W matrix or the measurements in a specific size class.

al scutes, the minimum value of each measurement needed to attain a back-calculated total length of 1 m is given in Table 5. However, as is the case with back-calculations based on lateral scutes, the TL of *A. sturio* will systematically be underestimated using the models in Table 5, while that of *A. oxyrinchus* will be overestimated. The percentages of *A. oxyrinchus*' back-calculated  $TL_{min} < 1$  m based on scutes from sturgeons  $> 1$  m TL vary between 6.5 to 22%, while those of *A. sturio* vary between 37 and 71%. The percentages of *A. oxyrinchus*' back-calculated  $TL_{min} > 1$  m based on scutes from sturgeons  $< 1$  m TL varies between 0 to 15%, while those of *A. sturio* varies between 0 and 1%. Again, a larger proportion of *A. sturio* will be excluded for species analysis, meaning that also for the dorsal scutes the ratio *A. sturio*/*A. oxyrinchus* in an archaeological assemblage cannot be inferred with this method.

#### Ventral scutes

For ventral scutes, models were constructed for the back-calculation of  $TL_{min}$  similar to those for the lateral and dorsal scutes, based on the 9 scute measurements (M1-M9) on the largest ventral scute from each specimen (Table 5). The last ventral scute was excluded for analysis since it has a distinctive and aberrant shape. With these models, with  $R^2$  values varying between 0.62 and 0.86, between 7.6 and 22.6% of the total lengths based on scutes from sturgeons  $< 1$  m TL were back-calculated larger than 1m, and between 14.6 and 27.3% of the lengths based on scutes from sturgeon  $> 1$  m TL were back-calculated smaller than 1 m. Similar to the back-calculations based on lateral and dorsal scutes, the TL of *A. sturio* will systematically be underestimated, while that of *A. oxyrinchus* will be overestimated. The percentages of *A. oxyrinchus*' back-calculated  $TL_{min} < 1$  m based on scutes from

sturgeons  $> 1$  m TL varies between 5 to 39%, while that of *A. sturio* varies between 2.5 and 11.5%. The percentages of *A. oxyrinchus*' back-calculated  $TL_{min} > 1$  m based on scutes from sturgeons  $< 1$  m TL varies between 7 to 24%, while those of *A. sturio* varies between 21 and 51%. Although the percentages of scutes from sturgeons  $> 1$  m TL that are back-calculated  $< 1$  m TL is smaller compared to the dorsal and lateral scutes, the percentage of scutes from sturgeons  $< 1$  m TL with back-calculated lengths  $> 1$  m TL is larger. It thus appears that ventral scutes are less reliable for size reconstruction than dorsal and lateral scutes, and therefore more difficult to identify to species. Ventral scutes with a tubercular ornamentation pattern should only be included for species identification when direct comparison with specimens of known length indicate that they are clearly from animals much larger than 1m.

#### Estimation of scute rank based on traditional and geometric morphometrics

Desse-Berset (2011) suggested that the accuracy of size reconstruction could increase if the exact place of the scute within the dorsal row could be established. This should also be the case for lateral and ventral scutes. Therefore, the correlation coefficients between the 9 measurements and TL and  $R^2$  values were calculated separately for each scute rank for the lateral (Table 2), dorsal (Table 3) and ventral scutes (Table 4). Most correlations were significant at the 0.05 significance level. For the lateral scutes an increase in both  $r$  and  $R^2$  values could be observed for all ranks, which was not always the case for the dorsal and ventral scutes. This suggests that especially for lateral scutes, knowing the original rank of the scute will pro-

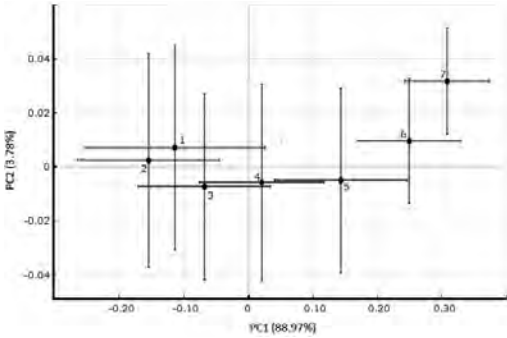


FIGURE 8

Scatterplot of PC2 against PC1, based on lateral scute measurements/TL on morphologically and genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean  $\pm$  standard deviation of the PC scores are shown per rank. 1: scutes 1-5; 2: Scutes 6-10; 3: Scutes 11-15; 4: Scutes 16-20; 5: Scutes 21-25; 6: Scutes 26-30; 7: Scute >30.

vide more accurate size reconstructions. For dorsal or ventral scutes, the effect of knowing the scute rank is less pronounced, but may also lead to an improvement of the size prediction accuracy. However, establishing the original scute rank of an isolated scute is not straightforward. In the following part, we explore different possibilities (traditional and geometric morphometrics) to determine the original place of an isolated scute within the row.

A PCA was performed on the measurements/TL on all specimens for the different scute rows. For the lateral scutes, the ordination plots categorized by ranks grouped per five (scute 1 to 5, 6 to 10, and so on) do not delineate any distinct groups, although there seems to be a gradual change in scute dimensions from the anterior part of the row, located more to the negative end of PC1, towards scutes at the posterior end of the row, located more to the positive end of PC1 (Figure 8). This explains the improvement mentioned above in  $r$  and  $R^2$  values when scutes are considered per rank for estimating TL (Table 2). Lateral scutes seem to cluster somewhat per individual (Figure 2), but scutes within the same group of ranks from different individuals also seem to group together. This might allow a rough estimation of the original rank of the scute based on traditional morphometric data. A CVA was performed on all morphologically identified animals with scutes grouped rank 1 to 5, rank 6 to 10 and so on. The analysis classified 31.8% of the cases correctly, versus 12.6% classified correctly with ungrouped ranks. Although an improvement in percentage of correct classification is observed

with the ranks grouped per five, this improvement does not allow an accurate estimate of the rank of an isolated scute. Therefore, the possibilities of geometric morphometric techniques to establish the provenance of an individual isolated scute within the row have been explored. The data points in the ordination plot of the PCA on the W matrix of the lateral scutes were categorized by rank (Figure 5b) instead of by individual (Figure 5a). A gradual change from scutes at the beginning of the row (at the positive end of PC1) towards scutes at the end of the row (at the negative end of PC1) can be observed, similar to the ordination plot of the PCA on scute dimensions (Figure 8). Landmark configurations on the two extreme ends of PC1 are shown (Figure 5b) to give an indication of the change in scute shape from the first to the last scute. A MANOVA on the W matrix of the scutes grouped per 5 indicated a significant overall difference between the different groups ( $l=0.27$ ,  $F_{(70,6601)}=23.40$ ,  $p<0.0001$ ). However, only 43.6% of the cases was classified correctly. When the CVA was repeated on the first two PC's, only 20.9% was classified correctly ( $l=0.95$ ,  $F_{(10,2282)}=6.24$ ,  $p<0.0001$ ).

For the dorsal and ventral scutes, no consistent improvement in  $r$  and  $R^2$  was observed (Table 3 and 4), which is reflected in the ordination plots. For the dorsal scutes, there seems to be a gradual change in scute dimensions from scutes at the beginning of the row (more located to the negative end of PC1 and the positive end of PC2, Figure 9) to scutes towards the caudal end of the row (more to the positive end of PC1 and negative end of PC2, Figure 9). However, this trend is much less

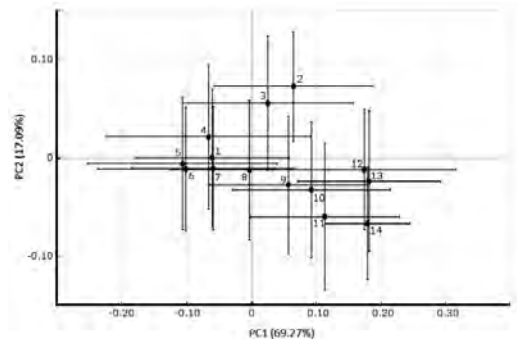


FIGURE 9

Scatterplot of PC2 against PC1, based on dorsal scute measurements/TL on morphologically and genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean  $\pm$  standard deviation of the PC scores are shown per rank. Numbers indicate the scute rank.

pronounced than in the lateral rows. Since traditional morphometry did not prove satisfactory for the estimation of lateral scute ranks, only geometric morphometric techniques are applied on dorsal scutes. When the data points from the PCA on the dorsal scutes' W matrix are categorized per rank (Figure 6b) instead of individual (Figure 6a), a gradual shape change from scutes at the anterior end of the row (at the positive end of PC1 and PC2) to scutes at the posterior end of the row (at the negative end of PC1 and PC2) can be observed, similar but more pronounced compared to the change in scute dimensions (Figure 9). A CVA on the W matrix and the dataset consisting of the first two PC's indicated a significant difference between the different ranks ( $p < 0.0001$ ), but also here the percentage of correct classification was low (18.76% for the W matrix, 12.58% for the dataset consisting of the first two PC's).

For the ventral scutes, the ordination plot of the first two PC's of a PCA on the measurements/TL did not show any clustering per rank or gradient change in scute dimensions (Figure 10). Therefore, no further attempts were made to classify the scutes according to their rank.

We can conclude that the percentage of correct classification for dorsal and lateral scutes is too low to allow a reliable estimate of the original rank of an individual scute. For ventral scutes, it was not tested if scutes could be classified to rank based on scute measurements, since - unlike the dorsal and lateral scutes - a first exploration of the data did not give any indications this would be possible.

#### *Scute dimensions or shape as an indication for wider size classes*

Since the scutes offer limited possibilities for an accurate estimation of TL, it was evaluated whether the shape or dimensions of individual scutes allow attributing them to a particular size range.

Different arbitrary chosen bin sizes were tested (25cm, 50cm and 1m). In Table 6 we present the percentages of correct classification from a CVA on the traditional measurements, on the W matrix and centroid size, and on the reduced datasets consisting of the first two PC's of a PCA on the measurements or the first two PC's of a PCA on the W matrix and centroid size. The percentages of correct classifica-

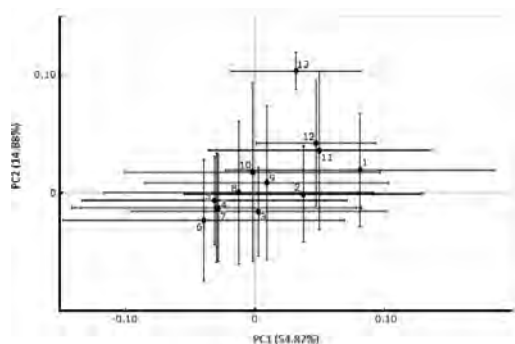


FIGURE 10

Scatterplot of PC2 against PC1, based on ventral scute measurements/TL on morphologically and genetically identified *A. sturio* and *A. oxyrinchus* museum specimens. Mean  $\pm$  standard deviation of the PC scores are shown per rank. Numbers indicate the scute rank.

tion of the CVA on the reduced datasets are, as expected, smaller than the ones based on the complete datasets. The difference between both is small for the dorsal scutes; only for the measurements in the 25 cm and 50 cm size class it is larger than 5%. For the ventral scutes, this difference is larger than 5% for the CVA in the 25 cm size class. For the lateral scutes, the difference was larger than 5% in all cases. This possibly indicates some overfitting when performing CVA on the complete datasets.

For the dorsal scutes, percentages of correct classification were highest with a CVA performed on the measurements; for the lateral scutes with a CVA on the W matrix. For all three scute types (except for the measurements on the ventral scutes), the percentage of correct classification increased when bin size increased. However, all percentages were quite low, with the best attained results around 80% of the dorsal scutes, around 70% of the ventral scutes and around 80% of the lateral scutes classified correctly in the 1m size class. In the 25 and 50 cm bin sizes, correct classifications are obtained in only 34% to 70% of the cases. These percentages might still be an overestimation since intra-individual scute similarity is not taken into account. However, because of the low percentages of correct classification, the models were not cross validated.

Next to the disappointing low accuracy of the models, this method is quite labor-intensive, requiring all nine measurements on the scutes, for only a rough estimation of size. Moreover, it is not always possible to take all measurements on archaeological scutes, which are often fragmented.

## CONCLUSION

In this study, different methods for size reconstruction based on sturgeon scutes were explored using traditional and geometric morphometric techniques. It appears that the back-calculation of TL or the estimation of size classes based on the scute shape or scute dimensions are not very accurate due to the wide variation among scutes within one row. A positive correlation between different scute measurements and TL does exist, but this correlation is not strong enough to allow a precise size reconstruction. This is partly due to the fact that the exact position of an isolated scute within a scute row cannot be accurately determined. Although a difference was observed in scute dimensions and shape from the anterior towards the posterior end of the dorsal and lateral row, this difference is not pronounced enough to accurately establish the rank of a scute within these rows. A size-related difference in scute shape and scute dimensions was also observed, but likewise, this difference is not marked enough to allow an adequate classification into size classes.

The regression equations based on scute measurements can be used to estimate whether an individual dorsal or lateral scute belonged to a sturgeon larger or smaller than 1m. Although the back-calculated length of many scutes from sturgeons > 1m TL will be smaller than 1m, the percentage of small sturgeon (< 1m TL) back-calculated as larger than 1m is small. The latter finding is of relevance for the adequate use of scutes for the discrimination between the *A. sturio* and *A. oxyrinchus* which is based on the ornamentation pattern of the external surface (Desse-Berset, 2009). The surface pattern is species-specific in most fish larger than 1m, but smaller individuals of *A. oxyrinchus* can show a more *A. sturio*-like pattern (Thieren *et al.*, in press). Scutes with a back-calculated TL over 1m, calculated with the regression equations mentioned above, can thus be safely used for species identification. However, it must be kept in mind that more *A. sturio* scutes than *A. oxyrinchus* scutes will be excluded for species identification. The length of *A. oxyrinchus* is systematically overestimated, while the length of *A. sturio* is underestimated using the proposed regression models: scutes of *A. sturio* are smaller than *A. oxyrinchus*, and the regression equations are based on the combined measurements of *A. sturio* and *A. oxyrinchus*. Therefore, scutes cannot be used to determine proportions of *A. oxyrinchus* and *A. sturio* in a given

archaeological assemblage. However, they can be used to indicate the presence or absence of the species. Preference for size reconstruction should be given to head elements, for which no difference in the regressions between the two species was observed (Thieren & Van Neer, 2014). Consequently, species identifications based on these elements can be used to determine the *A. sturio*/*A. oxyrinchus* ratio in an archaeological assemblage.

Given the difference in scute size and scute number between *A. sturio* and *A. oxyrinchus*, species-specific equations for size back-calculation might produce somewhat larger accuracy. However, this would require more modern reference specimens than presently available. Even with such equations, scutes will probably never allow precise length estimation because the number of scutes also tends to vary within species and because the size of scutes varies within one row.

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