Body length estimation of the European eel *Anguilla anguilla* on the basis of isolated skeletal elements

by

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ABSTRACT. - Using a large series of dry skeletons of modern European eel *Anguilla anguilla* (Linnaeus, 1758) from Belgium and the Netherlands, the relationship between fish length and individual bone measurements is investigated. The aim of the study is to provide adequate regression equations between both parameters. This methodology is relevant for both palaeoecological and ecological researches since isolated skeletal elements survive in large numbers on archaeological sites and in the stomach contents, faeces or regurgitations of piscivorous animals. The predictive value for the length estimations is explored for various skeletal elements and the accuracy of the obtained regression formulae is compared to that of the formulae already existing in literature. Particular attention is paid to the use of vertebrae, taking into account that different morphotypes can be distinguished amongst them.

RÉSUMÉ. - Reconstitution de la taille de l'anguille européenne *Anguilla anguilla* à partir d'éléments squelettiques isolés.

En utilisant une grande série de squelettes récents d'anguille européenne *Anguilla anguilla* (Linnaeus, 1758) provenant de Belgique et des Pays-Bas, la relation entre la taille du poisson et des mesures d'ossements isolés est étudiée. Le but de cette étude est de fournir des régressions adéquates entre ces deux paramètres. Cette approche est pertinente pour les études paléoécologiques et écologiques car ces éléments squelettiques isolés sont retrouvés en abondance dans les sites archéologiques et dans le contenu de l'appareil digestif d'animaux piscivores, leurs excréments ou leurs régurgitations. La valeur prédictive des différents éléments squelettiques est examinée et la précision des régressions établies est comparée à celle des formules existant dans la littérature. Une attention particulière est portée à l'utilisation des vertèbres, ceci en tenant compte des différents morphotypes que l'on peut distinguer entre elles.

Key words. - *Anguilla anguilla* - European eel - Archaeozoology - Ecology - Osteometry - Body length estimations.

The reconstruction of fish lengths on the basis of isolated skeletal elements is of relevance for both archaeology and biology. In modern ecological studies, the analysis of the stomach contents, faeces or regurgitations of piscivorous species, allows identification and size reconstruction of the prey species. This can be based on otoliths and scales, as well as on isolated bones (e.g., Fitch, 1968; Hyslop, 1980; Britton and Shepherd, 2005), and has been carried out for cetaceans, seals, otters, fish-eating birds (e.g., cormorants, herons, grebes,…) and predatory fish (pike, perch,…).

In archaeological studies, length reconstructions of fish are mainly based on (isolated) bones, although otoliths and scales are also sporadically used (Casteel, 1976; Wheeler and Jones, 1989). The reconstructed body lengths provide information on the fish captured and consumed by former human populations, on the fishing grounds exploited, the fishing methods applied, selective consumer behaviour in the past, and human impact on fish populations through time. For a considerable number of species, studies have been undertaken that allow the reconstruction of fish lengths on the basis of measurements taken from individual bones. However, the published approaches demonstrate a varying precision, depending on the method used. This ranges from crude estimations – in size classes with a width of 5 to 10 cm or even larger – obtained through direct comparison with modern specimens of known body length (e.g., Makowiecki, 2007), over bivariate plots graphically showing combinations between fish length and a given bone measurement (e.g., Desse, 1984; Desse *et al*., 1987), to linear regression equations statistically describing their relationship (e.g., Enghoff, 1983).

The aim of the present paper is to revise the methods for body length reconstruction of European eel *Anguilla anguilla* (Linnaeus, 1758) described thus far in the biological and archaeozoological literature. Consequently, on the basis of 69 modern specimens, new regressions were calculated between the fish length and the dimensions of the isolated skeletal elements that usually survive in large numbers on archaeological sites, or in the stomach contents of recent pis-

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civorous animals. The accuracy of the reconstructions was then tested, and on this basis recommendations are made regarding the choice of elements best suited for the adequate sizing of isolated eel bone finds.

Size reconstructions in the literature

Table I presents an overview of the skeletal elements and measurements that have been used for body length reconstruction of eel. Most of the publications provide simple linear regressions between fish total length (TL) and a given bone measurement (M): TL = a + b*M. Sometimes, logarithmic equations are used: TL = a + b*log(M). Lepiksaar and Heinrich (1977) and Heinrich (1987) applied the proportional method (TL = b*M), assuming a linear relationship between the bone measurements and fish length. However, these proportions are based upon only one (Lepiksaar and Heinrich, 1977) and three (Heinrich, 1987) individuals.

Although ten publications have already dealt with this topic for eel (see references in Table I), considerable variation seems to exist regarding the bones selected for the osteometrical investigations, the measurements taken, the size range represented by the sample set and the number of eels used as sample specimens. In the earliest studies (Lepiksaar and Heinrich, 1977; Heinrich, 1987; Brinkhuizen, 1989) a small number of animals was used, making the reconstruction less accurate. In later studies larger numbers of individuals were considered, but size ranges sometimes remained rather restricted (e.g., Prenda *et al.*, 2002), reducing the

Table I. - Skeletal elements used in the literature for the body length reconstruction of eel, with indication of the measurements retained, the number of individuals used and their total lengths (TL).

Skeletal element	Authors	Measurement	Number of specimens	Range of TL (mm)
Dentary	Lepiksaar and Heinrich, 1977	Greatest length	1	580
	Heinrich, 1987	Greatest length	3	375-635
	Libois *et al.*, 1987	Greatest length	68	64-585
	Prenda *et al.*, 2002	Greatest length	38	193-485
	Brinkhuizen, 1989	Internal length	4	324-1004
	Enghoff, 1994	Anterior width	14	not given
Articular	Libois *et al.*, 1987	Greatest length	66	64-585
		Height	59	80-585
Maxilla	Prenda *et al.*, 2002	Greatest length	38	205-514
	Libois *et al.*, 1987	Greatest length	64	64-585
		Height behind caput	58	64-585
Opercular	Prenda *et al.*, 2002	Greatest length	38	208-474
	Libois *et al.*, 1987	Greatest length	61	75-585
	Libois *et al.*, 1987	Minimum width behind articulation	56	80-585
Ceratohyal	Libois *et al.*, 1987	Greatest length	64	68-585
		Length of the margo anterior	64	68-585
	Enghoff, 1994	Minimum antero-posterior distance	14	not given
Cleithrum	Heinrich, 1987	Chord length	3	375-635
	Brinkhuizen, 1989	Chord length	4	323-1004
	Coy, 1989	Chord length	16	± 200-760
	Libois *et al.*, 1987	Chord length	67	64-585
		Antero-posterior distance in the middle	63	68-585
	Enghoff, 1994	Antero-posterior distance in the middle	12	not given
Frontal	Libois *et al.*, 1987	Greatest length	68	64-585
Basioccipital	Libois *et al.*, 1987	Greatest length	62	68-585
	Prenda *et al.*, 2002	Greatest length	31	200-498
First precaudal vertebrae	Enghoff, 1994	Greatest width	14	not given
Unspecified precaudal vertebrae	Lepiksaar and Heinrich, 1977	Greatest length	1	580
Precaudal vertebrae	Carrs and Elston, 1996	Greatest length	20	121-555
		Greatest length	40	147-590
	Wise, 1980	Greatest length	28	130-700
Caudal vertebrae	Wise, 1980	Greatest length	28	130-700
First six caudal vertebrae	Prenda *et al.*, 2002	Mean length	36	181-447

accuracy of the size prediction for larger or smaller animals falling outside the size range of the sample set. In only one osteometrical study were numerous specimens measured that represented a wide range of body lengths (Libois *et al*., 1987), albeit that we experienced that several bone measurements are not easily reproducible.

Only two archaeozoological studies (Lepiksaar and Heinrich, 1977; Enghoff, 1994) paid attention to vertebrae for the size reconstruction of eels, despite the fact that, compared to cranial bones, these elements are usually the most frequently represented in sieved samples from European archaeological inland sites. The studies of Wise (1980), Carss and Elston (1996) and Prenda *et al*. (2002), implemented to deal with eel bones found in the gut contents or droppings of recent predators, apparently escaped the attention of the archaeozoological community. For the calculation of his regression equations, Wise (1980) excluded the first 8 precaudal and the last 21 caudal vertebrae. In his report, a regression relationship is given between fish length and the centrum length of the retained vertebrae. Regressions were calculated separately for precaudals, caudals, and for all of the retained vertebrae together. Carrs and Elston (1996) graphically presented the relationship between the precaudal vertebrae lengths and fish length, using all precaudals of 20 eels as a sample set, but underlined the difficulties defining a good correlation. In addition, they provided a regression obtained on the precaudal vertebrae recovered in otter spraints during a controlled feeding experiment involving 40 eels. Caudal vertebrae were not included in that study. Prenda *et al*. (2002) worked with the mean length of the first six caudal vertebrae and concluded that, when body lengths were back-calculated, this gave a better fit compared to cranial measurements.

When testing the accuracy of the formulae existing in the literature on a large series of modern skeletons of eels of known length, it appeared that back-calculated body lengths differed markedly, depending on the skeletal element used and the fish size class sampled. Vertebrae seemed to give better body length estimations compared to cranial elements. It was hypothesized that this apparent poor performance of head bones could be related to the large variation in head shape documented for eel, which led to the distinction of a narrow-headed and a broad-headed morphotype (Proman and Reynolds, 2000; Ide *et al*., 2011). Therefore, in the present study the predictive value of the various skeletal elements is further explored and, in particular, the vertebrae are analysed in more detail, taking into account the different morphotypes that can be distinguished (see below).

MATERIAL AND METHODS

The modern reference collection housed at the Royal Belgian Institute of Natural Sciences (RBINS, Brussels) includes 69 skeletons of European eel with total lengths ranging between 8 and 76 cm. Four of these specimens derive from the Rhine basin in the Netherlands, whereas the remaining 65 were sampled from the Scheldt basin, in Belgium. This sample set was used to calculate regression equations, starting from measurements of isolated bone elements, and to test their accuracy by comparing the results with existing length reconstructions. To identify the skeletal elements with the best size predicting power, correlations between total length and the measurements on the bones were established through the non-parametric Spearman Correlation Coefficient. Power curves were used to model the relationship between total fish length and the different skeletal measurements. Model coefficients for the power curves were estimated with the least squares method. Power curves give greater accuracy in size prediction of animals with allometric growth (e.g., Leach *et al*., 1996; Grouard, 2001), but have never been used in previous studies dealing with body length reconstructions of eel (see Tab. I). The accuracy of each of the models was evaluated by calculating the Standard Error of Estimate (SEE), the Coefficient of Determination (R^2) and the relative number of back-calculated sizes with a deviation higher than 10% from the actual length. Student's t test was performed to analyse the difference between two groups. Analyses were performed using STATISTICA software (StatSoft Inc., 2011) at the 0.05 level of significance.

It must be noted that the regression equations calculated are not always based on the same skeletal elements and measurements that have already been published. Preferentially, bones were retained that are readily identifiable and that we know, by experience, to have good chances of being preserved more or less complete in an archaeological context. In addition, only well defined measurements were chosen that can easily be reproduced. The opercular, for instance, has not been retained for the present study because it is rarely found in archaeological contexts. Moreover, it has rounded structures, making measurements poorly reproducible. Other measurements on individual bones that were not retained are: the height of the maxilla, the width of the dentary, the height of the articular (all recordings that are not easily reproducible), and the length of the frontal, the articular, the basioccipital and of the maxilla (all bones that are rarely preserved complete).

In this study, the following cranial measurements (Fig. 1) were tested using the recent reference collection of 69 individuals:

- caudal width of the basioccipital,
- caudal height of the basioccipital,
- greatest length of the articular,
- greatest length of the dentary,
- internal body length of the dentary (from symphysis to incisure),
- greatest antero-posterior distance of the hyomandibular

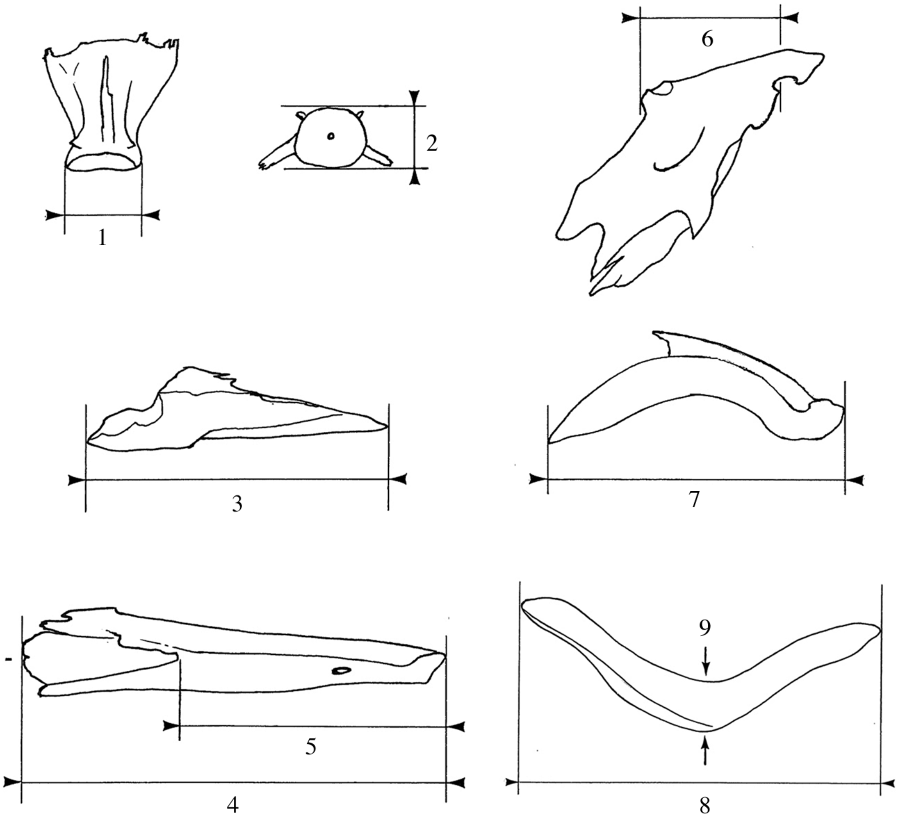

Figure 1. - Measurements on the cranial elements used in the present study: 1) caudal width of the basioccipital; 2) caudal height of the basioccipital; 3) greatest length of the articular; 4) greatest length of the dentary; 5) internal body length of the dentary; 6) greatest antero-posterior distance of the hyomandibular; 7) greatest length of the ceratohyal; 8) chord length of the cleithrum; 9) antero-posterior distance in the middle of the cleithrum.

(measured between the processus articularis sphenoticus and the processus articularis opercularis),
- greatest length of the ceratohyal,
- chord length of the cleithrum,
- antero-posterior distance in the middle of the cleithrum.

In the case of paired elements, the left side was used for the calculation of the regression equations. Of the vertebrae, width, height and length of the centrum were measured. The width and height were measured on the caudal end of the centrum, while the length was taken ventrally. The selection of vertebrae used is explained below, after the analysis of the variation in size and shape within the vertebral column.

All measurements were taken with digital calipers to the nearest 0.05 mm. Because of the whitish colour and glossy appearance of the reference specimens, a black background was used to enhance the exact location of the measuring points.

Shape and size variation of vertebrae within the vertebral column

Although European eels have a total number of vertebrae of around 115 (44 precaudals + 71 caudals) (Boëtius, 1980), earlier studies focusing on size reconstruction with the aid of vertebrae only made a distinction between precaudal and caudal vertebrae, using 'average data' for these skeletal elements as the input for the equations put forward (Wise, 1980; Carss and Elston, 1996; Prenda *et al.*, 2002). However, it is possible to attain more accuracy by distinguishing several morphotypes within both vertebral categories, as shown by Le Gall (1984, pp. 113-119). The first, second and third (precaudal) vertebrae are easily distinguishable, and also between each other (Fig. 2), but determining the exact position in the vertebral column of the remaining precaudal vertebrae is less straightforward, albeit that a number of morphotypes can indeed be distinguished (see also Le Gall, 1984). The next 6 to 7 precaudal elements (the 4th to 9th-10th precaudals) are here referred to as 'Type 4' vertebrae (types 1 to 3 being the first three precaudals). Typical for these elements are the two longitudinal ridges on the ventral side of the centrum and the elongated haemapophyses running over almost the entire length of the centrum but, at the same time, ventro-laterally poorly developed. The following 18 to 19 vertebrae have a 'Type 5' shape, characterised by the two haemapophyses being positioned at an angle of 90° to 45° to each other. In the remaining (usually 17) precaudal vertebrae, called 'Type 6', this angle is less than 45°.

The size variation within a particular (precaudal) morphotype has been evaluated by plotting the height, width and length measurements observed per vertebra within the precaudal part of the vertebral column of two modern specimens, one of 39 cm TL and one of 51.2 cm. The data are plotted here for the largest individual (Fig. 3, upper panel),

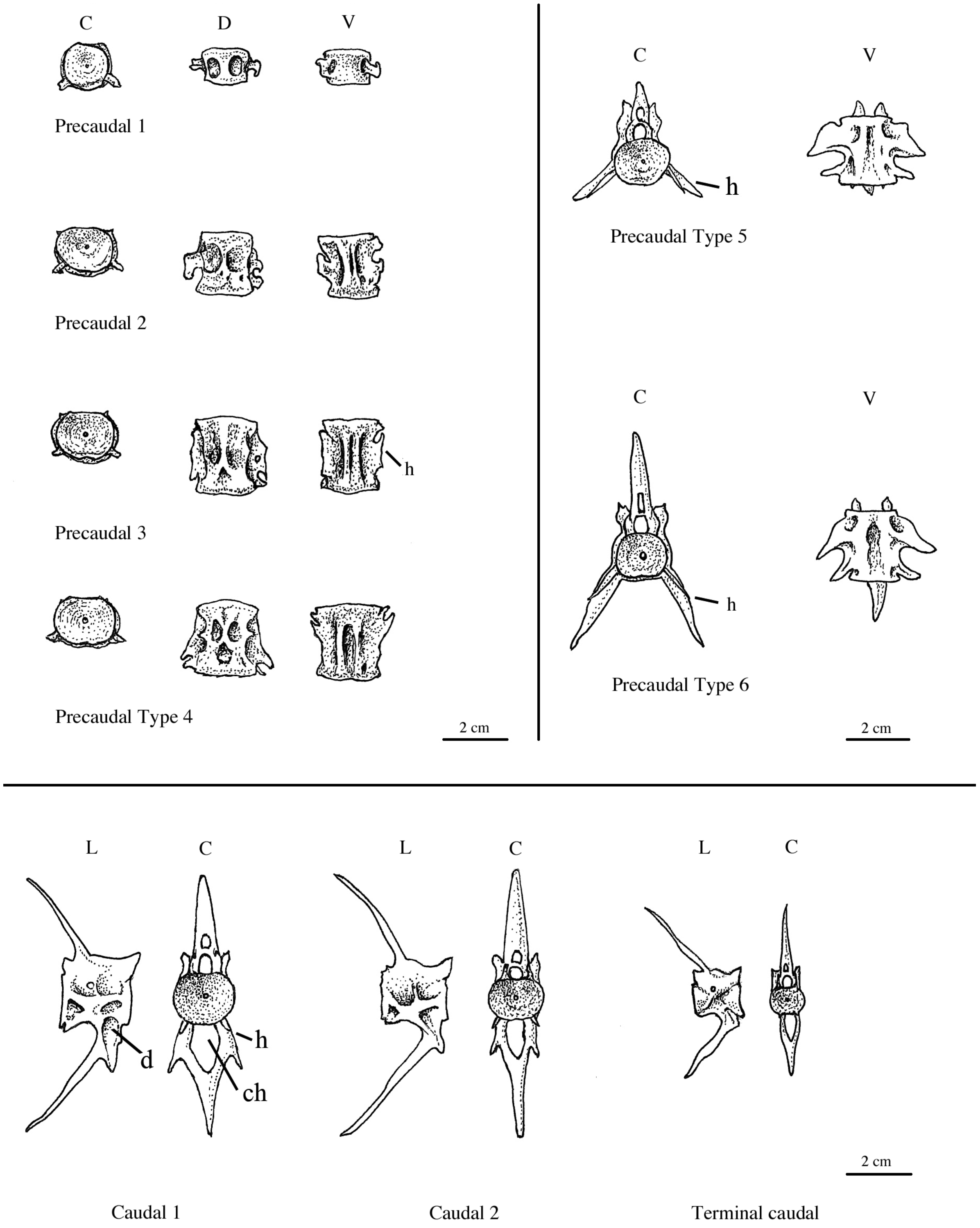

Figure 2. - Vertebrae morphotypes defined in the present study. Precaudal 1, 2, 3 and Type 4 vertebrae in cranial (C), dorsal (D) and ventral (V) view. Precaudal vertebrae Type 5 and 6 in cranial (C) and ventral (V) view. First caudal, second caudal and a terminal caudal vertebra in cranial (C) and right lateral (L) view. h = haemopophysis; ch = *canalis haemalis*; d = depression. The depicted vertebrae are from a specimen measuring 66.7 cm TL.

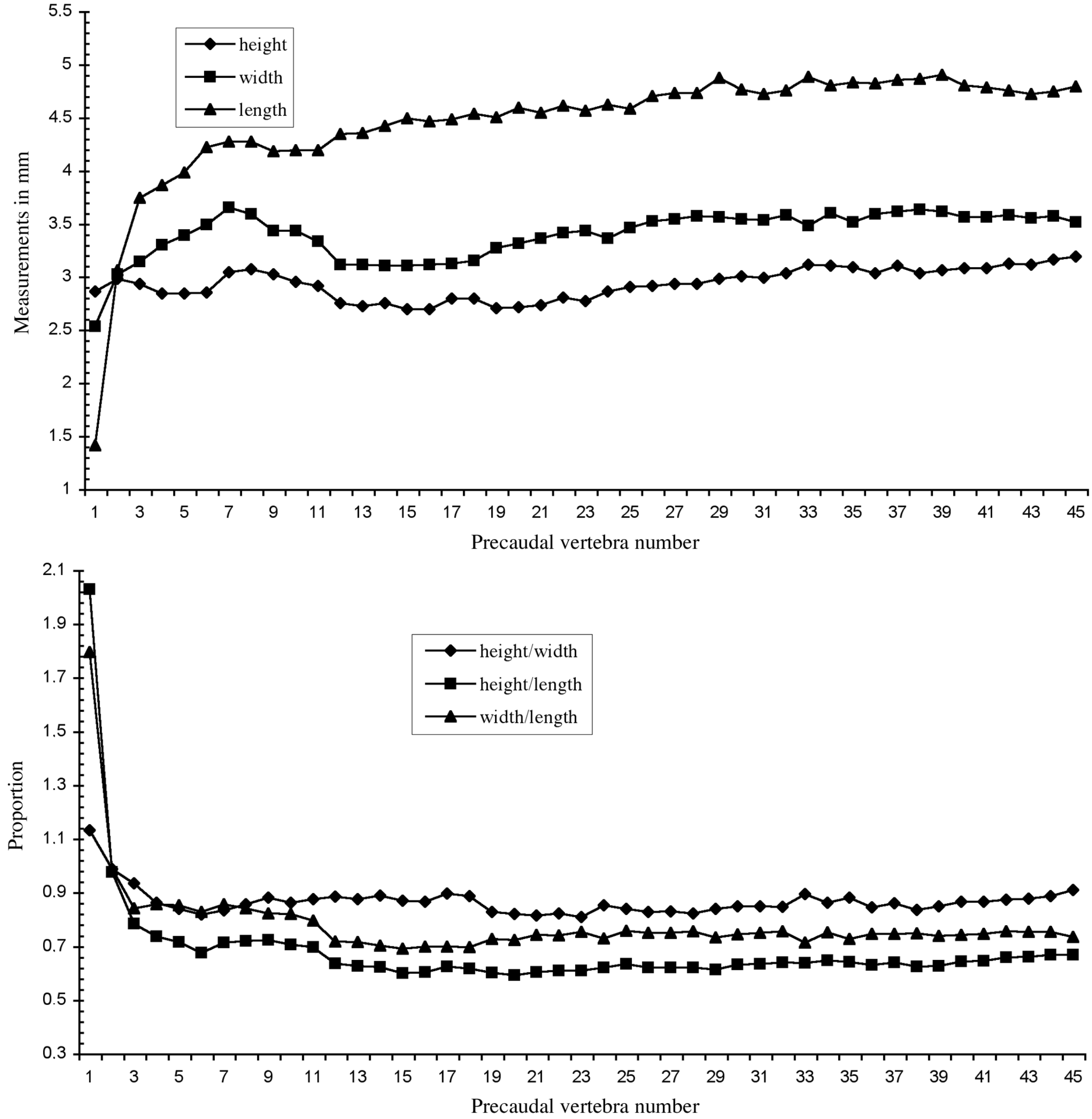

Figure 3. - Global Rachidian Profile of the precaudal segment of a modern eel of 51.2 cm TL. In the upper panel, the length, height and width of the centra are given separately. The lower panel shows the ratios.

which produced curves with an outline comparable to those of the smaller eel. This so-called 'Global Rachidian Profile' (Desse *et al*., 1989) allows the visual registration of the portions of the vertebral column that have centra with more or less similar dimensions. Such series of vertebrae with comparable dimensions are suitable for size reconstruction, because they can be used even when their exact rank within the vertebral column cannot be established. The graph clearly illustrates the large size differences between the first three precaudal vertebrae and the following skeletal elements. Considering the latter group, it appears that Types 4, 5 and 6 all show a similar size variation (between 0.20 and 0.25 mm difference between the largest and the smallest values observed), although it should be stressed that Type 4 contains a smaller number of vertebrae compared to Type 5 or 6. When proportions are used (Fig. 3, lower panel), the profiles are even more parallel to the X-axis. All this suggests, *a priori*, that isolated precaudal vertebrae may be suitable for size reconstructions even when they cannot be exactly positioned within the vertebral column.

Although it is possible to further subdivide the remaining, up to 70, caudal vertebrae in a number of morphotypes

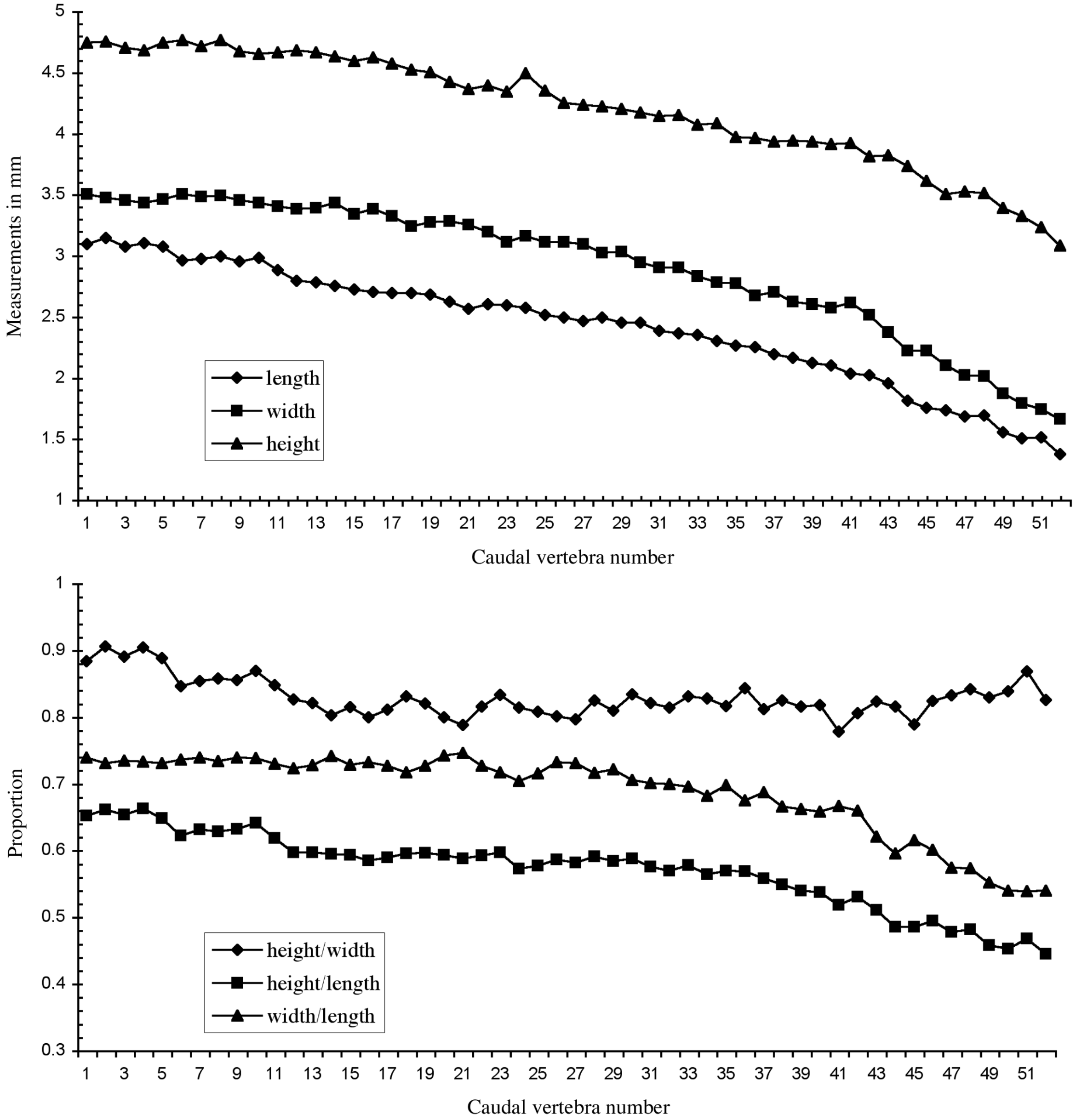

Figure 4. - Global Rachidian Profile of the caudal segment of a modern eel of 51.2 cm TL. The 20 terminal vertebrae are not shown. In the upper panel, the length, height and width of the centra are given separately. The lower panel shows the ratios.

(Le Gall, 1984), it appears that their shapes and dimensions change very gradually along the rachis, making it difficult to establish the provenance of a given, isolated, caudal vertebra within the vertebral column. An exception is the first caudal which can easily be recognized by its typical shape (Fig. 2). It has a closed haemal arch and a well-developed haemal spine. It is characterised by a well-developed haemapophysis similar to that seen in the precaudals, and with a clear triangular depression in its lateral side. In the other caudals the haemapophysis is less developed and has only a feeble or non-existant depression. In cranial view, the left and right haemal arches are at a wide angle, clearly extending laterally beyond the centrum. The canalis haemalis has a typical wide, oval, shape that is not seen in the following caudal vertebrae, which have a canal that is much narrower latero-medially. Fig. 4 (upper pane) gives the Global Rachidian Profile for the first 52 caudals of the modern specimen of 51.2 cm TL, implying that about 20 terminal vertebrae have not been considered (as was also done by Wise, 1980). These small, laterally very flattened, centra that have almost no ornamental structure on their lateral side (see ‘terminal caudal’ in Fig. 2), were excluded because their small sizes cause practical difficulties during measuring. In addition, the measuring errors increase too much in proportion to the actual measurements. Considering the caudal vertebrae retained, the Global Rachidian Profile shows that the first 15 elements have a more or less constant height and width, and then the vertebrae gradually become smaller. When the proportions are considered (Fig. 4, lower panel) it appears that this results in profiles that are more parallel to the X-axis, be it still less prominent than is the case for the precaudals. This suggests that more accurate size predictions can be obtained by combining different measurements of a caudal vertebra of unknown rank than when using individual measurements. It is also obvious that, compared to the precaudal elements, caudal vertebrae of which the exact position cannot be established are less suitable for length reconstructions.

For the calculation of the regression equations for the precaudal vertebrae of Type 4, 5 and 6, one precaudal vertebra of each type was randomly taken from each individual. Because most of the reference material is disarticulated, it was not possible to ascertain that, within each type, vertebrae of exactly the same rank were used. For the caudal vertebrae, on the contrary, this was possible because it was decided to measure only the first caudal.

RESULTS AND DISCUSSION

Table II lists the descriptive statistics for the measurements retained. The number of observations per measurement was lower than the number of analyzed eels, due to some missing skeletal elements. In some cases, however, the number of specimens that could be measured was markedly lower. This is the case for the internal body length of the dentary, which is often poorly ossified in the area of the caudally located measuring point, as a result of which the measurement could not be taken correctly. Similarly, there were problems with the accurate recording of short measuring distances in smaller individuals. This is the case, for instance, for the smallest antero-posterior distance in the middle of the cleithrum, and the measurements of the first precaudal.

The correlations between TL and the measurements on the bones were established through the non-parametric Spearman Correlation. All values appear to be relatively high (Tab. III), indicating a strong positive correlation between the total length and the skeletal measurements. The highest correlation coefficients seem to exist between the TL and the vertebrae measurements, suggesting that these elements are best suited for size reconstruction.

Different models, univariate as well as multivariate, were tested for the evaluation of the body size reconstruction potential of each skeletal element (Tab. IV). For each regression equation, the standard error of estimate (SEE), a measure of error in prediction, is given. The relative number of back-calculated sizes with a deviation higher than 10%

Table II. - Descriptive statistics for the different measurements, in millimetres, used in this study.

		N	Mean	Minimum	Maximum	SD
Total length		69	382.4	80	771	180.9
Dentary	Internal length	51	10.79	4.75	22.35	4.05
	Greatest length	66	15.10	3.15	35.00	7.50
Articular	Greatest length	66	10.59	2.40	20.55	4.77
Hyomandibular	Greatest a-p distance	57	5.47	2.30	13.00	2.20
Ceratohyal	Greatest length	62	11.29	2.50	25.25	5.14
Cleithrum	Chord length	62	16.50	3.60	35.30	7.55
	A-P distance in middle	51	1.86	0.70	5.20	0.82
Basioccipital	Caudal width	66	2.24	0.45	5.10	1.09
	Caudal height	60	2.09	0.75	5.40	0.96
Precaudal 1	Height	59	2.08	0.55	5.55	1.03
	Width	59	2.08	0.60	4.65	0.97
	Length	59	1.40	0.40	2.75	0.63
Precaudal 2	Height	64	2.08	0.50	5.30	1.04
	Width	64	2.25	0.55	5.30	1.08
	Length	64	2.49	0.80	4.65	1.06
Precaudal 3	Height	64	2.03	0.50	5.30	1.01
	Width	64	2.48	0.55	6.00	1.23
	Length	64	3.04	0.85	5.60	1.35
Precaudal Type 4	Height	64	2.12	0.50	6.15	1.09
	Width	64	2.54	0.61	6.55	1.27
	Length	64	3.20	0.90	7.10	1.45
Precaudal Type 5	Height	62	2.13	0.85	4.45	0.92
	Width	66	2.50	0.55	6.20	1.27
	Length	66	3.38	0.75	6.75	1.51
Precaudal Type 6	Height	62	2.38	0.90	4.65	0.99
	Width	66	2.58	0.60	6.00	1.27
	Length	66	3.39	0.80	6.75	1.51
First caudal	Height	59	2.51	0.90	4.90	1.02
	Width	61	2.58	0.60	5.75	1.20
	Length	61	3.46	0.80	6.70	1.45

Table III. - Spearman correlation coefficients (ρ), between the total length and the bone measurements described in table II, sorted in decreasing order ($p < 0.05$).

Parameter	ϱ
Length precaudal Type 6	0.994927
Length first caudal	0.994328
Length precaudal Type 5	0.992724
Height precaudal 3	0.992570
Width precaudal Type 6	0.991806
Height precaudal Type 4	0.990384
Height precaudal 2	0.989856
Caudal height basioccipital	0.989774
Width first caudal	0.988272
Width precaudal 3	0.988254
Greatest length dentary	0.986494
Height precaudal 1	0.986204
Width precaudal Type 5	0.985575
Chord length cleithrum	0.985104
Length precaudal 3	0.984030
Height precaudal Type 6	0.983730
Width precaudal 2	0.983491
Width precaudal Type 4	0.983252
Length precaudal Type 4	0.982473
Height precaudal Type 5	0.981676
Caudal width basioccipital	0.981504
Height first caudal	0.981105
Width precaudal 1	0.979191
Greatest length articular	0.975461
Internal length dentary	0.974364
Length precaudal 2	0.971414
Greatest A-P distance hyomandibular	0.967571
Greatest length ceratohyal	0.964629
A-P distance in middle cleithrum	0.947931
Length precaudal 1	0.879135

from the actual length is also given, as an indication for the accuracy of the size reconstruction.

The SEE values indicate which skeletal elements are better size predictors than others. Most cranial elements have higher SEE and lower R^2 values than the vertebrae, and are thus less suited as size predictors. The articular, ceratohyal, hyomandibular and basioccipital in particular do not score well, with both the highest SEE and lowest R^2. Up to 35% of the back-calculations based upon measurements taken from these skeletal elements show a deviation greater than 10% from the actual length.

In contrast to the cranial elements, measurements taken from the vertebrae yield more reliable size predictions. The first caudal vertebra and the Type 5 and Type 6 precaudals seem to be excellent size estimators, with high R^2 and low SEE values. Accordingly, none of the back-calculations exceeds 10% difference from the actual size and only 15% have more than a 5% error. In general, the length measurements of these precaudals produce better back-calculations than the height or width measurements. Type 4 gave the next best results, the three precaudal types, especially precaudal 1 and 2, performing less well when single measurements are used. A combination of measurements, however, increases the accuracy of the predictions considerably for the first three precaudals (Tab. IV, multiple regression).

It was also tested whether it was possible to construct a single regression equation for the three different types of precaudal vertebrae (Types 4, 5 and 6), obviously excluding the first three precaudals (see earlier). A t-test showed that the measurements taken from these three types did not differ statistically ($p > 0.05$) and an equation based upon the lengths and widths of Type 4, 5 and 6 vertebrae was thus constructed (see Tab. IV; Types 4, 5 and 6 combined). However, when this equation was tested against the measurements of the 69 eels from the reference collection, a relatively high number of deviations exceeding 10% between calculated and actual fish lengths, was observed for the Type 4 vertebrae. Therefore, the analysis was repeated excluding Type 4 vertebrae. Regarding Type 5 and 6, it was clear that, as the SEE and R^2 of the model of the combined types versus those of the separate types are more or less the same, a discrimination between vertebrae of Type 5 and 6 is not absolutely necessary. According to these results, regarding size estimation, the two types can be combined without an overall loss in accuracy.

As a final step, the equations calculated were compared with those given in the literature (Tab. V). Ideally, such an exercise should be performed on a test population of bones of eels with known sizes, not used in any previous analysis. Unfortunately, such a population was not at our disposal, so the reference collection used as sample set for the present study was tested again, possibly biasing the results in our advantage. In any case, the SEE of the equations described in the literature were generally significantly higher than ours, indicating that the size estimations put forward in this study are more accurate. Between 20-80% of the back-calculations using equations from the literature gave SEE-values exceeding 10% of the actual fish length. In contrast, the SEE values resulting from the regression equations presented in this study always yielded better values.

CONCLUSION

The results of this study indicate that, for body length reconstructions of the European eel, vertebrae provide the most accurate estimations, while cranial elements, frequently used in the literature, are less reliable. This pattern can probably be explained by the fact that European eel are

Table IV. - Regression equations for the different skeletal elements with indication of the type of regression retained, the coefficient of determination (R^2), the standard error of estimate (SEE) and the proportion of back-calculated fish lengths with a deviation of more than 10% from the actual length.

Skeletal element	Regression type	Equation	R^2	SEE	% with deviation > 10%
Dentary	Simple	$TL = 28.45 * \text{greatest length}^{0.9585}$	0.9816	31.13	23
		$TL = 52.74 * \text{internal length}^{0.8948}$	0.9562	36.03	23
Articular	Simple	$TL = 39.26 * \text{greatest length}^{0.9719}$	0.9728	38.63	21
Hyomandibular	Simple	$TL = 90.11 * \text{greatest A-P distance}^{0.9079}$	0.9519	43.02	19
Ceratohyal	Simple	$TL = 38.19 * \text{greatest length}^{0.9704}$	0.9637	56.10	29
Cleithrum	Simple	$TL = 26.67 * \text{chord length}^{0.9768}$	0.9842	27.45	16
		$TL = 278.60 * \text{A-P distance in the middle}^{0.7875}$	0.9165	56.79	35
Basioccipital 1	Simple	$TL = 171.95 * \text{caudal width}^{0.9966}$	0.9772	39.24	25
		$TL = 216.01 * \text{caudal height}^{0.891}$	0.9741	37.37	11
Precaudal 1	Simple	$TL = 219.74 * \text{height}^{0.8483}$	0.9782	36.71	17
		$TL = 213.85 * \text{width}^{0.8812}$	0.9737	35.86	17
		$TL = 299.02 * \text{length}^{0.8675}$	0.8185	86.88	59
	Multiple	$TL = 217.17 * \text{height}^{0.5456} * \text{width}^{0.3178}$	0.9802	34.33	14
Precaudal 2	Simple	$TL = 217.75 * \text{height}^{0.8492}$	0.9833	30.23	14
		$TL = 196.26 * \text{width}^{0.8845}$	0.9746	35.94	17
		$TL = 161.51 * \text{length}^{0.987}$	0.9582	43.37	37
	Multiple	$TL = 200.15 * \text{height}^{0.6333} * \text{length}^{0.2612}$	0.9864	26.97	6
Precaudal 3	Simple	$TL = 219.29 * \text{height}^{0.8627}$	0.9864	30.47	5
		$TL = 185.11 * \text{width}^{0.8624}$	0.9826	32.60	12
		$TL = 139.46 * \text{length}^{0.9478}$	0.9799	27.94	11
	Multiple	$TL = 184.58 * \text{height}^{0.5452} * \text{length}^{0.3546}$	0.9896	22.59	3
Precaudal Type 4	Simple	$TL = 214.28 * \text{height}^{0.8489}$	0.9820	37.47	8
		$TL = 180.76 * \text{width}^{0.8645}$	0.9821	33.66	9
		$TL = 134.20 * \text{length}^{0.9404}$	0.9821	25.96	14
	Multiple	$TL = 168.61 * \text{height}^{0.240} * \text{width}^{0.2803} * \text{length}^{0.3647}$	0.9880	27.54	3
Precaudal Type 5	Simple	$TL = 207.38 * \text{height}^{0.9154}$	0.9272	29.84	18
		$TL = 182.28 * \text{width}^{0.8649}$	0.9813	30.96	9
		$TL = 122.94 * \text{length}^{0.9616}$	0.9945	15.89	0
	Multiple	$TL = 129.45 * \text{width}^{0.1182} * \text{length}^{0.8322}$	0.9950	15.17	0
Precaudal Type 6	Simple	$TL = 184.57 * \text{height}^{0.9353}$	0.9784	27.10	10
		$TL = 172.42 * \text{width}^{0.8915}$	0.9883	23.54	6
		$TL = 120.71 * \text{length}^{0.975}$	0.9957	13.72	0
	Multiple	$TL = 127.88 * \text{height}^{0.1422} * \text{length}^{0.8324}$	0.9947	13.45	0
Precaudal Type 4, 5 and 6 combined	Multiple	$TL = 144.72 * \text{width}^{0.3592} * \text{length}^{0.5689}$	0.9900	Type 4 32,16	9
				Type 5 18.66	3
				Type 6 14,66	2
Precaudal Type 5 and 6 combined	Multiple	$TL = 127.68 * \text{width}^{0.1137} * \text{length}^{0.8444}$	0.9950	Type 5 15.22	0
				Type 6 13.69	0
First caudal	Simple	$TL = 176.24 * \text{height}^{0.9499}$	0.9798	26.49	12
		$TL = 176.57 * \text{width}^{0.9015}$	0.9842	26.17	8
		$TL = 119.61 * \text{length}^{0.9949}$	0.9942	15.28	0
	Multiple	$TL = 126.85 * \text{height}^{0.1765} * \text{length}^{0.8204}$	0.9939	15,18	0

Table V. - SEE of the equations obtained in this study, compared to the values calculated on the basis of the equations mentioned in the literature. 1 = Libois *et al*., 1987; 2 = Brinkhuizen, 1989; 3 = Lepiksaar and Heinrich, 1977; 4 = Prenda *et al*., 2002; 5 = Coy, 1989; 6 = Enghoff, 1994; 7 = Carss and Elston, 1996; 8 = Wise, 1980; 9 = Heinrich, 1987.

	This study	1	2	3	4	5	6	7	8	9
Dentary greatest length	31.13	51.26	–	36.9	42.04	–	–	–	–	–
Dentary internal length	36.03	–	43.54	–	–	–	–	–	–	–
Articular greatest length	38.63	54.39	–	–	–	–	–	–	–	–
Ceratohyal greatest length	56.10	74.4	–	–	–	–	–	–	–	–
Cleithrum chord length	27.45	57.13	48.55	–	–	72.07	–	–	–	43.02
Cleithrum A-P distance	56.79	74.92	–	–	–	–	56.07	–	–	–
Precaudal 1 width	35.86	–	–	–	–	–	41.08	–	–	–
Precaudal Type 5 length	15.89	–	–	17.21	–	–	–	16.64	85.85	–
First caudal length	15.28	–	–	–	22.88	–	–	–	82.3	–

characterised by a high intraspecific variation in head shape, leading to the distinction of two morphotypes, albeit that a strong overlap persists between these narrow-headed and broad-headed phenotypes (Proman and Reynolds, 2000; Ide *et al*., 2011). Without doubt, this phenomenon influences the shape and size of the cranial bones and may therefore also reduce the accuracy of size predictions based upon these elements. Vertebrae, on the other hand, are not expected to be influenced by this intraspecific variation, which may explain why they present a better alternative for size reconstruction. It appears from this study that the most accurate predictions can be made using the length measurements from the first caudal vertebra and from the precaudal vertebrae defined as Type 5 and 6 by their general morphology. A distinction between the latter two types does not seem to be a necessary step, as a single regression equation, combining both, can be used without a significant loss of precision. The first three precaudals and the Type 4 precaudals yield less accurate results than the first caudal vertebra and the Type 5 and 6 precaudals. Still, they remain better indicators compared to the cranial elements.

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