An elementary approach for estimating fossil volume: implications for allometric scaling

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Abstract

To calculate the volume of fossils based on Archimedes' principle, a simple experimental system for measuring underwater weight was constructed using a pole stand and a digital balance. As an initial step to examine fossil specimens, we validated the experimental system using 1 cm^3 metal cubes made of aluminium and iron. The average underwater weights of the aluminium and iron cubes were 0.997 g and 1.006 g, respectively. Utilising the density of fresh water, we determined the volumes calculated from underwater weights to be 1.001 cm^3 for the aluminium cube and 0.992 cm^3 for the iron cube, both of which corresponded to the product information for the metal cubes. Subsequently, when applying the experimental system to fossil specimens of the strophomenid brachiopod *Eoplectodonta transversalis*, our results indicated that the length and width of the shell exhibited an isometric and negative growth relationship relative to its volume, respectively. This morphological trend could potentially be attributed to the development of the ptycholophous lophophore, which caused a commensurate anterior growth to accommodate the increased metabolic rate.

Key words: Allometry, Brachiopoda, Strophomenida, Silurian, morphology, growth strategy.

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Introduction

Biomechanical approaches to fossil organisms significantly contribute to our understanding of adaptation and evolution in palaeontology (e.g., Koehl, 1996; Shiino et al., 2009, 2014; Fujiwara and Hutchinson, 2012). Because this approach allows numerical determination of functional thresholds and applicable ranges for adaptation capability and biological performance, the concept of treating an organism as a functionally integrated body serves as the "workhorse" of the functional morphological analyses (e.g., Shiino and Kuwazuru, 2010, 2011; Shiino et al., 2012). However, all organisms change their size and form during growth, which contrasts with mechanical designs that remain morphologically unchanged from production to disposal. The variable systems involved in the morphology of organisms do not collapse into dysfunction and continue to be maintained while changing size; additionally, and all systems maintain a balance without contradiction or fatal conflict. Biological scaling needs to be considered to understand biological design and its related ecology and evolution within the body plan.

Brachiopods are good examples for the study of biological scaling because their shells preserve their growth history as accrementition, showing a variety of morphology in terms of outline and convexity (Williams et al., 1997b). In general, the length of brachiopod shells is assumed to represent the size parameter for scaling (e.g., Zezina and Smirnova, 1977; Peck and Holmes, 1989; Saito and Tazawa, 2002). On the other hand, most of the interior of rhynchonelliformean brachiopods is a mantle cavity, which contains a tentaculate feeding organ, so called the lophophore (James et al., 1992; Williams et al., 1997b). Consequently, the total volume encapsulated by the shell is significantly correlated with the space available for filter feeding, which may be indicative of metabolic rates during growth.

For calculating the volume of an object, the underwater weight warrants consideration based on Archimedes' principle. When an object is submerged in water, the surrounding water exerts an upward buoyant force on the object (e.g., Ichinohe et al., 2019). Simultaneously, a downward force equal to the buoyant force acts on the water as a reaction. According to Archimedes' principle, the buoyant force is equal to the weight of the volume of the liquid displaced by the object. Therefore, the volume of an object based on its underwater weight can be calculated and represents the weight of the liquid displaced by the object.

As a preliminary step to understand growth strategies in fossil brachiopods, we constructed a simple experimental system to calculate the underwater weight of objects. Based on the validity and repeatability of the present system, we examined the growth pattern of Silurian brachiopods, with special reference to allometric scaling.

Material and methods

1. Metal material and fossil specimens

For the test experiments, we used aluminium and iron cubes of 1 cm^3, Density Measurement Cube (Artec Co., Ltd., Japan). The tolerances of these cubes are ±5%. We used 2.699 g/cm^3 and 7.874 g/cm^3 for the densities of aluminium and iron cubes, respectively.

For the examination of allometric scaling, we used 43 specimens of fossil brachiopod *Eoplectodonta transversalis* (Wahlenberg, 1818) from the lower Silurian Visby Formation of Gotland, Sweden (Fig. 1). All specimens have well-preserved conjoined valves, with size ranging from 2.12–12.28 mm in length. Prior to the calculation, nearly all the muddy particles on the specimens were removed using an ultrasonic cleaner.

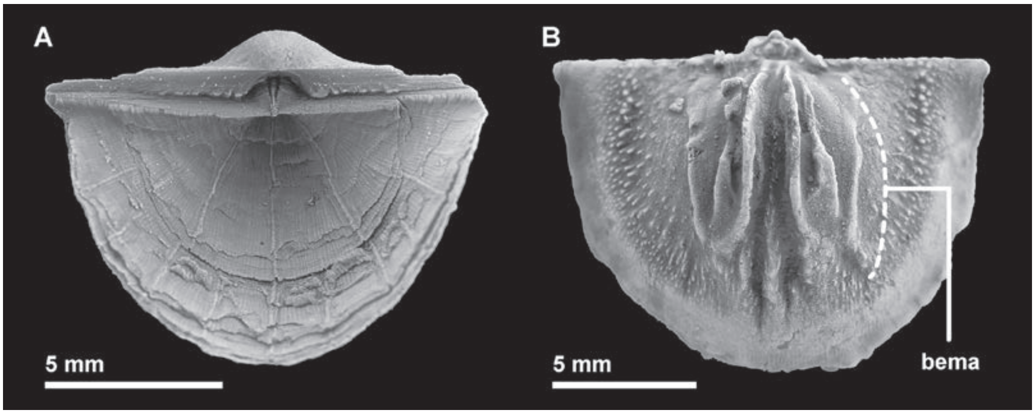

Fig. 1. Morphology of fossil brachiopod *Eoplectodonta transversalis* (Wahlenberg, 1818). **A**. Dorsal view of conjoined shell. **B**. Ventral (internal) view of dorsal valve. Several rows of the ridges, called bema, are attachment sites of ptycholophous lophophore. Photographs referenced from Shiino (2013).

2. Experimental protocols

To calculate the underwater weight of the fossil specimens, a simple experimental system using a pole stand and a digital balance was constructed (Fig. 2). The pole stand was equipped with a small stage with an iron beam (Fig. 2B). The stage was slightly submerged in a beaker filled with water in advance, and its weight was measured using a digital scale Precision Balance RJ-320 (Shinko Denshi Co., Ltd., Japan). Subsequently, the specimen was placed on the stage and slowly submerged, and the underwater weight was measured.

To examine the effect of rocks absorbing water, the differences in the underwater weights of the dry and wet specimens were compared. The weight of the fossil itself was also measured and compared with the volume calculated using the density of fossil. The shells of rhynchonelliformean brachiopods are primarily composed of calcium carbonate in the form of low-magnesian calcite (Jope, 1965). Furthermore, the present specimens occur in marlstone without sedimentary structures. Although there may be heterogeneity of

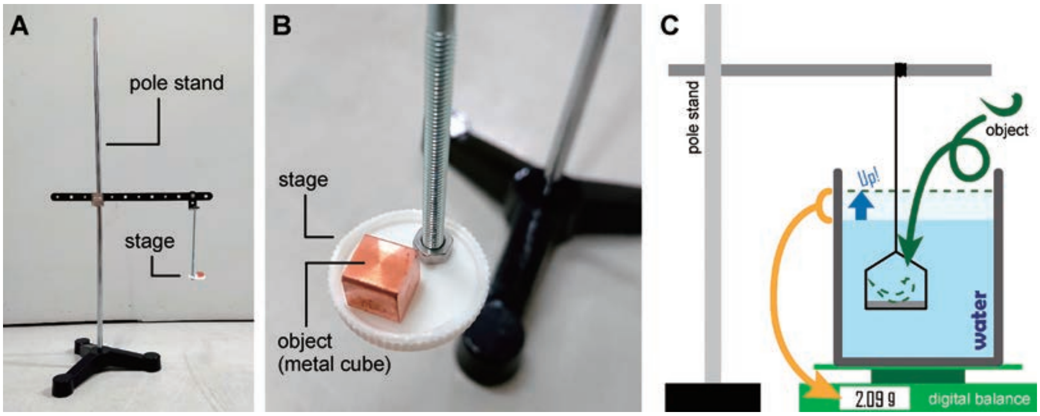

Fig. 2. Experimental system to calculate the underwater weight. **A**. Photograph of the experimental system without an electronic balance. **B**. Magnified photograph of the stage. **C**. Schematic illustration of the experimental system.

material inside the shell, we utilised the ideal density of calcite (2.71 g/cm^3) to estimate the volume based on the weight of the fossil.

3. Evaluation of brachiopod morphology

To evaluate the growth of *Eoplectodonta transversalis*, we measured the length L and width W using photographs of each specimen, and these measurements were compared with the calculated volume using the underwater weight. In the case of biological scaling, two variables of morphometric data were typically plotted on logarithmic coordinates, resulting in the linear-regression lines of the allometric equation, $y = ax^b$, where x and y are variables (Schmidt-Nielsen, 1984). Therefore, the graphs are shown with a double-logarithmic scale.

In general, component b in the allometric equation reflects the difference in growth strategy. When we compared two variables of the same dimension, such as a length relative to another length, a component greater than 1 could be interpreted as positive allometric growth, a component close to 1 could be interpreted as isometric growth, and a component smaller than 1 could be interpreted as negative allometric growth. The threshold value of the isometric growth differs in their dimensions; the volume increases as the cube of the length.

4. Statistical analysis

Statistical analyses were performed using R (The R Foundation for Statistical Computing, Vienna, Austria, version 4.2.1). To find correlations among the parameters, we conducted Pearson's correlation tests and set the significance level p-value at 0.05.

Results and discussion

1. Metal cubes

Table 1 shows the underwater weights of six experiments using aluminium and iron cubes. The range of numerical values for the aluminium cube was 0.978–1.054 g, with an average of 0.997 g, and the range of numerical values for the iron cube was 0.987–1.041 g, with an average of 1.006 g. Figure 3 shows box plots of the underwater weight using the aluminium and iron cubes. In both cubes, no significant differences were observed between the six experiments.

Table 2 shows numerical values of the volume *V* based on density *D* and weight *M* and the calculated volume *V*u based on the average underwater weight *M*u. The calculated volume *V*u of the aluminium cube was 1.001 cm^3 and that of the iron cube was 0.992 cm^3, both of which were similar to those of volume *V*. Therefore, our method could be applied to ensure the experimental validity of using the underwater weight to calculate its volume.

Table 1. Numerical values of underwater weight using aluminium and iron cubes.

Material	1 [g]	2 [g]	3 [g]	4 [g]	5 [g]	6 [g]	Average underwater weight *M*u [g]
Al	0.984	0.985	0.985	1.054	0.994	0.978	0.997
Fe	1.041	0.989	1.001	0.987	1.033	0.987	1.006

We demonstrated six times measurements, and then calculated average values.

Table 2. Numerical values of the test experiments using aluminium and iron cubes.

Material	Density *D* [g/cm^3]	Weight *M* [g]	Volume *V* (=*D*/*M*) [cm^3]	Average underwater weight *M*u [g]	Calculated volume *V*u (=*M*u/0.998) [cm^3]	Difference rate (*V*u-*V*)/*V*
Al	2.699	2.677	0.992	0.997	1.001	0.009
Fe	7.874	7.699	0.978	1.006	0.992	0.014

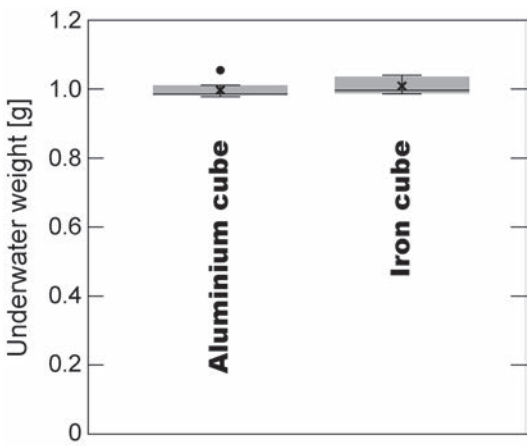

Fig. 3. Box plots of the numerical values using aluminium and iron cubes. The vertical lines with terminal cross bars are maximum and minimum values with the exception of an outlier value (black coloured circle). The lower and upper ends of each box indicate the 1st and 3rd quartiles, respectively. In each box, the horizontal black line shows the median, while the cross mark shows the average.

Table 3. Morphometric values of brachiopod *Eoplectodonta transversalis*.

Specimen ID	Length L [mm]	Width W [mm]	Weight M_f [g]	Volume V_s (= M_f/2.71) [cm^3]	Underwater weight of dry specimen M_{ds} [g]	Underwater weight of wet specimen M_{ws} [g]	Calculated volume of dry specimen V_{df} (= M_{ds}/0.998) [cm^3]	Calculated volume of wet specimen V_{ws} (= M_{ws}/0.998) [cm^3]
1	2.12	3.18	0.003	0.00111	---	0.001	---	0.00100
2	4.20	8.20	0.025	0.00923	0.005	0.008	0.00501	0.00802
3	3.92	6.13	0.018	0.00664	0.005	0.005	0.00501	0.00501
4	6.22	9.68	0.077	0.02841	0.026	0.028	0.02605	0.02806
5	5.60	9.83	0.055	0.02030	0.026	0.021	0.02605	0.02104
6	6.48	9.58	0.080	0.02952	0.032	0.030	0.03206	0.03006
7	3.78	7.14	0.016	0.00590	0.007	0.009	0.00701	0.00902
8	4.40	7.16	0.022	0.00812	0.008	0.009	0.00802	0.00902
9	3.12	5.15	0.005	0.00185	0.006	0.004	0.00601	0.00401
10	5.00	7.83	0.046	0.01697	0.016	0.018	0.01603	0.01804
11	11.11	12.99	0.378	0.13948	0.150	0.151	0.15030	0.15130
12	7.80	11.63	0.151	0.05572	0.056	0.057	0.05611	0.05711
13	8.42	10.91	0.208	0.07675	0.079	0.081	0.07916	0.08116
14	7.04	9.70	0.090	0.03321	0.026	0.036	0.02605	0.03607
15	4.86	7.55	0.038	0.01402	0.013	0.014	0.01303	0.01403
16	8.61	12.57	0.174	0.06421	0.065	0.066	0.06513	0.06613
17	11.25	13.05	0.424	0.15646	0.163	0.163	0.16333	0.16333
18	5.48	9.02	0.049	0.01808	0.021	0.016	0.02104	0.01603
19	7.03	10.85	0.105	0.03875	0.040	0.042	0.04008	0.04208
20	9.81	11.01	0.314	0.11587	0.119	0.120	0.11924	0.12024
21	5.28	8.66	0.037	0.01365	0.011	0.016	0.01102	0.01603
22	11.06	12.88	0.388	0.14317	0.140	0.149	0.14014	0.14915
23	8.91	12.14	0.180	0.06642	0.076	0.078	0.07608	0.07808
24	5.35	8.30	0.046	0.01697	0.008	0.020	0.00801	0.02002
25	6.73	10.15	0.096	0.03542	0.037	0.041	0.03704	0.04104
26	11.12	13.89	0.454	0.16753	0.179	0.181	0.17918	0.18118
27	6.77	9.33	0.077	0.02841	0.036	0.034	0.03604	0.03403
28	11.16	12.34	0.444	0.16384	0.180	0.183	0.18018	0.18318
29	11.35	12.20	0.369	0.13616	0.145	0.139	0.14515	0.13914
30	10.24	11.94	0.434	0.16015	0.158	0.165	0.15816	0.16517
31	10.25	11.19	0.313	0.11550	0.128	0.125	0.12813	0.12513

Specimen ID	Length L [mm]	Width W [mm]	Weight M_f [g]	Volume V_s (=M_f/2.71) [cm³]	Underwater weight of dry specimen M_{ds} [g]	Underwater weight of wet specimen M_{ws} [g]	Calculated volume of dry specimen V_{df} (=M_{ds}/0.998) [cm³]	Calculated volume of wet specimen V_{ws} (=M_{ws}/0.998) [cm³]
32	9.66	11.08	0.247	0.09114	0.101	0.102	0.10110	0.10210
33	7.80	11.11	0.160	0.05904	0.069	0.065	0.06907	0.06507
34	9.50	10.57	0.267	0.09852	0.104	0.105	0.10410	0.10511
35	5.72	9.16	0.058	0.02140	0.026	0.023	0.02603	0.02302
36	12.22	13.45	0.564	0.20812	0.214	0.222	0.21421	0.22222
37	6.26	8.81	0.080	0.02952	0.027	0.034	0.02705	0.03407
38	9.48	10.06	0.253	0.09336	0.094	0.101	0.09419	0.10120
39	9.28	11.21	0.237	0.08745	0.090	0.091	0.09018	0.09118
40	9.24	14.68	0.220	0.08118	0.092	0.083	0.09218	0.08317
41	12.28	12.75	0.570	0.21033	0.216	0.218	0.21643	0.21844
42	12.25	13.82	0.497	0.18339	0.210	0.209	0.21042	0.20942
43	11.84	13.13	0.490	0.18081	0.180	0.185	0.18036	0.18537

---: unmeasurable

2. Length, width and volume of *Eoplectodonta transversalis*

The length L, width W, weight M_f, underwater weight in dry M_{ds} and wet M_{ws} conditions of all specimens were measured, with the exception of the underwater weight of the dry specimen M_{ds} for specimen ID1. Because the specimen is too small with a length of 2.12 mm, the measurement display remained zero when the specimen in the dried condition was placed on the stage in the underwater setup. Using the specimen under the wet condition, 0.001 g of underwater weight was measured, though the numerical value was a detection limit. In our present experimental system, the underwater weight of the small specimens less than 4.4 mm in length was determined to be only one significant digit.

The width W and weight M_f increased with length increased as shown in Fig. 4A, B. For the allometric equation, we obtained $W = 2.70L^{0.66}$ ($R = 0.92$, $p < 0.01$) and $M_f = (3.0 \times 10^{-4}) L^{3.05}$ ($R = 0.95$, $p < 0.01$). In the former case, the length L has a positive allometric growth with respect to the width W because the exponent value was 0.66 (Fig. 4A). Qualitatively, this indicates that the greater the length, the greater will be the elongated appearance.

Figure 4C shows the numerical values of the volume relative to the length L or width W; the volume V_s (= Mf / 2.71), the calculated volume of dry specimen V_{df} (= M_{ds} / 0.998) and the calculated volume of wet specimen V_{ws} (= M_{ws} / 0.998). We obtained $V_s = (1.0 \times 10^{-4}) L^{3.05}$ ($R = 0.95$), $V_{ds} = (1.0 \times 10^{-4}) L^{3.07}$ ($R = 0.96$), $V_{ws} = (1.0 \times 10^{-4}) L^{3.01}$ ($R = 0.95$), and $V_{ws} = (4.0 \times 10^{-6}) W^{4.04}$ ($R = 0.81$), all of which have significant correlations ($p < 0.01$).

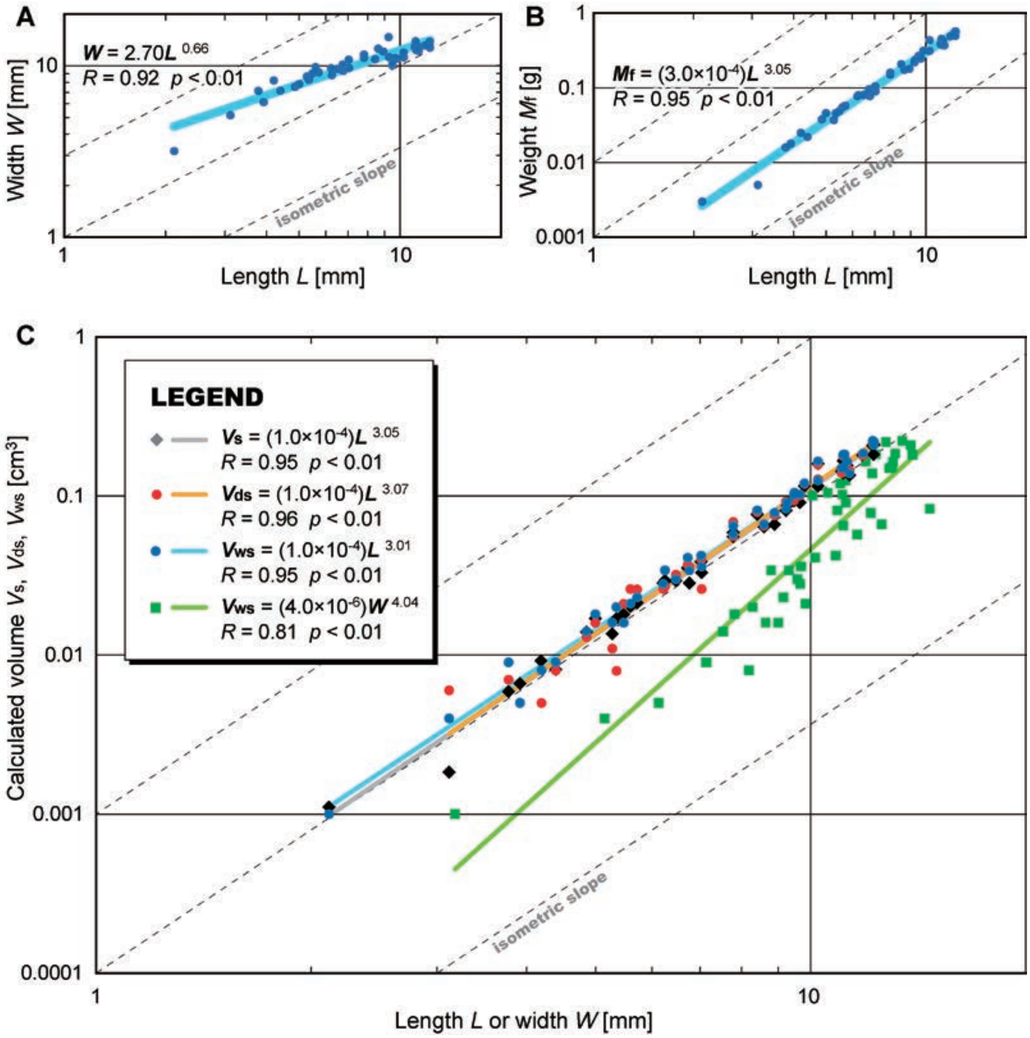

Fig. 4. Graphs of the numerical values. **A**. Width W with respect to length L ($p = 2.2 \times 10^{-16}$). **B**. Weight M_f with respect to length L ($p = 2.2 \times 10^{-16}$). **C**. Calculated volume V_s, V_{ds} and V_{ws} with respect to length L or width W. The block lines indicate the approximation with significant correlation based on the p-value.

All cases of the volume relative to length were closely similar to each other, with those components ranging from 3.01 to 3.07 (Fig. 4C). This relationship between the length and volume implies isometric growth. Unlike the comparison with length, the volume relative to width shows a larger increment in contrast to the isometric growth. Consequently, the width of the present species clearly shows a negative allometric growth with respect to either length or volume.

Several brachiopod species tend to have elongated shell outlines (e.g., Tazawa, 1974; Michalik, 1996). Because the brachiopod shell encapsulates soft parts responsible for biological performance, the changes of shell outline can be explained by the structure and function of the internal organs. The internal space of the shell is mainly subdivided into two parts; a body cavity and a mantle cavity (Williams et al., 1997b). The body cavity is a main part of the coelomic space in the posteromedian zone and contains the important organs such as muscles, digestive tract and reproductive structures (Williams et al., 1997b). The mantle cavity at the antero-lateral space inside the shell contains a food-collecting organ, called the lophophore; here, the flow of seawater enables passing (Williams et al., 1997b). In the case of typical rhynchonelliformeans including the present species, the space of the mantle cavity is greater than that of the body cavity (Williams et al., 1997b). This leads to the possibility that the difference in shell volume calculated herein is closely related to the development of the lophophore, reflecting metabolic requirements in each brachiopod species.

Eoplectodonta has a ptycholophous type of lophophore on the inner surface of the dorsal valve (Williams et al., 1997a; Clarkson, 1998). As the growth progresses, each lobe of ptycholophe extends in the anterior direction (Williams et al., 1997a). Therefore, the positive allometric growth of length relative to width can be interpreted as the development of the mantle cavity for the growth of the ptycholophous lophophore. This growth pattern could have allowed for isometric growth in length and volume, which is a similar trend to the case of extant terebratulid brachiopods (Peck and Holmes, 1989). By contrast, brachiopods with laterally extended lophophore may exhibit negative allometric growth of length relative to width. It is likely in spiriferid brachiopods with a long-winged appearance which have spiral lophophore with small diameter but larger number of spires, as observed in *Mucrospirifer* (Ager and Riggs, 1964; Carter et al., 2006).

3. Insights into the allometric scaling of brachiopod morphology

Based on Archimedes' principle, our study established a method to calculate volume based on the underwater weight. It is possible to uniformly compare three-dimensional body size data in terms of volume, even when the shapes of the objects are different. A problem is still present in the calculation of the small specimens of *Eoplectodonta* less than 4.4 mm in length; however, the volume calculated from the density of calcite and the weight of the specimen itself was effectively matched with the volume based on the underwater weight. This result indicates that the present specimens have similar physical properties to a calcareous shell and sediments with a lower amount of inside void space. By cross-checking the volume of the specimens based on the underwater weight and fossil weight, the validity of the calculated values to reflect the growth pattern of brachiopod morphology could be determined.

There are many smaller species of brachiopods. To unravel their growth strategies from morphological analysis, more advanced analysis, such as a microfocus X-ray CT, needs to be used (e.g., Shiino et al., 2020).

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