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# Large shell injuries in Middle Ordovician Orthocerida (Nautiloidea, Cephalopoda)

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# Large shell injuries in Middle Ordovician Orthocerida (Nautiloidea, Cephalopoda)

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**Abstract:** Sublethal injuries are described from six fragments of orthocerids, which belong to *Orthoceras regulare* Schlotheim, 1820, *Orthoceras scabridum* Angelin, 1880, *Nilssonoceras nilssoni* (Boll 1857) and *Plagiostomoceras laevigatum* (Boll 1857) from the Baltic Orthoceratite Limestone (Arenig-Llanvirn, Middle Ordovician) of Sweden, and of northern Germany. The injuries represent shell breakages with an exceptionally large absolute size. The largest observed injury measures more than 60 mm from the aperture to its distal rim. Injuries of that magnitude have previously never been described from Ordovician molluscs. All breakages represent aperture peelings, exclusively affecting the body-chamber of the living animal. The predators which are responsible for these injuries were most probably nautiloids or eurypterids. A calculation of the relative dimension of the shell loss which resulted in the breakage shows that these breaks were small in comparison with the maximum tolerated shell loss in Recent *Nautilus* or Mesozoic ammonoids.

**Keywords:** repaired injuries, sublethal injuries, palaeopathology, predation

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## Introduction

Cephalopods are an important part of the upper hierarchy of the food chain in the modern marine environment (Nesis 1987). There, they play their role both as highly developed predators and as nutritious prey. Parts of the cephalopods role in the Mesozoic are fairly well known even, based upon direct fossil evidence of predator-prey interactions like gut contents (e.g. Pollard 1968, 1990) or sublethal or lethal shell damage (e.g. Keupp & Ilg 1992; Kröger 2002; Mapes & Chaffin 2003). Also, the late Palaeozoic role of cephalopods in the marine drama of eat and be-eaten is fairly well reported (e.g. Bond & Saunders 1989; Mapes & Chaffin 2003), but direct evidence of a predator-prey interaction has rarely been reported for early Palaeozoic cephalopods (e.g. Stumbur 1960).

Predator-prey interactions in the early Palaeozoic are generally poorly understood at this time. We have some reason to expect that nautiloids (e.g. Alexander 1986), and arthropods (e.g. trilobites, Fortey & Owens 1999) were the top-predators of the Ordovician, but direct evidence is rare (Signor & Brett 1984; Brett 2003). In this study I describe healed shell injuries of orthocerid nautiloids. These shell breaks show an absolute size of several centimetres, which indirectly reveals the existence of durophagous predators with large absolute dimensions that were top-predators during the middle Ordovician.

The described specimens were examined from the collections of the Naturhistoriska riksmuseet in Stockholm, the Museum für Naturkunde der Humboldt-Universität Berlin and several small collections of northern Germany (Paläontologisches Museum and Geschiebearchiv Universität Greifswald, Paläontologisches Museum Universität Hamburg; Eiszeitmuseum Stolpe, Schleswig-Holstein; Müritzmuseum Waren/Müritz), where I studied the Orthocerida of the Baltoscandic Orthoceratite Limestone (Arenig–Caradoc, Ordovician; Kröger 2004). The nautiloids in these collections originate from outcrops of the Orthoceratite Limestone in Estonia and Sweden, and from Pleistocene erratic blocks of Orthoceratite Limestone in Northern Germany, Poland, Lithuania, Latvia, and Sweden. The collections contain more than 2000 fragments of orthoconic cephalopods including endocerid and actinocerid nautiloids. They have a size range from a few millimetres in depth to more that 150 mm in cross sectional diameter. Small healed shell injuries of <5 mm are relatively common. I did not count these injuries but would estimate a percentage of less than 10% of the total number of specimens. Large sized shell injuries are rare, only the six specimens that are described herein were discovered.

Ordovician healed shell breakages described previously on non-cephalopods are generally smaller in absolute size. Horný (1997) and Ebbestad & Peel (1997) described the frequency and morphology of sublethal injuries of Ordovician gastropods, and Alexander (1986) and Ebbestad & Högström (2000) described the morphology of healed injuries in Ordovician brachiopods. These injuries have a size range of only a few millimetres. It is interesting to compare these injuries with the large shell breakages of the nautiloids and consider whether these injuries bear information for the specific techniques of predation, identifica-

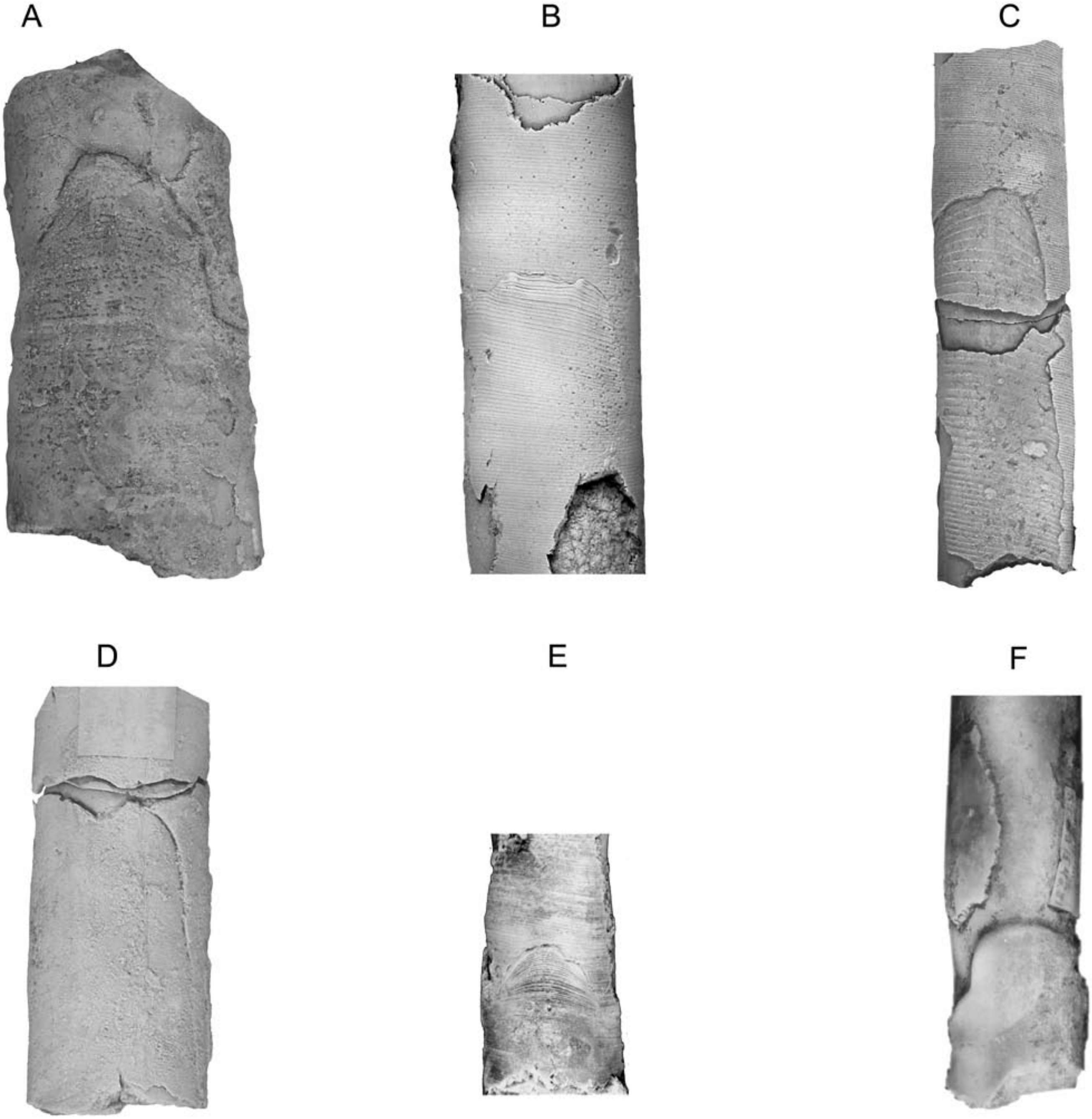


*Fig. 1*. Six Middle Ordovician orthocerids displaying major repaired shell injuries (aperture downward). **A.** *Orthoceras regulare* Schlotheim, 1820. **B.** *Orthoceras* sp. **C.** *Nilssonoceras nilssoni* (Boll 1857). **D.** *Plagiostomoceras laevigatum* (Boll 1857). **E.** *Orthoceras scabridum* Angelin, 1880. F. *Orthoceras scabridum* Angelin, 1880. A, C, D, E, F approx. ×1, B ×1.5.

tion of specific predators, and the pattern of healing of the injured animal. Additionally, it is important to compare these injuries with reported shell injuries in cephalopods. Therefore, I calculated the relative shell loss of some specimens and compared it with measurements in Mesozoic ammonoids (Kröger 2002) and recent *Nautilus* (Ward 1986).

*Abbrevations*. – NMB, Museum für Naturkunde der Humboldt Universität zu Berlin; DGG, Deutsches Geschiebearchiv Greifswald am Paläontologischen Institut der Universität Greifswald; PMH, Paläontologisches Museum der Universität Hamburg; NRM, Naturhistoriska riksmuseet Stockholm.

## Description

*Specimen A*. – The fragment of *Orthoceras regulare* Schlotheim, 1820, NMB C. 5386, comes from an erratic boulder of Upper Grey Orthoceratite Limestone (Llanvirnian) from the island of Vilm, Germany (Fig. 1A).

The fragment preserves a part of the mature body-chamber with its typical three equiangularly arranged longitudinal impressions (see Troedsson 1931); only the steinkern is preserved. The fragment has a maximum diameter of 33 mm and a length of 68 mm. The healed shell breakage has its origin at an interim aperture line, which is represented by a distinct growth line in the middle part of the fragment. From the growth line a widely v-shaped fracture extends 30 mm back toward the apex. The rim of the fracture is irregular.

The repaired shell bulges outward very strongly (3–4 mm) forming an acute apex at its deepest point. The growth lines, which are preserved in this area, initially mimic the rim of the fracture and successively compensate for the irregular aperture, caused by the breakage. Regular transversely directed growth lines are developed at the adoral part of the fragment.

*Specimen B*. – The fragment of an *Orthoceras* sp., DGG 00477e, comes from an erratic boulder of Upper Grey Orthoceratite Limestone (Llanvirnian) from Dranske, island of Rügen, Germany (Fig. 1B).

This fragment preserves part of the body-chamber of a nearly mature specimen; the fragment has a maximum diameter of 18 mm and a length of approx. 50 mm. The fragment preserves a recrystallized shell showing narrow imbricated growth lines typical for *Orthoceras* (see Troedsson 1931). The interim apertural margin, the position where the shell fracture begins, is not preserved at the fragment. However, a narrow, 'u'-shaped fracture, which extends more than 30 mm from the adoral end of the fragment, is visible. The lateral rim of the breakage is more or less smooth. The deepest, most apical part of the fracture is irregular and subdivided in small notches and wedges. The growth lines of the shell, which fill the area of the breakage (the repaired shell), run parallel to the regular growth lines of the undamaged shell. The distance between the growth lines of the repaired shell is slightly larger than in the regular shell. At its apical rim the fracture forms two slightly v-shaped notches. At this points two vertical lirae or scars originate within the repaired shell, which proceed about 5 mm in direction of growth. The phenomenon is known from ammonoids and is called "Rippenscheitel" (Hölder 1956, 1970; Keupp 1992) or *forma verticata* (sensu Hölder 1956). It marks an injury of the mantle epithelium.

*Specimen C*. – The fragment of *Nilssonoceras nilssoni* (Boll 1857), NMB C. 5387, is from an erratic boulder of the Upper Red Orthoceratite Limestone (Llanvirnian) from Gransee, northern Germany, (Fig. 1C).

This fragment preserved parts of the body chamber; the fragment has a maximum diameter of 20 mm and a length of 81 mm. The recrystallized shell, which is ornamented with narrow transverse lirae, is partially preserved. The interim apertural margin, the position where the shell fracture begins, is not preserved in the fragment, but, as in specimen B, a narrow, u-shaped fracture that extends more than 64 mm beginning at the adoral end of the fragment, is visible. The full extent of the breakage around the circumference of the shell is not visible. The fracture rim is irregular, and differentiated in small wedges and notches. The first four lirae of the ornamentation of the repaired shell run more or less parallel to the apical rim of the fracture, forming an u-shaped curvature; successively the ornamentation becomes regular in direction of growth. Notably the distance between the lirae is significantly larger in the repaired shell area.

*Specimen D*. – The fragment of *Plagiostomoceras laevigatum* (Boll 1857), NRM-Mo 31300, comes from the Upper Red Orthoceratite Limestone (Llanvirnian) of Sandby, island of Öland, Sweden (Fig. 1D).

This fragment preserves a part of a body-chamber of a nearly adult specimen. The length of the fragment is 80 mm, the maximum diameter 21 mm. The recrystallized shell of the specimen is smooth and without any growth lines or ornamentation. At the adoral half of the fragment a widely u-shaped shell fracture is preserved. The interim apertural margin, the position where the shell fracture begins, is not preserved. Nevertheless, the preserved part of the fracture measures more than 36 mm from the adoral end of the fragment. The fracture is smooth, forming three shallow arcs and wedges at its right side. The deepest part of the rim of the breakage is also smooth with only some minor shallow wedges. The area of the repaired shell is only slightly irregular with some shallow, wedge-shaped undulations.

*Specimen E*. – The fragment of a body chamber of a mature *Orthoceras scabridum* Angelin, 1880, NRM-Mo 154232, comes from the Upper Grey Orthoceratite Limestone (Llanvirnian) from Stora Mossen, island of Öland, Sweden (Fig. 1E).

The fragment preserves the entire length of the body-chamber with a maximum diameter of 17 mm, and a length of 80 mm. The shell of this specimen is recrystallized and almost completely

*Table 1*. The basic values and the results of the calculation of the relative shell loss of the two largest observed sublethal injuries in Middle Ordovician orthocerids.

| | specimen B | specimen C |
|---|---|---|
| Absolute shell loss in $mm^3$ | 1089 | 1263 |
| Diameter at position of the injury | 18 | 20 |
| Apical angle of cone in ° | 2.25 | 1.58 |
| Projected height of the cone | 916.92 | 1451.53 |
| Volume of the entire shell (incl. siphuncle and septa, Shell thickness 1 mm at aperture) in $mm^3$ | 22851 | 40427 |
| Shell loss in % of the entire shell | 4.8 | 2.7 |

The absolute shell loss gives the shell loss resulting from the breakage; the diameter at the position of injury gives the cross-sectional diameter at the interim apertural rim at the time of the injury; the volume of the shell is calculated assuming a straight conical conch with a shell thickness of 1 mm, which gives the volume of the outer shell, considering a factor of 1.4 for the volume of the septa and siphuncle (see appendix), the entire shell volume is calculated. The results show that the shell loss relative to the entire shell was relatively low.

preserved. One large repaired shell fractures is visible. The fracture begins at a distance of 30 mm from the terminal aperture of the specimen. The widely u-shaped breakage is 10 mm deep (Fig. 1E). The fracture is divided into small wedges and notches. The oldest growth lines of the repaired shell are strongly curved, and mimic the u-shape of the fracture. Successively the curvature and distance of the following growth lines decreases until the breakage is compensated.

*Specimen F*. – The fragment of the body-chamber of a mature *Orthoceras scabridum* Angelin, 1880, NRM-Mo 154281, comes from the Upper Grey Orthoceratite Limestone from Södra Bäck, island of Öland, Sweden (Fig. 1F).

The maximum diameter of the fragment is 17 mm, its length is about 85 mm. At the position of the shell fracture no shell material is preserved, therefore the extent of the breakage is documented only by parts of the inner impression of the shell. The position where the shell fracture begins is not preserved, but a wide, u-shaped fracture, which extends more than 10 mm beginning at the adoral end of the fragment, is visible. The area of the fracture is marked by the outward bulging of the mould of the body-chamber (approx. 3 mm). No details of the repaired shell are preserved.

## Calculation of the relative shell loss

The described shell breakages show an exceptional absolute size for middle Ordovician molluscs. But, are these breakages large compared with shell breakages reported from recent *Nautilus* or Mesozoic Ammonoids? The relative dimension of the injuries can be measured by calculating the relative shell loss that resulted from the breakage.

The calculation of the proportional shell loss begins with measuring the surface of the breakage. This is done by projecting the fracture line from the original conch on a surface and counting the area that is surrounded by the u, or v-shaped fracture line and the interim apertural rim of the conch. Because the results will give relative values, it is sufficient to calculate with a standard shell thickness (of 1 mm) at the position of the injury. (The introduced inaccuracy resulting from this simplification is not significant within this observation).

The volume of the conch of the injured orthocerid is calculated assuming a straight conical shell with a circular cross-section. The maximum diameter of this shell is the diameter at the position of the injury ($d_i$) with the projected height of the cone of the specimen ($h_p$). The volume of the outer shell, again, was calculated by assuming a standard shell thickness of 1 mm at the position of the injury. The volume of the outer shell is simply the difference of the volume of two cones with a given height ($h_p$). The larger cone is defined by the diameter at the time of the injury, the smaller has a diameter reduced by 1 mm. (The model assumes a simple linear increase in shell thickness.) The volume of septa and siphuncle is added by using a factor 1.4. This factor was measured and estimated at the actual specimens (Appendix), it is somewhat higher than the septal-sipho factor of Saunders & Shapiro (1986) used for their buoyancy calculations of *Nautilus*. Finally, the relation between the shell loss and the estimated shell volume can be calculated. For specimen B and specimen C the results of these calculations are given in Table 1.

The results of the calculation can be directly compared with calculations of observed maximum tolerated shell loss for *Nautilus* (Ward 1986) and ammonoids (Kröger 2002). Compared with maximum tolerated shell loss of ammonoids, the shell loss resulted in the reported breakages in Ordovician orthocerids is small. But the maximum tolerated shell loss reported from *Nautilus* matches the dimension of that of the Ordovician orthocerids. However, it is difficult to interpret these results because it is impossible, at this time, to evaluate whether the examined injuries in Ordovician orthocerids represent maximum tolerated shell loss or not. Further investigation is needed to resolve the problem.

*Table 2*. Comparison of the maximum tolerated shell loss in some ammonoids, the recent *Nautilus* and Middle Ordovician orthocerids.

| Genus | Tolerated shell loss, in % of the shell, incl. septa and sipho |
|---|---|
| Dactylioceras [#] | 10 |
| *Hildoceras* [#] | 18 |
| Lithacoceras [#] | 23 |
| *Lytoceras* [#] | 22 |
| *Nautilus** | 5 |
| *N. nilssoni* | 3 |
| *Orthoceras* sp. | 5 |

The table shows that the examined shell loss in Ordovician orthocerids is relatively low compared with other ectocochleate cephalopods. However, at this time it is not clear whether the reported Ordovician injuries reflect a maximum tolerated value or not.
[#] after Kröger (2002), * after Ward (1986).

## Discussion

Direct evidence of durophagous predation in the early Palaeozoic is described from the carapace of trilobites (e.g. Alpert & Moore 1975; Snajdr 1979; Conway Morris & Jenkins 1985; Babcock 2003), lip-peelings and borings of gastropods and bivalves (e.g. Ebbestadt & Peel 1997; Horný 1997; Lindström & Peel 1997; Alexander & Dietl 2003), and shell breakages of brachiopods (e.g. Alexander 1986; Ebbestad & Högström 2000; Leighton 2003). These authors discuss arthropods (naraoiids, trilobites, eurypterids, phyllocarids), nautiloids and in some cases ophiuroids and asteroids as possible predators.

The sheer dimension of the shell breakages described herein restricts the possible predators to large arthropods and nautiloids. In specimen C, D, and E (Fig. 1C–E) the rim of the shell fracture describes a deep, u-shaped slit with irregular lateral edges. These patterns strongly resemble a typical lip-peeling pattern that is commonly observed in recent gastropods. Papp et al. (1947), who described these breakages on recent marine gastropods called them “Bandschnitt”. Hollmann (1969) described in detail how these patterns originate as a result of the peeling by the recent crustacean *Hommarus*. Essentially, any “Bandschnitt” is caused by a more or less long lasting repeated sequence of shell breaking actions. The predator has to fix its prey and break out the shell piece by piece. In the Llanvirnian there were no armed crustaceans such as crabs or *Hommarus,* but it is conceivable that an ancient arthropod, as well as a nautiloid was able to fix its prey with its appendages or arms and thus followed the same practice.

All six specimens investigated here show the same repair pattern. In the beginning of the repair, the growth lines follow the edge of the breakage and the interspaces between the growth lines are larger than in the regular parts of the shell. This abnormal spacing and curvature of the ornamentation decreased successively until the area of shell loss was compensated. The injured *Nilssonoceras nilssoni* and the *Orthoceras* sp. (specimen B, and C, Fig. 1B, C) show a more or less regular ornamentation deep in the slit-like breakage. There, the ornamentation of the repaired shell is distorted only at the very beginning; later on it is more or less parallel to the regular striation. Molluscs are able to build a regular ornamentation exclusively by the peristome, because only the peristome is able to produce a periostracum. The periostracum serves as the necessary matrix for the underlying shell parts and is therefore responsible for the building of a regular sculpture (Clark 1976; Bandel 1981). The regular ornamentation deep in the slit-like breakages in specimen B and C indicates, therefore, that the peristomal rim could be withdrawn completely toward positions relatively deep in the body-chamber. This capability can be interpreted as an important antipredatory trait.

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# Appendix

For calculation of the relative volume of the septa and siphuncle of *Orthoceras* and *Nilssonoceras* I assumed a segmented cone. Every segment of the cone has the same proportion of septa, siphuncle and outer shell and is built by one septum, one connecting ring, and one ring of outer shell by the same length.

In *Nilssonoceras* and *Orthoceras* the distance between the septa normally varies strongly (Kröger 2004). I assumed that at the cross-section diameter of 20 mm the distance between two successive septa is 10 mm.

The ratio of shell thickness of the outer shell versus the shell thickness of the septum is 0.4. The height of a septum (h) is 6 mm and the radius of the sphere of the septum (r) is 11 mm. The area of the sector of the sphere, represented by the septum is then 213 $mm^2$ ($=\pi rh$). Given a thickness of 1 mm for the outer shell and 0.4 mm for the septum, the volume of the septum is $v_s = 85.19$ $mm^3$.

The diameter of the siphuncle is approx. 0.1 of that of the cross section of the entire shell. The sum of the volume of the septal necks and connecting ring was assumed to nearly compensate the septal perforation (The inaccuracy, which is introduced by this simplification is far below the inherent uncertainty of the entire calculation.)

The volume of the outer shell ($v_o$) of the segment is calculated by the volume of a frustum of the height of 10 mm and a basal diameter of 20 mm minus the volume of the same frustum with a basal diameter without shell of 19 mm. The result of this calculation is $v_o = 119$ $mm^3$.

Thus, the ratio between outer shell volume ($v_o$) and septa-sipho volume ($v_s$) is 1.4.