



The Morphology and Function of the Upper Valve of *Vaccinites vesiculosus* (Woodward)

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Abstract: The evolutionary transformation of the upper valve (UV) to a probable particle filter system in some hippuritid genera belongs to the most drastic changes in pelycipod shell structures. The basic architecture of this product is well known since long times. Again discussed is the functional role of the canal system. The bottom of the canals is very smooth. The canal system of *Vaccinites vesiculosus* is completely roofed by a particular graceful sieve. A water exchange between the canals did not exist. The uppermost part of the upper valve (the sieve) most probably was an endoskeleton. The upper valve was not accreted with the lower valve. Premortal damages of the canals and sieves could be repaired. It is discussed whether the oscules E and S really were places of exhalent currents. Early ontogenetic growth stages of the canal system are unknown. The pattern of the canal arrangement always is an individual one.

Key Words: palaeobiology, hippuritids, *Vaccinites*, feeding current, canal pattern, sieve structure, growth

Vaccinites vesiculosus (Woodward) Üst Kavkısının Morfolojisi ve Fonksiyonu

Özet: Üst kavkının (UV) evrimsel dönüşümü, pelesipod kavkı yapılarındaki köklü değişikliklerin birçoğuyla ilgili olan bazı hippuritid cinslerindeki parçalı filtre sistemiyle olasıdır. Bu ürünün temel mimarı uzun zamandanberi çok iyi bilinmektedir. Kanal sisteminin fonksiyonel rolü birkez daha tartışılmıştır. Kanalların dipleri oldukça düzdür. *Vaccinites vesiculosus*'un kanal sistemi tümüyle özel bir elek ile örtülmüştür. Kanallar arasında su değişimi olmamıştır. Üst kavkının en üst kısmı (elek) büyük bir olasılıkla endoskeletondu. Üst kavkı, alt kavkıyla eklenmemiştir. Kanal ve eleklerin ölüm öncesi hasarları onarılabildiği. E ve S boşluklarının gerçekten dış akıntılarının yeri olduğu tartışmalıdır. Kanal sisteminin erken ontogenetik büyüme evreleri bilinmemektedir. Kanal düzeninin modeli daima bireyseldir.

Anahtar Sözcükler: paleobiyoloji, hippuritids, *Vaccinites*, beslenme akımı, kanal modeli, elek yapısı, büyüme

Introduction

In the Early Campanian Samhan Formation of Central Oman (for localities and detailed lithological sections and stratigraphy see Platel *et al.* 1994 and Schumann 1995) large rudist associations with an extension of hundreds of square kilometres exist. The most common species within these autochthonous communities is *Vaccinites vesiculosus*. The last comprehensive studies of *Vaccinites* were done by Laviano *et al.* (1992), Simonpiétri (1993) and Simonpiétri *et al.* (1998). These investigations dealt mainly with stratigraphical, phylogenetical, palaeogeographical and biometric-statistical questions. The particular structure and function of

the upper valve was not described or discussed. Among the countless pieces from the Saiwan-localities are many specimens with best preserved upper valves (forthcoming called UV). The surfaces of the UV (sieves) and the underlying canal system of the UV were excellent prepared in all stages by the natural sand blasting of the desert (Plate 2, Figures 3-5). This enables unusual observations and leads to the questions discussed here.

For the principal function of these particular hippuritid UVs two hypothesises were made. First, according to Douvillé (1897) and Skelton (1976) the trapped particles (seize-controlled by the sieve) were leaded into the underlying radial canals and then

inside passing through the marginal openings which are distributed around the whole commissure of the UV. Second, Pons *et al.* (1994) and Seilacher (1998) on the other hand were more believing in a photosymbiotic function. Pons *et al.* described the probable existence of 'expansiones tentaculares' and 'asociación con zooxantellas' in connection with the left mantle of *Hippurites cornucopiae*. Seilacher had similar ideas with 'pallial diverticles, retractable papillae' and 'algal gardens' for photosymbiosis. For the older history see Dechaseaux & Coogan (1969)! Which hypothesis is more probable critically depends on nature and function of certain morphological features, such as the areas of the three infoldings in the UV, the areas of the ligamental ridge and the oscules S and E.

Materials, Locality

180 complete and well-preserved specimens, 22 isolated upper valves, mostly incomplete. Large cliffs 8 km south of the abandoned air strip Saiwan (Central Oman); GPS-coordinates: N 20° 3' 32,6" E 057° 36' 49,7".

Results

The Omani specimens, all belonging to *V. vesiculosus*, show a distinct individual variability of the canal arrangement (Plate 1, Figure 2a; Plate 2, Figures 1 & 2). Only the width of the canals and the socle distance (denticular base of the sieve on the canal ridges) are relatively identical in all pieces of *V. vesiculosus*.

The principal arrangement of the canal system is radial. The arrangement always comes in spacial conflict in the areas of the three infoldings L, E and S. There the canals are running individual ways onto or around the infoldings, and often collide with neighbouring canals (Plate 1, Figure 2a; Plate 2, Figures 1 & 2). At the end of each canal *V. vesiculosus* shows a main 'gully-hole' and in addition sometimes also some smaller openings around the whole margin. The floors of the canals are very smooth and there are no vascular impressions at all (REM control). The pores are not circular, they are polygonal, the pore's margins are spinose and often

sharply pointed. The surface of the sieve is densely equipped with short spines (Plate 1, Figure 2a; Plate 2, Figure 3). Some specimens show that also the areas of the oscules were roofed by a sieve. And around pillar E and S in the lower part of the UV always a ring of flat-oval vertical canals is visible, completely roofed by the sieve (Plate 1, Figures 1 & 2a, b). Already Vogel (1960) has observed such additional canals in his sections of *Hippurites socialis* and believed, that they probably 'washed' the pillars.

The uppermost structure of the UV of *V. vesiculosus* is a rather evolved one. The sieve is very thin, the diameter of the pores is 0.6 mm in average, often smaller. Somewhat bigger pores are subdivided by fine secondary net structures. Some areas show bushwoodlike thickenings. On the outermost margin the sieve has a very graceful finger-shaped zone (Plate 2, Figures 4 & 8).

Discussion

Douvillé (1897) suggested that the pillars of the lower valve correspond to inhalant (E) and exhalant (S) currents. Klinghardt (1930, 1931) and Wiontzek (1937) reported cavities within the pillars and were convinced that the pillars were siphonal tubes. Milovanovic (1933) and Kühn (1937) recognized these cavities as diagenetic structures, the pillars are massive structures. Vogel (1960) did careful sectioning in the area of the pillars of *Hippurites socialis*. He reported that the oscules were always open and therefore probably were places for sense organs or accessory gills. The last comprehensive palaeobiological publication dealing with these questions is the admirable analysis of Skelton (1976). He agreed with Vogel (1960) that the oscules were always open, but refused to believe the existence of sense organs or accessory gills in the oscules area. Pons (in Cestari & Sartorio 1995) showed the best published section with the structure of the UV of the Santonian species *Vaccinites oppeli*. The uppermost part of the UV (the sieve) of *V. vesiculosus* is definitely less compact in comparison with the illustrated specimen of *V. oppeli*.

Also the canals are described since more than a century, but I found a graphic presentation of a complete arrangement only in Seilacher (1998)

(remarkably an Omani specimen of *V. vesiculosus* from Saiwan). Even an ontogenetic or phylogenetic study of any canal system does not exist. Zapfe (1937), Vogel (1960), Skelton & Gili (1991) and Götz (2003) described early ontogenetic stages of hippuritids without mentioning any early stages of a canal system. The classic literature shows that the architecture of the canal system seems to be rather different within the taxonomic groups.

Skelton (1976) in his most interesting analysis interpreted the oscules E and S as places of exhalent currents. But, if covered by sieves, could they then have served for exhalent currents? A sieve normally is controlling the entrance of particles. Outgoing particles (faecal/pseudofaecal) often are bigger as the trapped ones. Is it eventually not more likely that the whole surface of the UV was used for the particle influx with the aid of ciliated epithelia? The exhalent currents could have been located on another place of the margin. As many modern pelycipods and brachiopods show a distinct morphology respective within the shell margin is not necessary for this function.

Because of the new observations I have doubts that the described system was exclusively or mainly used for photosymbiosis, with tentacles in the canals and/or retractable papillae. I believe more in a perfect water circulation system. The spiny surface of the sieve probably helped to reduce the flow velocity and therewith to trap useful particles. This does not mean that not any other parts of the mantle tissue with 'algal gardens' could have existed, a function which probably was of high significance in some rudist groups.

Conclusions

Generally pelycipods have an additive grown exoskeleton produced by a generative zone. But many inner parts do not grow simply additive. A bivalve tooth e.g. can grow only by a permanent secretion and resorption of shell material, nevertheless it is classified as an exoskeleton. I presume that the sieves of the UV of *V. vesiculosus* were growing in an analogue way. The lower part of

the UV grew principally as an exoskeleton, while the upper part (finally a sieve) evolved to an endoskeleton. Pons *et al.* and Seilacher also were convinced of a tissue-embedded UV. Considering the remarkable fine structure of the *vesiculosus*-sieve (Plate 1, Figures 1, 2b; Plate 2, Figures 3, 4 & 8), especially the very graceful finger-shaped marginal structures, it could be an embedded endoskeleton only. Presumably at least the whole uppermost part of the UV was embedded by a thin ciliated epithelial tissue. Thus it could grow and evolve with all the possibilities of an allometric growth.

The UV of *V. vesiculosus* was never accreted with the lower valve. There was no premortal settlement of any epibionts at all on the surface of the sieves. Between hundreds of specimens of my collection only one sieve was damaged during life and roughly repaired (Plate 2, Figure 2).

I have no idea why a functional important structure as the canalization of *Vaccinites* has such an individual arrangement. It is like a zebra: We see a significant pattern, but it is never the same two times.

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PLATE 1

Structures of *V. vesiculosus*.

Figure 1. Area of oscule E, particular canalization around the oscule, all canals were roofed by a sieve, UVCS-180.

Figure 2a. Complete canal arrangement. See specific arrangement around L, S, E!

Figure 2b. Detail of Figure 2a, oscule and pillar E. The surface of the pillar (sp) is crenulated. The steep canals around the oscule are roofed by a sieve. The canals end abruptly on the surface of the pillar, but there is a tiny gap (g) on the canals floor where water could pass through, UVCS-144. The black line is 5 mm.

Vaccinites vesiculosus
Canal arrangement
and sieve structure

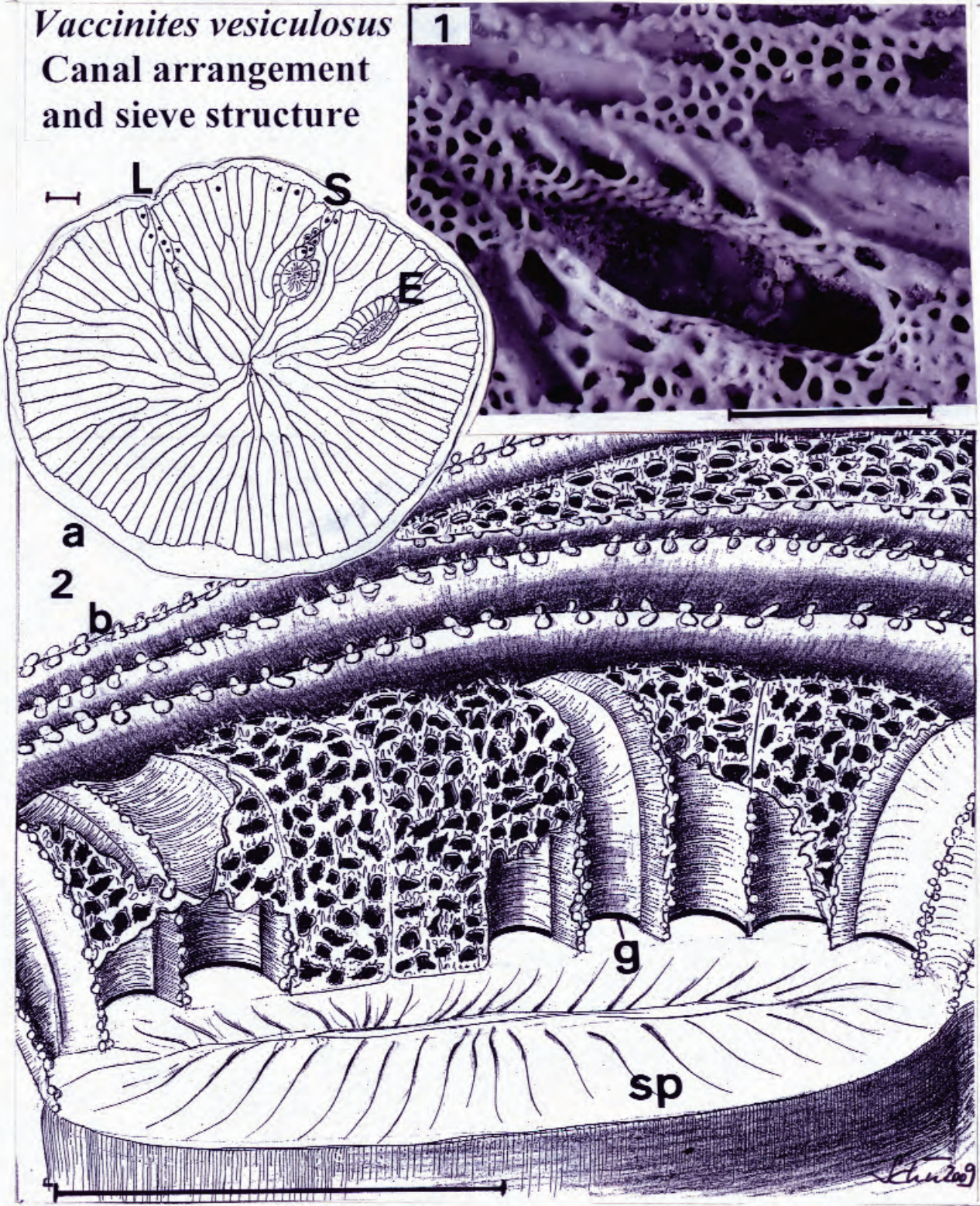


PLATE 2

Structures of *V. vesiculosus*.

- Figures 1, 2.** Individual canal arrangement of UVCS-23 and 24. The arrows in Figure 2 show an area where the sieve and the canals were damaged during life and roughly repaired.
- Figure 3.** A nearly complete roofed canalization, UVCS-32.
- Figure 4.** Canalization and sieve around S, UVCS-37.
- Figure 5.** Canalization and sieve around E, UVCS-25.
- Figure 6.** Vascular impressions on the margin, lower valve, UVCS-54.
- Figure 7.** Undersurface of upper valve, see structures of the oscules E, S and some of the main openings ('gully holes') at the margin, UVCS-147.
- Figure 8.** Finger-shaped sieve structure on the margin of UVCS-41. The black line is 5 mm.

