

1           **Systematics, functional morphology and distribution of a bivalve**  
2           **(*Apachecorbula muriatica* gen. et sp. nov.) from the “shores” of the**  
3           **“Valdivia Deep” brine pool in the Red Sea**

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11  
12  
13       **ABSTRACT**

14       *The deep brine pools of the Red Sea comprise extreme, inhospitable habitats, yet housing*  
15       *microbial communities which potentially may fuel adjacent fauna. We here describe a*  
16       *novel bivalve at a deep-sea (1525 m) brine pool in the Red Sea, where conditions of high*  
17       *salinity, lowered pH, partial anoxia and high water temperatures are prevalent. ROV*  
18       *footage showed that the clams were present in a narrow (20 cm) band along the*  
19       *“shores” of the brine, suggesting that the clam is not only tolerant of the extreme*  
20       *conditions but is also limited to them. The clam is attributed to the family Corbulidae and*  
21       *named as *Apachecorbula muriatica* gen et sp nov. The shell morphology is atypical of the*  
22       *family in being modioliform in outline and very thin. The semi-infaunal habit is seen in*  
23       *ROV images and is reflected in the anatomy by the lack of siphons. The ctenidium is large*  
24       *and typical of a suspension feeding bivalve, but the absence of “guard cilia” and the*  
25       *greatly reduced palps suggest that it is not selective and this is a response to low food*  
26       *availability. It is proposed that the low body mass observed is a consequence of the the*  
27       *extreme conditions and low food availability, yet higher than in the adjacent deep sea. It*  
28       *is postulated that the observed morphology of *Apachecorbula* is a result of*  
29       *paedomorphosis driven by the effects of the extreme environment on growth but is in part*  
30       *mitigated by the absence of high predation pressures.*

31

32 **Keywords:** Corbulidae, deep-hyper-saline anoxic basins (DHABs), Red Sea, Deep-sea,  
33 Apachecorbula gen. nov., Functional morphology, Valdivia Deep, Deep sea clams

34

## 35 INTRODUCTION

36

37 Deep-sea anoxic brine pools are formed by the solution of evaporate deposits and the  
38 stable accumulation of these hypersaline solutions in enclosed depressions on the sea  
39 floor (Bischoff 1969, Hartmann 1985). They are known from the Gulf of Mexico (Cordes  
40 et al. 2010), eastern Mediterranean and are widespread in the Red Sea with 25 known to  
41 date (Antunes et al., 2011). The brine pools are both highly saline and usually anoxic in  
42 addition to having a high metal content and low pH but harbour a unique microbial  
43 community of extremophiles (Antunes et al, 2011). Metazoans are absent from the  
44 extremes of anoxia but in the Red Sea have been recorded from the shores of a shallow  
45 and less saline site (Thuwal Seeps) (Batang et al, 2012) as well as along the Kebrit brine  
46 pool (Vestheim & Kaartvedt, *in prep.*). Bivalve mollusks including a species of  
47 Corbuloidea, were recorded from the Thuwal Seeps but have not been studied beyond a  
48 tentative identification (*Corbula cf. rotalis*) due to lack of samples. The presence of  
49 bacterial mats at the Thuwal deep suggest that this is an active cold seep site. The Kebrit  
50 brine shore hosted solemyid clams which are obligate chemosymbiotic and one live  
51 individual of a corbulid were also found (Vestheim & Kaartvedt, *in prep.*). In the Gulf of  
52 Mexico dense beds of the chemosymbiotic *Bathymodiolus childressi* (Gustafson et al.,  
53 1998) are found around the margins of a cold seep brine pool (MacDonald et al. 1990). In  
54 the eastern Mediterranean meiofaunal communities have been found in hypersaline  
55 sediments with sparse macrofauna at the margins. Juvenile bivalves were found in the  
56 meiofaunal samples but were not identified (Lampadariou et al., 2003).

57

58 In April 2013 the Valdivia Deep brine pool, situated in the central Red Sea (21° 20'  
59 49"N, 37° 57' 19"E) (Fig. 1) at a depth of 1525 metres was investigated by an expedition  
60 from the King Abdullah University of Science and Technology. Video footage from a  
61 ROV revealed small, black bivalves along the shores of the brine pool. Bivalves were  
62 sampled for further analyses together with analyses of environmental conditions, and

63 turned out to be a novel species and genera of clams. The Valdivia clams are living in  
64 conditions of high salinity, low oxygen, lowered pH and relatively high temperatures.  
65 This paper addresses their identity and systematic relationships and explores their  
66 functional morphology in relation to the extreme environmental conditions in which they  
67 are found.

68

## 69 MATERIALS AND METHODS

70

71 Data were collected in April 2013, using the RV Aegaeo (4th King Abdullah University  
72 of Science and Technology (KAUST) Red Sea Expedition.

73

### 74 **Environment**

75 Data on temperature, pH, salinity and oxygen were collected using a specially designed  
76 CTD, able to withstand the corrosive brine environment. The instrument package also  
77 included probes for measuring oxygen and pH.

78

### 79 **Underwater observation, collection and preservation**

80 Underwater observations were conducted using the ROV Max Rover (DSSI, USA)  
81 system as described in Batang et al. (2012) and Vestheim & Kaartvedt (*in prep.*).  
82 Sediment samples were collected using the ROV's robotic arm fitted with a fabric bag.  
83 The samples were then transferred to the surface in the bag and immediately inspected in  
84 the lab. Individual clams were picked out and either frozen in N<sub>2</sub>(l) or preserved in  
85 ethanol (70%), glutaraldehyde (EM grade) or 4% buffered formaldehyde solution, as  
86 further outlined in the Result & Discussion section. Preserved samples were stored at 4°C  
87 upon analysis.

88

89 No live macrofauna except for the corbulid clams were found in the sediments. The  
90 sediment mainly consisted of biogenic material being remains of shelled pelagic snails  
91 (pteropods) and some calcified foraminiferans along with mineral particles.

92

### 93 **Morphology**

94 Morphology was examined by gross dissection following staining of tissues in  
95 Haematoxylin. Scanning electron microscopy of tissues followed dehydration in 100%  
96 ethanol and critical point drying, gold coating and microscopy with a Jeol Neoscope;  
97 shell micrographs were taken on a FEI Quanta 200 or Jeol Neoscope. Shells were  
98 examined without cleaning and following cleaning with dilute bleach. The terminology  
99 associated with hinge structures follows that of Anderson & Roopnarine (2003). The shell  
100 measurements are shown in Fig. 4.

101

### 102 **Molecular data and analysis**

103 In order to confirm the family placement and ascertain affinities within the Corbulidae a  
104 molecular analysis was carried out. Total genomic DNA was extracted from ten ethanol  
105 preserved specimens using the DNA Easy Blood and Tissue Kit (Qiagen) following the  
106 manufacture's protocol for animal tissue. DNA yield of the extractions was quantified on  
107 a Qubit 2.0 fluorometer (Invitrogen) and partial COI, 28S, 18S and 16S sequences were  
108 generated by PCR using the primer pairs as described in Table 1. The 25  $\mu$ L PCR  
109 reactions included 5  $\mu$ L 5X Phusion buffer, 0.5  $\mu$ L 10 mM dNTPs, 1.25  $\mu$ L each primer  
110 (10  $\mu$ M), 1.25  $\mu$ L 50 mM MgCl<sub>2</sub>, 0.125  $\mu$ L Phusion High-Fidelity DNA polymerase and  
111 1  $\mu$ L DNA extract (~10 ng/ $\mu$ L). Thermal cycling conditions were: 98°C for 2 min, then 37  
112 cycles of 98°C for 30 s, 30-40 s at annealing temperature (see Table 1) and 72°C for 1  
113 min, followed by a final extension 10 min at 72°C. A negative (no template DNA) and  
114 positive control (template DNA known to amplify) were included in all PCRs. All PCR  
115 products were checked on a 1% agarose gel and cleaned with Illustra ExoStar 1-Step (GE  
116 Healthcare) before sequenced on an ABI 3730xl Capillary Sequencer (Applied  
117 Biosystems) using the respectively forward and backward PCR primer.

118

119 Table 1. List of PCR primers used in this study.

120

Primer pair	Target	Annealing temperature	Reference
LCO1490/HCO2198	COI	50°C	Folmer et al., 1994
16Sa/16Sb	16S	50°C	Xiong & Kocher, 1991

3F/18sbi, 1F/5R, 18Sa2.0/9R	18S	48°C	Giribet et al., 1996; Whiting et al., 1997
C1/C4	28S	52°C	Lorion et al., 2010

121

122 Contiguous sequences were after manually inspection compared with other corbulid  
123 sequences. No other, appropriately preserved, corbulids from the Red Sea were available  
124 for molecular analysis and all comparisons were made from previously published DNA  
125 sequences available through GenBank and from Anders Hallan (Hallan et al., 2013).  
126 There was only one 16S (*Corbula tunicata* KC429314, partial sequence, not overlapping)  
127 and no COI sequences from closely related corbulids available for comparison at the time  
128 of analysis, hence phylogentic analysis for those genes were not performed. For 28S and  
129 18S sequences phylogenetic analysis was executed on the Phylogeny.fr platform  
130 (Dereeper et al., 2008) using a MUSCLE alignment (Edgar, 2004), GBLOCKS curation  
131 of the nucleotide alignment allowing gaps in the final alignment (Castresana, 2000), the  
132 PhyML phylogeny package (Guindin & Gascuel, 2003) and the HKY85 nucleotide  
133 substitution model with approximate likelihood-ratio test for branch support (Anisimova  
134 & Gascuel 2006). Tree rendering was performed with TreeDyn (Chevenet et al. 2006).  
135

## 136 RESULTS AND DISCUSSION

137

### 138 **Environmental conditions**

139 Vertical profiles of temperature, salinity, dissolved oxygen and pH were almost constant  
140 with depth until close proximity to the surface of the brine pool. Within a five metre zone  
141 the water quality parameters change rapidly and significantly (Fig.2, Table 2). At 1525  
142 metres the salinity is 53 but within a further two metres depth it has risen to 220. Similar  
143 rapid changes in environmental parameters over this two metre range are seen in  
144 dissolved oxygen dropping from 2.9 mg/l to 0.9 mg/l; ph dropping from 7.8 to 6.5 while  
145 water temperature rises from 23.4°C to 26.1°C.

146

147 **Table 2.** CTD data for a depth range of 1525-1530 m indicating rapid and significant  
148 changes in salinity, dissolved oxygen, pH and temperature.

Water Depth (m)	Temperature (°C)	pH	Salinity	Oxygen (mg l <sup>-1</sup> )
1525.2	23.4	7.8	53	2.9
1526.0	23.9	7.1	82	2.4
1526.6	24.7	6.8	205	1.0
1527.2	25.5	6.7	219	0.9
1527.9	26.0	6.7	217	0.9
1528.7	26.6	6.6	222	0.8
1529.4	27.8	6.5	226	0.8
1530.2	28.7	6.5	231	0.7

149

150 **Video footage**

151 Video footage from the ROV revealed a barren fringe around the brine pool except for  
 152 small black clams living half buried in the sediment (Fig. 3A-C). The band of clams  
 153 could be seen stretching into the distance in Fig. 3C. The ROV footage showed that the  
 154 clams were present in a narrow (20 cm) band along the shores of the Valdivia deep. The  
 155 clams seemed to sit on the hill tops, not in the valleys (topographic depressions)  
 156 suggesting that they are responding closely to changes in water chemistry. Counting one  
 157 site (frame) gave an estimate of 130 individuals within 70x20 cm, though the distribution  
 158 was patchy. This high density corresponds to approximately 900 individuals m<sup>-2</sup>. The  
 159 distribution within a narrow band suggests that the clam is not only tolerant of the  
 160 extreme conditions but is also limited to them. This is unlike *Bathymodiolus childressi*  
 161 which tolerates hypersalinity but is not restricted to such environments (Carney et al.  
 162 2006).

163

164 No other live metazoans were observed in the sediments collected with the clams, which  
 165 therefore seem quite unique in inhabiting the Valdivia shore sediment. There was further  
 166 no evidence of a chemosynthetic community such as seen at the Thuwal Seeps (Batang et  
 167 al., 2012) or at the Kebrit brine pool (Vestheim & Kaartvedt, *in prep.*). This is in keeping  
 168 with the lack of hydrothermal activity at the Valdivia Deep as demonstrated by  
 169 Zierenberg & Shanks (1986).

170

171 One individual of the same species of clam were also found along the Kebrit brine pool  
172 (Vestheim & Kaartvedt, *in prep.*).

173

#### 174 **Phylogenetics**

175 There was no intraspecific variation among the clam individuals sequenced.

176 Representative contiguous sequences have been deposited to EMBL database under the  
177 accession numbers HG942537 (COI), HG942542 (16S), HG942541 (18S) and

178 HG942543 (28S). Based on comparison of 18S and 28S partial sequences (data not

179 shown), the Valdivia clam fits within the "Western pacific group" of Hallan et al. (2013)

180 that includes *Caryocorbula coxi* Pilsbry, 1897 and *Caryocorbula? zelandica* Quoy &

181 Gaimard, 1835, '*Corbula sinensis*' Bernard, Cai & Morton, 1993, *Notocorbula hydropica*

182 as well as '*Notocorbula coxi*' (AY192684, misidentified in GenBank (Hallan et al. 2013))

183 and *Corbula gibba* Olivi, 1792. The sequences available were not informative enough to

184 conclude anything more on the phylogenetic relationship to these species.

185

#### 186 TAXONOMY

187

#### SYSTEMATICS

188

Bivalvia Linnaeus, 1758

189

Heterodonta Neumayr, 1884

190

Order Myoida Stoliczka, 1870

191

Superfamily Myoidea Lamarck, 1809

192

Family Corbulidae Lamarck, 1818

193

Genus *Apachecorbula* Oliver & Vestheim, gen. nov.

194

Type species: *A. muriatica* Oliver, this paper, monotypic

195

#### **Definition**

196 Small, thin, translucent shelled, slightly inequivalve, strongly inequilateral, prosogyre  
197 beaks close to the anterior. Outline obliquely oval, modioliform. Hinge weak, right valve  
198 with a single anterior cardinal and a thin posterior flange; left valve with a cardinal  
199 complex of a cardinal socket, median projecting chondrophore and a small projecting  
200 knob behind the chondrophore; a narrow posterior flange also present.

## 201 **Etymology**

202 From the Greek apaches meaning “without thickness” (Brown, 1956); referring to the  
203 thin shell and insubstantial soft tissues.

## 204 **Comparisons**

205 There are few systematic studies of the Corbulidae but that of Anderson & Roopnarine  
206 (2003) lists forty genera of which fourteen are extant and of these only seven have an  
207 Indo-Pacific distribution. A very recent study by Hallan et al. (2013) presented the most  
208 comprehensive molecular based study to date and indicated that, for the marine genera  
209 included, the clades corresponded poorly with shell based genera. However, in general  
210 the marine Corbulidae have thick shells and are distinctly inequivalve. Two main shell  
211 forms are exhibited: (1) inflated, trigonal, posterior narrowly rostrate (2) subovate,  
212 posterior narrow, subtruncate. In the Red Sea the former is represented by *Corbula*  
213 (*Varicorbula*) *erythraeensis* Adams, 1871 and the latter by *Corbula* (*Anisocorbula*)  
214 *sulculosa* Adams, 1870. The thin, slightly inequivalve and modioliform shell is not seen  
215 in any of the described genera. The molecular study confirmed the placement within the  
216 Corbulidae and showed that *Apachecorbula* has closer affinity with other Indo- Pacific  
217 genera than those from the Western Atlantic/Caribbean. This distinction between the  
218 corbulids of the two regions was first noted by Anderson & Roopnarine (2003) and  
219 reiterated by Hallan et al. (2013).

220

221 *Apachecorbula muriatica* Oliver & Vestheim, gen. et sp. nov.



222 **Material examined**

223 40 specimens, Valdivia Brine Pool, Red Sea, 21° 20 49 N, 37° 57 19 E, 1525 m. R/V  
224 Aegaeo, 2013 KAUST Red Sea Expedition, 12/iv/2013.

225 Holotype, 1 specimen, as above. NMW.Z. 2013.058.1

226 Paratypes, 10 specimens as holotype, NMW.Z.2013.058.2; remaining specimens as  
227 holotype KAUST.

228 1 specimen, Kebrit Brine Pool, Red Sea, 24°43 00N, 36° 16 00E, 1465 m. R/V Aegaeo,  
229 2013 KAUST Red Sea Expedition, 15/iv/2013.

230 **Comparative material examined**

231 *Corbula (Varicorbula)* sp.1. 8 shells, Central Red Sea, RV “Valdivia” station 741GKW,  
232 24°43.100 N 36°15.500 E, 1465m. 08/03/1981. Senckenberg-Museum

233 *Corbula (Varicorbula) erythraeensis*. 20 shells, Gulf of Suez, Red Sea, ex Macandrew,  
234 National Museum of Wales, Melvill-Tomlin Coll. NMW.1955.158. 4 spec. Ras Budran  
235 Oilfield, Gulf of Suez, 28°57 N 33°10 E, ex Oil Pollution Rsearch Unit/ JP Hartley,  
236 1980-83, NMWZ. 1982.068.

237 *Corbula (Anisocorbula) sulculosa*. 20+ specimens, Ras Budran Oilfield, Gulf of Suez,  
238 28°57 N 33°10 E, ex Oil Pollution Rsearch Unit/ JP Hartley, 1980-83, NMWZ. 1982.068.

239 *Corbula (Anisocorbula) taitensis* 2 shells, Masirah, Oman, Arabian Sea, 20°12 N 58°42  
240 E, NMWZ 1993.61.1282.

241 *Corbula (Varicorbula) rotalis*. 10 shells, Hizen, Japan, Melvill-Tomlin Coll.  
242 NMW.1955.158.

243 *Corbua (Varicorbula) gibba* [Type species of *Varicorbula*]. Many specimens in  
244 collection of NMW from locations around the British Isles. Juveniles from the Irish Sea,  
245 NMWZ.2005.015.

246 *Corbula sulcata* [Type species of *Corbula*] 3 shells, Senegal, West Africa, ex Caziot,  
 247 Melvill-Tomlin Coll. NMW.1955.158.

248 *Corbula (Anisocorbula) macgillivrayi* [Type species of *Anisocorbula*] 1 shell, Australia,  
 249 Melvill-Tomlin Coll. NMW.1955.158.

250 **Table 3.** *Apachecorbula muriatica* sp. nov. Measurements (mm).

	Preservation	L (rv)	L (lv)	H (rv)	H (lv)	T (rv)	T (lv)	Total T	AL
1A	100% Eth	6.2	5.9	5	4.8	1.6	1.5	3.2	1.7
1B	100% Eth	6	5.7	4.7	4.4	2	1.1	3.1	1.5
1C	100% Eth	5.7	5.3	4.6	4.2	1.8	1.3	3.1	1.2
1D	100% Eth	5.4	4.9	4.6	4	2	1.6	3.6	1.4
1E	100% Eth	5.6	5.3	5.4	5.7	bk	bk	bk	1.6
2A	Form to 80% Eth	4.9	4.7	3.8	3.6	1.6	1	2.6	1.3
2B	Form to 80% Eth	4.9	4.6	4	3.7	1.5	1.2	2.7	1.2
2C	Form to 80% Eth	bk	bk	bk	bk	bk	bk	bk	bk
2D	Form to 80% Eth	5.7	5.4	4.7	4.5	bk	bk	bk	1.3
2E	Form to 80% Eth	4.6	4.4	3.8	3.5	1.3	1.2	2.5	1
3A	Form to 80% Eth	5.4	5.1	4.4	4	1.8	1.4	3.2	1
3B	Form to 80% Eth	4.7	4.4	3.8	3.5	1.5	1.1	2.6	1
3C	Form to 80% Eth	5.3	5.2	4.4	4.3	1.7	1.3	3	1.2
3D	Form to 80% Eth	5.6	5.2	4.5	4.1	1.5	1.2	2.7	1.2
3E	Form to 80% Eth	5.3	5	4.2	3.7	1.8	1.2	3	1
4A	Form to 80% Eth	5.1	4.8	4.2	3.9	1.7	1.6	3.3	1.2
4B	Form to 80% Eth	5	4.7	4.1	3.6	1.6	1	2.7	1.3
4C	Form to 80% Eth	5.1	4.8	4	3.4	1.5	1.2	2.7	0.9
4D	Glut to 80%Eth	6.1	5.7	4.7	4.3	1.6	1.5	3.1	1.4
4E	Glut to 80%Eth	5.6	5.2	4.3	3.7	1.7	1.4	3.1	1.3
5A	Glut to 80%Eth	5.4	5.1	4.3	3.7	1.9	1.2	3.1	1.4
5B	Glut to 80%Eth	4	3.9	3.2	2.8	1.2	1	2.2	0.9
5C	Glut to 80%Eth	5.6	5.3	4.2	3.8	1.8	1.3	3.1	1.2
5D	Glut to 80%Eth	4.6	4.2	4.1	3.6	1.5	1.1	2.6	1.1
5E	Glut to 80%Eth	5.2	4.8	4.1	3.5	1.6	1.3	2.9	1.1
6A	Glut to 80%Eth	5.5	5.2	4.2	3.5	1.8	1.3	3.1	1.1
6B	Glut to 80%Eth	4.3	4.1	3.5	3.2	1.4	1.3	2.7	0.9
6C	Glut to 80%Eth	4.2	4.1	3.4	3.1	1.3	1	2.3	0.8
6D	Glut to 80%Eth	4.4	4.1	3.6	3.2	1.5	1.1	2.6	0.9
6E	Glut to 80%Eth	5.2	4.9	4.3	3.8	1.6	1.4	3	1.5
7A	Glut to 80%Eth	4.8	4.5	3.9	3.5	1.6	1.3	2.9	1.2
7B	Glut to 80%Eth	4.1	3.9	3.6	3.1	1.3	0.8	2.1	0.8

7C	Glut to 80%Eth	4.4	4.2	3.7	3.2	1.6	1	2.6	1.1
7D	Glut to 80%Eth	bk	bk	bk	bk	bk	bk	bk	bk
7E	Glut to 80%Eth	bk	bk	bk	bk	bk	bk	bk	bk
8A	Glut to 80%Eth	bk	bk	bk	bk	bk	bk	bk	bk
HOLOTYPE	DRY	5.8	5.6	4.7	4.4	ds	ds	ds	1.4
SEM	DRY GOLD	9.2	8.7	6.9	6.2	ds	ds	ds	1.6

251

252 **Description – Shell Figs (5-7)**

253 To 9 mm in length. Typical shell as represented by the holotype (Fig. 5) very thin  
 254 approximately 16µm in cross section (Fig. 7A), translucent, fragile. Inequivalve, left  
 255 valve the slightly smaller, slightly less inflated fitting inside the larger right valve.  
 256 Outline inequilateral, prosogyrous beaks in the anterior fifth. Outline obliquely oval,  
 257 modioliform, anterior narrowly rounded, posterior expanded, subtruncate. Umbonal –  
 258 posterior ventral angle distinct but low, more strongly expressed in the right valve. Hinge  
 259 weak, LV (Fig. 6A,B) with a cardinal complex of a median narrow chondrophore (ch),  
 260 posterior to it a small projecting knob (kn), anterior to it a socket for the cardinal tooth in  
 261 the RV (c sk). RV (Fig. 6C) with a small cardinal peg-like tooth (c th) widely separated  
 262 from an elongate, thin, submarginal posterior, weakly serrated, flange (Fig. 6D), Internal  
 263 ligament attached to chondrophore and sub-umbonal gap, external ligament short, thin  
 264 (Fig. 6A, B, ext lig):

265 Sculpture weak, without magnification smooth with weak incremental lines except for the  
 266 margins of the RV of larger specimens where commarginal ridges develop and are best  
 267 seen with SEM (Fig. 6G). Under the SEM both valves with radial and commarginal  
 268 creasing of the periostracum (Fig. 6E), this reflected only very lightly as shell sculpture  
 269 (Fig. 6H, circled). LV with increasing lamellar periostracum at the margins with sparse  
 270 radial creases (Fig. 6F). Indications of shell spines on the dorsal margin of the RV (Fig.  
 271 6I, arrowed).

272 Shell colourless with sparse, black deposits. Deposits composed of aggregated spherules,  
 273 with a compact reticulate surface (Fig. 7B, C).

274 *Variation*

275 The shape of the shell is occasionally variable. Some shells are far less inequilateral and  
276 have a more rounded appearance (Fig. 5G) while some although strongly inequilateral  
277 have a more rounded posterior outline (Fig. 5E). This variability can be expressed in the  
278 “length : height” ratio of the right valves while there is a mean of 1.23 and a range from  
279 1.04 – 1.33. The inequilateral condition expressed as the ratio “length : anterior length”  
280 has a mean of 4.47 and a range from 3.47 to 5.67. The extent of the inequivalve condition  
281 is also variable, while the mean ratio for right and left valve tumidity is 1.33 the range is  
282 from 1.06 to 1.82.

283

284 **Description – Anatomy**\_ Figs 7-8

285 The mantle edge is thin (Fig. 8B) and largely fused except for an anterior pedal aperture  
286 Fig. 8A, pg) and small posterior inhalant and exhalant apertures (Fig. 8A, ex, in). The  
287 musculature of the posterior apertures is weak and siphons are not developed (Fig. 8C).  
288 The inner edge of the inhalant aperture bears minute widely spaced pointed papillae and a  
289 few papillae are also present on the outer edges (Fig. 8C). The exhalant aperture has a  
290 few papillae on the outer edge but the inner edge is smooth (Fig. 8C). The adductor  
291 muscles are small (Fig. 8A) and the pedal protractor muscles are very thin.

292 The volume of the shell is filled with the large ctenidium composed of two demibranchs  
293 with reflexed filaments, the outer demibranch is approximately two-thirds the size of the  
294 inner (Figs 8A, B). The filaments (Figs 9A-D) are narrow with heavily ciliated frontal  
295 surfaces (Fig. 9A) and are inter-connected with regularly spaced muscular junctions best  
296 seen from the abfrontal face (Fig. 9B). The frontal ciliation (Fig. 9D) is composed of a  
297 row of frontal cilia (fc) bounded on either side by a row of lateral frontal cirri (lfc), these  
298 bounded by a row of lateral cilia (lc) that lie slightly to the posterior and are seen from  
299 the abfrontal surface. The frontal cilia give way to longer terminal cilia (tc) towards the  
300 food groove. The lateral frontal cirri appear as lamellar structures with multiple fine ends

301 (Fig. 9C) and arise from prominent ridged bases (lfc[b]), this in contrast with the frontal  
302 and terminal cilia that arise from a punctate cushion-like surface (tc[b]).

303 Labial palps are vestigial and lack sorting ridges.

304 The foot and visceral mass are proportionately small compared to the mantle cavity and  
305 are contained within the anterior dorsal region (Fig. 8A). The foot (Fig. 8D, f) has a long  
306 toe and a short heel these separated by a small byssal groove. The byssus is active and  
307 produces a very fine thread that has a multiple split end (Fig. 8A, by).

308 The alimentary system (Figs 8A, D, E) is composed of a short oesophagus (oe), a  
309 stomach (st) with two distinct parts, a dorsal cavity and a ventral tube housing the style  
310 sac (ss). The digestive diverticula (dg) are confined to the immediate surrounds of the  
311 stomach and open by a single ventral aperture into the stomach. The remainder of the gut  
312 and rectum are not coiled.

313 A small portion of gonadal tissue (Fig. 8E, gd) was observed but the detailed structure  
314 and that of the heart and kidneys could not be discerned by gross dissection.

### 315 **Etymology**

316 From the Latin *muriaticus* meaning “of brine” (Brown, 1956); referring to the brine pool  
317 habitat.

### 318 **Comparisons**

319 Only three identified species of Corbulidae are recorded from the Red Sea, *C.*  
320 (*Varicorbula*) *erythraeensis* Adams, 1871 (Fig. 10A-B), *C. (Ansiocorbula) sulculosa*  
321 Adams, 1870 (Fig. 10D-E) and *C. (A.) taitensis* Lamarck, 1818 (Fig. 10G-H) (Oliver,  
322 1990). Unidentified species of *Corbula* were listed by Grill & Zuschin (2001) and a  
323 further but undescribed species has been collected from the deep central Red Sea and is  
324 referred to here as *C. (Varicorbula) sp. 1* (Fig. 11A-D, 12F-I). A fifth was recorded from  
325 the Thuwal Seep and tentatively identified as *C. (V.) rotalis* (Batang et al, 2012), shells  
326 from the type locality of Japan are illustrated here (Fig. 10C & F). Both species of

327 *Anisocorbula* have almost equilateral heavy strongly sculptured shells quite unlike  
328 *Apachecorbula*. The other three species can be assigned to the subgenus *Varicorbula* and  
329 have inequilateral, strongly inequivalve, robust shells with a prominent commarginal  
330 sculpture on the right valve. These characters contrast with the thin and modioliform shell  
331 of *Apachecorbula*. As stated under the generic remarks *Apachecorbula* is unlike all other  
332 corbulid genera in the weakly inequivalve, modioliform and thin shell but these are  
333 characters seen in the juvenile shells of some species. Juvenile *Anisocorbula* are  
334 distinctly carinate and some have a pustulose microsculpture (Fig 12C-D), both  
335 characters not seen in *Apachecorbula*. Juveniles of *Varicorbula* are quadrate in outline  
336 (Fig. 12A) with the anterior narrower than the posterior, with growth they become  
337 narrow, almost rostrate, posteriorly. These juveniles have a distinct umbonal angulation  
338 and are almost carinate in some, the left valve has a wide non calcified margin and is  
339 weakly pustulose in *C. (V.) erythraeensis* (Fig. 12A-B); this in contrast with the shell of  
340 *A. muriaticus*. In *Varicorbula* sp. 1 the ribbed sculpture of the right valve appears at an  
341 early stage, approximately at one millimetre (Fig. 12G) and has no radial sculptural element  
342 on the early shell (Fig. 12F). The indications of dorsal spines in *Apachecorbula* are  
343 reminiscent of the distinct spines present in juvenile of the European *C. (V.) gibba* (Fig.  
344 12E). Given the differences outlined here and the relatively large size of *Apachecorbula*  
345 we conclude that this does not represent a juvenile of any known species. The presence of  
346 gonadal tissue also suggests that these specimens are adult.

347

#### 348 DISCUSSION on FUNCTIONAL MORPHOLOGY

349

350 The footage from the ROV (Fig. 3) shows that *Apachecorbula* is semi-infaunal with only  
351 the anterior part of the shell within the sediment. Despite the slender nature of the byssus  
352 it is a constant feature and will help to stabilize this position. This life habit with the  
353 posterior part of the shell well above the sediment surface may account for the absence of  
354 well developed siphons in *Apachecorbula* and is in contrast with the siphonate condition  
355 found in all other corbulids studied (Yonge 1946, Morton 1990, Mikkelsen & Bieler  
356 2001). Shallow water corbulids are generally described as shallow burrowers with the

357 posterior part of the shell lying at or close to the sediment surface (Yonge 1946, Morton  
358 1990). Yonge (1946) makes reference to the heavy sediment load experienced by *C. (V.)*  
359 *gibba* and relates this to the form and function of the papillate siphons and the large  
360 quantities of pseudofaeces produced. Mikkelsen & Bieler (2001) record instances of *C.*  
361 *(V.) disparilis* being epifaunal but with no fixed position, rather living among shell hash.  
362 The morphology of *C. (V.) disparilis* is essentially similar to other shallow water species  
363 and has well developed papillate siphons. The paucity of siphonal papillae in  
364 *Apachecorbula* may be related to the semi-infaunal habit but may also reflect the  
365 potential paucity of suspended food particles available to it.

366 The large gill, its ciliation and lack of gut coiling suggest that *Apachecorbula* is a  
367 suspension feeder. Deep-sea deposit feeding bivalves typically have coiled mid and hind  
368 guts, and large labial palps or palp probosides (Allen, 1979). There is no abfrontal  
369 extension indicative of forms harbouring chemosymbiotic bacteria (Taylor & Glover,  
370 2010) and no bacteriocyte cells were observed. The diversity of suspension feeding  
371 bivalves in the deep sea is limited primarily to Arcidae and Limopsidae (Oliver, 1979)  
372 and for the relatively well studied Atlantic deep-sea fauna corbulids are all but absent  
373 from the bathyal and abyssal zones (Allen, 2008). As a suspension feeder *Apachecorbula*  
374 might be expected to have labial palps at least as large as other species in the family but  
375 this is not so as the palps are very small. This suggests that sorting of food particles is  
376 reduced and this is supported by the absence of guard cilia on the food groove of the  
377 ctenidium. Yonge (1946) suggested that the guard cilia in *C. (V.) gibba* functioned to  
378 prevent unwanted non-food particles being carried to the labial palps and mouth. Their  
379 absence, reduced palps and weak papillation of the inhalant aperture all suggest that  
380 *Apachecorbula* is not subjected to a large load of suspended particles entering the mantle  
381 cavity and does not sort particles to the same extent as shallow water species. Together  
382 this suggests that food is in short supply.

383

384 The overall appearance of the soft tissues is one of contracted size and lack of substance  
385 except for the ctenidia. We propose that the large ctenidium is maintained to facilitate

386 both food collection and respiration in conditions of low food and low oxygen. However,  
387 these adaptations do not overcome the severe conditions and the body mass is relatively  
388 small compared to the volume of the shell thus reducing the metabolic demand. A similar  
389 low body mass was reported in *Amygdalum anoxicolum*, a glassy mussel from the oxygen  
390 minimum zone off Oman (Oliver, 2001).

391

392 A number of studies on corbulids note the thick shell and presence of conchiolin layers  
393 Yonge (1946) on *C. (V.) gibba* from Scotland; Morton (1990) on *C. crassa* from Hong  
394 Kong and Mikkelsen & Bieler (2001) on *C. (V.) disparilis* from Florida. The conchiolin  
395 layers are postulated to prevent predation by shell-boring gastropods, their absence in *A.*  
396 *huriaticus* suggests that such predation pressures do not exist. The thin shell reduces the  
397 energy demand for shell production especially in an environment that is slightly acidic.

398

399 It has been noted above that the shell of *Apachecorbula* most resembles that of the  
400 juvenile shells of *Varicorbula* suggesting that paedomorphosis has occurred. The shells  
401 are relatively large (9 mm) compared with species that have evolved by progenesis, e.g.  
402 *Turtonia minuta* at 2 mm (Ockelmann, 1964) and *Notolimea clandestina* at 1mm (Salas,  
403 1994). Hayami and Kase (1993) cited abnormal salinity, metallic cat-ions (Fe, Cu),  
404 oxygen deficiency, high turbidity, strong water agitation, high population density,  
405 abnormal pH, temperature variations and deficient food supply as possible causes of  
406 stunting. Many of these factors apply to the extreme environment of the “shore” of the  
407 brine pool yet the size is not atypically small in comparison with other Red Sea corbulids  
408 that have a maximum size of 13 mm in *Varicorbula sp. 1* and *Anisocorbula taitensis*. The  
409 feeble musculature, small size of the visceral mass and small adductor muscles do  
410 however give an impression of stunting such that there is “a small body in a large shell”  
411 appearance to *Apachecorbula*. The shell although not smaller is much thinner than in  
412 most corbulids and in this could be regarded as stunted. We propose that progenesis has  
413 not occurred but the extreme conditions have stunted the growth of selected tissues and  
414 organs. The large ctenidium is retained in order to maximise food particle collection and



415 respiration, and the thin shell can reduce energy demand. The large, thin shell, which can  
416 be regarded as a neotenous character, does not increase predation pressure as predators  
417 are not abundant.

418

419 Colonisation of the shores of the brine pool is therefore negatively influenced by the  
420 extreme environmental parameters but these are partly mitigated by biological parameters  
421 such as lack of competition and few predators.

422

423 In the systematic section we noted that corbulids are infrequent in the bathyal and abyssal  
424 regions of the deep oceans across the world. The Red Sea appears to be an exception with  
425 species being recorded from the Thuwal seep at a depth of 840 – 850m (Batang et al,  
426 2012) and the *C. (Varicorbula)* sp. 1 from 1465m (this paper). Such bathymetric range  
427 extensions are not unusual for Red Sea invertebrates and it is argued that the high  
428 temperatures maintained in the deep Red Sea allow shallow warm water taxa to exist at  
429 greater depths (Turkay, 1996). High levels of endemism are recorded for the deep Red  
430 Sea fauna (Turkay, 1996) and to date corbulids have not been recorded from depths  
431 beyond the shelf in the adjacent Gulf of Aden and Arabian Seas. The deepest records are  
432 those of *Corbula subquadrata* Melvill & Standen, 1907 and *C. persica* Smith 1906 from  
433 285 m in the Gulf of Oman (Melvill & Standen, 1907).

434

435 Both *Apachecorbula* and *Corbula* sp. 1 can be added to the list of endemics from the Red  
436 Sea. The various environmental crisis experienced by the Red Sea including periods of  
437 hypersalinity and anoxia (Braithewaite, 1987) could have simulated current brine pool  
438 conditions at shallow depths creating an adaptive force in the shallow water fauna.

439

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449

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563

564

## 565 FIGURE LEGENDS

566

567 **Fig. 1.** Distribution of the major brine pools in the Red Sea.

568

569 **Fig. 2.** Chart of salinity, dissolved oxygen, pH and temperature with increasing depth in  
570 proximity to the Valdivia brine pool.

571

572 **Fig. 3.** Sea floor images at the margins of the Valdivia brine pool taken by the ROV Max  
573 Rover. *Apachecorbula* appear as black coloured clams in (A) and as small black objects  
574 arranged in a narrow band in (C). (B) shows the collecting bag of the ROV.

575

576 **Fig. 4.** Diagram showing the shell measurements used in the description.

577

578 **Fig. 5.** Shells of *Apachecorbula muriatica* gen et sp nov. (A-D): Holotype, NMW.Z.  
579 2013.058.1. (E-H): Variations in outline and tumidity.

580

581 **Fig. 6.** Scanning electron micrographs of the shell of *Apachecorbula muriatica*. (A) left  
582 valve hinge; (B) dorsal view of left valve hinge; (C) right valve hinge; (D) weak  
583 serrations on the posterior flange of the right valve; (E) microsculpture on the umbonal  
584 area of the left valve; (F) radial creases in the periostracum at the margins of the left  
585 valve; (G) commarginal ridges at the margins of the right valve; (H) radial impressions  
586 on the shell after removal of the periostracum; Small spines on the dorsal margin of the  
587 early shell.

588

589 **Fig. 7.** Scanning electron micrographs of the shell of *Apachecorbula muriatica*. (A) cross  
590 section of the shell; (B, C) black surface coating showing structure as an accumulation of  
591 reticulate spherules.

592

593 **Fig. 8.** Gross anatomy of *Apachecorbula muriatica*. after dissection from the left side and  
594 stained in haematoxylin. (A) semi-diagrammatic reconstruction of the gross anatomy; (B)  
595 whole animal after removal of left valve and mantle; (C) siphonal openings; (D) visceral  
596 mass; (E) visceral mass with digestive gland and epithelium dissected away.

597

598 **Fig. 9.** Scanning electron micrographs of the ctenidium of *Apachecorbula muriatica*. (A)  
599 frontal surface; (B) abfrontal surface; (C) lateral frontal cirri and lateral cilia; (D) ciliation  
600 at the ventral edge of the inner demibranch.

601

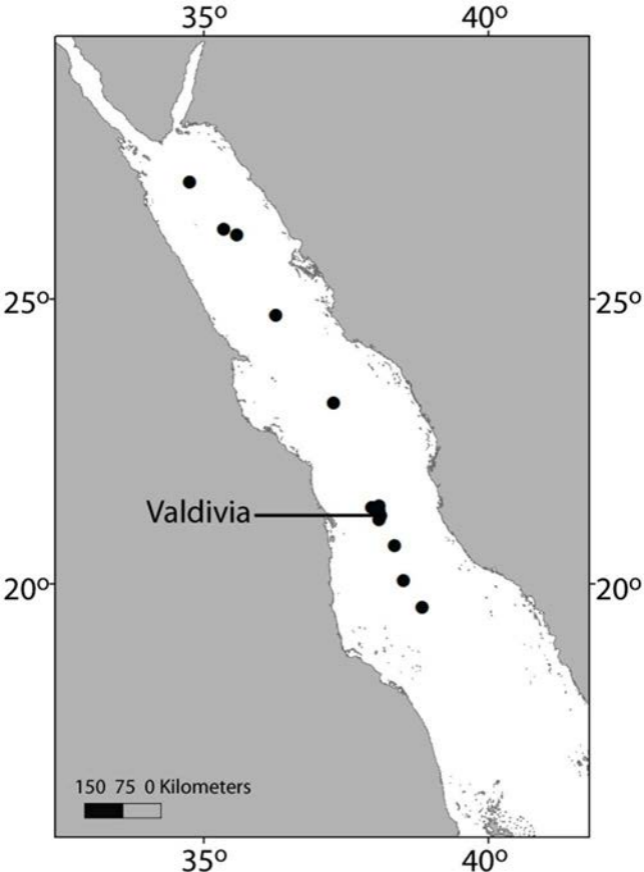
602 **Fig. 10.** Shells of comparative species recorded from the Red Sea. (A, B), *Corbula*  
603 (*Varicorbula*) *erythraeensis*; (C, F), *C. (V.) rotalis*; (D,E), *C. (Anisocorbula) sulculosa*;  
604 (G, H), *C. (A.) taitensis*.

605

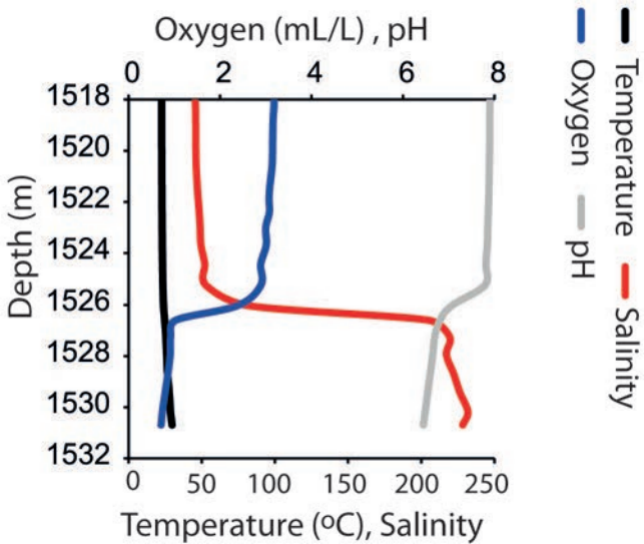
606 **Fig. 11(A-D):** Shells of *Corbula (Varicorbula)* sp. 1 Central Red Sea. E-F.  
607 *Apachecorbula muriatica*, large specimen for comparison.

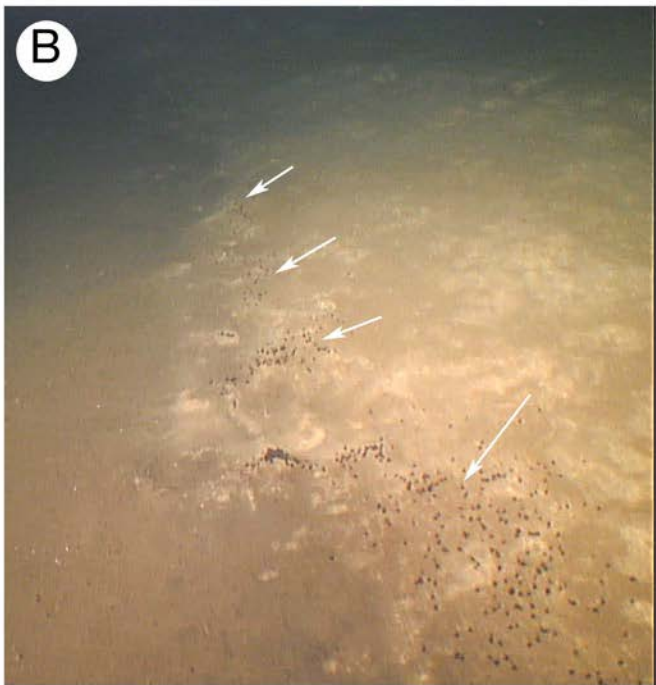
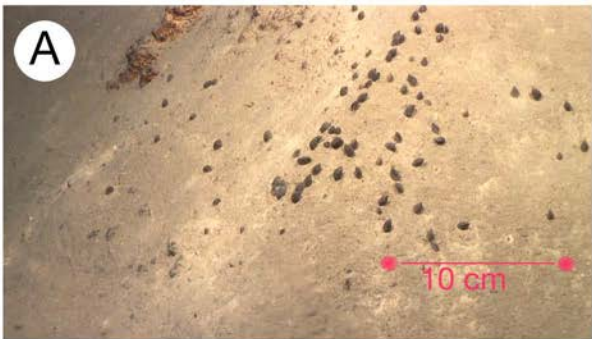
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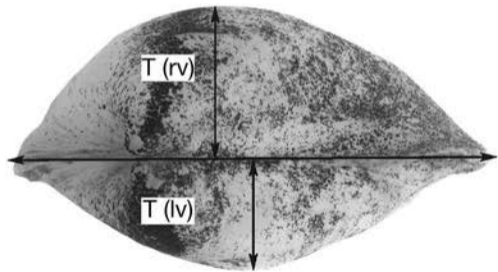
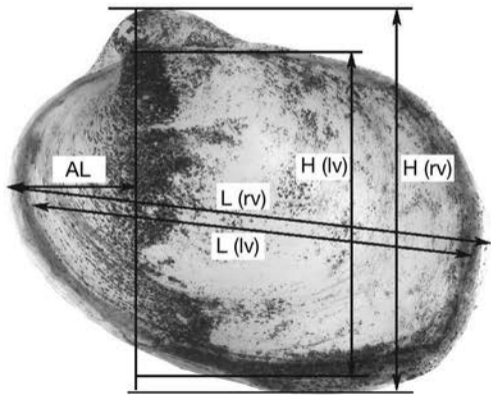
609 **Fig. 12.** Scanning electron micrographs of juvenile shells of corbulid species. (A-B) *C.*  
610 (*V.*) *erythraeensis*, (A) whole left valve; (B) pustules on anterior slope. (C,D), *C. (A.)*  
611 *sulculosa* (A) whole left valve; (D) posterior carina and radial rows of pustules. (E)  
612 Internal of right valve of *C. (V.) gibba* showing dorsal spines. (F-I): *A. (V.)* sp. 1 (F)  
613 whole left valve; (G) umbonal region of right valve; (H) hinge of left valve; (I) hinge of  
614 right valve.

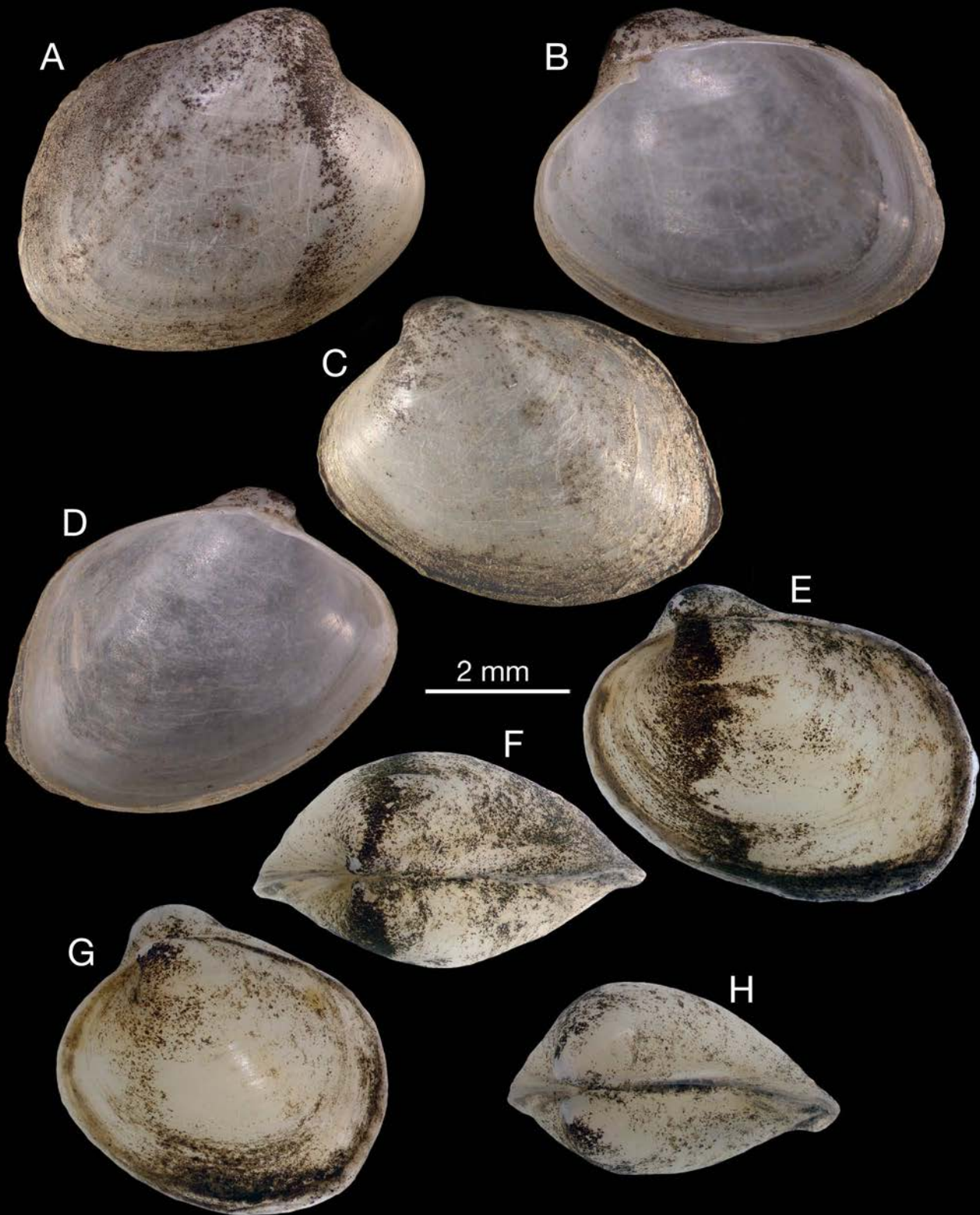


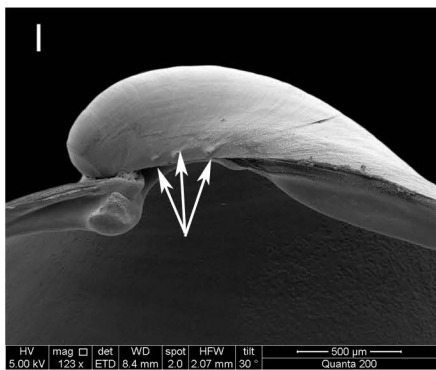
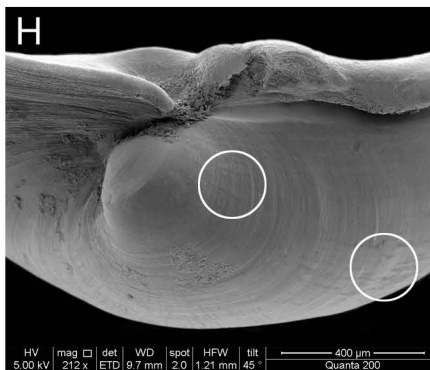
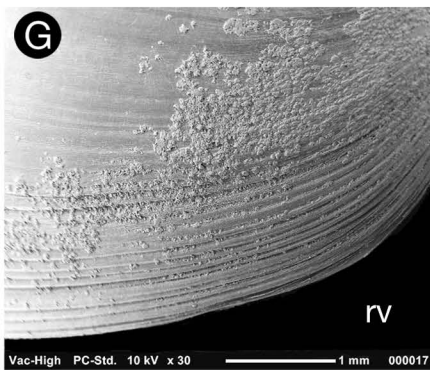
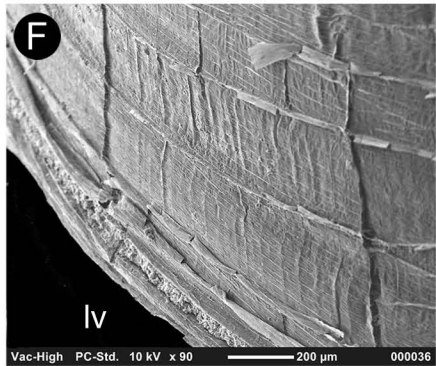
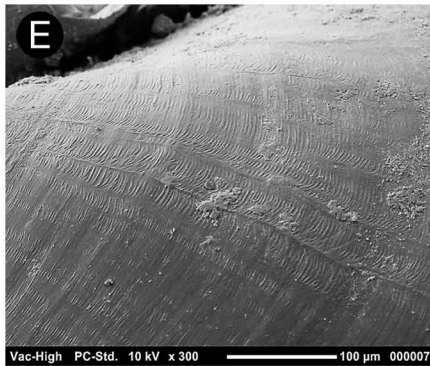
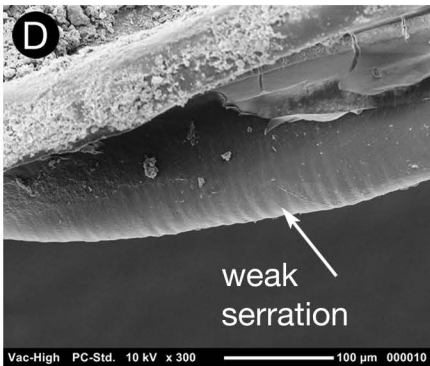
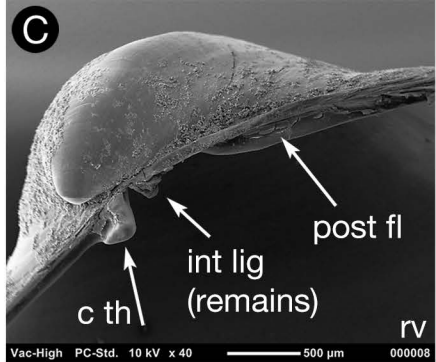
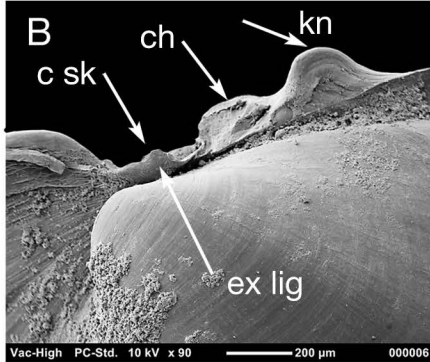
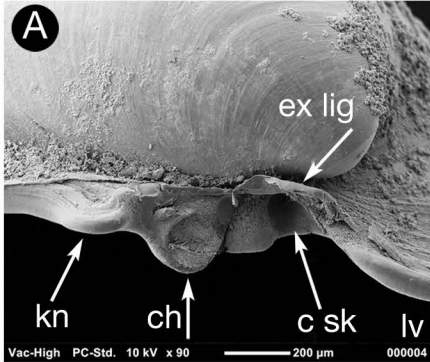


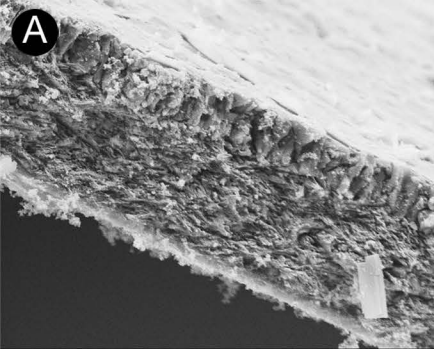




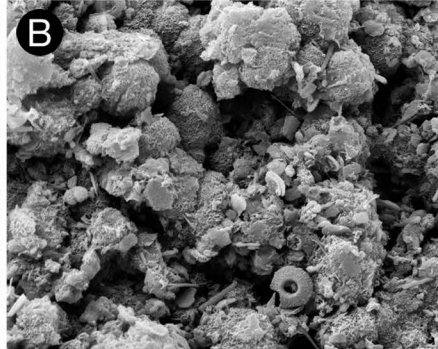




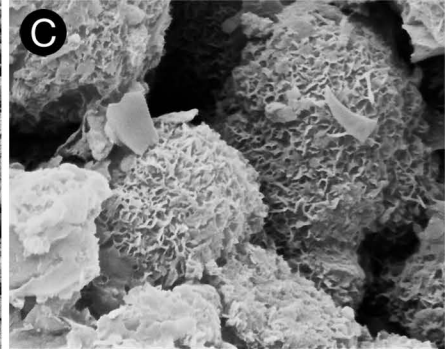




Vac-High PC-Std. 15 kV x 2700 10  $\mu$ m 000005

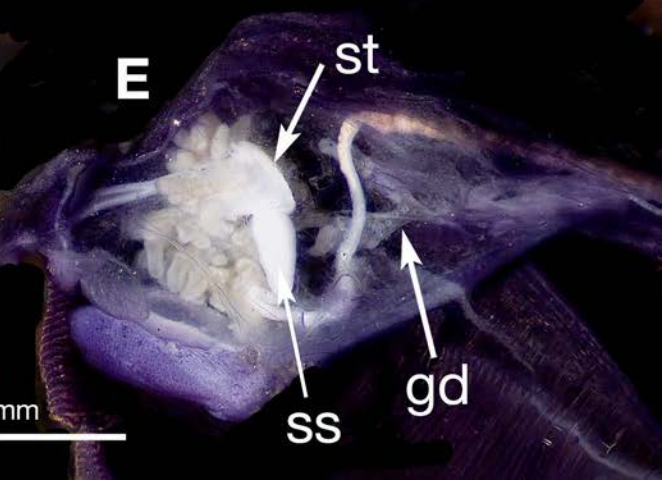
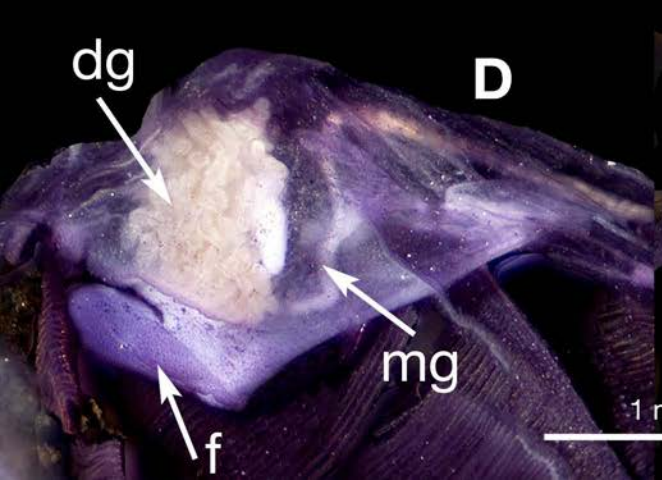
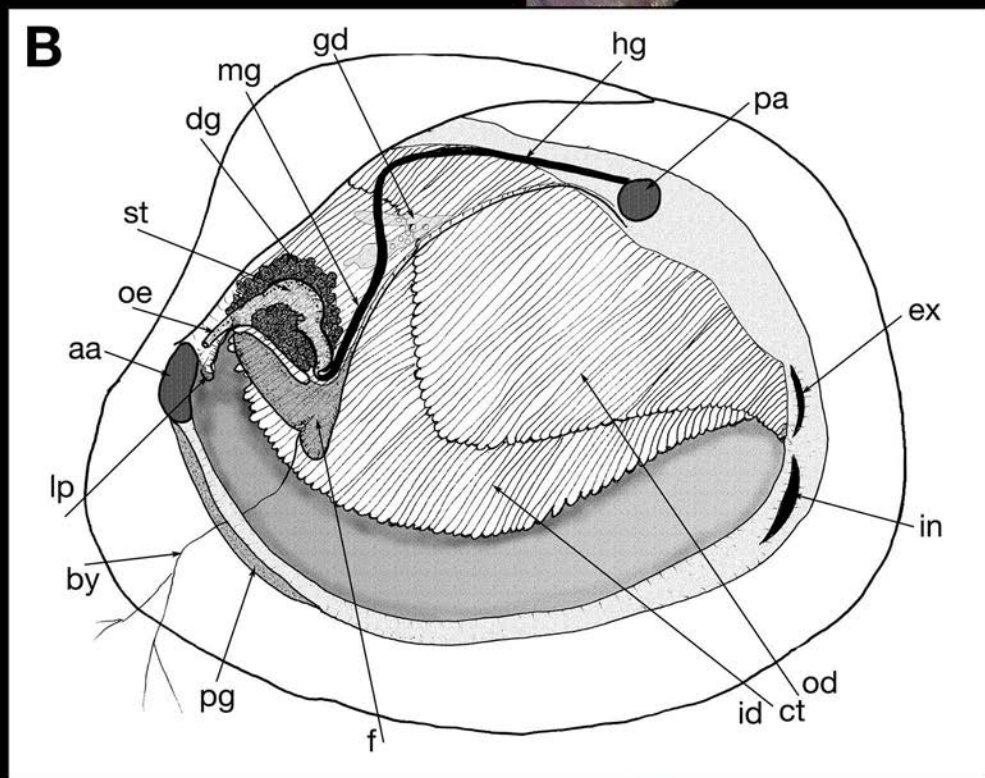
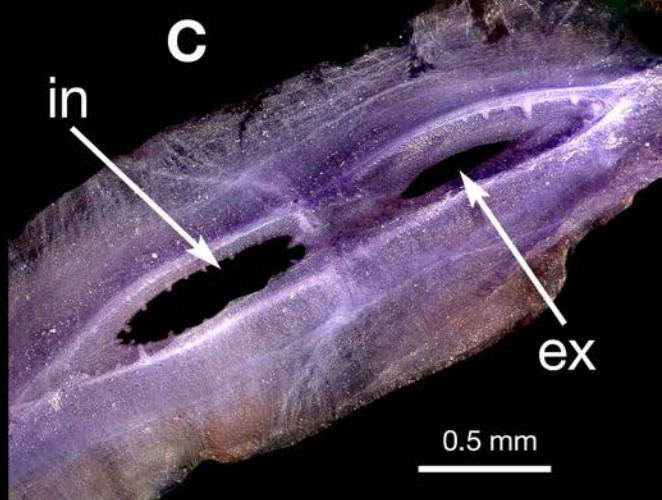
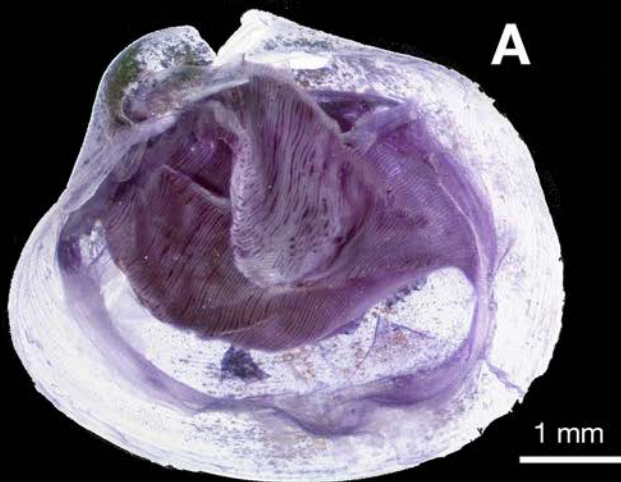


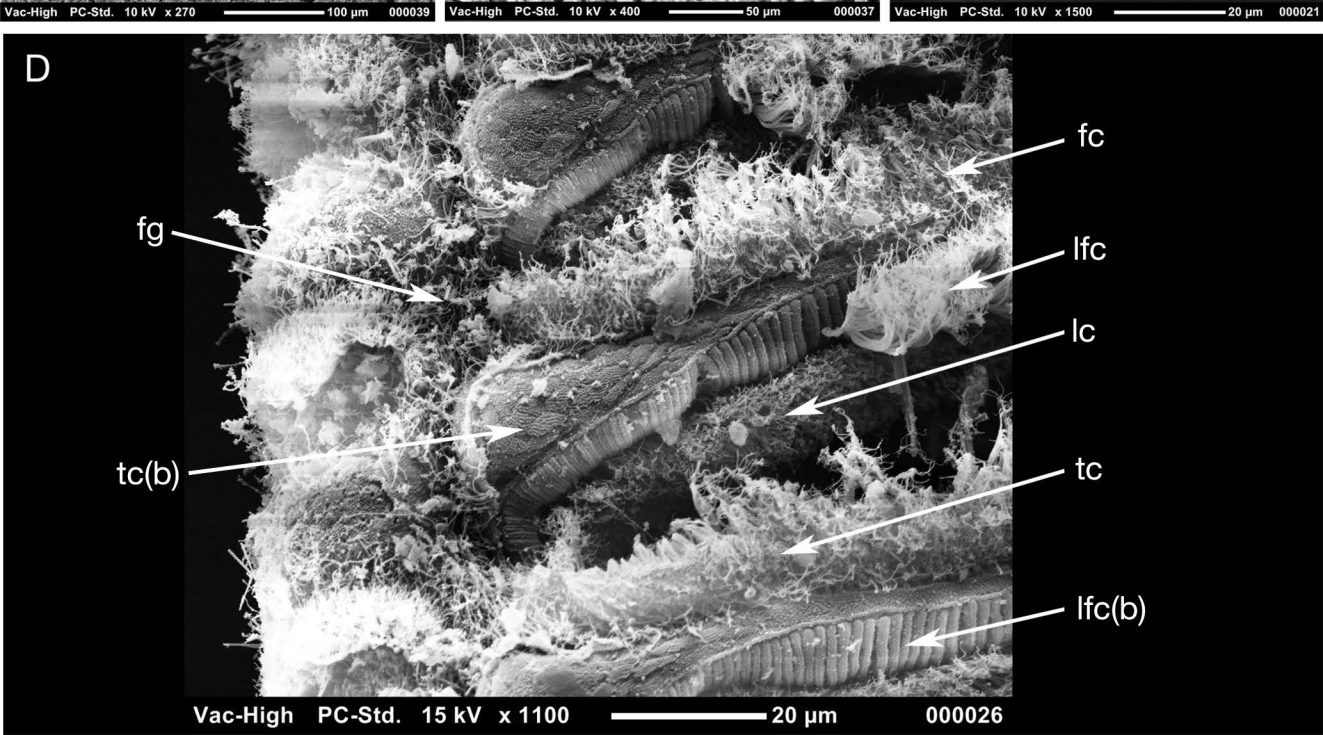
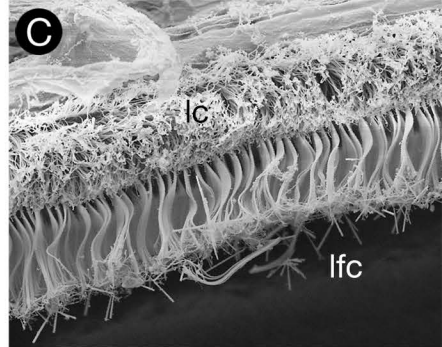
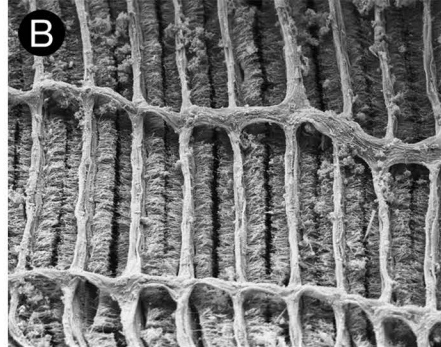
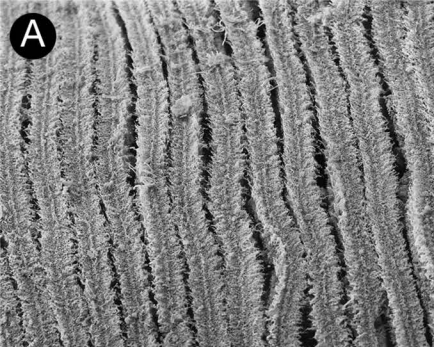
Vac-High PC-High 15 kV x 2000 10  $\mu$ m 000028



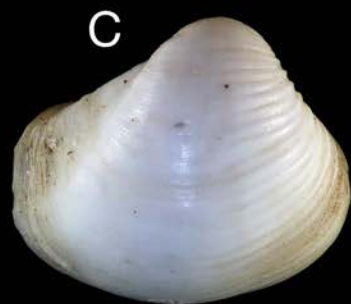
Vac-High PC-High 15 kV x 8000 2  $\mu$ m 000023









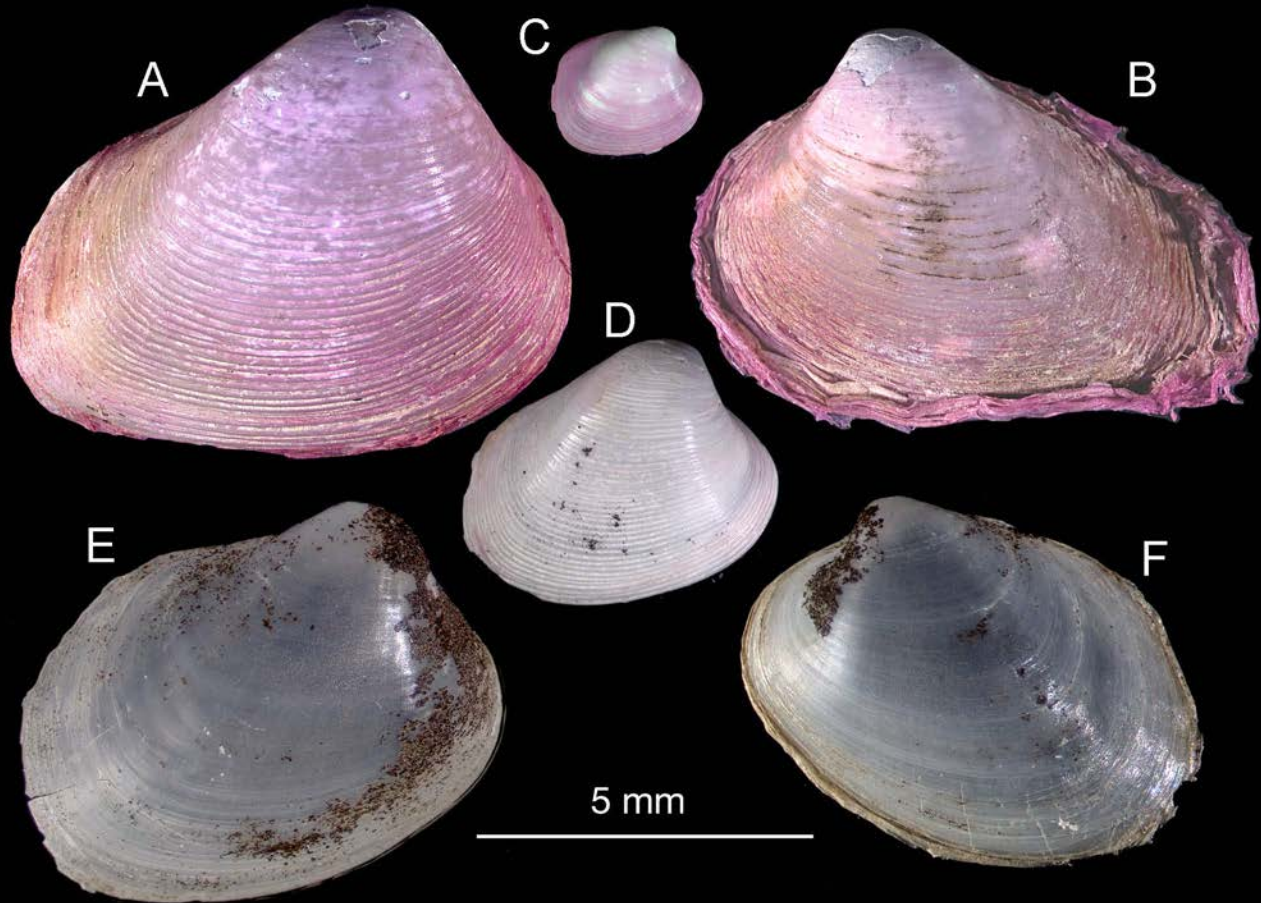


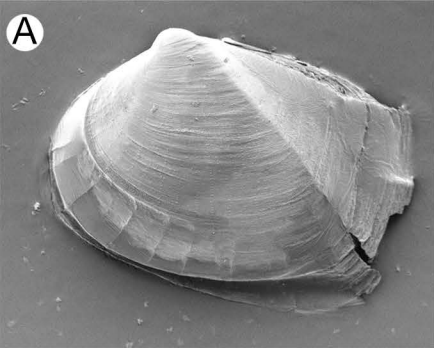
5mm



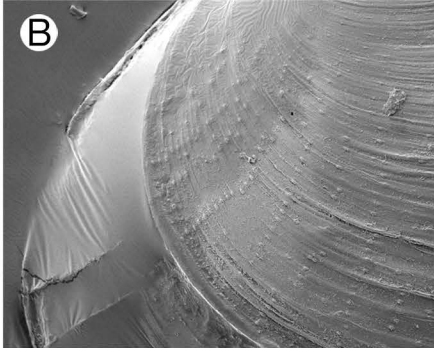
5mm



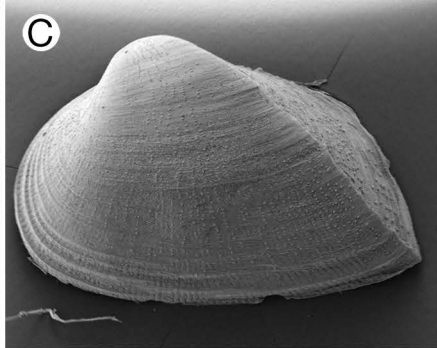




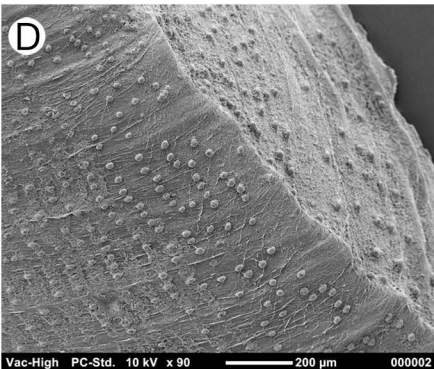
Vac-High PC-Std. 10 kV x 60 500  $\mu$ m 000003



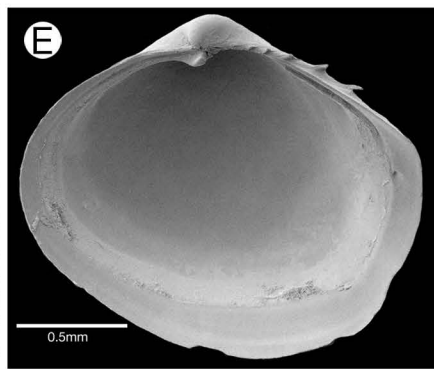
Vac-High PC-Std. 10 kV x 200 100  $\mu$ m 000004



Vac-High PC-Std. 10 kV x 27 1 mm 000001

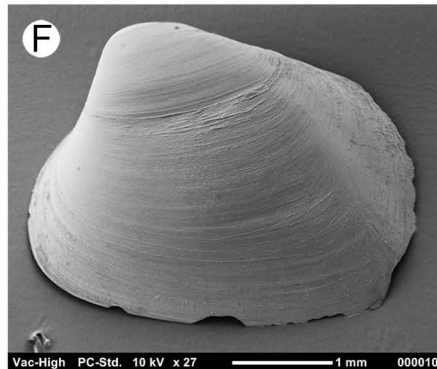


Vac-High PC-Std. 10 kV x 90 200  $\mu$ m 000002

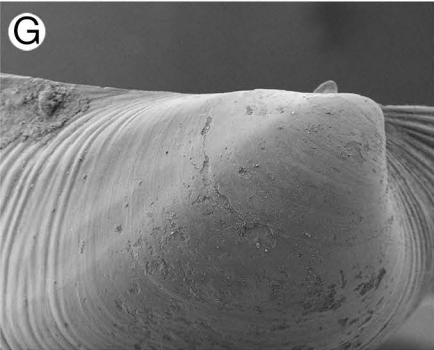


0.5mm

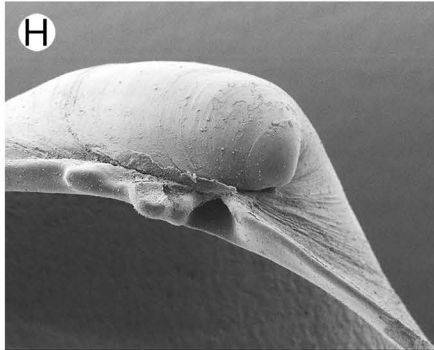
Vac-High PC-Std. 10 kV x 27 1 mm 000010



Vac-High PC-Std. 10 kV x 27 1 mm 000010



Vac-High PC-Std. 10 kV x 44 500  $\mu$ m 000007



Vac-High PC-Std. 10 kV x 80 200  $\mu$ m 000001



Vac-High PC-Std. 10 kV x 50 500  $\mu$ m 000006