

# ABYSSOGENA: A NEW GENUS OF THE FAMILY VESICOMYIDAE (BIVALVIA) FROM DEEP-WATER VENTS AND SEEPS

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## ABSTRACT

A new genus *Abyssogena* is established for *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986) and *A. kaikoi* (Okutani & Métivier, 1986), which were previously assigned to the genus *Calyptogena* Dall, 1891, and also for two new species, *A. southwardae* and *A. novacula*. The most characteristic features of *Abyssogena* are an elongate shell up to about 280 mm in length; a pallial line starting from the ventral margin of the anterior adductor scar; secondary pallial attachment scars developed dorsal to the pallial line; radially arranged hinge teeth with a reduced anterior cardinal tooth in the right valve; and presence of an inner ctenidial demibranch only. *Abyssogena* occurs in deep water from 2,985 to 6,400 m and is distributed in the Pacific and Atlantic Oceans at cold seeps along continental margins and hydrothermal vents at mid-oceanic ridges. Some species have a remarkably wide geographic distribution; *A. southwardae* is present throughout the Atlantic and *A. phaseoliformis* is present in Japan, Kuril-Kamchatka, as well as Aleutian Trenches. No fossils of *Abyssogena* are known.

## INTRODUCTION

The Vesicomylidae are a family of heterodont bivalves that includes specialized species occurring in sulphide-rich habitats at hydrothermal vents and cold seeps. All species studied so far contain sulphide-oxidizing bacteria in their ctenidia (Fisher, 1990). It is a diverse group comprising over 110 described and still undescribed Recent species (E.M. Krylova, H. Sahling and R. Janssen, unpubl.), distributed worldwide from the low sublittoral zone to the hadal depths. The combination of a pan-oceanic distribution and a high level of ecological isolation at separated habitats makes vesicomylids an interesting group in which to study dispersal patterns in the deep sea. However, the problematic taxonomy of vesicomylids still hinders use of this group in biogeographical analyses.

The generic structure of the family has not yet been fully determined (Krylova & Sahling, 2006). The absence of unambiguous generic diagnoses results from uncertainties in the definition of hinge characters, strong ontogenetic variation and much morphological convergence. As a consequence, recently described species have usually been assigned to the genera *Calyptogena* or *Vesicomya* (Coan, Scott & Bernard, 2000; Goffredi *et al.*, 2003), which, according to molecular analyses, are not monophyletic groups (Vrijenhoek *et al.*, 1994; Kojima *et al.*, 1995; Peek *et al.*, 1997; Kojima, Fujikura & Okutani, 2004).

Several recent studies have revealed that the generic composition of the family is more complex than previously thought. Von Cosel & Salas (2001) demonstrated the diversity of 'small' vesicomylids in the eastern Atlantic, where they recorded species of *Vesicomya* Dall, 1886, *Waisiuconcha* Beets, 1942, *Isorropodon* Sturany, 1896 and *Callogonia* Dall, 1889. Amano & Kiel (2007) have shown that the fauna of fossil vesicomylids from the North Pacific region comprises five genera: *Hubertschenckia* Takeda, 1953, *Adulomya* Kuroda, 1931, *Archivesica* Dall, 1908, *Isorropodon* and *Pliocardia* Woodring, 1925. Recently, the number of generic names applied to extant vesicomylids has increased. This results from the re-investigation and use of genera previously applied to fossil

species (Krylova & Janssen, 2006), as well as the introduction of new taxa (von Cosel & Olu, 2008, 2009).

Revision of the genus *Calyptogena* Dall, 1891 using morphological characters has shown that only four species, from 27 that were originally described as *Calyptogena*, match the diagnosis of *Calyptogena* based strictly on the type species (Krylova & Sahling, 2006). Among the species excluded from *Calyptogena* was a group comprising *Calyptogena* (*Ectenagena*) *phaseoliformis* Métivier, Okutani & Ohta, 1986, *C. (Ectenagena) kaikoi* Okutani & Métivier, 1986 and a yet undescribed species from the Mid-Atlantic Ridge (MAR) recorded as *Ectenagena* sp. aff. *kaikoi* (Gebruk *et al.*, 2000) and *C. (Ectenagena)* sp. (Southward *et al.*, 2001), respectively. The close relationship of two species from this group, '*C. phaseoliformis*' and '*C. kaikoi*', was shown by Horikoshi (1989), who pointed out the similarity of hinge structures, and by Kojima *et al.* (1995) on the basis of mitochondrial gene sequences. In addition, results of molecular investigations by Peek *et al.* (2000) indicated that '*C. phaseoliformis*' and *C. n. sp.* from the MAR, Barbados and Florida, form a well-supported monophyletic cluster separated from other vesicomylids. Preliminary morphological studies (Krylova & Sahling, 2006) discovered some common anatomical features that also suggested close relationship of these species and their distinction from other vesicomylids.

In this paper we review the above-mentioned group of species and propose a new genus *Abyssogena*, with *A. southwardae* n. sp. as its type. Originally this species was recorded as *Ectenagena* sp. aff. *kaikoi* from the 'Logatchev' site at the MAR (Gebruk *et al.*, 2000). In addition, we include other material of this species from the 'Wideawake Mussel Field' and Vima Fracture Zone located further to the south along the MAR, from off Barbados (West Atlantic Ocean), from off Virginia (Northwest Atlantic) and from the Canary Islands (East Atlantic). We also describe one more new species, *A. novacula*, from the Peru Trench. We provide detailed descriptions of the two previously described species that belong to the new genus, *C. (Ectenagena) phaseoliformis* and *C. (Ectenagena) kaikoi*. There are two additional undescribed forms that can be assigned to the new genus on the basis of molecular data, one

**Table 1.** Summary of cruises during which samples of *Abyssogena* were taken.

| Research vessel or programme | Cruise no. | Abbreviation | Year | Area   |
|------------------------------|------------|--------------|------|--|
| Vityaz                       | 45         |              | 1969 | Aleutian Trench  |
| Advance II                   |            |              | 1978 | Western Atlantic Ocean, continental margin offshore Virginia |
| BARESNAUT                    |            |              | 1987 | Western Atlantic Ocean, Barbados                             |
| VEMANAUTE                    |            |              | 1988 | Mid-Atlantic Ridge, Vima Fracture Zone                       |
| FARANAUT                     |            |              | 1992 | Mid-Atlantic Ridge, Logatchev area                           |
| Logatchev                    | 7          |              | 1994 | Mid-Atlantic Ridge, Logatchev area                           |
| Logatchev                    | 26         |              | 2005 | Mid-Atlantic Ridge, Vima Fracture Zone                       |
| Sonne                        | 97         | SO 97        | 1994 | Aleutian Trench  |
| Sonne                        | 110        | SO 110       | 1996 | Aleutian Trench  |
| Atlantis                     |            |              | 1997 | Mid-Atlantic Ridge, Logatchev area                           |
| KAIKO                        | 85         |              | 1998 | Kurile Trench  |
| Akademik Mstislav Keldysh    | 41         | Keldysh 12   | 1998 | Mid-Atlantic Ridge, Logatchev area                           |
| Meteor                       | 60/3       | ME 60        | 2004 | Mid-Atlantic Ridge, Logatchev area                           |
| Meteor                       | 64/1       | ME 64        | 2005 | Mid-Atlantic Ridge, Wideawake Field                          |
| Meteor                       | 66/1       | ME 66        | 2005 | Eastern Atlantic Ocean, offshore Canary Islands              |
| Pourquoi-pas?                |            |              | 2007 | Mid-Atlantic Ridge, Logatchev area                           |

from the West Florida Escarpment, West Atlantic (Peek *et al.*, 1997) and another from the Ryukyu Trench (Kojima *et al.*, 2004). Material of neither of these forms has been available to us. Genetic analysis suggests that bivalves from the West Florida Escarpment and Barbados are conspecific (Peek *et al.*, 1997).

## MATERIAL AND METHODS

The material examined comprises specimens that were collected during 16 expeditions (Table 1) as well as relevant type specimens (Table 2). The material in our collection comprises three species, one of which is already known and two other species are new. All species are represented by preserved, live-taken specimens. In addition, the type material of two earlier described species was studied.

For the morphological description the following measurements (Fig. 1) were made with callipers ( $\pm 0.1$  mm): length of valve ( $L$ ), height of valve ( $H$ ), width of valve ( $W$ ), length of fibrous part of ligament ( $F$ ) and length of posterior lamellar part of ligament ( $N$ ). For extremely elongated shells of adult specimens of *A. phaseoliformis* and *A. novacula*, height and width of valve were measured twice: at the level of umbo and where these were maximal (Fig. 1). Furthermore, the position of the umbo was defined as the distance of the umbo from the anterior margin relative to the shell length (Um, in %). For the description of the hinge teeth (Fig. 2) the terminology of Bernard (1895, 1896, 1897) was used, which is widely accepted in recent literature on vesicomysids (Horikoshi, 1989; Okutani, Fujikura & Kojima, 2000; von Cosel & Salas, 2001; Krylova & Sahling, 2006). Gross anatomy was observed on preserved live-taken specimens. Prodissoconchs and details of ctenidia were investigated by scanning electron microscopy (SEM).

Type specimens are deposited in the mollusc section of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt a. M.; Muséum National d'Histoire Naturelle, Paris; and Zoological Museum of Moscow State University, Moscow.

### Abbreviations of institutions

FMNH Field Museum of Natural History, Chicago, USA  
 MNHN Muséum National d'Histoire Naturelle, Paris, France  
 NMB Natural History Museum, Basel, Switzerland

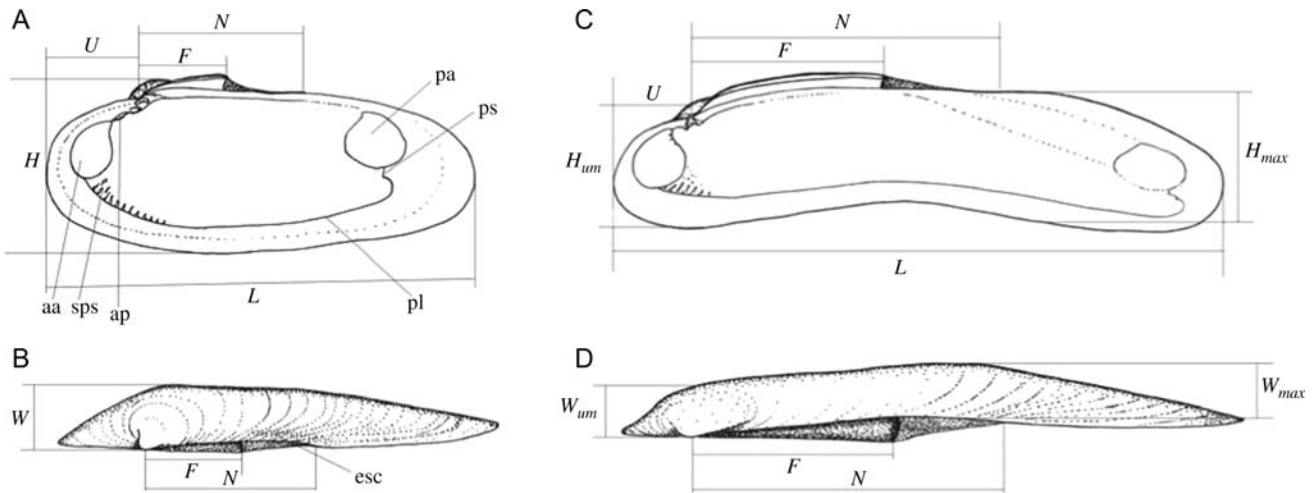
**Table 2.** Additional material of Vesicomysidae studied.

| Species   | Source of material   |
|---|--|
| <i>Ectenagena elongata</i> (Dall, 1916)                       | Albatross, Stn 4432, off Point Loma, California, 275 fm (502 m), type material, USNM 110774  |
| ' <i>Ectenagena</i> ' <i>extenta</i> Krylova & Moskalev, 1996 | RV <i>Keldysh</i> , Stn 2350, MIR, Monterey Bay, 3,041 m, type material, ZMMU Ld-2828; RV <i>Western Flyer</i> , <i>Tiburón</i> Dive 452, Northern Escanaba Trough, 3,217 m, FMNH 302093 |
| <i>Pleurophopsis unioides</i> Van Winkle, 1919                | Miocene, Trinidad, NMB 185, 186  |

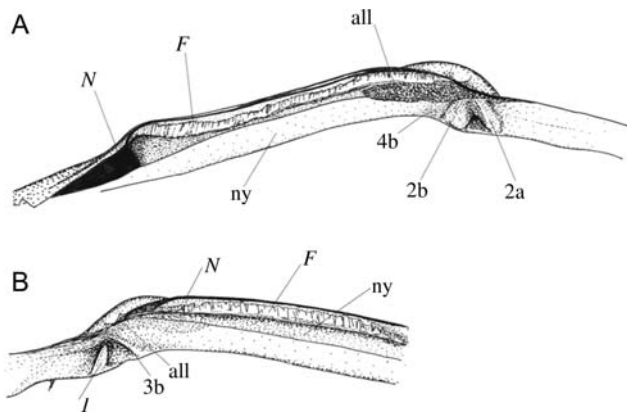
NSMT National Science Museum, Tokyo, Japan  
 SMF Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt a. M., Germany  
 USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA  
 ZMMU Zoological Museum of Moscow State University, Moscow, Russia

### Other abbreviations used in text

DD Drum dredge  
*F* Length of fibrous ligament  
*H* Height of valve  
 juv Juvenile specimen  
*L* Length of valve  
 MAR Mid-Atlantic Ridge  
*N* Length of posterior lamellar ligament  
 ROV Remote operated vehicle  
 RV Research vessel  
 Spm Specimen live-collected  
 TS Sigsbee trawl  
 TVG TV-guided grab  
 v Valve  
 Um Position of umbo (distance of the umbo from the anterior margin relative to the shell length as percentage)  
*W* Width of valve



**Figure 1.** Diagrammatic views of *Abyssogena* illustrating terminology and measurements taken. **A, B.** Juvenile specimen of *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986), RV *Vityaz*, Stn 6096-2,  $L = 20.2$  mm; **C, D.** Adult specimen of *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986), RV *Sonne-97*, Stn 66,  $L = 180$  mm. **A, C.** Right valve, internal view. **B, D.** Right valve, dorsal view. Abbreviations: aa, anterior adductor scar; ap, anterior pedal retractor scar; esc, escutcheon; *F*, fibrous ligament layer; *H*, height of valve;  $H_{um}$ , height of valve at the level of umbo;  $H_{max}$ , maximum height of valve; *L*, length of valve; *N*, posterior lamellar ligament layer; pa, posterior adductor scar; pl, pallial line; ps, pallial sinus; sps, secondary pallial attachment scars; *U*, distance from umbo to anterior margin; *W*, width of valve;  $W_{um}$ , width of valve at the level of umbo;  $W_{max}$ , maximum width of valve.



**Figure 2.** Hinge margins in *Abyssogena* (*A. southwardae* n. sp., holotype). **A.** Left valve. **B.** Right valve. 1, ventral cardinal tooth; 2a, anterior ramus of subumbonal cardinal tooth; 2b, posterior ramus of subumbonal cardinal tooth; 3b, posterior ramus of subumbonal cardinal; 4b, reduced posterodorsal cardinal tooth; all, anterior lamellar ligament layer; *F*, fibrous ligament layer; *N*, posterior lamellar ligament layer; ny, nymph.

## SYSTEMATIC DESCRIPTIONS

### Family Vesicomomyidae Dall & Simpson, 1901

Vesicomomyacidae Dall & Simpson, 1901: 496.

Vesicomomyidae Keen, 1969: 664.

### Genus *Abyssogena* new genus

*Type species:* *Abyssogena southwardae* n. sp.

*Etymology:* Referring to its distribution in abyssal depths; gender feminine.

*Diagnosis:* Shell medium- to large-sized,  $L$  to 277.4 mm, relatively thin-shelled, elongate to strongly elongate in outline, with nearly straight or concave ventral margin. Weakly defined, shallow escutcheon present only in juveniles, lunular incision missing. Pallial line starts from ventral margin of anterior

adductor scar; pallial sinus present as small irregular indentation. Pallial line with secondary pallial attachment scars developed especially near posterior limit of anterior adductor scar dorsal to pallial line. Anterior adductor scar broad, comma-like, somewhat impressed to rear. Anterior pedal retractor scar oval, impressed, located just above and behind the anterior scar. Posterior adductor scar larger, less distinct than anterior adductor scar, wider than high, fused with posterior pedal retractor scar. Ligament external, parivincular. Anterior lamellar layer of ligament running from front of the beak backwards under fibrous layer, subumbonal pit absent. Posterior lamellar layer running from the beak and overlaying externally shorter fibrous layer, subtended by slender nymph. Dentition of right valve: strong, upright, ventral cardinal (1) and subumbonal cardinal consisting of posterior ramus (3b) lower than (1); in adults anterior ramus (3a) is completely reduced. Dentition of left valve: subumbonal cardinal tooth with thin anterior ramus (2a) and stronger posterior ramus (2b), posterodorsal cardinal tooth (4b) reduced or very low. Ctenidia comprise inner demibranchs only, with descending and ascending lamellae; interlamellar septa divided into cylindrical channels. Inner valve of inhalant siphon without processes.

*Included species:* The genus at present comprises *A. southwardae* n. sp., *A. novacula* n. sp., *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986) and *A. kaikoi* (Okutani & Métivier, 1986). One more undescribed species from the Ryukyu Trench ('unidentified vesicomomyid' in Kojima *et al.*, 2004) may be assigned to this genus on the basis of molecular data only. The undescribed species from the West Florida Escarpment (referred to as '*Calyptogena* n. sp.' in Peek *et al.*, 1997) is on the basis of molecular data conspecific with *A. southwardae*.

*Distribution:* Pacific Ocean from Kuril-Kamchatka, Japan, Aleutian, Peru Trenches, Tenryu Submarine Canyon and Nankai Trough at depths from 3,540 to 6,400 m; possibly, Ryukyu Trench at depth 5,900 m (Kojima *et al.*, 2004). Atlantic Ocean along the MAR from the Wideawake Mussel Field to the Logatchev site, in the east Atlantic near the Canary Islands and in the west Atlantic in the Barbados Trench, in the West Florida Escarpment and offshore Virginia at depths 2,985–5,100 m.

*Remarks:* With its strongly elongated shell outline *Abyssogena* resembles three known vesicomyid genera: one Recent genus, *Ectenagena* Woodring, 1938, and two fossil ones, *Pleurophopsis* Van Winkle, 1919, and *Adulomya* Kuroda, 1931 (Table 3). *Ectenagena* was established with *Calyptogena elongata* Dall, 1916 (off Point Loma, California, 502 m) as the type. *Ectenagena* 'has a thinner and more elongate shell than *pacifica*; the right anterior cardinal is suppressed, the middle cardinal swings up to the umbo and the posterior cardinal is shorter and narrower than in *pacifica*; the left anterior cardinal is not so strongly joined to the middle one and is not parallel to the margin of the valve, and the posterior cardinal is short' (Woodring, 1938: 51). To the original description it can be added that the pallial line in *E. elongata* starts from the posterior margin of the anterior adductor scar; there is no pallial sinus and in the hinge margin of *E. elongata* there is a deep subumbonal pit (Figs 3, 6A). Anatomical details of *E. elongata* are unknown. Originally the species *Calyptogena phaseoliformis* and *C. kaikoi* were assigned to the subgenus *Ectenagena* on the basis of strong similarity in elongate shell shape and radiating teeth with a reduced 3a-tooth in the right valve (Métivier *et al.*, 1986; Okutani & Métivier, 1986). Nevertheless, *Abyssogena* is

distinguished from *Ectenagena* by the very characteristic form of the pallial line, starting from the ventral part of the anterior adductor scar (Figs 5, 6), the presence of a pallial sinus and secondary pallial attachments located mainly near posterior margin of anterior adductor scar dorsally to pallial line, and also by the absence of the subumbonal pit in the hinge margin. In addition, molecular analyses (Peek *et al.*, 1997, 2000; Kojima *et al.*, 2004) indicate that *Ectenagena*, including the species *phaseoliformis* and *kaikoi*, is a polyphyletic taxon and therefore also support separation of these species from *Ectenagena*.

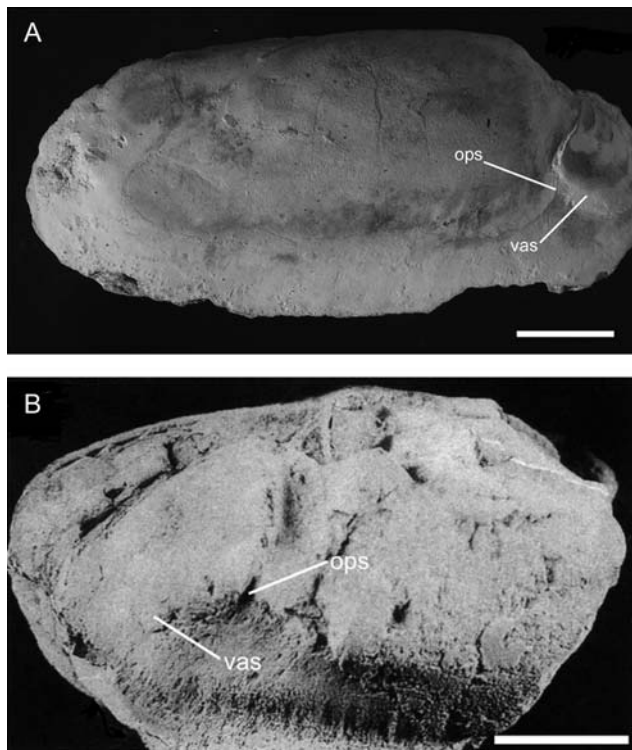
Van Winkle (1919) did not give a diagnosis for the genus *Pleurophopsis*, typifying it by the species *P. unioides* Van Winkle, 1919, known only from casts from the 'Oligocene' (now considered as Middle Miocene, see Gill *et al.*, 2005) of Trinidad. According to Van Winkle, *Pleurophopsis* is characterized by a large, elongated shell with beaks situated at the first fourth of the valve, two cardinal teeth in each valve with the left posterior tooth very large and both right cardinals of subequal size, deep anterior adductor scar and ridge between it and the umbonal area. Additional to this description, in the picture of *P. unioides* (Van Winkle, 1919: pl. 13, fig. 12) it is possible to

**Table 3.** Some conchological characters of genera of Vesicomyidae with elongate shell shape.

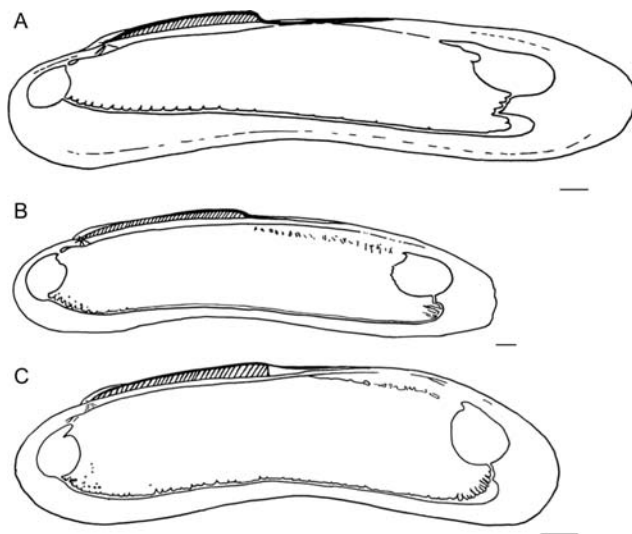
|   | <i>Abyssogena</i> n. gen.                             | <i>Ectenagena</i> Woodring, 1938                   | <i>Adulomya</i> Kuroda, 1931                       | <i>Pleurophopsis</i> Van Winkle, 1919              |
|---|---|--|--|--|
| Type species                                    | <i>Abyssogena southwardae</i><br>n. sp.               | <i>Calyptogena elongata</i> Dall,<br>1916          | <i>Adulomya uchimuraensis</i><br>Kuroda, 1931      | <i>Pleurophopsis unioides</i> Van<br>Winkle, 1919  |
| Maximal shell size for<br>genus (mm)            | 277.4   | 44   | 179.6  | 200  |
| Subumbonal pit                                  | Absent  | Present  | Present  | ?  |
| Start of pallial line                           | From ventral margin of<br>anterior adductor scar      | From posterior margin of<br>anterior adductor scar | From posterior margin of<br>anterior adductor scar | From posterior margin of anterior<br>adductor scar |
| Pallial sinus                                   | Present, small irregular                              | Absent   | ?  | Absent   |
| Secondary attachment<br>scar along pallial line | Present   | Absent   | ?  | Absent   |
| 4-b tooth                                       | Absent or developed less<br>than the other left teeth | Developed less than the<br>other left teeth        | Not reduced compared to the<br>other left teeth    | ?  |



**Figure 3.** *Ectenagena elongata* (Dall, 1916), Albatross, Stn 4432, USNM 110774,  $L = 44$  mm. **A.** Exterior of left valve. **B.** Interior of left valve. **C.** Left hinge plate. **D.** Right hinge plate. Abbreviation: ops, origin of pallial line; sup, subumbonal pit.



**Figure 4.** **A.** *Pleurophopsis unioides* Van Winkle, 1919, Trinidad, Miocene, type locality, NMB 186,  $L = 74$  mm, inner mold, right valve (Gill *et al.*, 2005). **B.** *Adulomya uchimuraensis* Kuroda, 1931, Japan, Shiga-mura, Miocene, inner mold, anterior part of left valve (from Kanno *et al.*, 1998: 27, fig. 10, 5a). Abbreviations: ops, origin of pallial line; vas, ventral margin of anterior adductor scar. Scale bar = 1 cm.



**Figure 5.** Semi-schematic line drawings of the interiors of right valves. **A.** '*Ectenagena*' *extenta* Krylova & Moskalev, 1996, paratype, MNHN. **B.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), paratype, MNHN. **C.** *Abyssogena novacula* n. sp., holotype, MNHN 21462. Scale: 1 cm.

see the outline of the pallial line, which begins at the posterior part of anterior adductor. It is also visible on an image of a specimen of *P. unioides* collected subsequently at the type locality (Fig. 4A; Gill *et al.*, 2005). Considering this description and figures, *Pleurophopsis* differs from *Abyssogena* in the absence

of the pallial sinus and secondary pallial attachments, and by a pallial line originating from the posterior margin of the anterior adductor scar.

The genus *Adulomya* Kuroda, 1931, with type species *A. uchimuraensis* Kuroda, 1931, from the Miocene of Japan, was originally described as completely edentulous and considered to belong to the family Solemyidae (Kanno & Ogawa, 1964; Cox, 1969; Boss & Turner, 1980). A possible close relationship between *A. phaseoliformis* and *Adulomya* was initially suggested by Métivier *et al.* (1986). They pointed out that the edentulous condition of the hinge could be explained by the fact that the type specimen of *A. uchimuraensis* is represented only by an inner mould. Kanno *et al.* (1998) provided a redescription of the type species of *Adulomya* based on new material and demonstrated that it is not edentulous, but has a well-developed hinge structure with teeth: there are two stout cardinal teeth in the right valve and three cardinals in the left. As a consequence, *Adulomya* was transferred to the family Vesicomyidae. It differs from the new genus, *Abyssogena*, by the presence of distinct subumbonal pits (Kanno *et al.*, 1998) and a pallial line originating from the posterior margin of the anterior adductor scar [Kanno *et al.*, 1998: 26, fig. 10 (5a)] (Fig. 4B).

Recently, Kiel (2007) suggested synonymizing all three genera, *Pleurophopsis*, *Adulomya* and *Ectenagena*, on the base of the shell shape and similar dentition. In spite of *Pleurophopsis* having priority as the oldest name, he proposed use of the name *Adulomya* because the holotype of the type species of *Pleurophopsis* described by Van Winkle was lost and the presently known material lacks 'critical hinge details'. Priority of the name *Pleurophopsis* could be reestablished if better preserved material of *P. unioides* becomes available. With regard to the incomplete and badly preserved material of *P. unioides*, which does not allow observation of some details of hinge margin, we agree that at present the species should be regarded as a *nomen dubium*. However, if the type species of the genus *Pleurophopsis* is considered a dubious taxon, the genus itself needs to be regarded as dubious. In this case it is impossible to synonymize *Pleurophopsis* with *Adulomya* as suggested by Kiel (2007). Comparison of the type species of *Ectenagena* and *Adulomya* revealed very similar dentition and shell shape (Kanno *et al.*, 1998). The distinguishing feature of these species is the presence of fine riblets on the ventral margin of *A. uchimuraensis* (Kanno *et al.*, 1998: 20) and a smooth ventral margin of *E. elongata* (Fig. 3). It might be reasonable to synonymize these genera when additional material of *A. uchimuraensis* and *E. elongata* becomes available for study.

#### *Abyssogena southwardae* new species

(Figs 2, 6C, D, 7–13, 14B, E, F, 15B, 28B)

*Calyptogena* n. sp. Clam#2 Peek *et al.*, 1997: 153.

*Calyptogena* n. sp. Olu *et al.*, 1997: 816.

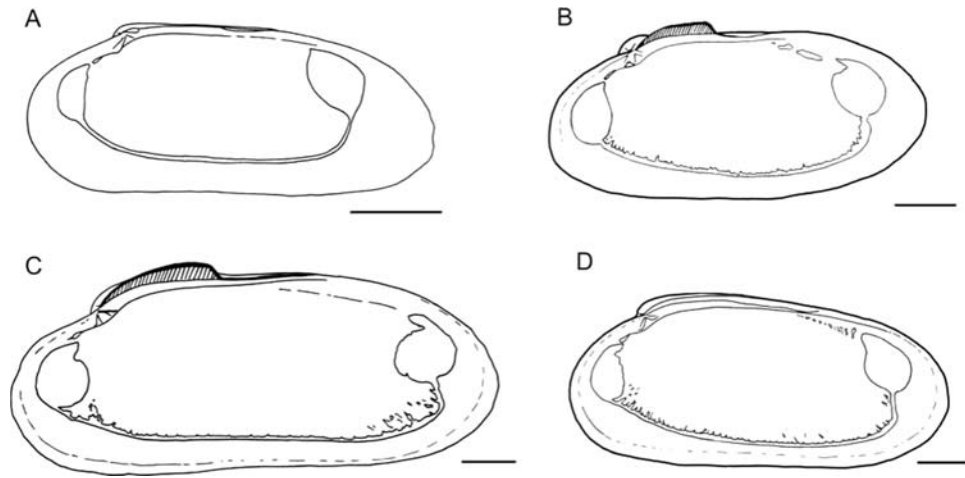
*Ectenagena* sp. aff. *kaikoi* Gebruk *et al.*, 2000: 387, fig. 4.

*Calyptogena* (*Ectenagena*) sp. Southward *et al.*, 2001: 658, fig. 1B.

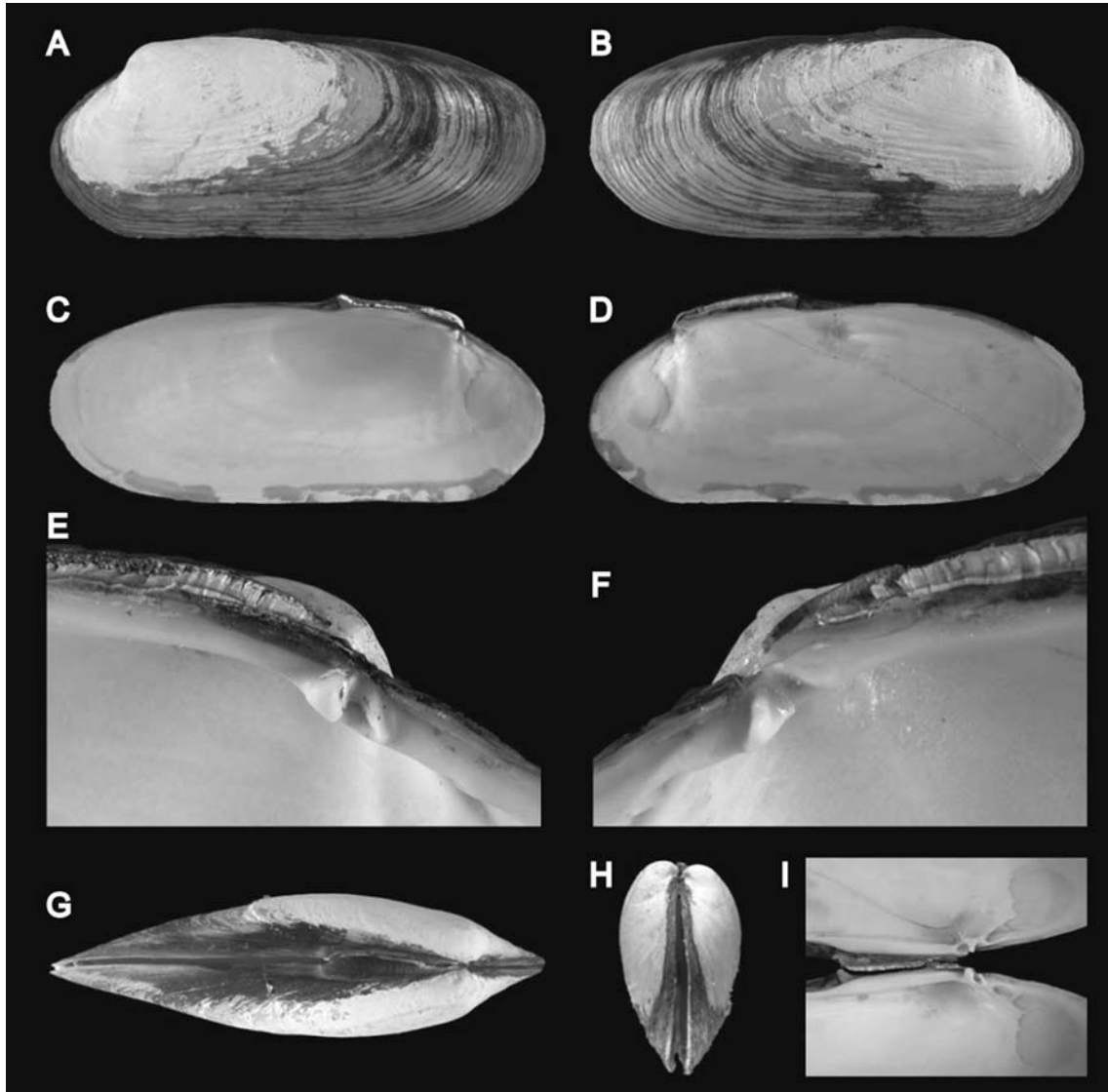
**Etymology:** This species is dedicated to Eve Southward (Marine Biological Association, Plymouth, UK) in acknowledgement of her investigations of the fauna from reducing habitats.

**Type material:** SMF 331775 (holotype, with soft parts); SMF 331776 (paratype, one spm with soft parts; RV *Akademik Mstislav Keldysh*, Stn 3869); SMF 331777 (paratypes, two pairs of conjoined valves; RV *Meteor*, Stn 66); ZMUU Ld-3026 (paratypes, two spms with soft parts; RV *Akademik Mstislav Keldysh*, Stn 3869). Type locality: MAR, Wideawake Mussel Field, 04°48.65'S, 12°22.35'W, 2,985 m (RV *Meteor*, Stn 125).

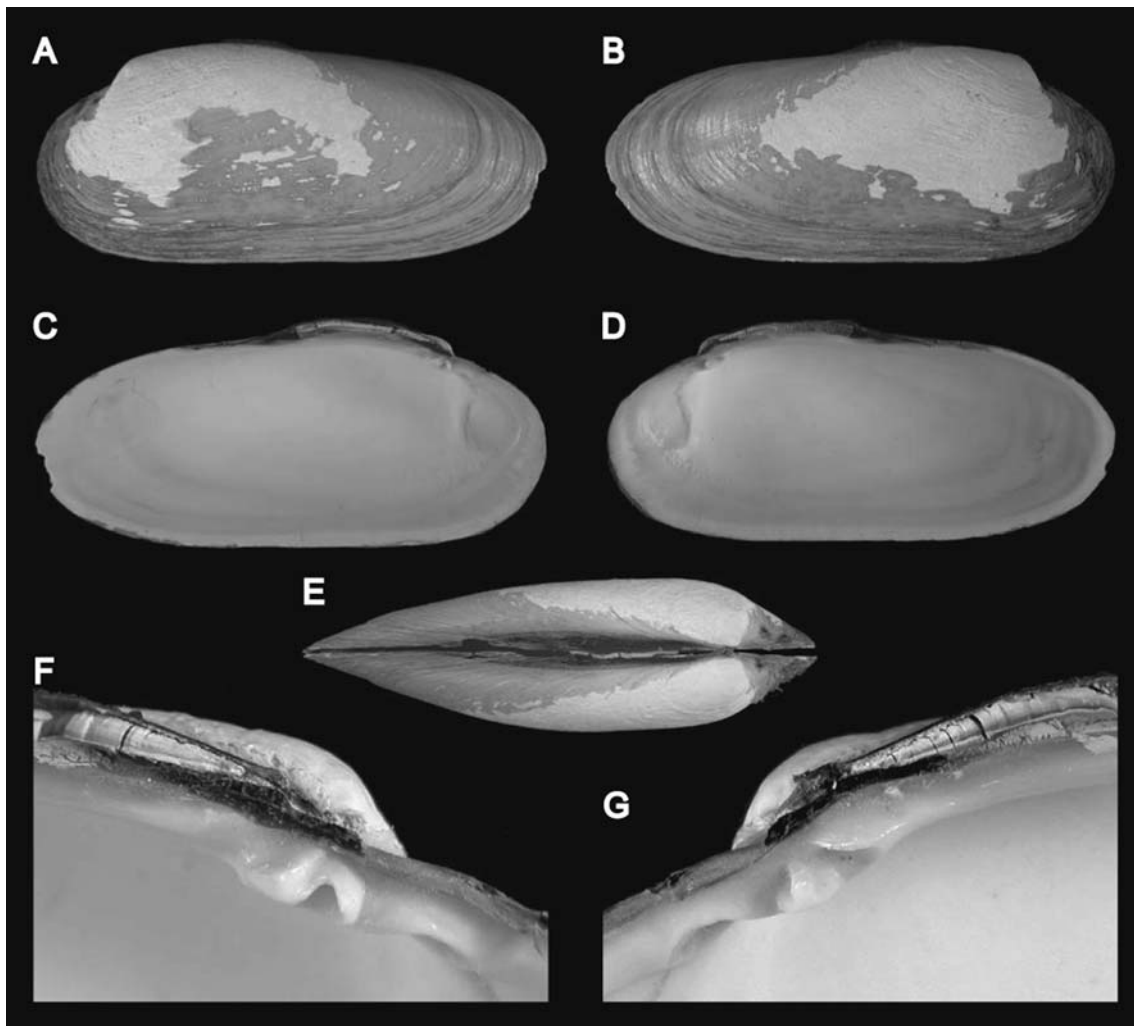
**Material examined:** RV *Advance II*, Stn 11, 45 Ft Sbt, 37°43.22'N, 70°29.24'W (offshore Virginia), 3,710 m, 26 June 1978, one spm with soft parts, USNM 832911. BARENAUT, PL 94,



**Figure 6.** Semi-schematic line drawings of the interiors of right valves. **A.** *Ectenagena elongata* (Dall, 1916), holotype. **B.** *Abyssogena kaikoi* (Okutani & Métiévier, 1986), holotype, MNHN. **C.** *A. southwardae* n. sp., from off Barbados. **D.** *A. southwardae* n. sp., paratype, SMF 331777. Scale bar = 1 cm.



**Figure 7.** *Abyssogena southwardae* n. sp., holotype, SMF 331775, RV *Meteor*-64/1, Stn 125, ROV 7,  $L = 103.4$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view. **I.** Hinge margin of both valves.

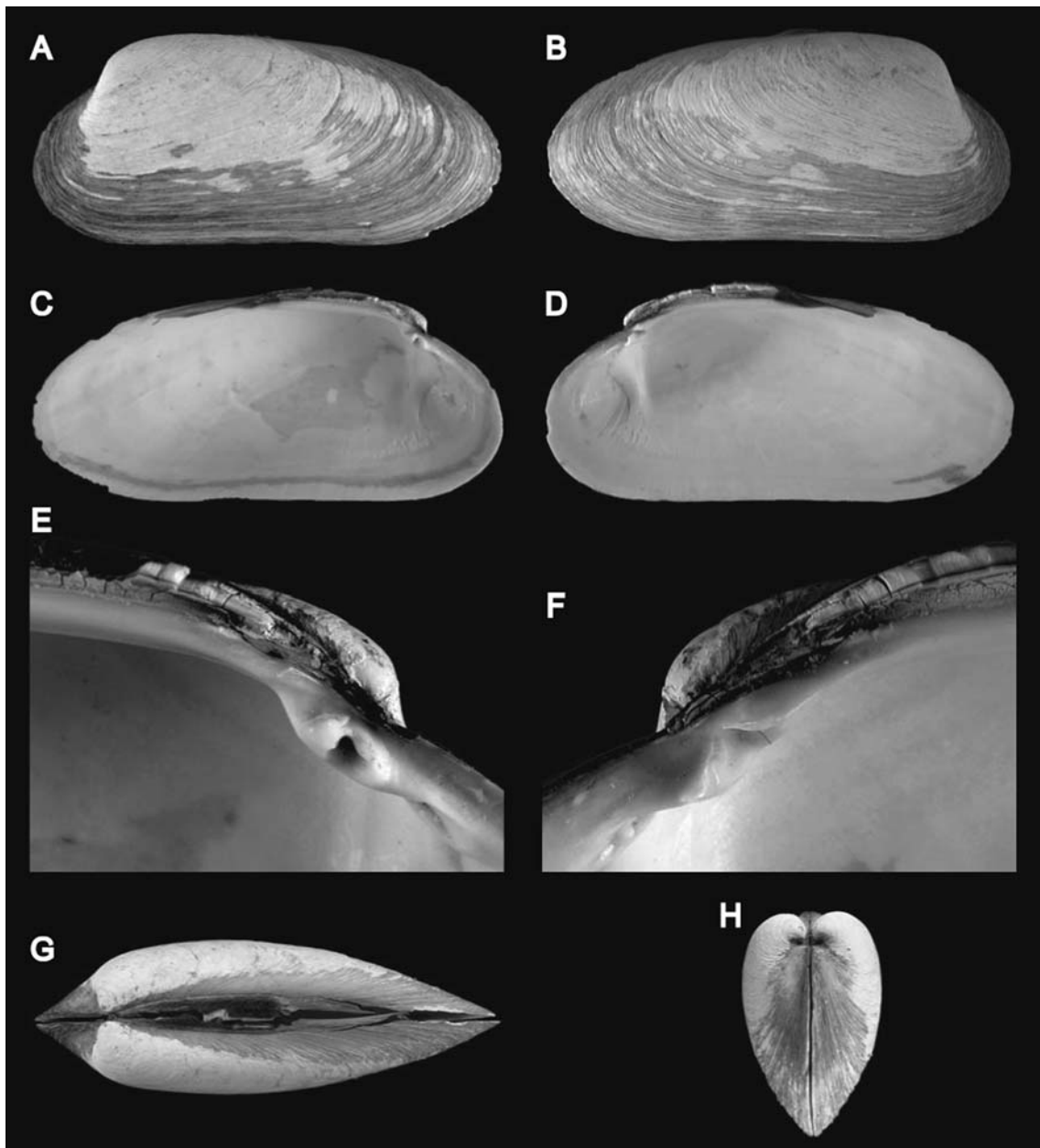


**Figure 8.** *Abyssosgena southwardae* n. sp., RV *Atlantis*, Alvin Dive 3133,  $L = 69.2$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Dorsal view. **F.** Left hinge plate. **G.** Right hinge plate.

13°49'N, 59°37'W (Barbados Accretionary Prism), 4,935 m, 24 September 1987, five spms without soft parts. FARANAUT, Stn FR 08, 15°07.07'N, 44°50.64'W (MAR), 3,424 m, 26 March 1992, broken valve. VEMANAUTE, Stn VE 1, 10°43.51'N, 42°42.98'W (Vema Fracture Zone), 5,107 m, 19 August 1988, one spm without soft parts. RV *Logatchev*, Cruise 7, Logatchev hydrothermal field, July 1994, one broken v. RV *Logatchev*, Cruise 26, 10°42.6'N, 40°57.4'W (Vema Fracture Zone), 4,600–5,100 m, 2005, one broken v. RV *Atlantis*, Alvin, Dive 3133, 14°45.189'N, 44°58.829'W (Anya's Garden, Logatchev area), 3,038 m, 27 July 1997, eight spms with soft parts. RV *Akademik Mstislav Keldysh*, Cruise 41, Stn 3869, MIR 10/232, 14°45.16'N, 44°58.61'W (Anya's Garden, Logatchev), 3,050–2,950 m, 18 November 1998, six spms (including three paratypes). RV *Meteor*, Cruise 60/3, Stn 66, ROV, 14°45.07'–14°45.19'N, 44°58.73'–44°58.75'W (Irina I and II, Logatchev), 3,050–2,950 m, 5 July 2004, 18 valves (including two paratypes). RV *Meteor*, Cruise 64/1, Stn 125, ROV 7, 04°48.65'S, 12°22.35'W (Wideawake Mussel Field), 2,985 m, 12 April 2005, two spms (including holotype). RV *Meteor*, Cruise 66/1, Stn 395, DD, 27°18'N, 17°45'W (off the Canary Archipelago, Henry Seamount), *c.* 3,500 m, 14 August 2005, two left entire valves and eight broken valves. SERPENTINE, RV *Pourquoi-pas*, Stn 315 – 06, Basket 18, 14°45.186'N, 44°58.769'W (Anya's Garden, Logatchev), 3,041 m, 21 March 2007, 2 v.

**Diagnosis:** *Abyssosgena* species with  $L$  to 220 mm, relatively thin-shelled, elongate, in adult specimens  $H/L = 0.37–0.52$ ,  $W/L = 0.11–0.15$ , dorsal and ventral margins nearly straight and sub-parallel to each other, valves somewhat depressed in the central segment, periostracum glossy, ochre coloured with close-set commarginal striae and elevated lamellae in the anterior and middle sectors of shell, prosogyrate low umbo situated at anterior 15–28% of valve length, beaks not enrolled, fibrous layer of ligament occupying 22–29% of valve length and 50–73% of posterior lamellar layer of ligament (Table 4).

**Description of holotype:** Shell medium-sized,  $L = 103.4$  mm, relatively thin-shelled, elongate in outline,  $H/L = 0.40$ , nearly equivalve. Periostracum thin, glossy, ochre coloured, remaining mainly at the periphery and on posterior part of shell, with short, close-set commarginal elevated lamellae developed mostly in the anterior and middle sectors of shell. Sculpture consisting of commarginal striae and inconspicuous radial lines running from umbo to posterior margin. There is a wide very shallow depression running from umbo to the middle of ventral margin. Inequilateral, umbo situated in anterior 20% of valve. Umbones prosogyrate, low; beaks not enrolled, not touching each other. Anterior–dorsal margin short, nearly straight; anterior margin rounded; ventral margin nearly straight with



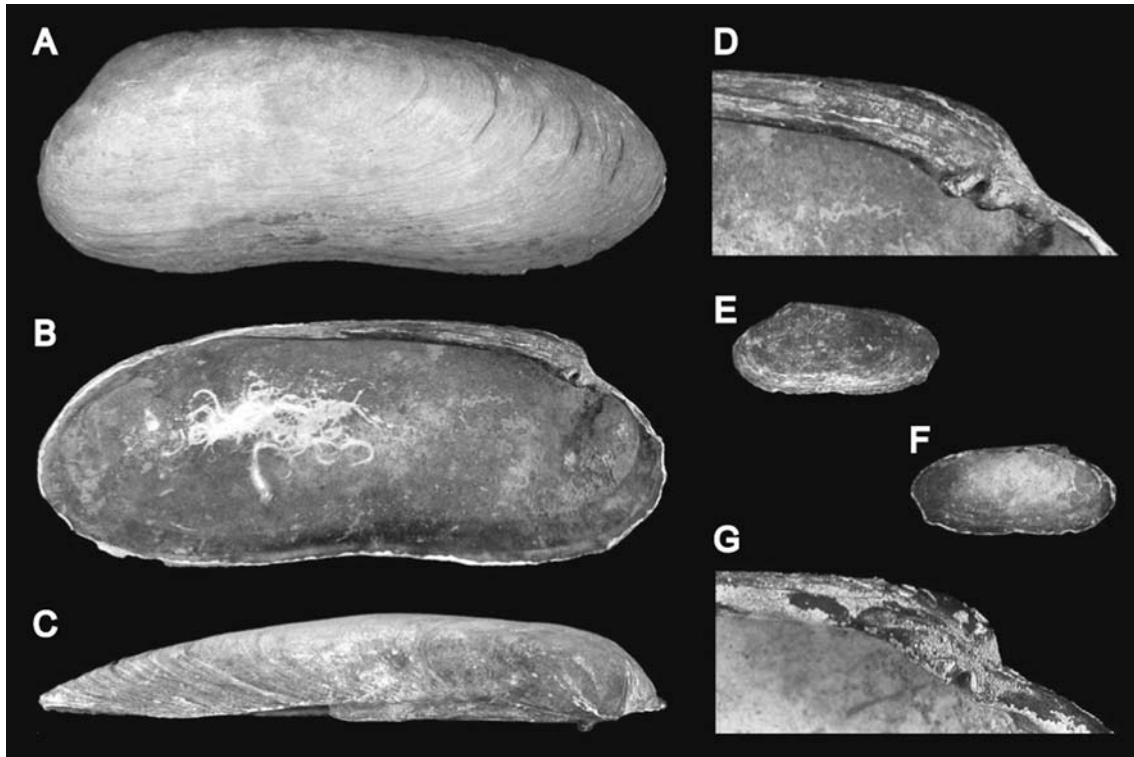
**Figure 9.** *Abyssogena southwardae* n. sp., RV *Advance II*, Stn 11, USNM 832911,  $L = 87.3$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

very slight depression in the middle; posterior margin broadly rounded, dorsal margin nearly straight. Internal shell surface white, with faint commarginal and radial striations. Pallial line slightly impressed anteriorly and hardly discernible posteriorly. Secondary pallial scars in the anterior part of the pallial line present (Fig. 12A). Pallial sinus is an irregular, very shallow indentation below posterior adductor scar (Fig. 12B). Anterior adductor scar ovately conical, somewhat impressed to rear. Posterior adductor scar larger, subcircular, hardly distinct. Anterior pedal retractor scar deeply impressed, located above anterior adductor scar, not fused with it. Posterior pedal retractor not impressed, fused to posterior adductor scar. Nymph weak, with smoothly sloping posterior end. Fibrous layer of ligament occupying 25% of valve length and 56% of posterior lamellar layer. Dentition of right valve (Fig. 2B): ventral cardinal (1) and subumbonal cardinal, consisting only of posterior

ramus (3b). Cardinal 1 upright, strong, wedge-shaped, bluntly pointed, with subtrigonal borders, radiating ventrally. 3b lower, with rather wide base, narrower at the top, anterior margin steeply sloping and the posterior smoothly sloping; radiating posteriorwards. No fusion between teeth 1 and 3b, their ventral parts diverging at about  $90^\circ$ . Dentition of left valve (Fig. 2A): subumbonal cardinal tooth with two rami (2a and 2b) and nearly totally reduced posterodorsal cardinal tooth (4b); 2b-ramus very stout, wedge-shaped, 2a-ramus lower and thinner, proximal part of 2a connected with lateral surface of 2b by low bridge, ventral parts diverge at a bit  $<90^\circ$ .

*Anatomy:* Mantle lobes thin, except at margins. Outer fold is most prominent and deeply folded. It secretes a two-layered periostracum, the outer one secreted within the periostracal groove, and the inner layer within one of the pleats of outer

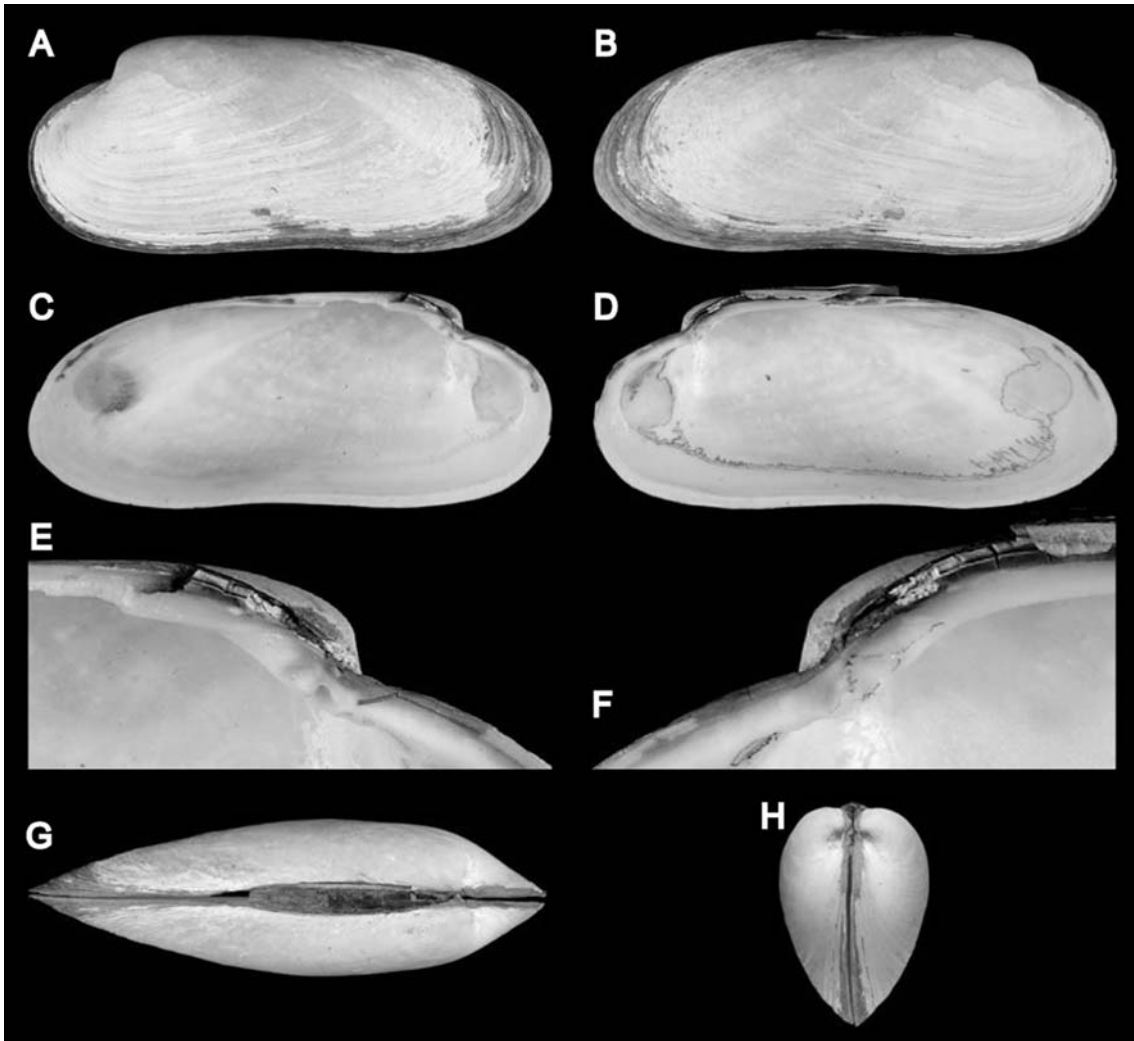




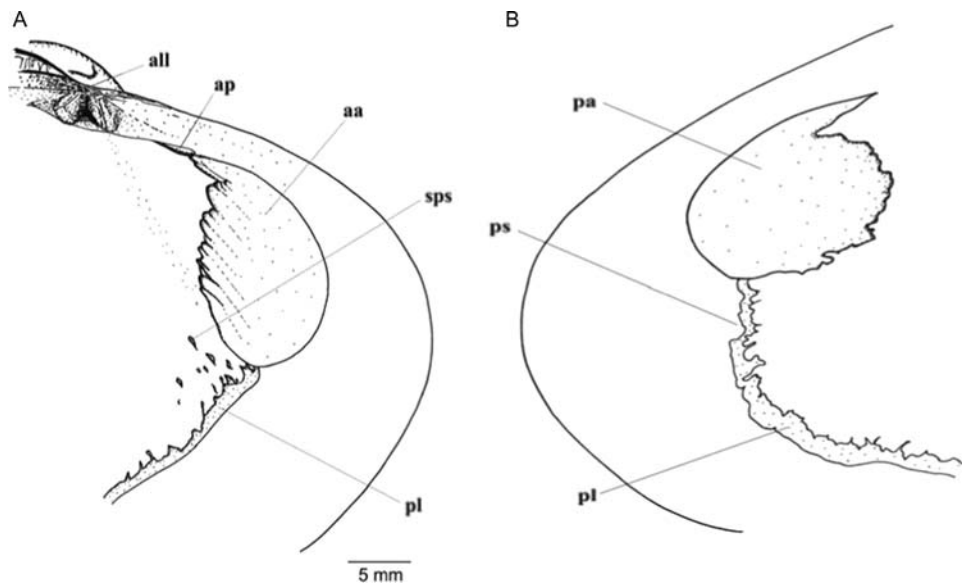
**Figure 10.** *Abyssogena southwardae* n. sp., RV Meteor 66/1, Stn 395. **A–D.**  $L = 148.2$  mm. **A.** Exterior of left valve. **B.** Interior of left valve. **C.** Dorsal view of left valve. **D.** Left hinge plate. **E–G.**  $L = 48.6$  mm. **E.** Exterior of left valve. **F.** Interior of left valve. **G.** Left hinge plate.

mantle fold (Fig. 15B). Middle fold composed of two subfolds, usually the external subfold is thinner, but relative thickness of subfolds changes along mantle margin. Internal subfold of middle fold is papillate anteriorly at level of anterior adductor. Inner fold is nearly inconspicuous forming a low ridge. Along mantle margin there is a vascularized thickening of the mantle lobe extending from anterior to posterior adductors as in all studied vesicomys. Mantle fusion forms three pallial apertures, the pedal gape and two posterior siphonal openings. Pedal gape occupies entire ventral edge from middle of frontal surface of anterior adductor to base of inhalant siphon. The posterior part of mantle including outer and external subfold of middle mantle fold forms a muscularized envelope around siphons. Internal subfold of middle mantle fold with tentacles; it borders both inhalant and exhalant apertures. Margin of inhalant aperture bears one row of small tentacles, the number of rows of tentacles increases in region between the apertures and at ventral margin. Tentacles of exhalant siphon are much shorter. Internally, inhalant siphon has on its dorsal side a ventrally directed, triangular flap of vascularized tissue. The volume of this flap can change and in some specimens it is so large that it nearly entirely closes the lumen of the siphon. Exhalant siphon with an internal, thin, transparent sleeve. Between siphons there is a septum, which joins with dorsal edge of descending lamellae of ctenidia. Anterior and posterior adductor muscles large, posterior muscle oval in section, anterior adductor muscle more elongate. Foot well developed, rugose, very muscular. Short (approximately one-sixth of sole length) and shallow byssal groove lies along mid-ventral line of foot and leads to byssal aperture located slightly anterior to heel. Ctenidia thick, non-plicate, comprising inner single demibranch with descending and ascending lamellae; the ascending lamellae two-thirds of the size of descending lamellae. Filaments of the same lamella connected with each other by

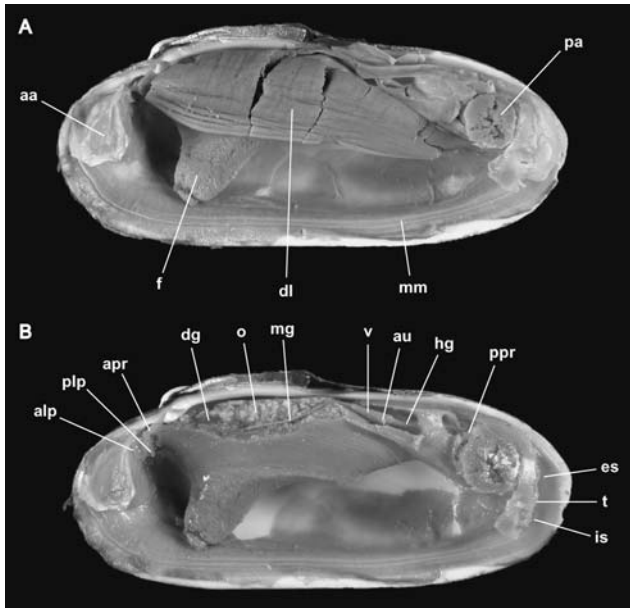
interfilamental junctions. From every filament of both descending and ascending lamellae septum runs towards inside, filling the entire interlamellar space. Approximately every fifth to seventh septum is united with the opposite one connecting descending and ascending lamellae. Every interlamellar septum divided into separate cylindrical tubes at full width of septum (Fig. 14). Outer parts of tubes wider than inner ones; tubes have a bead-like appearance with irregular enlargements and constrictions either along the whole length (Fig. 14E) or only in their inner parts (Fig. 14F). Inner parts of tubes united by thin transparent sheet of tissue. Ventral margin of demibranch with very shallow food groove. Margins of ctenidia fused along its entire length. Anteriorly filaments insert between palps, laterally gill connected by its ctenidial axis with visceral mass and by dorsal margin of ascending lamellae with the foot. Posterior to foot, margin of ascending lamellae fused with each other. Labial palps small; outer palps consist of thickened ridge, running along anteriormost part of ctenidia, inner labial palps smaller. Mouth small, rounded, located beneath the posterior face of anterior adductor, opening into oesophagus which enters the anterior part of thin-walled small stomach. There is no style sac. Gut leaves posterior part of stomach running straight, passing through the visceral mass to the pericardial cavity. Gut penetrating ventricle and ending in an anus located on posterior surface of posterior adductor muscle. Pericardial cavity large, elongate, with thin transparent walls; ventricle thick-walled, muscular, surrounding rectum; auricles thin-walled, with well-developed pericardial glands located on its surface, opening into ventricle approximately in its posterior third. Kidneys located between pericardium and posterior adductor muscle. Large gonads embedded in posterior–dorsal part of visceral mass, adjacent to digestive gland, occupying dorsal part of foot.



**Figure 11.** *Abyssogena southwardae* n. sp., BARESNAUT, PL 94.  $L = 91.6$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.



**Figure 12.** Pallial line in *Abyssogena southwardae* n. sp., holotype. **A.** Anterior region. **B.** Posterior region. Abbreviations: aa, anterior adductor scar; all, anterior lamellar ligament layer; ap, anterior pedal retractor scar; pa, posterior adductor scar; pl, pallial line; ps, pallial sinus; sps, secondary pallial scars.



**Figure 13.** *Abyssogena southwardae* n. sp., RV *Atlantis*, Alvin Dive 3133,  $L = 69.2$  mm. **A.** Body as seen from left. **B.** Body as seen from left, both gills removed. Abbreviations: aa, anterior adductor muscle; alp, anterior labial palps; apr, anterior pedal retractor muscle; au, auricle; dg, digestive gland; dl, descending lamella of demibranch; es, exhalant siphon; f, foot; hg, hindgut; is, inhalant siphon; mm, mantle margin; mg, midgut; o, ovarium; pa, posterior adductor muscle; ppr, posterior pedal retractor muscle; t, tentacles; v, ventricle.

**Variation:** Variation can be seen in shell shape and details of hinge margin. The outline of the shell can be more or less elongate. Dorsal shell margin can be parallel to the ventral margin or can be sloping, and in the latter case posterior part of shell is more tapering. The weak depression running from the umbo to the middle part of ventral margin can be absent in small specimens. The 4b-tooth can be weak or fully reduced. The secondary attachment scars at the inner surface of the shell may have different patterns. Specimens from Barbados, offshore Virginia and Vema Fracture Zone have higher umbo and more enrolled beaks compared to the specimens from the Logatchev and Wideawake fields.

**Distribution:** Central Atlantic Ocean along the MAR at the Logatchev site ( $14^{\circ}45'N$ ), 2,950–3,050 m, north to the Logatchev site ( $15^{\circ}07'N$ ), 3,424 m (valves only), in the region of Vema Fracture Zone ( $\sim 10^{\circ}N$ ), 4,600–5,107 m (valves only) and at the Wideawake Field ( $\sim 5^{\circ}S$ ), 2,985 m. In the eastern Atlantic near the Canary Islands off Henry Seamount (valves only) and in the western Atlantic off Barbados, West Florida Escarpment and offshore of Virginia, 2,985–5,100 m.

**Habitat:** In the MAR *A. southwardae* lived at the so-called Anya's Garden at the periphery of the Logatchev hydrothermal vent area described in detail in Gebruk *et al.* (2000). *Abyssogena southwardae* co-occurred with two species of Thyasiridae and *Bathymodiolus puteoserpentis* Cosel, Métivier & Hashimoto, 1994, but the different bivalve species were always encountered in separate clusters. While mytilids were observed in shimmering waters with temperatures several degrees above ambient bottom water, vesicomylid and thyasirid bivalves were not seen in shimmering waters, suggesting that they avoid zones of highest hydrothermal flow. In 1997, the highest density of *A. southwardae* reached 120 individuals per metre square. Recent scientific dives at Logachev hydrothermal vent reported only dead specimens of *A. southwardae*, suggesting

mass extinction perhaps due to a change in the hydrothermal activity (A. Gebruk, personal communication). In 2005, living specimens of *A. southwardae* were discovered at the Wideawake field with diffusive venting through jumbled sheet flow (Haase *et al.*, 2007). *Abyssogena southwardae* occurred with *B. puteoserpentis* and white filamentous bacteria but they were spatially segregated. The fluids that are expelled at the Wideawake field are strongly diluted by seawater compared to those that exit from the high-temperature black smoker vents. In the region of the MAR, *A. southwardae* was collected also in the Vema Fracture Zone with a maximal depth of 5,107 m; as yet there are no data concerning hydrothermal activity in that area. Near the Canary Islands shells of *A. southwardae* have been dredged along with hydrothermally altered trachytic rocks, barite, carbonate and soft sediments at Henry Seamount, which is a 126-million-year-old volcanic structure southeast of El Hierro (Klügel *et al.*, 2007). The clams and barite may be interpreted as evidence for hydrothermal circulation but details on the habitat are unknown so far. In the western Atlantic *A. southwardae* occurs at mud volcanoes located in the Barbados Trench. This species dominates the communities and can form beds of up to  $12\text{ m}^2$  with mean density up to 50 ind./ $\text{m}^2$  and maximum density up to 150 ind./ $\text{m}^2$  (Olu *et al.*, 1997). The habitat of *A. southwardae* from offshore Virginia is unknown.

**Remarks:** In spite of the fact that we have only one specimen from offshore Virginia and two entire valves from the Canary Islands and so cannot estimate the morphological variability of these populations, we suggest with a high level of probability that both these forms are conspecific with *A. southwardae*. Specimens of *A. southwardae* collected at different sites along MAR including the Logatchev site, the region of Vema Fracture Zone and the Wideawake Field appear to have a wide range of variability, and all available Atlantic specimens fit this range. The considerably more anterior placement of the umbo and a relatively longer fibrous part of the ligament in the valve from the Canary Islands could be related to allometric changes, since this valve is the longest measured.

In shell shape the new species is similar to *A. kaikoi*, from which it differs by the relatively more elongate fibrous layer of the ligament, weaker 4b-tooth in the left valve, less inflated umbo and less enrolled beaks (Table 8).

***Abyssogena novacula* new species**

(Figs 5C, 16, 17)

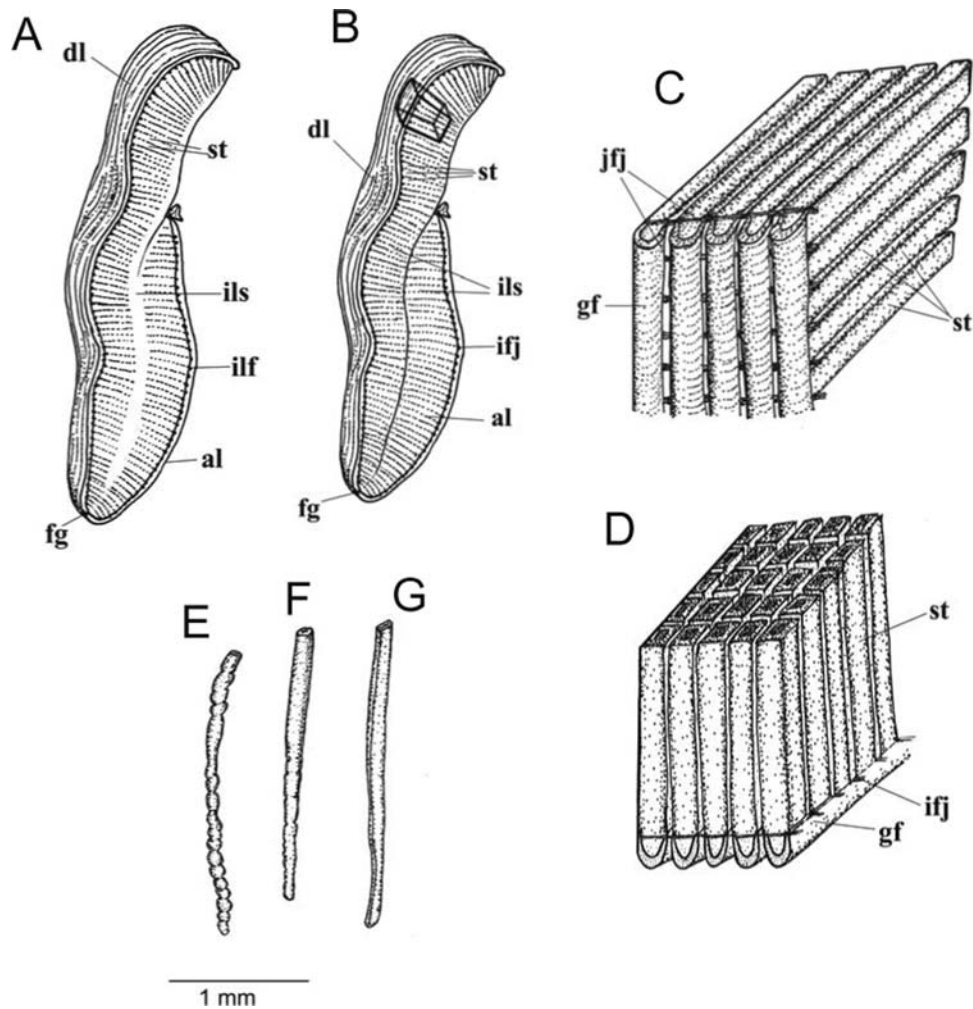
*Calyptogena* n. sp. 1 Olu *et al.*, 1996: 115, fig. 5A.

**Etymology:** Novacula (Latin): razor, named after the shell shape. Name used as noun in apposition.

**Type material:** MNHN 21462 (holotype, with soft parts); MNHN 21463 (three paratypes: spm with soft part; right valve intact, left valve broken, with soft parts; left valve intact, right valve broken, without soft parts). Type locality: East Pacific Ocean, Peru Trench,  $10^{\circ}02.2'S$ ,  $80^{\circ}08.3'W$ , 5,528 m, 2 April 1991 (NAUTIPERC, *Nautila*, dive PL-18).

**Material examined:** Type material. NAUTIPERC, R/V *Nadir*, submersible *Nautila*, dive PL-18,  $10^{\circ}02.2'S$ ,  $80^{\circ}08.3'W$ , 5,528 m, 2 April 1991, fragments of broken spms, partly with soft parts.

**Diagnosis:** *Abyssogena* species with  $L$  to 277.4 mm, thin-shelled, strongly elongate, in adult specimens  $H/L = 0.21-0.32$ ,  $W/L = 0.08-0.10$ , dorsal margin slightly convex, ventral margin concave, shell widening towards the posterior third, with light brownish periostracum with close-set commarginal striae and elevated lamellae at the periphery, umbones low, prosogyrate, situated at anterior 9–15% of valve length; fibrous layer of



**Figure 14.** Diagrammatic views of gills of *Abyssogena*. **A, B.** Transverse section through medial part of ctenidia. **A.** *Abyssogena phaseoliformis*. The medial part of interlamellar septum is not divided into separate tubes. **B.** *Abyssogena southwardae*. Interlamellar septum is divided into tubes at its whole width. **C, D.** Block diagrams of part of descending lamella of demibranch. **C.** Lateral view. **D.** Dorsal view. **E–G.** Separate tubes comprising interlamellar septum in different species. **E, F.** *Abyssogena southwardae*. **G.** *Abyssogena phaseoliformis*. Abbreviations: al, ascending lamella; dl, descending lamella; fg, food groove; gf, gill filament; ifj, interfilamental junctions; ils, interlamellar septum, composed of separate tubes (st).

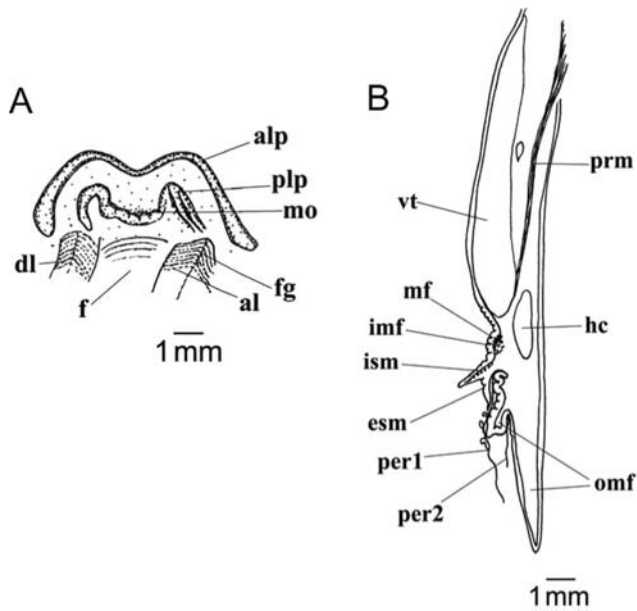
ligament occupying 26–40% of valve length and 55–69% of posterior lamellar layer of ligament (Table 5).

*Description of holotype:* Shell large,  $L = 158.2$  mm, relatively thin-shelled, strongly elongate in outline,  $H/L = 0.27$ , nearly equivalve. Periostracum thin, brownish, persistent mainly on ventral posterior area, with short commarginal elevated lamellae. Sculpture of commarginal striae and inconspicuous radial lines running from umbo to posterior margin. Very shallow and broad depression running from umbo to middle ventral margin. Inequilateral, umbones situated in anterior 15% of valves, prosogyrate, low; beaks pointed forward. Anterior–dorsal margin short, convex; anterior margin rounded, ventral margin concave. Posterior margin slightly tapering; posterior–dorsal margin straight proximally and convex distally with obtuse angle between these two parts. Shell widening towards its posterior third, where the maximum height ( $H_{um}/H_{max} = 0.91$ ) is situated. Internal shell surface white, with faint commarginal and radial striations. Row of small pallial scars running from umbonal cavity to posterior pedal retractor scar. Pallial line distinct, anteriorly impressed. Pallial sinus an irregular, very shallow indentation below posterior adductor scar (Fig. 5C). Well-developed secondary pallial scars present in anterior

part of pallial line near anterior adductor scar. Anterior adductor scar ovately conical, somewhat impressed to rear. Posterior adductor scar larger, suboval, well impressed at its anterior limit. Anterior pedal retractor scar deeply impressed, located above anterior adductor scar, not fused with it. Posterior pedal retractor slightly impressed, fused to posterior adductor scar. Nymph weak, with smoothly sloping posterior end. Fibrous layer of ligament occupying 34% of valve length and 60% of posterior lamellar layer.

Dentition of right valve: ventral cardinal (1) and subumbonal cardinal, consisting only of posterior ramus (3b). Cardinal 1 strong, wedge-shaped, pointed, radiating ventrally. 3b lower, thinner, radiating posteriorwards. No fusion between 1 and 3b, their ventral parts diverging at  $<90^\circ$ . Dentition of left valve: subumbonal cardinal with two rami (2a and 2b), posterodorsal cardinal (4b) absent. 2b-ramus very stout, wedge-shaped, upright, radiating posteriorwards; 2a-ramus lower and thinner, proximal part of 2a connected with lateral surface of 2b by low bridge, ventral parts diverge at  $<90^\circ$ .

*Anatomy:* All characters of genus. Interlamellar septum of gills consisting of more or less rectangular tubes. Margin of inhalant aperture bearing two rows of tentacles, the outer one consisting of larger and sometimes branching tentacles, those of inner



**Figure 15.** Anatomical details of *Abyssogena*. **A.** *Abyssogena phaseoliformis*. Ventral view of the labial palps. **B.** *Abyssogena southwardae*. Transverse section through mantle margin. Abbreviations: al, ascending lamella; alp, anterior labial palps; dl, descending lamella; esm, external subfold of middle mantle fold; f, foot; fg, food groove; hc, haemocoel; imf, inner mantle fold; ism, internal subfold of middle mantle fold; mf, muscle fibres; mo, mouth; omf, outer mantle fold; per1, outer layer of periostracum; per2, inner layer of periostracum; plp, posterior labial palps; prm, pallial retractor muscle; vt, vascularized thickening.

circle smaller. Margin of exhalant siphon bearing one row of quite small tentacles.

**Variation:** In left valve, cardinal 2a can be reduced. Shell may widen towards posterior to different degrees,  $H_{um}/H_{max}$  varying from 0.84 to 0.91. In some specimens a narrow central part of interlamellar septum is not divided into cylindrical channels, similar to gills of *A. phaseoliformis*, while some have interlamellar septum entirely divided into tubes.

**Table 4.** Measurements of right valves of *Abyssogena southwardae* n. sp.

|                                    | L (mm) | H (mm) | W (mm) | F (mm) | N (mm) | H/L  | W/L  | F/N  | F/L  | N/L  | Um (%) |
|------------------------------------|--------|--------|--------|--------|--------|------|------|------|------|------|--------|
| <b>MAR</b>                         |        |        |        |        |        |      |      |      |      |      |        |
| Holotype, SMF 331775               | 103.4  | 41.0   | 12.4   | 25.6   | 45.7   | 0.40 | 0.12 | 0.56 | 0.25 | 0.44 | 20     |
| RV <i>Atlantis</i> , Dive 3133     | 85.1   | 31.6   | 9.5    | 23.5   | 39.2   | 0.37 | 0.11 | 0.60 | 0.28 | 0.46 | 20     |
| Paratype, SMF 336777a              | 71.9   | 32.3   | 9.3    | 20.9   | 35.9   | 0.45 | 0.13 | 0.58 | 0.29 | 0.50 | 20     |
| RV <i>Atlantis</i> , Dive 3133     | 69.2   | 29.2   | 8.9    | 20.1   | 36.0   | 0.43 | 0.13 | 0.56 | 0.29 | 0.52 | 21     |
| Paratype, SMF 331777b              | 59.8   | 27.8   | 7.8    | 16.3   | 26.6   | 0.47 | 0.13 | 0.61 | 0.27 | 0.44 | 23     |
| RV <i>Meteor</i> , Stn 66          | 44.6   | 23.0   | 6.8    | 9.8    | 18.6   | 0.52 | 0.15 | 0.53 | 0.22 | 0.42 | 28     |
| RV <i>Meteor</i> , Stn 66          | 38.3   | 18.8   | 5.9    | 8.7    | 17.3   | 0.49 | 0.15 | 0.50 | 0.23 | 0.45 | 26     |
| <b>Barbados Accretionary Prism</b> |        |        |        |        |        |      |      |      |      |      |        |
| BARESNAUT, Pl. 94/3                | 127.0  | 52.5   | 15.7   | 37.3   | 60.0   | 0.43 | 0.12 | 0.62 | 0.29 | 0.47 | 20     |
| BARESNAUT, Pl. 94/3                | 92.2   | 39.3   | 12.0   | 23.5   | 39.0   | 0.43 | 0.11 | 0.60 | 0.25 | 0.42 | 22     |
| BARESNAUT, Pl. 94/3                | 91.6   | 38.0   | 11.7   | 23.0   | 40.0   | 0.41 | 0.13 | 0.58 | 0.25 | 0.44 | 21     |
| <b>Off Virginia</b>                |        |        |        |        |        |      |      |      |      |      |        |
| RV <i>Advance II</i> , Stn 11      | 87.3   | 38.6   | 12.0   | 26.8   | 45.0   | 0.44 | 0.14 | 0.60 | 0.31 | 0.52 | 19     |
| <b>Off Canary Islands</b>          |        |        |        |        |        |      |      |      |      |      |        |
| RV <i>Meteor</i> , Stn 395, N1     | 148.2  | 54.7   | 19.0   | 56.1   | 76.7   | 0.38 | 0.15 | 0.73 | 0.38 | 0.52 | 15     |
| N2                                 | 48.6   | 21.8   | 6.3    | 11.7   | 21.9   | 0.45 | 0.13 | 0.53 | 0.24 | 0.45 | 25     |

**Distribution:** East Pacific Ocean: Peru Trench, 3,500–5,528 m (Olu *et al.*, 1996).

**Habitat:** *Abyssogena novacula* occurs at cold seeps at the lower slope of the tectonically active continental margin. Clam clusters of 10–100 large individuals were observed mostly in sediments along the widely fractured bare cliffs (Olu *et al.*, 1996).

**Remarks:** This species is obviously closely related to *A. phaseoliformis*, from which it differs by shell shape. The shell of *A. novacula* is more widening towards the posterior: in *A. novacula*  $H_{um}/H_{max} = 0.84–0.91$ , whereas in adult *A. phaseoliformis*  $H_{um}/H_{max} = 0.94–1.0$ . For differences among all species of *Abyssogena* see Table 8.

***Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986)**

(Figs 1, 5B, 18–23, 28A)

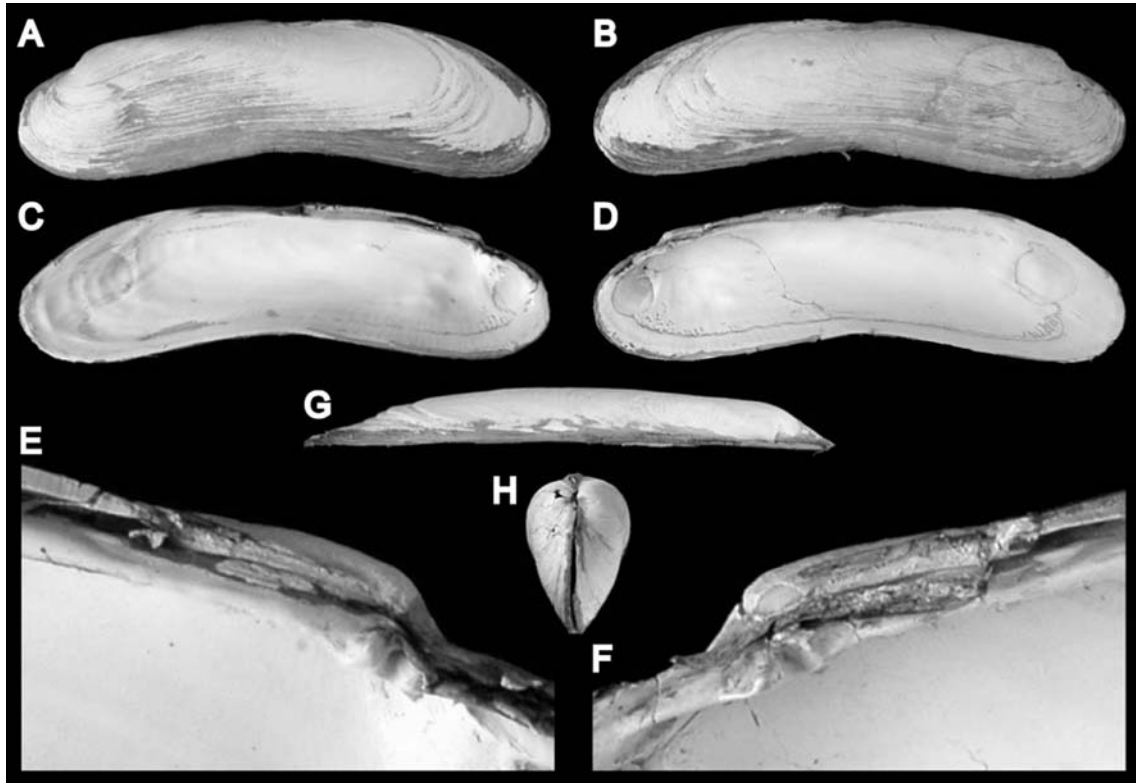
*Calyptogena* (*Ectenagena*) *phaseoliformis* Métivier *et al.*, 1986: 162, fig. 1, pls 1, 2. Okutani *et al.*, 2000: 96. Sasaki *et al.*, 2005: 101, fig. 8A, B.

*Calyptogena phaseoliformis*—Horikoshi, 1989: 156, pl. IV, figs 3, 7, 8.

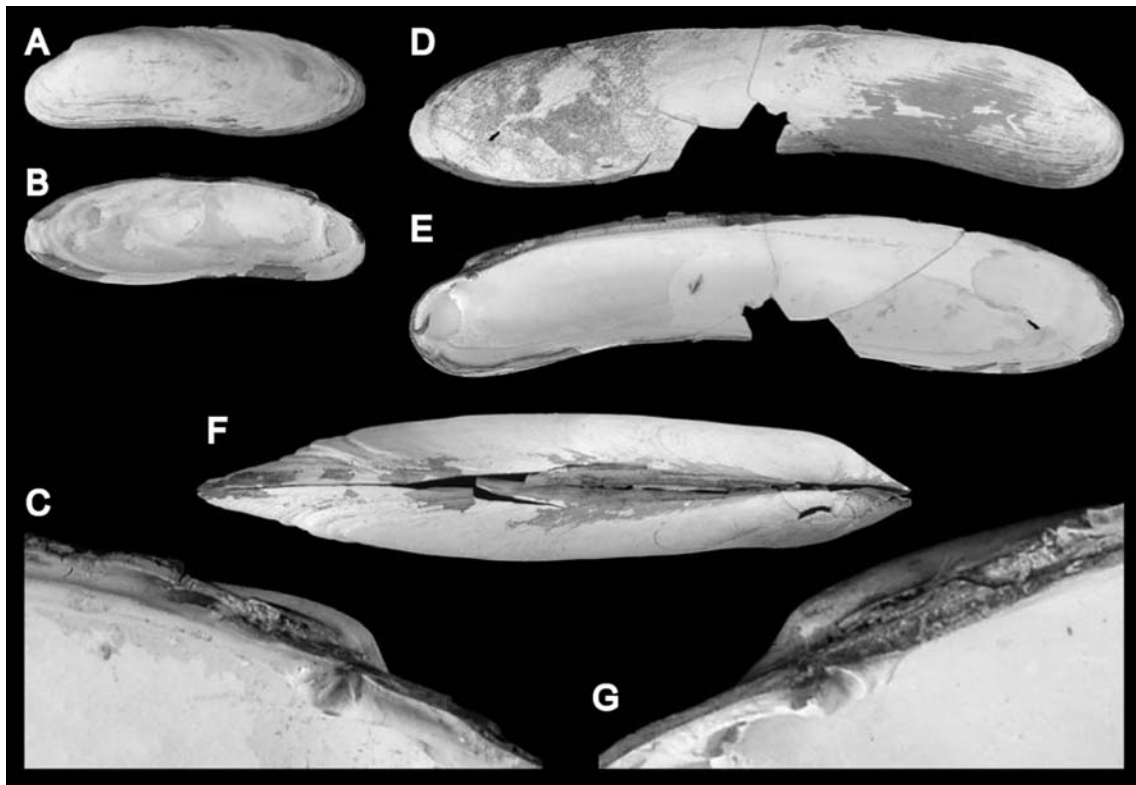
*Calyptogena* n. sp. (Aleutian) Peek *et al.*, 2000: 145.

**Type material:** USMT Mo 64164 (holotype); USMT Mo 64165 (paratype, spm without soft parts); MNHN (four paratypes, spms without soft parts). Type locality: West Pacific Ocean, Japan Trench, 35°54.2'N, 142°30.7'E, 5,640–5,695 m, 22 July 1985 (KAIKO, *Nautila*, dive KD-14).

**Material examined:** Type material: paratype, USMT Mo 64165, type locality; two paratypes, MNHN, KAIKO, *Nautila*, dive KD-18, 40°06.3'N, 144°10.6'E, 5,653–5,960 m, 31 July 1985; two paratypes, MNHN, type locality. Other material: KAIKO 85, KR 98-07, 40°06.4'N, 144°11.2'E, 6,329 m, 2 August 1998, one spm. RV *Vityaz*, Cruise 45, Stn 6096-2, TS, 57°18.0'N, 148°45.8'W, 4,190 m, 9 May 1969, five spms (juv). RV *Sonne*, Cruise 97, Stn 22, TVG, 57°26.6'N, 148°01.28'W, 4,740 m, 31 July 1994, five spms; Stn 66, TVG, 57°26.79'N, 147°59.98'W, 4,982 m, 10 August 1994, 38 spms, 30 spms without soft parts, 26 broken spms without soft parts, 11 v, fragments. RV *Sonne*, Cruise 110, Stn 23/1, *Ropos*, dive 344; 57°27.3'N, 147°59.7'W, 4,947 m, 23 July 1996, one fragment; Stn 24/1, TVG, 57°27.39'N, 148°00.01'W, 4,890 m, 24 July 1996, one broken spm, 2 v, fragments; Stn 28/2, TVG, 57°27.25'N, 147°59.67'W,



**Figure 16.** *Abyssogena novacula* n. sp., holotype, MNHN 21462, NAUTIPERC, *Nautila*, dive PL-18,  $L = 158.2$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view of left valve. **H.** Anterior view.



**Figure 17.** *Abyssogena novacula* n. sp., paratypes, MNHN 21463, NAUTIPERC, *Nautila*, dive PL-18. **A–C.**  $L = 132.4$  mm. **A.** Exterior of left valve. **B.** Interior of left valve. **C.** Left hinge plate. **D–G.**  $L = 277.4$  mm. **D.** Exterior of right valve. **E.** Interior of right valve. **F.** Dorsal view. **G.** Right hinge plate.

**Table 5.** Measurements of valves of *Abyssogena novacula* n.sp.

|                         | <i>L</i><br>(mm) | <i>H</i> <sub>um</sub><br>(mm) | <i>H</i> <sub>max</sub><br>(mm) | <i>W</i> <sub>um</sub><br>(mm) | <i>W</i> <sub>max</sub><br>(mm) | <i>F</i><br>(mm) | <i>N</i><br>(mm) | <i>H</i> <sub>max</sub> /<br><i>L</i> | <i>W</i> <sub>max</sub> /<br><i>L</i> | <i>H</i> <sub>um</sub> /<br><i>H</i> <sub>max</sub> | <i>F</i> / <i>N</i> | <i>F</i> / <i>L</i> | <i>N</i> / <i>L</i> | Um<br>(%) |
|-------------------------|------------------|--------------------------------|---------------------------------|--------------------------------|---------------------------------|------------------|------------------|---------------------------------------|---------------------------------------|---|---------------------|---------------------|---------------------|-----------|
| Holotype, MNHN, right v | 158.2            | 38.6                           | 42.6                            | 12.3                           | 13.2                            | 53.5             | 90.0             | 0.27                                  | 0.08                                  | 0.91  | 0.60                | 0.34                | 0.57                | 15        |
| Paratype, MNHN, right v | 277.4            | 47.9                           | 56.9                            | 17.6                           | 24.1                            | 112.0            | 163.0            | 0.21                                  | 0.09                                  | 0.84  | 0.69                | 0.40                | 0.59                | 9         |
| Paratype, MNHN, right v | 180.0            | 44.5                           | 52.1                            | 13.7                           | 18.6                            | 56.5             | 92.7             | 0.29                                  | 0.10                                  | 0.85  | 0.61                | 0.31                | 0.52                | 13        |
| Paratype, MNHN, left v  | 132.4            | 35.3                           | 41.9                            | 10.9                           | 13.4                            | 34.2             | 62.2             | 0.32                                  | 0.10                                  | 0.84  | 0.55                | 0.26                | 0.47                | 15        |

4,867 m, 28 July 1996, one broken spm without soft parts, one pair of conjoined valves, 6 v, fragments; Stn 40/1, TV box corer, 54°18.17'N, 157°11.82'W, 4,808 m, 2 August 1996, three pairs of conjoined valves (juv), fragments (juv); Stn 43/1, TVG, 54°18.19'N, 157°11.93'W, 4,810 m, 3 August 1996, one juv spm without soft parts, one broken spm without soft parts; Stn 48/1, TVG, 54°18.06'N, 157°11.89'W, 4,877 m, 8 August 1996, nine spms without soft parts (of different age), fragments of valves; Stn 49/1, TV box corer, 54°18.05'N, 157°12.11'W, 4,809 m, 8 August 1996, three juv spm without soft parts; Stn 63/1, TVG, 57°27.33'N, 148°01.27'W, 4,774 m, 13 August 1996, one spm, two spms without soft parts, 12 broken spms without soft parts, a lot of fragments of valves; Stn 64/1, TVG, 57°29.34'N, 148°01.01'W, 4,550 m, 14 August 1996, two broken spm without soft parts.

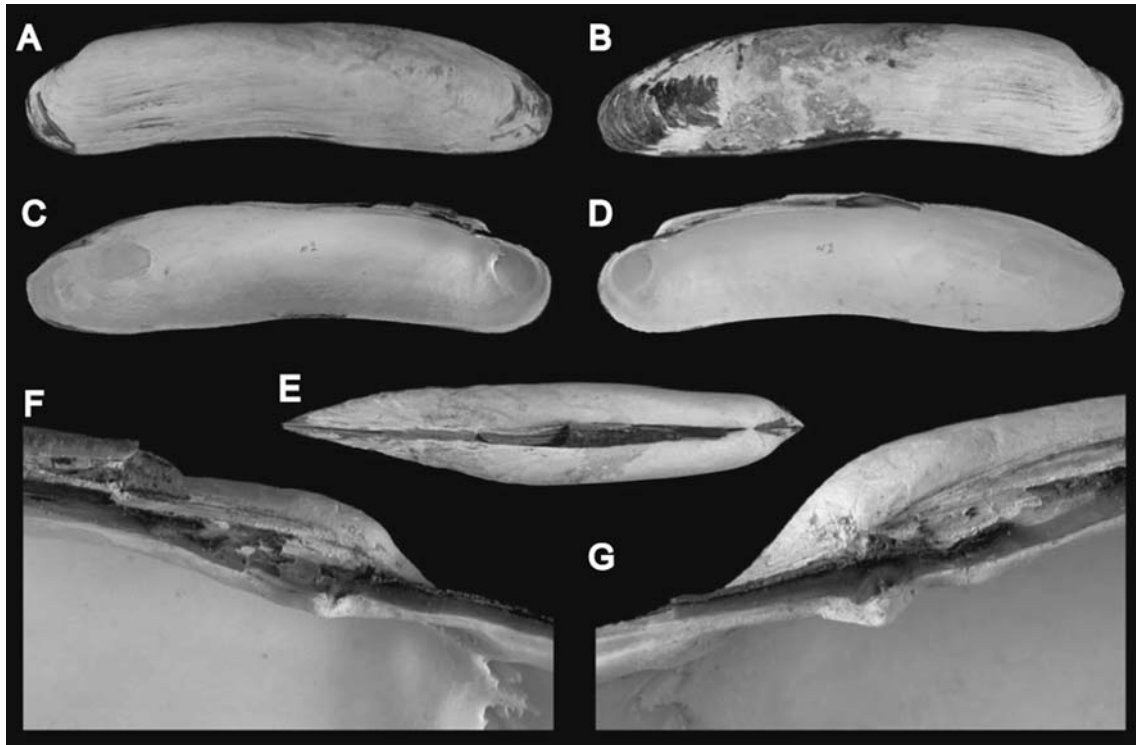
**Diagnosis:** *Abyssogena* species with *L* to 180 mm, thin-shelled, strongly elongate, in adult specimens *H*/*L* = 0.19–0.23, *W*/*L* = 0.08–0.10, dorsal margin slightly convex, ventral margin

concave, dorsal and ventral margins nearly parallel to each other, with light brownish periostracum with close-set commarginal striae and elevated lamellae at periphery, prosogyrate, low umbo situated at anterior 12–14% of valve length, beaks not enrolled, fibrous layer of ligament occupying 30–38% of valve length and 65–76% of posterior lamellar layer (Table 6).

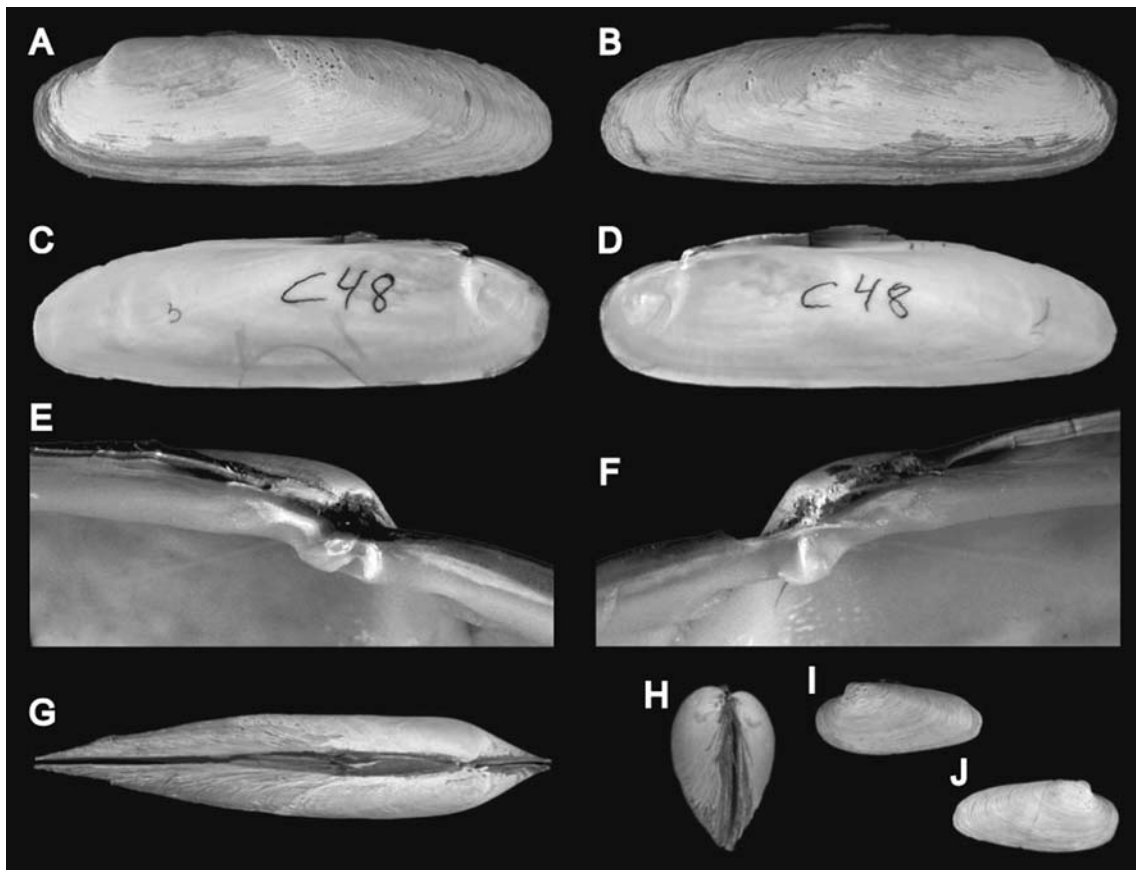
**Description:** Shell large, *L* to 180 mm, thin-shelled, strongly elongate in outline, *H*/*L* = 0.19–0.23, nearly equi-valve. Periostracum thin, brownish, remaining only on narrow peripheral area, with short commarginal elevated lamellae. Sculpture consisting of very close-set commarginal striae and inconspicuous radial lines running from umbo to posterior margin. Posterior sector of shell separated from middle one by a keel running from umbo to ventro-posterior margin. Inequilateral, umbo situated in anterior 12–14% of valve. Umbones prosogyrate, low; beaks not enrolled, touching each other. Anterior–dorsal margin short, convex; anterior margin



**Figure 18.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), paratype, NSMT Mo 64165, KAIKO, *Nautilé*, KD-14, *L* = 153.4 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

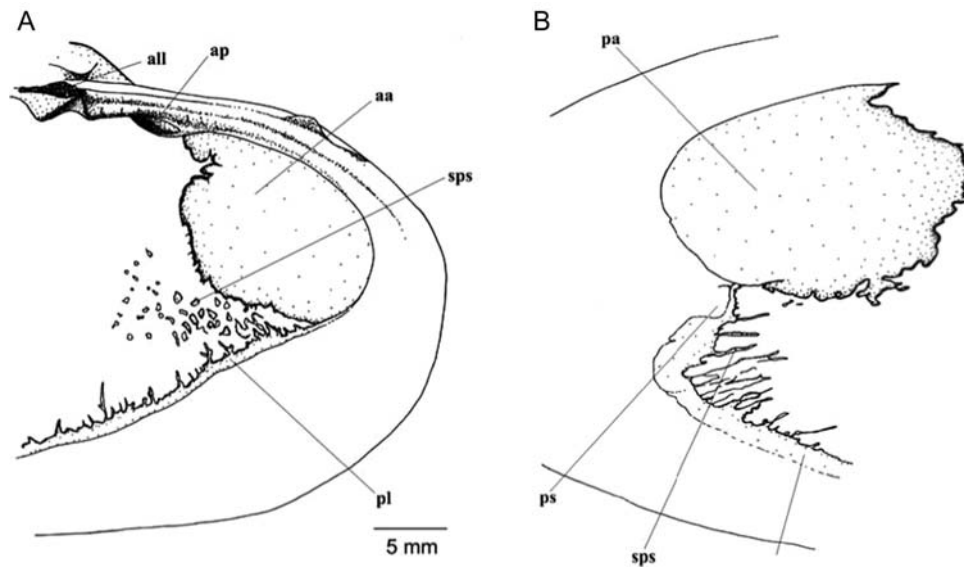


**Figure 19.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), RV *Sonne*-110, Stn 28/2,  $L = 179.0$  mm, University of Bremen. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Dorsal view. **F.** Left hinge plate. **G.** Right hinge plate.

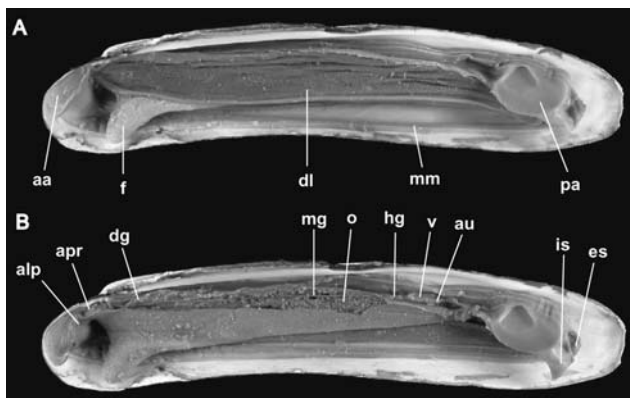


**Figure 20.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), **A–H.** RV *Sonne*-110, Stn 48,  $L = 60.8$  mm, University of Bremen. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view. **I, J.** RV *Sonne*-110, Stn 49,  $L = 18.5$  mm. **I.** Exterior of left valve. **J.** Exterior of right valve.





**Figure 21.** Pallial line in *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), RV *Sonne-97*, Stn 66, *L* = 156 mm, University of Bremen. **A.** Anterior region. **B.** Posterior region. Abbreviations: aa, anterior adductor scar; all, anterior lamellar ligament layer; ap, anterior pedal retractor scar; pa, posterior adductor scar; pl, pallial line; ps, pallial sinus; sps, secondary pallial scars.



**Figure 22.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986). RV *Sonne-97*, Stn 66, *L* = 180 mm, University of Bremen. **A.** Body as seen from left. **B.** Body as seen from left, left gill removed. Abbreviations: aa, anterior adductor muscle; alp, anterior labial palps; apr, anterior pedal retractor muscle; au, auricle; dg, digestive gland; dl, descending lamella of demibranch; es, exhalant siphon; f, foot; hg, hindgut; is, inhalant siphon; mm, mantle margin; mg, midgut; o, ovary; pa, posterior adductor muscle; v, ventricle.

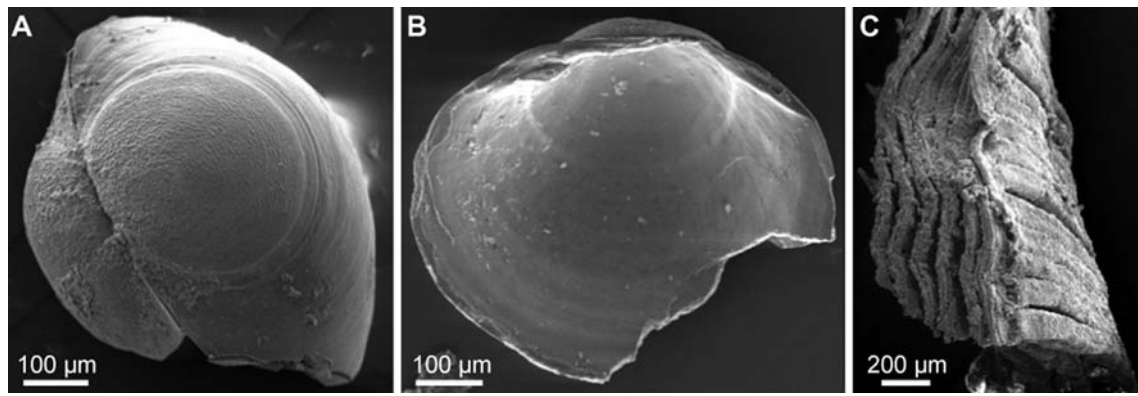
rounded, ventral margin concave. Posterior margin rounded, but more tapering than anterior one; posterior–dorsal margin straight proximally and convex distally. Internal shell surface white. There is a sulcus running from umbonal cavity to anteriormost point of posterior adductor scar with a row of small pallial scars just above this sulcus. Pallial line distinct. Secondary pallial scars in anterior part of pallial line very well developed; pallial sinus is a shallow irregular indentation just below posterior adductor scar, here also with secondary pallial scars (Fig. 21). Anterior adductor scar ovately conical, impressed. Posterior adductor scar larger, suboval, impressed towards front. Anterior pedal retractor scar deeply impressed, located above anterior adductor scar. Posterior pedal retractor slightly impressed, fused to posterior adductor scar. Nymph long and weak. Fibrous layer of ligament occupying 30–38% of valve length and 65–76% of

posterior lamellar layer. Dentition of right valve of adult specimens: ventral cardinal (1) and subumbonal cardinal consisting only of posterior ramus (3b). Tooth 1 strong, wedge-shaped, pointed, radiating ventrally. 3b much lower, radiating posteriorwards. There is no fusion between 1 and 3b, their ventral parts diverging  $<90^\circ$ . Dentition of left valve of adult specimens: subumbonal cardinal tooth with two rami (2a and 2b), posterodorsal cardinal tooth (4b) very inconspicuous, sometimes absent. 2b-ramus the most developed, upright, radiating posteriorwards; 2a-ramus lower, sometimes reduced and thinner, proximal part of 2a connected with lateral surface of 2b by low bridge, ventral parts diverge at about  $90^\circ$ . Dentition of right valve of juvenile specimen with shell length 20.2 mm: ventral cardinal tooth (1) is most developed, upright, shelf-like and nearly parallel to dorsal margin of shell. Subumbonal tooth with very short anterior ramus 3a, which is completely reduced in adults. Ramus 3b shelf-like, radiating posteriorwards. Behind 3b there is thickening on nymph separated from posterior part of nymph by shallow furrow radiating posteriorwards. In left valve, 2a-ramus shelf-like, parallel to anterior-dorsal shell margin, fused in its proximal part with proximal part of thicker 2b-ramus, which is also parallel to posterior-dorsal shell margin. Tooth 4b nearly totally reduced, looks like a slight ridge radiating posteriorly.

For further details see description of Métivier *et al.* (1986). Values showing shell differences from other species are given in Table 8.

SEM revealed a larval shell about  $640\ \mu\text{m}$  in length and  $550\ \mu\text{m}$  high (Fig. 23A, B). Prodissoconch rounded, convex, with a pitted sculpture, about  $350\ \mu\text{m}$  in diameter, with a margin sculptured by commarginal striae and irregular fine radial striation, about  $35\ \mu\text{m}$  broad. In right valve there are two elongated lamina-like teeth: ventral cardinal (1), and tooth III not yet differentiated into 3a and 3b. Left valve was not available.

**Anatomy:** Structure of gills and digestive tract of *A. phaseoliformis* were studied by Fiala-Médoni & Le Pennec (1988a, b). It was reported that ctenidia consist of only one demibranch; homorabdric filaments are connected by interfilamentary junctions and interlamellar septa and on ventral margin of each



**Figure 23.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986). **A, B.** RV *Sonne-97*, Stn 66, larval shells. **C.** RV *Sonne-97*, Stn 66,  $L = 165$  mm. Fragment of ascending lamella of gill with interlamellar septum.

**Table 6.** Measurements of right valves of *Abyssogena phaseoliformis*.

|                         | $L$<br>(mm) | $H_{um}$<br>(mm) | $H_{max}$<br>(mm) | $W_{um}$<br>(mm) | $W_{max}$<br>(mm) | $F$<br>(mm) | $N$<br>(mm) | $H_{max}/L$ | $W_{max}/L$ | $H_{um}/H_{max}$ | $F/N$ | $F/L$ | $N/L$ | Um<br>(%) |
|-------------------------|-------------|------------------|-------------------|------------------|-------------------|-------------|-------------|-------------|-------------|------------------|-------|-------|-------|-----------|
| Holotype* NSNT Mo 64164 | 139.6       |                  | 36.0              |                  |                   |             |             | 0.26        |             |                  |       |       |       |           |
| Paratype MNHN, KD 14    | 159.4       | 33.5             | 33.5              | 11.4             | 12.1              | 55.0        | 83.6        | 0.21        | 0.08        | 1.0              | 0.66  | 0.35  | 0.52  | 14        |
| Paratype† NSNT Mo 64165 | 153.4       | 32.3             | 33.4              | 10.0             | 13.8              | 50.2        | 74.2        | 0.22        | 0.09        | 0.98             | 0.68  | 0.33  | 0.48  | 14        |
| Paratype MNHN, KD 14    | 147.5       | 31.8             | 33.0              | 10.9             | 12.0              | 50.5        | 79.0        | 0.22        | 0.08        | 0.96             | 0.64  | 0.34  | 0.54  | 14        |
| Paratype MNHN, KD 18    | 120.0       | 26.6             | 26.6              | 9.1              | 11.2              | 37.5        | 53.1        | 0.21        | 0.09        | 1.0              | 0.71  | 0.30  | 0.42  | 18        |
| SO 97, Stn 66           | 180.0       | 35.8             | 36.8              | 12.0             | 15.3              | 58.8        | 90.1        | 0.20        | 0.08        | 0.97             | 0.65  | 0.33  | 0.50  | 12        |
|                         | 150.6       | 30.7             | 31.1              | 10.4             | 12.6              | 50.7        | 76.5        | 0.21        | 0.08        | 0.99             | 0.66  | 0.34  | 0.51  | 13        |
|                         | 150.6       | 27.3             | 28.2              | 10.1             | 11.6              | 57.3        | 81.7        | 0.19        | 0.08        | 0.97             | 0.70  | 0.38  | 0.54  | 12        |
| SO 110, Stn 63          | 167.0       | 30.1             | 32.2              | 8.9              | 13.6              | 61.8        | 86.4        | 0.19        | 0.08        | 0.94             | 0.72  | 0.37  | 0.52  | 13        |
| KAIKO 85, KR-9807       | 125.9       | 29.4             | 30.6              | 11.0             | 12.6              | 38.2        | 50.5        | 0.24        | 0.10        | 0.96             | 0.76  | 0.30  | 0.40  | 15        |
| SO 110, Stn 48          | 60.8        | 16.6             | 17.2              | 5.8              | 5.8               | 14.4        | 27.7        | 0.28        | 0.09        | 0.97             | 0.52  | 0.24  | 0.46  | 16        |
| SO 110, Stn 49          | 51.3        | 13.1             | 13.8              | 4.0              | 4.5               | 11.4        | 23.3        | 0.27        | 0.09        | 0.95             | 0.49  | 0.22  | 0.45  | 16        |
|                         | 37.5        | 12.4             | 12.4              | 4.1              | 4.5               | 7.5         | 17.6        | 0.33        | 0.12        | 1.0              | 0.43  | 0.20  | 0.47  | 21        |
|                         | 37.3        | 11.8             | 12.6              | 3.2              | 3.9               | 8.9         | 17.5        | 0.34        | 0.10        | 0.94             | 0.51  | 0.24  | 0.49  | 18        |

\*From Métivier *et al.* (1986).

†Specimen NSNT Mo 64165 examined in this paper differs from the specimen with the same number (NSNT Mo 64165) studied in Métivier *et al.* (1986).

demibranch there is a very thin food groove. It was shown that filaments bear frontal, latero-frontal and lateral cilia, and the epidermis of the interlamellar septum (inner part of the filament) is composed of bacteriocytes arranged in cylindrical channels. *Abyssogena phaseoliformis* has extremely reduced labial palps, a short oesophagus, a small stomach with plicated wall and reduced digestive diverticula; the intestine is thin, without convolutions, passing through the pericardium (Fiala-Médoni & Le Pennec, 1988b).

In addition, our studies show that in *A. phaseoliformis* a narrow central part of the interlamellar septum is not divided into cylindrical channels (Fig. 14A), as it is in *A. southwardae*, where the entire interlamellar septa are divided into tubes (Fig. 14B). Furthermore, the channels of *A. phaseoliformis* have a more or less rectangular shape (Fig. 14G) while those of *A. southwardae* are more cylindrical (Fig. 14F). Finally, the tubes of *A. phaseoliformis* lack the variability of the files observed in *A. southwardae* with thicker and thinner sections (Fig. 14E, F).

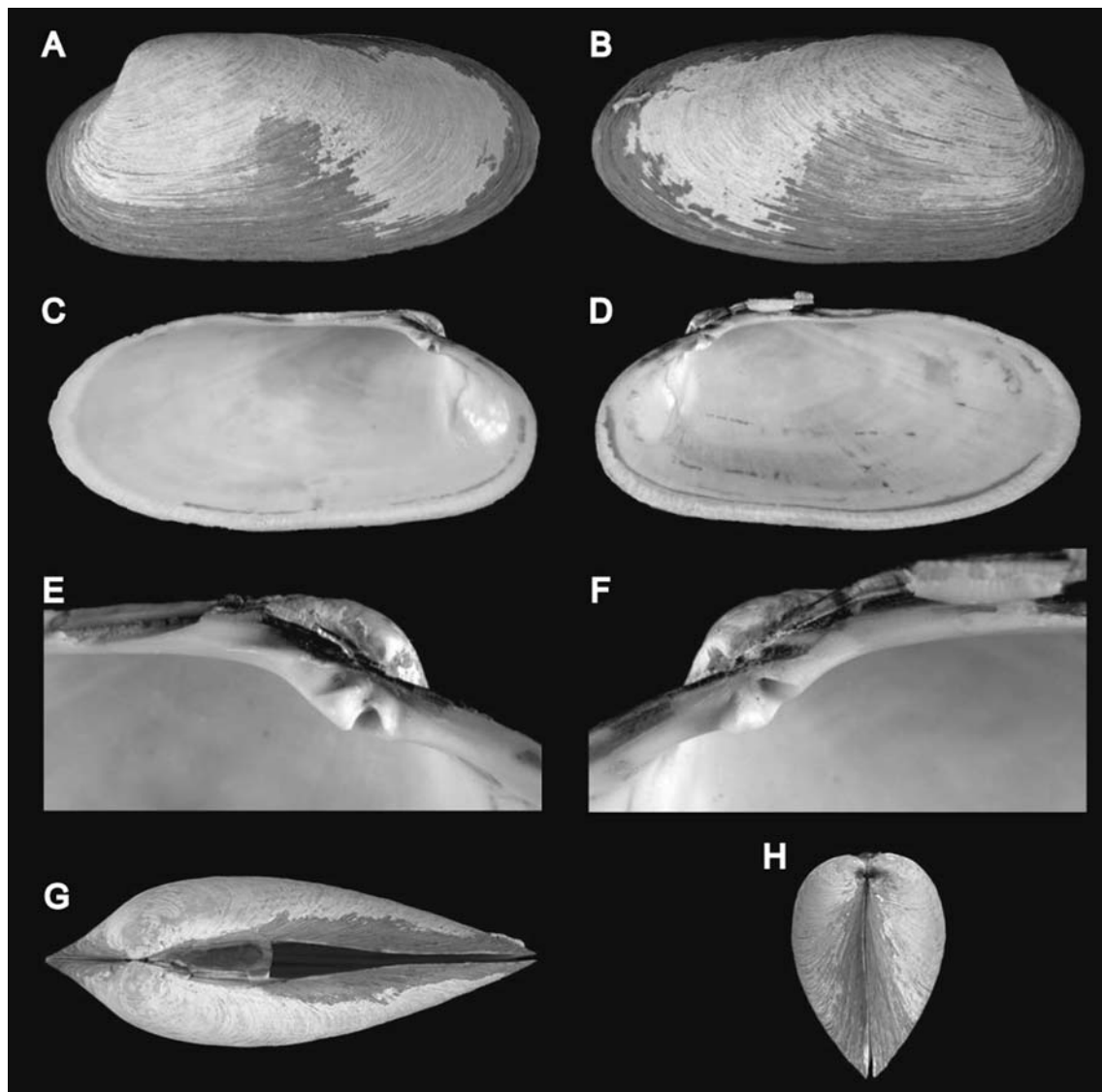
Margins of inhalant and exhalant apertures bear one row of tentacles. Tentacles of inhalant siphon larger, some of them can be branching; tentacles of exhalant siphon quite small.

**Variation:** In right valve, cardinal tooth 3b can be reduced to different degrees; in left valve 2a can be reduced and 4b can be

totally absent. Horikoshi (1989) described variations in hinge structure in detail. The shape of tentacles around inhalant siphon can vary from simple to slightly branching. Allometric changes are evident in a more elongate shell shape, longer fibrous and lamellar ligament, and more anterior placement of umbos in larger specimens. Smaller specimens have convex ventral margins and more inflated umbos with more enrolled beaks. Juvenile specimens usually have teeth placed parallel to the hinge margin compared to the radiating teeth of adults. Sometimes a very short ramus 3a is developed which is totally reduced in adults.

**Distribution:** North Pacific Ocean: Japan Trench, 5,400–6,400 m (Fujikura *et al.*, 2002; Kojima *et al.*, 2004), Kurile Trench, 4,700–6,200 m (Sasaki, Okutani & Fujikura, 2005), Aleutian Trench, 4,550–6,400 m.

**Habitat:** *Abyssogena phaseoliformis* occurs at cold seeps that are situated at the lower slope of convergent continental margins close to the trench axis. The geological and geochemical habitat of *A. phaseoliformis* has been studied in detail at the Aleutian convergent margin where tectonically induced dewatering causes the very slow seepage of methane-rich fluids at the seafloor (Suess *et al.*, 1998). Fluid flow is patchily distributed which is reflected in the typical occurrence of the clams in clusters of about 1 m in diameter.



**Figure 24.** *Abyssogena kaikoi* (Okutani & Métivier, 1986), holotype, MNHN, KAIKO, *Nautila*, KD-5,  $L = 61.1$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

*Remarks:* Molecular analyses reveal small differences in the COI sequences between samples of *A. phaseoliformis* from the Kuril-Kamchatka and Japan Trenches compared to samples from the Aleutian Trench (Peek *et al.*, 2000). Our study failed to find clear morphological differences between these populations. Until proof of the contrary we provisionally consider the populations from different trenches of the North Pacific to be conspecific. The view that these populations are indeed the same species is indirectly corroborated by the fact that in both trenches, Japan and Aleutian, *A. phaseoliformis* occurs together with the same species '*Ectenagena*' *fossajaponica* Okutani, Fujikura & Kojima, 2000 (Okutani *et al.*, 2000; E.M. Krylova, H. Sahling and R. Janssen, unpubl.). In addition, *A. phaseoliformis* from the Aleutian Trench was infested by the same species of parasitic polychaete *Nautilina calyptogenicola* Miura & Laubier, 1989 (D. Fiege, personal communication) as *A. phaseoliformis* from the Japan Trench (Miura & Laubier, 1989). In our material polychaetes usually occur between gill and inner mantle and can be up to 120 mm in length. Infested clams had damaged and deformed gills.

***Abyssogena kaikoi* (Okutani & Métivier, 1986)**

(Figs 6B, 24–26)

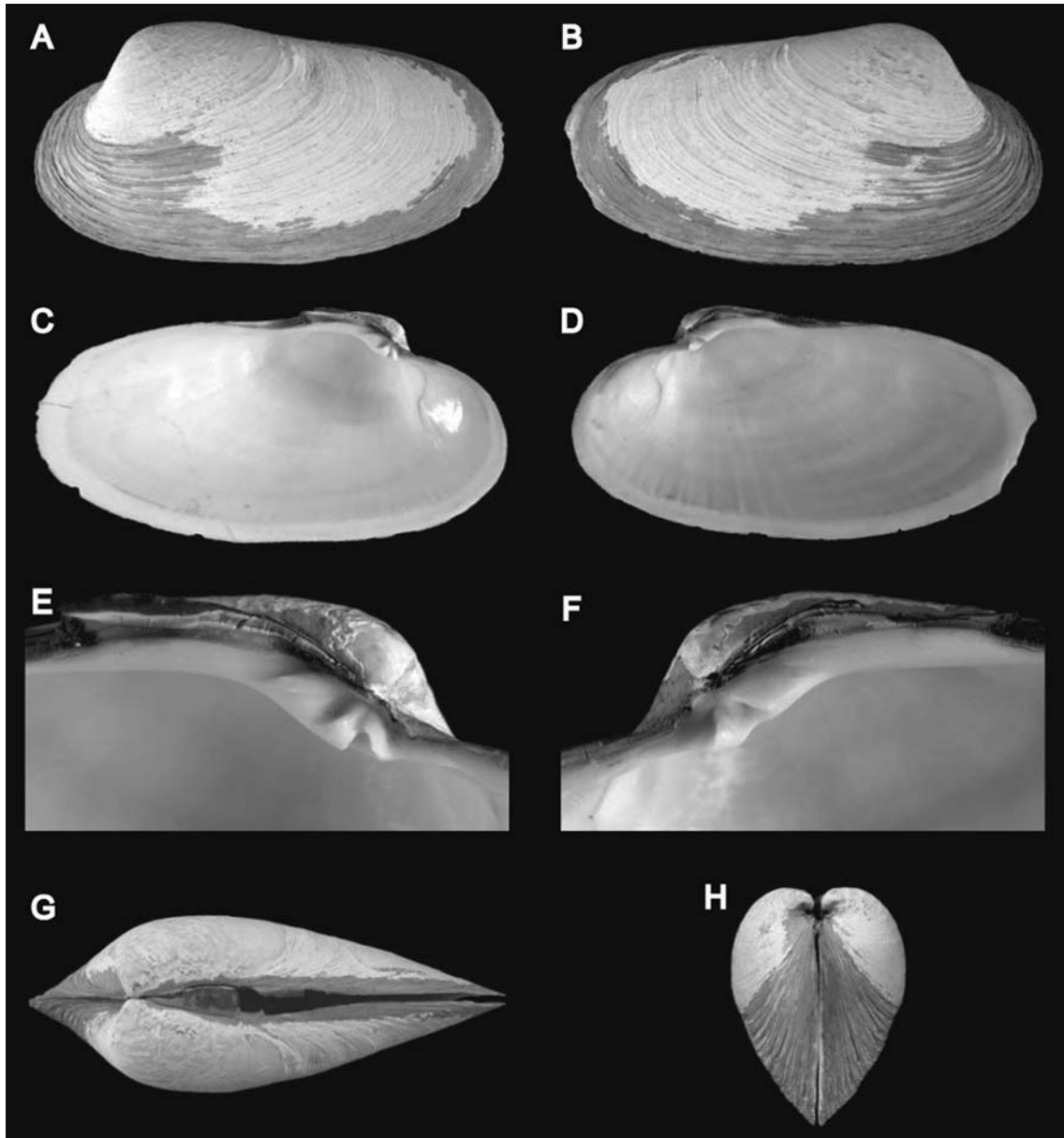
*Calyptogena* (*Ectenagena*) *kaikoi* Okutani & Métivier, 1986: 153, fig. 1c, pl. 3, figs 8–11. Okutani *et al.*, 2000: 96. Sasaki *et al.*, 2005: 99, fig. 7E, F.

*Calyptogena kaikoi*—Horikoshi, 1989: 151, pl. 4, figs 1, 2, 4–6.

*Type material:* MNHN (holotype, spm without soft parts; two paratypes, one spm with soft parts and one spm without soft parts); USMT Mo 64160 – 64163 (four paratypes, spms without soft parts). Type locality: West Pacific, Nankai Trough, Tenryu Submarine Canyon, 33°36.9'N, 137°32.0'E, 3,830 m, 10 June 1985 (KAIKO, *Nautila*, KD-5).

*Material examined:* Type material: holotype, two paratypes (MNHN); two paratypes (USMT Mo 64161, 64162).

*Diagnosis:* *Abyssogena* species with  $L$  to 61.1 mm, thin-shelled, elongate, in adult specimens  $H/L = 0.45–0.51$ ,  $W/L = 0.15–0.17$ , dorsal and ventral margins nearly straight and parallel to each other, light grey-brownish periostracum with close-set

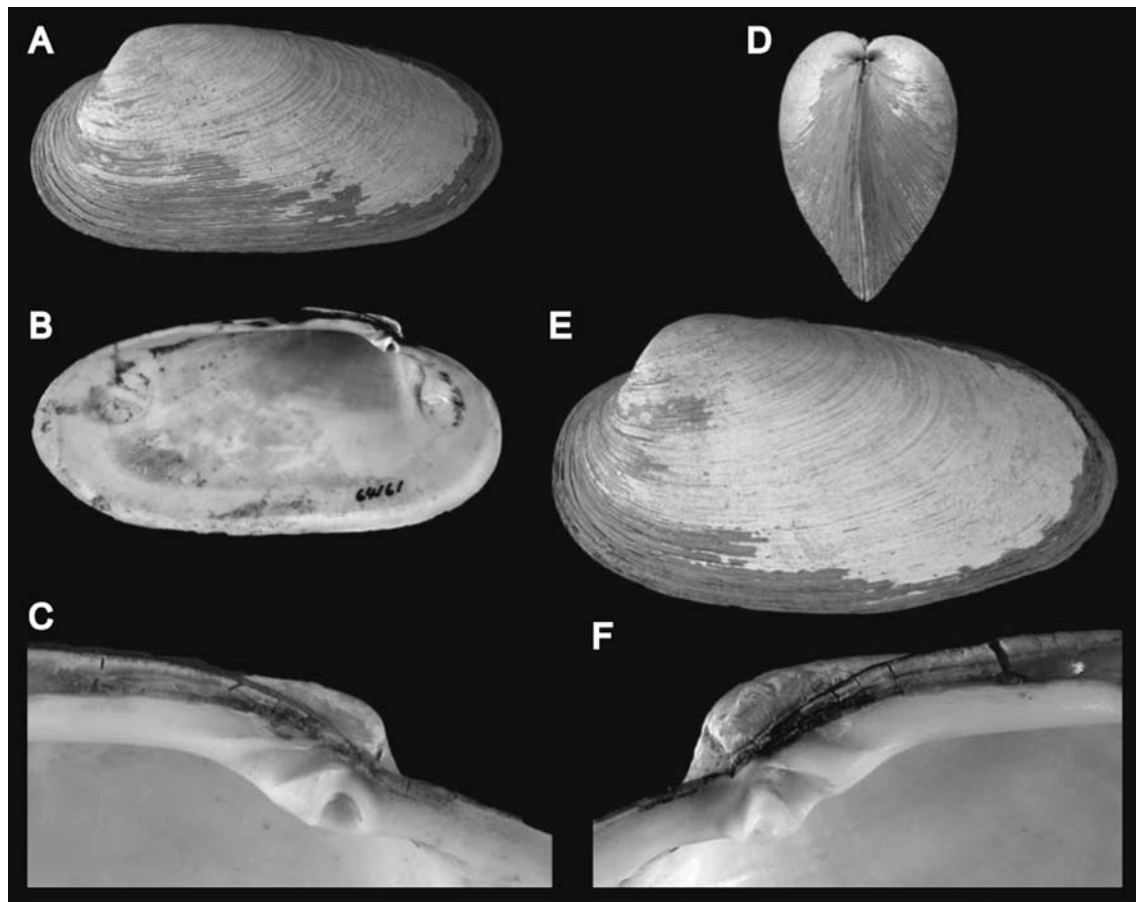


**Figure 25.** *Abyssogena kaikoi* (Okutani & Métivier, 1986), paratype, MNHN, KAIKO, *Nautila*, KD-5,  $L = 44.6$  mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

commarginal striae and elevated lamellae, umbo prosogyrate, inflated, situated at anterior 22–28% of valve length, beaks enrolled, fibrous layer of ligament occupying 20–22% of valve length and 49–53% of posterior lamellar layer (Table 7).

*Description:* Shell medium-sized,  $L$  to 61 mm, thin-shelled, elongate in outline,  $H/L = 0.45$ – $0.51$ , nearly equivalve. Periostracum thin, light grey-brownish, remaining only on peripheral area, with short, close-set commarginal, elevated lamellae developed mostly at anterior and ventral margins. Sculpture consisting of very close-set commarginal striae and inconspicuous radial lines running from umbo to posterior margin. Inequilateral, umbo situated in anterior 22–28% of valve. Umbones prosogyrate, inflated; beaks pointed, enrolled, touching each other. Anterior–dorsal margin short, convex; anterior margin rounded, ventral margin nearly straight in large specimens and slightly convex in smaller

specimens. Posterior margin rounded, but more tapering than anterior margin; posterior–dorsal margin nearly straight. Internal shell surface white, with faint radial striations. Pallial line very indistinct. Secondary pallial scars visible in anterior part of pallial line, pallial sinus hardly noticeable as a shallow irregular indentation just below posterior adductor scar. Anterior adductor scar ovately conical, somewhat impressed to rear. Posterior adductor scar larger, subcircular, hardly distinct. Anterior pedal retractor scar shallow or moderately impressed, located above anterior adductor scar. Posterior pedal retractor not impressed, fused to posterior adductor scar. Nymph weak, with smoothly sloping posterior end. Fibrous layer of ligament occupying 20–22% of valve length and 49–53% of posterior lamellar layer. Dentition of right valve: ventral cardinal (1) and subumbonal cardinal, consisting only of posterior ramus (3b).



**Figure 26.** *Abyssogena kaikoi* (Okutani & Métivier, 1986), paratypes, KAIKO, *Nautile*, KD-5. **A–C, F.** USMT Mo 64162, *L* = 60.8. **A.** Exterior of left valve. **B.** Interior of left valve. **C.** Left hinge plate. **F.** Right hinge plate. **D, E.** USMT Mo 64161, *L* = 50.6 mm. **D.** Anterior view. **E.** Exterior of right valve.

**Table 7.** Measurements of right valves of *Abyssogena kaikoi*.

|                         | <i>L</i> (mm) | <i>H</i> (mm) | <i>W</i> (mm) | <i>F</i> (mm) | <i>N</i> (mm) | <i>H/L</i> | <i>W/L</i> | <i>F/N</i> | <i>FL</i> | <i>N/L</i> | Um (%) |
|-------------------------|---------------|---------------|---------------|---------------|---------------|------------|------------|------------|-----------|------------|--------|
| Holotype, MNHN          | 61.1          | 27.6          | 9.4           | 13.7          | 25.7          | 0.45       | 0.15       | 0.53       | 0.22      | 0.42       | 22     |
| Paratype, MNHN          | 46.4          | 22.8          | 7.7           | 9.2           | 18.6          | 0.49       | 0.17       | 0.49       | 0.2       | 0.4        | 27     |
| Paratype, NSMT-Mo 64161 | 50.6          | 26            | 8.5           | 10.9          | 20.7          | 0.51       | 0.17       | 0.53       | 0.22      | 0.41       | 26     |
| Paratype, NSMT-Mo 64162 | 60.8          | 28.2          | 8.9           | 12.2          | 25.1          | 0.46       | 0.15       | 0.49       | 0.2       | 0.41       | 28     |

Tooth 1 upright, strong, wedge-shaped, bluntly pointed, radiating ventrally. 3b low, somewhat wide, with parallel anterior and posterior margins; anterior margin sharp, posterior margin always lower than anterior and smoothed; radiating posteriorwards. There is no fusion between 1 and 3b, their ventral parts diverging at about 90° or little more. Dentition of left valve: subumbonal cardinal tooth with two rami (2a and 2b) and posterodorsal cardinal tooth (4b). 2b-ramus stout, wedge-shaped, 2a-ramus lower and thinner, proximal part of 2a connected with lateral surface of 2b by low bridge, ventral parts diverge at about 90°; 4b-tooth thin, low, radiating posteriorwards.

For detailed description see Okutani & Metivier (1986). Differences from other *Abyssogena* species are given by comparison of morphometric shell values in Table 8.

**Anatomy:** Only gills were studied, which have a multichannelled structure characteristic for the genus.

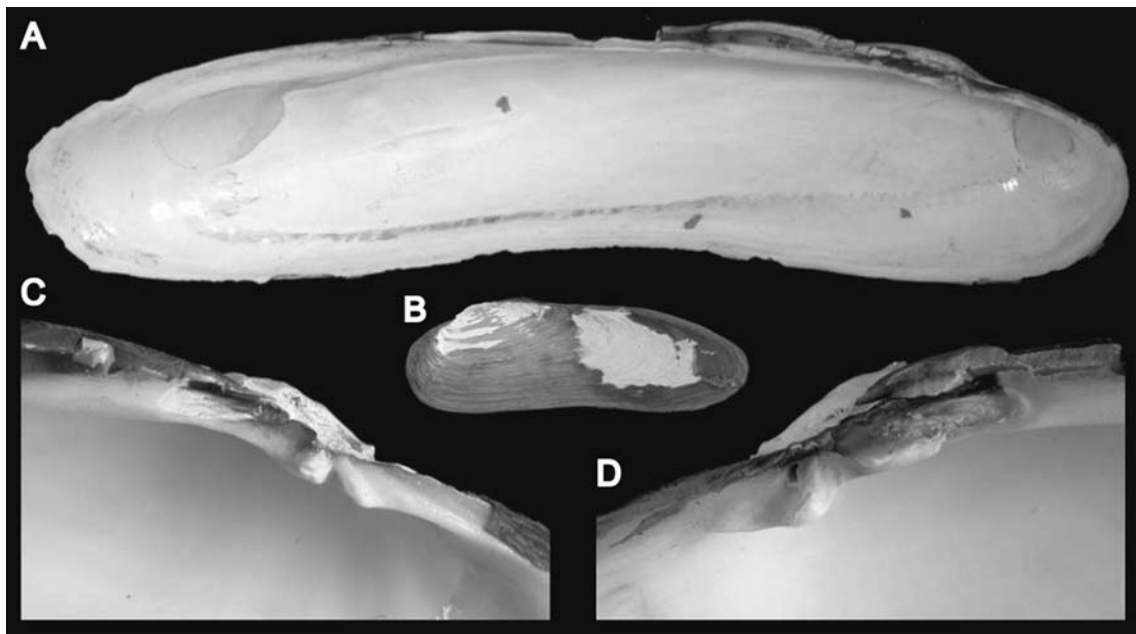
**Variation:** There are variations in shell outline: shell can be more or less elongated, ventral margin can be convex. The 4b-tooth in left valve can range from weak to moderate. For variations of hinge structure see Horikoshi (1989).

**Distribution:** West Pacific Ocean, Nankai Trough: Tenryu Submarine Canyon (Okutani & Metivier, 1986), Daisan Tenryu Submarine Canyon, off Muroto Point (Okutani *et al.*, 2002, Kojima *et al.*, 2004), 3,540–4,800 m (Sasaki *et al.*, 2005).

**Habitat:** Cold seeps related to the convergent continental margins offshore Japan.

## DISCUSSION

The new genus *Abyssogena*, consisting of new species as well as species previously assigned to *Ectenagena*, is a well-defined group distinguished morphologically, ecologically and



**Figure 27.** ‘*Ectenagena*’ *extenta* Krylova & Moskalev, 1996. **A.** Holotype, ZMUU Ld-2828,  $L = 235.2$  mm, interior of left valve. **B–D.** FMNH 302093,  $L = 76.4$  mm. **B.** Exterior of left valve. **C.** Left hinge plate. **D.** Right hinge plate.

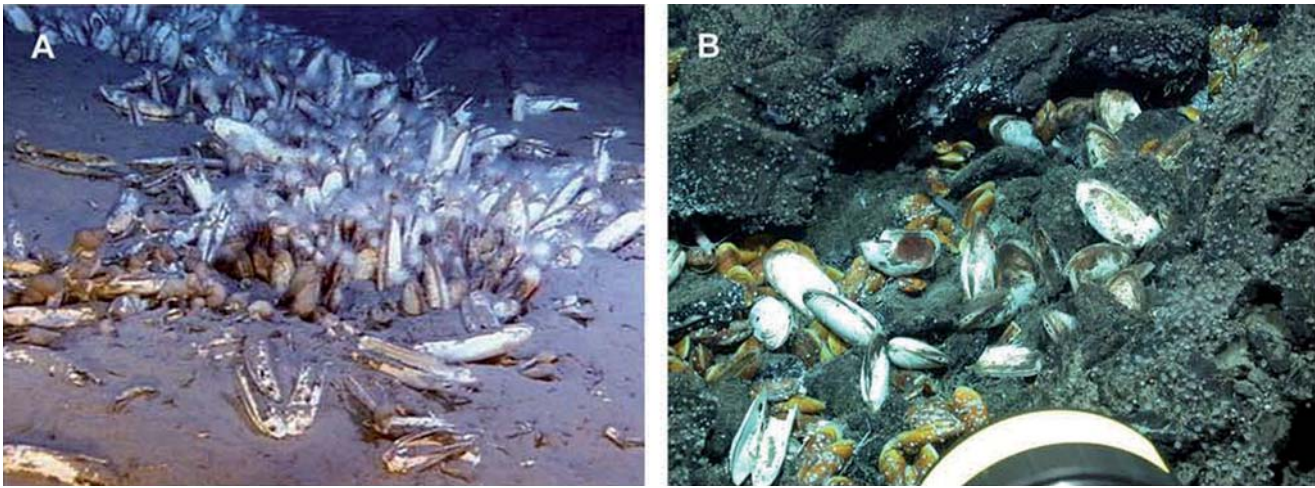
genetically from other vesicomids. Morphologically it is characterized by a complex of features such as elongated shell shape, weak hinge plate with reduced anterior ramus of subumbonal cardinal tooth (3a) in the right valve, absence of deeply placed anterior lamellar ligament located in the subumbonal pit, the pallial line originating in the ventral part of the anterior adductor scar, the presence of secondary pallial scars along pallial line and small irregular pallial sinus, the presence of only one pair of demibranchs with interlamellar septa consisting of cylindrical channels, a straight alimentary gut and the presence of an inner vulva of inhalant siphon lacking any processes.

Among Recent vesicomids there are some species having strong similarities with those included in *Abyssogena*. These species are *Calyptogena* (*Ectenagena*) *magnifica* Boss & Turner, 1980, *C. (Ectenagena) australis* Stuardo & Valdovinos, 1988, *Ectenagena extenta* Krylova & Moskalev, 1996 and *C. (Archivesica) tsubasa* Okutani, Fujikura & Kojima, 2000. These species have more or less strongly elongated shells and radiating teeth with more or less reduced anterior cardinal (3a) in the right valve (as an example *E. extenta* is shown in Fig. 27). Anatomical information is available for all these species (Boss & Turner, 1980; Morton, 1986; Stuardo & Valdovinos, 1988; Krylova & Moskalev, 1996) except *C. (A.) tsubasa*. The most obvious difference of *Abyssogena* compared to all these species is the presence of only one pair of demibranchs, namely the inner one. Furthermore, there are distinguishing characters of the pallial muscles, which are reflected in features of the shell: in *Abyssogena* the pallial line runs from the ventral part of the anterior adductor scar and has numerous secondary attachment scars along it. By contrast, *C. (E.) magnifica*, *C. (E.) australis* and *E. extenta* have two demibranchs and their pallial line originates from the posterior margin of the anterior adductor scar, the latter is also true for *C. (A.) tsubasa* (Okutani *et al.*, 2000: 89, fig. 10). The differences between *Abyssogena* on the one hand and *C. (E.) magnifica*, *E. extenta* and *C. (A.) tsubasa* on the other are further corroborated by molecular analysis (Peek *et al.*, 1997, 2000; Kojima *et al.*, 2004). Phylogenetic trees based on the molecular data show that the

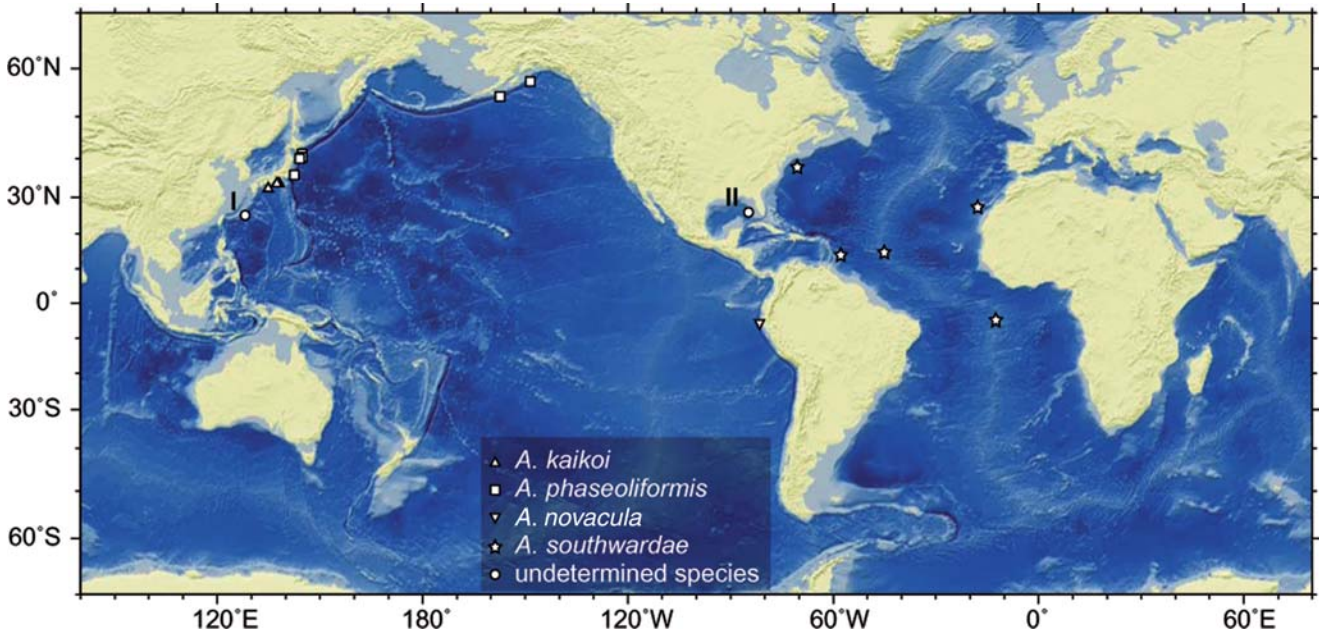
species of *Abyssogena* form a clade that is well separated from all other species.

In the gills of *Abyssogena* the interlamellar septa of the demibranch are divided into separate cylindrical tubes. Apparently such kind of structure was implied by Fiala-Médoni & Le Pennec (1988a), when they reported that bacteriocytes in gills of *A. phaseoliformis* were ‘arranged in files’ (p. 187; fig. 3D). This ‘multicylindrical organization’ was also reported for *A. southwardae* (*Calyptogena (Ectenagena)* sp.’ in Southward *et al.*, 2001). This character of *Abyssogena* is not unique among vesicomids, for example, the dividing of the peripheral part of the interlamellar septa into separate channels has been observed in adult specimens of *Phreagena edisonensis* (Okutani, Kojima & Kim, 2004) (Krylova & Janssen, 2006) and some other species, such as ‘*C. magnifica* and ‘*V. kwoshimana* Okutani, Fujikura & Kojima, 2000 (E.M. Krylova, H. Sahling and R. Janssen, unpubl.). However, in *Abyssogena* almost all of the interlamellar septa are divided into tubes and, furthermore, the structures are already developed in juveniles, which is in contrast to *P. edisonensis*. A very similar morphology of the gills has been reported for Lucinidae (Distel & Felbeck, 1987; Frenkiel *et al.*, 1996; Taylor & Glover, 2005). It seems that the structure of the interlamellar septum is an adaptive feature related to the symbiosis of the bivalves with chemosynthetic bacteria. It appears likely that this structure results in an enlargement of the surface area occupied by bacteriocytes, which facilitates chemical exchange processes between bacteria and the circulating water. Despite the fact that a tubulose structure of the septum has arisen independently several times within different groups of vesicomids, the highly developed structure which affects most of the septum and its presence in even early ontogenetic stages appears to be unique for *Abyssogena*.

Obviously, the character of an extremely elongated shell shape is homoplasious and has evolved within vesicomids independently in at least two different groups – species with a single demibranch and those with two demibranchs. The elongated shell as well as an overall body enlargement seems to be advantageous for some groups of vesicomids such as



**Figure 28.** **A, B.** *Abyssogena* in its natural habitat. **A.** *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986); Aleutian Trench, 4947 m (from Suess *et al.*, 1998; pl. 2a). **B.** *Abyssogena southwardae* with *Bathymodiolus puteoserpentis* Cosel, Metivier & Hashimoto, 1994; MAR, Wideawake vent site, 2,985 m (photo courtesy of MARUM).



**Figure 29.** Distribution of *Abyssogena* species. Locations of species designated by Roman numerals provisionally can be assigned to *Abyssogena* on the base of molecular data only. Abbreviations: **I**, unidentified vesicomyid (Kojima *et al.*, 2004); **II**, *Calyptogena* n. sp. (Peek *et al.*, 1997).

*Abyssogena*. The most obvious benefit of an elongated body might be the access of the bivalve to spatially separated chemical environments in order to provide the required chemical compounds to their symbiotic sulphur-oxidizing bacteria.

Typically, vesicomyid clams live buried in the sediments with about one half or less of the posterior part being exposed to the oxygenated bottom-waters (Fig. 28). The anterior part of the clam with the extendable foot has access to hydrogen sulphide in the sediments. Geochemical studies indicate that the concentration of hydrogen sulphide increases in the sediments below vesicomyid clam colonies and, furthermore, that the depth where the concentration increases is related to the size of the vesicomyid clam species. For example, maximal sulphide concentrations are reached at 25 cm sediment depth below the elongated *A. phaseoliformis* (Wallmann *et al.*, 1997)

whereas maximal concentrations are reached at 10 cm depth below the much shorter vesicomyid clam species *Calyptogena pacifica* and '*C. kilmeri*' (Sahling *et al.*, 2002). These examples show that there is interaction of vesicomyid clams with

**Table 8.** Some shell characteristics of Recent *Abyssogena* species (data for adult specimens).

|                              | Maximum length (mm) | H/L (%) | Position of umbo (%) | F/L (%) | F/N (%) |
|------------------------------|---------------------|---------|----------------------|---------|---------|
| <i>A. southwardae</i> n. sp. | 220                 | 36–47   | 15–23                | 25–38   | 44–73   |
| <i>A. novacula</i> n. sp.    | 277.4               | 21–32   | 9–15                 | 26–40   | 55–69   |
| <i>A. phaseoliformis</i>     | 180                 | 19–23   | 12–14                | 30–38   | 65–76   |
| <i>A. kaikoi</i>             | 61.1                | 45–51   | 22–28                | 20–22   | 49–53   |

biogeochemical processes and that the body size has an influence, but more studies are needed to understand these processes.

The concept that it is advantageous for species living in steep geochemical gradients to have elongated bodies and an overall increase in size is corroborated by the fact that another group of symbiont-bearing bivalves, the bathyomidiolines, follow this trend (von Cosel & Olu, 1998; von Cosel & Marshall, 2003; von Cosel & Janssen, 2008). To the contrary, there are bivalve groups such as the lucinids and thyasirids living in symbiosis with bacteria that are not characterized by body elongation. However, these bivalves have different strategies to reach and exploit reducing conditions. Most lucinids and thyasirids burrow in the sediment and construct tunnels, which draw in oxygenated water (Allen, 1958; Dando & Southward, 1986; Dando, Ridgway & Spiro, 1994). Furthermore, there is one lucinid species known that possesses long periostracal pipes used for exploitation of sulphides in sediment (Taylor & Glover, 1997).

*Abyssogena* species live in a wide variety of tectonic settings ranging from hydrothermal vents to cold seeps. Most often they are found in soft sediments, but the recent discovery of *A. southwardae* on jumbled, sheeted basalt shows that they can live on hard ground as well (Fig. 28B; Haase *et al.*, 2007). It would be interesting to compare the physicochemical habitat of *Abyssogena* species but, unfortunately, there is a lack of such data with the exception of *A. phaseoliformis* (Wallmann *et al.*, 1997). We speculate that the geochemical habitats of the species are not very different between the cold seep and hydrothermal settings because, for example, *A. southwardae* avoids areas with strong hydrothermal flow (Gebruk *et al.*, 2000).

Among the symbiont-bearing groups of vesicomids *Abyssogena* is the genus that occurs at the greatest water depths, in the range 2,985–6,400 m. It has a wide distribution in both the Pacific and Atlantic Oceans. Figure 29 shows the global distribution of *Abyssogena* species described in this study as well as locations of close relatives that have only been studied with molecular techniques (Peck *et al.*, 1997; Kojima *et al.*, 2004). The geographical ranges of separate species of *Abyssogena* are among the widest of all vesicomids; for example, *A. southwardae* occurs all over the Atlantic including both western and eastern regions and also the central part, and *A. phaseoliformis* occurs in the Kuril-Kamchatka, Japan and Aleutian Trenches.

The high level of specialization of the genus *Abyssogena*, indicated by a suite of morphological features such as relatively large body size, elongated shell shape, reduced outer pair of demibranchs and complicated structure of interlamellar septa, suggests that the genus *Abyssogena* is probably one of the most derived genera of vesicomids. There are no data on the time of origin of *Abyssogena*, for at present there are no fossils that can be certainly referred to the genus. The lack of fossils may be explained by the evolution of *Abyssogena* at great water depths, because deep-sea habitats are generally not well preserved in the geological record.

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