RECENT BIVALVE MOLLUSCS OF THE GENUS *CALYPTOGENA* (VESICOMYIDAE)

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ABSTRACT

The genus *Calyptogena* (Bivalvia: Vesicomyidae) comprises highly specialized bivalves living in symbiosis with sulphur-oxidizing bacteria in reducing habitats. In this study, the genus is revised using shell and anatomical features. The work is based on type material, as well as on the extensive collection of vesicomyids obtained during twelve expeditions to the Pacific and Indian Oceans. Nine Recent species are ascribed to the genus *Calyptogena*, four of which are new: *C. pacifica* Dall, 1891, *C. fausta* Okutani, Fujikura & Hashimoto, 1993, *C. rectimargo* Scarlato, 1981, *C. valdiviae* (Thiele & Jaeckel, 1931), *C. gallardoi* Sellanes & Krylova, 2005, *C. goffrediae* n. sp., *C. starobogatovi* n. sp., *C. makranensis* n. sp. and *C. costaricana* n. sp. The characteristic features of *Calyptogena* are: shell up to 90 mm in length, elongate-elliptical or elongate; presence of escutcheon; presence of broad posterior ramus (3b) of right subumbonal cardinal tooth as well as right posterior nymphal ridge; absence of pallial sinus as a result of attachment of intersiphonal septal retractor immediately adjacent to ventral surface of posterior adductor; absence of processes on inner vulva of inhalant siphon; presence of inner demibranch only, with descending and ascending lamellae with interlamellar septa not divided into separate tubes. The most closely related taxa to *Calyptogena* are probably the genus *Isorropodon* Sturany, 1896, and the group of species represented by '*Calyptogena*' *phaseoliformis* Métivier, Okutani & Ohta, 1986. These groups have several characters in common, namely absence of pallial sinus, presence of single inner pair of demibranchs and absence of processes on inner vulva of inhalant siphon. The worldwide distribution of the genus *Calyptogena* suggests that methane seeps at continental margins are the major dispersal routes and that speciation was promoted by geographical isolation. Recent species diversity and fossil records indicate that the genus originated in the Pacific Ocean. Sufficient data to discuss the distribution at species level exist only for *C. pacifica*, which has a remarkably narrow bathymetric range. Published studies on the physiology of *C. pacifica* suggest that adaptation to a specific geochemical environment has led to coexisting vesicomyid genera. The bacteria-containing gill of *C. pacifica* and other *Calyptogena* species is one of the most specialized in the family Vesicomyidae and may reflect these ecological adaptations.

INTRODUCTION

The family Vesicomyidae includes highly specialized bivalves known worldwide from continental slopes to hadal depths. Most, if not all, species of the family occur in reducing sulphide-rich habitats such as cold seeps, hydrothermal vents and whale carcasses, where they are often dominant in these chemosynthesis-based communities (Boss & Turner, 1980; Turner, 1985; Cosel & Salas, 2001; Krylova, 2002). All investigated vesicomyids harbour chemoautotrophic bacteria in their gills on which their nutrition depends (Fisher, 1990). Vesicomyids have been the subject of numerous studies involving physiological, biochemical, genetic, ecological and biogeographical approaches. In spite of this attention, the taxonomy of vesicomyids is far from being settled, both at species and supraspecific levels (Boss & Turner, 1980; Peek *et al*., 1997; Goffredi *et al*., 2003). The problematic taxonomy of this important group of animals frustrates the overall ecological and biogeographical investigation of chemosynthesis-based communities. Different authors estimate that the family includes from 50 to more than 70 Recent and fossil species (Peek *et al*., 1997; Cosel & Salas, 2001; Goffredi *et al*., 2003). Differences in the estimations of the species number reflect the uncertainties of taxonomic assignments.

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The type genus of the family Vesicomyidae Dall & Simpson, 1901, *Vesicomya* Dall, 1886, has similarities with *Kelliella* M. Sars, 1870, which is the type genus of the family Kelliellidae P. Fischer, 1887. If these two genera were united in the same family, the name Kelliellidae would take priority over Vesicomyidae. Relationships between these two groups have been debated for many years. Some authors have considered kelliellids and vesicomyids to be separate families (Dall, 1908; Thiele & Jaekel, 1931; Prashad, 1932; Woodring, 1938; Boss, 1967, 1968, 1970; Keen, 1969; Filatova, 1971; Bernard, 1974; Boss & Turner, 1980; Scarlato, 1981; Okutani, Fujikura & Kojima, 2000; Cosel & Salas, 2001), while others have united them (Thiele, 1935; Odhner, 1960; Clarke, 1962; Knudsen, 1970; Egorova, 1998; Allen, 2001).

The generic composition of the family has also been in question. Generic and subgeneric names of Recent and fossil groups that have been utilized are: *Akebiconcha* Kuroda, 1943, *Archivesica* Dall, 1908, *Callogonia* Dall, 1889, *Calyptogena* Dall, 1891, *Ectenagena* Woodring, 1938, *Hubertschenckia* Takeda, 1953, *Isorropodon* Sturany, 1896, *Phreagena* Woodring, 1938, *Pleurophopsis* van Winkle, 1919, *Pliocardia* Woodring, 1925, *Veneriglossa* Dall, 1886, *Vesicomya* Dall, 1886 and *Waisiuconcha* Beets, 1942 (see Table 12). Different authors have recognized from one to twelve genera and subgenera, by synonymizing part of them or placing some genera into other families (Dall, 1908; Woodring, 1938; Odhner, 1960; Keen, 1969; Bernard, 1974; Boss & Turner,

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1980; Okutani *et al*., 2000; Coan, Scott & Bernard, 2000; Allen, 2001; Cosel & Salas, 2001). Bernard (1974) proposed synonymizing *Ectenagena* and *Akebiconcha* with *Archivesica*. Boss & Turner (1980) synonymized *Pleurophopsis*, *Phreagena*, *Ectenagena*, *Akebiconcha* and *Hubertschenckia* with *Calyptogena*, and *Archivesica* with *Callogonia*. Vesicomyids from the Sea of Okhotsk have been assigned to *Calyptogena*, *Waisiuconcha*, *Akebiconcha* and *Archivesica* (Scarlato, 1981). Cosel & Salas (2001) showed that the genus *Isorropodon*, which has been placed in the family Trapeziidae, is a valid taxon of Vesicomyidae, and have assigned eastern Atlantic vesicomyids to *Vesicomya*, *Waisiuconcha*, *Isorropodon* and *Callogonia*. Allen (2001) synonymized *Vesicomya* with *Kelliella* and supposed that the genera and subgenera *Akebiconcha*, *Archivesica*, *Callogonia*, *Calyptogena*, *Ectenagena* and *Phreagena* were separated from *Kelliella* at least at subfamily level.

On the basis of shell morphology, Recent species have usually been assigned to *Vesicomya*, *Calyptogena s.l.* or *Ectenagena* (Boss, 1968; Boss & Turner, 1980; Okutani & Métivier, 1986; Krylova & Moskalev, 1996; Okutani *et al*., 1997; Barry & Kochevar, 1999; Okutani *et al*., 2000). However, there is much confusion in assignment of vesicomyid species to genera and molecular studies have revealed that the present genera do not comprise monophyletic species groups (Vrijenhoek *et al*., 1994; Kojima *et al*., 1995; Peek *et al*., 1997, Kojima *et al*., 2004). Coan *et al*. (2000) considered *Calyptogena s.l.* and *Ectenagena* to be 'poorly defined' taxa and at the present state of knowledge of vesicomyid taxonomy suggested using a single genus name, *Vesicomya*, for all species of the family. Some authors have followed this recommendation (Goffredi *et al*., 2003).

Nevertheless, in current literature dealing with chemosynthesis-based communities, *Calyptogena* is one of the most frequently used names, often for any large white clams. As a result, *Calyptogena* has become an inflated taxon combining phylogenetically distantly related species. At the same time, molecular studies have revealed that vesicomyids from the eastern Pacific which are usually attributed to *Calyptogena pacifica*, the type species of the genus, are actually composed of several morphologically cryptic species (Vrijenhoek *et al*., 1994; Peek *et al*., 1997). Recent studies have shown that the cryptic-species complex including *C. pacifica* contains at least five discrete evolutionary lineages (Goffredi *et al*., 2003). Clearly, *Calyptogena* needs an entire revision with an improved diagnosis based on both shell and anatomical features.

In this study, we attempt a taxonomic revision of *Calyptogena s.s*., which we regard as a separate genus in the family Vesicomyidae. The work is based on type material as well as on the extensive collection of vesicomyids obtained during twelve expeditions to the Pacific and Indian Ocean. The type species, *C. pacifica*, is redescribed based on the internal morphology. The paper includes a thorough description of *C. fausta*, *C. rectimargo* and *C. gallardoi* as well as four species that are new to science. Furthermore, we propose that *C. valdiviae* and *V. longa* are synonymous and that *C. valdiviae* is the appropriate species name.

We use a restrictive definition of the genus *Calyptogena*, which is in contrast to the ostensible likeness of the vesicomyid clams in general and the common use of the name '*Calyptogena*' in many studies. However, we found that the genus *Calyptogena s.s*. is a clearly defined taxon characterized by a set of conchological and anatomical features comprising species with common adaptive strategies. The results suggest that *Calyptogena s.s*. is a monophyletic group within the family Vesicomyidae, which is supporterd by molecular data. We are faced with the problem that the other vesicomyid genera are not yet well defined. As a consequence, we exclude species which have previously been ascribed to *Calyptogena*, without proposing to which other genera they should belong. This is the subject of future work. Despite the fact that the other genera in the family Vesicomyidae are yet not well defined, we summarize their main characters based on current knowledge.

This revision of the genus *Calyptogena s.s*. is a first step towards a revision of the family Vesicomyidae. Phylogenetic studies on available vesicomyid species are underway and will be published separately. Detailed discussion of the relationships between Vesicomyidae and Kelliellidae needs further investigation of so-called 'small vesicomyids', and is beyond the scope of this paper.

MATERIAL AND METHODS

The examined material was collected during 12 expeditions (Table 1). Altogether the collection comprises seven species of which four are new. Material of one species consists of shells only, and samples of six species consist of preserved live-taken specimens. In addition, the type material of six described species was studied.

For refining of anatomical details, material of species from other genera was used (Table 2).

For the morphological descriptions, 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), length of posterior lamellar part of ligament (N). The position of the umbo was defined as the distance of the umbo from the anterior margin relative to the shell length (Um, in %). The terminology of Bernard (1895, 1896, 1897), described in detail in Cox (1969), was applied to the description of the hinge teeth (Fig. 2). This terminology was modified for the hinge of vesicomyids by Okutani (1966) and is widely used in recent literature on the vesicomyids (Horikoshi, 1989; Okutani *et al*., 2000; Cosel & Salas, 2002). The posterior elongated ridge on the nymphal callosity of the right valve of *Calyptogena* is usually classified as a lateral tooth, although its origin is unknown. Here we designated it as posterior nymphal ridge. Gross anatomy was observed on preserved live-taken specimens.

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

Research vessel	Cruise no.	Abbreviation	Year	Area
Akademik Mstislav Keldysh	12	Keldysh 12	1986	Axial Seamount, Juan de Fuca Ridge
Akademik Mstislav Keldysh	22	Keldysh 22	1990	Piip Volcano, Bering Sea
Sonne	109	SO 109	1996	Continental margin off Oregon
Sonne	110	SO 110	1996	Continental margin off Oregon
Sonne	130	SO 130	1998	Makran Continental margin off Pakistan
Sonne	143	SO 143	1999	Continental margin off Oregon
Sonne	146	SO 146	2000	Continental margin off Peru
Meteor	54	M 54	2002	Continental margin off Costa Rica
Akademik M.A. Lavrentyev	28	Lv 28	1998	Sea of Okhotsk
Marshal Gelovani	1	Ge99	1999	Sea of Okhotsk
Atlantis	131	At 131	1993	Continental margin off Oregon
Atlantis	9906	AT9906	1999	Continental margin off Oregon

Table 2. Additional vesicomyid species studied.

	Source of material
Calyptogena (Archivesica) edisonensis Okutani, Kojima & Kim, 2004	SO 133, GTVA 34, 03°19.021′S, 152°34.849′E, 1448–1484 m
Calyptogena (Archivesica) kilmeri Bernard, 1974	SO 109/2, TVG 115, 44°40′1 N, 125°06′ W, 618 m
Calyptogena (Ectenagena) laubieri Okutani & Métivier, 1986	Kaikoi, Dive KD 5, 33°36.9′N, 137°32.0′E, 3830 m, paratype, MNHN
Calyptogena nankaiensis Okutani, Kojima & Ashi, 1996	JAMSTEC, Dive #897, 34°11.50′N, 137°45.50′E, 1911 m
Calyptogena similaris Okutani, Kojima & Ashi, 1997	Shinkai 6500, Dive #587, 33°40.557′N, 136°33.938′E, 1100 m

The type material is deposited in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M. (SMF) and Zoological Museum of Moscow State University, Moscow (ZMMU).

Abbreviations used in the text:

JAMSTEC, Japan Agency for Earth-Marine Science and Technology, Kanagawa
MNHNCL, National Museum of Natural History, Chile
MNHN, Muséum National d'Histoire Naturelle, Paris
NSMT, National Science Museum, Tokyo
SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M.
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZIN RAN, Zoological Institute of Russian Academy of Sciences; St Petersburg

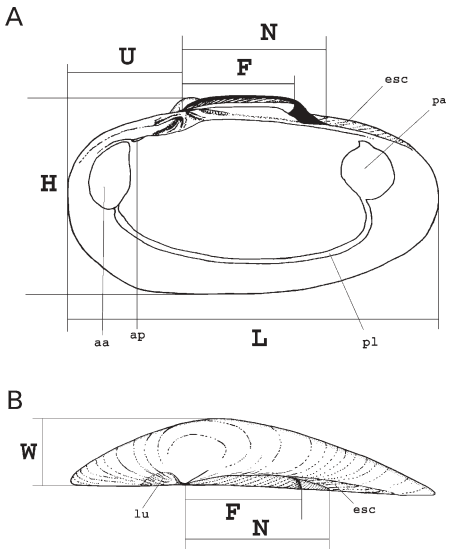

Figure 1. Diagrammatic views of *Calyptogena* illustrating the terminology and measurements applied in this study. **A.** Right valve, internal view. **B.** Right valve, dorsal view. Abbreviations: aa, anterior adductor scar; ap, anterior pedal retractor scar; esc, escutcheon; F, fibrous ligament layer; H, height of valve; L, length of valve; lu, lunule; N, posterior lamellar ligament layer; pa, posterior adductor scar; pl, pallial line; U, distance from umbo to anterior margin; W, width of valve.

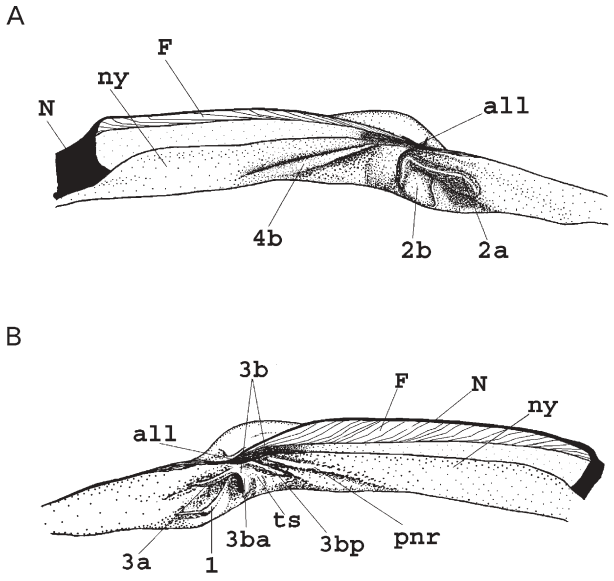

Figure 2. Hinge margins in *Calyptogena*. **A.** Left valve. **B.** Right valve. Abbreviations: 1, ventral cardinal tooth; 2a, anterior ramus of subumbonal cardinal tooth; 2b, posterior ramus of subumbonal cardinal tooth; 3a, anterior ramus of subumbonal cardinal; 3b, posterior ramus of subumbonal cardinal; 3ba, anterior edge of 3b; 3 bp, posterior edge of 3b; ts, top surface of 3b; 4b, posterodorsal cardinal tooth; pnr, posterior nymphal ridge; all, anterior lamellar ligament layer; F, fibrous ligament layer; N, posterior lamellar ligament layer; ny, nymph.

ZMB, Museum für Naturkunde der Humboldt-Universität Berlin, (formerly: Zoologisches Museum der Humboldt-Universität Berlin)
ZMMU, Zoological Museum of Moscow State University, Moscow
F, Length of fibrous ligament
H, Height of valve
L, Length of valve
N, Length of posterior lamellar ligament
RV, Research vessel
Spm, Specimen live-collected
V, Valve
s.l., *Sensu lato*
s.s., *Sensu stricto*
TVG, TV-guided grab
TV-MUC, TV-guided multicorer
Um, Position of umbo (defined above)
W, Width of valve

THE GENUS *CALYPTOGENA*

The nomenclatural history of *Calyptogena* is complicated and up to now the familial placement, composition and the level of the taxon has been the subject of discussion. The genus *Calyptogena* was erected by Dall (1891) for the species *C. pacifica* and placed in the family Carditidae. *Calyptogena pacifica* was the single representative of the genus until 1916, when one more species, *C. elongata*, was described by Dall. Woodring (1938) pointed out the similarity of the hinge structure of *Calyptogena* to that of vesicomyids, placing the genus in the family Vesicomyidae Dall & Simpson, 1901. He also, established two genera closely allied to *Calyptogena*, namely *Ectenagena* (type species *C. elongata* Dall, 1916) and *Phreagena* (fossil type species *P. lasia* Woodring, 1938). Then Woodring (written communication, 1952 in Winterer & Durham, 1962) indicated that *Phreagena* should be synonymized with *Calyptogena*. Later, Okutani (1966) discussed the taxonomic affinities of *Calyptogena* and

treated *Calyptogena* and *Akebiconcha* Kuroda, 1943 as separate genera belonging to the family Cyprinidae. Keen (1969) regarded *Calyptogena s.s.*, *Ectenagena* and *Phreagena* as subgenera of *Calyptogena* in the family Vesicomyidae. Bernard (1974) suggested distinguishing two subgenera of *Calyptogena*: *Calyptogena s.s.* and *Archivesica*. He proposed that *Calyptogena s.s.* should be used for 'heavy shelled forms with dehiscent periostraca and no vestige of the pallial sinus' (Bernard, 1974).

Boss & Turner (1980) distinguished in *Calyptogena s.l.* two subgenera: *Calyptogena s.s.* and *Ectenagena*, which differ from each other mainly by details of the hinge teeth. Their list of species currently referable to the genus *Calyptogena s.s.* includes 12 species, six of which are Recent: *C. pacifica*, *C. kawamurai* (Kuroda, 1943), *C. kilmeri* Bernard, 1974, *C. ponderosa* Boss, 1968, *C. soyoae* Okutani, 1957 and *C. valdiviae* (Thiele & Jaeckel, 1931).

Okutani *et al.* (2000) placed the vesicomyids collected by the Japan Marine Science and Technology Center into two genera, *Vesicomya* and *Calyptogena*. In *Calyptogena*, they distinguished three subgenera: *Calyptogena s.s.*, *Archivesica* and *Ectenagena*. According to the diagnosis, *Calyptogena s.s.* is characterized by thick short shell with apparent escutcheon, >-shaped subumbonal tooth overhanging ventral tooth on the right valve, >-shaped subumbonal tooth on the left valve and apparent posterior lateral tooth. Only one species, *C. fausta* Okutani, Fujikura & Hashimoto, 1993, was included in *Calyptogena s.s.*

In this paper, *Calyptogena* is regarded as a separate genus in the sense of Dall (1891), Woodring (1938) and Scarlato (1981) and corresponds to *Calyptogena s.s.* of Keen (1969), Bernard (1974) and Okutani *et al.* (2000).

SYSTEMATIC DESCRIPTIONS

Family Vesicomyidae Dall & Simpson, 1901

Vesicomyacidae Dall & Simpson, 1901.
Vesicomyidae Keen, 1969.

Genus *Calyptogena* Dall, 1891

Calyptogena Dall, 1891: 189.
Calyptogena—Woodring, 1938: 50.
Calyptogena (Calyptogena)—Bernard, 1974: 11. Okutani *et al.*, 2000: 94.
Calyptogena (Calyptogena)—Boss & Turner, 1980: 185 (in part).

Type species: *Calyptogena pacifica* Dall, 1891 (by monotypy).

Emended diagnosis: Shell usually medium-sized, L to 90 mm, from elongate-elliptical to elongate in outline, usually with nearly straight ventral margin. In nearly every species of genus there are two main variants in shape of posterior part of shell: one more expanded posterodorsally, the other with more elongated posterior part with sloping postero-dorsal margin. Escutcheon present, lunular incision indistinct or missing. Pallial line clearly visible, thick, with somewhat even margins, pallial sinus absent. Anterior adductor scar ovately triangular, somewhat impressed behind. Anterior pedal retractor scar not deeply impressed, located just above and behind anterior scar. Posterior adductor scar larger and less prominent than anterior adductor scar, pear-shaped, pointed dorsally, fused with posterior pedal retractor scar. Ligament external, parivincular, consisting of anterior and posterior lamellar layers and posterior fibrous layer. Anterior lamellar layer running from front of beak backwards behind posteriormost tooth just under fibrous layer, subumbonal pit absent. Posterior lamellar layer running from beak and overlain externally shorter fibrous layer, subtended by usually well-developed nymph. Dentition of right valve: ventral cardinal (1), subumbonal cardinal consisting of two rami (3a and 3b), 3b somewhat broad with anterior and posterior lamellate edges, and posterior nymphal ridge which may be nearly reduced or split into two parallel ridges. Dentition of left valve: subumbonal cardinal tooth with two rami (2a and 2b) and elongated posterodorsal cardinal tooth (4b). Ctenidia comprise inner demibranchs only with descending and ascending lamellae. Between lamellae there are fleshy septa. Retractor of intersiphonal septum fused with ventral surface of posterior adductor and attaches to shell immediately adjacent to it. Inner vulva of inhalant siphon does not bear processes.

Remarks: The genus *Calyptogena* differs from the genera *Phreagena*, *Archivesica*, *Akebiconcha* and *Ectenagena* by the presence of a broad 3b tooth and a right posterior nymphal ridge (see Table 12, Discussion). From *Phreagena*, *Archivesica* and *Akebiconcha*, it is also distinguished by an entire pallial line without a sinus. Additionally, from *Archivesica*, the genus *Calyptogena* differs by the presence of only inner demibranchs instead of both demibranchs, and by the absence of processes on the margin of the inner vulva of the inhalant siphon.

Calyptogena pacifica Dall, 1891
(Figs 3–6)

Calyptogena pacifica Dall, 1891: 190. Dall, 1895: 713, pl. 25, figs 4, 5. Woodring, 1938: 50. Okutani, 1966: 301, pl. 27, figs 1, 3. Boss, 1968: 739, figs 16, 17, 19, 20. Keen, 1969: N664, fig. E 138, 11a, b. Boss, 1970: 70.
Calyptogena (Calyptogena) pacifica—Bernard, 1974: 11, figs 1A, 2A, 3A, 4A–D. Boss & Turner, 1980: 188, figs 10B, C.
Vesicomya (Calyptogena) pacifica—Coan *et al.*, 2000: 341, pl. 70. Goffredi *et al.*, 2003.

Type material: USNM 122549 (syntypes, 59 entire valves, 6 broken valves); USNM 222323 (syntypes, 6 valves); USNM 206424 (syntypes, 2 specimens with dry bodies). Type locality: East Pacific Ocean, Dixon Entrance, Alaska (55°46′N, 132°24′W), 322 fm (580 m) (*Albatross* Stn 3077).

Material examined: Type material. Monterey Bay, Mount Crushmore (36°47.1′N, 122°02.6′W, Barry *et al.* 1996), 630 m, 3 spm. RV *Akademik Mstislav Keldysh*, 22nd cruise, Stn 2320, MIR-2 dive 15/28, 55°23′N, 167°15′E, 489 m, 7 August 1990, 14 spms. RV *Atlantis*, Cruise 131, Alvin dive 2646, 44°40.56′N, 125°06.85′W, 720 m, 3 September 1993, 16 dry spms, 2 intact and 2 broken vs; Alvin dive 2653, 44°40.58′N, 125°07.48′W, 680 m, 12 September 1993, 4 dry spms. RV *Atlantis*, Cruise 9906, Stn AD8, Alvin dive 3422, 44°34.23′N, 125°08.90′W, 778 m, 3 July 1999, 4 spms; Stn AD11, Alvin dive 3423, 44°40′N, 125°06′W, 603 m, 4 July 1999, 1 wet spm, 1 dry spm, 5 vs; Stn AD14, Alvin dive 3424, 44°34.23′N, 125°08.90′W, 777 m, 5 July 1999, 10 wet spms, 35 dry spms; Stn AD25, Alvin dive 3427, 44°40.2′N, 125°05.9′W, 580 m, 8 July 1999, 1 dry spm, 2 intact and 5 broken vs; Stn AD28, Alvin dive 3428, 44°34.13′N, 125°09.15′W, 784 m, 9 July 1999, 1 intact and 4 broken vs; Stn AD32, Alvin dive 3429, 44°34′N, 125°09′W, 774 m, 10 July 1999, 3 wet spms, 10 dry spms, 2 broken vs. RV *Sonne*, Cruise 109/2, Stn 43/1, TVG, 44°40.44′N, 125°06.41′W, 637 m, 2 June 1996, 1 v; Stn 109, TVG; 44°40.17′N, 125°05.796′W, 598 m, 22 June 1996, 23 spms, many vs; Stn 115, TVG; 44°40′N, 125°06′W, 618 m, 22 June 1996, 206 wet, 76 dry spms, many vs; St 121, TVG; 44°40.17′N, 125°05.79′W, 627 m, 22 June 1999, many subfossil valves. RV *Sonne*, cruise 110/1A, stn 4, Ropos dive N 339, sample 415, 44°40.2′N, 125°06.5′W, 635 m, 10 July 1996, 4 vs; st 8, Ropos dive N 340, sample tray 2/3, 44°40.2′N, 125°05.9′W, 600 m, 11 July 1996, 46 spms, 20 vs; stn 9, TVG, 44°40.167′N, 125°05.873′W, 596 m, 12 July 1996, 14 wet spms,

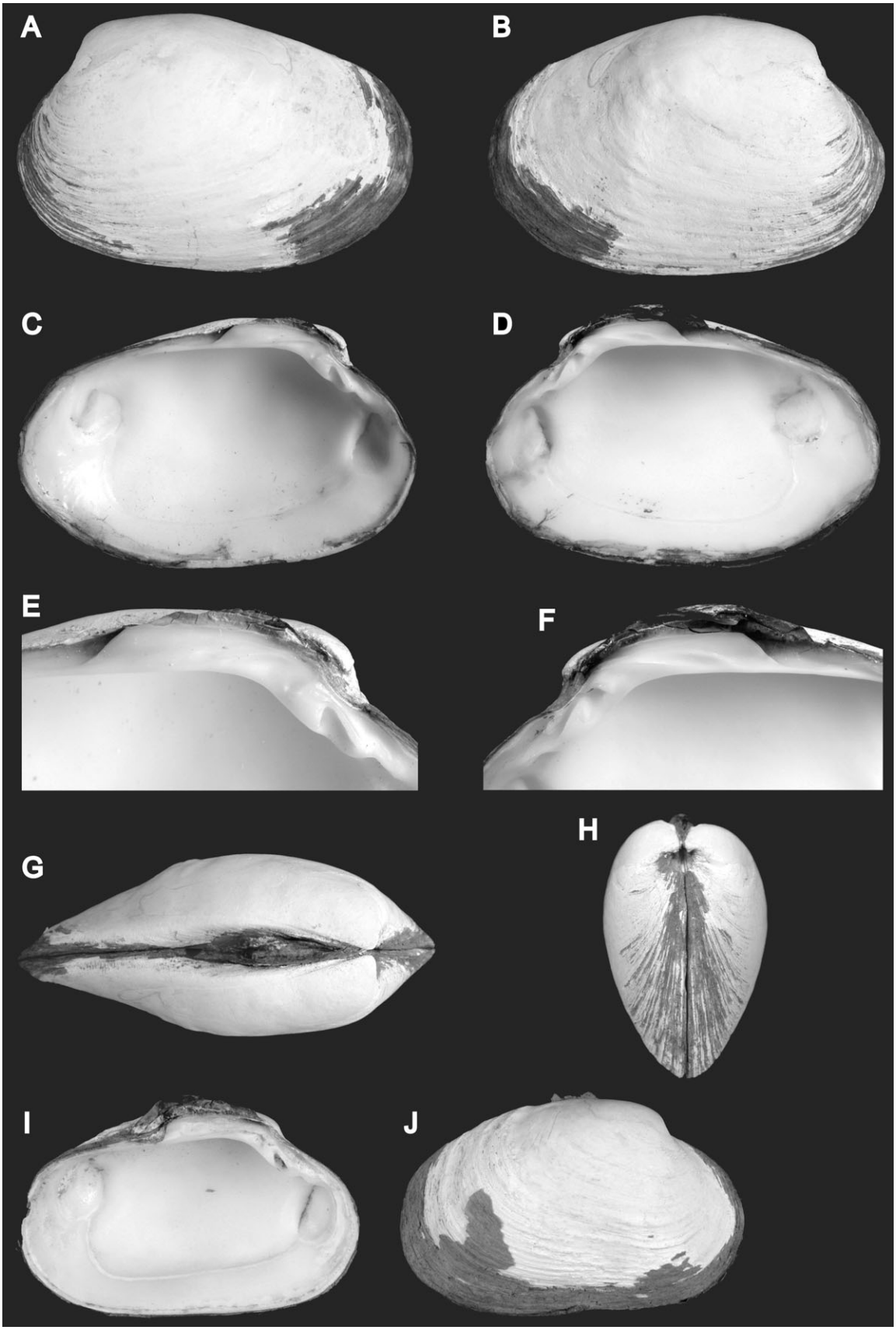

Figure 3. *Calyptogena pacifica* Dall, 1891. **A–H.** RV *Atlantis*, Alvin dive 2646, L = 38.00 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view. **I, J.** RV *Akademik Mstislav Keldysh*, stn 2320, L = 44.2 mm. **I.** Interior of left valve. **J.** Exterior of right valve.

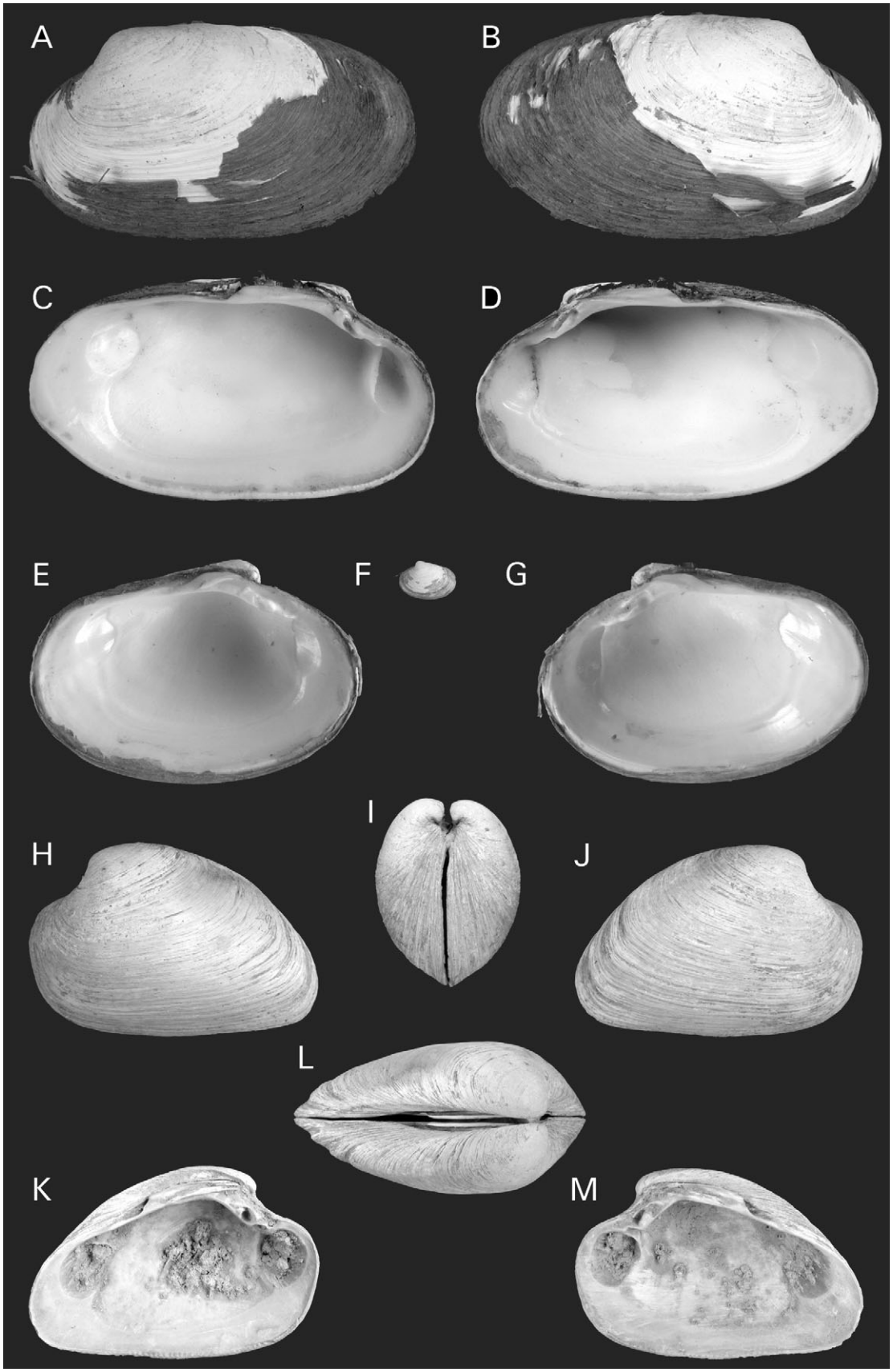

Figure 4. *Calyptogena pacifica* Dall, 1891. **A–D.** Monterey Bay, L = 53 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E–G.** *Sonne*, stn 115, L = 8.5 mm. **E.** Interior of left valve. **F.** Exterior of left valve. **G.** Interior of right valve. **H–M** *Sonne*, stn 121, L = 38.3 mm. **H.** Exterior of left valve. **I.** Anterior view. **J.** Exterior of right valve. **K.** Interior of left valve. **L.** Dorsal view. **M.** Interior of right valve.

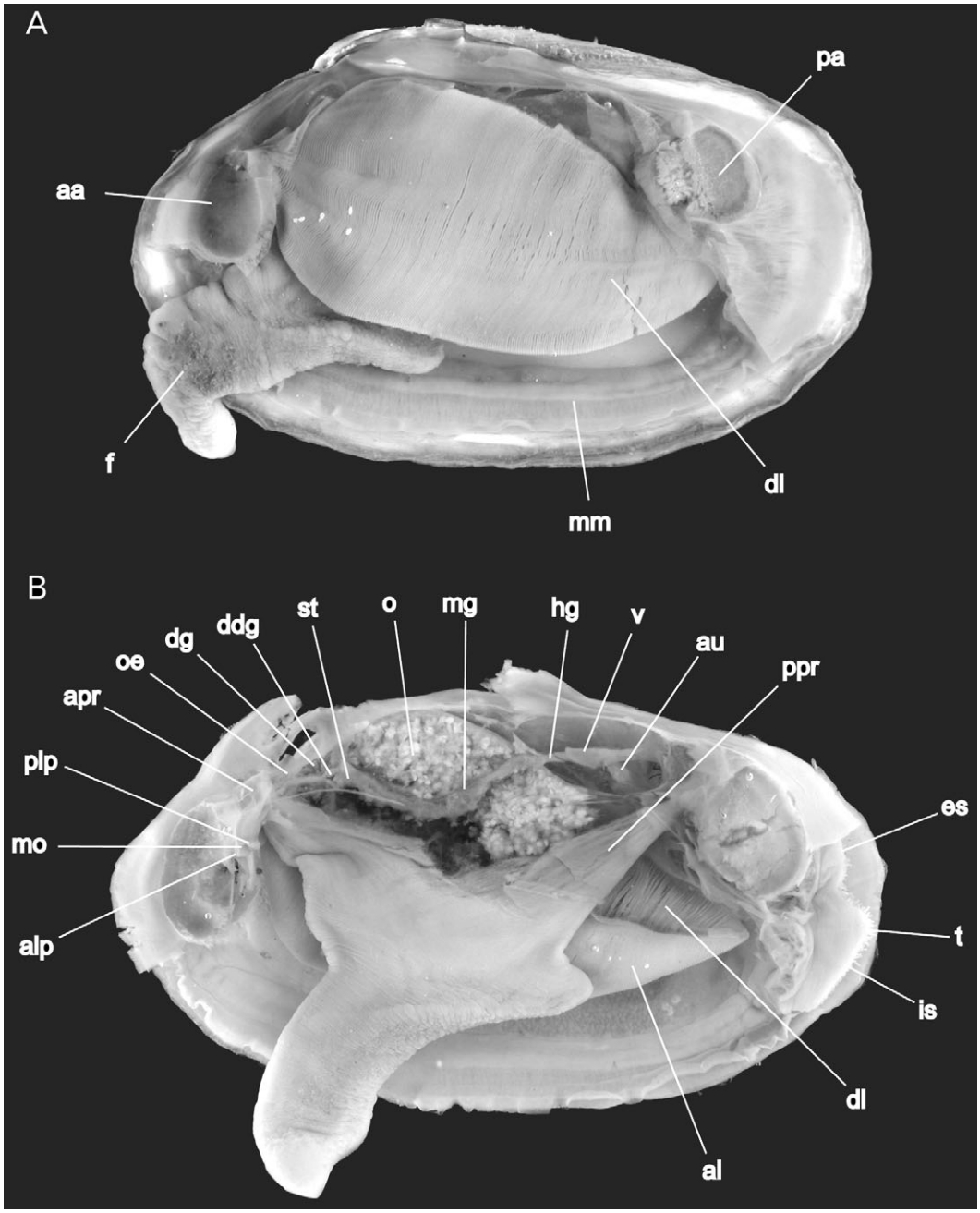

Figure 5. *Calyptogena pacifica* Dall, 1891, RV *Sonne*, st. 187, L = 25.2 mm. **A.** Soft parts as seen from left; L = 26.5 mm: **B.** Soft parts as seen from left, left gill removed. Abbreviations: aa, anterior adductor muscle; al, ascending lamella of demibranch; alp, anterior labial palps; apr, anterior pedal retractor muscle; au, auricle; ddg, ductus of digestive gland; dg, digestive gland; dl, descending lamella of demibranch; es, exhalant siphon; f, foot; hg, hindgut; is, inhalant siphon; mm, mantle; mg, midgut; mo, mouth; o, ovarium; oe, oesophagus; pa, posterior adductor muscle; plp, posterior labial palps; ppr, posterior pedal retractor muscle; st, stomach; t, tentacles; v, ventricle.

83 dry spms, many vs; stn 11, TVG, 44°40.134′N, 125°06.503′W, 524 m, 12 July 1996, 14 spms, many vs. RV *Sonne*, cruise 143, stn 21-1, TVG, 44°34.222′N, 125°08.827′W, 786 m, 15 July 1999, 5 vs; stn 24, MUC, 44°34.223′N, 125°08.805′W, 787 m, 16 July 1999, 2 vs; stn 29-4C, MUC, 44°34.222′N, 125°08.817′W, 787 m, 18 July 1999, 12 dry spms; stn 41-1, TVG, 44°39.957′N, 125°06.091′W, 610 m, 20 July 1999, 7 dry spms, 6 vs; stn 55, MUC, 44°34.2′N, 125°08.85′W, 790 m, 24 July 1999, 13 dry spms; stn 68-2, TVG, 44°43.880′N, 125°13.864′W, 946 m, 27 July 1999, many dry spms, many vs; stn 71-1, TVG (B-10 cm), 44°34.2′N, 125°08.84′W, 787 m, 27 July 1999, 6 vs; stn 105-1F, TV-MUC, 44°34.218′N, 125°08.823′W, 787 m, 6 August 1999, 5 spms; stn 167, TVG, 44°50.263′N, 125°55.681′W, 567 m, 16 August 1999, 2 wet spms, 3 dry spms; stn 185-1, TV-MUC, 44°34.190′N, 125°08.830′ W, 787 m, 18 August 1999, 2 dry spms; stn 187-2H, TV-MUC, 44°34.180′N, 125°08.820′W, 786 m, 19 August 1999, 7 spms; stn 206-2B, TV-MUC, 44°34.182′N, 125°08.835′W, 787 m, 22 August 1999, 2 spms; stn 206-3D, TV-MUC, 44°34.472′N, 125°08.842′W, 786 m, 22 August 1999, 5 spms. RV *Sonne*, Cruise 148, Stn 74, Ropos dive 570, 44°34.1′N, 125°09.2′W, 570 m, 8 August 2000, 13 dry spms.

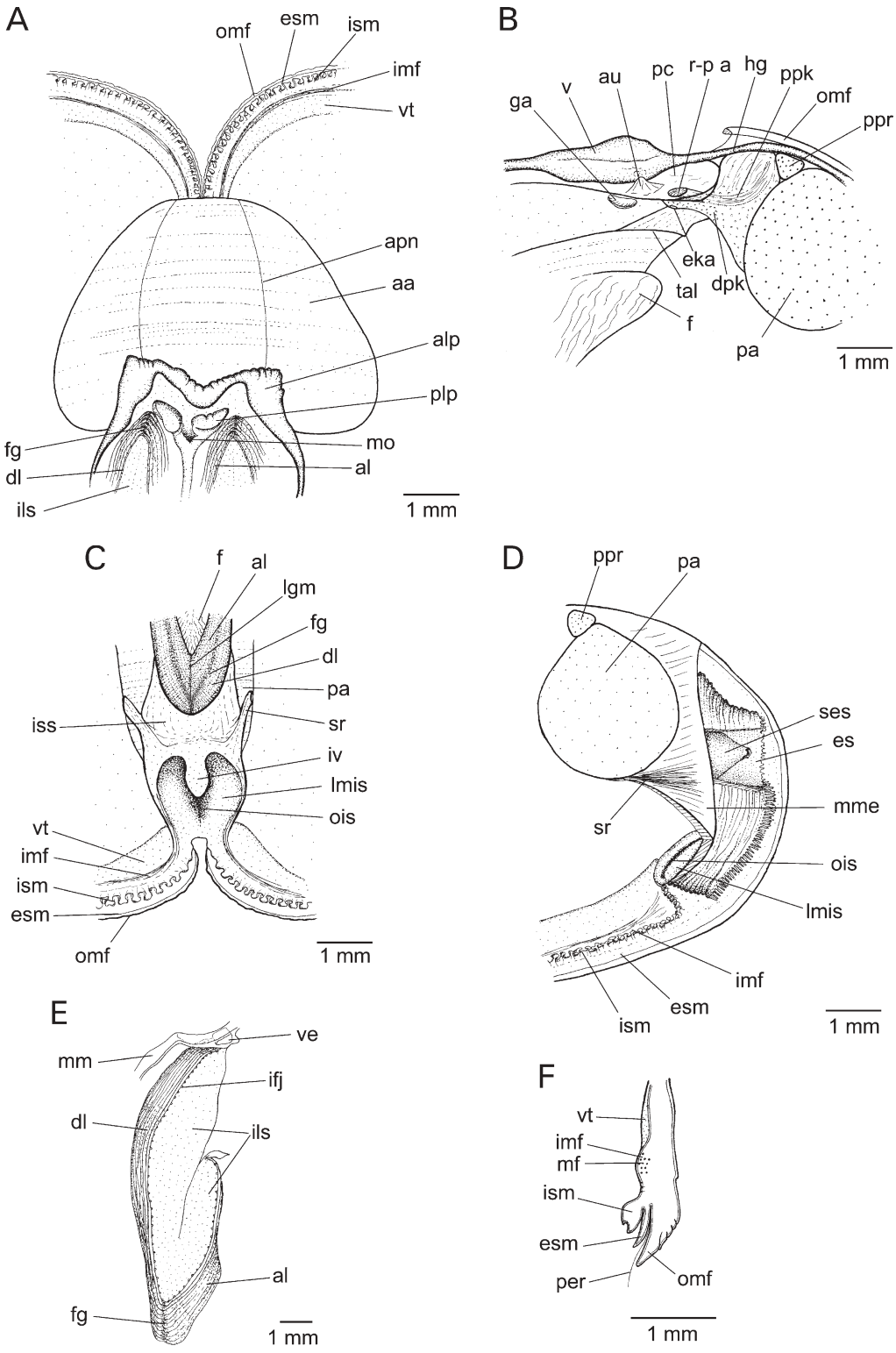

Figure 6. *Calyptogena pacifica* Dall, 1891. Anatomical details. **A.** Ventral view of the labial palps. **B.** Heart and kidney. **C.** Interior view of posterior part of mantle cavity. **D.** Posterior part of the body. **E.** Medial part of ctenidium. **F.** Transverse section through mantle margin. Abbreviations: aa, anterior adductor muscle; al, ascending lamella of demibranch; alp, anterior labial palps; apn, anterior pallial nerve; au, auricle; dl, descending lamella of demibranch; dpk, distal portions of kidney; eka, external kidney aperture; es, exhalant siphon; esm, external sub-fold of middle mantle fold; f, foot; fg, food groove; ga, genital apertures; hg, hindgut; ifj, interfilamental junctions; ils, interlamellar septum; imf, inner mantle fold; is, inhalant siphon; ism, internal sub-fold of middle mantle fold; iss, intersiphonal septum; iv, inner vulva of inhalant siphon; lgm, line of fusion of dorsal margin of ascending demibranchs; lmis, lateral margin of inhalant siphon; mf, muscle fibres; mm, mantle; mme, mantle muscularized envelope; mo, mouth; ois, inner opening of inhalant siphon; omf, outer mantle fold; pa, posterior adductor muscle; pc, pericardial cavity; per, periostracum; plp, posterior labial palps; ppk, proximal portion of kidney; ppr, posterior pedal retractor muscle; r-p a, reno-pericardial aperture; ses, sleeve of exhalant siphon; sr, siphonal retractor; tal – trace of attachment of dorsal margin of ascending lamellar; v, ventricle; ve, blood vessel; vt, vascularized thickening.

Diagnosis: *Calyptogena* species with L to 60 mm, stout, elongate-elliptical, H/L = 0.56–0.65, W/L = 0.18–0.25, ventral margin nearly straight along midpoint, with dehiscent dull periostracum, deep escutcheon, low umbo situated in anterior 24–31% of valve, prosogyrate beaks, stout nymph, fibrous layer of ligament occupying 20–34% of valve length and 61–80% of posterior lamellar layer, 4b-tooth occupying more than half of nymph length (Table 3).

Description: Shell medium-sized, L to 60 mm, solid, elongate-elliptical in outline, equivalve. Periostracum thick, dehiscent, brownish, at periphery with up-standing, short, concentric lamellae, giving velvety appearance. Sculpture consisting of irregular growth lines and low ridges. Nearly all shells corroded to varying extent, especially in umbonal region. Escutcheon deep. Inequilateral, umbo situated in anterior 24–31% of valve. Umbones prosogyrate, low, beaks not touching each other. Anterior margin rounded, ventral margin broadly convex with nearly straight region along ventral midpoint, posterior margin rounded, subtruncate, with postero-dorsal obtuse angle, posterior-dorsal margin slightly convex. Pallial line impressed. Anterior adductor scar ovate-triangular in outline, strongly impressed to rear. Posterior adductor scar more rounded, sometimes slightly impressed, but usually obsolete. Anterior pedal retractor scar shallowly impressed, located just above and behind anterior adductor scar. Posterior pedal retractor scar slightly impressed, fused to posterior adductor scar. Shell margin may be crenulate in anterior and ventral parts. Nymph strong, often with nearly abrupt posterior margin and weak lamellar-ligament fused just after it, fibrous layer of ligament occupying 20–34% of valve length and 61–80% of posterior lamellar layer. Dentition of right valve: ventral cardinal (1) stout, from wedge-like to shelf-like, radiates obliquely anterior; 3a-ramus lamellate, almost parallel to anterior-dorsal shell margin, nearly of same length as (1), more prominent in distal part, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus broad, with slightly concave top surface and lamellate anterior and posterior edges, posterior edge usually more developed and parallel to posterior nymphal ridge, anterior edge may not be parallel to posterior one; posterior nymphal ridge elongate, parallel to posterior-dorsal margin, more expressed in adult specimens and nearly indistinct in juveniles. Dentition of left valve: 2a-ramus lamellate, parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 2b-ramus; 2b-ramus broad, often with slightly rising anterior and posterior edges and concave top surface, radiates ventralwards; 4b-tooth elongate, lamellate in its proximal part, parallel posterior-dorsal shell margin and usually exceeds half of nymph length or more.

Anatomy: Mantle lobes, thin and transparent except at margins. Outer, middle and inner mantle folds present (Fig. 6F). Middle fold is duplicated, divided into internal and external sub-folds near frontal part of anterior adductor. External sub-fold of middle fold is simple and very thin, and borders periostracal groove. Internal sub-fold of middle fold is well developed, bears papillae, larger papillae particularly prevalent anterior-ventrally and posteriorly just below inhalant siphon. Above inner mantle

Table 3. Measurements of right valves of *Calyptogena pacifica*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
USNM no. 222323											
Syntype	43.8	24.7	8.4	11.6	17.3	0.56	0.19	0.67	0.26	0.39	26
Syntype	39.2	23.3	7.8	12.5	17.8	0.59	0.20	0.70	0.32	0.45	27
Syntype	38.9	22.4	7.9	10.7	14.3	0.58	0.20	0.75	0.28	0.37	28
USNM no. 122549											
Syntype	54.7	32.3	11.5	19.3	24.2	0.59	0.21	0.80	0.35	0.44	28
Syntype	41.7	25.2	8.2	11.8	16.3	0.60	0.20	0.72	0.28	0.39	29
Syntype	40.8	23.0	8.1	11.8	16.3	0.56	0.20	0.72	0.29	0.40	27
Syntype	32.0	17.4	6.9	9.5	13.5	0.54	0.22	0.70	0.30	0.42	27
Syntype	30.4	18.2	6.7	8.2	10.7	0.60	0.22	0.77	0.27	0.35	30
USNM no. 206424											
Syntype	37.7	22.9	7.5	10.0	14.4	0.61	0.20	0.69	0.26	0.38	25
Syntype	28.2	17.8	5.9	6.4	10.8	0.63	0.21	0.59	0.23	0.38	29
USNM no. 709147	29.7	17.7	5.2	6.0	10.7	0.60	0.18	0.56	0.20	0.36	29
RV *Sonne*, stn 121	38.3	25.4	9.4	12.1	17.0	0.66	0.25	0.71	0.32	0.44	26
RV *Atlantis*, dive 2646	38.0	24.5	7.3	10.3	16.8	0.64	0.19	0.61	0.27	0.44	30
	36.3	21.7	8.2	12.4	18.8	0.60	0.23	0.66	0.34	0.52	26
	35.3	22.7	7.8	10.3	15.1	0.64	0.22	0.68	0.29	0.43	27
	33.5	19.5	6.3	10.5	14.5	0.58	0.19	0.72	0.31	0.43	30
	32.9	19.4	6.6	9.2	13.0	0.59	0.20	0.71	0.28	0.40	25
	32.9	19.9	6.2	8.0	12.0	0.60	0.19	0.67	0.24	0.36	24
	32.5	20.4	6.4	9.8	15.0	0.63	0.18	0.65	0.30	0.46	22
	29.2	16.9	5.4	8.1	11.6	0.58	0.18	0.70	0.28	0.40	27
	27.2	17.0	5.3	6.7	11.0	0.62	0.19	0.61	0.27	0.40	25
	19.9	12.4	3.6	4.0	7.1	0.62	0.18	0.56	0.20	0.36	31
RV *Keldysh*, stn 2320	54.5	35.4	12.2	18.0	24.4	0.65	0.22	0.74	0.33	0.45	28
	44.4	27.6	9.8	14.0	19.5	0.62	0.22	0.72	0.32	0.44	27
	43.6	28.3	9.5	12.5	18.0	0.65	0.22	0.69	0.29	0.41	31
	42.9	26.6	8.5	12.9	16.4	0.62	0.20	0.79	0.30	0.38	24
	38.7	23.0	8.6	13.4	16.7	0.59	0.22	0.80	0.30	0.35	26

fold there is a vascularized thickening of mantle lobe extending from anterior to posterior adductors. Just dorsal of this vascularized zone there is line of attachment of pallial muscles to shell with the posterior muscles particularly stout. 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. Dorsal mantle fusion involves inner fold and both middle subfolds. Both siphons are formed from fused inner and internal sub-fold of middle folds. Siphons are short, united over their entire length, the posterior part of mantle forming a muscular envelope around them (Fig. 6D). Inhalant and exhalant apertures of nearly equal size, the inhalant siphon more muscular. Inhalant siphon bears 2–4 rows of small tentacles, sometimes the number of rows of tentacles increases in dorsal part of siphon. Exhalant siphon bears fewer rows of tentacles, usually only one. Tentacles differ in size, with rows of larger tentacles located more proximally. Internally, inhalant siphon has on its dorsal side a ventrally directed, triangular flap of muscular tissue. Proximal lateral margin of inhalant siphon thickened. Exhalant siphon with an internal, thin, transparent sleeve. Between siphons there is a septum, which joins with dorsal edge of descending lamellae of ctenidia (Fig. 6C). Intersiphonal septal retractor originating in lateral parts of siphonal septum is fused with ventral surface of posterior adductor and attaches to shell immediately adjacent to it. Anterior and posterior adductor muscles large, posterior muscle oval in section, anterior adductor muscle more elongate.

Foot well developed, rugose in its ventral part, very muscular. Short and shallow byssal groove lies along mid-ventral line of foot and leads to byssal aperture. Aperture of small byssal gland located slightly anterior to heel. Anterior and posterior pedal retractor muscles bifurcate before attaching to shell; anterior pedal retractor muscles insert on shell just posterior and dorsally to anterior adductor muscle, posterior pedal retractor muscles insert on shell dorsally to posterior adductor muscle.

Ctenidia thick, nonplicate, comprising inner demibranch only, with descending and ascending lamellae; the latter half the size of former (Fig. 6E). Filaments of the same lamella connected with each other by interfilamental junctions. Filaments of ascending lamella fused with the filaments of descending lamella by interlamellar septa. Ventral margin of demibranch with shallow food groove.

Margins of ctenidia fused along all its length and dividing mantle cavity into exhalant and inhalant chambers entirely isolated from each other. Anteriormost filaments insert between palps, laterally gill connected by ctenidial axis with visceral mass and by dorsal margin of ascending lamellae with proximal part of foot. Posterior to foot, margin of ascending lamellae fused with each other. Ctenidial muscle arising in distal end of ctenidial axis and inserting on lateral parts of pericardial walls.

Labial palps reduced; outer palps consist of thickened ridge with small plications, running along anteriormost part of ctenidia, inner labial palps smaller, with longitudinal ridges on inner surface (Fig. 6A). Mouth small, rounded, located beneath posterior face of anterior adductor, opening into thin-walled oesophagus. Inner epithelium of oesophagus bears longitudinal folds. Oesophagus enters anterior part of stomach. Anterior half of stomach covered by digestive gland. Stomach thin-walled, small, elongate, with low ridges and grooves on all inner surfaces. Digestive gland opens into anterior part of stomach by ducts, located laterally and lateral-ventrally on right side and laterally on left side. There is no style sac. Midgut leaves postero-ventral end of stomach, running nearly straight without any loops, penetrating ventricle. Rectum ends in an anus located on posterior surface of posterior adductor muscle.

Pericardial cavity large, elongate; pericardial glands located on lateral walls of pericardium and posterior part of auricles. Ventricle thick-walled, muscular, surrounding rectum (Fig. 6B). Auricles thin-walled, triangular, opening into ventricle in its posterior third. Kidneys located between pericardium and posterior adductor muscle. Paired reno-pericardial apertures locate on ventral side of pericardium posteriorly to ostia of auricles (on level of posterior part of ventricle). Pericardial (proximal) portions of kidney tube-like, with ridged inner epithelium. Distal portions of kidney not connected with each other. External apertures open just posterior to genital apertures in excurrent chambers. Sexes separate, large gonads embedded in posterior-dorsal part of visceral mass, adjacent to digestive gland. Genital apertures slit-like, located in excurrent chambers near base of posterior pedal retractor.

Variation: Variations can be seen in the shape and colour of shells, details of sculpture and hinge line. The outline of the shell can be more or less elongate. As in all species of *Calyptogena* there is a variation in the shape of posterior part of shell: some are more expanded posterodorsally (Figs 3A, 3J, 4A), while others are more elongated with sloping postero-dorsal margin (Fig. 4H). This variation in *C. pacifica* was pointed out before by Coan *et al*. (2000) who suggested sexual dimorphism. The relative length of different layers of ligament varies remarkably. The lunular region is usually not impressed, but sometimes incisions that limit the lunule are developed. Hinge teeth also vary: the right cardinal (3a) can be nearly fused with antero-dorsal margin of shell and the right posterior nymphal ridge can be reduced. There are variations in some anatomical details: the number of rows of tentacles around the inhalant siphon varies from 2 to 4, and the number of rows of tentacles around the exhalant siphon can be 1 or 2.

Remarks: Our observations on the anatomy of *C. pacifica* differ from the description by Bernard (1974). We found in our examined material, as well as in the dried soft tissue of syntypes (USNM No 206424), only one inner demibranch in the ctenidium, whereas Bernard noted that *C. pacifica* has ctenidia with both inner and outer demibranchs. Furthermore, at the base of the inhalant siphon of *C. pacifica* there is no flap of tissue with dendritic processes, as pointed out by Bernard (1974).

Distribution: Barents Sea (Piipa volcano), northwestern Pacific, and in eastern Pacific from Dixon Entrance, Alaska to Monterey Bay, California, 489–946 m.

Calyptogena fausta Okutani, Fujikura & Hashimoto, 1993

(Fig. 7)

Calyptogena (Ectenagena) fausta Okutani, Fujikura & Hashimoto, 1993: 122, figs 2–5.

Calyptogena (Calyptogena) fausta—Okutani, Fujikura & Kojima, 2000: 94.

Type material: USMT-Mo 69872 (holotype, 2 dry valves). Type locality: Suruga Bay, 34°55′N, 138°39′E, 1489 m, 29 March 1992 (Shinkai 2000 Dive 596).

Material examined: Holotype only.

Diagnosis: *Calyptogena* species with L to 70 mm, stout, elongate, H/L = 0.50, W/L = 0.14, nearly straight ventral margin, with adherent translucent glossy smooth periostracum becoming wrinkled towards periphery, shallow escutcheon, low umbo situated in anterior 26% of valve, prosogyrate beaks, strong nymph, fibrous layer of ligament occupying 30% of valve length and 66% of posterior lamellar layer, right posterior nymphal ridge split into two parallel ridges, 4b-tooth occupying more than half of nymph length (Table 4).

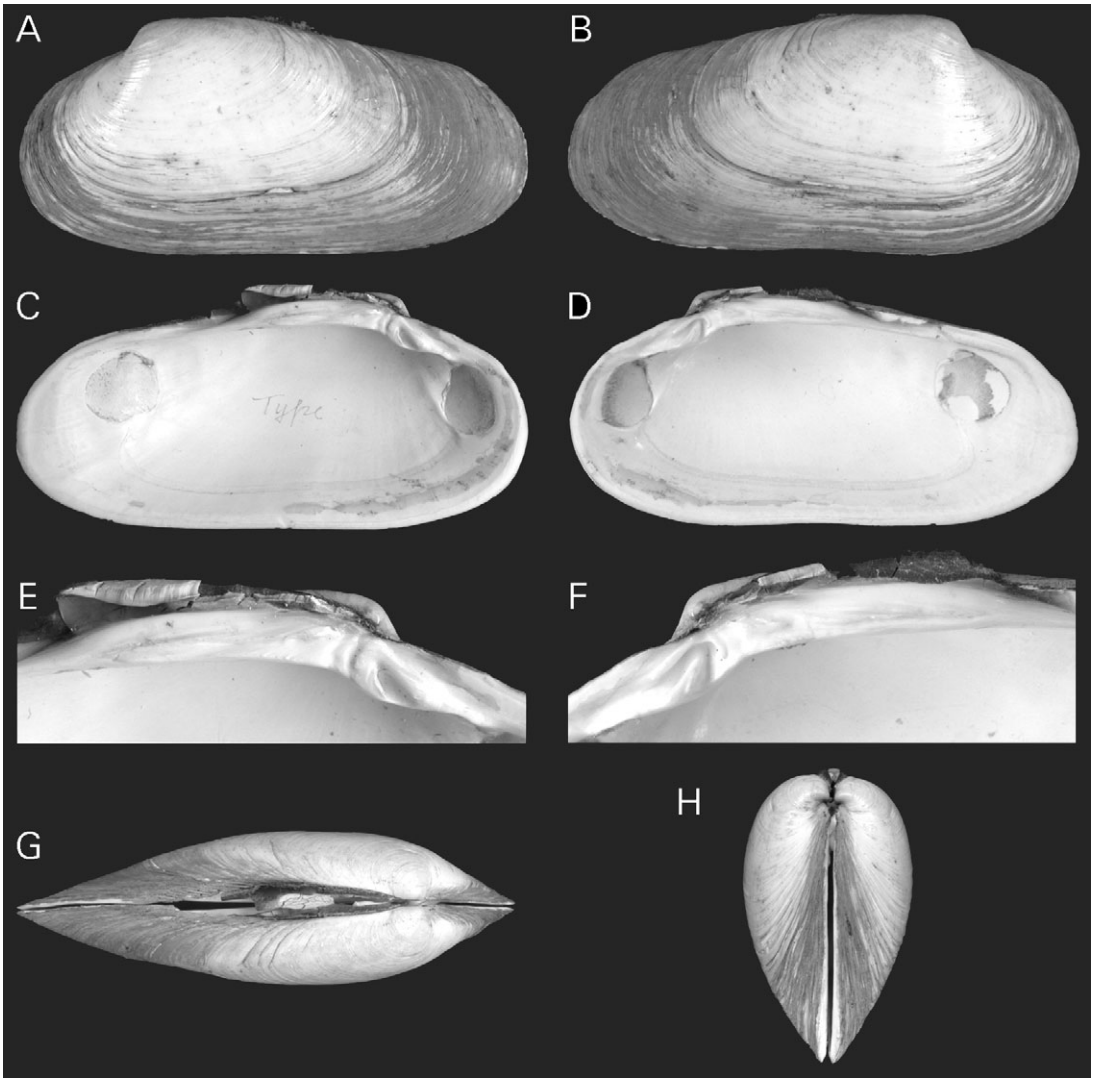

Figure 7. *Calyptogena fausta* Okutani, Fujikura & Hashimoto, 1993, *Shinkai 2000*, Dive 596, holotype, USMT-Mo 69872, L = 61.0 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

Description: Shell medium-sized, L to 70 mm, stout, elongate, equivalve. Periostracum adherent, thin, translucent and glossy in the umbonal region, thicker and wrinkled in marginal region. Sculpture of irregular growth lines and ridges. Escutcheon shallow, lunule indistinct. Inequilateral, umbo situated at 25% from anterior end of valve. Umbones prosogyrate, low. Beaks enrolled, nearly touching each other. Anterior and posterior margins rounded, posterior-dorsal margin has obtuse angle; ventral margin nearly straight, weakly concave. Pallial line distinct but barely impressed. Anterior adductor scar slightly impressed to rear. Posterior adductor clearly visible, shallowly impressed. Nymph strong, with smoothly sloping posterior end, fibrous ligament layer occupies 30% of valve length. Dentition of right valve: ventral cardinal (1) stout, shelf-like with two blunt points, radiates obliquely anteriorwards; 3a-ramus thin, lamellate, nearly parallel to anterior-dorsal shell margin, fused in its low proximal part with anterior edge of 3b-ramus; 3b-ramus broad, with slightly concave top surface and rising lamellate anterior and posterior edges; posterior nymphal ridge split into two low lamellate ridges, distal from which more elongated, parallel to posterior-dorsal margin, occupies nearly all length of nymph. Dentition of left valve: 2a-ramus shelf-like, radiates obliquely anterior, fused in its proximal part with proximal part of 2b-ramus; 2b-ramus broad, radiates ventralwards; 4b-tooth elongate, low and parallel to posterior-dorsal shell margin, occupying more that half of nymph length.

Remarks: The species is morphologically very close to *C. rectimargo* (Table 6). The holotype of *C. fausta* differs from *C. rectimargo* by the presence of a posterior nymphal ridge that is split into two

Table 4. Measurements of right valves of *Calyptogena fausta*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
Holotype, USMT-Mo 69872	61.0	30.0	8.6	18.0	27.1	0.49	0.14	0.66	0.30	0.44	25

low lamellate ridges, occupying more than half of the nymph length, by the more pointed, not truncated posterior margin, the less developed escutcheon and the adherent periostracum. The shape of the shell of *C. fausta* is also similar to that of *C. makranensis* n. sp., from which it differs by the presence of a posterior nymphal ridge that is split into two low lamellate ridges and more prominent umbo, which is placed more anteriorly.

Distribution: Suruga Bay and Yukie Ridge, western Pacific, 1,500–2,000 m (Kojima & Ohta, 1997).

Calyptogena rectimargo **Scarlato, 1981**
(Figs 8, 9)

Calyptogena rectimargo Scarlato, 1981: 390, fig. 410.

Type material: ZIN RAN 9970 (holotype, 2 dry valves). Type locality: East of north Sakhalin, 52°53′N, 144°54′E, 1643 m, 10 August 1932 (RV *Gagara*, St.231).

Material examined: Type material. RV *Akademik M.A. Lavrentyev*, Cruise 28, Stn 21-1, gravity corer, 54°26′N, 144°04′E, 702 m, 17 August 1998, 1 v, 1 broken v; Stn 36-1, dredge, 54°01′N, 146°15′E, 1490–1511 m, 20 August 1998, 1 sp; Stn 37-1, gravity corer, 53°59′N, 146°17′E, 1497 m, 20 August 1998, 2 vs, 4 broken vs; Stn 38-1, trawl, 54°05′N, 146°17′E, 1522–1642 m, 20 August 1998, 2 broken vs. RV *Marshal Gelovani*, Cruise 1, Stn 25-1, trawl, 54°26′N, 144°04′E, 700 m, 14 September 1999, 6 spms, 20 vs, 3 broken vs; Stn 28-1, trawl, 54°26′N, 144°04′E, 700 m, 14 September 1999, 2 spm, 30 vs, 34 broken vs; Stn 29-3, gravity-corer, 54°26′N, 144°04′E, 700 m, 15 September 1999, 8 vs, 8 broken vs.

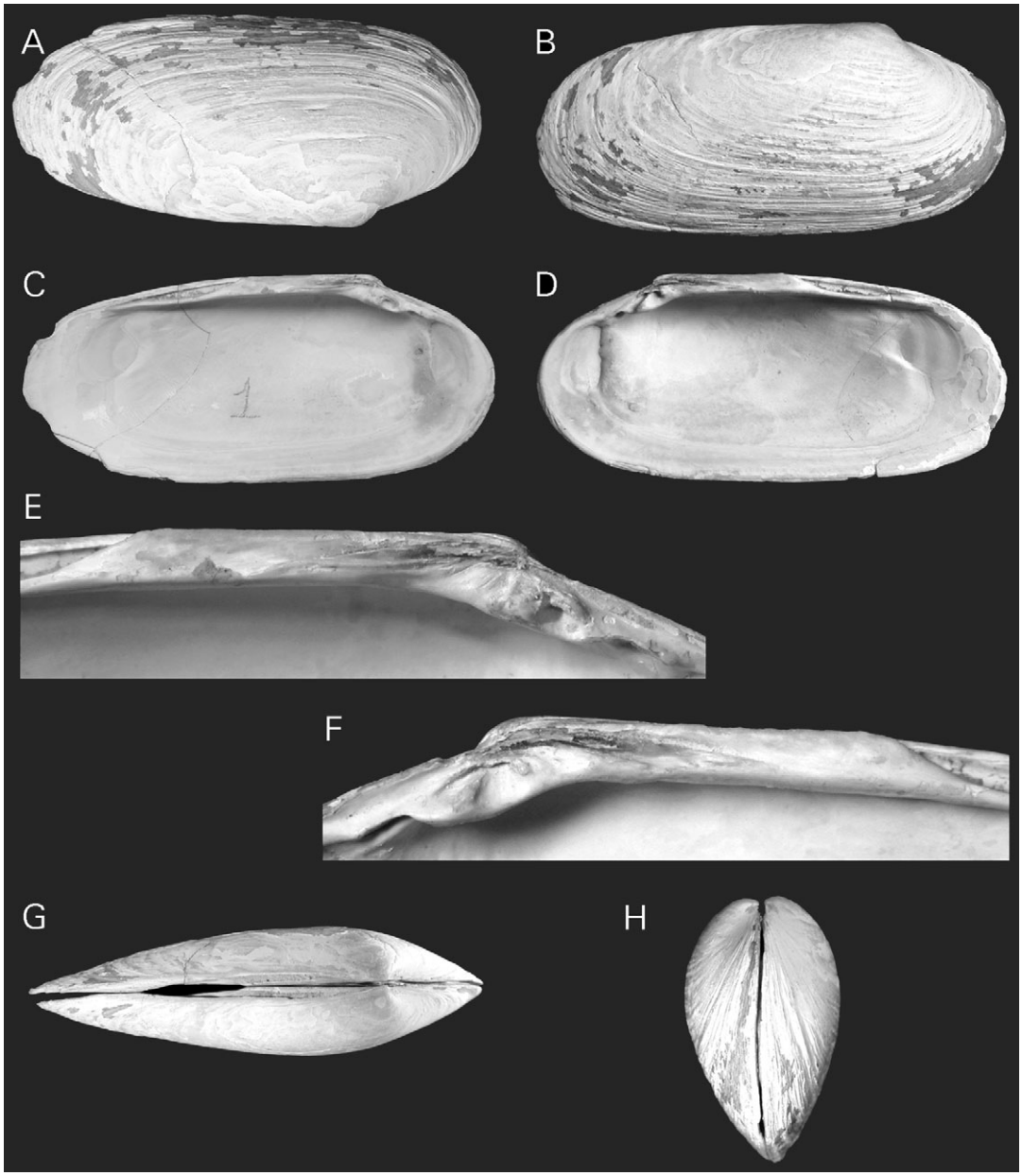

Figure 8. *Calyptogena rectimargo* Scarlato, 1981, RV *Gagara*, stn 231, holotype, ZIN RAN 9970, L = 48.2 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

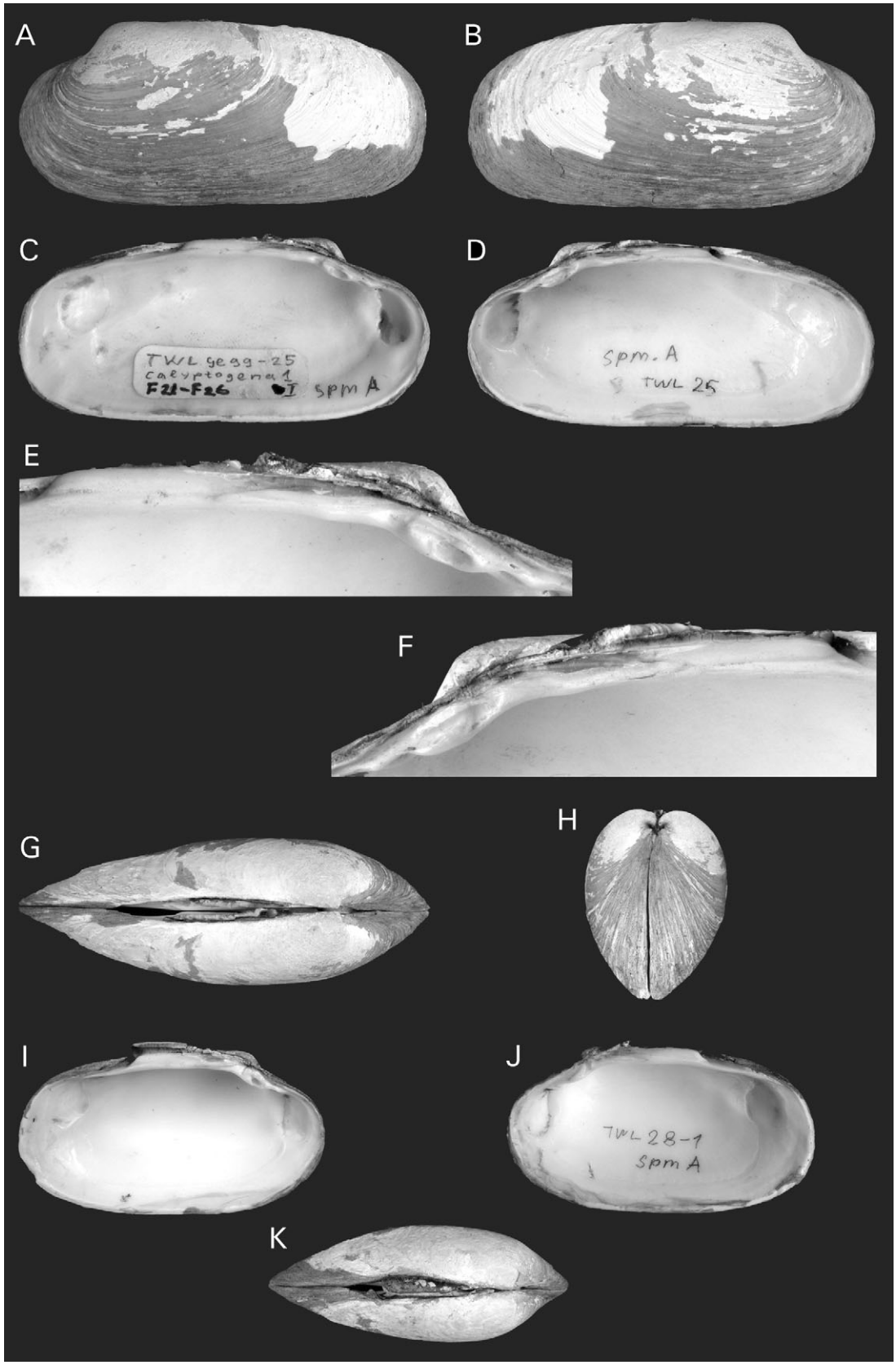

Figure 9. *Calyptogena rectimargo* Scarlato, 1981. **A–H.** RV *Marshal Gelovani*, stn 25-1, L = 68.4 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view. **I–K.** St 28-1, L = 57.5 mm. **I.** Interior of left valve. **J.** Interior of right valve. **K.** Dorsal view.

Diagnosis: *Calyptogena* species with L to 70 mm, stout, elongate, H/L = 0.45–0.56, W/L = 0.14–0.20, ventral margin nearly straight, with dehiscent periostracum becoming strongly wrinkled towards the periphery, moderate escutcheon, low umbo situated in anterior 25–29% of valve, prosogyrate beaks, strong nymph, fibrous ligament layer occupying 24–40% of valve length and 55–77% of posterior lamellar layer, 4b-tooth occupying nearly half of nymph length (Table 5).

Description: Shell medium-sized, L to 70 mm, solid, from elongate-elliptical to subquadrate elongate in outline, equivalve. Periostracum thick, dehiscent, dirty brownish, with short, concentric, upstanding lamellae developed at the periphery. Sculpture consisting of irregular growth lines and ridges. Escutcheon moderate to shallow, lunular region sometimes impressed. Inequilateral, umbo situated at 25–29% from anterior end of valve. Umbones prosogyrate, low. Anterior margin rounded, posterior margin rounded-truncate; ventral margin nearly straight and parallel to dorsal. Pallial line impressed. Anterior adductor scar strongly impressed to rear. Posterior adductor clearly visible. Nymph strong, fibrous ligament layer occupies 25–40% of valve length. Dentition of right valve: ventral cardinal (1) stout, wedge-shaped, radiates obliquely anteriorly; 3a-ramus thin, lamellate, parallel to anterior-dorsal shell margin, sometimes very low and nearly reduced, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus broad, with lamellate anterior and posterior edges and slightly concave top surface, posterior edge usually more developed and parallel to posterior nymphal ridge, anterior edge may not be parallel to posterior one; posterior nymphal ridge elongate, low, more expressed in its distal part, occupies nearly half of nymph length. Dentition of left valve: 2a-ramus lamellate, sub-parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 2b-ramus; 2b-ramus broad, radiates ventralwards; 4b-tooth elongate, low and parallel to posterior-dorsal shell margin, occupying nearly half of nymph length.

Anatomy: All features of genus.

Variation: The shape of shell can be more or less elongated. There is some variation in the size of the escutcheon. The relative length of the different layers of the ligament varies remarkably.

Remarks: Based on the shape of the shell, *C. rectimargo* is most similar to *C. fausta* and *C. makranensis* n. sp. (Table 11). From the first species *C. rectimargo* differs by not having a split posterior lateral tooth in the right valve, a shorter 4b-tooth, which usually occupies not much more than half of the nymph, a more developed escutcheon and dehiscent periostracum. *Calyptogena makranensis* n. sp. differs from the present species by the lower umbo placed more medially.

Distribution: Sea of Okhotsk, east of north Sakhalin, 700–1,643 m.

Calyptogena valdiviae (Thiele & Jaeckel, 1931)

(Figs 10–13)

Vesicomya valdiviae Thiele & Jaeckel, 1931: 229, pl. 9(4), fig. 101.
Calyptogena valdiviae—Boss, 1968: 742. Boss, 1970: 69, figs 3, 4, 22, 25.
Calyptogena (Calyptogena) valdiviae—Boss & Turner, 1980: 190.
'*Vesicomya*' *valdiviae*—Cosel & Salas, 2001: 362, figs 105.
Vesicomya longa Thiele & Jaeckel, 1931: 229, pl. 9(4), fig. 103.
Vesicomya (Archivesica) longa—Boss, 1970: 72, figs 11, 23, 26.
'*Vesicomya*' *longa*—Cosel & Salas, 2001: 363, figs 106.

Type material: Vesicomya valdiviae: ZMB 101.598a (lectotype, 2 valves of the same specimen, selected by Boss (1970)); ZMB 101.598b (paralectotypes, 31 valves, same locality); ZMB 101.599 (paralectotypes, 6 valves, RV *Valdivia*, Stn 103, 35°10.5′S, 23°02′E, 500 m). Type locality: about 230 km E of Morro Garnet, Rio de Oro, West Africa, East Atlantic Ocean, 24°35.3′N, 17°4.7′W, 2480 m, 25 August 1898 (RV *Valdivia*, Stn 33). *Vesicomya longa*: ZMB 101.601 (holotype, 1 right valve); ZMB 101.602 (paratypes, 6 intact valves and 2 broken valves, RV *Valdivia*, St 63, 2°N, 8°04.3′E, 2492 m).

Material examined: Type material.

Diagnosis: *Calyptogena*-species with L to 73 mm, stout, elongate-elliptical, H/L = 0.56–0.65, W/L = 0.19–0.26, with convex ventral margin, adherent, glossy, yellowish periostracum, rather deep escutcheon running along all dorsal-posterior margin, moderately low umbo situated in anterior 30–36% of valve length, prosogyrate beaks, moderately strong nymph, posterior lamellar layer of ligament encompassing 34–47% of length shell, 4b-tooth occupying nearly half of nymph length (Table 6).

Description: Shell medium-sized, L to 73 mm, solid, elongate-elliptical in outline, equivalve. Periostracum thin, adherent, glossy yellowish. Sculpture consisting of irregular growth lines and wrinkles. Escutcheon deep, bordered by sharp dorsal margin, running along all dorsal-posterior side, lunule impressed, indistinct, sometimes limited by shallow incision. Inequilateral, umbo situated 30–36% from anterior end of valve. Umbones prosogyrate, moderately low, beaks enrolled. Anterior-dorsal margin slightly concave and sometimes forms rounded angle with anterior margin, anterior-ventral margin broadly rounded, ventral margin slightly convex, posterior

Table 5. Measurements of right valves of *Calyptogena rectimargo*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
Holotype, ZIN RAN 9970	48.2	21.6	6.7	14.3	23.8	0.45	0.14	0.60	0.30	0.49	27
RV *Marshal Gelovani*											
stn 25-1	68.4	31.3	11.5	24.5	34.7	0.46	0.17	0.71	0.36	0.51	25
	56.3	30.2	10.6	22.6	29.6	0.54	0.19	0.76	0.40	0.53	25
	52.6	25.5	9.2	18.4	25.6	0.49	0.18	0.72	0.35	0.49	25
	51.0	28.2	8.8	12.6	21.6	0.55	0.17	0.58	0.25	0.42	29
	50.8	28.4	10.3	19.7	25.6	0.56	0.20	0.77	0.39	0.50	26
	50.6	28.0	8.6	11.9	21.7	0.55	0.17	0.55	0.24	0.43	28
stn 28-1	57.5	30.8	10.1	21.3	29.2	0.54	0.18	0.73	0.37	0.51	26
	43.4	23.3	7.0	11.3	19.7	0.54	0.16	0.57	0.26	0.45	29

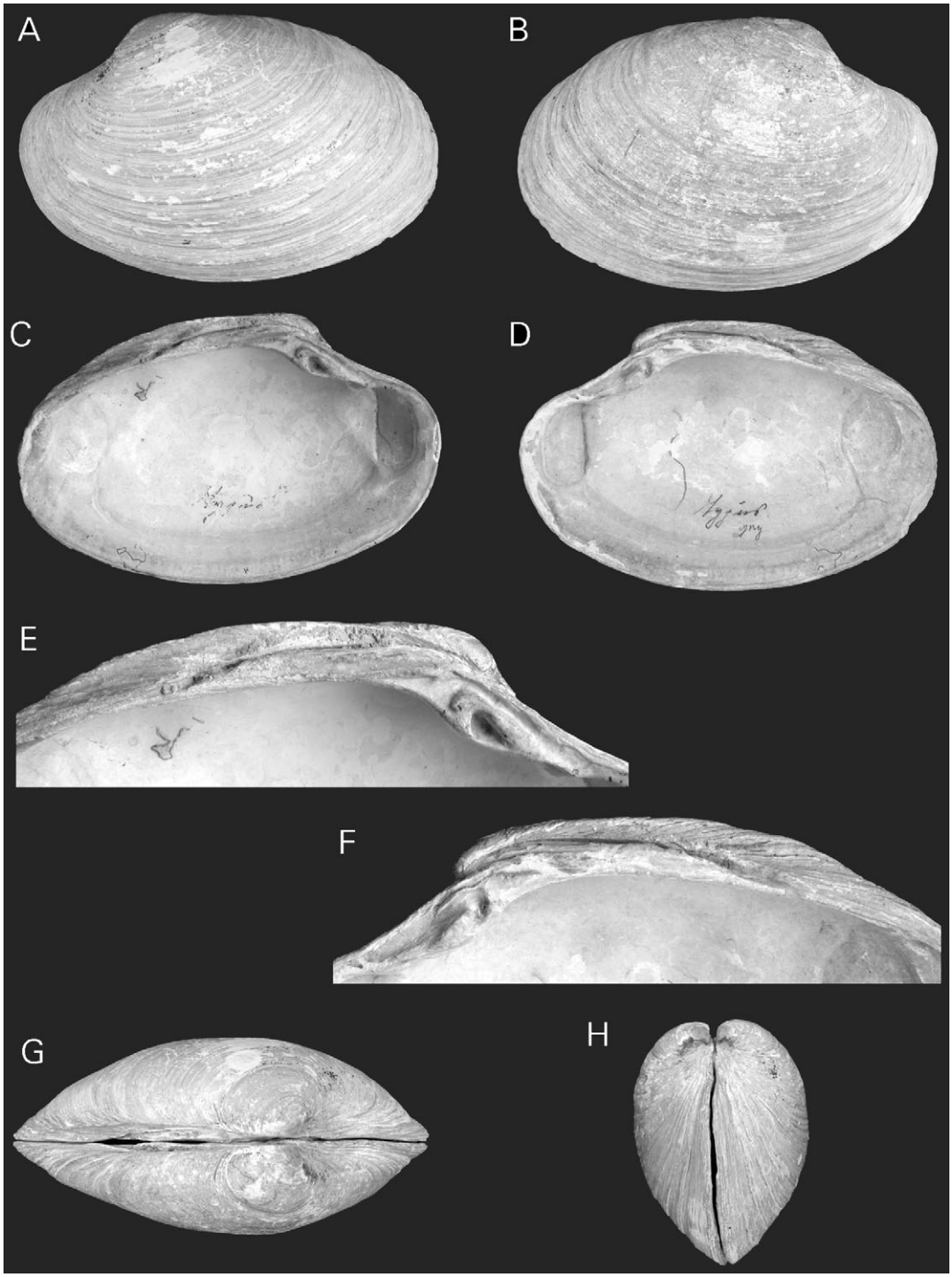

Figure 10. *Calyptogena valdiviae* (Thiele & Jaeckel, 1931), RV *Valdivia*, stn 33, lectotype, ZMB 101.598a, L = 59.2 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

margin rounded-truncate, posterior-dorsal margin usually slightly convex. Pallial line clearly visible, sometimes impressed, more strongly in its anterior part. Anterior adductor scar impressed to rear. Posterior adductor clearly visible, sometimes slightly impressed. Anterior pedal retractor scar shallowly impressed. Nymph moderately strong, with sloping posterior end. Dentition of right valve: ventral cardinal (1) stout, wedge-shaped, radiates obliquely anterior; 3a-ramus lamellate, low, parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus broad, low, with slightly rising anterior and posterior edges and therefore concave top surface, anterior edge usually radiates ventrally, posterior edge parallel to posterior nymphal ridge; posterior nymphal ridge elongate, parallel to posterior-dorsal margin. Dentition of left valve: 2a-ramus shelf-like, parallel to anterior-dorsal shell margin or slightly radiates anterior-ventrally, fused in its proximal part with proximal part of 2b-ramus; 2b-ramus thicker than 2a, radiates ventral-wards;

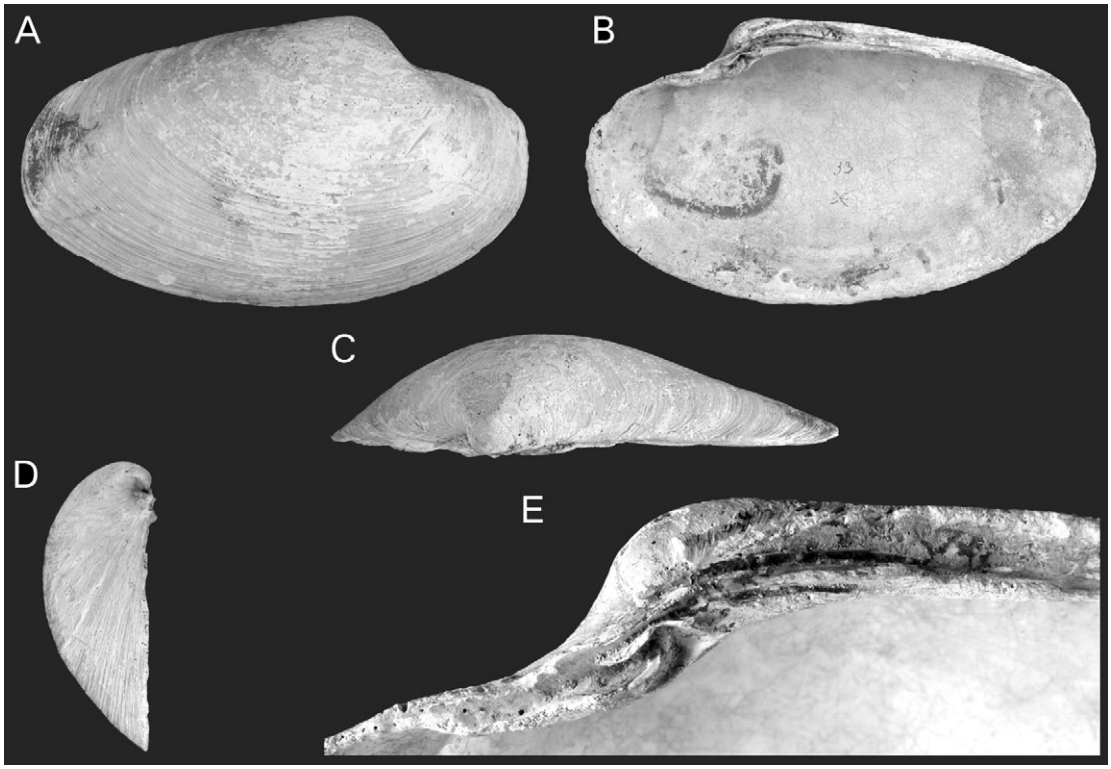

Figure 11. *Vesicomya longa* Thiele & Jaeckel, 1931 [=*Calyptogena valdiviae* (Thiele, & Jaeckel, 1931)], RV *Valdivia*, stn 33, holotype, ZMB 101.601, L = 70.6 mm. **A.** Exterior of right valve. **B.** Interior of right valve. **C.** Dorsal view. **D.** Anterior view. **E.** Right hinge plate.

4b-tooth elongate and parallel to posterior-dorsal shell margin, occupying nearly half of nymph length.

Variation: Variations are seen in the thickness and shape of valves, details of sculpture and dental configuration. The thickness of valves varies from heavy to moderate; the specimens described as *V. longa* are usually more thin-shelled. The escutcheon can be from moderately impressed to deep. The lunular incision, which sometimes limits the lunule, varies from shallow to deep (the deepest one is in the holotype of *V. longa*).

The shape of the shell can be more or less elongate. The position of the umbo and the lengths of the fibrous layers of the ligament vary. The right 3a-ramus can be nearly fused with the antero-dorsal margin, and therefore be indistinct; the posterior nymphal ridge can be reduced. In the left valve, the shape of 2a-ramus varies from lamellate to shelf-like and the angle between 2a- and 2b- rami can range from acute to obtuse. Sometimes the hinge margin is strongly corroded. Two usual main variants in the shape of posterior part of shell are: a more expanded (Figs 10A, 12A) and more elongated form with sloping postero-dorsal margin (Fig. 12E, G).

Remarks: Redescriptions of *Vesicomya valdiviae* and *V. longa* were made by Boss (1970). He selected a lectotype of *V. valdiviae*, compared it with *C. pacifica* and emphasized the similarity between them in the heaviness of the valves, dental configuration and 'weakly sinuate pallial line', which 'are all typical of *Calyptogena*'. On this evidence, he placed *V. valdiviae* in *Calyptogena*. Furthermore, Boss (1970) compared *V. longa* with *V. suavis* Dall, 1913 and found that they have much in common. Since Boss (1970) placed *V. suavis* Dall, 1913 in *Archivesica* Dall, 1925, *V. longa* was also provisionally assigned to *Archivesica*.

Our own comparison of *V. longa* with the holotype of *V. suavis* showed that these two species are remarkably different; for example, a pallial sinus is present in *V. suavis*, but absent in *V. longa*; an escutcheon is absent in *V. suavis*, but present in *V. longa*. Moreover, both species have different hinge margins.

In addition, we compared *V. longa* with *Archivesica gigas* Dall, 1895, the type species of the genus *Archivesica* and found differences between these two species. Firstly, *A. gigas* has an indistinct pallial line with a weak sinus, whereas the pallial line of *V. longa* is clearly visible, sometimes even impressed, and entire. Secondly, there are differences in the hinge structure: in *A. gigas*, the proximal part of the anterior lamellar ligament is placed in a special excavation, the subumbonal pit, just above the posterior hinge tooth, whereas in *V. longa* the subumbonal pit is absent; the 3b-ramus of the right valve of *A. gigas* is thin and lamellate and the posterior nymphal ridge is absent, whereas 3b-ramus of *V. longa* is broad, with concave top surface and slightly rising anterior and posterior ridges and the posterior nymphal ridge is present. Thirdly, *A. gigas* has no escutcheon, while in *V. longa* it is deep and long. These differences clearly demonstrate that *V. longa* should not be included in the genus *Archivesica*.

The shells selected as the types of *V. longa* and *V. valdiviae* were collected at the same station and represent near extreme variants in the range of variability of the available material. The main differences between the right valves of the types of *V. longa* and *V. valdiviae* are manifested in the thickness of valves, in the outline of shell (height/length ratio) and the extent of development of teeth, all of these features more or less fit the range of the variation observed in the paratypes. Some of these differences can be explained by allometric changes, since the length of specimens of *V. valdiviae* ranges from 36 to 62 mm, while the specimens of *V. longa* are larger ranging from 58 to 73 mm. This comparison of *V. longa* with *V. valdiviae* shows that the differences between these two forms fall within the usual range of the intraspecific variation of vesicomyids, and we therefore synonymize the two species.

Distribution: East Atlantic Ocean: off Morocco, 2480 m; Gulf of Guinea, 2492 m; off Knysna, Republic of South Africa, 500 m.

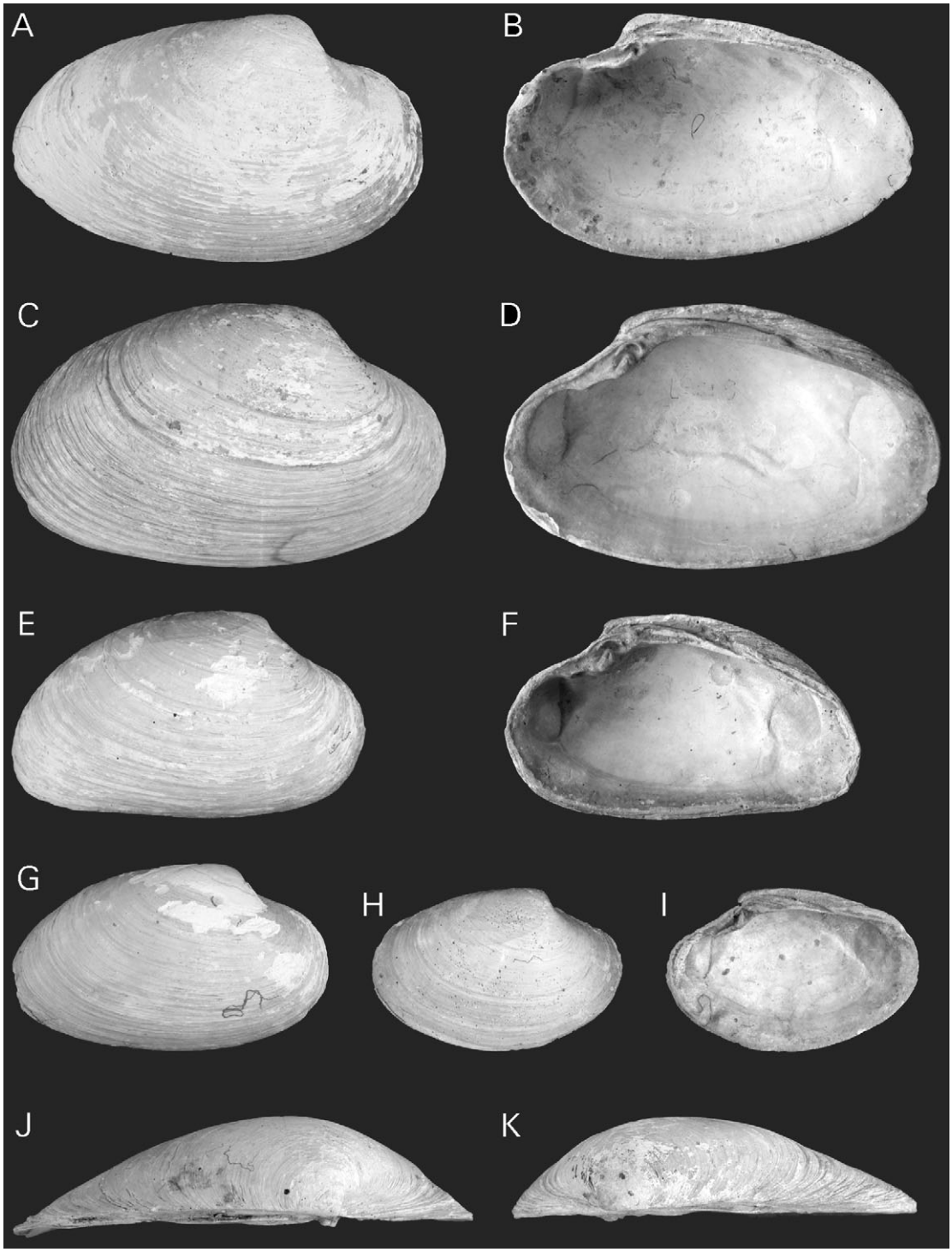

Figure 12. A, B, J. *Vesicomya longa* Thiele & Jaeckel, 1931 [=*Calyptogena valdiviae* (Thiele, & Jaeckel, 1931)], RV *Valdivia*, stn 63, ZMB 101.602, paratype, L = 57.9 mm. **A.** Exterior of right valve. **B.** Interior of right valve. **J.** Dorsal view. **C-I, K.** *Calyptogena valdiviae* (Thiele & Jaeckel, 1931), *Valdivia*, stn 33, ZMB 101.598b. **C, D, K.** Paralectotype, L = 61.9 mm. **C.** Exterior of right valve. **D.** Interior of right valve. **K.** Dorsal view. **E, F.** Paralectotype, L = 50.2 mm. **E.** Exterior of right valve. **F.** Interior of right valve. **G.** Paralectotype, L = 45.2 mm, exterior of right valve. **H, I.** Paralectotype, L = 35.9 mm. **H.** Exterior of right valve. **I.** Interior of right valve.

***Calyptogena gallardoi* Sellanes & Krylova, 2005**
(Fig 14)

Calyptogena gallardoi Sellanes & Krylova, 2005: 970, figs 1–3.

Type material: MNHNCL-200734 (holotype, 2 dry valves); MNHNCL-200735 (paratypes, 4 articulated valves); MNHNCL-200736 (paratypes, 13 separated valves); ZMMU-Ld2999 (2 articulated and 2 separated valves). Type locality: 72 km

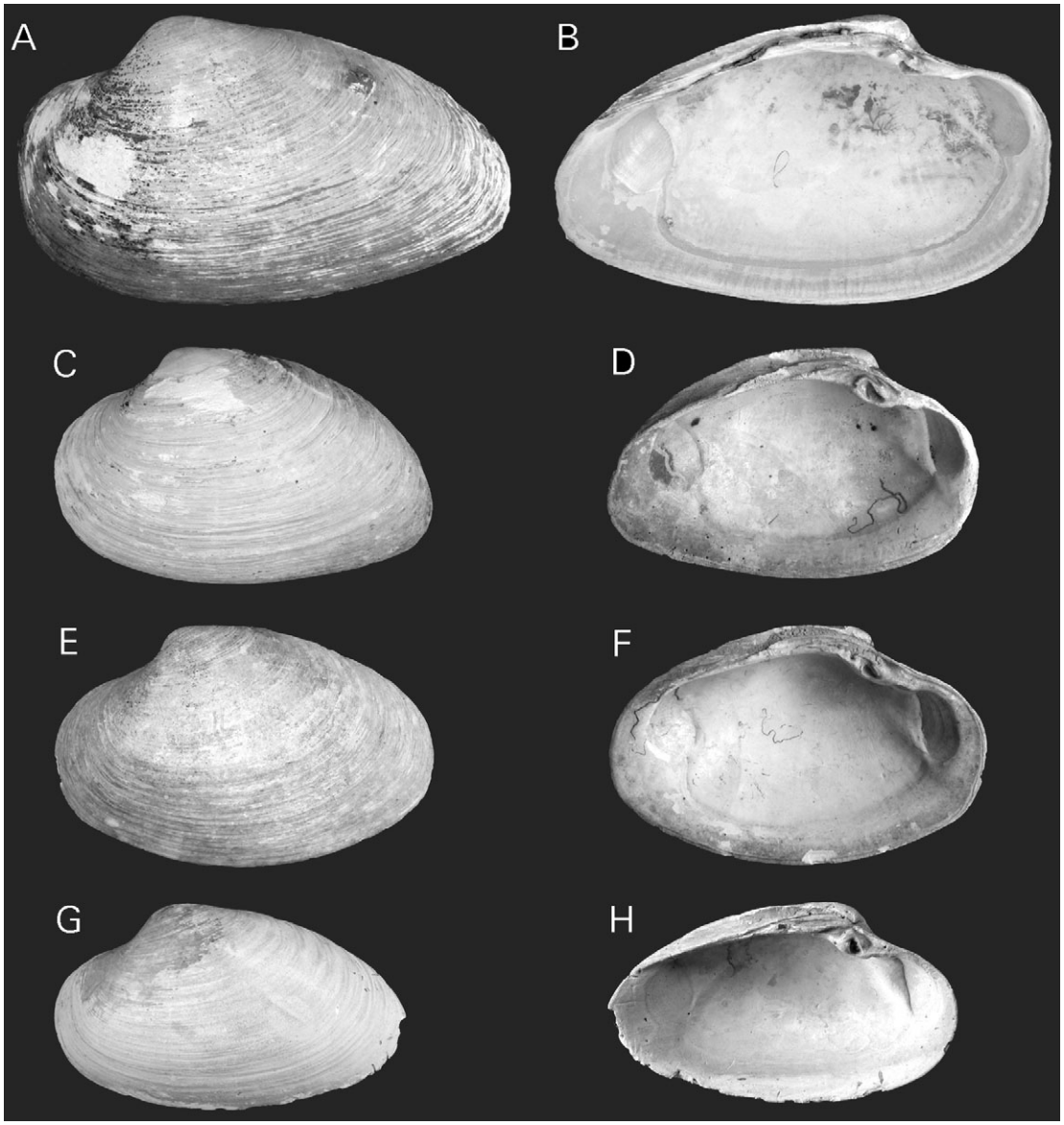

Figure 13. A, B. *Vesicomya longa* Thiele & Jaeckel, 1931 [=*Calyptogena valdiviae* (Thiele, Jaeckel, 1931)], RV *Valdivia*, stn 63, ZMB 101.602, paratype, L = 63.3 mm. **A.** Exterior of left valve. **B.** Interior of left valve. **C–H.** *Calyptogena valdiviae* (Thiele, Jaeckel, 1931). RV *Valdivia*, stn 33, ZMB 101.598b. **C, D.** Paralectotype, L = 47.5 mm. **C.** Exterior of left valve. **D.** Interior of left valve. **E, F.** Paralectotype, L = 49.0 mm. **E.** Exterior of left valve. **F.** Interior of left valve. **G, H.** Paralectotype, L = 45 mm. **G.** Exterior of left valve. **H.** Interior of left valve.

north-west off the Bay of Concepción, 36°22.21′S, 73°42.83′W, 760 m, 2 June 2004 (RV *Kay Kay*, Stn 40).

Material examined: Type material.

Diagnosis: *Calyptogena* species with L to 45 mm, stout, elongate-elliptical, H/L = 0.58–0.63, W/L = 0.18–0.21, ventral margin slightly convex, escutcheon not very deep, umbo situated in anterior 27–31% of valve, prosogyrate slightly enrolled beaks, moderate nymph, fibrous layer of ligament occupying 26–34% of valve length and 62–71% of posterior lamellar layer, 4b-tooth occupying a little more than half of nymph length.

Description: Shell medium-sized, L to 45 mm, stout, elongate-elliptical in outline, equivalve. Periostracum brownish, nearly absent except meagre remnant present mainly on periphery of ventral margin. Sculpture of irregular growth lines and wrinkles. Escutcheon moderate, sometimes lunular incision developed. Inequilateral, umbo situated at 27–31% from anterior end of valve. Umbones prosogyrate, not very low. Beaks slightly enrolled, not touching each other.

Antero-dorsal margin nearly straight or slightly convex, anterior margin broadly rounded, ventral margin slightly convex, posterior margin from tapering to rounded and postero-dorsal margin nearly straight or slightly convex. Pallial line somewhat broad, not impressed. Anterior adductor scar ovately conic, posterior margin of anterior adductor scar slightly impressed to rear. Anterior pedal retractor scar shallow. Posterior adductor scar slightly impressed anteriorly, square-rounded, fused to posterior pedal retractor scar. Nymph not strong, with sloping posterior end. Along posterior part of base of nymph, there is slight depression. Fibrous layer of ligament attaching to nymph comprises 62–71% of posterior lamellar layer and 26–34% of valve length. Dentition of right valve: ventral cardinal (1) stout, shelf-like, radiates obliquely

Table 6. Measurements of valves of *Calyptogena valdiviae* and *Vesicomya longa*.

	L (mm)	H (mm)	W (mm)	N (mm)	H/L	W/L	N/L	Um (%)
Lectotype *V. valdiviae* ZMB 101.598a								
Right valve	59.2	38.4	12.6	27.8	0.65	0.21	0.47	31
Paralectotypes *V. valdiviae* ZMB 101.598b								
Right valve	61.9	37.6	14.5	28.0	0.61	0.23	0.45	33
Right valve	60.0	38.4	14.3	24.0	0.58	0.24	0.40	32
Right valve	55.0	34.5	11.5	22.2	0.63	0.21	0.40	33
Right valve	51.6	33.5	10.9	23.7	0.65	0.21	0.46	34
Right valve	50.2	29.2	12.3	19.3	0.58	0.26	0.38	34
Right valve	49.2	28.1	10.6	18.0	0.57	0.22	0.37	35
Left valve	49.0	31.3	10.8	20.0	0.63	0.22	0.41	35
Right valve	45.2	26.5	10.0	19.0	0.59	0.22	0.42	33
Left valve	45.0	26.0	9.9	15.0	0.58	0.22	0.33	33
Right valve	35.9	23.4	7.1	13.1	0.65	0.20	0.36	36
Paralectotypes of *V. valdiviae* ZMB 101.599								
Right valve	56.0	35.2	12.5	23.0	0.63	0.22	0.41	33
Right valve	45.4	27.2	12.0	17.4	0.60	0.26	0.38	36
Holotype of *V. longa* ZMB101.601								
Right valve	70.6	39.7	14.7	26.0	0.56	0.21	0.37	34
Paratypes of *V. longa* ZMB 101.602								
Right valve	73.1	42.0	16.0	29.5	0.57	0.22	0.40	35
Left valve	72.0	41.8	15.2	30.0	0.58	0.21	0.42	31
Left valve	71.3	42.5	15.7	31.3	0.60	0.22	0.44	31
Left valve	63.3	36.4	14.4	26.5	0.58	0.23	0.42	30
Left valve	61.2	34.2	11.5	21.0	0.56	0.19	0.34	32
Right valve	57.9	34.3	12.2	25.0	0.59	0.21	0.43	34

anteriorwards; 3a-ramus lamellate, almost parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus broad, with slightly concave top surface and slightly rising anterior and posterior edges; posterior lateral obsolete, occupying a little more than half of nymph length. Dentition of left valve: 2a-ramus lamellate, parallel to anterior-dorsal shell margin, fused in its proximal part with the anterior edge of 2b-ramus; 2b-ramus broad, radiates ventralwards; 4b-tooth elongate, low, occupying a little more than half of nymph length.

Variation: The shape of the shell can be more or less elliptical. The nymph varies from weak to moderate; the depression along the posterior part of the base of the nymph can be more developed.

Remarks: Based on the elongate-elliptical shape of the shell, *C. gallardoi* is most similar to *C. pacifica*, *C. goffrediae* n. sp. and *C. starobogatovi* n. sp. From *C. pacifica* the present species differs by a less developed escutcheon, weaker nymph with sloping posterior margin, and less developed 4b-tooth in the left valve and posterior nymphal ridge in the right valve. *Calyptogena goffrediae* n. sp. differs from *C. gallardoi* by having a shallower escutcheon, more curved beaks and a more expanded antero-dorsal shell region. From *C. starobogatovi* the present species differs by the umbo, placed more anteriorly and by the absence of a glossy periostracum.

Distribution: 72 km north-west off the Bay of Concepción, south-central Chile East Pacific Ocean (36°22.21′S 73°42.83′W), 760 m.

***Calyptogena goffrediae* new species**
(Figs 15, 16)

Type material: SMF 327534 (holotype, dry valves); SMF 327535 (paratype, dry valves); SMF 327536 (paratype, dry valves); SMF 327537 (2 paratypes, dry valves); ZMMU Ld-3000 (4 paratypes, dry valves). Type locality: Paita, Peru, East Pacific Ocean (5°35.06′S, 81°38.53′W), 3136 m.

Material examined: RV *Sonne*, Cruise 146, Stn 1, TVG; 5°35.06′S, 81°38.53′ W, 3136 m, 17 March 2000, 10 specimens without soft parts (including holotype and 8 paratypes).

Diagnosis: *Calyptogena*-species with L to 38.1 mm, moderately stout, elongate-elliptical, H/L = 0.56–0.67, W/L = 0.17–0.22, ventral margin slightly convex with nearly straight region along ventral midpoint, with adherent grayish-brownish periostracum becoming more wrinkled towards periphery, shallow escutcheon, indistinct lunule, umbo situated in anterior 29–32% of valve length, prosogyrate enrolled beaks, weak nymph, fibrous layer of ligament occupying 17–30% of valve length and 47–75% of posterior lamellar layer (Table 7).

Description of holotype: Shell moderately solid, elongate-elliptical in outline, H/L = 0.56, equivalve. Periostracum adherent, translucent, thin, grayish. Sculpture of irregular growth lines and wrinkles. Escutcheon shallow, lunule indistinct. Inequilateral, umbo situated at anterior 29% of valve length. Umbones prosogyrate, not very low. Beaks enrolled, nearly touching each other. Antero-dorsal margin slightly convex, anterior margin rounded-truncated, ventral margin slightly convex, posterior margin rounded, posterodorsal margin straight. Pallial line not impressed, pallial sinus absent. Anterior adductor scar irregularly oval, posterior margin of anterior adductor scar slightly impressed to rear. Anterior pedal retractor scar shallow. Posterior adductor scar not impressed, pear-shaped, fused to posterior pedal retractor scar. Nymph weak, with sloping posterior end, occupies 23% of valve length. Along all the base of nymph, there is very slight depression. Fibrous layer of ligament, attaching to nymph, is 65% of posterior lamellar layer. Dentition of

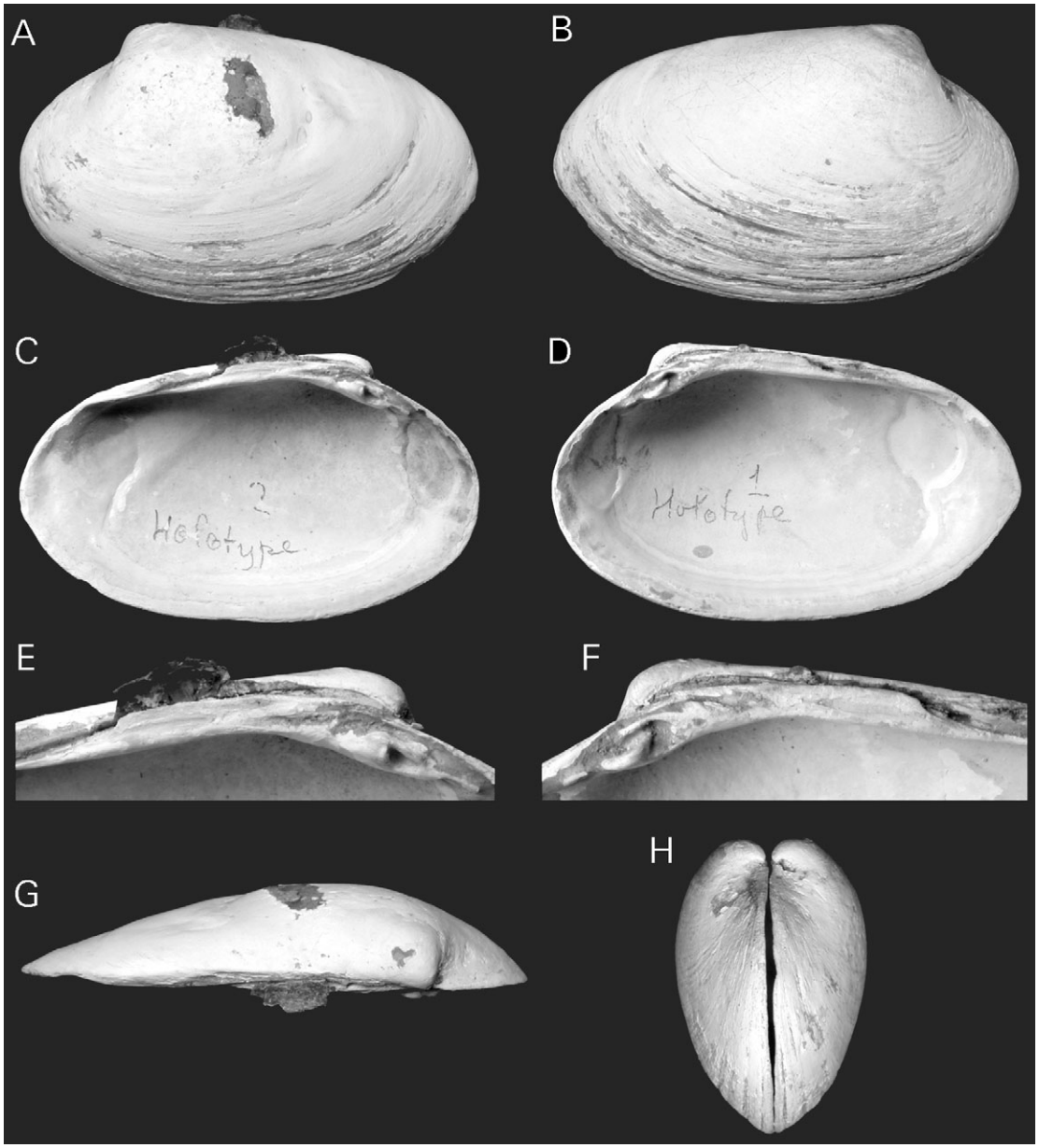

Figure 14. *Calyptogena gallardoi* Sellanes & Krylova, 2005, RV *Kay Kay*, stn 40, holotype, MNHNCL-200734, L = 41.3 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view of left valve. **H.** Anterior view.

right valve: ventral cardinal (1) stout, shelf-like, radiates obliquely anterior-wards; 3a-ramus lamellate, short, almost parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus broad, with slightly concave top surface and slightly rising anterior and posterior edges; posterior nymphal ridge very low. Dentition of left valve: 2a-ramus lamellate, parallel to anterior-dorsal shell margin, fused in its proximal part with anterior edge of 2b-ramus; 2b-ramus broad, radiates ventralwards; 4b-tooth elongate, low, weak, occupying less than half of nymph.

Variation: Variations can be seen in the shape of valves and in the dental configuration. Shell shape can be more or less elongate and the outlines of the anterior and posterior margins can vary from rounded to subtruncate. Younger specimens usually have more rounded anterior margins and truncate posterior margins. The ventral margin can be more or less convex. The lengths of fibrous layers vary; more elongate fibrous layers of the ligament are found in larger specimens. In the right valve, the ventral cardinal (1) can range from thin and shelf-like to stout and wedge-like; the 3a-ramus can be nearly fused with the antero-dorsal margin, and therefore be indistinct; the right posterior nymphal ridge can be reduced.

Remarks: The elongate-elliptical shape of *C. goffrediae* n. sp. is most similar to *C. pacifica*, *C. gallardoi* and *C. starobogatovi* n. sp., from all of which it differs by the enrolled beaks, adherent periostracum and more expanded anterior-doral shell region (Table 11). Additionally, from *C. pacifica* the present species differs by having a thinner shell, a shallower escutcheon and a weaker nymph, and from *C. starobogatovi* by the more anteriorly placed umbo.

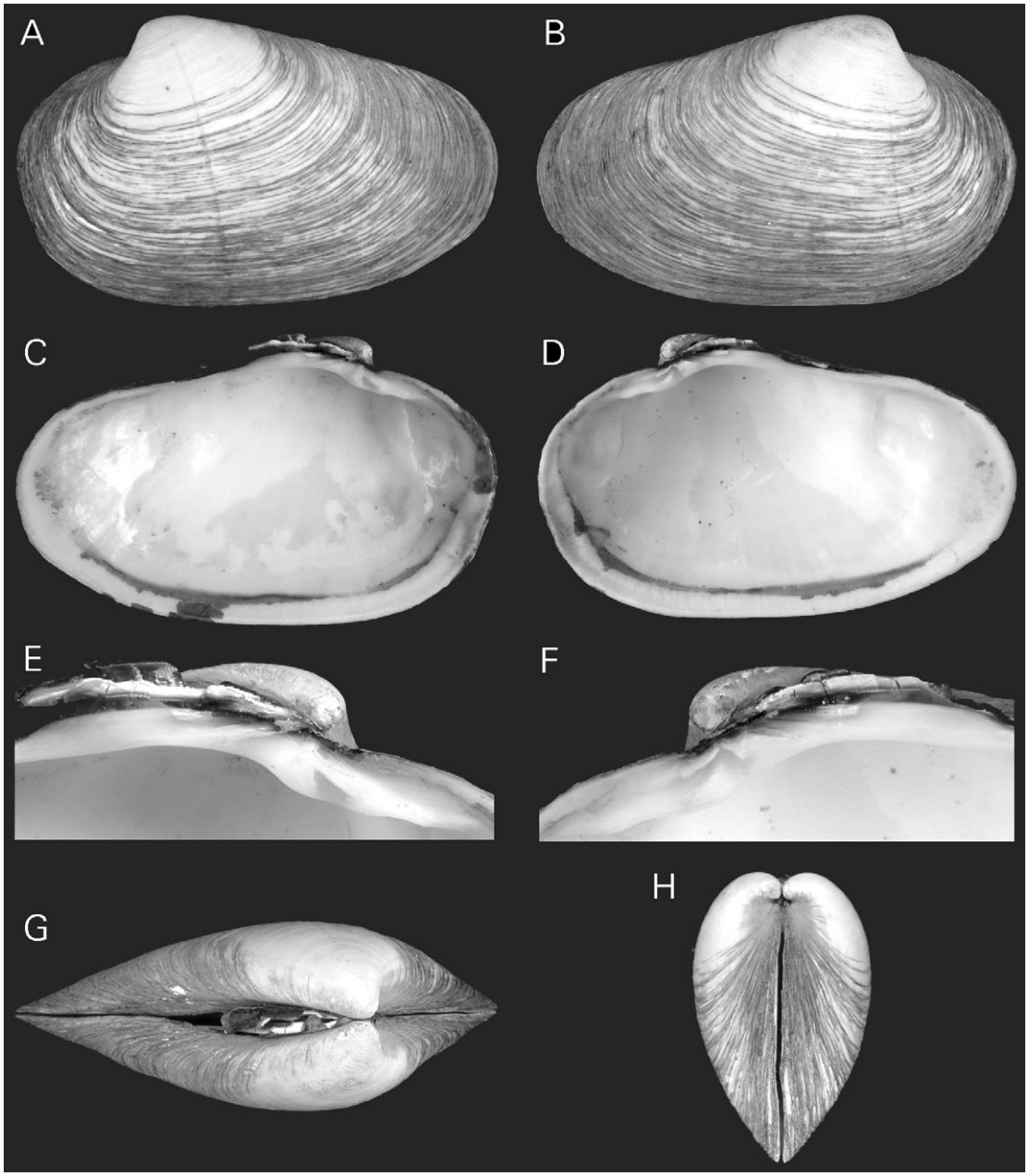

Figure 15. *Calyptogena goffrediae* n. sp., RV *Sonne*, stn 1, holotype, SMF 327534, L = 38.1 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

Distribution: Paita, Peru, East Pacific (5°35.06′S, 81°38.53′W), 3136 m.

Etymology: Named for Shana Goffredi (California Institute of Technology, USA) who has made a great contribution to the biology of symbiotrophic bivalves.

***Calyptogena starobogatovi* new species**
(Figs 17, 18)

Type material: ZMMU Ld-3001 (holotype, with soft parts); ZMMU Ld-3002 (2 paratypes, dry valves); SMF 327538 (paratype, dry valves); SMF 327539 (3 paratypes, dry valves). Type locality: Axial Seamount, Juan de Fuca Ridge, East Pacific Ocean (45°55.63′N, 130°01.81′W), 1540 m.

Material examined: RV *Akademik Mstislav Keldysh*, 12th cruise, stn 1505, 'Pisces XI', 45°55′N, 130°01′W, 1540 m, 26 September 1986, 36 specimens (including holotype and 6 paratypes).

Diagnosis: *Calyptogena* species with L to 42 mm, moderately stout, elongate-elliptical, H/L = 0.58–0.66, W/L = 0.16–0.21, with slightly convex ventral margin, adherent glossy yellowish periostracum, shallow escutcheon, low umbo situated in anterior 32–39% of valve length, usually corroded nearly orthogyrate beaks, nymph moderately strong but short, fibrous layer of ligament occupying 12–24% of valve length and 44–59% of posterior lamellar layer (Table 8).

Description of holotype: Shell subsolid, elongate-elliptical in outline, H/L = 0.59, equivalve. Periostracum adherent, thin, glossy,

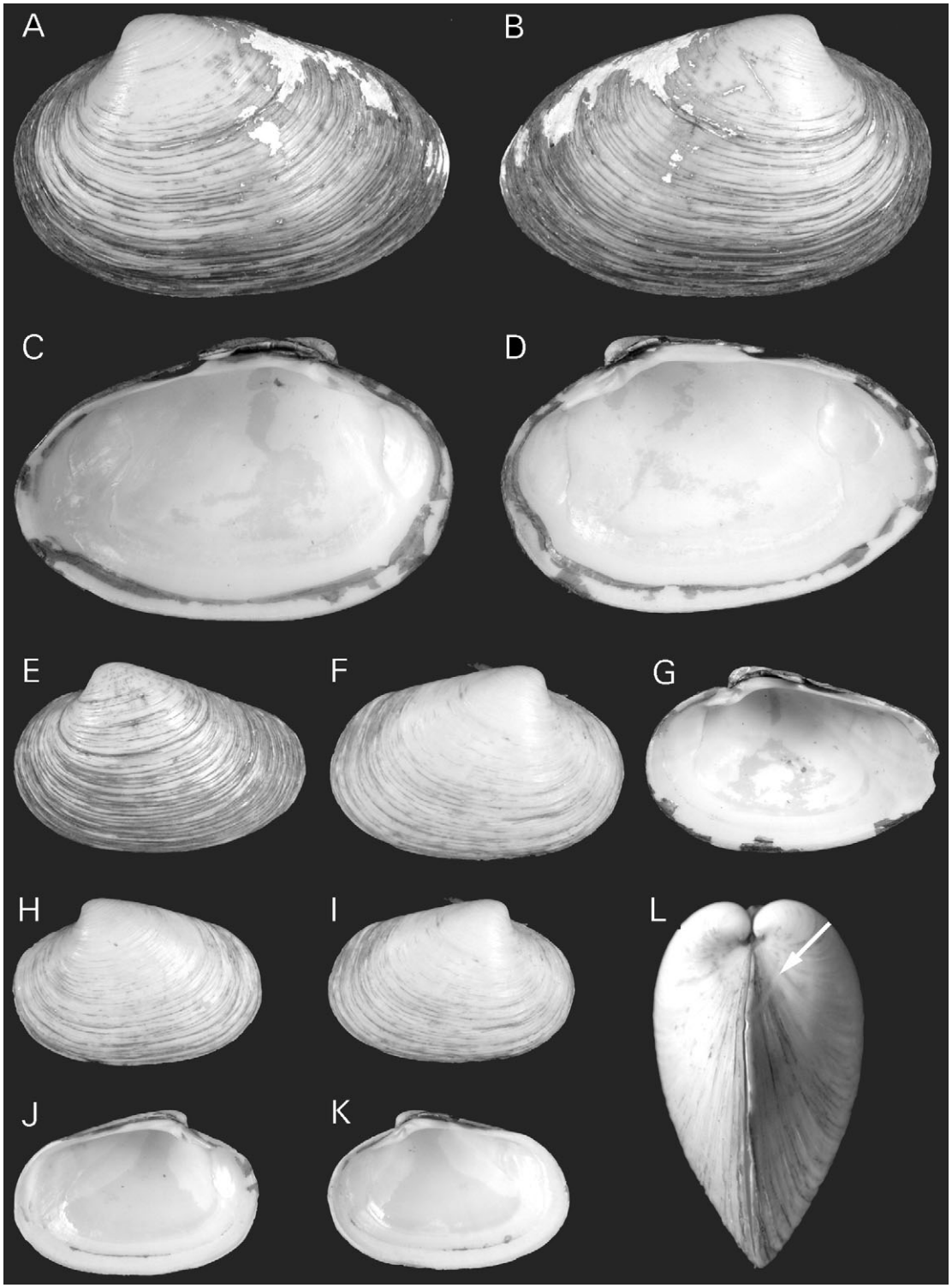

Figure 16. *Calyptogena goffrediae* n. sp., RV *Sonne*, stn 1. **A–D.** Paratype, SMF 327535, L – 36.4 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E–G.** Paratype, SMF 327536, L = 24.6 mm. **E.** Exterior of left valve. **F.** Exterior of right valve. **G.** Interior of right valve. **H–L.** Paratype, L = 20.6 mm. **H.** Exterior of left valve. **I.** Exterior of right valve. **J.** Interior of left valve. **K.** Interior of right valve. **L.** Anterior view; arrow indicates lunular incision.

yellowish, pinkish in posterior part and at periphery, with thin radiating striation, smooth in region of umbo, becoming wrinkled in marginal region and with short, concentric, up-standing lamellae developed mostly at periphery. Sculpture consisting of irregular concentric growth lines and inconspicuous lirae radiating from umbo to posterior margin. Escutcheon shallow. Inequilateral, umbo situated in anterior 37% of valve length. Umbo highly corroded and therefore very low. Anterior margin rounded, ventral margin convex, posterior margin rounded subtruncate with postero-dorsal obtuse angle and posterodorsal

Table 7. Measurements of right valves of *Calyptogena goffrediae*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
Holotype, SMF 327534	38.1	21.4	6.5	8.8	13.5	0.56	0.17	0.65	0.23	0.35	29
Paratype 1, SMF 327537	38.1	23.0	6.8	10.4	14.1	0.60	0.18	0.74	0.27	0.37	30
Paratype 2, ZMMU Ld-3000	36.5	23.1	7.5	10.9	15.6	0.63	0.21	0.70	0.30	0.43	31
Paratype 3, SMF 327535	36.4	22.0	6.4	8.5	12.3	0.60	0.18	0.69	0.23	0.34	29
Paratype 4, ZMMU Ld-3000	36.2	23.4	7.8	10.5	14.0	0.65	0.22	0.75	0.29	0.39	30
Paratype 5, ZMMU Ld-3000	34.7	21.4	7.1	9.0	13.5	0.62	0.20	0.67	0.26	0.39	30
Paratype 6, SMF 327537	28.5	18.8	6.3	6.8	10.0	0.66	0.22	0.68	0.24	0.35	32
Paratype 7, SMF 327536	24.6	15.7	5.4	5.3	8.2	0.64	0.22	0.65	0.22	0.33	32
Paratype 8, ZMMU Ld-3000	22.3	14.8	4.4	4.5	7.8	0.66	0.20	0.58	0.20	0.35	32
	20.6	13.8	3.9	3.5	7.5	0.67	0.19	0.47	0.17	0.36	32

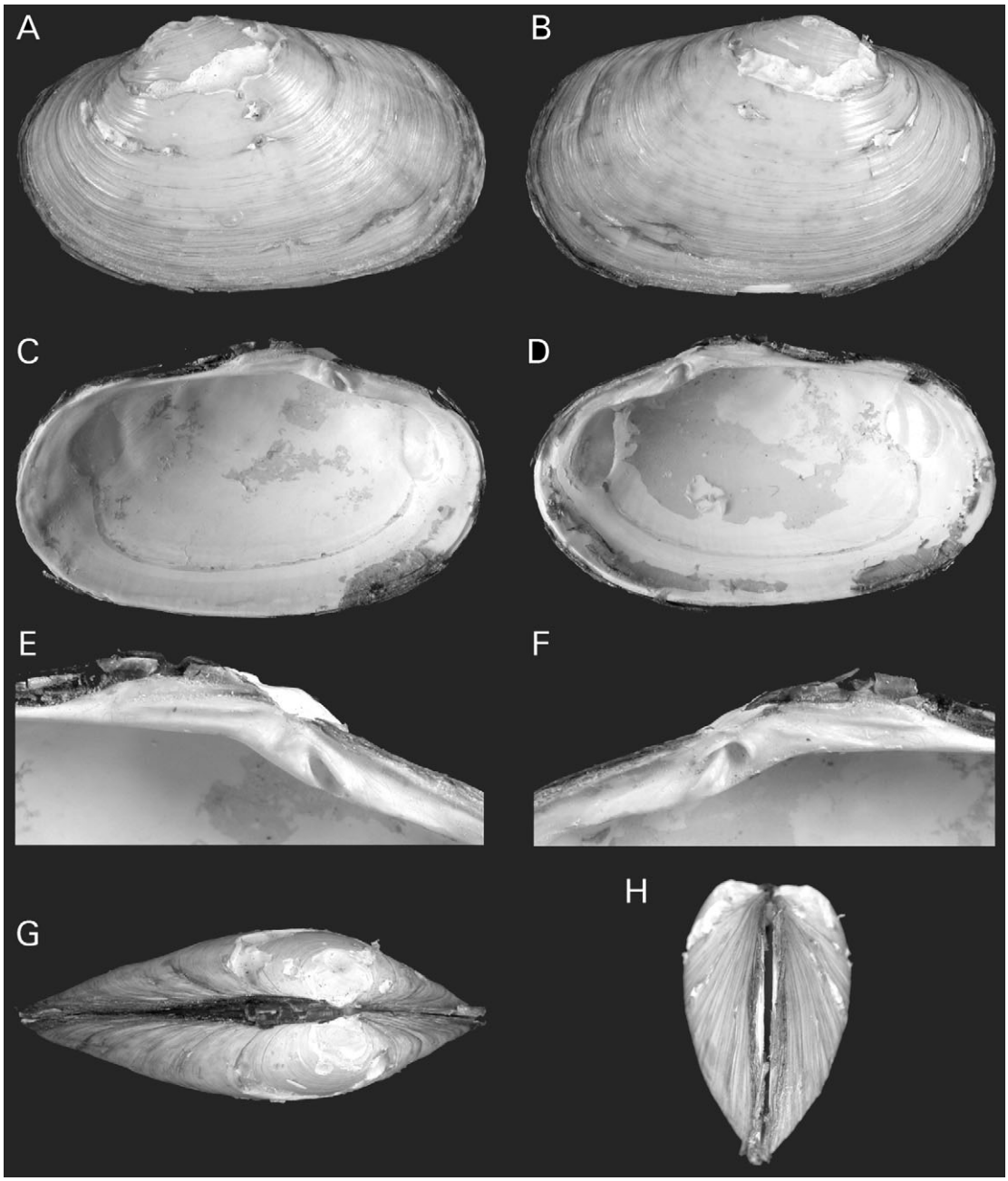

Figure 17. *Calyptogena starobogatovi* n. sp. RV *Akademik Mstislav Keldysh*, stn 1505, holotype, ZMMU Ld-3001, L = 33.8 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

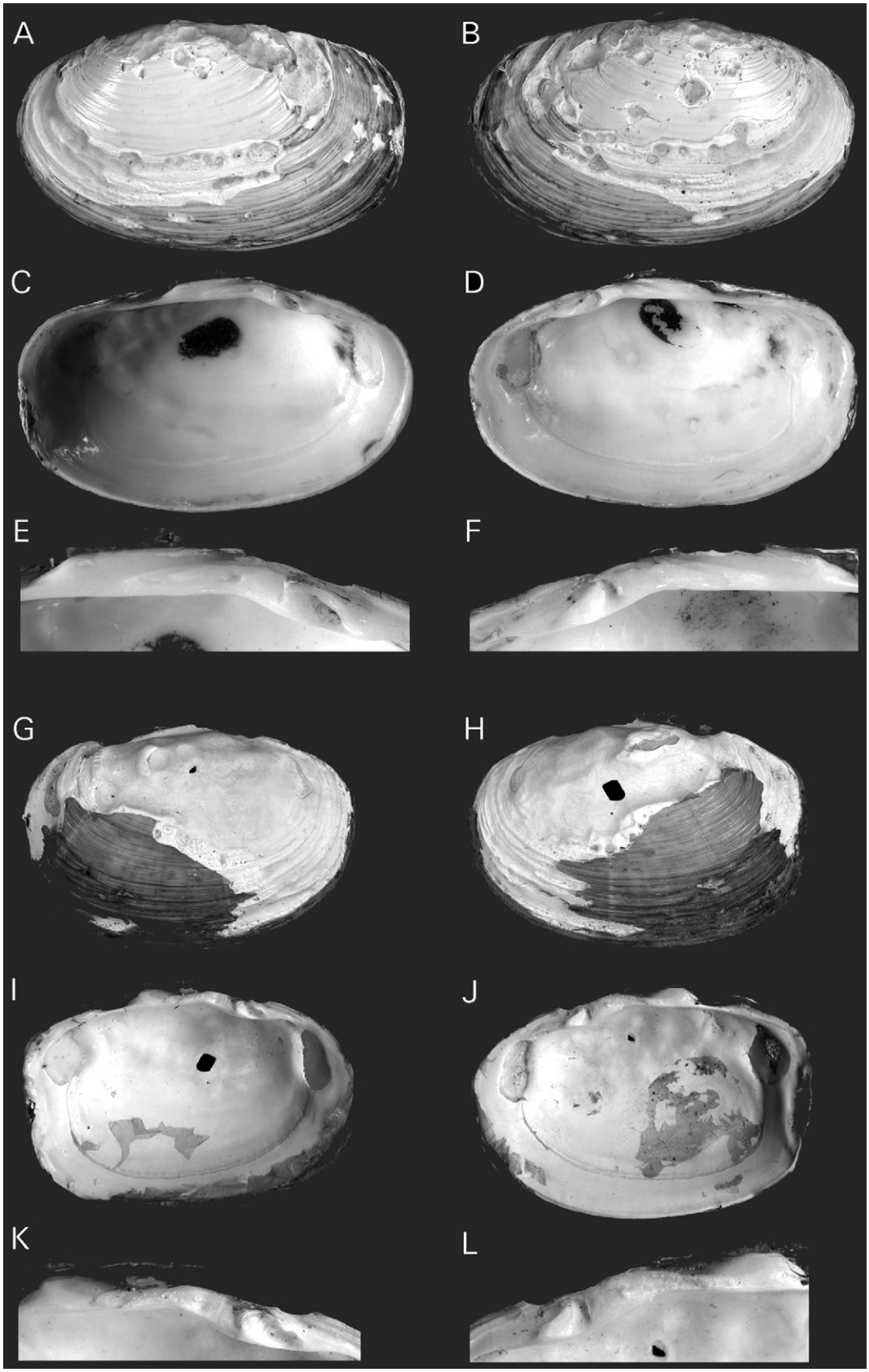

Figure 18. *Calyptogena starobogatovi* n. sp., RV *Akademik Mstislav Keldysh*, stn 1505. **A–F.** Paratype, SMF 327538, L = 41.4 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G–L.** L = 36.4 mm. **G.** Exterior of left valve. **H.** Exterior of right valve. **I.** Interior of left valve. **J.** Interior of right valve. **K.** Left hinge plate. **L.** Right hinge plate.

Table 8. Measurements of right valves of *Calyptogena starobogatovi*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
Holotype, ZMMU Ld-3001	33.8	19.9	5.6	6.6	13.0	0.59	0.17	0.51	0.20	0.38	37
Paratype 1, SMF 327538	41.4	24.1	7.2	9.2	15.7	0.58	0.17	0.59	0.22	0.38	32
Paratype 2, ZMMU Ld-3002	39.3	25.4	6.9	9.0	17.3	0.65	0.18	0.52	0.23	0.44	35
	37.4	24.0	6.7	8.6	15.0	0.64	0.18	0.57	0.23	0.40	37
Paratype 3, ZMMU Ld-3002	33.2	21.6	7.0	7.7	13.2	0.65	0.21	0.58	0.23	0.40	35
Paratype 4, SMF 327539	32.4	19.3	6.1	7.1	13.4	0.60	0.19	0.53	0.22	0.41	34
	30.5	18.5	5.7	7.2	12.6	0.61	0.19	0.57	0.24	0.41	30
Paratype 5, SMF 327539	30.5	17.9	5.5	6.6	11.4	0.59	0.18	0.58	0.22	0.37	36
	26.8	15.5	4.4	5.1	10.1	0.58	0.16	0.50	0.19	0.38	35
	26.2	15.1	5.0	4.9	9.8	0.58	0.19	0.53	0.19	0.37	35
Paratype 6, SMF 327539	14.0	9.3	2.9	1.7	3.9	0.66	0.21	0.44	0.12	0.28	39

margin straight. Pallial line not impressed. Anterior adductor scar and posterior adductor slightly impressed. Anterior pedal retractor scar shallow. Nymph moderately strong, short, occupies 20% of valve length. Fibrous layer of ligament is 51% of posterior lamellar layer. Dentition of right valve: ventral cardinal (1) stout, shelf-like, radiates obliquely anteriorwards; 3a-ramus lamellate, thin, nearly twice shorter than (1), subparallel to anterior-dorsal shell margin, depressed in its proximal part and fused with anterior edge of 3b-ramus; 3b-ramus broad, with slightly elevated narrow anterior and posterior edges, posterior edge lower and parallel to posterior nymphal ridge, anterior edge radiates anteriorwards; posteral nymphal ridge low, elongate, occupies nearly all the length of nymph, parallel to posterior-dorsal margin, more developed in distal part. Dentition of left valve: 2a-ramus lamellate, thin, radiates anteriorwards, fused in its proximal part with 2b-ramus; 2b-ramus broad, with more developed proximal posterior part, radiates ventralwards; 4b-tooth elongate, lamellate in its proximal part and parallel posterior-dorsal shell margin, occupying more than half of nymph.

Anatomy: All features of genus.

Variation: Variations can be shown in the colour and shape of shells, in details of sculpture and of the hinge line. Shell colour varies from nearly white through yellowish to pinkish. The number of lirae radiating from the umbo to the posterior margin also varies and they can be absent. As a result of corrosion, the beaks can be nearly absent. If not corroded, the beaks are placed very closely and touch each other. The outline of the shell can be more or less elongate. The position of the umbo, the length of the nymph and the length of the fibrous layer of the ligament vary remarkably. Variations in the dentition: the right cardinal 3a can be nearly fused with the antero-dorsal margin and therefore may be indistinct; the length of the right posterior nymphal ridge can vary from 3/4 length of nymph to full length; sometimes it can be reduced. Sometimes the hinge margin can be highly corroded. Allometric changes are evident in the slightly more elongate ligament and more truncate posterior margin of larger specimens.

Remarks: The elongate-elliptical shell shape of the *C. starobogatovi* n. sp. is close to those of *C. pacifica*, *C. goffrediae* n. sp. and *C. gallardoi* (Table 11). From all these species *C. starobogatovi* n. sp. differs by the presence of a glossy, smoother periostracum, a lower umbo placed more medially and the more expanded posterior portion of shell. In addition, from *C. pacifica* the present species differs by the thinner shell, shallower escutcheon and shorter fibrous ligament layer.

Distribution: Eastern Pacific in the region of Juan de Fuca Ridge, 1540 m.

Etymology. Named after the late Ya. I. Starobogatov, outstanding Russian zoologist, who began to study this material and recognized a new species.

***Calyptogena makranensis* new species**

(Figs 19, 20)

Type material: SMF 327540 (holotype, dry valves); SMF 327541 (paratype, dry valves); SMF 327542 (paratype, dry valves); SMF 327543 (paratype, dry valves); ZMMU Ld-3003 (3 paratypes, dry valves). Type locality: Makran continental margin off Pakistan, Indian Ocean (24°32.94′N, 64°15.70′E), 2336 m.

Material examined: RV *Sonne*, Cruise 130, Stn 320, TVG, 24°33.09′N, 64°15.79′E, 2215 m, 28 April 1998, 75 intact and 54 broken vs; Stn 322, TVG, 24°32.94′N, 64°15.70′E, 2336 m, 28 April 1998, 132 intact and 9 broken vs (including holotype and six paratypes); Stn 330, TVG, 24°33.00′N, 64°15.64′E, 2334 m, 01. Mai 1998, 2 spms, 54 vs.

Diagnosis: *Calyptogena* species with L to 87 mm, stout, elongate, H/L = 0.45–0.56, W/L = 0.13–0.18, with nearly straight ventral margin, with glossy, smooth, brownish periostracum becoming wrinkled at periphery, moderate escutcheon, limited by sharp ridge, very low umbo situated in anterior 31–35% of valve length, weakly prosogyrate beaks, nymph strong, fibrous layer of ligament occupying 28–43% of valve length and 64–80% of posterior lamellar layer, 4b-tooth occupying nearly half of nymph length (Table 9).

Description of holotype: Shell stout; elongate in outline, H/L = 0.50, equivalve. Valves more flattened towards dorsal margin. Periostracum eroded in the umbonal region, thin, glossy, yellow-brownish and darker and wrinkled towards periphery. Sculpture of growth lines and low irregular concentric ridges. Escutcheon moderate, limited by sharp ridge; lunule narrow and long, limited by slightly raised ridges. Inequilateral, umbo situated at 34% of length from anterior end of valve. Umbones prosogyrate low. Beaks slightly enrolled and nearly touching each other. Anterior-dorsal margin straight, anterior and posterior margins rounded, ventral margin nearly straight, posterior-dorsal margin straight with posterior obtuse angle. Pallial line distinct, slightly impressed. Anterior adductor scar irregularly oval, slightly impressed to rear. Anterior pedal retractor scar shallowly impressed, not fused with anterior adductor scar, but connected to it by narrow line. Posterior adductor scar clearly visible but not impressed, as wide as high, pear-shaped, fused to posterior pedal retractor scar. Nymph strong, with sloping posterior end, occupies 32% of

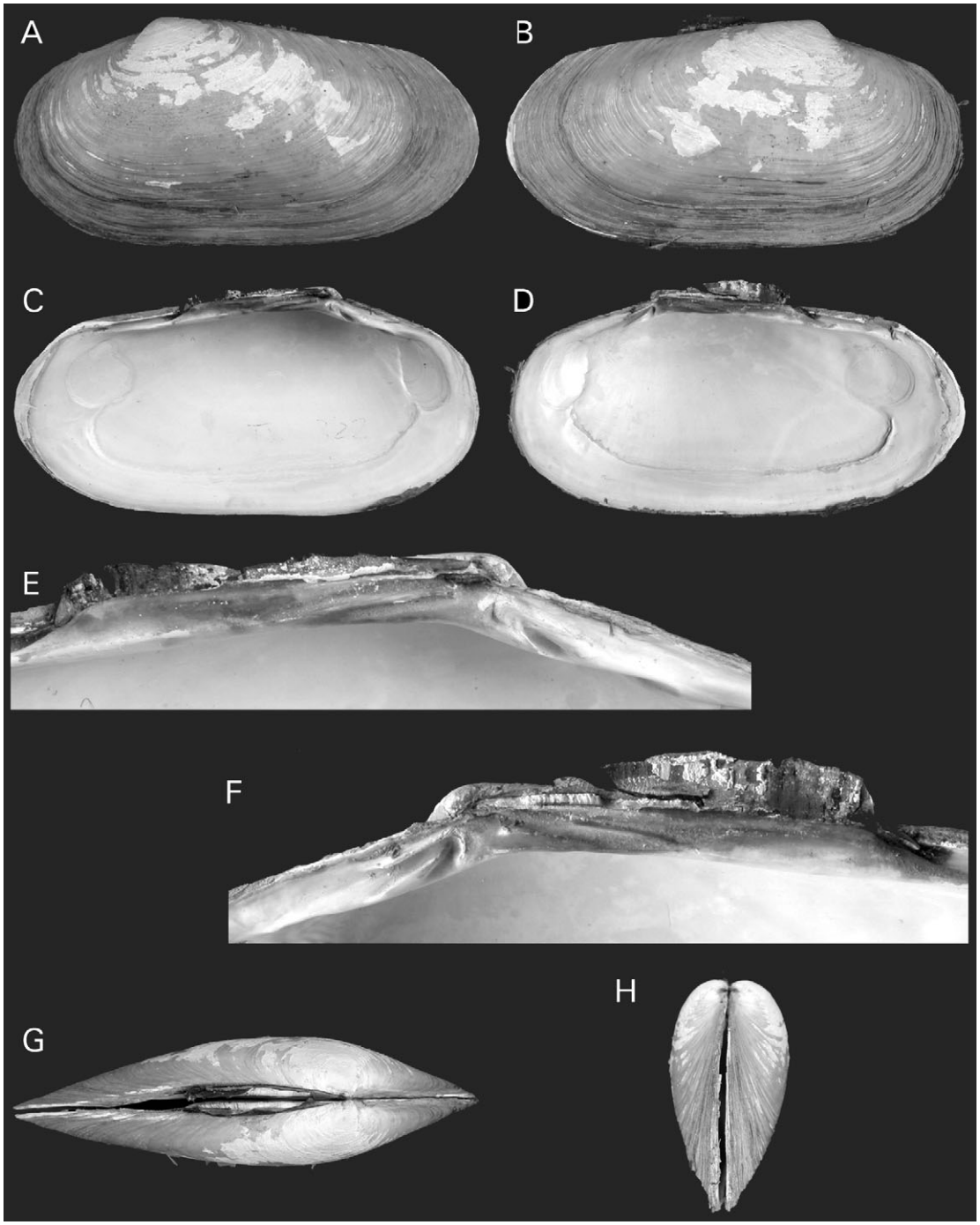

Figure 19. *Calyptogena makranensis* n. sp., RV *Sonne*, stn 322, holotype, SMF 327540, L = 62.8 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

valve length. Fibrous layer of ligament, which attaches to nymph, is 77% of posterior lamellar layer. Dentition of right valve: ventral cardinal (1) thin, shelf-shaped, radiates obliquely anteriorwards; 3a-ramus thin, lamellate, parallel to anterior-dorsal shell margin, fused in its low proximal part with anterior edge of 3b-ramus; 3b-ramus broad, low, with slightly elevated anterior and posterior edges and concave top surface, anterior edge usually radiates ventrally, posterior edge parallel to posterior nymphal ridge; posterior nymphal ridge elongate, occupying nearly half of nymph. Dentition of left valve: 2a-ramus shelf-like, sub-parallel to anterior-dorsal shell margin, fused in its proximal part with proximal part of 2b-ramus; 2b-ramus thicker and shorter than 2b, radiates ventralwards; 4b-tooth elongate, occupying nearly half of nymph, sub-parallel to posterior-dorsal shell margin.

Anatomy: All features of genus.

Variation: The shape of the shell can be more or less elongate. The length of the fibrous layer of the ligament varies. The postero-dorsal margin can be convex, sloping posteriorly, so that the posterior margin is acute. The lunular region may not be impressed at all. In the right valve the ventral cardinal (1) can range from

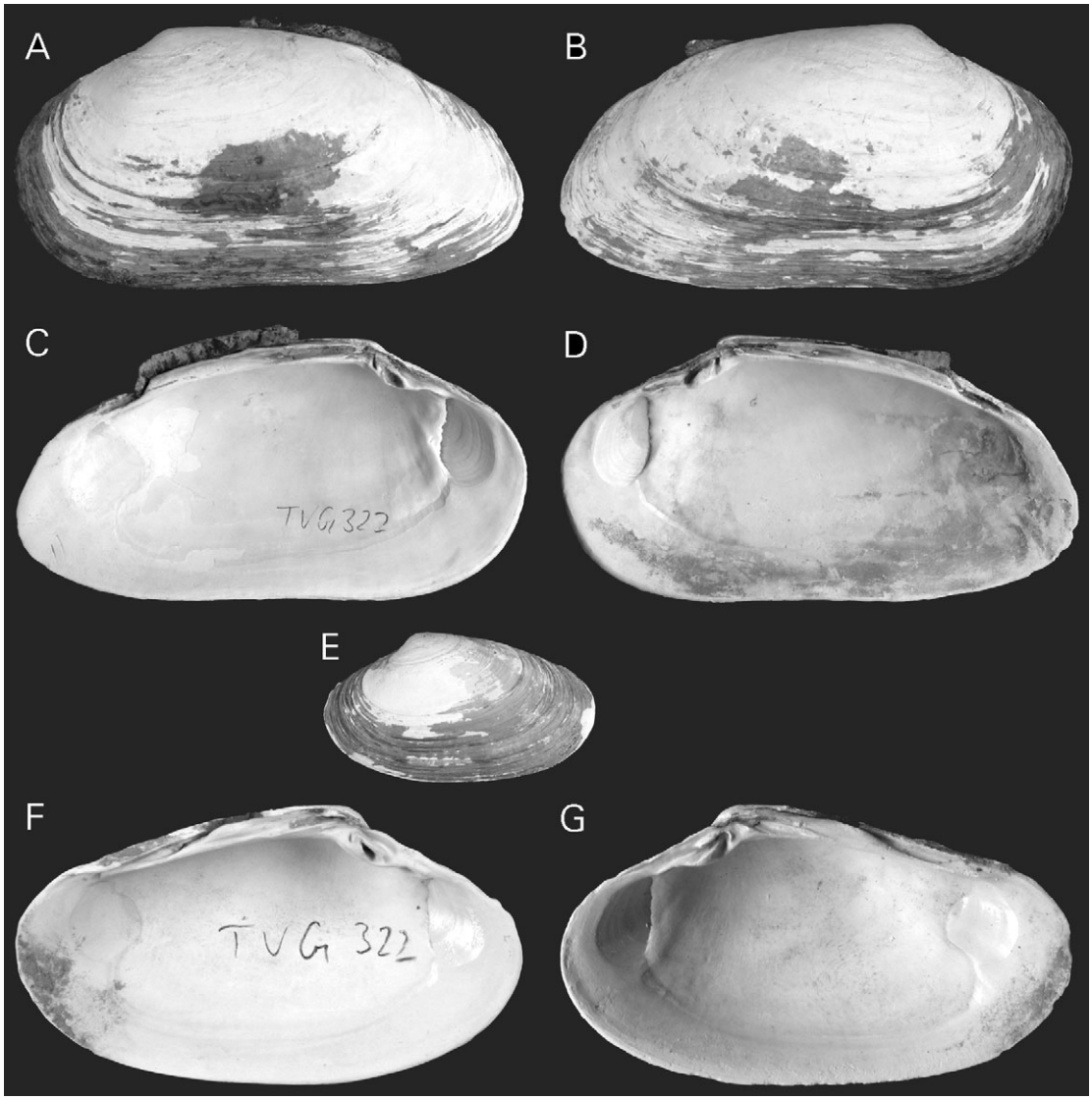

Figure 20. *Calyptogena makranensis* n. sp., RV *Sonne*, stn 322. **A–D.** Paratype, SMF 327541, L = 66.5 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E–G.** Paratype, SMF 327542, L = 33.7 mm. **E.** Exterior of left valve. **F.** Interior of left valve. **G.** Interior of right valve.

Table 9. Measurements of right valves of *Calyptogena makranensis*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
Holotype, SMF327540	62.8	31.2	8.3	20.3	26.3	0.50	0.13	0.77	0.32	0.42	34
Paratype 1, ZMMULd-33003	86.4	41.3	13.1	29.0	39.3	0.48	0.15	0.74	0.34	0.45	31
Paratype 2, SMF 327543	76.5	34.3	10.2	29.0	36.1	0.45	0.13	0.80	0.38	0.47	32
Paratype 3, ZMMU Ld-3003	67.2	34.4	10.2	29.0	36.2	0.51	0.15	0.80	0.43	0.54	34
Paratype 4, SMF 327541	66.5	32.6	10.0	22.3	30.4	0.49	0.15	0.73	0.34	0.46	31
Paratype 5, ZMMU Ld-3003	57.1	26.2	7.5	17.7	26.4	0.46	0.13	0.67	0.31	0.46	31
Paratype 6, SMF 327542	33.7	18.8	5.5	9.4	14.6	0.56	0.16	0.64	0.28	0.43	35
RV *Sonne* 130, stn 320	52.1	26.2	7.4	15.4	23.1	0.50	0.14	0.67	0.30	0.44	33
RV *Sonne*, stn 330	82.7	44.2	15.0	28.1	38.3	0.53	0.18	0.73	0.34	0.46	31
	81.2	41.6	13.4	25.3	38.6	0.51	0.17	0.66	0.31	0.48	31

thin and shelf-like to stout and wedge-like; the 3a-ramus can be nearly fused with the antero-dorsal margin; the anterior and posterior edges of the 3b-ramus may not be parallel to each other.

Remarks: Based on the elongate shape of the shell, *C. makranensis* n. sp. is most similar to *C. rectimargo*, *C. fausta* and *C. costaricana* n. sp. (Table 11). From *C. rectimargo* and *C. fausta* it differs by the less prominent umbo, placed more medially. From

C. fausta the new species differs also by the shorter and not split posterior nymphal ridge in the right valve. It differs from *C. costaricana* by the relatively longer right posterior nymphal ridge, a longer nymph, longer posterior lamellar ligament and the deeper escutcheon that is limited by a sharp ridge.

There are few records of vesicomyids from the Indian Ocean; three species were described by Smith (1904, 1906) from material obtained by R/V *Investigator* off the coast of India and Ceylon, and two species were collected recently from the eastern part of the Indian ocean, off Sunda Strait (Kojima *et al*., 2004). The species described by Smith are: *Vesicomya indica* Smith, 1904, from off Travancore coast, 666 m and off Andamans, 749 m; *V. cretacea* Smith, 1906, from off Burma, 754 m and off Ceylon, 2007 m; and *V. brevis* Smith, 1906 from the Laccadive Sea, 546–666 m. All of these species are closely related to each other and Boss (1970) supposed that these species together with *V. compressa* Prashad, 1932 may prove to be a single Indo-Pacific species. These species differ from *Calyptogena* by their subovate shell shape, well-developed lunule, presence of a pallial sinus that is weakly developed, and by the absence of right posterior nymphal ridge. Similar to *Calyptogena*, however, these species have a well-developed escutcheon.

Both species collected from off the Sunda Strait, 2100 m (Kojima *et al*., 2004) were studied only by molecular methods. One of these species formed a well-supported group with *V. crenulomarginata* Okutani, Kojima & Iwasaki (2002), described from the Nankai Trough, and the other species is closely related to *Calyptogena (Archivesica) similaris* Okutani, Kojima & Ashi (1997), also known from the Nankai Trough. From *V. crenulomarginata* our species differs by the more elongated shell, absence of well-developed lunule and pallial sinus and by different hinge margin. From '*C. (Archivesica)*' *similaris*, *C. makranensis* is distinguished by the absence of a pallial sinus, a quite different hinge margin without a subumbonal pit and with a right posterior nymphal ridge, and also by presence of only one demibranch. Consequently, *C. makranensis* n. sp. is the first record of the genus *Calyptogena* in the Indian Ocean.

Distribution: Makran continental margin off Pakistan, northwestern Indian Ocean, 2213–2336 m.

Etymology: Named after type locality.

Calyptogena costaricana **new species**

(Figs 21, 22)

Type material: SMF 327544 (holotype, with soft parts); SMF 327545 (paratype, with soft parts; Stn 123); SMF 327546

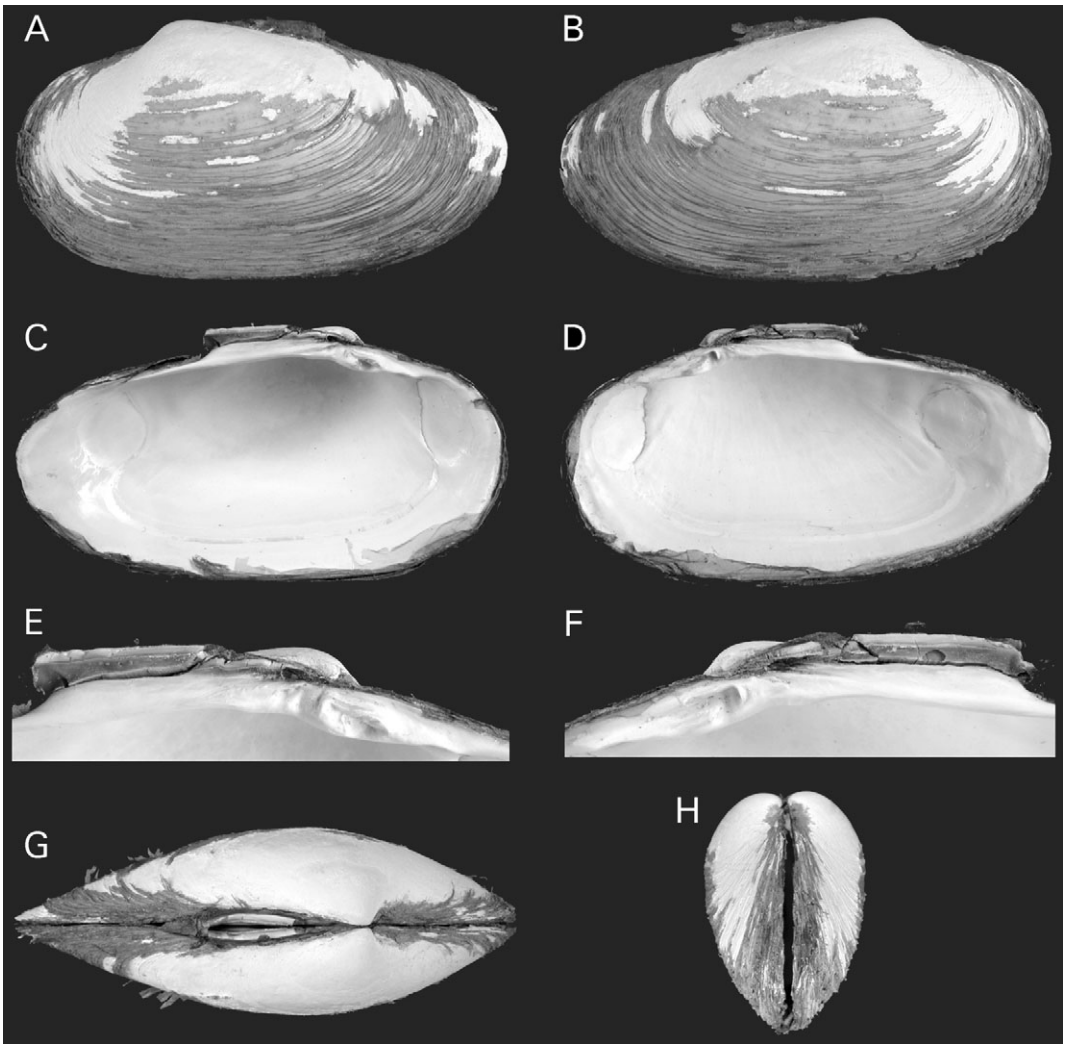

Figure 21. *Calyptogena costaricana* n. sp., RV *Meteor*, stn 123, holotype, SMF 327544, L = 50.8 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G.** Dorsal view. **H.** Anterior view.

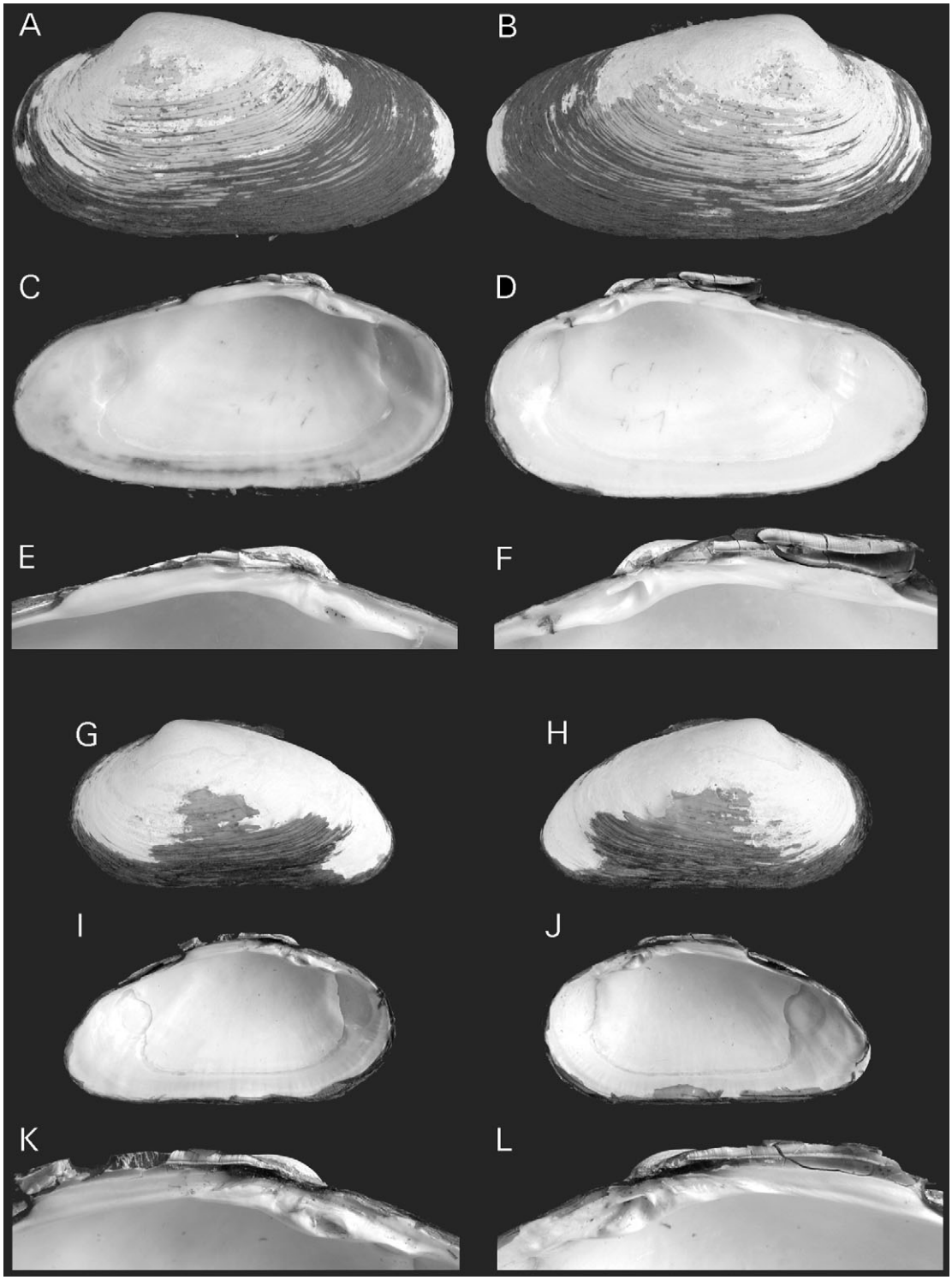

Figure 22. *Calyptogena costaricana* n. sp., RV *Meteor*, stn 134. **A–F.** Paratype, ZMMU Ld-3004, L = 52.0 mm. **A.** Exterior of left valve. **B.** Exterior of right valve. **C.** Interior of left valve. **D.** Interior of right valve. **E.** Left hinge plate. **F.** Right hinge plate. **G–L.** Paratype, ZMMU Ld-3004, L = 38.4 mm. **G.** Exterior of left valve. **H.** Exterior of right valve. **I.** Interior of left valve. **J.** Interior of right valve. **K.** Left hinge plate. **L.** Right hinge plate.

(paratype, dry valves; Stn 134); ZMMU Ld-3004 (3 paratypes, with soft parts; 1 paratype, dry valves; Stn 134). Type locality: Mound 10, off Costa Rica, East Pacific Ocean (10°00.43′N, 86°11.45′W), 2263 m.

Material examined: RV *Meteor*, Cruise 54/3, Stn 123, TV-MUC, 10°00.43′N, 86°11.45′W, 2263 m, 14 September 2002, 2 spms (including holotype and paratype); Stn 134, TVG, 10°00.52′N, 86°11.41′W, 2258 m, 16 September 2002, 3 spms and 4 vs (paratypes).

Diagnosis: *Calyptogena* species with L to 52 mm, stout, elongate, H/L = 0.50–0.59, W/L = 0.16–0.21, with nearly straight ventral margin, dehiscent glossy periostracum becoming

strongly wrinkled to periphery, shallow escutcheon, low umbo situated in anterior 31–35% of valve length, prosogyrate beaks, moderate nymph, fibrous layer of ligament occupying 28–33% of valve length and 66–87% of posterior lamellar layer, 4b-tooth occupying less than a half of nymph length, right posterior nymphal ridge sometimes reduced (Table 10).

Description of holotype: Shell stout, elongate in outline, H/L = 0.53, equivalve. Periostracum eroded in umbonal region, dehiscent, thin, glossy, dirty-pinkish, wrinkled, with short concentric lamellae perpendicular to surface, developed mostly at periphery. Sculpture of growth lines and low irregular concentric ridges. Escutcheon shallow, lunule indistinct. Inequilateral, umbo situated at 33% from anterior end of valve. Umbones prosogyrate, low. Beaks slightly enrolled and nearly touching each other. Anterior-dorsal margin straight, anterior margin broadly rounded, ventral margin nearly straight, posterior margin acutely rounded and posterior-dorsal margin nearly straight. Pallial line distinct, slightly impressed. Anterior adductor scar irregularly oval, slightly impressed to rear. Anterior pedal retractor scar shallow. Posterior adductor scar clearly visible but not impressed, as wide as high, pear-shaped, fused to posterior pedal retractor scar. Nymph strong, with nearly abrupt posterior end, occupies 29% of valve length. Along distal part of the base of nymph there is very slight depression. Fibrous layer of ligament, which attaches to nymph, is 70% of posterior lamellar layer. Dentition of right valve: ventral cardinal (1) stout, shelf-shaped, radiates obliquely anteriorwards; 3a-ramus thin, lamellate, parallel to anterior-dorsal shell margin, fused in its low proximal part with anterior edge of 3b-ramus; 3b-ramus broad, low, with slightly raising anterior and posterior edges and concave top surface, anterior edge usually radiates ventrally, posterior edge radiates posteriorly; posterior nymphal ridge elongate, very low, occupying less than a half of nymph. Dentition of left valve: 2a-ramus thin, shelf-like, sub-parallel to anterior-dorsal shell margin, fused in its proximal part with proximal part of 2b-ramus; 2b-ramus thicker and shorter than 2a, radiates ventrally; 4b-tooth elongate, occupying less than a half of nymph, radiates posteriorwards.

Anatomy: All features of genus.

Variation: The shape of the shell can be more or less elongate. The postero-dorsal margin can be strongly convex, sloping posteriorly, and the ventral margin can be weakly concave. The location of the umbo and the length of the fibrous layers of the ligament also vary. The right posterior nymphal ridge can be reduced. The 4b-tooth can sometimes be slightly longer than half of the nymph. The colour of the periostacum of live-collected specimens is pinkish-brown, while the colour of dead valves is greyish-brown. The lunular region can sometimes be slightly impressed.

Remarks: The elongate shape of the shell of *C. costaricana* is most similar to *C. rectimargo*, *C. fausta* and *C. makranensis* (Table 11). From *C. rectimargo* and *C. fausta*, it differs by the more medially placed umbo. From *C. fausta* the new species differs also by the absence of a slit in the posterior nymphal ridge of the right valve. *Calyptogena costaricana* differs from *C. makranensis* by the shorter nymph, shorter right posterior nymphal ridge and shallower escutcheon.

Calyptogena costaricana very much resembles in proportion and gross outline the fossil species *C. panamensis* Olsson (1942), from sandstones of the uppermost Miocene and lower Pliocene beds on the Burica Peninsula (boundary between Panama and Costa Rica). Comparison between these two species is difficult because the only specimen of *C. panamensis* showing the hinge has an obsolete tooth (Olsson, 1942), however *C. panamensis* differs from *C. costaricana* by more solid shell with broader hinge plate and shorter ligament.

Table 10. Measurements of right valves of *Calyptogena costaricana*.

	L (mm)	H (mm)	W (mm)	F (mm)	N (mm)	H/L	W/L	F/N	F/L	N/L	Um (%)
RV *Meteor*, stn 123											
Holotype, SMF 327544	50.8	26.8	8.7	14.8	21.1	0.53	0.17	0.70	0.29	0.42	33
Paratype 1, SMF 327545	33.2	19.5	6.9	9.4	14.3	0.59	0.21	0.66	0.28	0.43	33
RV *Meteor*, stn 134											
Paratype 2, ZMMU Ld-3004	52.0	26.2	8.5	16.6	21.6	0.50	0.16	0.77	0.32	0.42	31
Paratype 3, ZMMU Ld-3004	40.8	21.1	6.8	12.7	16.5	0.52	0.17	0.77	0.31	0.40	33
Paratype 4, ZMMU Ld-3004	38.4	19.8	6.8	12.2	16.6	0.52	0.18	0.73	0.32	0.43	35
Paratype 5, SMF 327546	37.1	19.0	6.0	12.2	14.0	0.51	0.16	0.87	0.33	0.38	32
Paratype 6, ZMMU Ld-3004	37.0	19.0	6.3	11.8	16.5	0.51	0.17	0.72	0.32	0.45	33

Table 11. Shell characteristics of recent *Calyptogena* species.

Species	Maximum length (mm)	Shell shape	Escutcheon	H/L	Periostracum	Position of umbo (%)	Length of 4b-tooth
C. pacifica	60	Elongate-elliptical	Deep	0.55–0.65	Dehiscent	24–31	More than half nymph length
C. starobogatovi n. sp.	42	Elongate-elliptical	Shallow	0.58–0.66	Adherent	32–39	More than half nymph length
C. goffrediae n. sp.	38.1	Elongate-elliptical	Shallow	0.56–0.67	Adherent	29–32	Less than half nymph length
C. valdiviae	73	Elongate-elliptical	Deep	0.56–0.65	Adherent	30–36	Nearly half nymph length
C. gallardoi	45	Elongate-elliptical	Moderate	0.58–0.63	Dehiscent	27–31	Nearly half nymph length
C. costaricana n. sp.	52	Elongate	Shallow	0.50–0.59	Dehiscent	31–35	Less than half nymph length
C. rectimargo	70	Elongate	Moderate	0.45–0.56	Dehiscent	25–29	Nearly half nymph length
C. fausta	70	Elongate	Shallow	0.50	Adherent	26	More that half nymph length
C. makranensis n. sp.	87	Elongate	Moderate	0.45–0.56	Dehiscent	31–35	Nearly half nymph length

Distribution: Off Costa Rica, eastern Pacific Ocean, 2258–2263 m.

Etymology: Named after the type locality.

DISCUSSION

Our study reveals that *Calyptogena* represents a compact group of species united by common adaptive strategies with similar morphological features. The most characteristic conchological and anatomical features of *Calyptogena* are: shell is usually medium-sized, up to 90 mm in length; elongate-elliptical or elongate shape of valves; presence of an escutcheon; presence of a broad posterior ramus (3b) of the right subumbonal cardinal tooth, as well as presence of a right posterior nymphal ridge and left elongated posterodorsal cardinal tooth (4b); absence of pallial sinus as a result of fusion of intersiphonal septal retractor in its distal part to the ventral surface of the posterior adductor and inserting on the shell immediately adjacent to it; absence of processes on inner vulva of inhalant siphon; ctenidia with inner demibranch only, with descending and ascending lamellae with interlamellar septa not divided into separate cylindrical tubes.

The taxonomic composition of the entire family Vesicomyidae is still uncertain. We have summarized the characteristic features of all genera that are currently referred to the family on the basis of the type species and species unequivocally closely related to the type species (Table 12). The large differences of *Calyptogena* from all other genera demand the separation of this group at the generic level. Several species were originally described as *Calyptogena* which we exclude from the genus. Table 13 lists those species and the main diagnostic characters which distinguish them from *Calyptogena s.s*. Further studies are needed in order to refine the generic allocation of these species.

Our concept of *Calyptogena* is supported by molecular investigations. Preliminary molecular studies on *C. pacifica*, *C. rectimargo*, *C. makranensis* and *C. costaricana* indicate that they form a well-supported monophyletic group separated from other known vesicomyid groups (Goffredi, personal communication). This cluster also includes those species closely related to *C. pacifica*, which have been termed the '*pacifica-lepta*' complex (Peek *et al*., 1997; Goffredi *et al*., 2003). Goffredi *et al*. (2003) showed evidence for five putative species at 15 localities in the eastern Pacific Ocean, including *C. pacifica* and *Vesicomya lepta* (Dall, 1896), with three probable new species. Some of these putative new species may be identical to the species described in this study. However, further investigations are needed to resolve this. In addition, the recent publication by Kojima *et al*. (2004) indicated the placement of *C. fausta* in the '*pacifica-lepta*' complex.

The close proximity of *V. lepta* to *C. pacifica* in the molecular tree is puzzling; therefore, we studied the type material of *V. lepta*, with the aim of ascertaining its relationship to *Calyptogena*. We found that *V. lepta* differs from 'typical' *Calyptogena* in having a much more convex ventral shell margin, a well-developed lunule and lacks a right posterior nymphal ridge. At the same time, *V. lepta* shares features with *Calyptogena* such as the presence of an escutcheon, a broad posterior ramus (3b) of the right subumbonal cardinal tooth and the absence of the pallial sinus. In conclusion, we hesitate to assign *V. lepta* to the genus *Calyptogena*. Additional studies of anatomy and the variability of shell characters of *V. lepta* are needed. Furthermore, it needs to be confirmed that the species investigated genetically is actually identical to the type material of *V. lepta*.

The taxa most closely related to *Calyptogena* are probably the genus *Isorropodon* Sturany, 1896, and the group of species, including '*Calyptogena*' *phaseoliformis* Métivier, Okutani & Ohta, 1986, '*C*'. *kaikoi* Okutani & Métivier, 1986 and '*Calyptogena*' n. sp. from Logatchev (Peek *et al*., 2000). These three groups have several characters in common, such as the absence of a pallial sinus, the presence of a single inner pair of demibranchs and the absence of dendritic processes on the inner vulva of the inhalant siphon. The close relationship of *Calyptogena* with the '*phaseoliformis*' – group is also supported by Horikoshi (1989), who pointed out the similarity of hinge structure in *C. pacifica*, '*C*'. *phaseoliformis* and '*C*'. *kaikoi*. Molecular data have also revealed the affinity of *C. fausta* with '*C*'. *phaseoliformis* and '*C*'. *kaikoi* (Kojima *et al*., 1995). Nevertheless, there are considerable differences in the shell shape and hinge margins, which separate *Calyptogena* from both *Isorropodon* and the '*phaseoliformis*' – group. *Calyptogena* is distinguished from *Isorropodon* by a larger, thicker shell, a broader hinge line with radiating teeth and the presence of a posterior nymphal ridge in the right valve (Table 12). From the '*phaseoliformis*' – group, *Calyptogena* differs by its shorter, more elliptical shell with a well-marked escutcheon and a much stronger hinge plate. Species of the "*phaseoliformis*" – group lack the anterior ramus of the subumbonal cardinal and the posterior nymphal ridge in the right valve. Also, in the '*phaseoliformis*' – group the interlamellar septa of the demibranchs are divided into separate cylindrical tubes (Fiala-Médoni & Le Pennec, 1988; Southward *et al*., 2001; unpublished observations), whereas in *Calyptogena* the interlamellar septa are not divided. Quite probably the '*phaseoliformis*' – group should be placed in the genus *Pleurophopsis* van Winkle (1919), based on the fossil middle Tertiary species *P. unioides* from Trinidad (van Winkle, 1919).

The bacteria-containing gill of *Calyptogena* with its entirely reduced outer demibranchs and wide interlamellar septa is one of the most specialized in the family Vesicomyidae. The specialized gill may reflect ecological adaptations that have been studied in two species belonging to different vesicomyid genera, *C. pacifica* and '*C.*' *kilmeri*. The different physiologies were shown to be related to different pore water compositions leading to spatial segregation of these two species within a seep site (Barry, Kochevar & Baxter, 1997). The physiological adaptations include differences in, for example, the sulphide-binding affinity of the blood, the sulphide consumption rates and densities of bacterial symbionts, as well as different growth rates (Barry & Kochevar, 1998; Goffredi & Barry, 2002). It might be expected that these physiological peculiarities are typical not merely for *C. pacifica*, but for the entire genus *Calyptogena*. This may allow niche differentiation amongst coexisting vesicomyid genera. Further examples are in the Sea of Okhotsk with the occurrence of *C. rectimargo* together with *Akebiconcha soyoae ochotensis* Scarlato, 1981 and *Archivesica ochotica* Scarlato, 1981 (Sahling *et al*. 2003, unpubl.), as well as the Yukie Ridge in the Nankai Trough with coexisting *C. fausta* and '*C.*' *similaris* (Kojima & Ohta, 1997).

Calyptogena's endosymbionts, and thus *Calyptogena* species themselves, rely on energy-rich hydrogen sulphide for chemotrophy. At methane seeps (cold seeps) this is produced by the anaerobic oxidation of methane. At hydrothermal vents it is provided by the hydrothermal fluids that are enriched in reduced compounds due to seawater circulation through the upper ocean crust. Despite the vast geological differences there is evidence that sediment-covered hydrothermal vents and methane seeps can be geochemically similar and that the concentration and flux of sulphide is a key factor in understanding the distribution of chemosynthetic species (Sahling *et al*., 2005). We lack data on the geochemical habitat for all *Calyptogena* species, with the exception of *C. pacifica* off Monterey and Oregon (Barry, Kochevar & Baxter, 1997; Sahling *et al*., 2002). In general, most species occur in areas with methane seepage: *C. goffrediae* off Peru (Olu *et al*., 1996), *C. costaricana* of Costa Rica (Mau *et al*., 2006), *C. rectimargo* in the Sea of Okhotsk (Greinert *et al*., 2002; Sahling *et al*., 2003), *C. makranensis* off Pakistan

Table 12. Main characters of genera currently referred to the family Vesicomyidae.

	Calyptogena Dall, 1891	*Phreagena* Woodring, 1938	*Ectenagena* Woodring, 1938	*Archivesica* Dall, 1908	*Akebiconcha* Kuroda, 1943	*Isorropodon* Sturany, 1896	*Vesicomya* Dall, 1886	*Pliocardia* Woodring, 1925	*Callogonia* Dall, 1889	*Waisiuconcha* Beets, 1942	*Hubertschenckia* Takeda, 1953	*Pleurophopsis* van Winkle, 1919
Type species	*Calyptogena pacifica* Dall, 1891	*Phreagena lasia* Woodring, 1938	*Calyptogena elongata* Dall, 1916	*Vesicomya gigas* Dall, 1895	*Akebiconcha kawamurai* Kuroda, 1943	*Isorropodon peplexum* Sturany, 1896	*Callocardia atlantica* Smith, 1885	*Anomalocardia bowdeniana* Dall, 1903	*Callocardia* (*Callogonia*) *leeana* Dall, 1889	*Waisiuconcha alberdinae* Beets, 1942	*Tapes ezoensis* Yokoyama, 1890	*Pleurophopsis unioides* van Winkle, 1919
Maximal shell size for genus (mm)	90	250	44	111	60	47	10	44	34	24	65	200
Shell outline	From elongate-elliptical to elongate	Elongate	Elongate	From subovate to elongate-elliptical	Elongate-elliptical	From subcircular to subovate	Subcircular	Subovate	Subovate	Subcircular	Subovate	Elongate
Tumidity	Not inflated	Not inflated to moderately inflated	Not inflated	Moderately to very inflated	Not inflated	Moderately to very inflated	Very inflated	Inflated to very inflated	Moderately inflated	Moderately inflated	Moderately inflated	Not inflated
Orientation of teeth	Diverging	Diverging	Diverging	Diverging	Diverging	Parallel	Parallel	Diverging	Parallel	Diverging	Diverging	Diverging
Subumbonal pit	Absent	Present	Present	Present	Present	Absent	Absent	Absent	Present	Absent	?	?
3-a tooth	Present	Reduced or absent (often in adults)	Absent	Present	Present	Present	Present	Present	Present	Present	Reduced	Absent
3-b tooth	Broad	Thin	Thin	Thin	Thin	Thin	Thin	Broad	Thin	Thin	Thin	Thin
Posterior nymphal ridge	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Pallial sinus	Absent	Small sinus present	Absent	Small sinus present	Small sinus present	Absent	Absent	Small sinus present	Well developed	Absent	Small sinus present	Absent
Anterior pedal retractor scar	Shallow	Deep	Shallow	Shallow	Deep	Shallow	Shallow	Shallow	Shallow	Shallow	?	?
Numbers of demibranchs	1	?	?	2	?	1	2	?	?	?	?	?
Processes on inner vulva of inhalant siphon	Absent	?	?	Present	?	Absent	Absent	?	?	?	?	?

Table 13. List of Recent species originally described as *Calyptogena* or usually referred to *Calyptogena*, which we exclude from the genus.

Original generic assignment	Species epithet	Reference of original description	Distinguishing features from *Calyptogena*
Calyptogena (Ectenagena)	*australis*	Stuardo & Valdovinos, 1988	Narrow 3b tooth, completely reduced 3a tooth, absence of right posterior nymphal ridge, presence of pallial sinus
Calyptogena (Calyptogena)	*birmani*	Domaneschi & Lopes, 1990	Absence of right posterior nymphal ridge, presence of pallial sinus
Calyptogena	*diagonalis*	Barry & Kochevar, 1999	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes
Calyptogena (Archivesica)	*edisonensis*	Okutani, Kojima & Kim, 2004	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit, pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes*
Calyptogena	*elongata*	Dall, 1916	Narrow 3b tooth, absence of right posterior nymphal ridge, completely reduced 3a-tooth
Ectenagena	*extenta*	Krylova & Moskalev, 1996	Narrow 3b tooth, absence of 3a-tooth and right posterior nymphal ridge, presence of pallial sinus, two demibranchs, horseshoe-like aperture of inhalant siphon
Calyptogena (Ectenagena)	*fossajaponica*	Okutani, Fujikura & Kojima, 2000	Narrow 3b tooth, absence of right posterior nymphal ridge, completely reduced 3a tooth
Calyptogena (Archivesica)	*garuda*	Okutani & Soh, 2005	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit, pallial sinus
Calyptogena (Ectenagena)	*kaikoi*	Okutani & Métivier, 1986	Narrow 3b tooth, absence of right posterior nymphal ridge, completely reduced 3a tooth
Calyptogena (Archivesica)	*kilmeri*	Bernard, 1974	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes*
Calyptogena (Ectenagena)	*laubieri*	Okutani & Métivier, 1986	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit, pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes*
Calyptogena (Ectenagena)	*magnifica*	Boss & Turner, 1980	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of two demibranchs
Calyptogena (Archivesica)	*magnocultellus*	Okutani, Kojima & Iwasaki, 2002	Narrow 3b tooth, presence of subumbonal pit and pallial sinus
Calyptogena	*nankaiensis*	Okutani, Kojima & Ashi, 1996	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit, pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes*
Calyptogena (Ectenagena)	*nautilei*	Okutani & Métivier, 1986	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit and pallial sinus
Calyptogena	*okutanii*	Kojima & Ohta, 1997	Narrow 3b tooth, absence of right posterior nymphal ridge, presence pallial sinus
Calyptogena	*packardana*	Barry, Kochevar, Baxter & Harrold, 1997	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes
Calyptogena (Ectenagena)	*phaseoliformis*	Métivier, Okutani & Ohta, 1986	Narrow 3b tooth, completely reduced 3a tooth, absence of right right posterior nymphal ridge
Calyptogena (Calyptogena)	*ponderosa*	Boss, 1968	Absence of right posterior nymphal ridge, presence of pallial sinus
Calyptogena	*similaris*	Okutani, Kojima & Ashi, 1997	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of pallial sinus, two demibranchs, inner vulva of inhalant siphon with processes*
Calyptogena	*solidissima*	Okutani, Hashimoto & Fujikura, 1992	Narrow 3b tooth, absence of right posterior nymphal ridge, presence of subumbonal pit and pallial sinus
Calyptogena	*soyoae*	Okutani, 1957	Narrow 3b tooth, absence of right posterior nymphal ridge, presence pallial sinus
Calyptogena (Archivesica)	*tsubasa*	Okutani, Fujikura & Kojima, 2000	Narrow 3b tooth, absence of right posterior nymphal ridge, presence pallial sinus

*Data of authors.

(von Rad *et al*., 2000), *C. fausta* off Japan (Henry *et al*., 2002) and *C. valdivia* in the Gulf of Guinea (Sibuet *et al*., 2002). The geochemical habitat of *C. pacifica* at Piip Volcano in the Bering Sea is very similar to that of methane seeps, too. Warm fluids circulate through sediments causing the dissolution of gas hydrate and, subsequently, the release of methane (Taran *et al*., 1992). *Calyptogena starobogatovi* is the only species that occurs at a hydrothermal vent, southwest of the caldera of Axial Seamount on the Juan de Fuca Ridge. We agree with Goffredi *et al*. (2003), who also found species at Juan de Fuca Ridge which they discuss as not specific to the hydrothermal vent system, but restricted to the bathymetric depths at which the hydrothermal vent is located. The authors found that the putative '*Vesicomya* sp. mt-II' (which is probably identical to *C. starobogatovi*) is not only present at hydrothermal vents, but also at methane seeps occurring at a narrow bathymetric range between 1500 and 2200 m. Similar results were found off Japan, where vesicomyid clams were found at hydrothermal vents as well as methane seeps within restricted vertical ranges (Kojima & Ohta, 1997; Fujikura *et al*., 2000). In this study, we also found a remarkably narrow bathymetric range for *C. pacifica*, between about 500 and 950 m within a wide geographic range from the Bering Sea to Monterey Bay off California. The depth as well as the geographic range for all other *Calyptogena* species is not well defined due to the limited sampling. Only *C. valdiviae* has a wide distribution along the continental margin of Africa. In addition, dead shells were found at a wide variety of depths between 500 and 2500 m. Most *Calyptogena* species occur along continental margins (Fig. 23), suggesting that these are major spreading pathways. Methane seepage is a widespread phenomenon that is not limited to tectonically active compressional margins, e.g. off Pakistan (von Rad *et al*., 2000) or the Circum-Pacific 'fire belt' in which the seeps off Japan (Henry *et al*., 2002), Oregon (Sahling *et al*., 2002), California (Barry *et al*., 1996), Costa Rica (Mau *et al*., 2006) and Peru (Olu *et al*., 1996) are located. It is also caused by various geological processes such as salt tectonics, faults tapping into methane-rich sediments or landslides. Respective examples are the pockmarks in the Gulf of Guinea (Sibuet *et al*., 2002), the gas seeps in the Sea of Okhotsk (Sahling *et al*., 2003) and the slump off Peru (Olu *et al*., 1996). Intensive research in areas such as the continental margin off Japan (Kojima, 2002) and California (Barry *et al*., 1996) revealed very high frequencies of individual methane seeps. Despite the small spatial scale of individual methane seeps, we suggest that the various geological phenomena leading to abundant seep sites result in a near-continuous linear system along continental margins through which vesicomyid clams can spread. We further propose that geographic isolation is a major factor for the speciation within the genus *Calyptogena*. Molecular studies support the view that vesicomyid clams spread easily along continental margins. Kojima *et al*. (2004) recognized six pairs of closely related vesicomyid species, each comprising one species from the western Pacific and one from the eastern Pacific, which indicates multiple migrations across the Pacific. Furthermore, molecular phylogenies indicate that vesicomyid clams have diversified at methane seeps and, later, have also exploited hydrothermal vents and decomposing whale bones (Peek *et al*., 1997, 2000; Baco *et al*., 1999).

Among numerous fossils of vesicomyids, only some can be more or less certainly referred to *Calyptogena*. All these species (Table 14) are characterized by the presence of an escutcheon, the absence of a pallial sinus and a dentition which fits the diagnosis of *Calyptogena*. The species *C. moraiensis* (Suzuki, 1941) may be synonymous with *C. pacifica* (Boss & Turner, 1980; Okutani, 1962). *Calyptogena gibbera* Crickmay (1929) was also considered a possible synonym of *C. pacifica* (Boss & Turner, 1980), but a recent complete redescription of *C. gibbera* shows that it differs markedly from *C. pacifica* (Squires, 1991). The distinguishing features are the presence of a short hinge plate with narrow 3b-tooth in right valve, short 4b-tooth in the left valve and the absence of the right posterior nymphal ridge, which indicate that *C. gibbera* is not a representative of the genus *Calyptogena s.s*. *Calyptogena (Calyptogena) chinookensiis* Squires & Goedert, 1991, known from late middle Eocene to late Oligocene of Washington, is also characterized by a short hinge plate with diverging teeth without nymphal ridge in the right valve. Thus, we suggest that it should be excluded from the genus *Calyptogena s.s*.

The earliest records for the entire family Vesicomyidae are from the early Cretaceous (Kanie & Sakai, 1997). The first representatives of *Calyptogena* appeared later, with a first record in the Miocene (Table 14) in the northwestern and north Pacific. Later records of *Calyptogena s.s*. date from the uppermost Miocene of the eastern Pacific. The earliest fossil records in combination with the observed high diversity of Recent species in the northwest Pacific (Fig. 23) suggets that this was the site of origination of the genus. The modern distribution of *Calyptogena s.s*. leads to the hypothesis that dispersal of the genus took place from the northwestern Pacific in two main directions: to the East

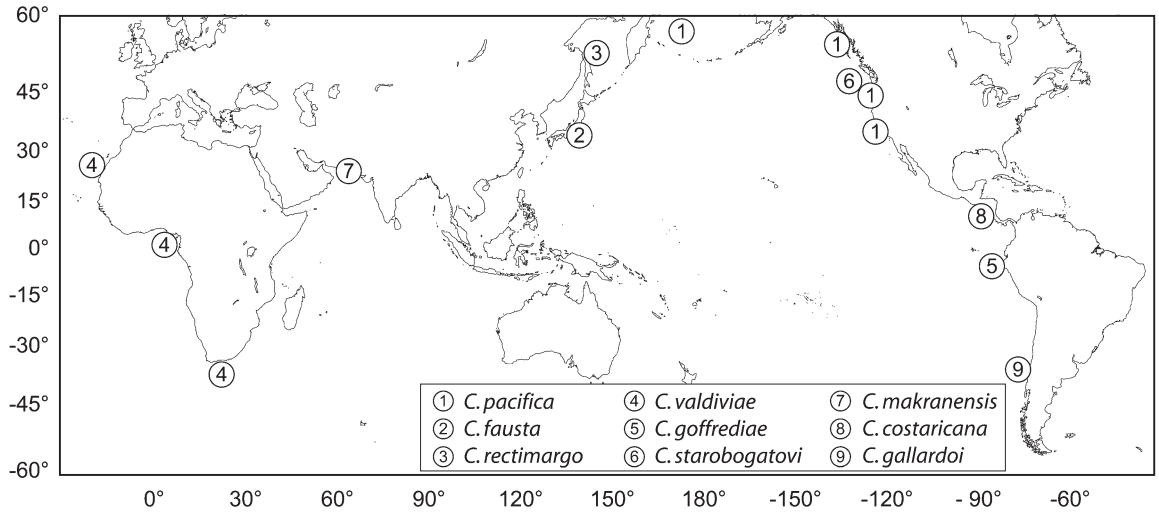

Figure 23. Distribution of *Calyptogena* species based on the material examined in this study.

Table 14. Palaeontological records of *Calyptogena*.

Species	Age	Region	Reference
C. pacifica	Pliocene	California	Grant & Gale, 1931
C. pacifica	Miocene, Pliocene	Honshu, Japan	Kanno *et al.*, 1989
C. moraiensis	Mio-Pliocene	Japan	Suzuki, 1941
C. panamensis	Uppermost Miocene and lower Pliocene	Costa-Rica and Panama, Pacific Coast	Olsson, 1942

Pacific along the continental margin of North America and to the west into the Indian Ocean via abundant seep sites in the Indo-West Pacific region. Colonization of the Atlantic Ocean could have been accomplished along the continental margin of Africa, reflected in the distribution pattern of *C. valdiviae*.

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