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A new species of *Calyptogena* (Bivalvia: Vesicomyidae) from a recently discovered methane seepage area off Concepción Bay, Chile (~36°S)

Javier Sellanes*†ʃ and Elena Krylova‡

*Centro de Investigación Oceanográfica en el Pacífico Sur-Oriental (COPAS), Casilla 160-C, Concepción, Chile.
†Universidad Católica del Norte, Departamento de Biología Marina, Larrondo 1281, Coquimbo, Chile.
‡Shirshov Institute of Oceanology, Nakhimovskii prospect, 36, Moscow, 117851, Russia.
ʃCorresponding author, e-mail: jsellane@udec.cl

Calyptogena gallardoi sp. nov. is described from eight articulated and 15 separated valves collected by dredge at ~760 m depth off the Bay of Concepción, central Chile (~36°S). In general outline, *C. gallardoi* sp. nov. is close to *C. pacifica* and to a new species of *Calyptogena* from Peru, from which it differs in details of the shell shape and hinge margin. Bivalves of the genus *Calyptogena* are typical constituents of marine chemosynthesis-based communities, and are therefore indicators of reducing environments. In the area of occurrence, the presence of *C. gallardoi* sp. nov. is related to methane seepage, associated in turn with the extensive gas–hydrate fields recently reported for the Chilean margin along 35°S to 45°S. Gas-saturated sediments as well as fragments of other chemosynthetic endosymbiont-containing clams of the families Vesicomyidae, Lucinidae, Thyasiridae and Solemyidae were also retrieved in the area.

Calyptogena gallardoi sp. nov. is the first species of *Calyptogena* s.s. and the second species of the family Vesicomyidae so far described for the south-eastern Pacific area.

INTRODUCTION

The central Chilean margin has an ideal geological setting for the occurrence of methane seepage, as indicated by two types of evidence. First, based on acoustic surveys, the presence of extensive gas–hydrate fields has been inferred for the Chilean margin between 35°S and 45°S (Grevemeyer et al., 2003; Morales, 2003). Conservative estimates of the volume of gas stored in this form in subsurface sediments of the area are in the order of $3.2\times10^{13}\,m^3$, roughly 3% of the world total (Morales, 2003). Second, this convergent margin area is characterized by intense tectonic activity, as exemplified by the occurrence of the largest earthquakes yet recorded, i.e. the great Chile earthquake of 1960.

Some families of bivalves are known to make their living by harbouring chemosynthetic endosymbiont bacteria, and are therefore associated with reducing environments (e.g. methane and brine seeps, hydrothermal vents etc.). For this reason, these molluscs are among the main visible indicators of fluid expulsion at the sea-floor (Paull et al., 1984; Kennicutt et al., 1989; Sahling et al., 2002; Sibuet & Olu-Le Roy, 2002).

Sellanes et al. (2004) reported for bathyal depths (651–934 m), north-west off the Bay of Concepción (~36°S), the presence of important accumulations of carbonate blocks, indicative of anaerobic oxidation of methane in the surface-sediment layer, accompanied by fragmented shells of chemosymbiotic bivalves of the families Vesicomyidae and Solemyidae. The taxonomic status of the bivalve-fragments reported in that first communication was unclear, and regarding the vesicomyids, only some of them seemed to correspond to the single so far described local species (*Ectenagena australis* Stuardo & Valdovinos, 1988). Further exploration of the nearby bathyal area resulted in the discovery of additional shell fragments, including some living bivalves belonging to other families that probably rely on chemosynthesis for their existence.

In this paper we describe a new species of *Calyptogena*, collected nearby the Concepción methane seep area (CMSA) as reported by Sellanes et al. (2004), and report, for the first time, the presence of representatives of other families of chemosymbiotic bivalves in the area. These findings further add to the general picture that the Chilean margin methane seep assemblages may be highly endemic and that their study would constitute a major contribution to unveiling biogeographical patterns of chemosymbiotic assemblages in the Pacific area.

MATERIALS AND METHODS

Samples were taken with an Agassiz trawl (mouth opening 1×0.4 m, mesh size 10×10 mm at the cod-end), in a 20 min haul, operated from the RV 'Kay Kay' of the University of Concepción, Chile.

The description of the new species is based on eight articulated and six left and nine right separated valves collected at a single site (~36°S) off Concepción Bay, central Chile. For comparison with already described species, the type material of *C. pacifica* Dall, 1891 deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), was used.

For the morphological description, the following measurements were recorded: valve length, valve height, valve width, length of the fibrous part of the ligament (or length of nymph for valves without preserved ligaments) and length of the posterior lamellar part of the ligament (or length of the ligament groove for valves without preserved ligaments) (Figure 1D & F). The situation of the umbo was determined as the ratio of the distance from the umbo to the anterior shell margin to the length of the valve. Measurements were made with a hand-held calliper (±0.1 mm).

For the descriptions of the hinge teeth, the terminology of Bernard (1895, 1896, 1897) was used (Cox, 1969) (figure 1G,H). The type material will be deposited in the National Museum of Natural History of Chile (MNHNCL) and the Zoological Museum of Moscow State University, Moscow, Russia (ZMMU).

RESULTS

As in previous dredging in the area (Sellanes et al., 2004), carbonate and mud-breccia blocks, indicative of carbonate-saturated porewater due to the process of anaerobic oxidation of methane (Boetius et al., 2000), were retrieved. Dominant non-chemosymbiotic specimens collected during this trawl included two species of ophiuroids (*Asteronyx loveni* and *Ophiurolepis carinata*), tube-building polychaetes (*Hyalinoecia* sp. and *Eunice* cf. *magellanica*) and solenocerid shrimps (*Haliporoides diomedeae*). Other groups represented by only one or two individuals were Pycnogonida, Mollusca (*Limopsis ruizana* and a scaphopod), Sipunculida, a scleractinid coral, an anemone and some gorgonians.

Besides the newly described species, fragments of at least five species of chemosymbiotic bivalves, belonging to the families Lucinidae, Thyasiridae and Solemyidae and what seems to be another species of a fairly large vesicomyid (probably *Archivesica* sp.), were also retrieved. Table 1 summarizes the taxonomic status at a generic level, quantities and characteristics of those fragments. Although they are presumably undescribed species, the general condition of most of them still does not allow their exact identification. Only the smaller vesicomyid species was present in sufficient quantity and good enough condition to allow its description, which is presented below.

Table 1. *Summary of the chemosymbiotic bivalve fragments and articulated valves retrieved during the dredge haul off Concepción (coordinates: 36°22.21′S 73°42.83′W; water depth ~760 m), in which the representatives of* Calyptogena gallardoi *sp. nov. were collected.*

Taxa	Left valves	Right valves	Articulated
Vesicomyidae			
Calyptogena gallardoi sp. nov.	6	9	8
Archivesica sp.	7	5	2
Lucinidae			
Lucinoma sp.	1	1	
Thyasiridae			
Thyasira sp.	2	3	
Conchocele sp.		1	
Solemyidae			
Acharax sp.	2	2	4

SYSTEMATICS

Class BIVALVIA Linnaeus, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. & A. Adams, 1856
Family VESICOMYIDAE Dall & Simpson, 1901
Genus *Calyptogena* Dall, 1891

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

Type species
Calyptogena pacifica Dall, 1891 (by monotype).

Diagnosis
Shell medium-sized, up to 90 mm in length, from elongate–elliptical to elongate in outline, usually with ventral margin nearly straight along midpoint. Escutcheon present, lunular incision indistinct or missing. Pallial line clearly visible, pallial sinus absent. Anterior pedal retractor scar not deeply impressed. Ligament external, parivincular, consists of anterior and posterior lamellar layers and posterior fibrous layer, subtending by nymph, subumbonal pit is absent. Right valve with ventral cardinal tooth (1), situated beneath 3a; sub-umbonal cardinal tooth consisting of two rami (3a and 3b); and posterior lateral tooth which may be nearly reduced or split into two parallel ridges. Rami 3a and 3b fusing by their proximal parts, 3a thin and sub-parallel to the dorsal margin, 3b somewhat broad with anterior and posterior lamellate ridges, radiating ventralwards. Left valve with sub-umbonal cardinal tooth with two rami (2a and 2b) and posterodorsal cardinal tooth (4b).

At present, the genus *Calyptogena* s.s. contains nine recent species (Krylova & Sahling, unpublished), including *Calyptogena gallardoi* sp. nov.

Calyptogena gallardoi sp. nov.
(Figures 1–3)

Type material
Holotype: two articulated valves (RV 'Kay Kay', Cruise 2 June, 2004, Station 40, 36°22.21′S 73°42.83′W, 760 m) [MNHNCL-200734].

Paratypes (all from the same station): 4 articulated valves [MNHNCL-200735], 13 separated valves [MNHNCL-200736], 2 articulated (paratype N 3) and 2 separated valves (paratypes N 2, 4) [ZMMU-Ld2999].

Comparative material examined
Calyptogena pacifica Dall, 1891. Syntypes, 59 entire valves, 6 broken valves (Albatross, Station 3077, 55°46′N 132°24′W, 322 fm (580 m)) [USNM 122549], 6 valves (from the same station) [USNM 222323], 2 specimens with dry soft parts (same station) [USNM 206424].

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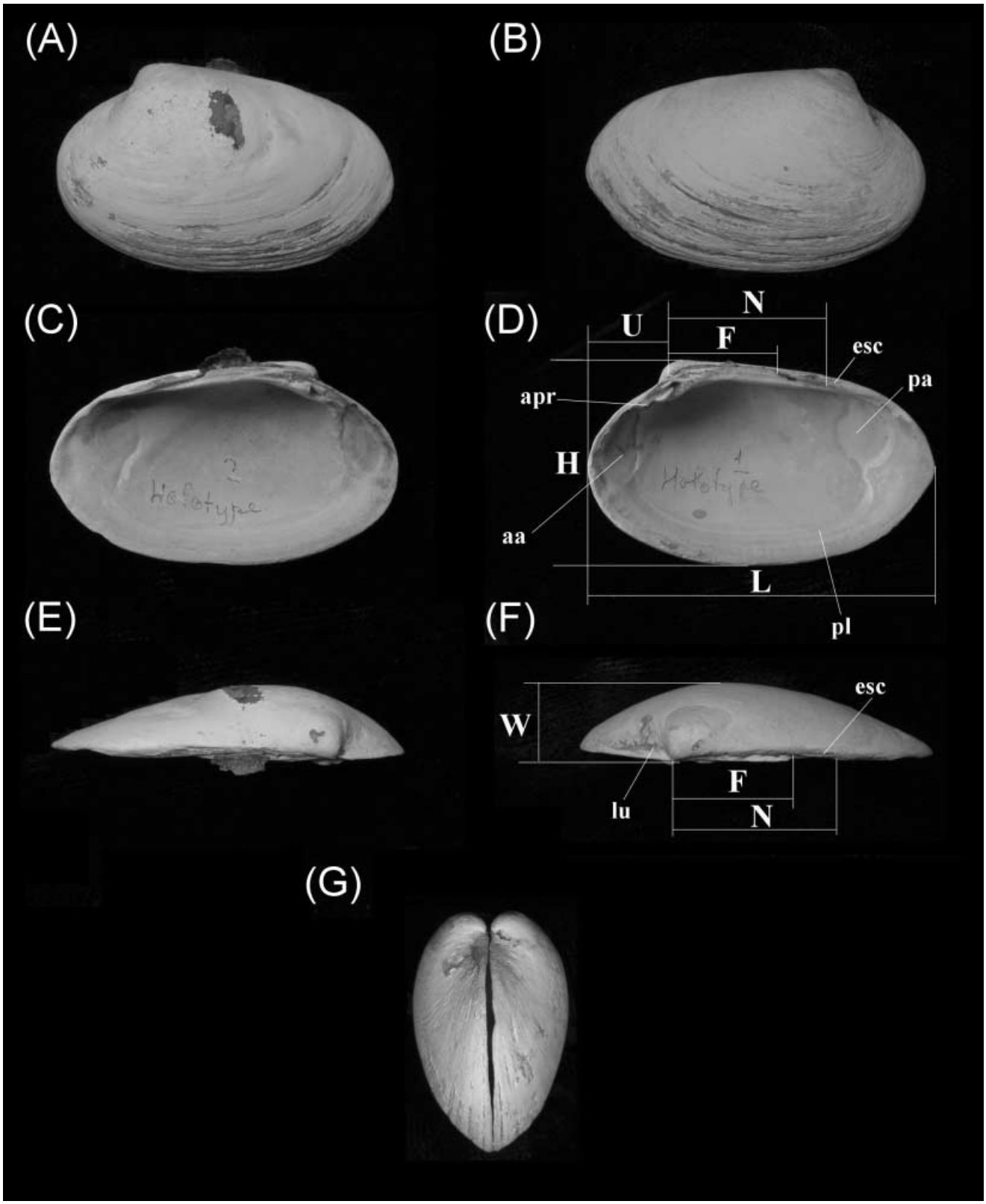

Figure 1. *Calyptogena gallardoi* sp. nov. (A–G) Holotype, length 41.3 mm. (A) Exterior of left valve; (B) exterior of right valve; (C) interior of left valve; (D) interior of right valve; (E) dorsal view of left valve; (F) dorsal view of right valve; (G) anterior view. aa, anterior adductor scar; apr, anterior pedal retractor scar; esc, escutcheon; F, length of the fibrous ligament layer; H, valve height; L, valve length; lu, trace of the lunule; N, length of the posterior lamellar ligament layer; pl, pallial line; U, distance from the umbo to the anterior margin; W, valve width.

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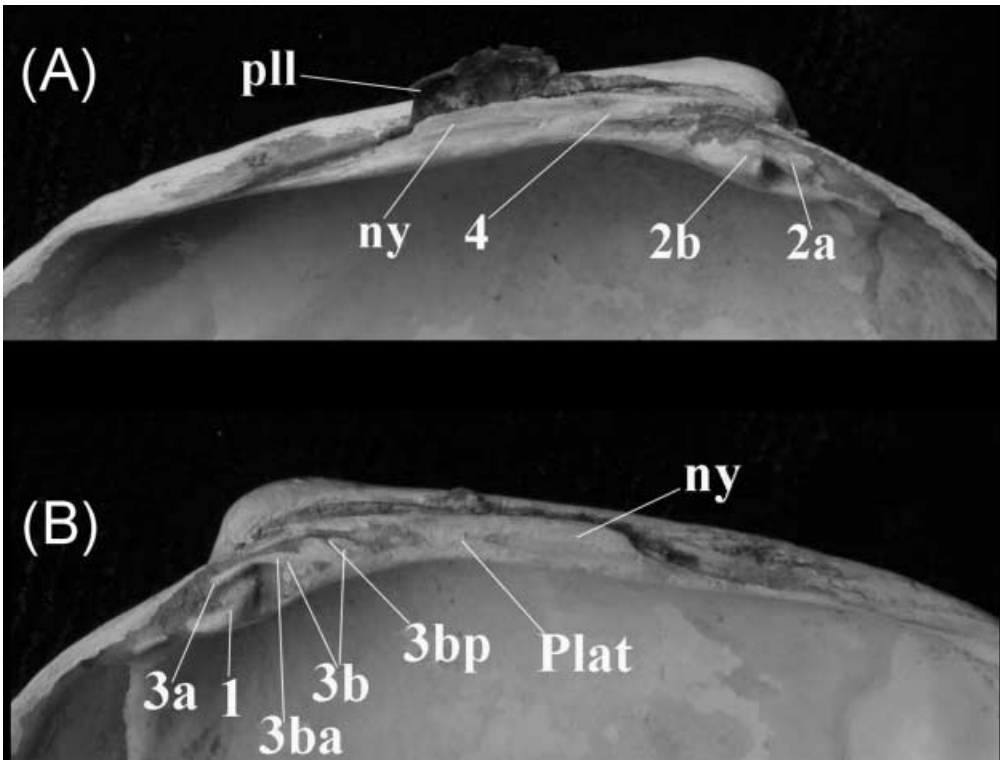

Figure 2. *Calyptogena gallardoi* sp. nov., detail of the left and right hinges of the holotype. Holotype length 41.3 mm. (A) Left hinge plate; (B) right hinge plate. ny, nymph; pll, remnants of posterior lamellar ligament. Teeth of right valve: 1, ventral cardinal tooth; 3a, anterior ramus of subumbonal cardinal; 3b, posterior ramus of subumbonal cardinal; 3ba, anterior ridge of 3b; 3bp, posterior ridge of 3b; Plat, posterior lateral tooth; teeth of left valve: 2a, anterior ramus of subumbonal cardinal tooth; 2b, posterior ramus of subumbonal cardinal tooth; 4, posterodorsal cardinal tooth.

Calyptogena goffrediae sp. nov. (Krylova & Sahling, unpublished). Nine specimens without soft parts (RV 'Sonne', Cruise 146, Station 1, TV-guided grab (TVG); 5°35.06′S 81°38.53′W, 3136 m).

Type locality

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

Diagnosis

Calyptogena species up to 45 mm, stout, elongate–elliptical, height 58–63% of the length, width 18–21% of the length, ventral margin slightly convex, escutcheon not very deep, umbo situated at the anterior 27–31% of the valve, prosogyrate slightly enrolled beaks, moderate nymph, fibrous layer of the ligament occupying 26–34% of the valve length and 62–71% of the posterior lamellar layer (Table 2).

Description of the holotype

Shell stout, elongate–elliptical in outline, height 59% of the length, equivalve. Periostracum of brownish colour, nearly absent except meagre remnant present mainly on periphery of ventral margin. Sculpture consisting of irregular growth lines and wrinkles. Escutcheon moderate, trace of lunular incision on the right valve. Inequilateral, umbo situated at the anterior 28% of the valve length. Umbones prosogyrate, not very low. Beaks slightly enrolled, not touching each other. Antero-dorsal margin nearly straight, anterior margin broadly rounded, ventral margin slightly convex, posterior margin tapering and postero-dorsal margin nearly straight.

Pallial line somewhat broad, not impressed, pallial sinus absent. Anterior adductor scar ovately conic, posterior margin of anterior adductor scar slightly hollowed behind. Anterior pedal retractor scar shallow. Posterior adductor scar slightly impressed, square–rounded, fused to posterior pedal retractor scar.

Nymph not strong, with sloping posterior end. Along the posterior part of the base of the nymph there is a very slight depression. The fibrous layer of the ligament attaching to the nymph comprises 68% of the posterior lamellar layer and 30% of the valve length.

Dentition of the left valve (Figure 2A): 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 the nymph length. Dentition of the right valve (Figure 2B): ventral cardinal (1) stout, shelf-like, radiates obliquely 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

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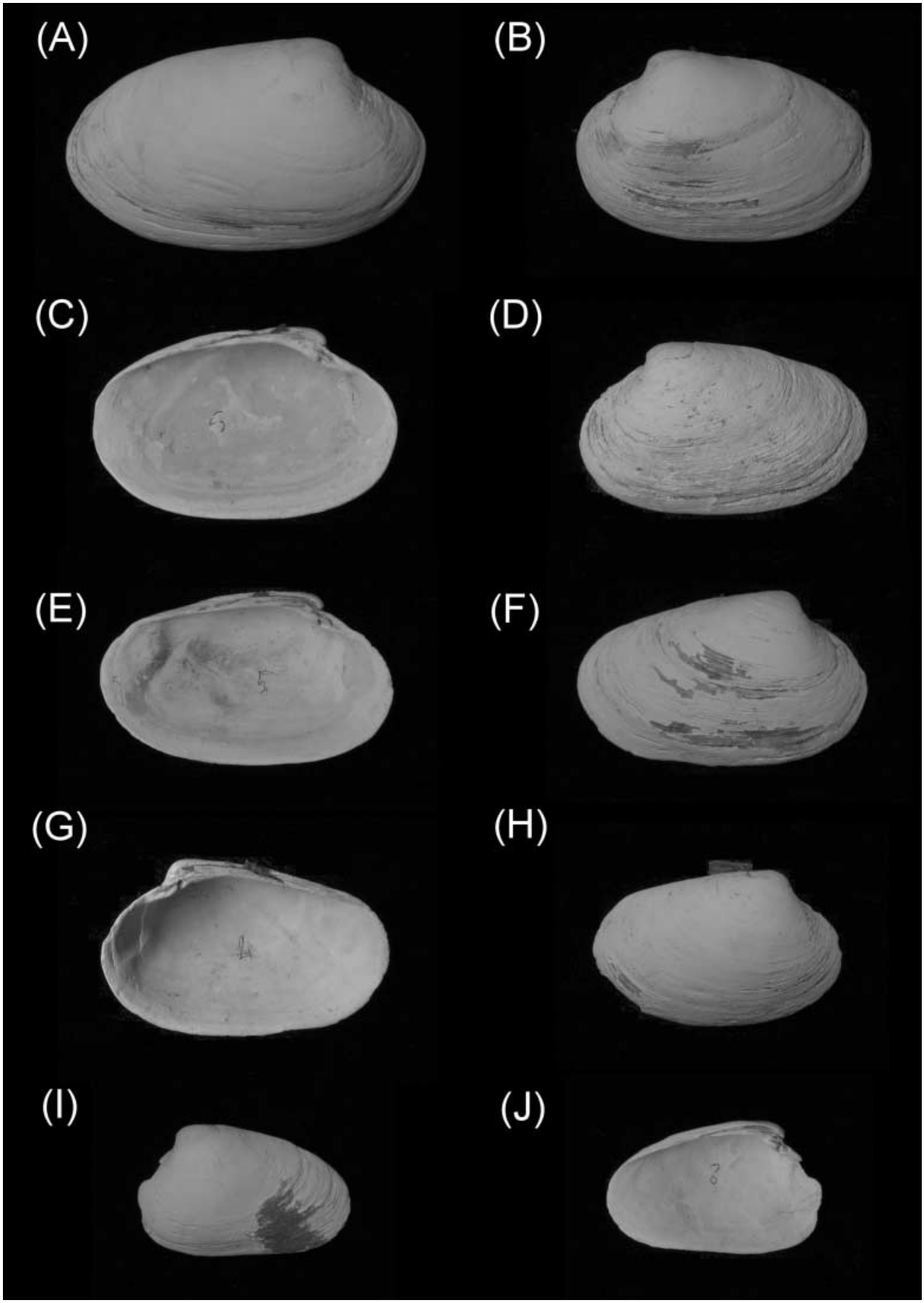

Figure 3. *Calyptogena gallardoi* sp. nov. (A) Paratype 1, length 44.4 mm, exterior of right valve; (B, C) paratype 2, length 36.4 mm; (B) exterior of left valve; (C) interior of left valve; (D–G) paratype 3, length 35.6 mm; (D) exterior of left valve; (E) interior of left valve; (F) exterior of right valve; (G) interior of right valve; (H) paratype 4; length 31.0 mm; exterior of right valve; (I, J) paratype 5, length 26.3 mm; (I) exterior of left valve; (J) interior of left valve.

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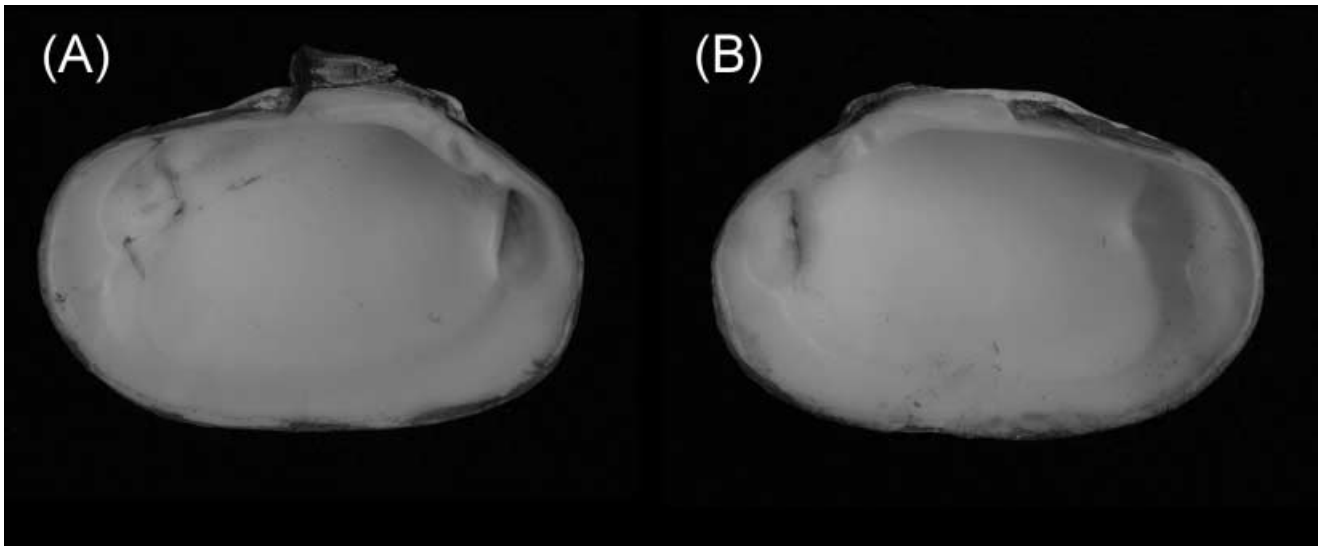

Figure 4. *Calyptogena pacifica* Dall, 1891, RV 'Atlantis', Cruise 131, Alvin dive 2646, 44°40.56′N 125°06.85′W, 720 m, length 35.3 mm. (A) Interior of left valve; (B) interior of right valve.

posterior edges; posterior lateral obsolete, occupying a little more than half of the nymph length.

Variation

It should be pointed out that the described material is in sub-fossil condition. It might be expected that in some features, such as the degree of development of the tooth and lunular incision, valves of living specimens could be different from the ones described here. Variations can be observed in the outline of the shells and in the hinge line. The shape of the shell can be more or less elongate. Outline of posterior margin can vary from rounded to tapering. Smaller specimens have usually more rounded posterior margins. The nymph can be developed to different degrees and varies from weak to moderate. The position of the umbo and the length of the different layers of the ligament vary unremarkably. There are two main variations in the shape of the shell: some specimens being more expanded posterodorsally, while the others have a more elongated posterior part, sloping postero-dorsal margin and a nearly straight ventral margin. This variation has been described in all species of the genus *Calyptogena* s.s. for which large collections of shells exist (Krylova & Sahling, unpublished), and it is suggested represents exhibitions of sexual dimorphism (Coan et al., 2000).

Remarks

Based on the elongate–elliptical shape of the shell, *C. gallardoi* sp. nov. is most similar to *C. pacifica* Dall, 1891 and *Calyptogena goffrediae* sp. nov. collected off Peru (5°35.06′S 81°38.53′W), 3136 m (Krylova & Sahling, unpublished). From *C. pacifica* (Figure 4), the present species differs in the following aspects: *C. gallardoi* sp. nov. has a less developed escutcheon and the nymph of *C. gallardoi* sp. nov. is weaker and usually with sloping posterior margin, while *C. pacifica* has a strong nymph often with a nearly abrupt posterior end. *Calyptogena pacifica* has a longer posterior edge of 3b-ramus. The posterior lateral tooth in the right valve and postero-dorsal cardinal tooth (4b) in the left valve are more strongly developed than in *C. gallardoi* sp. nov. The new species from Peru (Krylova & Sahling, unpublished) differs from *C. gallardoi* sp. nov. by having a shallower escutcheon, more curved beaks and a more expanded antero-dorsal shell region.

Distribution

Known only from the type locality.

Biotope

Sticky dark grey mud with a sulphidic smell. The presence of sulphide in the sediment, as well as methane,

Table 2. *Meristic and morphometric characteristics of* Calyptogena gallardoi *sp. nov.*

	L	H	W	F	N	H/L	W/L	F/N	F/L	N/L	U
Holotype, right valve	41.3	24.4	7.7	12.4	18.2	0.59	0.19	0.68	0.3	0.44	28
Paratype 1, single right valve	44.4	25.8	8.6	15	21	0.58	0.19	0.71	0.34	0.47	28
Paratype 2, single left valve	36.4	23	7.7	10	14.6	0.63	0.21	0.68	0.27	0.4	31
Paratype 3, right valve	35.6	21.3	6.5	10.5	16.2	0.59	0.18	0.65	0.3	0.46	30
Paratype 4, single right valve	31	18.6	5.7	8.2	13.3	0.6	0.18	0.62	0.26	0.43	29
Paratype 5, single left valve	26.3	16.3	5.4	7	10	0.62	0.21	0.7	0.27	0.38	27

L, length; H, height; W, width; F, length of the fibrous ligament; N, length of the posterior lamellar ligament; U, situation of the umbo (% of shell length from the anterior margin). All measurements in millimetres.

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was later corroborated by gas chromatography analysis at the Microbiology Department of the University of Concepción (V. Campos, personal communication).

Etymology

Named after Professor Dr Victor A. Gallardo from the University of Concepción, who participated in the collection of the type material, and also in recognition of his devotion to the development of marine sciences in Chile.

DISCUSSION

In the current literature dealing with chemosynthesis-based megafaunal communities, *Calyptogena* is one of the most often mentioned genera, which sometimes refers to any large white clams. As a consequence, *Calyptogena* became a complex taxon containing species not closely related. Recently, a revision of the genus *Calyptogena* is being made by Krylova & Sahling (unpublished), and as a result only four previously known species are retained in the genus (*Calyptogena pacifica* Dall, 1891; *Calyptogena fausta* Okutani, Fujikura & Hashimoto, 1993; *Calyptogena rectimargo* Scarlato, 1981 and *Calyptogena valdiviae* Thiele & Jaeckel, 1931). All species of the genus have shell characters in common such as the presence of an escutcheon, absence of a pallial sinus and presence of broad 3b-ramus and a posterior lateral tooth in the right valve. So far the genus *Calyptogena* s.s., together with the newly described species, includes nine recent species distributed along the continental parts of the Pacific, Indian and the East Atlantic Oceans. The region with most species is the East Pacific. Before the present finding, the southernmost locality of *Calyptogena* s.s. was off Peru, 5°35′S (Goffredi et al., 2003; Krylova & Sahling, unpublished). The discovery of *C. gallardoi* sp. nov. extends the range of the genus to 36°22′S.

Given that the slope fauna of the south-eastern Pacific is, in general, poorly known, and that communities associated with methane seepage are in general highly localized, it is not surprising that at the Chilean margin their existence has been only recently confirmed (Sellanes et al., 2004). Nevertheless, a first clue of their presence was the description of *Ectenagena australis* Stuardo & Valdovinos, 1988, whose relationship with cold seeps was at the time still not known.

It is noteworthy that, though scarce, the evidence so far obtained indicates that the CMSA seems to be quite rich in symbiont-containing bivalve families, if compared with other thoroughly described sites in the Pacific. Fragments of at least five still unidentified species, belonging to different families, were collected together with those of *C. gallardoi* sp. nov. (Table 1). It is known that in general the number of symbiont-containing species decreases with the depth at which seeps occur (Olu et al., 1996; Sibuet & Olu-Le Roy, 2002). So far, the only well studied cold-seep areas in the Pacific Ocean, laying at comparable depths with the present study are those of Monterey Bay, north-east Pacific margin (600–1000 m) and in Sagami Bay, north-west Pacific margin (900–1200 m), recently reviewed by Sibuet & Olu-Le Roy (2002). Although, five species of endosymbiont-containing bivalves are reported for the Monterey Bay area, they belong only to two families. On the other hand, at Sagami Bay the diversity at the family level is slightly higher, with eight species belonging to five families.

Due to the large extent of the gas–hydrate fields reported by Morales (2003) below the slope area off central Chile (about 1000 km from north to south), it could be expected that methane seep communities will prove to be quite a common feature in the Chilean bathyal landscape. They could thus be playing some role in the energy flux of the corresponding benthos. From the present study, a circumstantial proof suggesting that chemosynthesis could be subsidizing heterotrophic food webs at these depths, is that one of the valves of *C. gallardoi* sp. nov. presented a mollusc bore hole, probably of a muricid of the genus *Trophon*. Further, many lost hooks and weights used by artisanal fishermen of deep-sea cod (*Dissostichus eleginoides*), dredged in and around the study area, indicate a potential link between this important Chilean fishery and methane seepage, probably by providing a favourable habitat (e.g. carbonate hard-grounds, enhanced biological activity) to this large predator. Nevertheless, MacAvoy et al. (2002) indicated, by means of stable isotope analysis, that large mobile predators captured on-site from three chemosynthetic communities showed significant incorporation of chemosynthetic material. It still has to be proven if this is also the case for predators associated with Chilean seep communities.

It is thus expected that in the near future further explorations of the bathyal area, using modern technologies, will yield exciting results in diverse aspects such as trophodynamics, biogeography and phylogenetics of this kind of community, as well as of the related non-chemosymbiotic fauna.

We wish to thank the captain and crew of RV 'Kay Kay' for their skilful assistance at sea. Our thanks also to Graham Oliver of the National Museums & Galleries of Wales for his help with the lucinids and thyasirids. Victor Campos at the Microbiology Department of the University of Concepción is thanked for the analysis of methane and sulphide in the sediments. For loan of the type material of *Calyptogena pacifica* we thank Tyjuana Nickens and Jerry Harasevich (NMNH). Figures of *C. pacifica* were made by Heiko Sahling (University of Bremen, Germany). Funding for E.K. was provided by a grant of the Russian Foundation for Basic Research (project no. 05-05-65283). The Census of Marine Life programme and its field project ChEss (Biogeography of Deep-water Chemosynthetic Ecosystems) are thanked for inviting J.S. to a first implementation meeting on future activities in the south-east Pacific margin and for subsequent support. This is a contribution of the Center for Oceanographic Research in the eastern South Pacific (COPAS).

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