

Methane seep molluscs from the Sinú–San Jacinto fold belt in the Caribbean Sea of Colombia

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Several species of bivalves belonging to families which are typically associated with reducing conditions, like those observed at methane seep sites, have been obtained in recent explorations of the Caribbean Sea margin off the coast of Colombia. The material has been collected at depths of around 500 m west of the Magdalena and Sinú deltas, located in the Sinú–San Jacinto fold belt. These bivalves correspond to the families Vesicomidae (Calyptogena ponderosa, Vesicomya caribbea and Ectenagena modioliforma), Lucinidae (Graecina colombiensis and three unidentified species of Lucinoma), Solemyidae (Acharax caribbaea) and Thyasiridae (Conchocele bisecta). In addition, for the first time off Colombia empty tubes of vestimentiferan polychaetes, belonging to the family Siboglinidae, were collected. At some of these sites the presence of authigenic carbonates has been observed together with the biological material. Although the obligate seep fauna generally contains relatively few and endemic species, a large suite of accompanying heterotrophic species (here we report only the molluscs) has been found at the seep sites. The occurrence of carbonates, the geological characteristics of the area and the new biological evidence confirms the presence of methane seep ecosystems in the Caribbean Sea off Colombia.

Keywords: methane seeps, chemosynthesis, chemosymbiotic bivalves, Caribbean Sea, Colombia

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INTRODUCTION

Reducing systems in which carbon is fixed chemosynthetically by bacteria, e.g. methane, hydrocarbon and brine seeps, dead whale-falls, hypoxic sulphidic settings and hydrothermal vents, are now known to be conspicuous components of the benthic realm (Gage & Tyler, 1991; Duperron *et al.*, 2005). A particular type of these systems are those associated with the seafloor seepage of hydrocarbons (e.g. methane), also known as cold-seeps. These systems are known from both active and passive continental margins worldwide, and cover a vast bathymetric range, from the shelf to trenches (Barry *et al.*, 1996; Corselli & Basso, 1996; Olu *et al.*, 1997; Olu-Le Roy *et al.*, 2004; Campbell, 2006). Biological communities at methane seeps are in general dominated by highly endemic chemosymbiotic metazoans, such as bivalves of the families Vesicomidae, Lucinidae, Thyasiridae, Mytilidae (bathymodiolin mussels), Solemyidae, Manzanellidae and Teredinidae (Cosel & Olu, 2008, 2009), together with vestimentiferan tube-worms and free living filamentous bacteria. These particular systems are found where methane or other hydrocarbons are expelled from the seafloor at accretionary prisms, mud

and salt diapirs, buried organic-rich sediments associated to slope mass-wasting processes and also nearby sites with high sedimentation rates close to river deltas (Barry *et al.*, 1996; Tunnicliffe *et al.*, 2003). At the western Atlantic, the presence of these systems has been well documented in the Gulf of Mexico, the Florida escarpment, and in the slope off the coast of Louisiana (Paull *et al.*, 1984; Carney, 1994; Sibuet & Olu, 1998; Cordes *et al.*, 2007). Reports of recent seep communities or taxa off the South American coasts exist also for north-eastern Brazil (e.g. *Calyptogena birmani*—Domaneschi & Lopes, 1990), Uruguay (e.g. *Lamellibrachia victori*—Mañé-Garzón & Montero, 1986), Chile (e.g. *Ectenagena australis*—Stuardo & Valdovinos, 1988; a seep site off Concepción—Sellanes *et al.*, 2004, 2008; Sellanes & Krylova, 2005), and the Yaquina Basin methane seeps off Peru (Olu *et al.*, 1996). Palaeontological and recent evidences for the presence of these communities are also available for the Paleogene and Neogene in Barbados, Trinidad and Venezuela (Gill *et al.*, 2005), where their presence has been associated with the accretionary prism at the subduction site of the Caribbean plate below the North Atlantic plate. As in most recent seep sites, the assemblages were dominated by bivalves of the above mentioned families. But Gill *et al.* (2005) also show a comparative list of the taxa from modern seep communities of the Barbados Prism and Gulf of Mexico.

The occurrence of gas hydrates in the Colombian Caribbean was first described by Shipley *et al.* (1979) in

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López & Ojeda (2006). However, only geological research has been conducted on this topic and this was aimed at exploring hydrocarbon sources. In Colombia, the presence of some of these bivalve families has been sparsely reported in taxonomic studies or inventories of the continental margin fauna, but lacking any ecological information. For the family Vesicomidae, Boss (1967a, 1968) described some species based on material collected off northern Colombia. Most recently, Taylor & Glover (2009) described two species of the family Lucinidae, found on the middle of the Colombian Caribbean coast. Nearby this area the presence of gas escaping from the seafloor at the shelf and slope (to 1370 m depth) has been reported from off Ciénaga Grande de Santa Marta (Shepard *et al.*, 1968; Shepard, 1973), towards the Gulf of Urabá and has been associated with the presence of diapirs and mud volcanoes (Duque-Caro, 1984; Ojeda *et al.*, 2004; López & Ojeda, 2006).

Recently, several projects have improved our knowledge of the shelf and slope (20 to 940 m depth) benthic fauna of the Caribbean Sea off Colombia (e.g. Macrofauna I, 1998; Macrofauna II, 2001; ANH-I, 2008; and ANH-II, 2009). Among the results of these studies, most relevant are the discoveries of deep water coral habitats off La Guajira, Magdalena and Bolívar (Reyes *et al.*, 2005; Santodomingo *et al.*, 2007), evidence of deep water calcareous algae (unpublished data), and now, biological and geological evidence supporting the presence of cold-seeps in the Sinú and Magdalena areas.

This paper reports on new findings of chemosymbiotic species off Colombia, as well as the presence of other indicators of seep activity, such as authigenic carbonates. These results help to elucidate the biogeographical patterns of chemosymbiotic assemblages in the Caribbean Sea and the western Atlantic area, and are discussed within the geological context of the area.

MATERIALS AND METHODS

Geological setting

The Colombian Caribbean is located in an active tectonic zone in which the Caribbean and South American plates interact (Figure 1). This interaction has generated magmatic arches (from the Jurassic to the Paleogene), the accretion of ophiolitic fields (e.g. ophiolitic series of the Jurassic) and the formation of a wedge or folded belts denominated in the literature as Sinú and San Jacinto (Duque-Caro, 1979; Toto & Kellogg, 1992; Flinch, 2003; Sánchez & Permanyer, 2006). These belts have created a sedimentary basin up to 12 km thick, which was accreted to the South-American margin during the Cenozoic, and extends from Urabá (south-west—Caribbean of Colombia) to Venezuela (Duque-Caro, 1979; Toto & Kellogg, 1992).

All the continental shelf and slope areas of the southern Colombian Caribbean belong to the Sinú belt, which is bounded to the east by the Romeral fault system and to the west by the Colombia fault system. Lithologically this belt constitutes rocks from the lower Eocene to sediments of recent alluvial and marine origin. The majority is formed by a turbiditic sequence of very fine sediments up to 5000 m thick (Duque-Caro, 1980) and the main characteristic of this belt is the widespread presence of mud diapirism.

According to the geomorphological conditions the southern part of the Colombian Caribbean, where the stations discussed in the present work are distributed, can be separated into two very distinct areas: (i) Magdalena, or the Magdalena Turbidity System (MTS); and (ii) Sinú, or the Accretionary Sinú Prism (ASP).

Magdalena constitutes a wide sedimentary accumulation on the northern part of the continental margin of Colombia. This system began to develop during the Pliocene, forming a sedimentary wedge that remains practically undeformed (Kolla *et al.*, 1984). According to Ercilla *et al.* (2002) the MTS is ~230 km long, covers an area of ~53,000 km², has a volume of 180,000 km³ and extends into water more than 4000 m deep. This turbidite system is fed by the Magdalena River, which has an average fluvial discharge of 5000 m³ s⁻¹ (Kolla *et al.*, 1984; Kolla & Buffler, 1985; Pujos & Javelaud, 1991). The main geomorphologic features that characterize the seafloor of the MTS are: (i) submarine canyons; (ii) structural highs; (iii) levees and channels; (iv) mass flow deposits; (v) ridges; and (vi) scarps.

The Sinú sector covers most of the area named ASP. The features occurring within this area include drainage systems (broad channels and turbidity channels), anticlinal ridges with associated faults, seabed mounds and mass-transport systems such as slumps and debris flows. The drainage systems include broad lower relief drainage channels occurring mostly in the southern and northern parts of the area and thin high relief turbidity channels that generally occur in the central part of the area (similar to the Magdalena sector). The pathways or directions of flow of these drainage systems are structurally influenced. These drainage systems originate at the shelf and flow down into the abyssal plain. Small seabed mounds occur throughout the Sinú area. The mounds are probably buried mud diapirs, which are common in this area of offshore Colombia. As shortening occurs in some anticlines the mud is concentrated within the core of the anticline and is eventually pushed upwards. However, not all mud diapirs extrude to the seabed—some are trapped by sedimentation. The smaller seabed mounds occur in the east central part of the survey area and they range from 5 m to 10 m height (Rangel-Buitrago & Idarraga, 2010).

Biological sampling

Present investigations were carried out within ongoing research projects INVEMAR–Macrofauna I (1998 and 1999 on the Colombian Caribbean coast, which included samples taken broadly within 300 and 500 m depth), INVEMAR–ANH I (2008, sampled within 170 and 940 m depth) and INVEMAR–ANH II (2009, sampled within 30 and 700 m depth) (Figure 1).

These projects surveyed the area located between La Guajira peninsula (12°34'N–71°50'W) and the Gulf of Urabá (09°02'N–76°02'W). Most of the sampled areas comprised shelf and slope soft bottoms. Samples were obtained aboard BI 'Ancón' using a semiballoon trawling net with a mouth opening of 9 × 1 m, equipped with a protective bag of polyethylene with 10 mm stretched mesh-size at the cod-end, and operated at 3 knots in 10 minute hauls. The samples were carefully washed with water in a 500 µm sieve. Each sample was separated immediately, preserved in 70% ethanol and then transported to INVEMAR laboratories

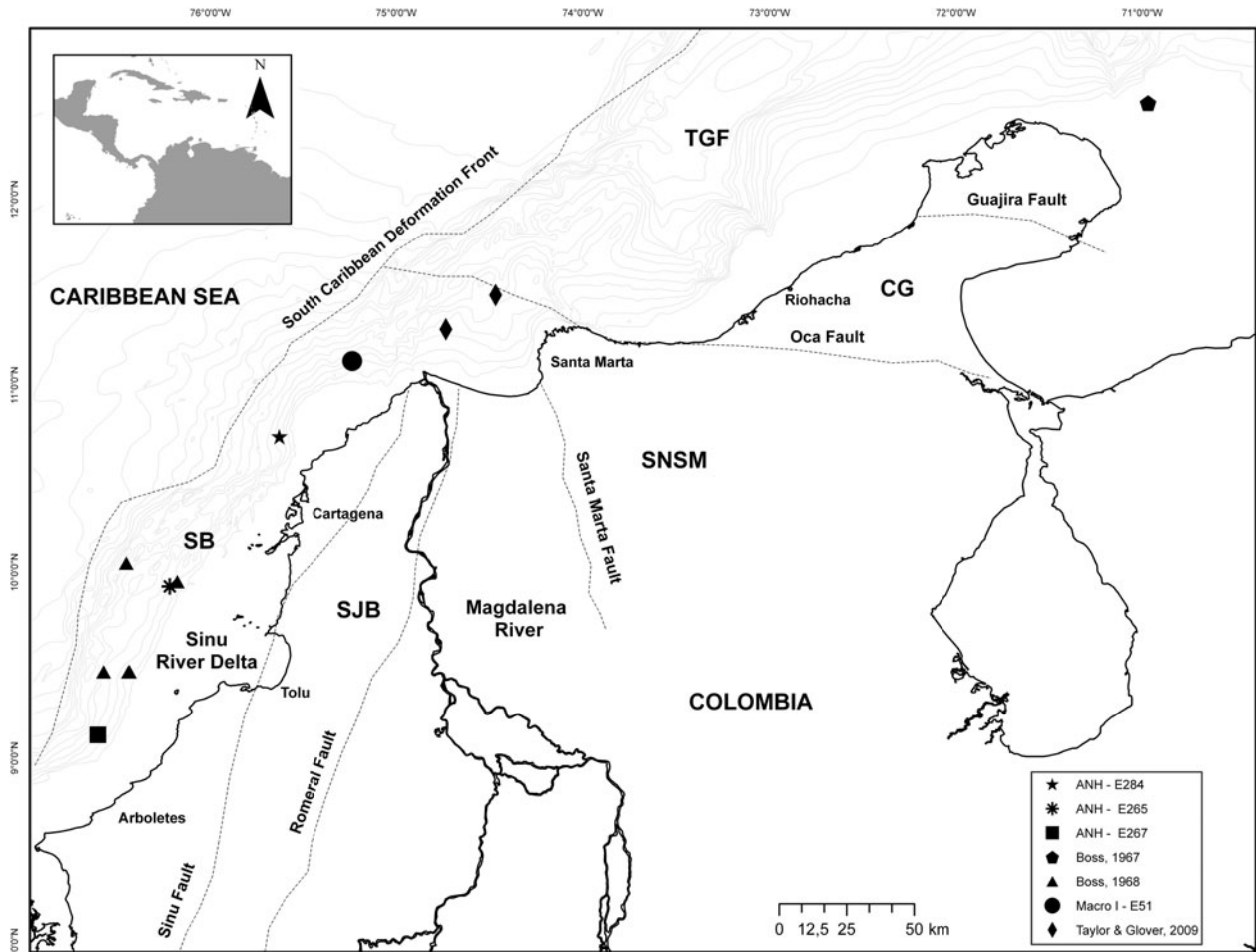


Fig. 1. Map showing the location of the sampling stations, as well as previous references indicating the presence of representatives of the families Vesicomidae, Solemyidae, Lucinidae and other species associated with methane seeps in the Colombian Caribbean. The stations located in the middle of the Colombian Caribbean belong to the Magdalena area and those located in the southern area correspond to Sinú. Boss (1967a): *Vesicomya caribbea*; Boss (1968): *V. cordata*, *Ectenagena modioliforma*, *Calyptogena ponderosa*; Macrofauna I (E51): *C. ponderosa*, *V. caribbea*, *Lucinoma* sp. 1, *Graecina colombiensis*, *Acharax caribbaea*, *E. modioliforma*; ANH I E265: *C. ponderosa*, *Lucinoma* sp. 1; ANH E267: *E. modioliforma*, *Lucinoma* sp. 2, *Lucinoma* sp. 3. and various pieces of Vesicomidae; ANH II E284: *Cantrainea macleani* and tubes of *Lamellibrachia* sp.; Taylor & Glover (2009): *G. colombiensis* and *Jorgenia gracile*; TGF: Guajira-Falcon Terrain; CG: Guajira Basin; SJB: San Jacinto Belt; SB: Sinú Belt.

for further processing. In the present work we review and discuss only the mollusc collections, with the exception of additional seep indicator taxa (e.g. vestimentiferan tube-worms). Living organisms and shells were counted and identified to the lowest taxonomic level possible, with particular attention given to chemosymbiotic fauna. The taxonomic work was performed at the Museo de Historia Natural Marina de Colombia (MHNMC). The material is deposited in the Molluscs Collection of the MHNMC, Santa Marta, Colombia.

The information presented here is further complemented with a review of the existing records of chemosymbiotic taxa for the area (e.g. Boss, 1967a, 1968; Bayer *et al.*, 1970; Taylor & Glover, 2009).

RESULTS

From the INVEMAR–Macrofauna I expedition, the most interesting finding regarding seep fauna was at Station E51 located west of the Magdalena River delta. At this site, the assemblage of chemosymbiotic bivalves included the families

Solemyidae, Vesicomidae, Lucinidae (Figure 2A–E, H & K–P) and Thyasiridae. Solemyids were represented by *Acharax caribbaea* (Vokes, 1970) (13 articulated valves) constituting the second known record for the species and extending its local range southward. Vesicomids included *Calyptogena ponderosa* Boss, 1968 (a single valve and a matching pair) and *Vesicomya caribbea* Boss, 1967 (a living specimen and a set of articulated valves). Locally the latter was known only from La Guajira, thus its local range was extended by our new records. Lucinids were represented also by two species, *Lucinoma* sp. 1 (a living specimen) and *Graecina colombiensis* Taylor & Glover, 2009 (a living specimen). The most conspicuous non-chemosymbiotic bivalves at this site included *Limopsis sulcata* Verrill & Bush, 1898 (Limopsidae), *Acesta colombiana* (Vokes, 1970) (Limidae) and *Neilo* sp. (Neilonellidae). The complete inventory, including sample numbers of all the molluscs obtained at each station, is detailed in Table 1.

During the INVEMAR–ANH I survey, evidence from seep habitats was obtained from three sampling stations. Articulated valves of *C. ponderosa* were found at Station E265, located off Golfo de Morrosquillo. At Station E267

Table 1. Species of molluscs found at the sampling stations which recorded the presence of families inhabiting reducing settings. *, indicate stations in the southern Colombian Caribbean surveyed by the RV 'Pillsbury' (see Bayer *et al.*, 1970). Some records in Boss 1968: (-). Where information is available, the condition of the material is specified: empty shells (s) or shells with soft-body (sb).

Species	*E364 (937 m)	*E391 (1485 m)	*E394 (525 m)	MACROI E51 (500 m)	ANH-I E265 (500 m)	ANH-I E267 (500 m)	ANH-II E284 (705 m)
Class Polyplacophora Gray, 1821							
Order Neoloricata Bergenhayn, 1855							
Leptochitonidae Dall, 1889							
<i>Leptochiton binghami</i> (Boone, 1928). In Bayer <i>et al.</i> (1970): <i>Lepidopleurus pergranatus</i> (Dall, 1889)	x (sb)		x (sb)			x (sb)	x (sb)
Class Bivalvia Linné, 1759							
Subclass Protobranchia Pelseneer, 1889							
Order Solemyoidea Dall, 1889							
Solemyidae Gray, 1840							
<i>Acharax caribbaea</i> (Vokes, 1970)				x (s)			x (s)
Order Nuculoida Dall, 1889							
Nuculidae Gray, 1824							
Nuculidae sp.							x (sb)
Nuculanidae H. & A. Adams, 1858							
<i>Nuculana acuta</i> (Conrad, 1832)						x (s)	
Nuculanidae sp.			x				
Malletiidae H. & A. Adams, 1858							
<i>Malletia</i> sp. 1			x				
<i>Malletia dilatata</i> (Philippi, 1844)						x (sb)	
<i>Neilo</i> sp.				x (s)			
Yoldiidae Dall, 1908							
<i>Orthoyoldia scapania</i> (Dall, 1890)						x (s)	x (s)
<i>Portlandia nigromaculata</i> Okutani, 1983							x (sb)
<i>Portlandia</i> sp.				x			
<i>Yoldia liorhina</i> Dall, 1881			x				
Tindariidae Verrill & Bush, 1897							
<i>Tindaria amabilis</i> (Dall, 1889)	x						
<i>Tindaria cytherea</i> (Dall, 1881)						x (sb)	
Subclass Pteromorpha Beurlen, 1944							
Order Arcoida Stoliczka, 1870							
Arcidae Lamarck, 1809							
<i>Barbatia</i> sp.						x (s)	
<i>Batharca glomerula</i> (Dall, 1881)							x (sb)
<i>Bentharca sagrinata</i> (Dall, 1886)						x (sb)	
Limopsidae Dall, 1895							
<i>Limopsis sulcata</i> Verrill & Bush, 1898				x (sb)	x (sb)	x (sb)	x (sb)
<i>Limopsis</i> sp. 1	x		x				
Order Mytiloidea Férussac, 1822							
Mytilidae Rafinesque, 1815							
<i>Amygdalum politum</i> (Verrill & Smith, 1880)			x				
<i>Modiolus americanus</i> Leach, 1815	x						
<i>Modiolus</i> sp. 1			x				
Mytilidae sp. 2							x (sb)
Order Limoida Waller, 1978							
Limidae Rafinesque, 1815							
<i>Acesta colombiana</i> (Vokes, 1970)			x	x (sb)	x (sb)		x (sb)
Order Pectinoidea Adams & Adams, 1857							
Propeamussiidae Abbott, 1954							
<i>Parvamussium pourtalesianum</i> (Dall, 1886)					x (sb)	x (sb)	
<i>Propeamussium dalli</i> (Smith, 1885)			x				x (sb)
<i>Propeamussium</i> sp. 1	x	x					
<i>Propeamussium</i> sp. A							x (sb)
<i>Propeamussium</i> sp. B							x (sb)
Pectinidae Rafinesque, 1815							
<i>Pseudohinnites adamsi</i> (Dall, 1886) In Bayer <i>et al.</i> (1970): <i>Pseudamussium adamsi</i> (Dall, 1886)	x						
Dimyidae Fischer, 1886							
<i>Dimya argentea</i> Dall, 1886			x				
Subclass Heterodonta Neumayr, 1884							

Continued

Table 1. Continued

Species	*E364 (937 m)	*E391 (1485 m)	*E394 (525 m)	MACROI E51 (500 m)	ANH-I E265 (500 m)	ANH-I E267 (500 m)	ANH-II E284 (705 m)
Order Veneroida H. & A. Adams, 1856							
Lucinidae Fleming, 1828							
<i>Graecina colombiensis</i> Taylor & Glover, 2009				x (sb)		x (s)	
<i>Lucinoma filosa</i> (Stimpson, 1851) In Bayer <i>et al.</i> (1970): <i>Lucina filosa</i> Stimpson, 1851			x				
<i>Lucinoma</i> sp. 1				x (sb)	x (s)		x (s)
<i>Lucinoma</i> sp. 2						x (s)	
<i>Lucinoma</i> sp. 3						x (s)	
Thyasiridae Dall, 1900							
<i>Conchocele bisecta</i> (Conrad, 1849) In Boss (1967b) and Bayer <i>et al.</i> (1970): <i>Thyasira</i> <i>disjuncta</i> (Gabb, 1866)			x				x (s)
Thyasiridae sp.						x (s)	
Vesicomomyidae Dall & Simpson, 1901							
<i>Calyptogena ponderosa</i> Boss, 1968	x	–	x (s)	x (s)	x (sb)		x (sb)
<i>Ectenagena modioliforma</i> Boss, 1968			– (sb)	x (s)		x (s)	
<i>Vesicomya caribbea</i> Boss, 1967				x (sb)			
<i>Vesicomya cordata</i> Boss, 1968			– (sb)				x (sb)
Vesicomomyidae sp.							x (sb)
Vesicomomyidae remains						x (s)	
Semelidae Stoliczka, 1870							
<i>Abra longicallus</i> (Scacchi, 1835). In Bayer <i>et al.</i> (1970): <i>Abra americana</i> Verrill & Bush, 1898	x					x (sb)	x (sb)
Trapezidae Lamy, 1920							
<i>Glossocardia agassizii</i> (Dall, 1886) In Bayer <i>et al.</i> (1970): <i>Meiocardia agassizii</i> Dall, 1886			x				
Order Anomalodesmata Dall, 1889							
Cuspidariidae Dall, 1886							
<i>Cardiomya perrostrata</i> (Dall, 1881)						x (sb)	
<i>Cuspidaria</i> sp.						x (s)	
<i>Myonera paucistriata</i> Dall, 1886							x (sb)
Verticordiidae Stoliczka, 1870							
<i>Haliris fischeriana</i> (Dall, 1881)					x (sb)		
<i>Euciroa elegantissima</i> (Dall, 1881)			x		x (s)		
<i>Sinospinella agnes</i> Simone & Cunha, 2008						x (s)	
Poromyidae Dall, 1886							
<i>Cetoconcha margarita</i> (Dall, 1886)						x (sb)	
<i>Poromya rostrata</i> Rehder, 1943						x (sb)	
Cephalopoda Schneider, 1784							
Subclass Coleoidea Bather, 1788							
Superorder Octopodiformes Berthold & Engeser, 1987							
Order Octopoda Leach, 1818							
Octopodidae d'Orbigny, 1840							
<i>Benthoctopus januarii</i> (Hoyle, 1885)				x			
Superorder Decapodiformes Leach, 1817							
Order Sepioidea Naef, 1916							
Sepiolidae Leach, 1817							
<i>Semirossia</i> sp.						x	
Gastropoda Cuvier, 1797							
Subclass Eogastropoda							
Order Patellogastropoda Lindberg, 1986							
Acmaeidae Carpenter, 1857							
<i>Pectinodonta arcuata</i> Dall, 1882						x (s)	
Subclass Orthogastropoda							
Superorder 'Cocculiniformia' Haszprunar, 1987							
Cocculinidae Dall, 1882							
Cocculinidae sp.						x (sb)	x (sb)
Superorder Vetigastropoda Salvini-Plawen, 1980							

Continued

Table 1. Continued

Species	*E364 (937 m)	*E391 (1485 m)	*E394 (525 m)	MACROI E51 (500 m)	ANH-I E265 (500 m)	ANH-I E267 (500 m)	ANH-II E284 (705 m)
Fissurellidae Fleming, 1822							
<i>Diodora tanneri</i> (Verrill, 1882)				x (sb)			
<i>Diodora</i> sp.			x				
<i>Cornisepta acuminata</i> (Watson, 1883)						x (sb)	
Fissurellidae sp.						x (s)	
Colloniidae Cossmann, 1917							
<i>Cantrainea macleani</i> Warén & Bouchet, 1993							x (sb)
<i>Homalopoma</i> sp. 1			x				
<i>Homalopoma</i> sp. 2	x		x				
<i>Homalopoma</i> sp. 3			x				
Calliostomatidae Thiele, 1924							
<i>Calliostoma rosewateri</i> Clench & Turner, 1960			x				
Chilodontidae Wenz, 1938							
<i>Calliotropis actinophora</i> (Dall, 1890)	x	x					
<i>Calliotropis</i> sp.							x (sb)
<i>Cataegis meroglypta</i> McLean & Quinn, 1987							x (sb)
<i>Cataegis finkli</i> (Petuch, 1987)							x (sb)
Trochidae Rafinesque, 1815							
<i>Gaza olivacea</i> Quinn, 1991				x (s)			x (sb)
Superorder Caenogastropoda Cox, 1960							
Order Sorbeoconcha Ponder & Lindberg, 1997							
Capulidae Fleming, 1822							
<i>Capulus</i> sp.				x (sb)			
Xenophoridae Troschell, 1852							
<i>Xenophora longleyi</i> Bartsch, 1931. In Bayer et al. (1970): <i>Tugurium longleyi</i> Bartsch, 1931			x			x (s)	x (sb)
Naticidae Guilding, 1834							
<i>Polinices</i> sp.			x				
Cassidae Latreille, 1825							
<i>Eucorys bartschi</i> (Rehder, 1943). In Bayer et al. (1970): <i>Oocorys bartschi</i> Rehder, 1943			x				
Tonnidae Suter, 1913							
<i>Eudolium crosseanum</i> (Monterosato, 1869)			x				
<i>Eudolium</i> sp.							x (sb)
Muricidae Rafinesque, 1815							
<i>Boreotrophon aculeatus</i> (Watson, 1882)							x (sb)
<i>Coralliophila squamosa</i> (Bivona, 1838)						x (s)	
<i>Murex</i> sp.						x (s)	
<i>Laevityphis</i> sp.					x (sb)		
<i>Paziella oregonia</i> (Bullis, 1964)				x (s)			
<i>Siphonochelus riosi</i> (Bertsch & D'Attilio, 1980)							x (sb)
<i>Poirieria actinophora</i> (Dall, 1889). In Bayer et al. (1970): <i>Trophon actinophorus</i> (Dall, 1889)			x			x (sb)	
Turbinellidae Swainson, 1840							
<i>Fulgurofusus brayi</i> (Clench, 1959). In Bayer et al. (1970): <i>Columbarium brayi</i> Clench, 1959			x			x (sb)	x (sb)
Buccinidae Rafinesque, 1815							
<i>Manaria canetae</i> (Clench & Aguayo, 1944)				x (sb)			x (sb)
<i>Plicifusus</i> sp.	x		x				
Volutidae Rafinesque, 1815							
<i>Scaphella</i> sp.			x				
Marginellidae Fleming, 1828							
<i>Prunum roscidum</i> (Redfield, 1860) In Bayer et al. (1970): <i>Marginella limatula</i>			x				
<i>Marginella</i> sp. 3			x				
<i>Volvarina hennequini</i> Boyer, 2001				x			x (sb)
<i>Volvarina bayeri</i> Gracia & Boyer, 2004							x (sb)

Continued

Table 1. Continued

Species	*E364 (937 m)	*E391 (1485 m)	*E394 (525 m)	MACROI E51 (500 m)	ANH-I E265 (500 m)	ANH-I E267 (500 m)	ANH-II E284 (705 m)
Volutomitridae Gray, 1854							
<i>Volutomitra persephone</i> Bayer, 1971							x (sb)
Turridae Swainson, 1840							
<i>Benthomangelia</i> sp.				x		x (sb)	
<i>Stenodrillia gundlachi</i> (Dall & Simpson, 1901)				x (s)			x (s)
<i>Compsodrillia</i> sp.						x (s)	
<i>Globidrillia smirna</i> (Dall, 1881) In Bayer <i>et al.</i> (1970): <i>Drillia smirna</i> Dall, 1881			x				
<i>Gemmula periscelida</i> (Dall, 1889)			x			x (sb)	
<i>Gymnobela</i> sp.							x (s)
<i>Hindsiclava polytorta</i> (Dall, 1881)						x	
<i>Leucosyrinx tenoceras</i> (Dall, 1889)	x						
<i>Leucosyrinx verrillii</i> (Dall, 1881)					x (s)	x (sb)	
Turridae sp.			x				
Superorder Heterobranchia Gray, 1840							
Order Opisthobranchia Milne-Edwards, 1848							
Scaphandridae Sars, 1878							
<i>Scaphander punctostriatus</i> (Mighels & Adams, 1842). In Bayer <i>et al.</i> (1970): <i>Scaphander clavus</i> Dall, 1889			x				
<i>Scaphander watsoni rehderi</i> Dall, 1881					x (sb)	x (s)	

located off Arboletes, many fragments and shells corresponding to the above mentioned families of chemosymbiotic bivalves were collected, including two morphotypes of the family Lucinidae (Figure 2F, G). This station was also characterized by the presence of pieces of authigenic carbonates, corresponding to 16.5 kg in weight (Figure 3A).

From the INVMAR-ANH II survey, living specimens of *C. ponderosa* were obtained at Station E284, north of Cartagena, and also some shells of *A. caribbaea*, *Conchocele bisecta* (Conrad, 1849) (Figure 2I, J) and fragments and shells of lucinids. It was remarkable that this station was also characterized by a significant number (>1000) of live specimens of the gastropod *Cataegis meroglypta* McLean & Quinn, 1987 (Figure 3B, C). Other conspicuous non-chemosymbiotic molluscs at this site included *A. colombiana* (Limidae), *Manaria canetae* (Clench & Aguayo, 1944) (Buccinidae) and *Cantrainea macleani* Warén & Bouchet, 1993 (Colloniidae). Also remarkable was the presence for the first time at this site of empty tube worms of the family Siboglinidae (Figure 3D, E).

DISCUSSION AND CONCLUSIONS

Due to the particular geomorphological conditions, it is possible to find well developed sedimentary basins in an active margin at both studied areas (Magdalena and Sinú). These processes contribute to the formation of mud diapirs, which in turn constitute optimal scenarios for the occurrence of seeps. Methane-rich fluids exiting over-pressured regions migrate along low permeability pathways upward or outward, supporting the chemosynthetic communities (Barry *et al.*, 1996; Tunnicliffe *et al.*, 2003). However, as in most of the South American margin, no cold seep research

has been carried out in Colombia so far, and the characteristic of these reducing systems is almost completely unknown.

Previous research that complements our findings includes the reports of Boss (1967a, 1968) and Taylor & Glover (2009). Boss (1967a) reported the presence of a living specimen of *Vesicomya caribbea*, off La Guajira peninsula (MV 'Oregon', Station 5692), at 375 m depth. Boss (1968) reported and described *Vesicomya cordata* Boss, 1968 and *Ectenagena modioliforma* Boss, 1968 from material collected off 'Golfo de Morrosquillo' (north-north-east of Punta Caribana), at 421–641 m depth (Station Pillsbury 394). At this station the lucinid *Conchocele bisecta* (Boss, 1967b) was also present. *Calyptogena ponderosa* was reported off 'Golfo de Morrosquillo' (north-north-east of Punta Caribana), at 933–961 m (Station Pillsbury 364), off 'Golfo de Morrosquillo' (north-north-east of Punta Caribana), 421–641 m depth (Station Pillsbury 394) and off Cartagena, at 1417–1767 m depth (Station Pillsbury 391). Recently Taylor & Glover (2009) described the lucinid *Graecina colombiensis*, found off Ciénaga Grande de Santa Marta, at 366 m depth (RV 'Oregon', Station 4840, 16 May 1964), and *Jorgenia gracile* Taylor & Glover, 2009 found off southern Isla de Salamanca, at 600 m (RV 'Oregon II', Station 11248, 9 November 1970), however no information on the habitat at the collection sites was provided.

The presence of living specimens of the bivalves '*Calyptogena*' *ponderosa* (its generic placement within vesicomysids is still uncertain; E. Krylova, personal communication) and *V. caribbea* constitute strong evidences suggesting that active methane seep sites hosting chemosynthetic communities exist from north of the mouth of the Magdalena River (~500 m depth) to the southernmost Colombian Caribbean sea (~1700 m). Vesicomysids are highly adapted to sulphur-rich environments and they are often the dominant taxa in these reducing environments (Krylova & Sahling, 2006).



Fig. 2. Some species of chemosymbiotic bivalves found in the projects Macrofauna I, ANH I and II. (A) Exterior view of *Acharax caribbaea*, a relatively rare species, of which only the holotype, collected off Palomino was known; (B, C) exterior and interior views of *Graecina colombiensis*; (D, E) exterior and interior views of *Lucinoma* sp. 1; (F) exterior view of *Lucinoma* sp. 2; (G) exterior view of *Lucinoma* sp. 3; (H) exterior view of *Ectenagena modioliforma*; (I, J) exterior and interior views of *Conchocele bisecta*; (K, M) exterior, interior and dorsal views of *Calyptogena ponderosa*, T 40.15 mm; (N, O) exterior and interior views of *Vesicomya caribbea*; (P) dorsal view of articulated valves of *V. caribbea*, T 47.67 mm. T, tumidity. Scale bars: (A–H & K–P) = 1 cm, and (I–J) = 2 mm.

They host and derive their nutrition from symbiotic chemoautotrophic bacteria (Krylova & Jenssen, 2006; Krylova & Sahling, 2006). *Calyptogena ponderosa* has been also reported from the Gulf of Mexico (upper slope off Louisiana) as a typical constituent of the cold seep assemblages (Cordes *et al.*, 2007), in addition to the siboglinid tubeworm *Lamellibrachia* cf. *luymesii* van der Land & Nørrevang, 1975, which is most probably the species recorded at Station E284. At hydrocarbon seeps in the Gulf of Mexico these vestimentiferan tubeworms form large bush-like aggregations and obtain their nutrition from sulphide-oxidizing endosymbiotic bacteria (Dattagupta *et al.*, 2006). It is also interesting to note that other non-chemosymbiotic species, like the Chilodontidae *Cataegis meroglypta*, which occurred at high densities at Station E284, has been also reported at the Bush

Hill Seep (a hydrocarbon seep with thick growth of tube worms, mussel beds and bacteria mats off Louisiana) and also in Colombia, Trinidad and Barbados (Warén & Bouchet, 1993; Gill *et al.*, 2005). Similarly, the buccinid *Manaria canetae* and the colloniid *Cantrainea macleani* are also known to be associated with vestimentiferan bushes at seeps off Louisiana (Bergquist *et al.*, 2003). It is necessary to highlight that a fraction of the material (Table 1) was not identified to species level. It is therefore imperative to continue with this process since these data would provide further information about the composition of the communities present in these habitats off Colombia and their connections with other faunas in the Caribbean and Atlantic Ocean.

The generation of authigenic carbonate, as observed at Station E267, is a typical feature of the sites where methane

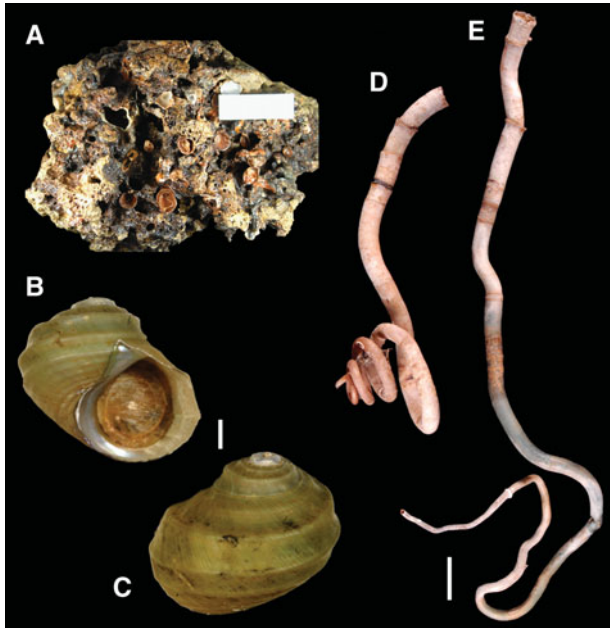


Fig. 3. Further evidence of the presence of seep habitats in the study area. (A) Authigenic carbonates collected off Arboletes (Station E267), scale bar = 4 cm; (B, C) frontal and dorsal views of *Cataegis meroglypta*, scale bar = 2 mm; (D, E) *Lamellibrachia* sp. tubes found off northern Cartagena (Station E284), scale bar = 2 cm.

is expelled from the seafloor. Crusts are formed by the precipitation of methane-derived bicarbonate released to pore-water during the anaerobic oxidation of methane (AOM) via sulphate reduction. A consortium of archaea and bacteria mediates the process (Boetius *et al.*, 2000). Sulphide, the other by-product of AOM, is in turn used by free-living filamentous bacteria, e.g. *Beggiatoa* and endosymbiont sulphide-oxidizing chemosynthetic prokaryotes (e.g. those present in vesicomysids, solemyids and lucinids), as an energy source for primary carbon fixation.

According to Barry *et al.* (1996), the geological complexity and tectonically dynamic nature of continental margins favour cold seep formation in a variety of geological settings including subduction zones, accretionary complexes, and transform faulted boundaries that produce fault zones, channels and canyons, mud volcanoes or diatremes and submarine artesian springs. Thus, along active tectonic boundaries, faults can intercept and focus fluid migration, enhancing the development and persistence of chemosynthetic communities. These geomorphological characteristics are common at the study area and in this sense it is expected that such environments should be widespread in the Colombian Caribbean. The available data indicate that at least the southern part (Sinú area), where most of our records of chemosymbiotic species occur (Table 1), should be considered as a priority area for the study of seep environments. The scarcity of direct observations of seep communities for the Colombian Caribbean highlights a challenge that should be tackled in the short and medium term in order to gain sufficient information for assessing the current conservation status of these fragile communities. In Colombian waters it is important to improve characterization studies, complement information about taxonomically enigmatic species, carry out DNA sequencing (to establish whether there is gene-flow between zones), describe the ecology of the autotrophic and

heterotrophic fauna and describe the geology and geochemistry of the habitats. Support also needs to be found for studies of deeper sites to continue filling gaps in our knowledge about the biogeographical patterns of seep communities at a global scale (Ramírez-Llodra *et al.*, 2003).

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