

ORIGINAL ARTICLE

Patchiness of deep-sea communities in Papua New Guinea and potential susceptibility to anthropogenic disturbances illustrated by seep organisms

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Abstract

The deep-sea part of the 'Papua Niugini Biodiversity Expedition' surveyed the deep-sea environments along the coasts of New Guinea Island in the Bismarck Sea, from the Vitiav Strait to the border between Papua New Guinea (PNG) and Irian Jaya. This expedition was a follow-up of the BIOPAPUA cruise (2010) that gave some of the first insights into the diversity of the deep-sea fauna of the Bismarck and Solomon Seas for environments other than deep-sea hydrothermal vents. The main aims of the cruise were to survey the diversity of the fauna of (i) hard bottoms that are typically found on deep seamounts, (ii) Astrolabe Bay from 200 m to about 1000 m, (iii) the chemosynthetic environments of the deep sea, including cold-seep environments and plant debris. Astrolabe Bay was one of our targets because its topography allows sampling over the complete bathymetric gradient covered by our sampling gear (down to 1000 m depth), and the recent start of nickel refining activities in the bay is a potential threat to its marine fauna for which little reference data are available. Sampling in the bay revealed not only a diversified fauna associated with soft bottoms and plant debris, but also a chemosynthetic fauna typical of cold-seep environments (e.g. siboglinid worms and bathymodioline mussels) below the Ramu refinery. Although the refinery activities had officially started just one week before our work in the area, we observed impacts of these activities. Our molecular work indicates that the siboglinid tubeworm species and one of the two mussel species collected below the Ramu refinery have so far only been documented from this location, despite intensive sampling effort. This illustrates the potential destructive effects of human activities in areas where the diversity and uniqueness of deep-sea communities are poorly understood.

Introduction

Despite some significant exploration efforts, notably during the last decade (e.g. Costello *et al.* 2010), the deep-sea

realm remains among the least known biodiversity compartments on Earth, even for macro-organisms. As it is difficult to protect what we do not know exists, this knowledge gap makes the deep sea particularly vulnerable

to human disturbances. Pioneering work in the 1960s with the development of appropriate tools revealed that deep-sea biodiversity was greatly underestimated and rivals that of shallow tropical communities (e.g. Hessler & Sanders 1967). Later studies also revealed that deep-sea assemblages are far from homogenous, with substantial among-site differences, and some endemism (Levin *et al.* 2001; Brandt *et al.* 2007). Despite ongoing efforts to describe deep-sea biodiversity, working in this environment is challenging and much remains to be learned.

As a result of this knowledge gap, many common assumptions on the structure of deep-sea biodiversity, upon which many environmental policies are based, are questionable. Among them, the seemingly uniform nature of the deep sea ('everything is everywhere') is potentially one of the most damaging assumptions. This assumption is mainly based on the observation that many deep-sea organisms have a cosmopolitan distribution. However, most of these cosmopolitan species are patchily distributed over their wide geographic range (McClain & Hardy 2010 and references therein). More generally, recent studies have revealed an unexpected heterogeneity of deep-sea habitats linked to geomorphologic, geochemical and hydrographic features and stressed the resulting vulnerability of associated communities to human activities (e.g. Levin & Dayton 2009; Levin & Sibuet 2012). Thus, considering that 'everything is everywhere' leads to a minimized assessment of the potential effect of the destruction of discrete habitats. In this communication we illustrate this problem by reporting the discovery of two chemosynthetic sites in Papua New Guinea (PNG), one of them being impacted by the tailings rejected by a nickel mine refinery.

The first chemosynthetic site was discovered during the BIOPAPUA cruise off the Sepik River (Pante *et al.* 2012). The discovery of the impacted site, in Basamuk Canyon near Astrolabe Bay, occurred during the deep-sea leg of the 'Papua Niugini Biodiversity Expedition' (hereafter PAPUA NIUGINI), the latest expedition of the 'Our planet reviewed' program (www.laplaneterevisitee.org). This program is an international scientific project whose goals are to provide better estimates of the magnitude of biodiversity worldwide and to provide baseline data for several sites that are particularly rich or vulnerable on our planet. The most recent expedition of the program targeted PNG and the surrounding Bismarck and Solomon Seas. PNG is located in the Coral Triangle, a region of exceptional zooxanthellate coral diversity (Veron *et al.* 2009). Its forests count among the most important in the world in terms of diversity of plant species (Joppa *et al.* 2011). The marine part of the expedition included a shallow-water sampling workshop and a deep-sea cruise. Over 3 months, the marine expedition involved a total of

88 scientists from 18 countries, in addition to 51 trainees, media, logistics co-ordinators and visitors. Prior to this expedition, exploration of PNG's marine biodiversity had been minimal, and had mostly focused on shallow-water coral reefs (e.g. Drew *et al.* 2012) and hydrothermal vents in the Manus Basin (e.g. Levin *et al.* 2009). Other deep-sea habitats of PNG's waters were particularly poorly explored, including during great historical expeditions (Pante *et al.* 2012).

The BIOPAPUA cruise and the deep-sea part of the 2012 marine expedition used the RV *Alis* for deploying hauls from 100 to 1000 m depth. The BIOPAPUA cruise covered a wide area surrounding the Bismarck Sea and the Solomon Sea (Pante *et al.* 2012). The 2012 (PAPUA NIUGINI) cruise surveyed the deep-sea environments along the coasts of New Guinea Island in the Bismarck Sea, from the Vitiaz Strait to the border between PNG and Irian Jaya. Both expeditions aimed at covering as well as possible the diversity of deep-sea habitats. Seamounts were one of the targets because they generally have hard bottoms with a fauna dominated in terms of biomass by suspension-feeding organisms that shelter an important diversity of associated organisms. Another goal was to sample the organisms associated with soft bottoms that can be found in sedimentary basins separating islands, or, when the topography allows the accumulation of sediments, on the slopes of the islands. Preliminary work during the BIOPAPUA cruise allowed us to focus in 2012 on sampling the fauna of soft bottoms in Astrolabe Bay. Additionally, the start of refinery activities had already been identified as a potential threat to the marine fauna but little biological data were available (e.g. Reichelt-Brushett 2012). Finally, we targeted chemosynthetic habitats as they are among the most productive environments in the deep sea. In PNG, hydrothermal vents are easily accessible, and have been intensively studied for many years (e.g. Erickson *et al.* 2009; Levin *et al.* 2009). For the same reason of accessibility, the hydrothermal deposits characterized by a high grade of precious ore in the Bismarck Sea represent a prime target for deep-sea refinery activities (Van Dover 2011). Other types of deep-sea chemosynthetic environments (*i.e.* cold seeps and accumulations of decaying terrestrial plant debris) remain poorly surveyed in PNG, although geological surveys in this active area have provided sporadic records of cold-seep environments (e.g. Tappin *et al.* 2001). The BIOPAPUA cruise allowed us to discover a site off the Sepik River (facing Broken Water Bay), at about 400 m depth, with fauna typically associated with cold-seep environments. This area, which we revisited during the 2012 cruise, is close to the area detected by the JAMSTEC cruise (Tappin *et al.* 2001), which provided the only report of chemosynthetic organisms from cold-seep environments in PNG

waters (e.g. Kyuno *et al.* 2009 for Bathymodiolinae, Kojima *et al.* 2003 for Siboglinidae). Additionally, off the Ramu refinery, the deeper operations that we performed have unexpectedly brought back bathymodioline mussels and siboglinid tubeworms, revealing a new location of chemosynthetic habitat.

In these poorly explored deep-sea regions, chemosynthetic organisms are perhaps the best studied, especially at vents in the Manus Basin. The two seep sites sampled in 2012, in combination with the data available from the Japanese geological surveys and the 2010 data from the BIOPAPUA cruise, offered the opportunity to compare the specific diversity of bathymodioline mussels and siboglinid tubeworms at a relatively small spatial scale (the Astrolabe Bay and Broken Water Bay sites are separated by only about 250 km). Moreover, operations off the Ramu refinery revealed the presence of a brick-red deposit. The activities of the Ramu refinery started by the end of November 2012, and tailings were announced to be released from the refinery at 200 m depth. The deposits observed off the Ramu refinery were found nowhere else during either the BIOPAPUA cruise or the PAPUA NIUGINI expedition. Dredging operations brought back a dark gray mud (as found in many other locations) but overlaid by a brick-red deposit, consistent with the release of tailings from the refinery, suggesting that the newly discovered site is potentially threatened by rapidly accumulating tailings from the refinery.

The bathymodioline mussels and siboglinid worms sampled in the two discovered seep sites in PNG waters offer the opportunity to illustrate the patchiness of distribution of organisms, even at small scales, and to question some common misconceptions about the pattern of

diversity in the deep sea that result from the paucity of available knowledge.

Material and Methods

Sampling

During the deep-sea leg of the 2012 expedition, 137 hauls (92 trawling and 45 dredging operations) were conducted. These samples were added to the ones collected during the BIOPAPUA cruise (Pante *et al.* 2012). Out of all of the 2012 sampling operations (Fig 1), five contained fauna typically found in cold-seep environments, and in particular representatives of the Siboglinidae (Polychaeta) and Bathymodiolinae (Bivalvia). Three were conducted in Broken Water Bay, off the Sepik River (stations CP4040, CP4042, CP4043, depth range 400–800 m), a site where cold seeps were discovered during a previous expedition in 2010 (BIOPAPUA, stations CP3703 and CP3704, depth range 400–800 m), and two in Basamuk Canyon facing the Ramu refinery, near Astrolabe Bay (stations CP4020 and CP4081, depth range 400–860 m). During the 2012 cruise, a total of 16 *Lamellibrachia* (siboglinid tubeworms) and 52 bathymodioline mussels (Table 1) were preserved in 90% alcohol for molecular analyses. Out of the 11 Siboglinidae in the small aggregation sampled in Basamuk Bay, however, only four provided DNA that could be amplified. These animals are thought to have been dead, buried under an accumulation of tailings. To facilitate preservation of tissues in alcohol, mussels were first microwave following the procedure described in Galindo *et al.* (2014).

Fig. 1. Map of Papua New Guinea with locations of stations sampled during the BIOPAPUA (2010) cruise and PAPUA NIUGINI expedition (2012). Stations where cold-seep organisms were found are represented by white squares (left of arrows: station numbers). Other stations are represented by gray circles. The map was prepared based on NOAA's ETOPO1 data using the *marmap* package in R (Pante & Simon-Bouhet 2013). Stations CP4020 and 4081: Basamuk Canyon, canyon below the Ramu refinery. Stations CP3703, 3704, 4040, 4042 and 4043: Broken Water Bay, Sepik site.

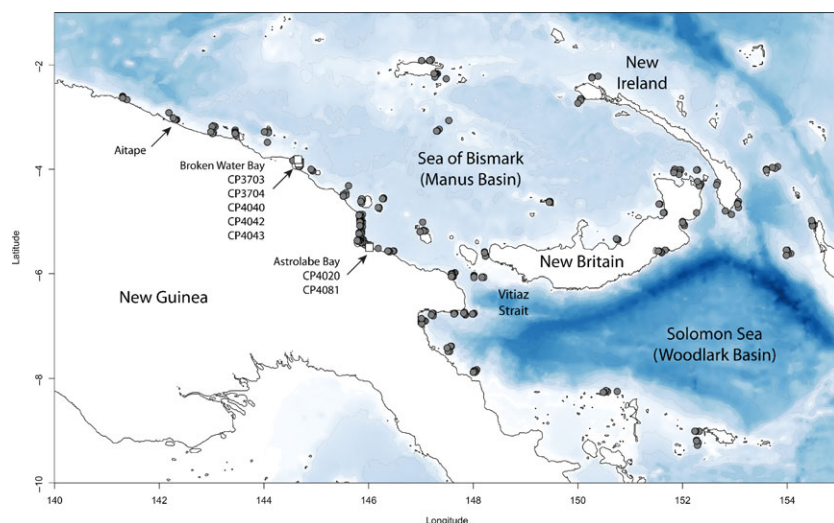


Table 1. List of analyzed specimens. For specimens analysed in this study the registration number in the collection of the Muséum National d'histoire Naturelle in Paris are given (MNHN ID), taxon refers to higher rank classification. Identification provides valid species names when available and/or identification labels referring to genetic lineages or haplotypes as given in GenBank or in the literature or as displayed in the tree included in this study. For bathymodiolineae the identification follows the classification proposed in Thubaut *et al.* 2013. For specimens analysed in this study the name of the expedition and the associated station number are provided.

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
IM_2013_17293	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210291	KP210343
IM_2013_17294	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210290	KP210342
IM_2013_17295	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210289	KP210341
IM_2013_17296	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210288	KP210340
IM_2013_18626	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210287	KP210339
IM_2013_18628	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210295	KP210347
IM_2013_18629	Bathymodiolineae	<i>Gigantidas</i> sp. 2 Broken Bay	PAPUA NIUGINI	CP4042	KP210292	KP210344
IM_2013_18630	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210286	KP210338
IM_2013_18631	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210285	KP210337
IM_2013_18632	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210284	KP210336
IM_2013_18634	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210283	KP210335
IM_2013_18656	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210282	KP210334
IM_2013_18670	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210293	KP210345
IM_2013_18674	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210294	KP210346
IM_2013_18675	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210296	KP210348
IM_2013_18717	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210297	KP210349
IM_2013_18719	Bathymodiolineae	new species 2	PAPUA NIUGINI	CP4042	KP210298	KP210350
IM_2013_18722	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210299	KP210351
IM_2013_18723	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210249	KP210301
IM_2013_18724	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210300	KP210352
IM_2013_18725	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210281	KP210333
IM_2013_18726	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210280	KP210332
IM_2013_18727	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210279	KP210331
IM_2013_18728	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210278	KP210330
IM_2013_18729	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210277	KP210329
IM_2013_18730	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210276	KP210328
IM_2013_18731	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210275	KP210327
IM_2013_18732	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210274	KP210326
IM_2013_18733	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210273	KP210325
IM_2013_18734	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210272	KP210324
IM_2013_18735	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210271	KP210323
IM_2013_18736	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210270	KP210322
IM_2013_18737	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210269	KP210321
IM_2013_18738	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210268	KP210320
IM_2013_18739	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210267	KP210319
IM_2013_18740	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210266	KP210318
IM_2013_18741	Bathymodiolineae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210265	KP210317

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
IM_2013_18742	Bathymodiolinae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210264	KP210316
IM_2013_18743	Bathymodiolinae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210263	KP210315
IM_2013_18744	Bathymodiolinae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210262	KP210314
IM_2013_18745	Bathymodiolinae	<i>Gigantidas</i> sp. 1 Broken Bay	PAPUA NIUGINI	CP4042	KP210261	KP210313
IM_2013_18746	Bathymodiolinae	new species 2	PAPUA NIUGINI	CP4042	KP210260	KP210312
IM_2013_18747	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4042	KP210259	KP210311
IM_2013_19398	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210258	KP210310
IM_2013_19399	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210257	KP210309
IM_2013_19400	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210256	KP210308
IM_2013_19401	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210255	KP210307
IM_2013_19403	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210254	KP210306
IM_2013_19406	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210253	KP210305
IM_2013_19408	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210252	KP210304
IM_2013_19409	Bathymodiolinae	<i>Gigantidas</i> sp. 2 Broken Bay	PAPUA NIUGINI	CP4020	KP210251	KP210303
IM_2013_19411	Bathymodiolinae	new species 1	PAPUA NIUGINI	CP4020	KP210250	KP210302
GenBank	Bathymodiolinae	<i>Terua arcuatilis</i>	GenBank		FJ937033	GU065879
GenBank	Bathymodiolinae	<i>Gigantidas crypta</i> B'	GenBank		EU702319	EU683298
GenBank	Bathymodiolinae	<i>Gigantidas crypta</i> B''	GenBank		EU702315	EU683301
GenBank	Bathymodiolinae	<i>Idas iwaotakii</i> A'	GenBank		EU702333	EU683288
GenBank	Bathymodiolinae	<i>Idas iwaotakii</i> A''	GenBank		EU702322	EU683295
GenBank	Bathymodiolinae	<i>Benthomodiolus lignicola</i>	GenBank		AY275545	AY781131
GenBank	Bathymodiolinae	<i>Bathymodiolus boomerang</i>	GenBank		FJ890503	FJ890505
GenBank	Bathymodiolinae	<i>Bathymodiolus aff. thermophilus</i>	GenBank		AF456317	AY781140
GenBank	Bathymodiolinae	<i>Bathymodiolus azoricus</i>	GenBank		AY649795	AY781148
GenBank	Bathymodiolinae	<i>Bathymodiolus breviar</i>	GenBank		AY649799	AY781150
GenBank	Bathymodiolinae	<i>Bathymodiolus brooksi</i>	GenBank		AY649798	AY781135
GenBank	Bathymodiolinae	<i>Bathymodiolus heckerae</i>	GenBank		AY649794	AY781138
GenBank	Bathymodiolinae	<i>Bathymodiolus puteoserpentis</i>	GenBank		AY649796	AY781151
GenBank	Bathymodiolinae	<i>Gigantidas tangaroa</i>	GenBank		AY608439	AY781149
GenBank	Bathymodiolinae	<i>Vulcanidas</i> ESU E	GenBank		FJ937079	GU065791
GenBank	Bathymodiolinae	<i>Vulcanidas</i> ESU F	GenBank		FJ937127	GU065809
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> ESU G	GenBank		FJ937161	GU065778
GenBank	Bathymodiolinae	<i>Nypamodiolus</i> ESU H	GenBank		FJ937073	GU065856
GenBank	Bathymodiolinae	<i>Nypamodiolus</i> ESU I	GenBank		FJ937188	GU065774
GenBank	Bathymodiolinae	<i>Nypamodiolus</i> ESU J	GenBank		FJ937189	GU065842
GenBank	Bathymodiolinae	<i>Idas</i> ESU K	GenBank		FJ937192	GU065868
GenBank	Bathymodiolinae	<i>Idas</i> ESU L	GenBank		FJ937193	GU065767
GenBank	Bathymodiolinae	<i>Idas</i> ESU M	GenBank		FJ937202	GU065845
GenBank	Bathymodiolinae	<i>Idas</i> ESU N	GenBank		FJ937205	GU065843
GenBank	Bathymodiolinae	<i>Idas</i> ESU O	GenBank		FJ937211	GU065763

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Bathymodiolinae	<i>Idas</i> ESU P	GenBank		FJ937222	GU065846
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> ESU Q	GenBank		FJ937230	GU065875
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> ESU R	GenBank		FJ937239	GU065877
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> ESU S'	GenBank		FJ937240	GU065816
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> ESU S''	GenBank		FJ937258	GU065829
GenBank	Bathymodiolinae	<i>Terua</i> ESU T	GenBank		FJ937283	GU065804
GenBank	Bathymodiolinae	<i>Gigantidas gladius</i>	GenBank		AY649802	AY781134
GenBank	Bathymodiolinae	<i>Idas macdonaldi</i>	GenBank		AY649804	AY781145
GenBank	Bathymodiolinae	<i>Idas modiolaeformis</i>	GenBank		FJ158585	FJ159555
GenBank	Bathymodiolinae	<i>Idas</i> sp. C	GenBank		EU702376	EU683260
GenBank	Bathymodiolinae	<i>Idas</i> sp. D	GenBank		EU702357	EU683275
GenBank	Bathymodiolinae	<i>Idas washingtonius</i>	GenBank		AY275546	AY781146
GenBank	Bathymodiolinae	<i>Benthomodiolus</i> sp. Juan de Fuca	GenBank		KF611694	KF611699
GenBank	Bathymodiolinae	<i>Nypamodiolus longissimus</i>	GenBank		DQ340773	DQ863945
GenBank	Bathymodiolinae	<i>Nipponiomodiolus manusensis</i>	GenBank		GU966637	GU966642
GenBank	Bathymodiolinae	<i>Gigantidas mauritanicus</i>	GenBank		FJ890502	FJ890504
GenBank	Bathymodiolinae	<i>Idas</i> SAL1	GenBank		DQ340775	DQ863944
GenBank	Bathymodiolinae	<i>Vulcanidas</i> SAL3	GenBank		DQ340772	DQ863946
GenBank	Bathymodiolinae	<i>Lignomodiolus</i> SAL4	GenBank		DQ340776	DQ863947
GenBank	Bathymodiolinae	<i>Nypamodiolus simpsoni</i>	GenBank		KF611695	KF611700
GenBank	Bathymodiolinae	<i>Gigantidas</i> sp. 1 Broken Bay	GenBank		KF611693	KF611696
GenBank	Bathymodiolinae	<i>Gigantidas</i> sp. 2 Broken Bay	GenBank		KF611692	KF611697
GenBank	Bathymodiolinae	<i>Benthomodiolus</i> sp. South Atlantic	GenBank		KF611691	KF611698
GenBank	Bathymodiolinae	<i>Gigantidas taiwanensis</i>	GenBank		GU966638	GU966641
GenBank	Bathymodiolinae	<i>Bathymodiolus thermophilus</i>	GenBank		GU966639	GU966640
GenBank	Bathymodiolinae	<i>Tamu fisheri</i>	GenBank		AY649803	AY781132
GenBank	Bathymodiolinae	<i>Vulcanidas insolatus</i>	GenBank		FJ767936	FJ767937
GenBank	Bathymodiolinae	<i>Modiolus modiolus</i>	GenBank		FJ890501	EF526455
MNHN-IA-2013-77	Vestimentifera	<i>Escarpia</i>	BIOPAPUA	CP3703	KP203873	–
MNHN-IA-2013-78	Vestimentifera	<i>Escarpia</i>	BIOPAPUA	CP3704	KP203874	–
MNHN-IA-2013-79	Vestimentifera	Lam1	PAPUA NIUGINI	CP4040	KP203875	–
MNHN-IA-2013-80	Vestimentifera	Lam2	PAPUA NIUGINI	CP4040	KP203876	–
MNHN-IA-2013-81	Vestimentifera	LamB	PAPUA NIUGINI	CP4042	KP203877	–
MNHN-IA-2013-82	Vestimentifera	LamC	PAPUA NIUGINI	CP4042	KP203878	–
MNHN-IA-2013-83	Vestimentifera	LamD	PAPUA NIUGINI	CP4043	KP203879	–
MNHN-IA-2013-84	Vestimentifera	LamC	PAPUA NIUGINI	CP4081	KP203880	–
MNHN-IA-2013-85	Vestimentifera	LamD	PAPUA NIUGINI	CP4081	KP203881	–
MNHN-IA-2013-86	Vestimentifera	LamE	PAPUA NIUGINI	CP4081	KP203882	–
MNHN-IA-2013-87	Vestimentifera	LamF	PAPUA NIUGINI	CP4081	KP203883	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp L4	GenBank		AB0552091	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp L5	GenBank		AB0552101	–
GenBank	Vestimentifera	<i>Arcovestia ivanovi</i>	GenBank		AB0734911	–
GenBank	Vestimentifera	<i>Cf Alaysia</i> sp A1	GenBank		AB0886701	–
GenBank	Vestimentifera	<i>Cf Alaysia</i> sp A2	GenBank		AB0886711	–
GenBank	Vestimentifera	<i>Cf Alaysia</i> sp A3	GenBank		AB0886721	–
GenBank	Vestimentifera	<i>Cf Alaysia</i> sp A4	GenBank		AB0886731	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp L6	GenBank		AB0886741	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp L7	GenBank		AB0886751	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp L1 DH-2004	GenBank		AB1811611	–
GenBank	Vestimentifera	<i>Oasisia fujikurai</i>	GenBank		AB2428571	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i>	GenBank		AB2428581	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i> haplotype1	GenBank		AB2646011	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i> haplotype2	GenBank		AB2646021	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i> haplotype3	GenBank		AB2646031	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i> haplotype4	GenBank		AB2646041	–
GenBank	Vestimentifera	<i>Lamellibrachia juni</i> haplotype5	GenBank		AB2646051	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 1	GenBank		AB7214791	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 2	GenBank		AB7214801	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 3	GenBank		AB7214811	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 4	GenBank		AB7214821	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 5	GenBank		AB7214831	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 6	GenBank		AB7214841	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 7	GenBank		AB7214851	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 8	GenBank		AB7214861	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 9	GenBank		AB7214871	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 10	GenBank		AB7214881	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 11	GenBank		AB7214891	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 12	GenBank		AB7214901	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 13	GenBank		AB7214911	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 14	GenBank		AB7214921	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 15	GenBank		AB7214931	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 16	GenBank		AB7214941	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 17	GenBank		AB7214951	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i> haplotype 18	GenBank		AB7214961	–
GenBank	Vestimentifera	<i>Ridgeia piscesae</i>	GenBank		AF0222331	–
GenBank	Vestimentifera	<i>Ridgeia piscesae</i>	GenBank		AF0222341	–
GenBank	Vestimentifera	<i>Ridgeia piscesae</i>	GenBank		AF0222351	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i>	GenBank		AF3172871	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB425	GenBank		AF3172881	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC234	GenBank		AF3172891	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate TAMU-17	GenBank		AF3172901	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i>	GenBank		AF3426711	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> individual 2	GenBank		AY1291211	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC354	GenBank		AY1291221	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB535	GenBank		AY1291231	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> individual 6	GenBank		AY1291241	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> individual 1	GenBank		AY1291251	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> isolate GC354	GenBank		AY1291261	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> individual 3	GenBank		AY1291271	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> individual 41314	GenBank		AY1291281	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> individual 35-11	GenBank		AY1291291	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> individual 35-2	GenBank		AY1291301	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> individual 2	GenBank		AY1291311	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> individual 1	GenBank		AY1291321	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> individual 2	GenBank		AY1291331	–
GenBank	Vestimentifera	<i>Escarpia</i> sp. GB425-GoM	GenBank		AY1291341	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> isolate GB425	GenBank		AY1291351	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i> isolate GC234	GenBank		AY1291361	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 10	GenBank		AY1291371	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 11	GenBank		AY1291381	–
GenBank	Vestimentifera	<i>Lamellibrachia cf. luymesi</i>	GenBank		AY1291391	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate TAMU-17	GenBank		AY1291401	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 9	GenBank		AY1291411	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i>	GenBank		AY1291421	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB425	GenBank		AY1291431	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC234	GenBank		AY1291441	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 8	GenBank		AY1291451	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 7	GenBank		AY1291461	–
GenBank	Vestimentifera	<i>Lamellibrachia barhami</i> individual 4	GenBank		AY1291471	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> haplotype 2	GenBank		AY3263031	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> haplotype 1	GenBank		AY3263041	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i> haplotype A	GenBank		AY6459891	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i> haplotype B	GenBank		AY6459901	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i> haplotype C	GenBank		AY6459911	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype A	GenBank		AY6459921	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype B	GenBank		AY6459931	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype C	GenBank		AY6459941	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype D	GenBank		AY6459951	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype E	GenBank		AY6459961	–
GenBank	Vestimentifera	<i>Tevnia jericchonana</i> haplotype F	GenBank		AY6459971	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Tevnia jerichonana</i> haplotype G	GenBank		AY6459981	–
GenBank	Vestimentifera	<i>Tevnia jerichonana</i> haplotype H	GenBank		AY6459991	–
GenBank	Vestimentifera	<i>Tevnia jerichonana</i> haplotype I	GenBank		AY6460001	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype A	GenBank		AY6460011	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype B	GenBank		AY6460021	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype C	GenBank		AY6460031	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype D	GenBank		AY6460041	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype E	GenBank		AY6460051	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype F	GenBank		AY6460061	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype G	GenBank		AY6460071	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype H	GenBank		AY6460081	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype I	GenBank		AY6460091	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype J	GenBank		AY6460101	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype K	GenBank		AY6460111	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype L	GenBank		AY6460121	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype M	GenBank		AY6460131	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype N	GenBank		AY6460141	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype O	GenBank		AY6460151	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype P	GenBank		AY6460161	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype Q	GenBank		AY6460171	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype R	GenBank		AY6460181	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype S	GenBank		AY6460191	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i> haplotype T	GenBank		AY6460201	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i>	GenBank		AY7416621	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp	GenBank		D380292	–
GenBank	Vestimentifera	<i>Lamellibrachia satsuma</i>	GenBank		D380302	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp	GenBank		D505922	–
GenBank	Vestimentifera	<i>Paraescarpia</i> cf <i>echinospica</i> isolateE1	GenBank		D505932	–
GenBank	Vestimentifera	<i>Paraescarpia</i> cf <i>echinospica</i> isolateE2	GenBank		D505942	–
GenBank	Vestimentifera	<i>Paraescarpia</i> cf <i>echinospica</i>	GenBank		D505951	–
GenBank	Vestimentifera	<i>Lamellibrachia columna</i> isolate Lcolumna C JII145	GenBank		DQ9966451	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp SMH-2007a	GenBank		EU0466161	–
GenBank	Vestimentifera	<i>Ridgeia piscesae</i> isolate T449A1-1	GenBank		EU1904941	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i> isolate 97	GenBank		FJ6675291	–
GenBank	Vestimentifera	<i>Arcovestia ivanovi</i> isolate JII142	GenBank		FJ6675301	–
GenBank	Vestimentifera	<i>Tevnia jerichonana</i> isolate 92	GenBank		FJ6675311	–
GenBank	Vestimentifera	<i>Tevnia jerichonana</i> isolate 351	GenBank		FJ6675321	–
GenBank	Vestimentifera	<i>Oasisia</i> sp SBJ-2009 isolate NZ	GenBank		FJ6675331	–
GenBank	Vestimentifera	<i>Oasisia</i> sp SBJ-2009 isolate S	GenBank		FJ6675341	–
GenBank	Vestimentifera	<i>Oasisia</i> sp SBJ-2009 isolate 25	GenBank		FJ6675351	–
GenBank	Vestimentifera	<i>Alaysia</i> sp SBJ-2009 isolate JII145	GenBank		FJ6675361	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate T548	GenBank		FI6675371	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E6 1	GenBank		GU0591631	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GB697 E205 10	GenBank		GU0591641	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate WR269 102	GenBank		GU0591651	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate AT340 L1	GenBank		GU0591661	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate WR269 L9 104	GenBank		GU0591671	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate WR269 L2 105	GenBank		GU0591681	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate AC601 L13 107	GenBank		GU0591691	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GB829 E4 11	GenBank		GU0591701	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate AC601 L2 110	GenBank		GU0591711	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 2 MPM-2010 isolate GC852 L5 118	GenBank		GU0591731	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GB829 E5 12	GenBank		GU0591741	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 2 MPM-2010 isolate AT340 L39 122	GenBank		GU0591751	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 2 MPM-2010 isolate WR269 123	GenBank		GU0591761	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 2 MPM-2010 isolate AC601 L1 124	GenBank		GU0591771	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 2 MPM-2010 isolate AC601 L81 126	GenBank		GU0591781	–
GenBank	Vestimentifera	<i>Lamelibrachia</i> sp 1 MPM-2010 isolate AT340 L2 128	GenBank		GU0591791	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB697 S3 130	GenBank		GU0591801	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S10 131	GenBank		GU0591811	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC234 LV3 132	GenBank		GU0591821	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC234 EV3 134	GenBank		GU0591831	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GC234 EV7 134b	GenBank		GU0591841	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GC852 E23B 14	GenBank		GU0591851	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S12 141	GenBank		GU0591861	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S6 143	GenBank		GU0591871	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S5 144	GenBank		GU0591881	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E5 145	GenBank		GU0591891	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S11 147	GenBank		GU0591901	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB647 S7 148	GenBank		GU0591911	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GC852 E47 17	GenBank		GU0591921	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GC852 E35 18	GenBank		GU0591931	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate GC852 newVest 19	GenBank		GU0591941	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E93 19B	GenBank		GU0591951	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E2 2	GenBank		GU0591961	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E4 20	GenBank		GU0591971	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E5 21	GenBank		GU0591981	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E6 22	GenBank		GU0591991	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E75 23	GenBank		GU0592001	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E9S 24	GenBank		GU0592011	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT340 Efat 27	GenBank		GU0592021	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT340 E2 28	GenBank		GU0592031	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT 340 E4 29	GenBank		GU0592041	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E2 3	GenBank		GU0592051	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT340 E1 30	GenBank		GU0592061	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT340 E5 31	GenBank		GU0592071	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT341 E2 32	GenBank		GU0592081	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AT340 E6 33	GenBank		GU0592091	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate WR269 E5 35	GenBank		GU0592101	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E3 37	GenBank		GU0592111	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E4 38	GenBank		GU0592121	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 L2 39	GenBank		GU0592131	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E3 4	GenBank		GU0592141	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E3 40	GenBank		GU0592151	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC602 E5 42	GenBank		GU0592161	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E2 43	GenBank		GU0592171	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC602 E6 44	GenBank		GU0592181	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E4 45	GenBank		GU0592191	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 L2 47	GenBank		GU0592201	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E9 49	GenBank		GU0592211	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E4 5	GenBank		GU0592221	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 L7 50	GenBank		GU0592231	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 E1 54	GenBank		GU0592241	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH L7 55	GenBank		GU0592251	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate GC234 V1 57	GenBank		GU0592261	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC852 L33 58	GenBank		GU0592271	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E6 6	GenBank		GU0592281	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH LA V9 62	GenBank		GU0592291	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH LV1 66	GenBank		GU0592311	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH V2 68	GenBank		GU0592321	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH V3 69	GenBank		GU0592331	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC818 E4 7	GenBank		GU0592341	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH V4 70	GenBank		GU0592351	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BP LV8 72	GenBank		GU0592361	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GB697 L13S 73	GenBank		GU0592371	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GB829 L1 76	GenBank		GU0592381	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate GC234 LV5 83	GenBank		GU0592401	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate GC234 LV6 86	GenBank		GU0592411	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC600 L4 88	GenBank		GU0592421	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC600 L5 89	GenBank		GU0592431	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC852 L4 90	GenBank		GU0592441	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC852 L6 92	GenBank		GU0592451	–
GenBank	Vestimentifera	<i>Lamellibrachia luymeri</i> isolate BH V10 93	GenBank		GU0592461	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Lamellibrachia luymesi</i> isolate GC234 V4L 99	GenBank		GU0592471	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601 L8 95 149	GenBank		GU0592481	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GB697 L13 157	GenBank		GU0592491	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB697 L5 160	GenBank		GU0592511	–
GenBank	Vestimentifera	<i>Seepiophila jonesi</i> isolate GB697 S3P 160	GenBank		GU0592521	–
GenBank	Vestimentifera	<i>Lamellibrachia luymesi</i> isolate GC234 LaV2 152	GenBank		GU0592531	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp 1 MPM-2010 isolate GC600 L3 417 153	GenBank		GU0592541	–
GenBank	Vestimentifera	<i>Escarpid</i> sp n MPM-2010 isolate GB425 154	GenBank		GU0592551	–
GenBank	Vestimentifera	<i>Escarpid</i> sp n MPM-2010 isolate GC234 155	GenBank		GU0592561	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp Lam1	GenBank		HQ1545251	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp Lam2	GenBank		HQ1545261	–
GenBank	Vestimentifera	<i>Lamellibrachia</i> sp DBUA 1146	GenBank		HQ3968911	–
GenBank	Vestimentifera	<i>Escarpia</i> sp 1 JMP-2012	GenBank		JN0212671	–
GenBank	Vestimentifera	<i>Escarpia</i> sp 2 JMP-2012	GenBank		JN0212681	–
GenBank	Vestimentifera	<i>Escarpia</i> sp 3 JMP-2012	GenBank		JN0212691	–
GenBank	Vestimentifera	<i>Escarpia</i> sp 4 JMP-2012	GenBank		JN0212701	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate AC601-S03-41	GenBank		KC3573211	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-14	GenBank		KC3573221	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-17	GenBank		KC3573231	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-18	GenBank		KC3573241	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-19	GenBank		KC3573251	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-45	GenBank		KC3573261	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-7	GenBank		KC3573271	–
GenBank	Vestimentifera	<i>Escarpia laminata</i> isolate DC673-S10-9	GenBank		KC3573281	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-102	GenBank		KC3573291	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-103	GenBank		KC3573301	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-107	GenBank		KC3573311	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-92	GenBank		KC3573321	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-94	GenBank		KC3573331	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Regab-S11-19	GenBank		KC3573341	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Regab-S11-21	GenBank		KC3573351	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Regab-S11-27	GenBank		KC3573361	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-35	GenBank		KC3573371	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-40	GenBank		KC3573381	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-43	GenBank		KC3573391	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-45	GenBank		KC3573401	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-47	GenBank		KC3573411	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-50	GenBank		KC3573421	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-58	GenBank		KC3573431	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Baboon-S11-83	GenBank		KC3573441	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Baboon-S11-62	GenBank		KC8709531	–

Table 1. Continued

MNHN ID	Taxon	Identification	Expedition	Station	GenBank COI	GenBank 28S
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Baboon-S11-61	GenBank		KC8709541	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-37	GenBank		KC8709551	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-33	GenBank		KC8709561	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Regab-S11-16	GenBank		KC8709571	–
GenBank	Vestimentifera	<i>Escarpia southwardae</i> isolate Worm Hole-S11-31	GenBank		KC8709581	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-101	GenBank		KC8709591	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-110	GenBank		KC8709601	–
GenBank	Vestimentifera	<i>Escarpia spicata</i> isolate TF4-S11-116	GenBank		KC8709611	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Eratosthenes	GenBank		KF1992561	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Palmachim 1	GenBank		KF1992571	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Palmachim 2	GenBank		KF1992581	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Palinuro 1	GenBank		KF1992591	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Palinuro 2	GenBank		KF1992601	–
GenBank	Vestimentifera	<i>Lamelibrachia anaximandri</i> isolate Palinuro 3	GenBank		KF1992611	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i>	GenBank		U740531	–
GenBank	Vestimentifera	<i>Lamelibrachia barhami</i>	GenBank		U740541	–
GenBank	Vestimentifera	<i>Lamelibrachia barhami</i>	GenBank		U740551	–
GenBank	Vestimentifera	<i>Ridgeia</i> sp Southern Explorer Ridge	GenBank		U740561	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U740571	–
GenBank	Vestimentifera	<i>Lamelibrachia columna</i>	GenBank		U740611	–
GenBank	Vestimentifera	<i>Escarpia laminata</i>	GenBank		U740631	–
GenBank	Vestimentifera	<i>Escarpia spicata</i>	GenBank		U740641	–
GenBank	Vestimentifera	<i>Escarpia spicata</i>	GenBank		U740651	–
GenBank	Vestimentifera	<i>Oasisia alvinae</i>	GenBank		U740691	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U740731	–
GenBank	Vestimentifera	<i>Riftia pachyptila</i>	GenBank		U740741	–
GenBank	Vestimentifera	<i>Tevnia jerichonana</i>	GenBank		U740751	–
GenBank	Vestimentifera	<i>Basibranchia</i> sp Mariana Trough	GenBank		U740781	–
GenBank	Vestimentifera	<i>Escarpia spicata</i>	GenBank		U842621	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U879751	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U879761	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U879771	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U879781	–
GenBank	Vestimentifera	<i>Ridgeia piscisae</i>	GenBank		U879791	–
GenBank	OUTGROUP (Siboglinidae)	<i>Pogonophora</i> sp Kushiuro-SK-2003	GenBank		D505982	–
GenBank	OUTGROUP (Siboglinidae)	<i>Osedax roseus</i>	GenBank		JF5099491	–
GenBank	OUTGROUP (Siboglinidae)	<i>Sclerolinum brattstromi</i>	GenBank		FJ3476441	–
GenBank	OUTGROUP (Siboglinidae)	<i>Sclerolinum contortum</i> Scon COI-1	GenBank		FMI1784801	–
GenBank	OUTGROUP (Siboglinidae)	Loihi Seamount perviate pogonophoran	GenBank		U740681	–

DNA amplification and sequencing

DNA from mussel specimens was extracted using a QIAmp™ DNA Micro Kit (Qiagen, Valencia, CA, USA). After removal of excess ethanol, total DNA from tube-worms was isolated using a cetyltrimethylammonium bromide (CTAB) - polyvinylpyrrolidone (PVPP) protocol derived from Doyle & Doyle (1987). For the Siboglinidae, only the barcode fragment of the cytochrome oxidase subunit I (COI) gene was amplified using the Folmer primers LCO1490 and HCO2198 (Folmer *et al.* 1994). For the Bathymodiolinae both the barcode fragment of the COI gene and a fragment of the rDNA 28S gene were amplified using the Folmer primers and the C1 and D2 primers (Jovelin & Justine, 2001), respectively. All PCR reactions were performed in 20 µl, using 3 ng DNA, 10× reaction buffer containing 15 mM MgCl₂, 0.26 mM deoxynucleotides (dNTP), 0.3 µM of each primer, 5% dimethyl sulfoxide (DMSO), 1 mg · ml⁻¹ Bovine Serum Albumin (BSA) and 1 unit QBIotaq (MP Biomedicals, Illkirch Graffenstaden, France). Amplification consisted of an initial denaturation step at 95 °C for 5 min, followed by 40 cycles of denaturation at 95 °C for 1 min, annealing at 48 °C for the COI gene and 55 °C for the 28S gene for 30 s, followed by extension at 72 °C for 30 s. The final extension was at 72 °C for 5 min. PCR products were purified and sequenced in both forward and reverse directions by the Genoscope or the Eurofins sequencing facilities.

Phylogenetic analyses

Sequences were aligned automatically using MUSCLE 3.8.31 (Edgar 2004). Both maximum likelihood (ML) and Bayesian analyses (BA) were performed for the inference of phylogenetic relationships. ML analyses were performed using RAxML 7.0.4 (Stamatakis, 2006) with a GTR-GAMMAI model. Three partitions were defined for the COI gene, corresponding to each position of the codon. RAxML analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2/>) using the RAxML-HPC2 on TG Tool (Miller *et al.* 2010). Node support was estimated by bootstrapping (1000 replicates). For the Bathymodiolinae, a concatenated data set (COI+28S) was also analysed, with four partitions defined (the three codon positions of COI and one for 28S). BA were performed by running two parallel analyses in MRBAYES (Huelsenbeck *et al.* 2001), each consisting of four Markov chains of 30,000,000 generations each with a sampling frequency of one tree each 1000 generations. The number of swaps was set to two, and the chain temperature to 0.02. Similarly to the ML approach, unlinked models (each with six substitution categories, a gamma-distributed rate variation across sites approximated in

four discrete categories and a proportion of invariable sites estimated during the analysis) were applied for each partition. Convergence of each analysis was evaluated using TRACER 1.4.1 (Rambaut and Drummond, 2007), and analyses were terminated when ESS values were all greater than 200. A consensus tree was then calculated after discarding the first 25% of trees as burn-in.

Additional sequences from GenBank and outgroups

Within the Siboglinidae, vestimentiferans constitute a monophyletic group (*e.g.* Eichinger *et al.* 2013). We thus downloaded all the COI sequences of vestimentiferans from GenBank. Four sequences (GU059239.1, GU059172.1, GU059250.1 and GU059230.1), obviously contaminated or misidentified (they clustered within groups of specimens with different species and genus names), were removed from the data set. To reduce computational times, 215 *Ridgeia piscesae* sequences (EU190494.1–EU190709.1, all highly similar and belonging to the NCBI PopSet 158516272) were removed from the data set. Only one sequence from the PopSet was kept. In total, 283 COI sequences from GenBank were included in the alignment (Table 1). COI sequences of *Sclerolinum* were used as closely related outgroups, and a sequence of *Osedax roseus* was used to artificially root the tree, following the results of Eichinger *et al.* (2013). Additionally, two sequences obtained from two escarpiids collected in 2010 during the BIOPAPUA cruise from Broken Water Bay off the Sepik River (stations CP3703 and CP3704) were added to the data set (Table 1).

For the Bathymodiolinae, we used the data set from Thubaut *et al.* (2013), which is representative of the known diversity of the subfamily (Table 1). *Modiolus modiolus* was used as an outgroup.

Results and Discussion

New data and collections of deep-sea habitats in PNG

Due to a very active tectonic regime, the bottom topography around PNG is very uneven. Bathymetric data sets are also scarce. The 2012 deep-sea expedition largely took advantage of the deep-sea results of the BIOPAPUA cruise that both allowed us to identify the most interesting spots and provided preliminary bathymetric maps that were added to during the 2012 expedition. During each cruise, when the topology of the bottom allowed, each selected spot was explored over a depth range of 100–1000 m. Depending upon the topology and the type of substrate (*i.e.* hard or soft bottom), either a trawl or a dredge was used. Each collection was sieved onboard, using seawater to separate animals from the substrate into

different size classes. Specimens were then quickly sorted and preserved. All invertebrates were then integrated into the collections of the Muséum national d'Histoire naturelle (MNHN) in Paris and then distributed over an international network of taxonomists for study (Bouchet *et al.* 2008; Richer De Forges *et al.* 2013).

Seamounts were particularly difficult to localize and to sample, but a diversified fauna was obtained when operations were successful. On the slope of New Guinea island, from the Sepik River to Vanimo, collections were characterized by soft bottom associated with low diversity vastly dominated in biomass by irregular sea urchins (morphologically resembling *Sarsiaster greigii*, S. Hourdez, personal observations), most of which contained an Amphinomidae (Annelida) in the terminal portion of their digestive tube. Sunken plant remains associated with their typical fauna were present in most of the operations. The typical fauna associated with cold-seep environments was only found in a very restricted area off Broken Water Bay. From Manam Island to the Vitiaz Strait, *i.e.* the limit between the Bismark and Solomon Seas, the slopes of New Guinea island are very steep. Consequently, hauls mainly contained round stones, suggesting that strong currents do not allow settlement of sessile organisms or sediment accumulation. When terrestrial plant remains were found, these were large pieces of wood, in the early stages of decomposition but greatly abraded. Accumulations of sediments and/or of terrestrial plant remains were mostly found in small canyons and in large bays, notably in Astrolabe Bay.

Fauna sampled off Broken Water Bay (Sepik River)

In a very restricted area at the Sepik site, off Broken Water Bay, at stations dominated by irregular sea urchins (*cf.* *Sarsiaster greigii*), a fauna typical of cold seeps was collected (Fig. 2), including Bathymodiolineae mussels and siboglinid tubeworms [sampled during both the BIOPAPUA cruise in 2010 and Niugini in 2012 Expedition]. Irregular sea urchins are often found at seeps, although rarely properly identified (*e.g.* Olu-Le Roy *et al.* 2004; Cordes *et al.* 2009). The other bivalves sampled at this location were typical of seep environments. Among these, Rudo Von Cosel (personal communication) identified two species of Vesicomidae, one species of Thyasiridae attributed to the genus *Conchocele* and one species of Nuculidae attributed to the genus *Acila*. Among gastropods, predatory snails attributed to the genera *Phymorhynchus* (Raphitomidae) and *Manaria* sp. (Buccinidae closely related to *Eosipho*) are also typical of chemosynthetic environments (Warén 2011; Kantor *et al.* 2013). Among the Nassariidae, this location was the only one where a specimen attributed to the genus *Profundinassa* was sam-

pled. For the crustacean fauna, a hippolytid shrimp typical of deep-sea reducing environments, attributed to the genus *Lebbeus*, was identified (Komai *et al.* 2012; Nye *et al.* 2012), while other specimens were not typical of chemosynthetic environments. The ethusid crab *Ethusa curvipes*, a species typical of muddy deep-sea bottoms (P. Castro, personal communication), was also found among the animals collected.

Fauna sampled below the Ramu refinery

Off the Ramu refinery, specimens were sampled from 200 to 1000 m depth. The samples contained fauna associated with both soft bottoms and plant remains. Sampling off the Ramu refinery indicated a heavy release of tailings (Fig. 3) although refining activities had only started 10 days prior to our sampling operations. These tailings formed a layer of color and texture consistent with the known nickel-refining protocols used at the Ramu refinery. The tailings overlay the otherwise gray sediment, very similar to sediment sampled elsewhere during the expedition, including the Broken Water Bay cold-seep site. Shallower operations (*c.* 250–400 m) brought back sediments only slightly stained by the tailings (Fig. 3A), while in deeper collections (400–700 m) sediments were covered by a thick layer of red sediment (Fig. 3B). In the impacted sediments, we notably sampled polychaete tubes that had incorporated red particles over a few centimeters. The topography of Basamuk Canyon, off the Ramu refinery, rendered the operations difficult, with many instances of damage to the trawls for the deeper sites (hard bottoms). Although the catch was not very abundant in this canyon, we unexpectedly captured organisms typical of cold-seep environments (Bathymodiolineae mussels and Siboglinidae tubeworms; Fig. 4). As for Broken Water Bay, other fauna typical of seep environments was identified, notably bivalves of the families Thyasiridae and Nuculidae (genus *Acila*). The crustacean fauna was mostly composed of species that were not specific to reducing environments (*e.g.* *Ethusa curvipes* as in Broken Water Bay), with the exception of the hippolytid shrimp *Lebbeus* sp. (also found in Broken Water Bay). The squat-lobster *Munidopsis andamanica*, largely distributed in the Indo-Pacific and frequently found associated with sunken wood (Hoyoux *et al.* 2009), was also found in these samples.

Bathymodioline mussel diversity

All phylogenetic trees (COI, 28S and COI+28S) are very congruent. Specimens collected in Broken Water Bay (Sepik) and in Basamuk Canyon (Astrolabe Bay) cluster into four distinct groups (Fig. 5), some of which also include sequences from GenBank. The specimens from



Fig. 2. Broken Water Bay fauna. Photos taken onboard. (A) Bathymodiolinae mussels, PAPUA NIUGINI, CP4042; (B) *Gigantidas* sp. 2, Broken Bay BIOPAPUA, CP3703; (C) *Gigantidas* sp. 1, Broken Bay, BIOPAPUA, CP3703; (D) *Lamellibrachia* sp., BIOPAPUA, CP3703; (E) *Acila* sp., BIOPAPUA, CP3703; (F) *Conchocele* sp., BIOPAPUA CP3703; (G) Buccinidae gastropod *Manaria* sp., PAPUA NIUGINI, CP4042.

Broken Water Bay (Sepik station CP4042), are divided into three groups. One well-supported clade (three specimens) is sister to *Gigantidas taiwanensis*. This new clade is closely related to but distinct from *G. taiwanensis* which is only known from a shallow vent off Taiwan. The second group clusters 39 newly collected specimens, including one collected during the BIOPAPUA cruise in Broken Water Bay (labeled in Thubaut *et al.* 2013 as '*Gigantidas* sp 1 Broken Bay'). Finally, one specimen clustered with one specimen collected in 2010 (labeled '*Gigantidas* sp. 2 Broken Bay' in Thubaut *et al.* 2013). Interestingly, this cluster also included one sequence from a specimen collected in Basamuk Canyon (CP4042). Based on COI data, this species was also collected earlier in a site off the nearby Aitape village, at 420 m depth (Kyuno *et al.* 2009). The 2012 expedition also explored the Aitape area but did not bring back any catch of fauna typical of seep environments. In this area, two additional

undescribed *Gigantidas* species (assignment based on COI data) were collected from greater depths during a Japanese cruise (1600–1900 m, Kyuno *et al.* 2009). These species were not collected during our expeditions, probably because they live deeper than the explored bathymetric range. The eight other specimens from Basamuk Canyon (CP4020) cluster into a distinct group and form a well-supported group, sister to *Nypamodiolus longissimus* (new genus name under description, R. Cosel & J. Thubaut, unpublished data). These specimens are thus attributed to a potential new species of the genus *Nypamodiolus*.

If we consider the high genetic distances found within and among these clusters, and the fact that the phylogenetic information from mitochondrial and nuclear genes is congruent, we can conclude that four putative species were found at the Broken Water Bay site and in Basamuk Canyon, two of which were previously collected during the BIOPAPUA cruise. Overall, the three explorations in

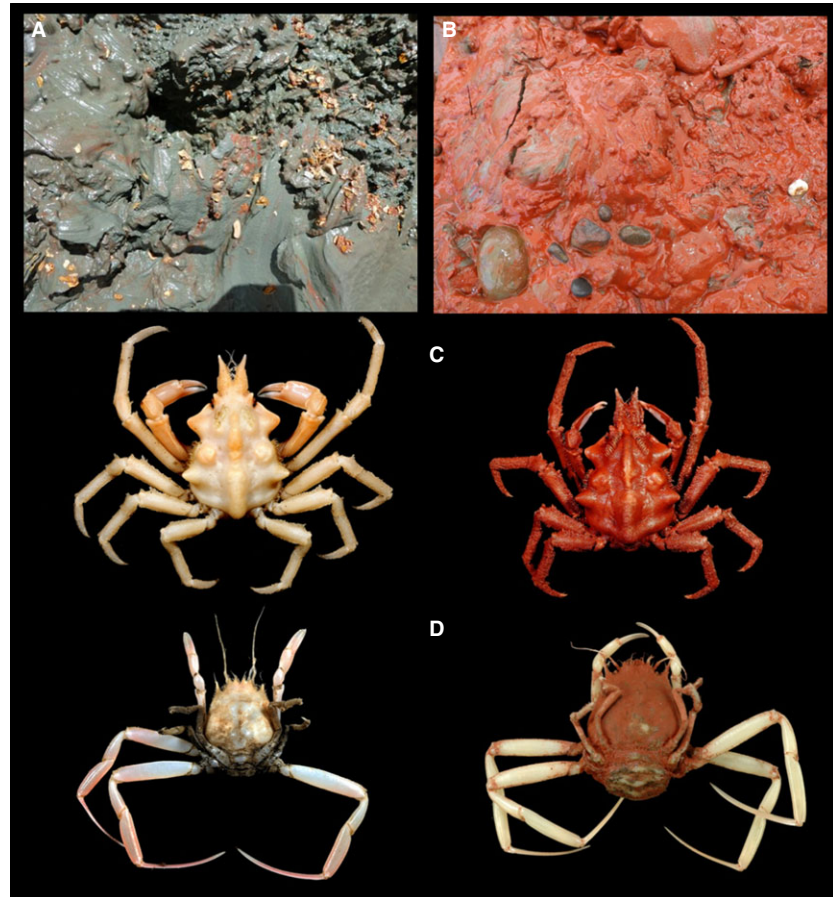


Fig. 3. Basamuk Canyon, below the Ramu refinery. (A) Muddy sediment collected 50 m below pipe opening (DW 4018). (B) Red muddy sediment collected 200 m below pipe opening (DW 4019). (C) *Goniopugettia sagamiensis*. (D) *Ethusa curvipes*. Illustrations of the red mineral deposit covering animals. Specimens on the left collected outside the refinery area. Specimens on the right collected at station CP4081.

this area (JAMSTEC cruise, BIOPAPUA cruise and PAPUA NIUGINI expedition) identified five different *Gigantidas* species and one *Nypamodiolus* species. Interestingly, only one of these species was found at all locations (including at Aitape), the five others each being restricted to a single location. Similarly, *Nipponiomodiolus manusensis* (new genus under description, R. Cosel & J. Thubaut, unpublished data) has only been found at hydrothermal vent sites in the Manus Basin and was not found in our cold-seep collections (Thubaut *et al.* 2013).

The genus *Nypamodiolus* contains species that are very ecologically diverse (*i.e.* associated with plant remains, whale bones or seep environments over a wide bathymetric range). For example, the geographic range of *N. longissimus* coincides with that of the *Nypa* palm although it is sometimes associated with other types of wood; *Nypamodiolus simpsoni* has been collected in both the Mediterranean and in the Atlantic over a wide range of depths, and associated with whale carcasses, sunken wood and cold seeps (Thubaut *et al.* 2013). The specimens attributed to *Nypamodiolus* collected below the Ramu refinery belong to an unknown species: they have never been found elsewhere in our collections (neither in Astrolabe

Bay in general nor on the abundant plant debris often collected at other sites during our expeditions).

Siboglinidae diversity

Siboglinid tubeworms were only found at two locations (Broken Water Bay and Astrolabe Bay sites). In Astrolabe Bay, tubeworms were only found in Basamuk Canyon off the Ramu refinery. Part of the COI gene was sequenced for a total of 11 siboglinid specimens collected from these locations. The specimens fall into three distinct lineages (Fig. 6) that are not shared between locations: two of these clades are only found at the Sepik River site and the third has only been collected at the Astrolabe site during our expeditions.

Two specimens from the Broken Water Bay collections (BIOPAPUA cruise) cluster among the escarpiids but clearly form a separate clade. Although clearly distinct, the sequences of the Broken Water Bay escarpiid species most closely resemble that of a distinct isolate of an animal identified as *Paraescarpia cf. echinospica* (isolate E1) collected near Japan (Andersen *et al.* 2004). Sequences from two other specimens of *Paraescarpia cf. echinospica*,

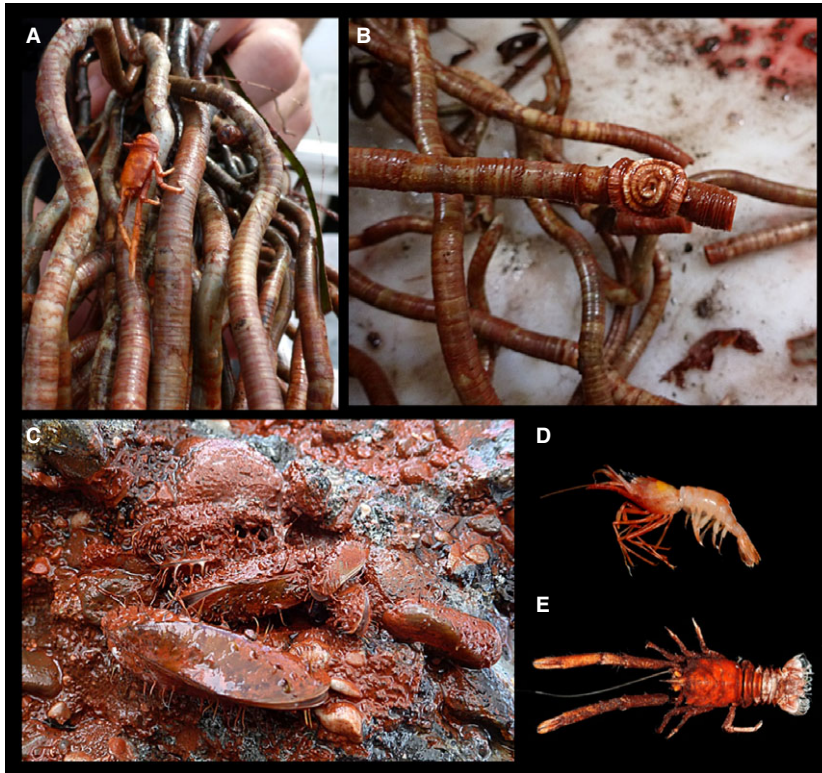


Fig. 4. Basamuk Canyon fauna (PAPUA NIUGINI, CP4081). (A and B) Siboglinidae (*Lamellibrachia* sp.); (C) Bathymodiolinae (*Gigantidas* sp.); (D) *Lebbeus* sp.; (E) *Munidopsis andamanica*. The red coloration of the specimens is due to the Ramu refinery tailings.

also collected near Japan, however, form a different clade. Closer examination of the morphology of all these worms (if vouchers are available) will be necessary to determine species identities.

The sequences for five specimens of *Lamellibrachia* from the Broken Water Bay site most closely cluster with the sequence of a *Lamellibrachia* specimen collected about 325 km west of the Broken Water Bay collection site (Aitape site *Lamellibrachia* L6 in Kojima *et al.* 2003). Although distinct in sequence, two other species of *Lamellibrachia* are closely related to this group: *L.* sp. L4, from the PACMANUS vent site in the Manus Basin (about 650 km east of the Broken Water Bay site), and *L.* sp. L5, from the cold-seep sites of Kuroshima Knoll, about 3 000 km north-northwest of the Broken Water Bay site (Kojima *et al.* 2001). Additional samples from the different locations will be necessary to study this lineage further and determine whether there is genetic continuity between the groups identified.

Sequences from Basamuk Canyon specimens all cluster with different haplotypes of *Lamellibrachia juni*, including four specimens collected from the DESMOS hydrothermal vent site in the Manus Basin, about 770 km to the east. However, some genetic structure exists in this clade, and the haplotype network produced for this lineage (Fig. 7) revealed some geographic pat-

terns that could correspond to different species occupying different locations. Basamuk Canyon specimens ($n = 4$) represent three distinct haplotypes differing by two mutations at the most. These differ from the DESMOS specimens ($n = 4$) by at least 10 fixed mutational steps. Sequences from specimens collected 1600 km to the north (TOTO Caldera, South Mariana) differ from Basamuk Canyon sequences by six fixed mutational steps. At the Brothers Caldera (4600 km southeast of the TOTO Caldera, and 3500 km southeast of Astrolabe Bay), there are two haplotype groups, one of which only differs from the TOTO haplotype by a single mutational step, possibly corresponding to a single species. The other haplotypic group from Brothers Caldera differs from all the other haplotypes by at least four fixed mutational steps.

For at least two clades, although sequence polymorphism does exist, inter-specific variation is no greater than intra-specific variation (Miglietta *et al.* 2010). This observation does not reflect within-species morphological variation but a reduced divergence of the mitochondrial genome (Miglietta *et al.* 2010; Cowart *et al.* 2013). The COI marker thus offers a very conservative estimation of specific diversity in Siboglinidae. Based solely on COI sequence data, there is therefore little doubt that the species studied here represent new species that have only

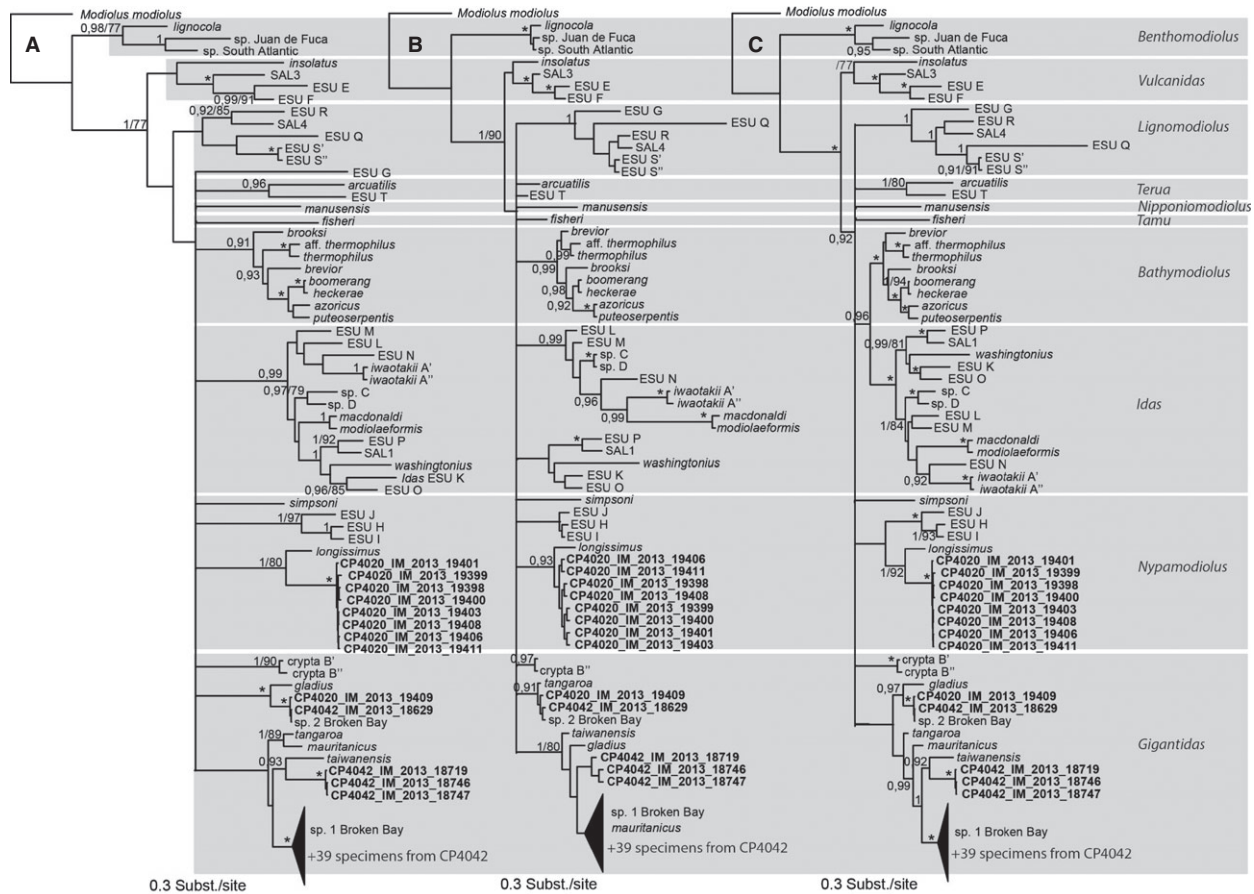


Fig. 5. (A) Cytochrome oxidase subunit I (COI), (B) 28S and (C) COI+28S. Bayesian phylogenetic trees obtained from sequences of 105 Bathymodiolinae specimens. Posterior probabilities (>0.90) and bootstrap values (>75%) are shown for each node. *posterior probabilities >0.98 and bootstrap values >95%. For clarity, support values for within-species relationships are not shown. Specimens from the PAPUA NIUGINI expedition are in bold.

been collected in the sampled area so far. The *Lamellibrachia* specimens collected at Broken Water Bay probably correspond to the same species as the specimen collected at the Aitape site, further west on the PNG coast (Kojima *et al.* 2001, 2003). A population genetics study including more variable markers (*e.g.* microsatellites) could reveal whether or not these populations separated by 350 km are genetically connected. The number of specimens collected in Basamuk Canyon (*Lamellibrachia juni* clade), and other specimens of the same clade from different locations, was sufficient to initiate a study of connectivity. The specimens from Astrolabe Bay were only found at the site below the Ramu refinery. Although close to *L. juni*, there are some fixed differences in the COI sequences that strongly suggest that this lineage should be separated into at least four species (non-inter-breeding populations), two of which are found in PNG. Except for the Brothers Caldera site where two species co-occur, only a single haplotypic group (= species) occurs at each

site. Even within the Manus Basin, the sequences of the specimens from the hydrothermal vent site DESMOS are 10 mutational steps distant from the sequences of the specimens collected at the cold-seep site in Astrolabe Bay, indicating that they belong to reproductively isolated evolutionary units.

Conclusions

Deep-sea chemosynthetic environments are rare and very patchy (Levin & Sibuet 2012; Van Dover *et al.* 2012). Some organisms can live in several types of chemosynthetic environments (*e.g.* *Idas washingtonius* is present at vents and on sunken wood or bones in the Eastern Pacific; *Gigantidas platifrons* is present both at vent and seep environments in the Western Pacific, Thubaut *et al.* 2013; *Pyropelta musaica* is found at cold seeps, hot vents and on sunken whale carcasses, Smith & Baco 2003), and some have a very wide distribution, sometimes spanning

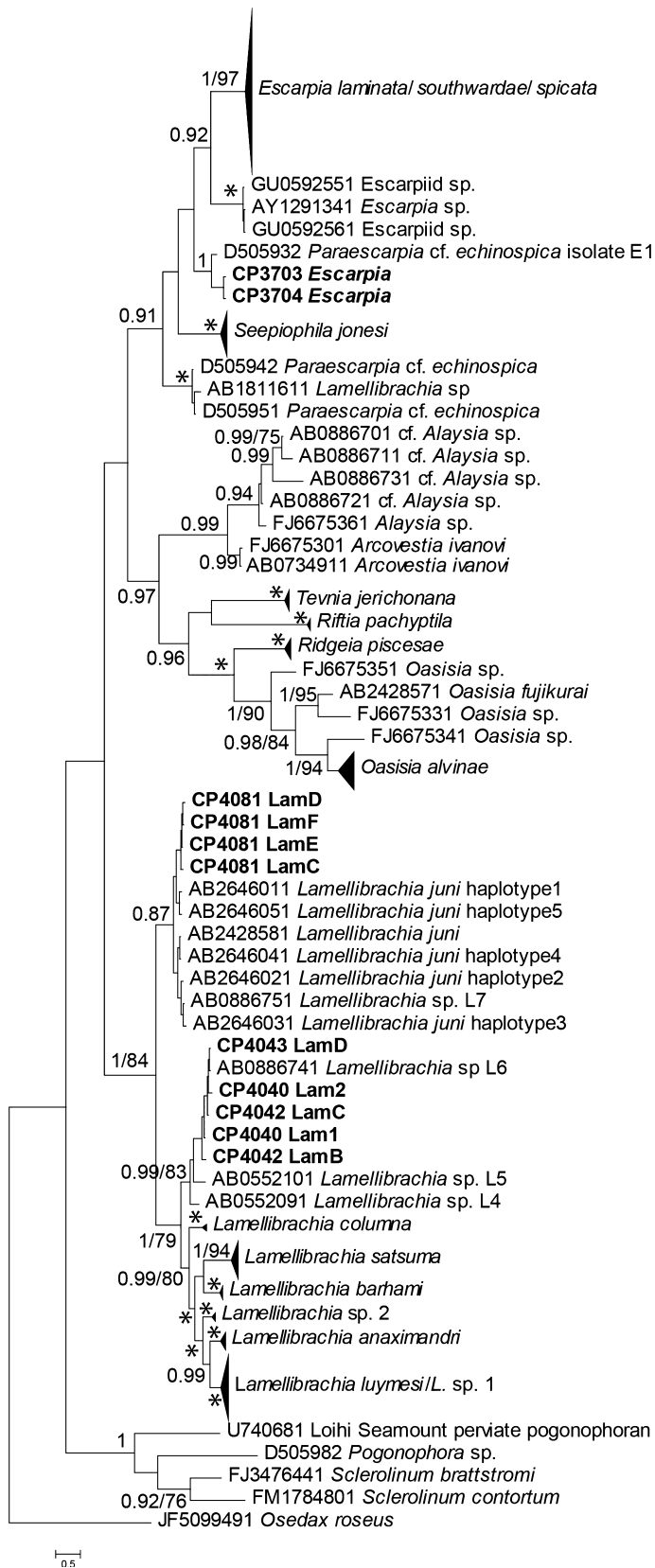


Fig. 6. Bayesian phylogenetic tree obtained from 298 Vestimentifera cytochrome oxidase subunit I sequences. Posterior probabilities (>0.85) and bootstrap values (>75%) are shown for each node. *posterior probabilities >0.98 and bootstrap values >95%. For clarity, support values for within-species relationships are not shown and clades that included sequences from the same species or the same species complex were collapsed into triangles (as long as they did not include PAPUA NIUGINI sequences). Specimens from the PAPUA NIUGINI expedition are in bold. Specimens of the species *Gigantidas* sp. 1, Broken Water Bay, were collapsed into a triangle (details in Table 1).

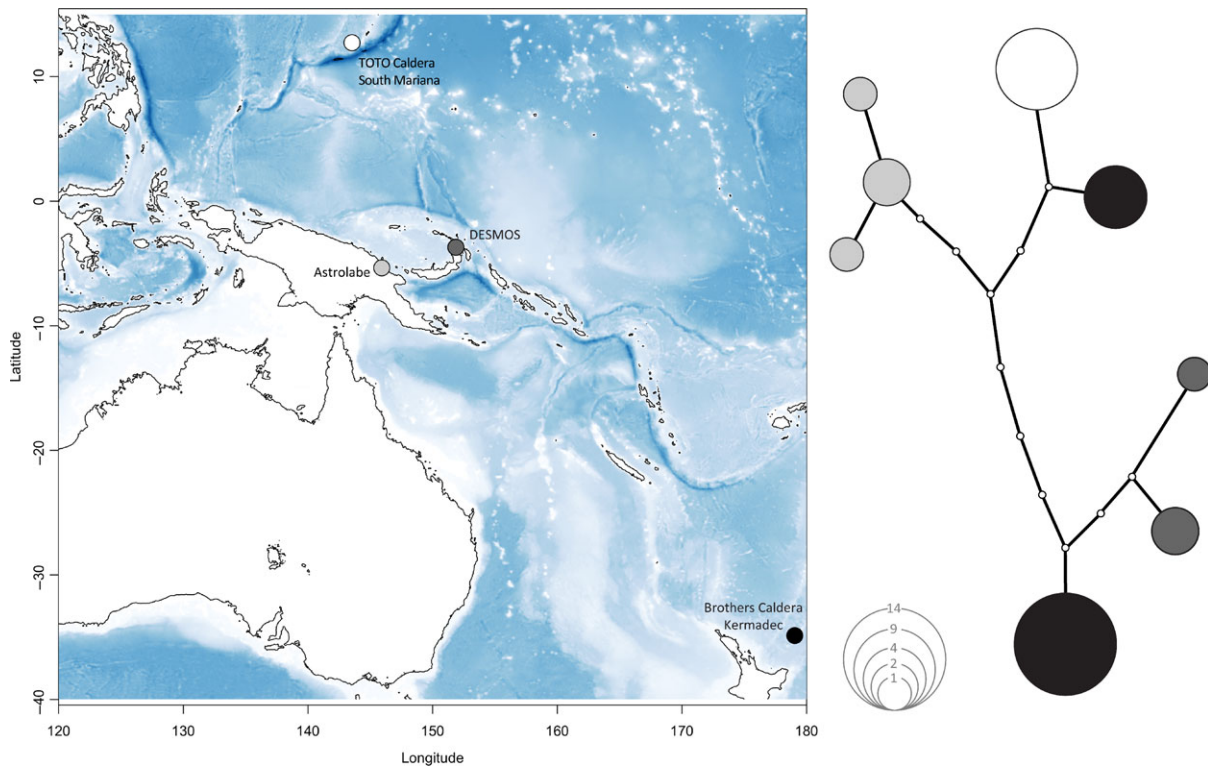


Fig. 7. Sampling locations (left) and TCS haplotype network (Clement *et al.* 2000) of the *Lamellibrachia juni* clade (right). Circles on the network represent unique mitochondrial cytochrome oxidase subunit I haplotypes; circle diameters are proportional to the number of individuals (key: bottom right). Intermediate mutations (*i.e.* unsampled haplotypes) are represented by small white circles. Site shading levels on the map correspond to circle shading levels on the network. The map was prepared based on NOAA's ETOPO1 data using the *marmap* package in R (Pante & Simon-Bouhet 2013).

thousands of kilometers (*e.g.* *Rimicaris exoculata* on the Mid-Atlantic Ridge, Teixeira *et al.* 2013). In the Atlantic Ocean, the among-site faunal similarity is better explained by depth than by geographic distances (Olu *et al.* 2010). The potential threat to the fauna associated with deep-sea chemosynthetic habitats should therefore take into account a complex pattern of patchiness and connectivity at small and large geographic scales.

Although intensive, our sampling in the area probably missed some chemosynthetic sites. For instance, we re-visited the Aitape site sampled earlier with a remotely operated vehicle (Tappin *et al.* 2001), and did not find any fauna typical of cold seeps in our collections. The area is characterized by very complex bottom structures that are difficult to sample using dredges and trawls. In addition, the sampled animals formed very small clumps (Tappin *et al.* 2001) that are easily missed. It is therefore very likely that there are sites with chemosynthetic fauna elsewhere in the sampled area.

However, the collections so far clearly reveal not only the great patchiness in the distribution of different environments (cold-seeps, hydrothermal vents, sedimentary

areas, rubble, plant debris), which has a direct effect on the distribution of species, but also differences in the species that occupy different sites of the same habitat type, in particular for the cold-seep sites studied so far in PNG.

In other words, although some species are shared between the two locations sampled, each location is also characterized by unique assemblages. The Broken Water Bay site does share some species with the Aitape site (*Lamellibrachia* L6 and *Gigantidas* sp. 2, this latter also found in Astrolabe Bay) but the Astrolabe Bay site is characterized by some species that have so far only been found there. Interestingly, the northern sites (Aitape and Broken Water Bay) receive currents from the northwest (with occasional upwellings) while Astrolabe Bay receives currents coming from the southeast through the Vitiaz Strait (Hasegawa *et al.* 2011), suggesting that each location may receive larvae from different sources.

Our results provide clear evidence of the patchiness of the cold-seep habitats in PNG and of the limited connectivity between the two studied locations. Although

more exploration remains to be performed, it is clear that the assertions that impact of human activities on deep-sea species is limited because the deep sea is uniform and that all species are present everywhere are inherently wrong. In the case of the Ramu refinery in Astrolabe Bay, we can not exclude the possibility that the major impact that it has on the local deep-sea habitat in Basamuk Bay could result in species extinction. These concerns call for major exploration efforts and studies of connectivity in the hotspot of biodiversity that PNG represents.

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