Deep-Sea Research II 58 (2011) 196–204

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

The Southern Ocean: Source and sink?

J.M. Strugnell [a,b,*], Y. Cherel [c], I.R. Cooke [b,d], I.G. Gleadall [e], F.G. Hochberg [f], C.M. Ibáñez [g], E. Jorgensen [h], V.V. Laptikhovsky [i], K. Linse [j], M. Norman [k], M. Vecchione [l], J.R. Voight [m], A.L. Allcock [n]

[a] Department of Genetics, La Trobe Institute for Molecular Science, La Trobe University, Bundoora 3086, Australia
[b] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[c] Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS, BP 14, 79360 Villiers-en-Bois, France
[d] Department of Biochemistry, La Trobe Institute for Molecular Science, La Trobe University, Bundoora 3086, Australia
[e] Department of Applied Biosciences, Faculty of Agriculture, Tohoku University, Amamiya 1-1, Sendai, Japan
[f] Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, CA 93105, USA
[g] Laboratorio de Ecología Molecular, Instituto de Ecología y Biodiversidad, Dpto. Ciencias Ecoloígicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile
[h] NMFS, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA
[i] Falkland Island Fisheries Department, PO Box 598, Stanley FIQQ IZZ, Falkland Islands
[j] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK
[k] Sciences, Museum Victoria, GPO Box 666, Melbourne, Vic. 3001, Australia
[l] NMFS National Systematics Laboratory, National Museum of Natural History, MRC-153, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA
[m] Department of Zoology, Field Museum of Natural History, 1400 S. Lake Shore Dr, Chicago, IL 60605-2496, USA
[n] Martin Ryan Marine Science Institute, National University of Ireland Galway, University Road, Galway, Ireland

ARTICLE INFO

Article history:
Received 18 May 2010
Accepted 18 May 2010
Available online 11 June 2010

Keywords:
Benthoctopus
Antarctic zone
Phylogenetics
Marine molluscs
Thermohaline circulation

ABSTRACT

Many members of the benthic fauna of the Antarctic continental shelf share close phylogenetic relationships to the deep-sea fauna adjacent to Antarctica and in other ocean basins. It has been suggested that connections between the Southern Ocean and the deep sea have been facilitated by the presence of a deep Antarctic continental shelf coupled with submerging Antarctic bottom water and emerging circumpolar deep water. These conditions may have allowed 'polar submergence', whereby shallow Southern Ocean fauna have colonised the deep sea and 'polar emergence', whereby deep-sea fauna colonised the shallow Southern Ocean. A recent molecular study showed that a lineage of deep-sea and Southern Ocean octopuses with a uniserial sucker arrangement on their arms appear to have arisen via polar submergence. A distantly related clade of octopuses with a biserial sucker arrangement on their arms (historically placed in the genus *Benthoctopus*) is also present in the deep-sea basins of the world and the Southern Ocean. To date their evolutionary history has not been examined. The present study investigated the origins of this group using 3133 base pairs (bp) of nucleotide data from five mitochondrial genes (12S rRNA, 16S rRNA, cytochrome *c* oxidase subunit I, cytochrome *c* oxidase subunit III, cytochrome b) and the nuclear gene rhodopsin from at least 18 species (and 7 outgroup taxa). Bayesian relaxed clock analyses showed that *Benthoctopus* species with a high-latitude distribution in the Southern Hemisphere represent a paraphyletic group comprised of three independent clades. The results suggest that the *Benthoctopus* clade originated in relatively shallow Northern Hemisphere waters. *Benthoctopus* species distributed in the Southern Ocean are representative of polar emergence and occur at shallower depths than non-polar *Benthoctopus* species.

1. Introduction

The Southern Ocean is recognised as an evolutionary centre of origin for marine species (Crame, 1993; Briggs, 2003). A recent molecular study showed that a major global lineage of deep-sea octopods had its evolutionary origins in Antarctica (Strugnell et al., 2008) and proposed that the global thermohaline circulation acted as an evolutionary driver enabling the Southern Ocean to become a centre of origin for deep-sea fauna. Members of that octopod lineage examined have a uniserial arrangement of

* Corresponding author. Tel.: +61 394793663; fax: +61 394791226.
E-mail addresses: J.Strugnell@latrobe.edu.au (J.M. Strugnell), cherel@cebc.cnrs.fr (Y. Cherel), octopus@bios.tohoku.ac.jp (I.G. Gleadall), fghochberg@sbnature2.org (F.G. Hochberg), christianibez@yahoo.com (C.M. Ibáñez), Elaina.Jorgensen@noaa.gov (E. Jorgensen), vlaptikhovsky@Fisheries.gov.fk (V.V. Laptikhovsky), kl@bas.ac.uk (K. Linse), mnorman@museum.vic.gov.au (M. Norman), VecchioneM@si.edu (M. Vecchione), jvoight@fieldmuseum.org (J.R. Voight), louise.allcock@gmail.com (A.L. Allcock).

0967-0645/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2010.05.015

Table 1
Purported valid species in the genus *Benthoctopus* Grimpe, 1921 and nominal species removed from the genus *Benthoctopus* Grimpe, 1921.

Species	ML	TL	Distribution	Depth (m)	Status/refs.
(a) Purported valid species in the genus *Benthoctopus* Grimpe, 1921					
Benthoctopus abruptus (Sasaki, 1920)	100	520	NW Pacific, Pacific Coast of Japan	1074	Poorly known
Benthoctopus berryi (Robson, 1924)	47	–	Off Cape Town, South Africa	2196	Known only from type
Benthoctopus canthylus Voss and Pearcy, 1990	50	250	NE Pacific, off Oregon, USA	3000	Voss and Pearcy (1990)
Benthoctopus clyderoperi O'Shea, 1999	90	380	S Pacific, E of North Is, NZ	840–1100	O'Shea (1999)
Benthoctopus eureka (Robson, 1929)	–	300	S Atlantic, N Argentina to Falklands	119–299	Nesis (1987)
Benthoctopus fuscus (Taki, 1964)			NW Pacific, off Japan	ukn	Nesis (1987), Norman and Hochberg (2005)
Benthoctopus hokkaidensis (Berry, 1921)	58	245	N Pacific, Japan to Oregon	130–1000	Nesis (1987)
Benthoctopus januarii (Hoyle, 1885)	70	–	W Atlantic, Gulf of Mexico to Brazil	350–732	Toll (1981), Nesis (1987), Gleadall (2004)
Benthoctopus johnsonianus, Allcock et al. 2006	113	510	Atlantic coast of Europe between 49–59°N	1800–2540	Allcock et al. (2006)
Benthoctopus karubar Norman, Hochberg and Lu, 1997	100	400	W Pacific, Arafura Sea, Indonesia	400–800	-
Benthoctopus leioderma (Berry, 1911)	70	270	N Pacific, Sea of Okhotsk to California, USA	90–500	Hochberg (1998)
Benthoctopus levis (Hoyle, 1885)	50	180	S Indian, Heard Island	13–404	Vecchione et al. (2009)
Benthoctopus longibrachus Ibáñez, Sepúlveda and Chong 2006	115	695	SE Pacific, off Chile	436–1000	Ibáñez et al. (2006)
Benthoctopus normani (Massy, 1907)	64	320	Atlantic coast of Europe between 38–60°N	537–1865	Allcock et al. (2006)
Benthoctopus oregonae Toll, 1981	58	300	Southern Caribbean Sea	640–1080	Nesis (1987)
Benthoctopus oregonensis Voss and Pearcy, 1990	93	-	NE Pacific, off Oregon, USA	1000–2750	Strugnell et al. (2009)
Benthoctopus profundorum Robson, 1932	-	290	N Pacific, Japan to Gulf of Alaska	150–3400	Nesis (1987)
Benthoctopus pseudonymus (Grimpe, 1922)			South of Flores Island (Azores Island)	1599	Robson (1932), Norman and Hochberg (2005)
Benthoctopus rigbyae, Vecchione et al. 2009	105	400	South Shetland Islands, Antarctica	250–600	Vecchione et al. (2009)
Benthoctopus robustus Voss and Pearcy, 1990	142	-	NE Pacific, Oregon, USA to Baja California, Mexico	1200–3850	Hochberg (1998)
Benthoctopus sibiricus Loyning, 1930	–	–	Eastern Arctic	38–220	Nesis (1987, 2001)
Benthoctopus tangaroa O'Shea, 1999	122	720	S Pacific, E and S of New Zealand	500–1500	–
Benthoctopus tegginmathae, O'Shea, 1999	96	330	S Pacific, E of New Zealand	777–1723	–
Benthoctopus thielei Robson, 1932	65	–	S Indian Ocean, Kerguelen Plateau	126–507	Nesis (1987)
Benthoctopus violescens Taki, 1964			NW Pacific, off Japan	ukn	Norman and Hochberg (2005)
Benthoctopus yaquinae Voss and Pearcy, 1990	83	–	NE Pacific, off Oregon, USA	1000–3000	Strugnell et al. (2009)
Vulcanoctopus hydrothermalis González and Guerra, 1998	55	180	NE Pacific, East Pacific Rise	2495–2832	González et al. (1998), Strugnell et al. (2009)

Species	Distribution	Depth	Status/refs
(b) Nominal species removed from the genus *Benthoctopus*, Grimpe 1921			
Benthoctopus ergasticus (Fischer and Fischer, 1892)	N Atlantic, Ireland to Senegal	450–1400	Moved to *Bathypolypus* by Muus (2002)
Benthoctopus lothei (Chun, 1913)	Atlantic Ocean, SE of Fuerteventura	1365	Synonym of *Bathypolypus ergasticus*, Norman and Hochberg (2005)
Benthoctopus piscatorum	Arctic Ocean	220–2492	Type shown to be a female *Bathypolypus*, see Voss and Pearcy (1990), Muus (2002). Most specimens previously identified as *B. piscatorum* are actually *B. normani* or *B. johnsonianus*. Placed in *Bathypolypus* Grimpe, 1921 by Muus (2002) as junior synonym of *Bathypolypus bairdii* (Verrill, 1873)
Benthoctopus salebrosus (Sasaki, 1920)	NW Pacific, Japan and Okhotsk Sea	212–1160	Placed in *Benthoctopus* by Muus (2002). Moved to *Sasakiopus* by Jorgensen et al. (2010)

suckers on their arms and include the majority of endemic octopods in the Southern Ocean (members of the Antarctic genera *Pareledone*, *Adelieledone* and *Megaleledone*) and more widely distributed deep-water genera (including *Thaumeledone*, *Velodona* and *Graneledone*, the latter extending into deep waters of the Northern Hemisphere).

Octopods with a biserial sucker arrangement on their arms are more rarely captured in the Southern Ocean and comprise only a small proportion of catch records (e.g. $<2\%$ of octopod fauna sampled, Vecchione et al., 2009). All lack an ink sac and as a consequence have been placed in the genus *Benthoctopus*, defined as octopods with two rows of suckers on the arms, which lack an ink sac and possess a simple unlaminated ligula at the tip of the hectocotylised arm (Nesis, 1987). The taxonomic status of the genus *Benthoctopus* is discussed in detail in Strugnell et al. (2009) and the valid species currently contained within the genus are detailed in Table 1. Strugnell et al. (2005, 2008) showed that *Benthoctopus* is only distantly related to the monophyletic members of the clade with a uniserial sucker arrangement discussed above (Strugnell et al., 2005, 2008). The phylogenetic relationships and origins of the Southern Ocean *Benthoctopus* are unknown.

The genus *Benthoctopus* (as it currently stands) contains member species in deep waters of all oceans of the world from the equator to polar seas, and to depths of almost 4 km (Table 1). *Benthoctopus* species are also known from hydrothermal vents (Strugnell et al., 2009) and *Vulcanoctopus hydrothermalis* (a hydrothermal vent octopus species) was recently proposed to belong in the genus *Benthoctopus* (Strugnell et al., 2009). Due to their occurrence at great depths, limited well-preserved specimens have been collected for most *Benthoctopus* species. More than 30 nominal species have been described with around 27 currently considered to be valid (Table 1). Norman and Hochberg (2005) proposed that the genus may be polyphyletic as it is united by only two simple characters—possession of biserial suckers, and the absence of an ink sac, and suggested that the genus requires thorough revision.

To date, only two *Benthoctopus* species have been formally described from the Southern Ocean (here defined as south of the Polar Front). *Benthoctopus levis* (Hoyle, 1885) was described from off Heard Island and is known from shallow depths of 13–404 m (Fig. 1). *Benthoctopus rigbyae* (Vecchione et al., 2009) was collected from off the Antarctic Peninsula from the relatively shallow depths of 250–600 m (Fig. 1). This same study also reported an undescribed *Benthoctopus* species from the Weddell Sea. An additional species, *Benthoctopus thielei* (Robson, 1932), has been described from off the sub-Antarctic Kerguelen Island, which lies just north of the Southern Ocean in the Polar Frontal Zone (Fig. 1). *Benthoctopus eureka* (Robson, 1929) has been described from the Falkland Islands and descriptions of an additional Falkland Island species and a subspecies of the Chilean *Benthoctopus longibrachus* are in press (Gleadall et al., 2010) (Fig. 1).

Southern Ocean *Benthoctopus* may be a product of one of two major evolutionary pathways. The first hypothesis is that these species represent a radiation into Southern Ocean waters associated with polar emergence (i.e. shallow depth distribution of *B. rigbyae* and *B. levis*). The second hypothesis is that the Southern Ocean *Benthoctopus* species are the surviving members of a genus that originated in Antarctica and moved into the deep sea via polar submergence, as was proposed for the Antarctic and deep-sea octopod clade with a uniserial sucker arrangement (Strugnell et al., 2008).

The aims of this study were to (1) conduct a broad molecular phylogenetic analysis of the genus *Benthoctopus*, with species collected throughout its range (North and South Atlantic, North and South Pacific, Falkland Islands, the Southern Ocean

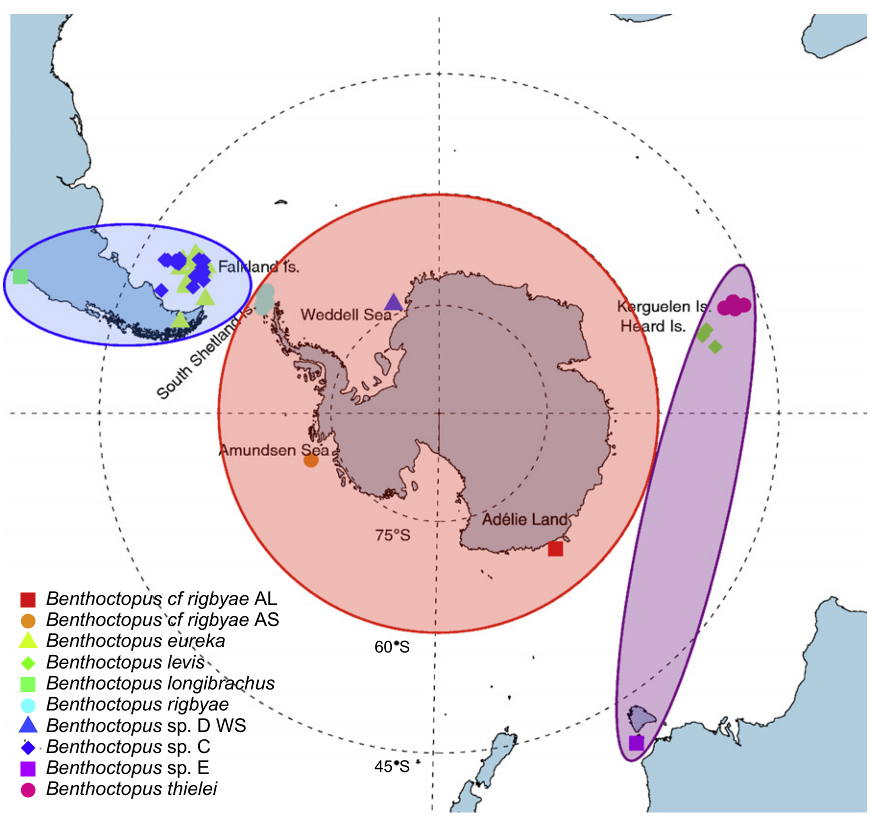

Fig. 1. Distribution of *Benthoctopus* spp. in the Southern Hemisphere. The three clades of *Benthoctopus* recovered in the phylogenetic analysis are indicated; clade 1 (blue oval, far left), clade 2 (orange circle, centre) and clade 3 (purple oval, far right) (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

and sub-Antarctic Islands) in order to examine the evolutionary history of *Benthoctopus* species with a Southern focus in their distribution and (2) to further investigate the theory of polar submergence or polar emergence in *Benthoctopus* by analysing the relationship between catch depth and latitude for *Benthoctopus* and *Vulcanoctopus* species using all available catch records.

2. Methods

2.1. Sample collection

The 24 octopodid representatives included in the present study were kindly provided by colleagues or collected by the authors on research expeditions. Full details of capture locations and catalogue numbers where available are provided in Table 2. Tissue samples were preserved in 70–100% ethanol for subsequent DNA extraction. In addition to *Benthoctopus* and *Vulcanoctopus* species, *Enteroctopus* spp. and *Octopus* s.l. *californicus* were also included because previous studies have shown a close phylogenetic relationship between these taxa and *Benthoctopus* (Carlini et al., 2001; Allcock et al., 2006; Strugnell et al., 2005, 2008, 2009). It is recognised that *Octopus* s.l. *californicus* will be transferred to a genus distinct from *Octopus* s.s. in the near future (Norman and Hochberg, 2005). *Octopus vulgaris* and *Bathypolypus* were included as outgroup taxa, as this has been shown to be appropriate in previous studies (Allcock et al., 2006; Strugnell et al., 2009).

2.2. Molecular sequencing techniques

Genomic DNA was extracted using a high salt method (Sambrook et al., 1989). PCR conditions and primers for fragments of four mitochondrial genes (12S rRNA, 16S rRNA, cytochrome *c* oxidase subunit I [COI], cytochrome *c* oxidase subunit III [COIII]) and the nuclear gene rhodopsin are detailed in Allcock et al. (2008). Primers for the mitochondrial gene cytochrome b (cytb) are detailed in Guzik et al. (2005). An additional primer pair for rhodopsin was also used to amplify a larger fragment. These primer sequences are as follows: Rh1243 gatcgttataacgtcattggaagacc and Rh1793 gtagacaatygggttgtggatagcctg, used at an annealing temperature of 50 °C. The majority of sequencing was carried out by Macrogen (Korea). Five COI sequences were obtained from the barcode of life database (http://www.barcodinglife.org).

2.3. Genetic datasets

DNA sequences for each gene were compiled and aligned by eye in Se-Al v.2.0a11 (Rambaut, 1996). Secondary structural information was used as a guide for alignment of 12S rRNA and 16S rRNA. All genes were concatenated into a dataset containing all genes.

The homogeneity of the signal from the mitochondrial genes was compared to the nuclear gene, rhodopsin using a series of partition homogeneity tests (1000 replicates) based on the incongruent length difference, ILD (Farris et al., 1995) as implemented in PAUP*.

2.4. Phylogenetic analysis

The nucleotide sequence data were partitioned using BEAST v1.4.8 (Drummond and Rambaut, 2007) to allow different evolutionary models to be assigned to the mitochondrial sequence data and the nuclear gene rhodopsin.

The dataset was analysed using Bayesian relaxed phylogenetic methodologies implemented within BEAST v1.4.8. An uncorrelated log-normal model of rate variation among branches in the tree was assumed and a Yule prior on branching rates was employed. Substitution models for each partition for the nucleotide sequence data were chosen on the basis of the Akaike information criterion (AIC; Akaike, 1974) implemented in ModelTest 3.7 (Posada and Crandall, 1998).

A prior normal distribution with a mean of 125 Ma and a standard deviation of 40 Ma was selected for the root height of the tree (i.e. the divergence time between *O. vulgaris* and all remaining taxa included in the analysis). In addition a uniform prior with a lower value of 40 Ma and an upper value of 210 Ma was placed on the same node. These values were obtained from the estimated divergence time of *Octopus* and *Benthoctopus normani* in Strugnell et al. (2008). Strugnell et al. (2008) also utilised relaxed phylogenetic methodologies (Drummond et al., 2006) incorporating constraints based on four fossil octopodiform taxa and a biogeographical constraint to estimate divergence times within Octopodiformes.

These values were used within this study to obtain a computationally economical approximation of mean divergence times within *Benthoctopus* on a time scale comparable to that in Strugnell et al. (2008). Mean divergence time estimates are given as are 95% highest posterior density intervals (HDP). The 95% highest posterior density interval is the shortest interval in parameter space that contains 95% of the posterior probability.

Two independent Monte Carlo Markov Chain (MCMC) analyses were run. Acceptable mixing was determined using Tracer v1.4.1 which was also used to determine an appropriate ‘burnin’ to be discarded. Independent tree files for each analysis were combined using LogCombiner v1.4.8 (Rambaut and Drummond, 2006a) and summarised using TreeAnnotator v1.4.8 (Rambaut and Drummond, 2006b).

The phylogenetic tree was rooted using *O. vulgaris* (Fig. 1) as previous studies have shown *Octopus* to be a suitable outgroup to *Benthoctopus* (Strugnell et al., 2004, 2005, 2008; Allcock et al., 2006).

2.5. Analysis of catch records

The relationship between catch depth and latitude was investigated using all available catch records for *Benthoctopus* and *Vulcanoctopus* specimens. For each trawl in which at least one specimen was caught, the mean depth and latitude was recorded. Trawls had an average depth range of 28 m and since it is impossible to know the depth at which individual specimens were caught, the mean depth is the best estimate of species depth. Wherever specimens from different species were recorded in the same trawl we considered these as separate catches. A quantile regression (Koenker and Bassett, 1978) was performed on the shallowest 10% of catches against latitude, pooling data from both hemispheres. This statistical method was used because it focuses on the biologically relevant portion of the catch data (the shallowest records), and because it makes no assumptions about the shape, or homoscedasticity of depth records (Cade and Noon, 2003). Quantile regressions were performed using the package *quantreg* (Koenker, 2008) in the R statistical environment (R Development Core Team, 2008).

3. Results

Nucleotide sequences generated in this study were deposited in GenBank (accession numbers HM572142-HM572229.)

Alignment of COI, COIII and cyt b required no insertion/deletion events (indels). Indels were required to align 12S rRNA, 16S rRNA and the 3′ end of rhodopsin. Highly variable loop regions of 16S rRNA (minimum 29 bp, maximum 52 bp) that

Table 2
Cephalopod tissue samples used for molecular analyses in this study.

Species	Station	Date	Depth (m)	Latitude and longitude	Museum catalogue
Octopus vulgaris	Banyuls, France	1994			Not extant
Bathypolypus sponsalis	RV *Discovery* Stn 14170#1	1 September 2001	775–842	51°36′24″N 11°53′18"W	NMSZ 2002126.002
Bathypolypus sp.	North East Atlantic Ocean				
Enteroctopus dofleini	Living Elements Research, North Vancouver, Canada				
Enteroctopus megalocyathus	RV *Falkland Protector*, stn 368, Falkland Islands	12 July 1992	121	52°21′S 60°43′48″W	SBMNH 00000
Enteroctopus megalocyathus	*Golden Chicha*, ZDLC1, stn 260, Falkland Islands,	24 April 2003	142	52°34S 58°35W	Not extant
Octopus s.l. *californicus*	Santa Barbara, CA				SBMNH 00000
Benthoctopus normani	RV *Discovery* Stn 14163#1	29 August 2001	1340–1397	49°27′N 12°41′W	NMSZ 2002126.001
Benthoctopus normani	Porcupine Seabight, North Atlantic MC				Not extant
Benthoctopus salebrosus	FV *NW Explorer*	6 August 2004	495	54°29′24″N, 166°19′12″W	NMNH 1125287
Benthoctopus yaquinae	*Alvin* Dive 4045	02 September 2004	2213	47°56′52″N 129°05′51″W	FMNH 308673
Benthoctopus cf. *profundorum*	*Alvin* Dive 3934	15 November 2003	2492	11°24′54″N 103°47′12″W	FMNH 307179
Benthoctopus sp. B (embryo)	*Tiburon* Dive 884, Gorda Ridge, GR14	23 August 2005	2751.7	42°45′18″N 126°42′35″W	FMNH 309724
Benthoctopus sp. A	*Alvin* Dive 4046	03 September 2004	2658	47°47′11″N 127°41′53″W	FMNH 308674
Benthoctopus sp A	Sta. 3, off the coast of Oregon, USA	17 April 1997	2850	44°45′57″N 125°31′44"W–44°36′54″N 125°37′24"W	FMNH 278117
Benthoctopus eureka	RV *Falklands Protector*, Stn 366, Falkland Islands	07 October 1992	230	51°57′S 61°58′W	SBMNH 423134
Benthoctopus eureka	*Manuel Angel Nores*, EBZJ St. 18, Falkland Islands	13 March 2006	766–771	53°01′S 57°48′30″W–53°10′24″S, 58°22′36"W	Not extant
Benthoctopus eureka	G-06 ZDLR1, stn 143, Falkland Islands	3 April 2003	136	51°10′S, 56°59′W	BMNH 20090263
Benthoctopus longibrachus	Off Valparaíso coast, Chile	September 2008	515	33°29′S71°52′W	Laboratorio de Ecología Molecular, Instituto de Ecología y Biodiversidad, Dpto, Universidad de Chile
Benthoctopus sp. C	ZDLV stn 361, Falkland Islands	30 September 2002	174	52°30′36″S, 58°21′54″W	NMSZ 2010053.01
Benthoctopus sp. C	G-57.2 6NKQ stn 26, Falkland Islands	23 May 2003	258	49°22′S, 60°7′W	BMNH 20090272 Holotype of new subspecies of *B. longibrachus*
Benthoctopus sp. C	FI-93, EAOD, stn 76, Falkland Islands	11 April 1994	212	49°47′S 60°05′W	Not extant
Benthoctopus cf. *rigbyae* AL	CEAMARC, East Antarctica, Voyage 3, stn 3452, CT938	16 January 2008	1138–1231	65°26′41″S 139°19′07″E	Museum Victoria
Benthoctopus sp. D WS	*Polarstern,* ANTXIII/3, GSN 39/014, Weddell Sea	14 February 1996	850–889	73°36′S 22°36′W	Not extant
Benthoctopus rigbyae	61/048-1	16 March 2002	343.2	61°10′S 54°34′W	NMSZ 2002037.032
Benthoctopus cf. *rigbyae* AS	RRS *James Clark Ross*, JR179-971, BIO6_AGT-1B, Amundsen Sea	13 March 2008	1485–1491	71°09′S 110°00′35″W	NMSZ 2008090.16
Benthoctopus oregonensis	Sta. 15, off the coast of Oregon, USA	21 April 1997	2750	44°45′47′N 125°31′14′W–44°37′06′N 125°36′00″W	FMNH 278314
Benthoctopus sp. E	RV *Southern Surveyor*, stn SS01/00/260 CT043, CSIRO, off Victoria, Australia	29 April 2000	1923–1962	39°48′27″S 149°06′02″E–39°47′06″S 149°05′19″E	Museum Victoria
Benthoctopus johnsonianus	RV *Discovery*, Cruise D260, stn 14309	16 March 2002	2011–2218	49°44.2′N 13°10.4′W	NMSZ 2002159.2
Benthoctopus johnsonianus	G.O. *Sars*, MAR-ECO cruise, SS68 LS384	25 July2004	2349.8	53°08′19.21"N 34°45′57.60"W	Bergen Museum
Benthoctopus levis	Western Plateau, Haul ID 166	30 April 2003	404	52°18′S 72°36′E	NMSZ 2010053.02
Benthoctopus thielei	*Austral*, POKER 2006 cruise Stn 53	13 September 2006	475–507	46°58′57"S 70°26′40" E–46°58′20"S 70°28′49"E	Centre d'Etudes Biologiques de Chizé
Vulcanoctopus hydrothermalis	East Pacific Rise, *Alvin* Dive 3926,	07 November 2003	2541	08°38′15"N 104°12′54"W	FMNH 307184
Vulcanoctopus hydrothermalis	East Pacific Rise, Dive 3938, Genesis	19 November 2003	2619	12°48′39"N 103°56′26"W	FMNH 307185

could not be unambiguously aligned were excluded from the analysis. Sequence alignments are available from the first author on request.

The AIC (implemented within ModelTest) favoured the GTR+G+I model for the mitochondrial sequence data and the HKY+G+I model for the rhodopsin sequence data. However, the addition of a proportion of invariable sites has been shown to create a strong correlation between the proportion of invariable sites and the alpha parameter of the gamma distribution (Yang, 1993; Sullivan et al., 1999; Mayrose et al., 2005), making it impossible to estimate both parameters reliably. Therefore we repeated our analyses without +I. The topology and divergence time estimates were constant between analyses. Posterior probabilities differed marginally for only a few nodes between analyses. Six rate categories were selected for gamma distributed rate heterogeneity in all analyses.

Partition homogeneity tests of the mitochondrial sequence data and rhodopsin revealed no significant inconsistencies in phylogenetic signal ($p=0.026$) at the significance levels suggested by Cunningham (1997). Cunningham (1997) suggested that combining data above a probability value of 0.01 improved

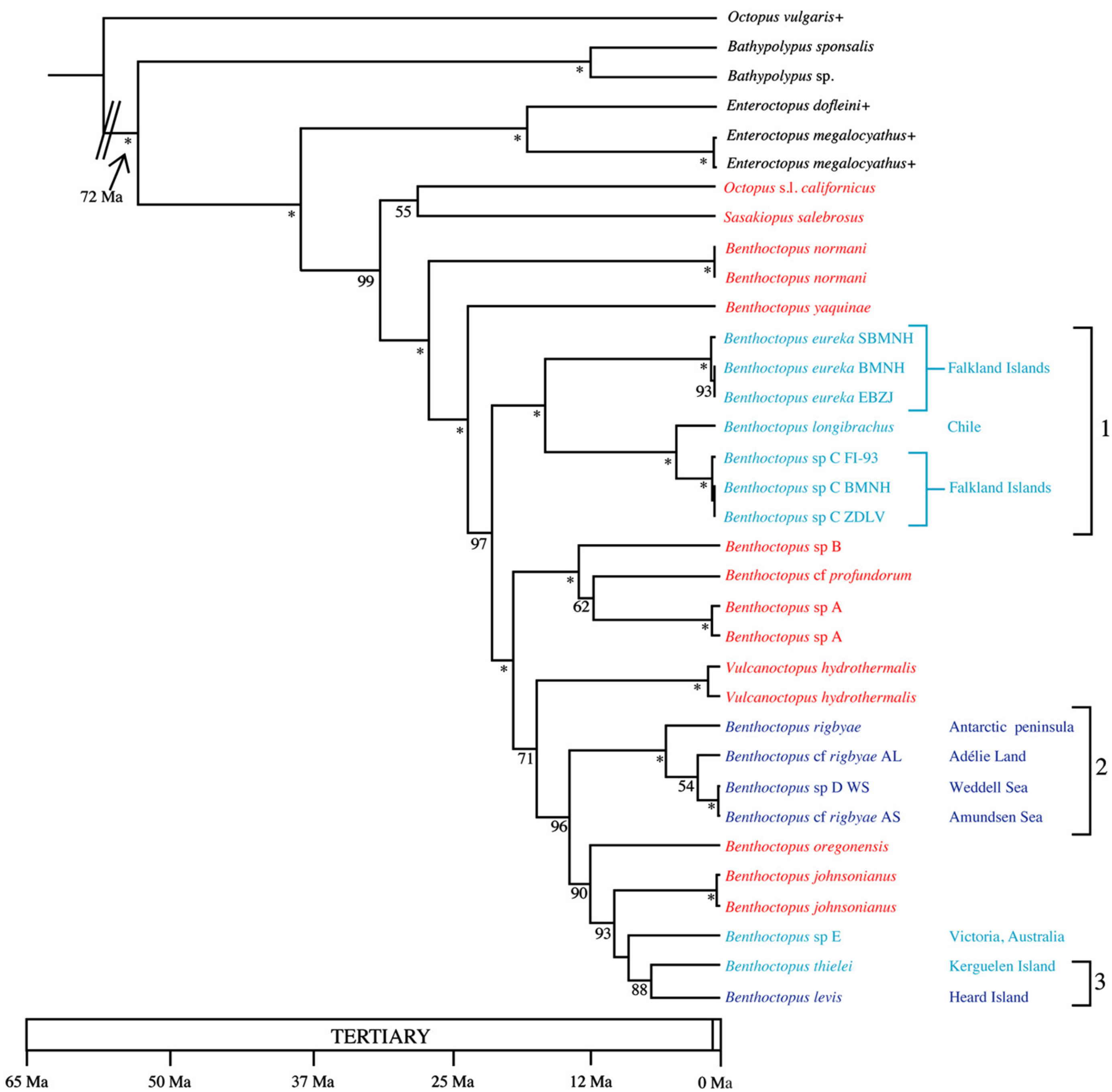

Fig. 2. Bayesian phylogenetic tree based on the results of the relaxed phylogenetic analysis using six genes: rhodopsin, 12S rDNA, 16S rDNA, cytochrome oxidase subunit I (COI), cytochrome oxidase subunit III (COIII) and cytochrome b (cytb) of 25 *Benthoctopus* individuals, 2 *Vulcanoctopus* individuals and 7 outgroup taxa. The topology is that from the posterior sample which has the maximum product of posterior clade probabilities. Each node in the tree is labeled with its posterior probability, '*' indicates posterior probability of 1.0. The divergence times correspond to the mean posterior estimate of their age in millions of years. The *Benthoctopus* species collected from the Southern Ocean (south of the polar front) are shown in dark blue and represent a paraphyletic group. Other *Benthoctopus* species collected from the Southern Hemisphere are shown in light blue. *Benthoctopus* and *Vulcanoctopus* species collected from the Northern Hemisphere are shown in red. Outgroup taxa are shown in black. '+' indicates species that possess an ink sac. Clade 1 was estimated to had a common ancestor around 16 million years ago (Ma; 95% HPD interval 4–32 Ma), Clade 2 was estimated to have had a common ancestor around 5 Ma (95% HPD interval 1–11 Ma) and Clade 3 was estimated to had a common ancestor around 6 Ma (95% HPD interval 1–13 Ma). Clade 2 was estimated to have diverged from its sister clade around 14 Ma (95% HPD interval 4–27 Ma) (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

phylogenetic accuracy (and suggested that the accuracy of the combined data decreased relative to the partitions when $p < 0.001$).

A clade containing *Bathypolypus sponsalis and Bathypolypus* sp. is the sister taxon to a well-supported clade (posterior probability [PP]=1.00) containing *Enteroctopus* spp., *Sasakiopus salebrosus*, *Octopus* s.l. *californicus*, and all *Benthoctopus* and *Vulcanoctopus* species (Fig. 2).

A very weakly supported clade containing *Octopus* s.l. *californicus* and *S. salebrosus* is the sister taxon to a well-supported clade (PP=1.00) containing the *Benthoctopus* species and *Vulcanoctopus.*

B. normani is the sister taxon to the remaining *Benthoctopus* and *Vulcanoctopus* species which group in a highly supported clade (PP=1.00). Excluding *B. normani*, *Benthoctopus yaquinae* is the sister taxon to the remaining *Benthoctopus* and *Vulcanoctopus* species. This clade is also well supported (PP=0.97).

B. eureka, *B. longibrachus* and *Benthoctopus* sp. C (an undescribed species from the Falkland Islands) group in a highly supported clade (PP=1.00) (Clade 1). It is estimated that this clade had a common ancestor 16 Ma (95% HPD 4–32 Ma).

B. levis and *B. thielei* are sister taxa (PP=0.88) and are estimated to have diverged 6 Ma (95% HPD interval 1–13 Ma). These species form a well-supported monophyletic group with *Benthoctopus* sp. E. (an undescribed species from off the south of Australia), *Benthoctopus johnsonianus* and *Benthoctopus oregonensis* (PP=0.90) (Clade 3).

This clade is the sister taxon to a well-supported clade containing four morphologically similar, but molecularly distinct species, termed here *B. rigbyae*, *Benthoctopus* cf. *rigbyae* AL (Adélie Land), *Benthoctopus* sp. D WS (Weddell Sea) and *Benthoctopus* cf. *rigbyae* AS (Amundsen Sea) (PP=1.00) (Clade 2). It is estimated that these four species had a common ancestor 5 Ma (95% highest posterior density [HPD] 1–11 Ma) which is estimated to have diverged from its sister clade (detailed above) around 14 Ma (95% HPD interval 4–27 Ma).

The shallowest depths at which *Benthoctopus* species have been caught, show a clear trend towards shallower values at higher latitudes (Fig. 3). In particular, there is a striking absence of shallow (< 300 m) catches in tropical and subtropical regions, whereas catches in shallow water (< 100 m) are relatively common at latitudes higher than about 50°. A regression of the shallowest 10% of depth records against latitude had a slope of -6.6 metres/degree ($p < 0.00001$). Both hemispheres show qualitatively similar catch depth to latitude profiles, but it was necessary to pool data from both in order to obtain sufficient records for a regression to the 10% quantile.

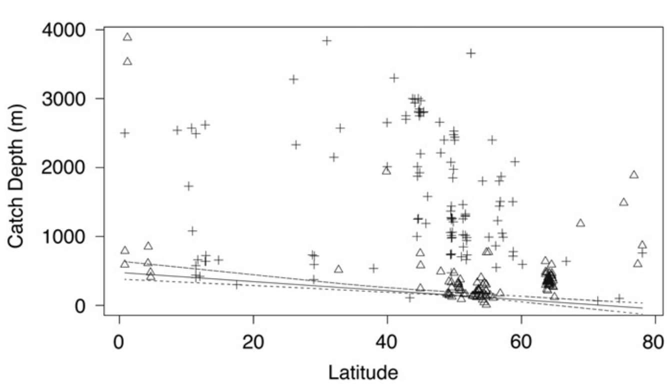

Fig. 3. Variation of catch depth with latitude. Depth values are averages for trawls in which at least one *Benthoctopus* or *Vulcanoctopus* specimen was present. Catch depths from the Northern and Southern Hemispheres are represented by crosses and triangles, respectively. The solid line is a regression to the 0.1 (shallowest) quantile of depths obtained using the *quantreg* package in R. Dashed lines are 95% confidence intervals for predictions based on this regression.

4. Discussion

The present molecular phylogenetic study indicates that *Benthoctopus* species with a high-latitude distribution in the Southern Hemisphere represent a paraphyletic group. They are representative of polar emergence, tending to occur at shallower depths at high latitudes than do their congeners elsewhere in the world's oceans. The results suggest that the *Benthoctopus*/*Vulcanoctopus* clade had its evolutionary origin in relatively shallow Northern Hemisphere waters.

The *Benthoctopus* species included in this study form a well-supported clade which also contains the deep-sea hydrothermal vent species *V. hydrothermalis.* Placement of *Vulcanoctopus* within the *Benthoctopus* clade was presented and discussed by Strugnell et al. (2009). Potential polyphyly of *Benthoctopus* as discussed by Norman and Hochberg (2005) is not supported for the member species examined in this study.

The sister taxon to the *Benthoctopus*/*Vulcanoctopus* clade is a clade containing *S. salebrosus* and *Octopus* s.l. *californicus*, both restricted to the waters of the Northern Pacific Ocean. *S. salebrosus* is known from the Bering Sea, Sea of Okhotsk and the Sea of Japan at depths of 212–1160 m. *Octopus* s.l. *californicus* is distributed in the north-east Pacific Ocean from Baja California to the Gulf of Alaska at depths of 100–900 m (Hochberg, 1998). Both species possess functional, if small, ink sacs. A clade containing *Enteroctopus dofleini* and *Enteroctopus megalocyathus* is the sister taxon to the clade containing *Benthoctopus*/*Vulcanoctopus*/*Sasakiopus*/*Octopus* s.l. *californicus.* Both *Enteroctopus* species also possess an ink sac and are known from depths of 0–1500 and 5–300 m, respectively (Hochberg, 1998; Allcock personal communication).

Voss (1988) proposed that the possession of an ink sac was the ancestral state for extant cephalopods and that loss of an ink sac in deep-sea octopods represented an adaptation for lightless habitats. Ink release in the dark is of limited value as a visual decoy or screen from potential predators (although chemical defence components of ink such as tyrosinase may also play a role, Prota et al., 1981). Most deep-water benthic octopods lack an ink sac (e.g. *Graneledone*, *Thaumeledone*, *Praealtus*, *Bathypolypus*). Our analyses support that the common ancestor of *S. salebrosus*, *O.* s.l. *californicus*, *Benthoctopus* and *Vulcanoctopus* possessed an ink sac and is likely to have inhabited relatively shallow waters where possession of an ink sac would be of benefit. The loss of the ink sac in the *Benthoctopus/Vulcanoctopus* lineage is proposed here to be a product of their evolutionary shift to a deep-sea habit. The loss of the ink sac has occurred independently in a number of deep-sea octopod lineages (Voss, 1988).

In addition to the Northern Hemisphere distribution of *S. salebrosus* and *O.* s.l. *californicus*, *B. normani*, the sister taxon to the remaining *Benthoctopus*/*Vulcanoctopus* clade, is also distributed in the Northern Hemisphere, specifically North Atlantic waters. Similarly, *B. yaquinae*, the sister taxon to the *Benthoctopus/Vulcanoctopus* clade (excluding *B. normani*) is also known from Northern hemisphere waters, off the Oregon coast. The Northern Hemisphere distribution of these 'basal' *Benthoctopus* species further supports a Northern Hemisphere origin for the clade. *B. normani* and *B. yaquinae* are known from relatively deep water, 537–1865 m (Allcock et al., 2006) and ~1000–3000 m (Strugnell et al., 2009), respectively.

The *Benthoctopus* species with a high latitude distribution in the Southern Hemisphere fall into three distinct clades with non-overlapping distributions and appear to represent independent invasions of this region.

Clade 1 is a well-supported monophyletic group containing *B. longibrachus*, known from the coast of central Chile, a subspecies of *B. longibrachus* and *B. eureka*, both from the Falkland Islands shelf. These species are not known from sub-antarctic or Antarctic waters.

Clade 2 contains four very closely related *Benthoctopus* taxa, possibly comprising a single species captured from a diverse range of locations off the Antarctic coast. These include the Amundsen Sea, the Weddell Sea, the Antarctic Peninsula and off the coast of Adélie Land representing a probable circum-Antarctic distribution for this clade.

Clade 3 contains *B. levis* and *B. thielei* known to be distributed around the Antarctic Heard Island and sub-antarctic Kerguelen Island, respectively. Both Heard and Kerguelen Islands are located on the Kerguelen Plateau. This clade forms a monophyletic group along with an undescribed *Benthoctopus* species collected off the coast of Victoria, Australia. Together these three species form the sister taxon to *B. johnsonianus* distributed in the North East Atlantic, a notable distance from this clade of Southern Hemisphere species.

Clades 2 and 3 may have arisen via 'polar emergence' from the deep sea. Submerging Antarctic bottom water and emerging circumpolar deep water along the Antarctic continental margin provide unique connections between the deep sea and coastal Antarctic waters (Menzies et al., 1979). These connections, in conjunction with the 500–900 m deep Antarctic continental shelf (with an average shelf depth up to four times more than other continents) (Johnson et al., 1982) have been suggested to have allowed deep-sea fauna to emerge across the Antarctic continental shelf (polar emergence) and Antarctic shelf fauna to submerge into the deep sea (polar submergence) (Zinsmeister and Feldmann, 1984; Clarke and Crame, 1989).

The mean estimated divergence time of Clades 2 and 3 was 14 Ma (95% HPD interval 4–27 Ma). In this timeframe there was an increased production and northward spreading of Antarctic Bottom Water (Wright and Miller, 1993; Maldonado et al., 2003), facilitating direct connections between the deep sea and coastal Antarctic waters. Given that the most recent common ancestor of the Southern Ocean clade was estimated to have occurred at a mean of 5 Ma (95% HPD interval 1–11 Ma) it is likely that this clade 'emerged' after establishment of these deep-sea connections.

It must be noted that although the Kerguelen Plateau may not have been subject to submerging and emerging water masses to the same extent as was the Antarctic continent, its surface waters (at 15 m) have a mean annual temperature of around 4 °C, comparable to those of the deep sea (Barnes et al., 2006; Herring, 2002). This suggests that an isothermic water column in itself may allow these *Benthoctopus* species to have colonised relatively shallow waters.

The quantile regression is in support of this, indicating a trend towards shallower catch values of *Benthoctopus* at higher latitudes. This is likely to reflect a preference or constraint of this genus to cooler water temperatures.

It is of interest that this pattern is also evident in the Northern Hemisphere. *Benthoctopus sibiricus* (which unfortunately could not be included in this study) is also known from shallow waters, 38–220 m (Table 1), and may also be indicative of Arctic polar emergence. Nesis (2001) suggested that the ancestor of *B. sibiricus* migrated from the North Pacific to the eastern Arctic through the Bering Strait in the mid-Pliocene.

This polar emergence of high latitude Southern Ocean *Benthoctopus*, a predominantly deep-sea genus, contrasts with the polar submergence of a distantly related clade of octopods with a single series of suckers reported recently (Strugnell et al., 2008). The latter study reported the radiation of a clade of Southern Ocean octopodids into the deep sea, reaching the Northern Hemisphere and suggested that the thermohaline circulation acted as an evolutionary driver with the Southern Ocean as its centre of origin. The present study indicates the radiation of an octopus clade in the opposite direction, from the deep sea in the Northern Hemisphere via the deep sea into Southern Ocean waters. The estimated divergence times suggest that the polar emergence of the *Benthoctopus* species occurred within a similar timeframe as the polar submergence of the octopus clade with a single series of suckers, suggesting that the 'thermohaline expressway' is bi-directional.

The fact that both of these octopus clades have representatives in the Southern Ocean and also in the far North of the world's oceans also has clear implications in understanding the presence and processes leading to apparent bipolar 'species' distributions. A total of 235 animal 'species' was suggested to be present in both poles in a recent Census of Antarctic Marine Life press release (Kinver, 2008). A number of recent studies of the morphological taxonomy and molecular phylogenetics of polar and deep-water octopus clades (Allcock and Piertney, 2002; Allcock et al., 2003, 2006; Allcock, 2005; Vecchione et al., 2009; Strugnell et al., 2008, 2009; Jorgensen et al., 2010) have led to the description and redescription of a number of species, many of which had not been recognised as distinct. Additional collections followed by detailed morphological and molecular studies of other benthic 'bipolar' species will likely uncover closely related, but distinct, species at each pole.

Acknowledgments

We thank the Alfred Wegner Institute and the British Antarctic Survey for provision of sea time. We are grateful to all colleagues who facilitated sea-time or assisted on board, and to David Carlini, Annie Lindgren, Kirrily Moore and Marc Eleaume who supplied tissue samples. We thank the CEAMARC sampling effort onboard the *Aurora Australis* and the voyage leader Martin Riddle (Australian Antarctic Division). We thank the Barcode of Life Database team (BOLD), particularly Dirk Steinke for providing COI sequences. JS is supported by a Lloyd's Tercentenary Fellowship. Part of this work was supported by a grant to IGG from the Falkland Islands Government Fisheries Department. Thanks to the Systematic Association, the Edith Mary Pratt Musgrave fund and Antarctic Science Bursaries. We thank the National Science Foundation Grants DEB 0072695 and 0103690 to JRV. This work was a contribution to Evolution and Biodiversity in the Antarctic: the Response of life to Change (EBA) and the International Polar Year. This is CAML publication #30 and ANDEEP publication #144.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19 (6), 716–723.

Allcock, A.L., Piertney, S.B., 2002. Evolutionary relationships of Southern Ocean Octopodidae (Cephalopoda: Octopoda) and a new diagnosis of *Pareledone*. Marine Biology 140, 129–135.

Allcock, A.L., Hochberg, F.G., Rodhouse, P.G.K., Thorpe, J.P., 2003. *Adelieledone*, a new genus of octopodid from the Southern Ocean. Antarctic Science 15, 415–424.

Allcock, A.L., 2005. On the confusion surrounding *Pareledone charcoti* (Joubin, 1905) (Cephalopoda: Octopodidae): endemic radiation in the Southern Ocean. Zoological Journal of the Linnean Society 143, 75–108.

Allcock, A.L., Strugnell, J.M., Ruggierio, H., Collins, M.A., 2006. Redescription of the deep-sea octopod *Benthoctopus normani* (Massy, 1907) and a description of a new species from the Northeast Atlantic. Marine Biology Research 2, 372–387.

Allcock, A.L., Strugnell, J.M., Johnson, M.P., 2008. How useful are the recommended counts and indices in the systematics of the Octopodidae (Mollusca: Cephalopoda)? Biological Journal of the Linnean Society 95, 205–218.

Barnes, D.K.A., Fuentes, V., Clarke, A., Schloss, I.R., Wallace, M.I., 2006. Spatial and temporal variation in shallow seawater temperatures around Antarctica. Deep-Sea Research II 53, 853–865.

Briggs, J.C., 2003. Marine centres of origin as evolutionary engines. Journal of Biogeography 30, 1–18.

Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and Environment 1, 412–420.
Carlini, D.B., Young, R.E., Vecchione, M., 2001. A molecular phylogeny of the Octopoda (Mollusca: Cephalopoda) evaluated in light of the morphological evidence. Molecular Phylogenetics and Evolution 21, 388–397.
Clarke, A., Crame, J.A., 1989. The origin of Southern Ocean marine fauna. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota. Special Publication No. 47. Geological Society, London, pp. 253–268.
Crame, J.A., 1993. Latitudinal range fluctuations in the marine realm through geological time. Trends in Ecology and Evolution 8, 162–166.
Cunningham, C.W., 1997. Can three incongruence tests predict when data should be combined? Molecular Biology and Evolution 14 (7), 733–740.
Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7, 214.
Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4, e88.
Farris, J.S., Källersjö, M., Kluge, A.G., Bult, C., 1995. Testing significance of incongruence. Cladistics 10, 315–319.
Gleadall, I.G., 2004. Some old and new genera of octopus. Interdisciplinary Information Sciences 10, 99–112.
Gleadall, I.G., Guerrero Kommritz, J., Hochberg, F.G., Laptikhovsky, V.V., 2010. The inkless octopuses (Cephalopoda: Octopodidae) of the Southwest Atlantic. Zoological Science 27, 528–553.
González, A.F., Guerra, A., Pascual, S., Briand, P., 1998. *Vulcanoctopus hydrothermalis* gen. et sp. nov. (Mollusca, Cephalopoda): an octopod from a deep-sea hydrothermal vent site. Cahiers de Biologie Marine 39, 169–184.
Guzik, M.T., Norman, M.D., Crozier, R.H., 2005. Molecular phylogeny of the benthic shallow-water octopuses (Cephalopoda: Octopodinae). Molecular Phylogenetics and Evolution 37, 235–248.
Herring, P., 2002. The Biology of the Deep Sea. Oxford University Press, Oxford 314 pp.
Hochberg, F.G., 1998. Class Cephalopoda (pp. 175–236). In: Scott, Blake (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 8: The Mollusca Part 1, The Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. Santa Barbara Museum of Natural History, Santa Barbara, 250 pp.
Ibáñez, C.M., Sepúlveda, R.D., Chong, J., 2006. A new species of *Benthoctopus* Grimpe 1921 (Cephalopoda: Octopodidae) from the southeastern Pacific Ocean. Proceedings of the Biological Society of Washington 119, 355–364.
Johnson, G.L., Vanney, J.R., Hayes, D., 1982. The Antarctic continental shelf. In: Craddock, C. (Ed.), Antarctic Geoscience. University of Wisconsin Press, Madison, pp. 995–1002.
Jorgensen, E.M., Strugnell, J.M., Allcock, A.L., 2010. Description and phylogenetic relationships of a new genus of octopus, *Sasakiopus* (Cephalopoda: Octopodidae) from the Bering Sea, with a redescription of *Sasakiopus salebrosus* (Sasaki, 1920) Nov. Comb. Journal of Molluscan Studies 76, 57–66.
Kinver, M., 2008. Octopus share 'living ancestor'. BBC news. Sunday 9 November 2008. Available from: 〈http://news.bbc.co.uk/1/hi/sci/tech/7715741.stm〉.
Koenker, R., Bassett, G., 1978. Regression quantiles. Econometrica. 46, 33–50.
Koenker, R., 2008. Quantreg: Quantile Regression. R package version 4.26. Available from: 〈http://www.r-project.org〉.
Maldonado, A., Barnolas, A., Bohoyo, F., Galindo-Zaldívar, J., Hernández-Molina, J., Lobo, F., Rodriguez-Fernandez, J., Somoza, L., Tomas Vazquez, J., 2003. Contourite deposits in the central Scotia Sea: the importance of the Antarctic Circumpolar Current and the Weddell Gyre flows. Palaeogeography Palaeoclimatology Palaeoecology 198, 187–221.
Mayrose, I., Friedman, N., Pupko, T., 2005. A Gamma mixture model better accounts for among site rate heterogeneity. Bioinformatics 21, 151–158.
Menzies, R.J., George, R.Y., Rowe, G.T., 1979. Abyssal Environment and Ecology of the World Oceans. Wiley, New York 488 pp.
Muus, B.J., 2002. The *Bathypolypus–Benthoctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). Malacologia 44, 175–222.
Nesis, K.N., 1987. Cephalopods of the World. TFH Publications, Neptune City, NJ.
Nesis, K.N., 2001. West-Arctic and East-Arctic distributional ranges of cephalopods. Sarsia 86, 1–11.
Norman, M.D., Hochberg, F.G., 2005. The current state of octopus taxonomy. In: Proceedings of the International Workshop and Symposium of Cephalopod International Advisory Council, Phuket, 2003. Phuket Marine Biological Center Special Publication, vol. 66, pp. 127–154.
O'Shea, S., 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). NIWA Biodiversity Memoirs 112, 1–280.
Posada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14 (9), 817–818.
Prota, G., Ortonne, J.P., Voulot, C., Khatchadourian, C., Nardi, G., Palumbo, A., 1981. Occurrence and properties of tyrosinase in the ejected ink of cephalopods. Comparative Biochemistry and Physiology B—Biochemistry and Molecular Biology 68, 415–419.
R Development Core Team, 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. Available from: 〈http://www.R-project.org〉.
Rambaut, A., 1996. Se-Al Version 2.0a11 [Computer Program]. Available from: 〈http://tree.bio.ed.ac.uk/software/seal/〉.
Rambaut, A., Drummond, A.J., 2006a. LogCombiner v1.4.1 [Computer Program]. Available from: 〈http://beast.bio.ed.ac.uk/Programs〉.
Rambaut, A., Drummond, A.J., 2006b. TreeAnnaotator v1.4.1 [Computer Program]. Available from: 〈http://beast.bio.ed.ac.uk/Programs〉.
Robson, G.C., 1932. A Monograph of the Recent Cephalopoda Based on the Collections in the British Museum (Natural History), Part II: The Octopoda (excluding the Octopodinae). British Museum (Natural History), London 359 pp., 6 plates.
Sambrook, J., Fritsch, E.F., Maniatis, T., 1989. Molecular Cloning: A Laboratory Manual second ed. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY.
Strugnell, J., Norman, M., Drummond, A.J., Cooper, A., 2004. Neotenous origins for pelagic octopuses. Current Biology 14, R300–R310.
Strugnell, J., Norman, M., Jackson, J., Drummond, A.J., Cooper, A., 2005. Molecular phylogeny of coleoid cephalopods (Mollusca: Cephalopoda) using a multigene approach; the effect of data partitioning on resolving phylogenies in a Bayesian framework. Molecular Phylogenetics and Evolution 37, 426–441.
Strugnell, J., Rogers, A.D., Prodöhl, P.A., Collins, M.A., Allcock, A.L., 2008. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. Cladistics 24, 1–8.
Strugnell, J.M., Voight, J.R., Collins, P.C., Allcock, A.L., 2009. Molecular phylogenetic analysis of a known and a new hydrothermal vent octopod: their relationships with the genus *Benthoctopus* (Cephalopoda: Octopodidae). Zootaxa 2096, 442–459.
Sullivan, J., Swofford, D.L., Naylor, G.J.P., 1999. The effect of taxon sampling on estimating rate heterogeneity parameters of maximum-likelihood models. Molecular Biology and Evolution 16, 1347–1356.
Toll, R.B., 1981. *Benthoctopus oregonae*, a new species of octopod (Mollusca; Cephalopoda) from the southern Caribbean with a redescription of *Benthoctopus januarii* (Hoyle, 1885). Bulletin of Marine Science 31, 83–95.
Vecchione, M., Allcock, L., Piatkowski, U., Strugnell, J., 2009. *Benthoctopus rigbyae*, n. sp., a new species of cephalopod (Octopoda; Incirrata) from near the Antarctic Peninsula. Malacologia 51, 13–28.
Voss, G.L., 1988. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In: Clarke, M.R., Trueman, E.R. (Eds.), The Mollusca, Paleontology and Neontology of Cephalopods, vol. 12. Academic Press, San Diego, pp. 253–276.
Voss, G.L., Pearcy, W.G., 1990. Deep-water octopods of the Northeastern Pacific. Proceedings of the California Academy of Sciences 37, 47–94.
Wright, J.D., Miller, K.G., 1993. The Antarctic Paleoenvironment: a perspective on global change. Antarctic Research Series 60, 1–25.
Yang, Z., 1993. Maximum-likelihood estimation of phylogeny from DNA sequences when substitution rates differ over sites. Molecular Biology and Evolution 10, 1396–1401.
Zinsmeister, W.J., Feldmann, R.M., 1984. Cenozoic high latitude heterochroneity of southern hemisphere marine faunas. Science 224, 281–283.