Systematics and Phylogenetic Relationships of New Zealand Benthic Octopuses (Cephalopoda: Octopodoidea)

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The systematics of the New Zealand octopods have only been reviewed twice in the last 100 years. In these revisions many species have been provisionally classified in the genus *Octopus*. Recent genetic studies have synonymized some New Zealand species with octopuses from other regions. The present study investigates the systematics and phylogeny of octopuses from New Zealand using eighty eight specimens, three mitochondrial genes (16S rRNA, cytochrome c oxidase subunit I, and cytochrome c oxidase subunit III) and one nuclear gene (Rhodopsin). Forty-four new octopod DNA sequences (belonging to 13 species) were included, adding to the 83 existing sequences from GenBank. All sequences were used to generate phylogenetic trees based on Maximum Likelihood (ML) and Bayesian inference (BI), with a data set composed by 97 species, including octopod sister groups and *Vampyroteuthis infernalis* as an outgroup. Gene tree and species delimitation analyses revealed a distinct genetic difference between two sympatric *Graneledone* subspecies, which we propose as valid species. *Muusoctopus tangaroa* is a sister species of *M. thielei* from Kerguelen; while *Enteroctopus zealandicus* forms a clade with *E. megalocyathus* from South America and *E. dofleini* from the North Pacific. Similarly, *Octopus campbelli*, *O. huttoni,* and *O. mernoo* form a monophyletic group with *Robsonella fontaniana* from South America, *Scaeurgus unicirrhus* from the Atlantic and *O. pallidus* from Australia. *Pinnoctopus cordiformis* is close to *Grimpella thaumastocheir* and several species of *Octopus* sensu lato as in previous phylogenetic studies. This study suggests that octopuses from New Zealand have different phylogenetic and biogeographic origins and represent independent radiations into this region.

Keywords: taxonomy, Cephalopoda, Octopodiformes, species delimitation, octopus

INTRODUCTION

The incirrates include benthic and pelagic octopods in two superfamilies: Argonautoidea Cantraine, 1841 (pelagic octopods), and Octopodoidea (d'Orbigny, 1840) (benthic and pelagic octopods). Benthic octopuses are a group of over 200 species inhabiting all oceans of the world, from tropical to polar regions, and from the intertidal to at least 3,000 m depth (Norman, 2000; Nesis, 2003; Hoving et al., 2014; Jereb et al., 2014). Despite this diversity, the current systematic relationships within the group are still poorly understood given their variable morphology and lack of suitable characters for morphological analysis (Strugnell et al., 2014). In recent years, several changes in octopod taxonomy have been proposed, including a new phylogenetic classification that positions incirrate octopuses in the superfamily Octopodoidea, which is composed of six families: Octopodidae, Megaleledonidae, Enteroctopodidae, Amphitretidae, Eledonidae, and Bathypolypodidae (Strugnell et al., 2014).

Considering that nearly 200 species are currently incorporated within this categorization, most of the octopod phylogenies published to date have included only few species (<30) (Carlini et al., 2001; Guzik et al., 2005; Strugnell et al., 2005; Strugnell et al., 2014), with just a few studies considering more than fifty species (see Lindgren et al., 2012; Ibáñez et al., 2014, 2018). Incorporating much more species into octopod phylogenies seems problematic, as most species are recognized only from type material that has been fixed in formaldehyde and consequently lacks color and characters seen only in living specimens, and for which DNA sequences are not available. This has hindered the analysis of phylogenetic relationships as missing taxa can significantly influence tree topology (Graybeal, 1998; Poe and Swofford, 1999; Rosenberg and Kumar, 2003); therefore, including missing and poorly studied species in new DNA sequence analyses is important to provide a more complete and updated understanding of the phylogenetic relationships among benthic octopuses.

In the specific case of octopod fauna from New Zealand, this was initially reported by Dell (1952) in a monograph describing 14 species of benthic and pelagic octopuses. O'Shea (1999) revised New Zealand octopod fauna, placing 39 octopod species in six families and 14 genera, with two new genera and 16 new species. Many new species were assigned to an unplaced genus provisionally called 'Octopus' (Norman and Hochberg, 2005; Jereb et al., 2014); however, neither Dell nor O'Shea had the benefit of obtaining genetic information for complementing their morphologic approach. The most recent review of New Zealand biodiversity includes 41 octopod taxa (Spencer et al., 2009), although recent genetic studies have synonymized two of the New Zealand species (Octopus gibbsi O'Shea, 1999; Amor et al., 2014 and O. jollyorum Reid and Wilson, 2015; Gleadall, 2016).

Biogeographically, New Zealand's marine fauna comprises both subtropical and tropical species (Shears et al., 2008). The relationships among benthic octopuses from New Zealand, Australia, and South America has been hypothesized from evidence based on morphology and distribution (O'Shea, 1999). Previous biogeographic studies based on ancestral distribution

inferred from phylogenies did not include the New Zealand octopod fauna (i.e., Strugnell et al., 2008, 2011; Ibáñez et al., 2016), suggesting that the inclusion of those species could dramatically change not only the phylogenetic hypothesis but also our knowledge of the biogeographic events that would explain the origin of the octopus in this region.

The aims of this study were to: (i) determine the evolutionary relationships within the New Zealand octopuses and their genetic relationships in the context of octopus phylogeny and (ii) clarify the current status of some species identities. Furthermore, establishing taxonomic clarity on a regional subset of species is prerequisite to larger scale revisions of the broader group. For this purpose, we constructed a molecular phylogeny of 88 species of benthic octopuses, in addition to nine outgroups to estimate their phylogenetic relationships.

MATERIALS AND METHODS

Sampling

A total of 88 octopuses were obtained and examined from stored collections (**Table 1** and **Figure 1**). Of these, 20 specimens were captured by bottom trawl during fisheries research voyages aboard the National Institute of Water and Atmospheric Research, Ltd. (NIWA) vessel *R/V Tangaroa*. A further set of 38 specimens were collected by New Zealand Ministry for Primary Industries scientific observers program from New Zealand fishing vessels. Finally, 30 octopuses were collected by NIWA staff during the annual Bluff oyster survey in South Island (**Figure 1**). Specimens were captured at depths ranging from 38 to 1208 m.

All specimens are deposited at NIWA Invertebrate Collection, Wellington, New Zealand (**Table 1**) and are available for examination. Additionally, we reviewed some type specimens from NIWA to confirm their identification and taxonomic status.

Type Material Examined

Pinnoctopus cordiformis (Quoy and Gaimard, 1832): Neotype NIWA 43044 (H-668), ML 120 mm, 41°09.14′ S, 173°15.07′ E, 23–24 m, 21/03/1997.

Octopus mernoo (O'Shea, 1999): Holotype NIWA 7555 (H-666), ML 33.5 mm, 43°51.19′ S, 178°58.81′ E, 480 m, 13/09/1989.

Graneledone taniwha (O'Shea, 1999): Holotype NIWA 662, ML 121 mm, 44°41.90′ S, 177°23.71′ W, 1135–1157 m, 17/10/1995.

Muusoctopus tangaroa (O'Shea, 1999): Holotype NIWA 7546 (H-660), ML 97 mm, 44°06.99′ S, 178°26.01′ E, 936–999 m, 11/10/1995.

Muusoctopus clyderoperi (O'Shea, 1999): Holotype NIWA 7556 (H-667), ML 80 mm, 39°58.55′ S, 178°14.80′ E, 900 m, -/04/1994.

Muusoctopus tegginmathae (O'Shea, 1999): Holotype NIWA 7545 (H-659), ML 64.5 mm, 39°57′ S, 178°16′ E, 1020–1250 m, 25/09/1995.

Most specimens were frozen at sea prior to being shipped to NIWA where they were defrosted. In the laboratory, mantle tissue samples were taken and stored in 99% ethanol until required for the molecular analysis. Foveaux Strait specimens

TABLE 1 | Octopod species included in the phylogenetic analyses and their GenBank code for each mitochondrial gene.

Species	NIWA code	Depth (m)	Latitude	Longitude	16S	COI	COIII
Argonauta nodosus	95200-A	80	−37.1	174.1	MT216948	MT216541	MT225040
Argonauta nodosus	95200-B	80	−37.1	174.1	MT216949	MT216542	MT225041
Enteroctopus zealandicus	104973	424	−43.8346666	−178.834	MT216950	MT216543	
Enteroctopus zealandicus	105194	459	−43.2553333	176.228666	MT216951	MT216544	MT225042
Enteroctopus zealandicus	106215	394	−43.3713333	178.943833	MT216952	MT216545	MT225043
Enteroctopus zealandicus	95204	350	−47.03	165.695	MT216953	MT216546	MT225044
Enteroctopus zealandicus	NZ9	−	−	−	MT216954	MT216547	MT225045
Enteroctopus zealandicus	NZP13	−	−	−	MT216955		MT225046
Graneledone challengeri	88912	1012	−34.8158333	171.6606667	MT216957		MT225048
Graneledone challengeri	95213	1090	−42.653333	−179.925	MT216956	MT216548	MT225047
Graneledone challengeri	NZP30	−	−	−	MT216958		MT225049
Graneledone taniwha kubodera	85918	779	−42.8706667	−179.739667	MT216959	MT216556	
Graneledone taniwha kubodera	105193	928	−44.6903333	173.693	MT216960	MT216549	MT225050
Graneledone taniwha kubodera	105195	652	−42.8616667	175.925	MT216961	MT216550	MT225051
Graneledone taniwha kubodera	106060	566	−44.1628333	174.6704	MT216962	MT216551	MT225052
Graneledone taniwha kubodera	106065	577	−44.1761667	174.6696			MT225053
Graneledone taniwha kubodera	106227	523	−43.118	−179.623333	MT216963		MT225054
Graneledone taniwha kubodera	NZ1	−	−	−	MT216968	MT216557	MT225059
Graneledone taniwha kubodera	NZ6	−	−	−	MT216969	MT216558	MT225060
Graneledone taniwha taniwha	95210	836	−46.665	170.595	MT216964	MT216552	MT225055
Graneledone taniwha taniwha	95211	878	−46.716667	170.588333	MT216965	MT216553	MT225056
Graneledone taniwha taniwha	95212	977	−46.793333	170.453333	MT216966	MT216554	MT225057
Graneledone taniwha taniwha	95214	820	−46.103333	171.123333	MT216967	MT216555	MT225058
Muusoctopus tangaroa	106245-B	654	−44.2691667	179.6023333	MT216979	MT216567	MT225072
Muusoctopus tangaroa	95205	562	−49.046667	166.575			MT225068
Muusoctopus tangaroa	95207	624	−49.22	166.643333	MT216981	MT216565	MT225069
Muusoctopus tangaroa	95208	562	−49.046667	166.575	MT216980	MT216566	MT225070
Muusoctopus tangaroa	95209	562	−49.046667	166.575			MT225071
Octopus campbelli	106213	394	−42.7278333	178.1041667	MT216983	MT216568	MT225073
Octopus huttoni	105445	38	−42.653333	−179.925	MT216986	MT216571	MT225076
Octopus huttoni	105446-A	38.4	−46.6019667	168.0571	MT216987	MT216572	MT225077
Octopus huttoni	105446-B	38.4	−46.6019667	168.0571	MT216988	MT216573	MT225078
Octopus huttoni	105446-C	38.4	−46.6019667	168.0571	MT216989	MT216574	MT225079
Octopus huttoni	105446-D	38.4	−46.6019667	168.0571	MT216990	MT216575	MT225080
Octopus huttoni	105448-A	42	−46.70555	167.9718167	MT216991	MT216576	MT225081
Octopus huttoni	105452-D	42	−46.6578667	168.1598833	MT216992	MT216577	MT225082
Octopus mernoo	105443-A	369	−43.4925	176.1533333	MT216994	MT216578	MT225083
Octopus mernoo	105443-B	369	−43.4925	176.1533333	MT216995	MT216579	MT225084
Octopus mernoo	106116-C	465	−43.8043333	176.5976667	MT216996	MT216580	MT225085
Octopus mernoo	106232	461	−43.273	179.0375	MT216984	MT216569	MT225074
Octopus campbelli	NZP25	−	−	−	MT216985	MT216570	MT225075
Opisthoteuthis chathamensis	NZP22	−	−	−	MT216982		
Opisthoteuthis mero	106093	442	−43.1838333	175.8743333	MT216997		
Opisthoteuthis mero	95194	492	−46.463333	166.181667	MT216998		
Pinnoctopus cordiformis	105449	32.9	−46.7388833	168.22715	MT216970		MT225061
Pinnoctopus cordiformis	105451	32.9	−46.66285	168.2126333	MT216971	MT216559	MT225062
Pinnoctopus cordiformis	95192		−43.403333	−176.338333	MT216972	MT216560	MT225063
Pinnoctopus cordiformis	95196	130	−44.041667	173.623333	MT216973	MT216561	MT225064
Pinnoctopus cordiformis	95197	130	−44.041667	173.623333	MT216974	MT216562	MT225065
Pinnoctopus cordiformis	95198	130	−44.041667	173.623333	MT216975	MT216563	MT225066
Pinnoctopus cordiformis	95216-A	98	−38.248333	174.033333	MT216976	MT216564	MT225067
Pinnoctopus cordiformis	95215	105	−38.138333	174.065	MT216978		

(Continued)

TABLE 1 | Continued

Species	NIWA code	Depth (m)	Latitude	Longitude	16S	COI	COIII
Pinnoctopus cordiformis	104974	424	−41.0166667	174.8833333	MT216977		
Thaumeledone zeiss	105435	1208	−44.716	176.6798333	MT216999		MT225086
Thaumeledone zeiss	NZP31	−	−	−	MT217000	MT216581	MT225087
Thaumeledone zeiss	NZP32	−	−	−	MT217001		MT225088
Vitreledonella richardi	106147	947	−42.7278333	178.1041667		MT216582	

Samples without coordinates were collected from the Chatham Rise, New Zealand. The NIWA code correspond to the voucher specimen catalog number.

were shipped in plastic bags on ice, inside an insulated box to NIWA, Wellington, and processed immediately. Small whole animals were preserved in 99% ethanol. Tissue subsamples were taken from larger animals before they were fixed in a buffered 5% formaldehyde solution, then transferred to 80% ethanol, for anatomical and morphological analyses.

DNA Extraction, PCR Amplification, and Sequencing

Total DNA was extracted from 66 specimens of the total 88 examined using a high-salt extraction protocol (Aljanabi and Martinez, 1997), the phenol/chloroform method (Sambrook et al., 1989), or DNeasy® purification kits (mouse tail protocol, Qiagen GmbH, Germany). Polymerase Chain Reaction (PCR) amplifications were carried out in 25 μL volumes with 5 units of Platinum^{TM} *Taq* DNA polymerase (Invitrogen) with 20 mM Tris HCl (pH 8.4), 50 mM KCl, 2.5 mM dNTPs, 3 mM MgCl$_2$ and 0.5 μM each of primers of the mtDNA genes Cytochrome Oxidase I (COI), Cytochrome Oxidase III (COIII) and 16S rRNA (Simon et al., 1991). Primers for COI were modified from Folmer et al. (1994) to match octopus DNA sequences in GenBank (Forward: TYTCAACAAATCATAAAGAYATTG G, Reverse: TATACTTCTGGRTGACCAAARAATCA). Primers for COIII were also modified from the literature (Forward: CAATGATGACGWGAYATTATTCG; Guzik et al., 2005 and Reverse: TCTACAAAATGTCAYTATCA; Simon et al., 1994). After an initial denaturation (2 min at 94°C), the reaction mixtures were subjected to 30–40 cycles of 94°C (30 s), [40–50°C (30 s) for COI; 45–65°C (30 s) for 16S; 40–45°C (30 s) for COIII], and 72°C (60 s) followed by a final extension at 72°C (10 min) using a thermal cycler. PCR products were purified using ExoSAP-IT and the DNA sequences were determined using a 3730 ABI Genetic Analyzer at Macrogen, Inc. (Seoul, South Korea). The resultant DNA sequences were aligned by Muscle using default parameters (Edgar, 2004) implemented in MEGA ver. X software (Kumar et al., 2018). Sequences generated in this study are available from GenBank (**Table 1**). Protein-coding sequences (COI and COIII) were translated to amino acids using the invertebrate mitochondrial genetic code to check for errors or gaps in MEGA.

Species Delimitation

Species delimitation was evaluated by using the Bayesian Poisson tree processes (bPTP) analyses (Zhang et al., 2013). Previously, Maximum Likelihood and Bayesian phylogenetic analyses were performed, including two preliminary steps on the aligned DNA

sequences. First, Xia's test for saturation of the phylogenetic signal of each gene was performed using Dambe ver. 6.0 (Xia, 2017). Second, the best substitution model for each gene was estimated with jModelTest (Posada, 2008) using the Bayesian Information Criterion (BIC).

The phylogenetic relationships of the benthic octopuses were examined using a Maximum Likelihood (ML) reconstruction via the IQ-TREE online server (Trifinopoulos et al., 2016) with hill-climbing NNI tree search strategy (Nguyen et al., 2015). The ModelFinder option (Kalyaanamoorthy et al., 2017) was used under a partition scheme including codon position for coding genes (COI, and COIII). Statistical support was estimated using 5,000 ultrafast bootstrap replicates (Minh et al., 2013). The trees were rooted using the cirrates *Opisthoteuthis mero* O'Shea (1999) and *O. chathamensis* O'Shea (1999) as outgroups, as Cirrata is well-established as the sister group of Incirrata (Voight, 1997; Young et al., 1998; Lindgren et al., 2012).

Phylogenetic reconstruction was inferred from a partitioned matrix (16S, COI, COIII) with a different substitution model for each gene. Bayesian analyses were conducted using MrBayes ver. 3.2 (Ronquist et al., 2012) with four chains, each with 10 million generations, sampled every 1,000 generations. Bayesian analyses were performed several times to compare the likelihood values of each run using Tracer ver. 1.5 (Rambaut and Drummond, 2009). The first 1,000 trees of each run were discarded as burn-in, and a consensus of the remaining trees was calculated. FigTree ver. 1.4 was used to edit the trees (Rambaut, 2009). In both phylogenetic analyses (ML and BI), we used specimens for which all mitochondrial genes were available (44 specimens, **Table 1**). The consensus tree was finally used as input for the species delimitation analysis with the Bayesian Poisson Tree Process method (bPTP; Zhang et al., 2013) as implemented in the web server[1].

Additional species boundaries were delimited using the Automatic Barcode Gap Discovery method (ABGD; Puillandre et al., 2012). The ABGD method recursively searches for major changes in the slope of ranked pairwise genetic distances between groups of individual sequences. Through this, ABGD proposes a distance superior to maximal intraspecific sequence divergences, as determined using a coalescent model. These distances potentially correspond to the frontiers between intra and interspecific distances, or the so-called barcode gap. ABGD analyses were performed online[2] using both the COI and COIII

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[1]https://species.h-its.org/ptp/
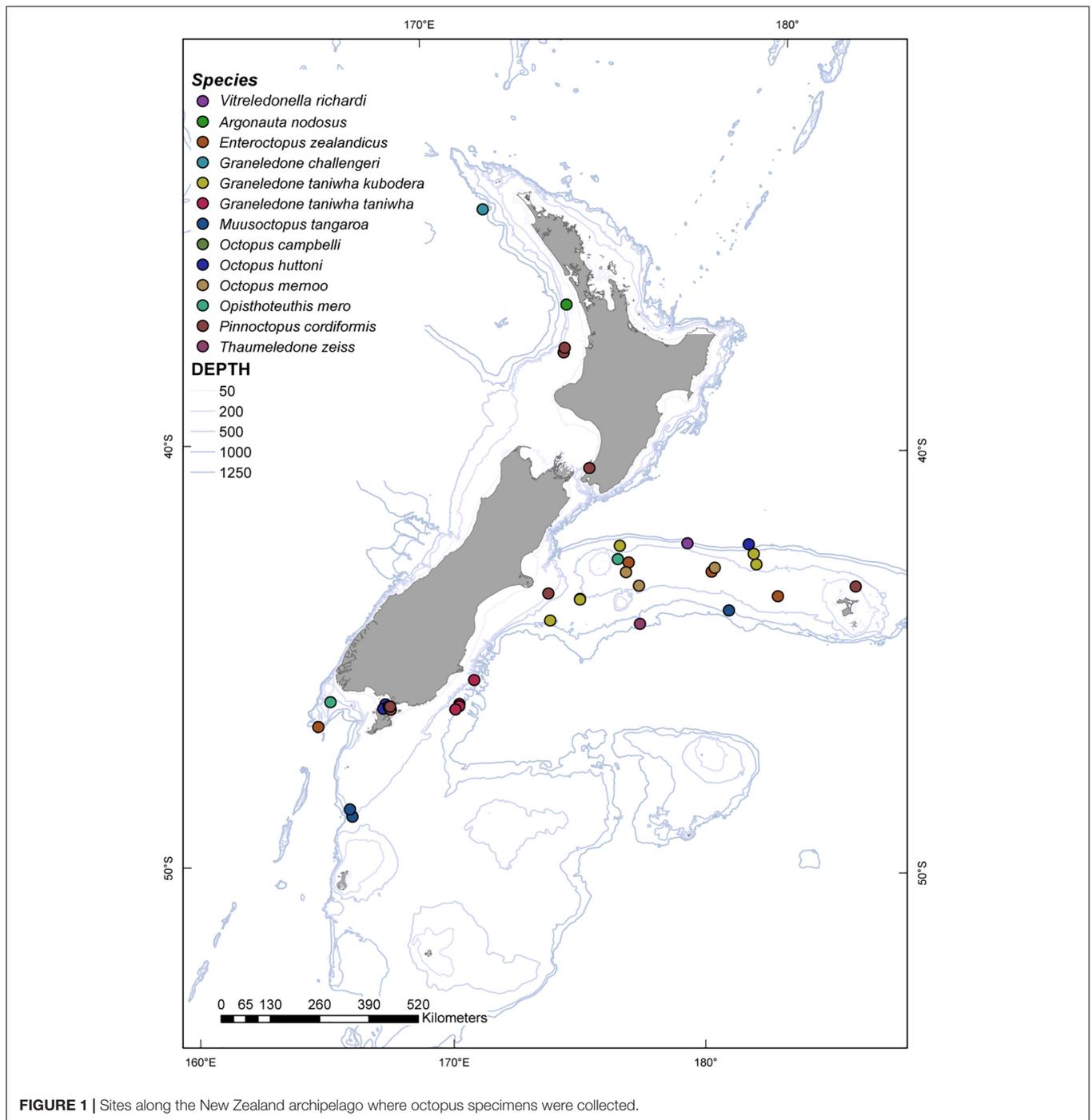[2]http://wwwabi.snv.jussieu.fr/public/abgd/

FIGURE 1 | Sites along the New Zealand archipelago where octopus specimens were collected.

data sets independently, excluding outgroups. The p-distance with a minimum gap width of 1.5 were selected. The remaining parameters were set as default (Pmin = 0.001, Pmax = 0.100, Steps = 10, Number of bins = 20).

Phylogenetic Analysis

In a second phylogenetic analysis, mitochondrial DNA sequences obtained during the present study were combined with those of other species available at GenBank (16, COI, COIII,

and Rhodopsin) to explore the phylogenetic position of the New Zealand taxa. These included Rhodopsin (RHO) sequences in a matrix with 97 species (**Table 2**), including 88 species of octopuses from the superfamily Octopodoidea, in addition to outgroups from two pelagic octopuses of the superfamily Argonautoidea (*Argonauta argo* and *Argonauta nodosus*), six cirrates (*Opisthoteuthis mero*, *O. chathamensis*, *O. depressa*, *O. massyae, Cirroctopus glacialis,* and *Stauroteuthis gilchristi*), and the vampire squid *Vampyroteuthis infernalis*. These analyses were

performed in the same way as the previous analysis in IQ-TREE and MrBayes.

RESULTS

Xia's test found no saturation of coding genes (COI: Iss = 0.170 < Iss.c = 0.732, P < 0.001 and COIII: Iss = 0.210 < Iss.c = 0.702, P < 0.001). jModeltest result in a different substitution model for each gene (16S: HKY85 + G; COI: GTR + I; COIII: TN93 + G + I) (BIC, **Table 3**). The consensus of 9,000 phylogenetic trees from MrBayes showed high posterior probabilities (PP values > 0.9) for most of the nodes (**Figure 2**). ML trees from IQ-TREE reported the same topology with high bootstrap support (>70, **Figure 2**).

Species Delimitation

Species delimitation using bPTP agreed in defining the clusters of our dataset, with both analyses identifying 12 entities of New Zealand octopuses with posterior probabilities of conspecificity ranging from 0.90 to 1.0 (**Figure 2**). In this phylogeny, we found four clades within the Incirrata: Clade 1, compound by *A. nodosus (*Lightfoot, 1786); and Clade 2 compound by four species of deep-sea dwelling *Graneledone* and *Thaumeledone* (family Megaleledonidae), all of them recognized by a single sucker row. Within this clade, the reciprocal monophyly between *G. taniwha taniwha* O'Shea, 1999 and *G. taniwha kubodera* (O'Shea, 1999), in addition to the species delimitation analysis (bPTP and ABGD), suggest they would correspond to separate species (**Figure 2**). In Clade 3, species delimitation analyses evidenced two species, *Enteroctopus zealandicus* (Benham, 1944) and *Muusoctopus tangaroa* (O'Shea, 1999); whereas Clade 4 was compound by species of the family Octopodidae: *P. cordiformis* (Quoy and Gaimard, 1832), *Octopus mernoo* (O'Shea, 1999), *Octopus huttoni* (Benham, 1943) and *Octopus campbelli* (Smith, 1902) (**Figure 2**). Species delimitation analyses with ABGD for both coding genes (COI and COIII) identified 12 genetic groups of 11 morphological species based on p-distances on the gene tree (**Figure 2**).

Molecular Phylogeny

The consensus tree from the Bayesian analysis of the combined sequences (GenBank and new sequences) had high posterior probability values (>0.95) for most nodes, and a similar topology compared to the ML tree (**Figure 2**). The ML tree from IQ-TREE had a better topology, resolving the polytomies present in the Bayesian tree with high bootstrap support (>70, **Figure 3**, Mendeley Dataset: DOI: 10.17632/5vkm46hm49.2). For this reason, we present the ML tree with posterior probability values from the Bayesian analysis. Within this tree, the genus *Octopus* is polyphyletic, probably related to the fact that many *Octopus* species are poorly described (c.f. Norman and Hochberg, 2005). New Zealand benthic octopuses are placed in clades that correspond to three distinct families. Clade 1, Enteroctopodidae, is compound by the species *Enteroctopus dofleini* (Wülker, 1910) from Alaska, *Enteroctopus megalocyathus* from Chile and *E. zealandicus* from New Zealand (**Figure 3**). In the same

clade, *Muusoctopus thielei* (Robson, 1932) from Kerguelen is closely related to *M. oregonensis* (Voss and Pearcy, 1990) from the North Pacific and *M. tangaroa* from New Zealand. Within clade 2, Megaleledonidae, *Thaumeledone zeiss* O'Shea, 1999 was included in a clade comprising *T. gunteri* (Robson, 1930), *T. rotunda* (Hoyle, 1885) and *T. peninsulae* (Allcock, Collins, Piatkowski and Vecchione, 2004) from Antarctica (**Figure 3**). In the same clade, *Graneledone taniwha taniwha* and *G. taniwha kubodera* are sister taxa, as *G. challengeri* (Berry, 1916) and *G. antarctica* (Voss, 1976) (**Figure 3**). Clade 3 comprised the family Octopodidae (**Figure 3**), where *P. cordiformis* was a sister species of *Grimpella thaumastocheir* (Robson, 1928), both species nearly related to the *Octopus s.l.* clade composed by Indo-Pacific species. The phylogenetic position of *P. cordiformis* and *G. thaumastocheir* was similar to previous phylogenetic analysis, with the absence of ink sac in *G. thaumastocheir* being an apparent adaptation to deep sea (Guzik et al., 2005; Strugnell et al., 2014). *Octopus campbelli*, *O. huttoni* and *O. mernoo* formed a monophyletic group with *Robsonella fontaniana* (d'Orbigny, 1834) from Chile, *Scaeurgus unicirrhus* (Delle Chiaje in d'Orbigny, 1841) from the Atlantic, and *O. pallidus* (Hoyle, 1885), from Australia. Clade 4 was composed of *O. fitchi* (Berry, 1953), *Paroctopus digueti* (Perrier and Rochebrune, 1894) from Northeastern Pacific and *O. tehuelchus* (d'Orbigny, 1834), from the Southwest Atlantic (**Figure 3**). Clade 5 included *Ameloctopus litoralis* (Norman, 1992) from Australia, *Cistopus* (Gray, 1849) and *Octopus s. l.* from the West Pacific. Clade 6 included *Abdopus aculeatus* (d'Orbigny, 1834), *O. cyanea* (Gray, 1849), and *O. laqueus* (Kaneko and Kubodera, 2005) from the West Pacific (**Figure 3**). Clade 7 contained the genus *Amphioctopus* (Fischer, 1882) and *Hapalochlaena* (Robson, 1929), from the West Pacific (**Figure 3**). Finally, clade 8 was composed by octopodid species including *O. oliveri* (Berry, 1914) with members of the *Octopus sensu stricto* clade including *O. tetricus* (Gould, 1852), from Australia/New Zealand and others from America (**Figure 3**).

DISCUSSION

This study evidenced that benthic octopuses from New Zealand have different phylogenetic and biogeographic origins. Our review based on museum collections and phylogenetic analyses indicated that the New Zealand octopod fauna is composed of 16 species distributed in eight genera. This is a low diversity compared to tropical regions, but higher than cold and temperate ecosystems (Rosa et al., 2019). Only four shallow-water species [*Octopus mernoo*, *O. campbelli*, *O. kaharoa* O'Shea, 1999 and *Callistoctopus kermadecensis* (Berry, 1914)], and six deep-sea species (*Graneledone taniwha taniwha*, *G. taniwha kubodera*, *Thaumeledone zeiss*, *T. marshalli*, *M. tegginmathae,* and *M. tangaroa*) are endemic to New Zealand. The remaining octopuses are widely distributed and are known to occur near Australia and Japan (*Octopus oliveri*, *O. huttoni*, *O. sinensis*, *O. tetricus*, *P. cordiformis*, and *G. challengeri*).

TABLE 2 | Species included in phylogenetic analyses from GenBank.

Species	16S rRNA	COI	COIII	Rhodopsin
Abdopus aculeatus	GQ900717	AB430514	AB573185	HM104287
Adelieledone piatkowski	EU071431	EU071444	EU071455	EU086511
Adelieledone polymorpha	EF102194	EF102173	EF102153	EF102113
Ameloctopus litoralis	HM104245	HM104255	AJ628207	
Amphioctopus aegina	FJ800371	AB430515	AB573189	HM104289
Amphioctopus kagoshimensis	AJ311108	AB430520	AB573193	
Amphioctopus marginatus	GQ900709	AB430521	AB573195	
Argonauta argo	AB191108	AB191273	GU288523	
Bathypolypus arcticus	DQ280044	AF000029	KP693813	KP693815
Bathypolypus sponsalis	EF016338	EF016329	FJ603530	HM104289
Callistoctopus luteus	GQ900707	AB430526	AB573208	
Callistoctopus minor	AB191110	AB430540	AB573201	
Callistoctopus ornatus	GQ900705	AY616892	AB573209	AY616926
Cirroctopus glacialis	AF487304	AF377962		
Cistopus chinensis	KF017606	KF017606	KF017606	
Cistopus indicus	AJ252744	AB385878	AB573210	HM104291
Cistopus taiwanicus	KF017605	KF017605	KF017605	
Eledone cirrhosa	KC792309	AY557520	KC792300	AY617043/HM104292
Enteroctopus dofleini	AY545109	AB191272	AB573211	AY545174
Enteroctopus megalocyathus	KC792314	KF774312	KC792304	
Graneledone antarctica	EU071436	AF377973	EU071461	EU086518
Graneledone boreopacifica	EU071435	EU071448	EU071460	EU086516
Graneledone verrucosa	AY545111	EU071449	EU071462	EU086517/HM104293
Grimpella thaumastocheir	HM104246	HM104259	AJ628209	
Hapalochlaena fasciata	GQ900711	AB430529	AB573212	
Hapalochlaena lunulata	AB191113	AB430530	AB573213	
Hapalochlaena maculosa	AY545107	AF000043	AB573214	AY545171
Megaleledone setebos	EF102195	EF102174	EF102154	EF102114
Muusoctopus eicomar	KM459467	KM459480	KM459495	
Muusoctopus eureka	HM572155	HM572170	HM572191	HM572221
Muusoctopus januarii	EF016344	EF016335	HM572188	EF016318/EF016311
Muusoctopus johnsonianus	HM572162	EF016333	HM572197	
Muusoctopus levis	FJ428007	FJ428012	EF016323	
Muusoctopus longibrachus	KC792311	KF774314	KC792302	HM572219
Muusoctopus oregonensis	FJ603543	HM572180	FJ603538	GQ226016
Muusoctopus profundorum	FJ603542	HM572176	FJ603537	GQ226022
Muusoctopus rigbyae	FJ428011	FJ428014	FJ603528	HM572226
Muusoctopus thielei	FJ428009	HM572185	HM572198	
Muusoctopus yaquinae	FJ603539	HM572182	FJ603532	
Octopus bimaculatus	KT581981	KT581981	KT581981	KT335846
Octopus bimaculoides	KC792308	KF774309	KC792299	AY545172
Octopus californicus	HM572164	AF377968	HM572187	HM572214
Octopus conispadiceus	AB191116	AB430533	AB573222	
Octopus cyanea	GQ900721	AB430535	AB573224	
Octopus fitchi	KT335838	KT335832	KT335844	
Octopus hongkongensis	AB302174	AB430538	AB573221	
Octopus insularis	KF843968	KP056555	KX219649	MH550449
Octopus kaurna	AY545106	AY545188	AJ628227	AY545169
Octopus laqueus	AB302177	AB430543	AB573215	
Octopus maya	KC792312	KF774310	KC792303	
Octopus mimus	KC792313	KF774308	KC792305	KT335848
Octopus oliveri	GQ900712	AB430532	AB573226	
Octopus pallidus	AJ252754	KP693817	AJ628236	

(Continued)

TABLE 2 | Continued

Species	16S rRNA	COI	COIII	Rhodopsin
Octopus parvus	AB191106	AB430544	AB573216	
Octopus rubescens	AJ252755	HM431980	KC792306	AY545170
Octopus salutii	AJ390323	KC894941	AJ250484	
Octopus tehuelchus	AJ252761	GU355936	GU355937	
Octopus tetricus	KJ605236	MH289826	KJ60530	
Octopus vulgaris	KC792315	KF774311	KC792307	HM104297
Octopus wolfi	AJ311111	AB430545	AB573227	
Opisthoteuthis depressa	AB191117	AB191282		
Opisthoteuthis massyae	AY545103	AY545187	EU071451	HM104301
Pareledone aequipapillae	EF102201	EF102179	EF102160	EF102119
Pareledone albimaculata	EF102203	EF102182	EF102162	EF102122
Pareledone aurata	EF102199	EF102177	EF102158	EF102118
Pareledone charcoti	EF102197	EF102175	EF102156	EF102115
Pareledone cornuta	EF102207	EF102185	EF102165	EF102125
Pareledone felix	EF102205	GU806449	EF102163	
Pareledone panchroma	EF102214	EF102193	EF102172	EF102133
Pareledone serperastrata	EF102209	EF102187	EF102167	EF102127
Pareledone subtilis	EF102210	EF102189	EF102169	EF102129
Pareledone turqueti	EF102213	EF102192	EF102171	EF102132
Paroctopus digueti	KT335839	KT335833	KT335845	
Praealtus paralbida	HM104247	HM104261	HM104252	
Robsonella fontaniana	KC792310	KF774313	KC792301	
Scaeurgus unicirrhus	AJ390324	HM104263	AJ012129	HM104298
Stauroteuthis gilchristi	AY545102	AY545186	EU071450	
Thaumeledone gunteri	AF299266	AY557521	EU148470	EU086513
Thaumeledone peninsulae	EU148474	EU071446	EU071458	EU086514
Thaumeledone rotunda	EU071432	EU071445	EU071456	EU086512
Vampyroteuthis infernalis	DQ280043	AF000071	GU288521	AY545163
Velodona togata	EU071434	EU071447	EU071459	EU086515
Vulcanoctopus hydrothermalis	HM572163	HM104264	HM572200	GQ226020/HM104300

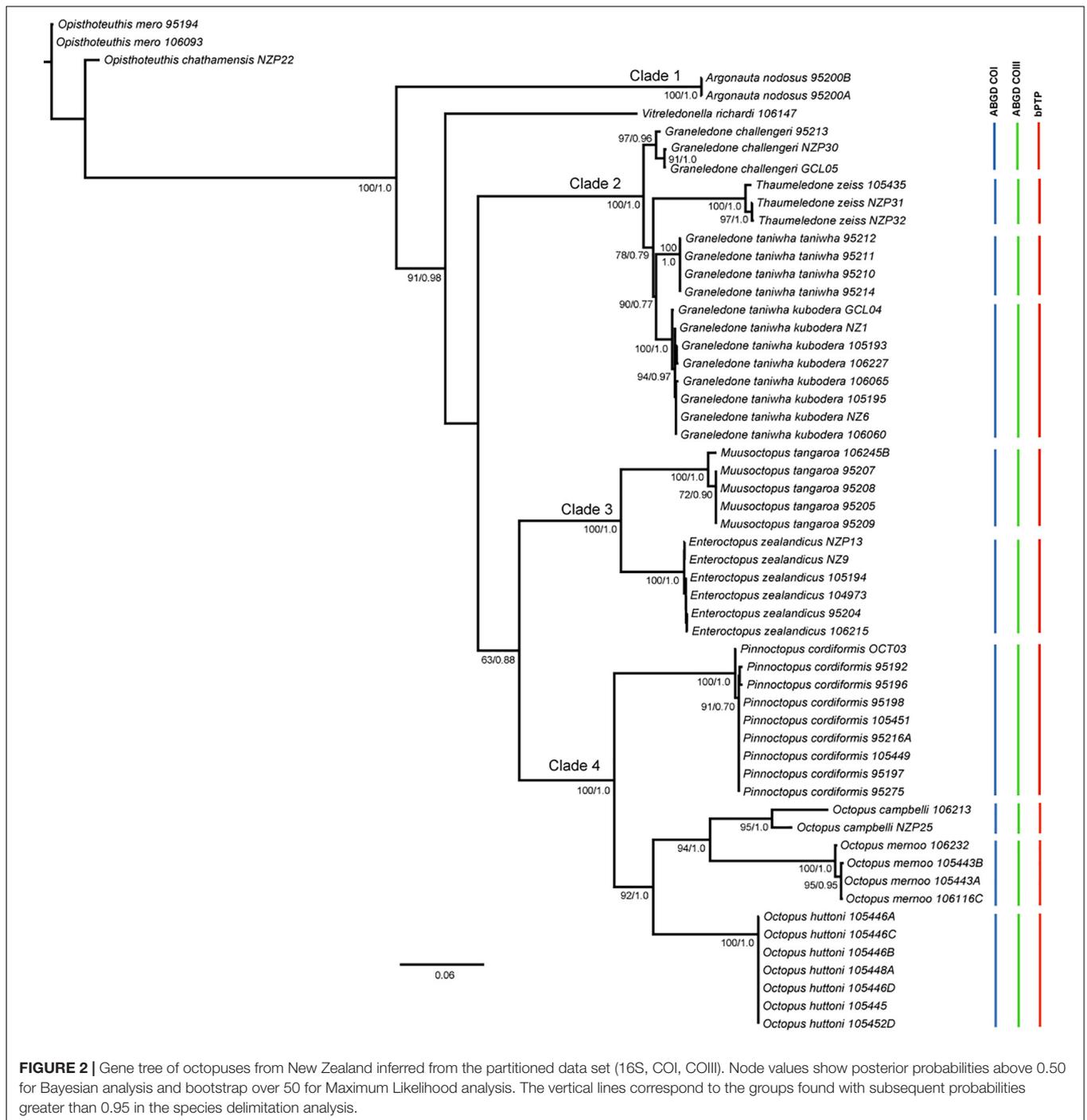**TABLE 3 | Results of substitution model selection for each gene.**

Gene	Model	#Parameters	BIC	lnL
16S	TN93 + G	121	4382.08	−1578.34
COI	GTR + I	110	7948.06	−3401.50
COIII	TN93 + G + I	118	7511.33	−3150.34
RHO	T92 + G	92	6934.84	−3014.33

BIC, Bayesian Information Criterion; lnL, likelihood values.

New Zealand Octopus Systematics

The most complete information to date on octopod fauna from New Zealand waters correspond to O'Shea's (1999) monograph; however, considering the limitation imposed by the lack of any genetic analysis, identifying octopuses solely using O'Shea's descriptions can be challenging. Norman et al. (2014) were critical on this revision and questioned the validity of some species (e.g., *Thaumeledone*, *Pinnoctopus*). In fact, Norman and Hochberg (2005) placed several species from New Zealand in different genera than those proposed by O'Shea (1999) (e.g., *P. cordiformis* and *P. kermadecensis*). O'Shea (1999) resurrected *P. cordiformis*

designating a neotype in the absence of type material, but other authors argued that morphologically, this species is a senior synonym of *Macroctopus maorum* (Hutton, 1880) (Robson, 1929; Norman and Hochberg, 2005). Our phylogenetic results added to the review of the neotype (NIWA 43044, H-668) agreed with O'Shea (1999) and suggest placing the currently recognized species *Octopus cordiformis* in the genus *Pinnoctopus*. Similarly, previous studies also placed *P. kermadecensis* within the genus *Callistoctopus* (Norman and Hochberg, 2005; Reid and Wilson, 2015); however, molecular information would first be required in order to confirm the valid status of the species. In this context, O'Shea (1999) suggested both *Macroctopus* and *Callistoctopus* are junior synonyms of *Pinnoctopus*, and Voss (1981) suggested that no valid basis exist for recognizing any distinction between *Callistoctopus* and *Octopus*. Therefore, and based on this information, our study suggests that *P. cordiformis* and *P. kermadecensis* would remain as the correct names. Indeed, the name *P. cordiformis* has been consistently used in several studies recently carried out in New Zealand and Australia (see Carrasco, 2014; Orbach and Kirchner, 2014; Briceño et al., 2015, 2016).

FIGURE 2 | Gene tree of octopuses from New Zealand inferred from the partitioned data set (16S, COI, COIII). Node values show posterior probabilities above 0.50 for Bayesian analysis and bootstrap over 50 for Maximum Likelihood analysis. The vertical lines correspond to the groups found with subsequent probabilities greater than 0.95 in the species delimitation analysis.

In the present study, most New Zealand octopodids (*P. cordiformis*, *O. campbelli*, *O. huttoni* and *O. mernoo*) were found within Clade 3 (see **Figure 3**), sharing a common ancestor with other Pacific species from different genera (*Grimpella, Octopus, Robsonella,* and *Scaeurgus*). In fact, Robson (1929) observed morphological similarities between *Robsonella* and *Scaeurgus* in the terminal organ's shape and the presence of a ligula with robust cheeks. The specimens examined from our Clade 3 (New Zealand and Chile) shared a similar hectocotylus

shape, suggesting this clade require a new classification. Our genetic analyses suggest that some shallow-water, small-bodied octopuses from New Zealand (*Octopus campbelli, O. huttoni,* and *O. mernoo*) currently placed in *Octopus sensu lato* would belong to the *Robsonella* clade. In fact, Adam (1938) recognized only two species (*R. fontaniana* and *R. campbelli*), while Pickford (1955) recognized three species (*R. fontaniana, R. campbelli,* and *R. huttoni*). Clearly all these species share a recent common ancestor and have similar morphologies. Based on this
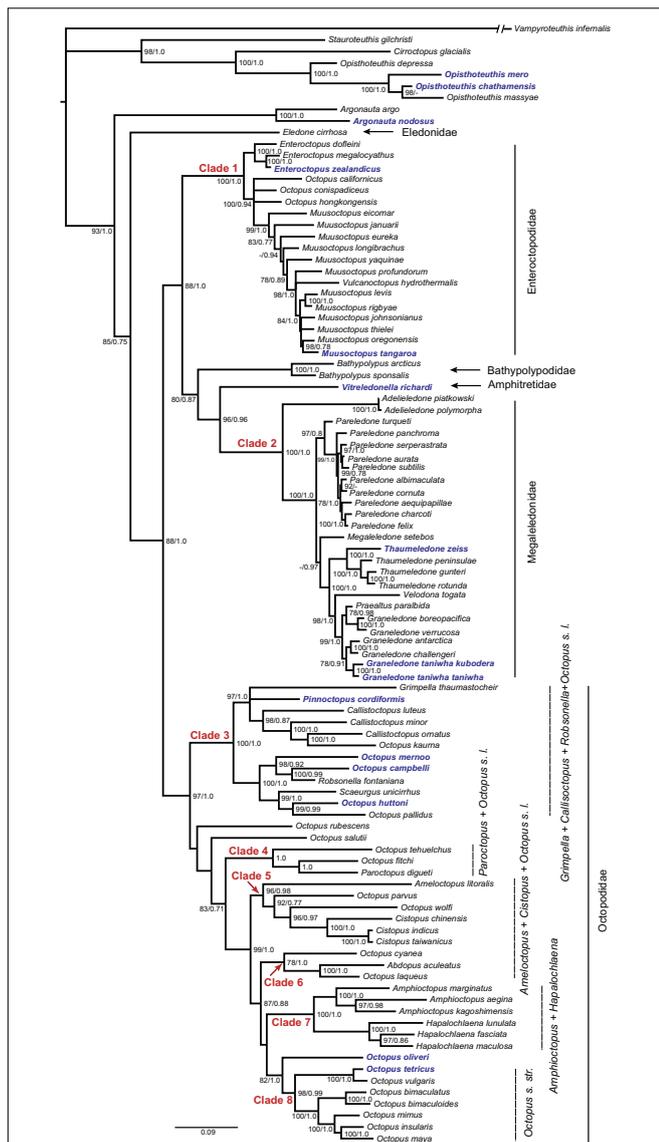
FIGURE 3 | Phylogram of octopuses from the partitioned data set (16S, COI, COIII, RHO) including sequences from the present study and from GenBank. Node values show posterior probabilities above 0.50 for Bayesian Inference and bootstrap over 50 for Maximum Likelihood analysis. Species in blue are from New Zealand.

information, we suggest identifying the New Zealand species *O. campbelli*, *O. huttoni* and *O. mernoo* as species within the genus *Robsonella*, as they shared several morphological features (radula, skin, hectocotylus) following the diagnosis of the genus (Ibáñez et al., 2008). Other authors have also used this identification (Sweeney and Roper, 1998; Sweeney, 2017).

Our DNA sequence data suggests that there was a close relationship (99% similarity in 16S and COIII, and 100% similarity in COI) between *E. zealandicus* (yellow octopus) from New Zealand and *E. megalocyathus* (red octopus) from Chile, relationship that deserve an improved revision as Hudelot (2000) also suggested that *E. magnificus* (Villanueva et al.,

1992) and *E. zealandicus* may be conspecific. Both species (*E. zealandicus* and *E. megalocyathus*) are similar but have slight differences in morphometric, meristic measurements and coloration, which require further investigation (M.C. Pardo-Gandarillas et al. unpublished data). Norman and Hochberg (2005) and Jereb et al. (2014) classified *Octopus oliveri* in *Octopus sensu lato* provisionally, but our phylogenetic analysis suggests that this species is a close relative to the *Octopus sensu stricto* group to retain it in this genus. Another species not included in our genetic study, a recently described species from the Kermadec Islands (*Octopus jollyorum;* Reid and Wilson, 2015) has been suggested as a junior synonym of *O. sinensis* (d'Orbigny, 1841) (Amor et al., 2017), although Gleadall (2016) identified them as different species with clear morphological differences.

The finding of reciprocal monophyly and species delimitation analyses suggested that the subspecies *G. taniwha taniwha* and *G. taniwha kubodera* are different species. Both sub-species have similar morphological features, including suckers, gills, and wart counts (Ibáñez et al., 2012). O'Shea (1999) suggested that future descriptions of *Graneledone* species should provide more morphological detail (cartilaginous cluster distribution and composition, and arm sucker counts), and proposed that the only way to differentiate these two species is by the number of cartilaginous processes per cluster (i.e., *G. taniwha taniwha* 1–37 and *G. taniwha kubodera* 4–13). Similarly, specimens of each taxon were also examined here, suggesting they had different wart head counts (i.e., *G. taniwha taniwha* 10–14, *G. taniwha kubodera* 5–8) and confirming the distinction observed within the molecular phylogeny.

The genus *Benthoctopus* is not sustainable, as Gleadall et al. (2010) pointed out that *Benthoctopus* is a junior synonym of *Bathypolypus* and identified species in genus *Benthoctopus* as species of *Muusoctopus*. Therefore, there is no reason in retaining both *Benthoctopus* and *Muusoctopus* (e.g., Norman et al., 2014). In this context, Ibáñez et al. (2016) also suggested (based on morphology and genetics) that all New Zealand species of *Benthoctopus* should be included within the genus *Muusoctopus*. Future research should therefore target to compare morphometrics and genetic data to specifically determine the number of *Muusoctopus* species present in New Zealand waters.

Octopus Phylogeny

The phylogeny reported here contains several groups, represented by the families Bathypolypodidae, Eledonidae, Megaleledonidae, Enteroctopodidae, and Octopodidae (**Figure 3**). Within Octopodidae, we recognized two monophyletic groups, one composed by *Octopus sensu stricto* (Clade 8) and the other by species of the genera *Amphioctopus* and *Hapalochlaena* (Clade 7). Two other groups were paraphyletic, being composed by species of *Octopus sensu lato* (Clades 3, 4, and 5) in addition to *Abdopus*, *Callistoctopus*, *Cistopus*, *Pinnoctopus*, *Robsonella*, and *Scaeurgus*. Our finding of *Octopus* as a polyphyletic group is consistent with previous studies (e.g., Strugnell et al., 2005; Lindgren et al., 2012;

Ibáñez et al., 2014, 2018), suggesting that the genus *Octopus* need an urgent revision.

Recent studies carried out by Strugnell et al. (2014) evaluated the phylogenetic relationships of 23 octopods using four mitochondrial and three nuclear genes, and evidenced a similar topology compared to that obtained with our fewer genes (three mtDNA regions) and higher number of species (88 spp. in five families; see **Figure 3**). In this context, increasing the coverage of species and including additional characters is a well-recognized approach to improve phylogenetic analyses (Graybeal, 1998; Poe and Swofford, 1999; Rosenberg and Kumar, 2003), suggesting that our phylogeny is a solid estimation of the evolutionary relationships. Since our phylogenetic reconstruction was based only on three mitochondrial genes and one nuclear gene, it is plausible to expect that the inclusion of more markers would improve our understanding of the evolutionary relationships of the New Zealand octopuses. However, the polyphyletic nature of the genus *Octopus* is clearly an artifact of poorly described species being placed into the genus because of uncertainty about their true taxonomic positions (sensu Norman and Hochberg, 2005). As suggested by previous authors (Gleadall, 2004; Kaneko et al., 2011), *Octopus* systematics still requires an extensive revision in order to solve some of the difficulties in finding informative morphological characters. Based on this information, we suggest that several species included in Clade 1 (representing the family Enteroctopodidae) may not belong to the genus *Octopus* (e.g., *O. californicus*, *O. conispadiceus*, *O. hongkongensis*).

The presence in New Zealand of 16 species of benthic octopus from different genera and environments suggests a history of several radiations from tropical and cold-water ancestors. Most octopuses included in the present study inhabit the Indo-Pacific, a region that based on the high diversity of benthic octopuses is recognized as the potential origin of the family Octopodidae, and from where many species radiated worldwide (Rosa et al., 2019). Close biogeographic relationships of benthic octopuses from New Zealand, Australia and the Southern Ocean have been recently revealed (Rosa et al., 2019), confirming the taxonomic relationships proposed by O'Shea (1999). The close phylogenetic relationships of the New Zealand *O. campbelli*, *O. huttoni* and *O. mernoo* with *O. pallidus* from Australia and *R. fontaniana* from South America is probably related to dispersal events after the circumpolar current was established during the Cenozoic (Strugnell et al., 2008). The same pattern would be expected for the *Octopus* s.s. clade with species from America, Australia and New Zealand, and the Mediterranean, which suggests a classic Tethyan distribution. For the deep-sea species of the genera *Graneledone* and *Thaumeledone*, an Antarctic origin is probable based on the findings by Strugnell et al. (2008). In the case of *Muusoctopus*, dispersal events from the North

Pacific to the Southern Ocean and Atlantic (Gleadall, 2013) and from the Atlantic to the Southern Ocean (Ibáñez et al., 2016) have been previously proposed. The molecular phylogenetic approach presented here has added important information to the current systematics of the New Zealand octopod fauna; nonetheless, further studies are still required considering larger sampling sizes and a mixture of both mitochondrial and nuclear molecular markers to properly clarify their biogeographic origin and diversification.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

ETHICS STATEMENT

The animal study was reviewed and approved by the Universidad Andres Bello.

AUTHOR CONTRIBUTIONS

CI and MP-G conceived the idea, designed the study, analyzed the data, and led the writing of the manuscript. MF, SC, and PR collaborated in writing and provided editorial advice. All authors have read and commented on the manuscript.

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REFERENCES

Adam, V. W. (1938). *Robsonella* nom. nov. für Joubinia Robson, 1929 (Cephalopoda. Octopoda). *Zool. Anz.* 121, 223–224.

Aljanabi, S. M., and Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nuc. Acids Res.* 25, 4692–4693. doi: 10.1093/nar/25.22.4692

Amor, M. D., Norman, M. D., Cameron, H. E., and Srugnell, J. M. (2014). Allopatric speciation within a cryptic species complex of Australasian octopuses. *PLoS One* 9:e98982. doi: 10.1371/journal.pone.0098982

Amor, M. D., Norman, M. D., Roura, A., Leite, T. S., Gleadall, I. G., Reid, A., et al. (2017). Morphological assessment of the *Octopus vulgaris* species complex evaluated in light of molecular-based phylogenetic inferences. *Zool. Scrip.* 46, 275–288. doi: 10.1111/zsc.12207

Briceño, F., León, R., Gardner, C., Hobday, A. J., André, J., Frusher, S. D., et al. (2016). Spatial variation in mortality by in−pot predation in the Tasmanian rock lobster fishery. *Fish. Oceanogr.* 25, 6–18. doi: 10.1111/fog.12115

Briceño, F., Linnane, A. J., Quiroz, J. C., Gardner, C., and Pecl, G. T. (2015). Predation risk within fishing gear and implications for South australian rock lobster fisheries. *PLoS One* 10:e0139816. doi: 10.1371/journal.pone.0139816

Carlini, D. B., Young, R. E., and Vecchione, M. (2001). A molecular phylogeny of the Octopoda (Mollusca: Cephalopoda) evaluated in light of morphological evidence. *Mol. Phyl. Evol.* 21, 338–397.

Carrasco, S. A. (2014). The early life history of two sympatric New Zealand octopuses: eggs and paralarvae of *Octopus huttoni* and *Pinnoctopus cordiformis*. *New Zeal. J. Zool.* 41, 32–45. doi: 10.1080/03014223.2013.827126

Dell, R. K. (1952). The recent Cephalopoda of New Zealand. *Dominion Museum Bulletin* 16, 1–157.

Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32, 1792–1797.

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3, 294–299.

Gleadall, I. G. (2004). Some old and new genera of octopus. *Interdiscip. Inf. Sci.* 10, 99–112. doi: 10.4036/iis.2004.99

Gleadall, I. G. (2013). A molecular sequence proxy for *Muusoctopus januarii* and calibration of recent divergence among a group of mesobenthic octopuses. *J. Exp. Mar. Biol. Ecol.* 447, 106–122. doi: 10.1016/j.jembe.2013.02.017

Gleadall, I. G. (2016). *Octopus sinensis* d'Orbigny, 1841 (Cephalopoda: Octopodidae): valid species name for the commercially valuable east asian common octopus. *Species Divers.* 21, 31–42. doi: 10.12782/sd.21.1.031

Gleadall, I. G., Guerrero-Kommritz, J., Hochberg, F. G., and Laptikhovsky, V. V. (2010). The inkless octopuses (Cephalopoda: Octopodidae) of the Southwest Atlantic. *Zool. Sci.* 27, 528–553. doi: 10.2108/zsj.27.528

Graybeal, A. (1998). Is it better to add taxa or characters to a difficult phylogenetic problem? *Syst. Biol.* 47, 9–17. doi: 10.1080/106351598260996

Guzik, M. T., Norman, M. D., and Crozier, R. H. (2005). Molecular phylogeny of the benthic shallow-water octopuses (Cephalopoda: Octopodinae). *Mol. Phyl. Evol.* 37, 235–248. doi: 10.1016/j.ympev.2005.05.009

Hoving, H. J. T., Perez, J. A. A., Bolstad, K. S., Braid, H. E., Evans, A. B., Fuchs, D., et al., (2014). The study of deep-sea cephalopods. *Adv. Mar. Biol.* 67, 235–359.

Hudelot, C. (2000). *La Systèimatique des Octobrachia (Mollusca; Cephalopoda): une Approche Molèiculaire*. Ph.D thesis, Paris: Musèium National d'Histoire Naturelle.

Ibáñez, C. M., Pardo-Gandarillas, M. C., Peña, F., Gleadall, I. G., Poulin, E., and Sellanes, J. (2016). Phylogeny and biogeography of *Muusoctopus* (Cephalopoda: Enteroctopodidae). *Zool. Scrip.* 45, 494–503. doi: 10.1111/zsc.12171

Ibáñez, C. M., Pardo-Gandarillas, M. C., Poulin, E., and Sellanes, J. (2012). Morphological and molecular description of a new record of *Graneledone* (Cephalopoda, Octopodidea) in the southeastern Pacific Ocean. *Rev. Biol. Mar. Oceanogr.* 47, 439–450. doi: 10.4067/s0718-19572012000300007

Ibáñez, C. M., Peña, F., Pardo-Gandarillas, M. C., Méndez, M. A., Hernández, C. E., and Poulin, E. (2014). Evolution of development type in benthic octopuses: holobenthic or pelago-benthic ancestor? *Hydrobiologia* 725, 205–214. doi: 10.1242/jeb.109603

Ibáñez, C. M., Rezende, E., Sepúlveda, R. D., Avaria-Llautureo, J., Hernández, C. E., Sellanes, J., et al. (2018). Thorson's rule, life history evolution and diversification of benthic octopuses (Cephalopoda: Octopodoidea). *Evolution* 7, 1829–1839. doi: 10.1111/evo.13559

Ibáñez, C. M., Sepúlveda, R. D., Guerrero, J., and Chong, J. (2008). Redescription of *Robsonella fontaniana* (Cephalopoda: Octopodidae). *J. Mar. Biol. Ass. UK* 88, 617–624. doi: 10.1017/s002531540800101x

Jereb, P., Roper, C. F. E., Norman, M. D., and Finn, J. K. (2014). *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Volume 3. Octopods and Vampire Squids*. Rome: FAO Species Catalogue for Fishery Purposes, 370.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., Von Haeseler, A., and Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* 14, 587–589. doi: 10.1038/nmeth.4285

Kaneko, N., Kubodera, T., and Iguchis, A. (2011). Taxonomic study of shallow-water octopuses (Cephalopoda: Octopodidae) in Japan and adjacent waters

using mitochondrial genes with perspectives on octopus DNA barcoding. *Malacologia* 54, 97–108. doi: 10.4002/040.054.0102

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. (2018). MEGA X: molecular evolutionary genetics analysis across computing platforms. *Mol. Biol. Evol.* 35, 1547–1549. doi: 10.1093/molbev/msy096

Lindgren, A. R., Pankey, M. S., Hochberg, F. G., and Oakley, T. H. (2012). A multi-gene phylogeny of Cephalopoda supports convergent morphological evolution in association with multiple habitat shifts in the marine environment. *BMC Evol. Biol.* 12:129. doi: 10.1186/1471-2148-12-129

Minh, B. Q., Nguyen, M. A., and Von Haeseler, A. (2013). Ultrafast approximation for phylogenetic bootstrap. *Mol. Biol. Evol.* 30, 1188–1195. doi: 10.1093/molbev/mst024

Nesis, K. N. (2003). Distribution of recent Cephalopoda and implications for plio-pleistocene events. *Berliner Paläobiol. Abh.* 3, 199–224.

Nguyen, L. T., Schmidt, H. A., Von Haeseler, A., and Minh, B. Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* 32, 268–274. doi: 10.1093/molbev/msu300

Norman, M. D. (2000). *Cephalopods: a World Guide*. Hackenheim: Conch Books.

Norman, M. D., Finn, J. K., and Hochberg, F. G. (2014). "Family Octopodidae," in *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*, eds P. Jereb, C. F. E. Roper, M. D. Norman, and J. K. Finn (Rome: FAO Species Catalogue for Fishery Purposes), 36–215.

Norman, M. D., and Hochberg, F. G. (2005). The current state of Octopus taxonomy. *Phuket Mar. Biol. Cent. Res. Bull.* 66, 127–154.

Orbach, D. N., and Kirchner, T. (2014). Armed escorts: Dusky dolphin (*Lagenorhynchus obscurus*) interactions with octopuses (*Pinnoctopus cordiformis*) in New Zealand. *Aquat. Mamm.* 40, 285–292. doi: 10.1578/am.40.3.2014.285

O'Shea, S. (1999). *Octopoda (Mollusca: Cephalopoda)*. Wellington: NIWA Biodiversity Memoir.

Pickford, G. E. (1955). A revision of the Octopodinae in the collections of the British Museum. Part II. A re-examination of the specimens of *Robsonella fontaniana* in the collections of the British Museum. *Bull. Br. Mus. Nat. Hist. Zool.* 3, 163–167.

Poe, S., and Swofford, D. L. (1999). Taxon sampling revisited. *Nature* 398, 299–300. doi: 10.1038/18592

Posada, D. (2008). jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.* 25, 1253–1256. doi: 10.1093/molbev/msn083

Puillandre, N., Lambert, A., Brouillet, S., and Achaz, G. (2012). ABGD. Automatic barcode gap discovery for primary species delimitation. *Mol. Ecol.* 21, 1864–1877. doi: 10.1111/j.1365-294X.2011.05239.x

Rambaut, A. (2009). *FigTree v1.4*. Available online at: http//tree.bio.ed.ac.uk/ software/tracer (accessed 11 June 2018).

Rambaut, A., and Drummond, A. J. (2009). *Tracer v1.5*. Available online at: http: //tree.bio.ed.ac.uk/software/tracer/ (accessed June 11, 2018).

Reid, A. L., and Wilson, N. G. (2015). Octopuses of the Kermadec Islands: discovery and description of a new member of the *Octopus 'vulgaris'* complex (*O. jollyorum, sp. nov.*) and the first description of a male *Callistoctopus kermadecensis* (Berry, 1914). *Bulletin of the Auckland Museum* 20, 349–368.

Robson, G. C. (1929). *A Monograph of the Recent Cephalopoda. Part I. Octopodinae*. London: British Museum, 236.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D., Darling, A., Höhna, S., et al. (2012). MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 22, 539–542. doi: 10.1093/sysbio/sys029

Rosa, R., Pissarra, V., Borges, F., Xavier, J., Gleadall, I. A., Golikov, A., et al. (2019). Global patterns of species richness in coastal cephalopods. *Front. Mar. Sci.* 6:469. doi: 10.3389/fmars.2019.00469

Rosenberg, M. S., and Kumar, S. (2003). Taxon sampling, bioinformatics, and phylogenomics. *Syst. Biol.* 52, 119–124. doi: 10.1080/10635150390132894

Sambrook, J., Fritsch, E. F., and Maniatis, T. (1989). *Molecular Cloning: A Laboratory Manual*, 2nd Edn. Cold Spring Harbor, N.Y: Cold Spring Harbor Laboratory.

Shears, N. T., Smith, F., Babcock, R. C., Duffy, C. A. J., and Villouta, E. (2008). Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal marine environment. *Conserv. Biol.* 22, 467–481. doi: 10.1111/j.1523-1739.2008.00882.x

Simon, C., Franke, A., and Martin, A. P. (1991). "The polymerase chain reaction: DNA extraction and amplification," in *Molecular Techniques in Taxonomy*, eds G. M. Hewitt, A. W. B. Johnston, and J. P. W. Young (New York, NY: Springer Verlag), 329–355.

Simon, C., Frati, F., Beckenback, A., Crespi, B., Liu, H., and Flook, P. (1994). Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved. *PCR primers. Ann. Entomol. Soc. Am.* 87, 651–701.

Spencer, H. G., Marshall, B. A., Maxwell, P. A., Grant-Mackie, J. A., Stilwell, J. D., Willan, R. C., et al. (2009). "Chapter 10: phylum mollusca, chitons, clams, tusk shells, snails, squids, and kin," in *New Zealand Inventory of Biodiversity*, ed. D. P. Gordon (Christchurch: Canterbury University Press), 161–254.

Strugnell, J. M., Cherel, Y., Elaume, M., Gleadall, I. G., Hochberg, F. G., Ibáñez, C. M., et al. (2011). The Southern Ocean: source and sink? *Deep Sea Res.* 58, 196–204.

Strugnell, J. M., Norman, M. D., Jackson, J., Drummond, A. J., and 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. *Mol. Phyl. Evol.* 37, 426–441. doi: 10.1016/j.ympev.2005.03.020

Strugnell, J. M., Norman, M. D., Vecchione, M., Guzik, M., and Allcock, A. L. (2014). The ink sac clouds octopod evolutionary history. *Hydrobiologia* 725, 215–235. doi: 10.1007/s10750-013-1517-6

Strugnell, J. M., Rogers, A. D., Prodöhl, P. A., Collins, M. A., and Allcock, A. L. (2008). The thermohaline expressway: the Southern Ocean as a centre of origin for deep−sea octopuses. *Cladistics* 24, 853–860. doi: 10.1111/j.1096-0031.2008.00234.x

Sweeney, M. J. (2017). *Recent Cephalopod Primary Type Specimens: a Searching Tool*. Available online at: https://cephalopoda.org (accessed 04 July 2019).

Sweeney, M. J., and Roper, C. F. (1998). Classification, type localities, and type repositories of recent Cephalopoda. *Smith. Contr. Zool.* 586, 561–595.

Trifinopoulos, J., Nguyen, L. T., Von Haeseler, A., and Minh, B. Q. (2016). W-IQ-TREE: a fast-online phylogenetic tool for maximum likelihood analysis. *Nucl. Acids Res.* 44, W232–W235. doi: 10.1093/nar/gkw256

Voight, J. R. (1997). Cladistic analysis of the octopods based on anatomical characters. *J. Moll. Stud.* 63, 311–325. doi: 10.1093/mollus/63.3.311

Voss, G. L. (1981). A redescription of *Octopus ornatus* Gould, 1852 (Octopoda: Cephalopoda) and the status of *Callistoctopus* Taki, 1964. *Proc. Biol. Soc. Wash.* 94, 525–534.

Xia, X. (2017). DAMBE6: new tools for microbial genomics, phylogenetics, and molecular evolution. *J. Heredity* 108, 431–437. doi: 10.1093/jhered/esx033

Young, R. E., Vecchione, M., and Donovan, D. T. (1998). The evolution of coleoid cephalopods and their present biodiversity and ecology. *South Afr. J. Mar. Sci.* 20, 393–420. doi: 10.2989/025776198784126287

Zhang, J., Kapli, P., Pavlidis, P., and Stamatakis, A. (2013). A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29, 2869–2876. doi: 10.1093/bioinformatics/btt499