

Global biodiversity of the genus *Ommastrephes* (Ommastrephidae: Cephalopoda): an allopatric cryptic species complex

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Received 21 August 2019; revised 30 December 2019; accepted for publication 2 February 2020

Cryptic speciation among morphologically homogeneous species is a phenomenon increasingly reported in cosmopolitan marine invertebrates. This situation usually leads to the discovery of new species, each of which occupies a smaller fraction of the original distributional range. The resolution of the taxonomic status of species complexes is essential because species are used as the unit of action for conservation and natural resource management politics. Before the present study, *Ommastrephes bartramii* was considered a monotypic cosmopolitan species with a discontinuous distribution. Here, individuals from nearly its entire distributional range were evaluated with mitochondrial DNA (cytochrome *c* oxidase subunit I and 16S rRNA). Four distinct species were consistently identified using four molecular species delimitation methods. These results, in combination with morphological and metabolic information from the literature, were used to resurrect three formerly synonymized names (*Ommastrephes brevimanus*, *Ommastrephes caroli* and *Ommastrephes cylindraceus*) and to propose revised distributional ranges for each species. In addition, diagnostic characters from the molecular sequences were incorporated in the species description. At present, only one of the four newly recognized species (*Ommastrephes bartramii*) is commercially exploited by fisheries in the North Pacific, but it now appears that the distributional range of this species is far smaller than previously believed, which is an essential consideration for effective fisheries management.

ADDITIONAL KEYWORDS: Cephalopoda – *Ommastrephes brevimanus* – *Ommastrephes caroli* – *Ommastrephes cylindraceus* – phylogeny – systematics – taxonomy.

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[Version of record, published online 19 March 2020; <http://zoobank.org/urn:lsid:zoobank.org:pub:69C6D660-9970-4ED0-943E-067F183867B9>]

INTRODUCTION

Traditionally, species descriptions were based solely on morphological characters. However, reliance on morphological characters alone can overlook species

that evolved and developed genetic barriers (e.g. habitat, life history or recognition systems) without a parallel morphological differentiation, leading to species complexes (Knowlton, 1993). Species complexes can be either cryptic (i.e. there are no morphological differences) or pseudocryptic (i.e. there are morphological differences that might be overlooked or considered as intraspecific variation owing to mistaken or overconservative taxonomic practices). For marine animals, this situation is common owing to the long-standing general belief that the oceanic realm is a continuum, devoid of barriers for genetic exchange. As a result, many marine taxa with relatively homogeneous morphology have been assigned to species described previously from a distant place (e.g. Carrera-Parra *et al.*, 2011) or several similar species from distant areas have been synonymized under a single cosmopolitan morphospecies, but in fact represent different biological species (e.g. Valdés *et al.*, 2017). With a recent increase in the inclusion of molecular tools in taxonomy, it was revealed that many 'cosmopolitan' species in fact represent multiple morphologically similar species (e.g. Kawauchi & Giribet, 2010). This is a direct consequence of physical barriers to dispersal in marine environments and several biological and physiological factors that affect the dispersal capabilities in species.

Conservation and natural resource management are limited by taxonomic resolution. However, recently there appears to be an increase in the recognition of cryptic species of marine invertebrates, which typically results in species that occupy a small portion of the original distribution described for the previously cosmopolitan species (e.g. Bickford *et al.*, 2007; Calvo *et al.*, 2009; Amor *et al.*, 2017). Given that conservation and resource management politics work at the species level, it is especially important to ascertain how many cryptic species are involved in problematic taxa and to describe and name the newly discovered species (Templado *et al.*, 2016). However, owing to practical reasons or journal requirements (Jörger & Schrödl, 2013), many researchers postpone formal description of discovered cryptic species, and they remain unnamed and, therefore, excluded from conservation planning and natural resource management.

Squids of the family Ommastrephidae Steenstrup, 1857 are considered the most economically and commercially important cephalopods worldwide (Roper *et al.*, 2010). Their abundance, rapid growth and massive body size make them one of the most exploited invertebrate fishing resources (Arkhipkin *et al.*, 2015b). Ecologically, these oceanic squids are both important prey (Romeo *et al.*, 2012) and predators (Villanueva *et al.*, 2017), occupying a wide range of trophic levels in marine pelagic food webs (Coll *et al.*, 2013). They are

characterized by a short life span, usually < 2 years (Arkhipkin *et al.*, 2015a), and by a unique paralarval phase known as rhynchoteuthion (Roper *et al.*, 2010; Fernández-Álvarez *et al.*, 2017), with a detritivore diet (Fernández-Álvarez *et al.*, 2018a). The neon flying squid, *Ommastrephes bartramii* (Lesueur, 1821), is the second largest representative of the family, exceeded in size only by the Humboldt flying squid, *Dosidicus gigas* (d'Orbigny, 1835). Neon flying squids can reach a maximal size of 1020 mm in dorsal mantle length (DML) and 35 kg in weight (Guerra *et al.*, 2010), but usually attain smaller sizes. *Ommastrephes* d'Orbigny, 1834 is currently considered a monotypic genus with a cosmopolitan distribution, with three distinct populations defined by region (Nesis, 1987; Roper *et al.*, 2010): the North Atlantic, the Southern Hemisphere and the North Pacific. These undescribed populations were defined according to differences in the size structure (Zalygalin *et al.*, 1983), the spermatophore structure (Nigmatullin *et al.*, 2003) and the substrate-inhibitory traits of optic ganglia cholinesterases (Shevtsova *et al.*, 1979; Rozengart & Basova, 2005). These morphological and metabolic differences have created some doubts regarding the taxonomic accuracy of considering the genus *Ommastrephes* to be monotypic. Some literature before the 1990s considered at least two species to exist within the genus (e.g. Roper *et al.*, 1984; Lozano Soldevilla & Franquet Santaella, 1986; Clarke, 2003). The ocean basins inhabited by *Ommastrephes* are also fragmented (Roper *et al.*, 2010), containing geographical barriers that might lead to speciation events. The aim of this study, therefore, was to use molecular analyses of two mitochondrial markers in order to resolve this long-standing debate among the cephalopod research community.

MATERIAL AND METHODS

SAMPLE COLLECTION

Ommastrephes samples were obtained from local markets (specimen ICMC000070), from land strandings or were collected by jigging during the Atlantic research cruises MAFIA (Olivar *et al.*, 2017) and BATHYPELAGIC. After collection, a small piece of the mantle was preserved in 96% ethanol for molecular analysis. In some cases, a morphological voucher was preserved in 4% buffered seawater formalin and deposited in the following collections: the Biological Reference Collections of the Institut de Ciències del Mar (Barcelona, Spain; CBR-ICM); Museu Oceanográfico of the Rio Grande Federal University (Rio Grande, Rio Grande do Sul, Brazil; MORG); the Central Marine Fisheries Research Institute (Kerala, India; CMFRI); and the National Museum of New

Table 1. Sample data of the *ommastrephid* squid individuals studied, including their accession numbers for GenBank and the morphological vouchers

Species	Locality	N	Voucher accession number	GenBank accession number		Reference
				COI	16S	
<i>Ommastrephes</i> group 1	Arguineguín, Las Palmas de Gran Canaria, Spain; NE Atlantic	1	ICMC000070*	MK995126	–	This study
	Gijón, Asturias, Spain; NE Atlantic	1	Whole specimen: Parque de la Vida (La Mata, Asturias, Spain; http://www.parquedelavida.org)*. Tissue snips: ICMC000398* Whole specimen: Parque de la Vida (La Mata, Asturias, Spain; http://www.parquedelavida.org)*. Tissue snips: ICMC000399*	MK995127	MK991813	This study
	Colunga, Asturias, Spain; NE Atlantic	1	Whole specimen: Parque de la Vida (La Mata, Asturias, Spain; http://www.parquedelavida.org)*. Tissue snips: ICMC000398*	MK995128	–	This study
	40.12°N, 19.99°W, NE Atlantic	1	ICMC000110*	MK995129	MK991814	This study
	Luka Šipanska, Island of Šipan, Croatia; Mediterranean Sea	1	–	KF212462	–	Franjevic <i>et al.</i> (2015)
<i>Ommastrephes</i> group 2	Selvagem Grande island, Portugal; NE Atlantic	8	–	–	KC603479, KC603482–KC603484, KC603486–KC603489	Alonso <i>et al.</i> (2014)
	Cape Verde. 18.11°N, 20.20°W, E Tropical Atlantic	1	ICMC000059*	MF980596	MK991815	Fernández-Álvarez <i>et al.</i> (2018a); this study
	Parana State, Brazil. 25.86°S, 45.75°W, SW Atlantic	4	ICMC000400*, MORG 51418*	MK995138–MK995141	MK991824–MK991827	This study
	S Atlantic	6	–	–	AB635411–AB635416	Wakabayashi <i>et al.</i> (2012b)
	40.20°S, 58.41°E, SW Indian Ocean	2	DE.2.1.5.4.2 and DE.2.1.5.4.3*	MK995134–MK995135	MK991820–MK991821	This study
<i>Ommastrephes</i> group 3	30.95°S, 57.52°E, SW Indian Ocean	4	DE.2.1.5.4, DE.2.1.5.4.1, DE.2.1.5.4.4, DE.2.1.5.4.5*	MK995132–MK995133, MK995136–MK995137	MK991818–MK991819, MK991822–MK991823	This study
	34–36°N, 40–50°E, SW Indian Ocean	2	–	–	AB635465–AB635466	Kurosaka <i>et al.</i> (2012)
	Mangaia, Cook Islands (William F. Gilly, pers. comm.); Central S Pacific	2	–	HQ829183, HQ829184	HQ829182	Unpublished

Table 1. Continued

Species	Locality	N	Voucher accession number	GenBank accession number		Reference
				COI	16S	
<i>Ommastrephes</i> group 4	Princess Bay, Wellington, New Zealand; SW Pacific	1	NMNZ M.318162 [¶]	MK995130	MK991817	This study
	Off Manukau Harbour entrance, New Zealand; SW Pacific	1	NMNZ M.318203 [¶]	MK995131	MK991816	This study
	Rapa Nui, Chile; SE Pacific	1	–	MH347315	–	Carrasco <i>et al.</i> (2018)
	Cruise Hokusei-Marui, NW Pacific	1	–	AF000057	–	Carlini <i>et al.</i> (1999)
	Northern Hawaiian waters, Central N Pacific	2	–	AB199549, AB199551	–	Wakabayashi <i>et al.</i> (2006)
	Cruise Shunyo-Marui, Northern Hawaiian waters, Central N Pacific	1	–	AB270941	–	Wakabayashi <i>et al.</i> (2012a)
	N Pacific	7	–	–	AB635404–AB635410	Wakabayashi <i>et al.</i> (2012b)
	39–46°N, 163–173°W; NW Pacific and Central N Pacific	30	–	–	AB509422–AB509451	Kurosaka <i>et al.</i> (2012)
	<i>Dosidicus gigas</i> (d'Orbigny, 1835)	1	–	–	AB270944	Wakabayashi <i>et al.</i> (2012a)
	<i>Sthenoteuthis pteropus</i> (Steenstrup, 1855)	1	–	–	AB270942	Wakabayashi <i>et al.</i> (2012a)
<i>Sthenoteuthis oualaniensis</i> (Lesson, 1830–1831)	1	–	–	AB270943	Wakabayashi <i>et al.</i> (2012a)	
<i>Eucleoteuthis luminosa</i> (Sasaki, 1915)	1	–	–	AB270945	Wakabayashi <i>et al.</i> (2012a)	
<i>Hyaloteuthis pelagic</i> (Bosc, 1802)	1	–	–	AB270947	Wakabayashi <i>et al.</i> (2012a)	

Coordinates are included only when available.

Abbreviations: COI, cytochrome c oxidase subunit I; 16S, 16S rRNA.

[¶]CBR-ICM, Barcelona, Spain.[†]No voucher accession number available.[‡]Museu Oceanográfico de Rio Grande (Morg), Rio Grande, Brazil.[§]Central Marine Fisheries Research Institute (CMFRI), Kochi-682018, Kerala, India.[¶]National Museum of New Zealand Te Papa Tongarewa (NMNZ), New Zealand.

Zealand Te Papa Tongarewa (Te Aro, Wellington, New Zealand; NMNZ). Information on the locality and GenBank and collection accession numbers is summarized in Table 1.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA was extracted from ethanol-fixed tissue using the NZY Tissue gDNA isolation kit (NZYTech, Lisbon, Portugal), following the manufacturer's protocol, and resuspended in a final volume of 100 µL. A negative control that contained no tissue was included in every round of DNA extraction to check for contamination. Sequences from the partial mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene were amplified using the primer pair LCO1490 and HCO2198 (Folmer *et al.*, 1994). The partial mitochondrial 16S rRNA (16S) fragment was amplified using the primer pair 16sbr-H-myt and 16sar-L-myt (Lydeard *et al.*, 1996). Standard polymerase chain reactions (PCRs) were performed using the NZYTaQ Green PCR Master Mix (NZYTech), following the manufacturer's protocol, in a total volume of 25 µL, which included 0.5 µM of each primer, 25 ng of template DNA and PCR-grade water up to 25 µL. The PCRs consisted of an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 50 °C for *COI* and 45 °C for 16S for 30 s and extension at 72 °C for 45 s, with a final extension of 5 min at 72 °C. The amplified products were sequenced using both forward and reverse PCR primers on an ABI 3730xl sequencer. DNA sequence data were edited and aligned with GENEIOUS v.8.1.5 (<http://www.geneious.com>). Ommastrephid squids have duplicated regions of the mitochondrial genome, including the gene *COI* (Yokobori *et al.*, 2004; Staaf *et al.*, 2010). Although it is assumed that concerted evolutionary mechanisms apply in ommastrephid mitochondria (Allcock *et al.*, 2015), several variable positions were found. The International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes were used to codify these nucleotide variable positions, as in the study by Fernández-Álvarez *et al.* (2015a).

PHYLOGENETIC ANALYSIS

Sequences generated in the present study and available in GenBank from previous studies were used for the development of *COI* and 16S rRNA databases (Table 1). Sequences lacking locality data or with *COI* sequences with stop codons or indels were excluded from our analysis. The final alignment included 25 individuals for *COI* and 69 individuals for 16S. Sequences were aligned manually using the software BIOEDIT v.7.0.1 (Hall, 1999). Sequences were trimmed to be the same

length, resulting in 612 and 467 bp alignments for *COI* and 16S, respectively. For the 16S alignment, a single gap needed to be added to the sequence KC603489 owing to the presence of a single nucleotide deletion.

As a preliminary species delimitation analysis, the software TCS v.1.21 (Clement *et al.*, 2000) was used to construct the haplotype networks with a maximal connectivity limit of 95% with the *COI* database. This analysis resulted in four separate networks that were named as *Ommastrephes* groups 1–4 to simplify the nomenclature (Table 1). This nomenclature was applied to both matrices. The TCS function of the software PopART (Leigh & Bryant, 2015) was used to represent the statistical parsimony networks. Uncorrected *p*-distances within each *Ommastrephes* group and between groups were calculated with MEGA v.6.06 (Tamura *et al.*, 2013) for both molecular markers. The online version of the software Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012) was used to check the distribution and size of a potential barcoding gap for both databases.

The phylogenetic relationships of Ommastrephidae are not yet fully resolved. According to different authors, the sibling genus of *Ommastrephes* might be either *D. gigas* or *Sthenoteuthis* spp. (Lindgren *et al.*, 2012; Strugnell *et al.*, 2017; Pardo-Gandarillas *et al.*, 2018). Uncorrected *p*-distances of both *COI* and 16S show a closer relationship between *Ommastrephes* and *D. gigas* (F.Á.F.-Á., pers. obs.). This species was selected as the outgroup for the phylogenetic analyses. Both gene regions were also analysed using Poisson tree processes (PTP; Zhang *et al.*, 2013). The starting maximum likelihood (ML) trees were constructed with the online version of RaxML (<https://raxml-ng.vital-it.ch/#/>) using the GTR gamma model, with bootstrap values calculated from 100 replicates. The obtained tree was visualized and converted to Newick format using FigTree v.1.4.3 (Rambaut, 2006–2009) and submitted to the PTP portal (<http://species.h-its.org/ptp/>). The default parameters and 300 000 Markov chain Monte Carlo generations were used.

In this work, the unified species concept (De Queiroz, 2007) was applied. The concordance of results of molecular species delimitation methods was considered as confirmation of the reproductive isolation between groups and therefore the species status for each *Ommastrephes* group.

DNA DIAGNOSTIC CHARACTERS

DNA sequences contain valuable diagnostic characters for species descriptions, especially when species complexes are involved. Here, *COI* and 16S rRNA were examined for diagnostic characters. Diagnostic molecular characters are nucleotides in a

specific position and gene region that are the same in all individuals examined for a single species and consistently distinct from all other known species (autapomorphies). Only homogeneous characters were considered. Special care was taken to avoid the inclusion of plesiomorphic characters as diagnostic characters by the inclusion of the putative sister species of the genus (*D. gigas*; see above) and the remaining members of the subfamily Ommastrephinae Posselt, 1891, as outgroups (Table 1). For the presentation of the results and to ensure the reproducibility of this work, the general recommendations of Jönger & Schrödl (2013, 2014) were followed. To ensure transparency in our selection of diagnostic nucleotides, the alignments of *COI* and 16S matrices are provided (Supporting FASTA Files S1 and S2, respectively).

RESULTS

The haplotype parsimony statistical network analysis of *COI* identifies four groups with conspicuous geographical patterns (Fig. 1A). *Ommastrephes* group 1 includes exclusively North Atlantic individuals, and 45 mutations separate it from the closest group. *Ommastrephes* groups 2–4 are more closely related, with 15–20 mutations between them. *Ommastrephes* group 2 is represented by individuals from Tropical and South Atlantic and South Indian waters, whereas groups 3 and 4 occur exclusively in the South and North Pacific, respectively. The *COI* intragroup *p*-distances range from 0.0 to 0.8% (Table 2), whereas intergroup *p*-distances are 2.4–9.0% (Table 3). The ABGD analysis of *COI* identifies four groups (prior maximal distance $P = 0.001$) and a clear barcoding gap between intra- and intergroup distances. Although there is a tendency to group the sequences by geographical origin, the statistical parsimony network analysis of the 16S database (Fig. 1B) reveals a pattern that is not as clear as for *COI*. The four *Ommastrephes* networks are separated by two to five mutations. Intragroup and intergroup distances are 0.0–0.9 and 0.7–1.9%, respectively (Tables 2 and 3); therefore, there is an overlap between the maximal intraspecific distance and the minimal interspecific distance for 16S.

The ML analyses of *COI* reveal four clades consistent with the four *Ommastrephes* groups identified in the haplotype parsimony analysis (Fig. 2). *Ommastrephes* groups 2 and 3 are recovered as sister taxa, *Ommastrephes* group 4 is the sister group of this clade, and *Ommastrephes* group 1 is the sister group of the clade formed by groups 2–4. Bootstrap values of each group are high (96–98%), with the exception of *Ommastrephes* group 4 (68%). The PTP analysis recovers four species, which are consistent

with the four clades revealed in the ML analyses. The ML analysis of 16S shows two well-supported clades formed by *Ommastrephes* group 1 and another clade formed by the remaining *Ommastrephes* sequences (data not shown). The PTP analysis for 16S recovers two species consistent with two clades from the ML analysis. This indicates that 16S might be too conserved to resolve the taxonomy of this genus. Figure 2 summarizes the results of all the species molecular delimitation methods for *COI* [haplotype networks (TCS), *p*-distance, ABGD and PTP] and the TCS and PTP analyses for 16S.

For *COI*, a total of 23 diagnostic positions are identified (Table 4). *Ommastrephes* group 1 has 16 diagnostic positions, whereas *Ommastrephes* groups 2, 3 and 4 have four, three and one diagnostic position, respectively. No diagnostic positions for 16S are recognized in *Ommastrephes* groups 1 and 4, but one is identified for group 2 (435, G) and one for group 3 (16, C) (Table 5). It is important to note that diagnostic characters (as considered here) are not the only variable positions among species, because only homogeneous autapomorphies were considered.

DISCUSSION

SPECIFIC BIODIVERSITY OF THE GENUS *OMMASTREPHESES*

Previous empirical studies have shown that individuals assigned to a statistical parsimony network with a 95% probability for *COI* correspond to species (Pons *et al.*, 2006; Hart & Sunday, 2007; Bond & Stockman, 2008; Kang *et al.*, 2015). Statistical parsimony network analysis of *COI* in the present study with 95% confidence intervals identified four isolated groups with a recognizable geographical pattern: north-east Atlantic samples belong to group 1; eastern tropical and South Atlantic together with south Indian samples belong to group 2; South Pacific samples belong to group 3; and north-western and central-north Pacific individuals belong to group 4 (Fig. 1). This pattern is also found in the statistical parsimony networks of 16S. The maximal intragroup *COI* *p*-distance is 0.8% (Table 2), whereas intergroup distances range from 2.4 to 9.0% (Table 3), suggesting the existence of a barcoding gap. This is supported by the recognition of four different groups with the ABGD analysis. Similar distances have been reported between several other cephalopods, such as octopuses (Allcock *et al.*, 2011) and bobtail squids (Gebhardt & Knebelberger, 2015), and in other invertebrates, such as land planarians (Lago-Barcia *et al.*, 2015), crustaceans (Robles *et al.*, 2007) and annelids (Tomioka *et al.*, 2016), even including

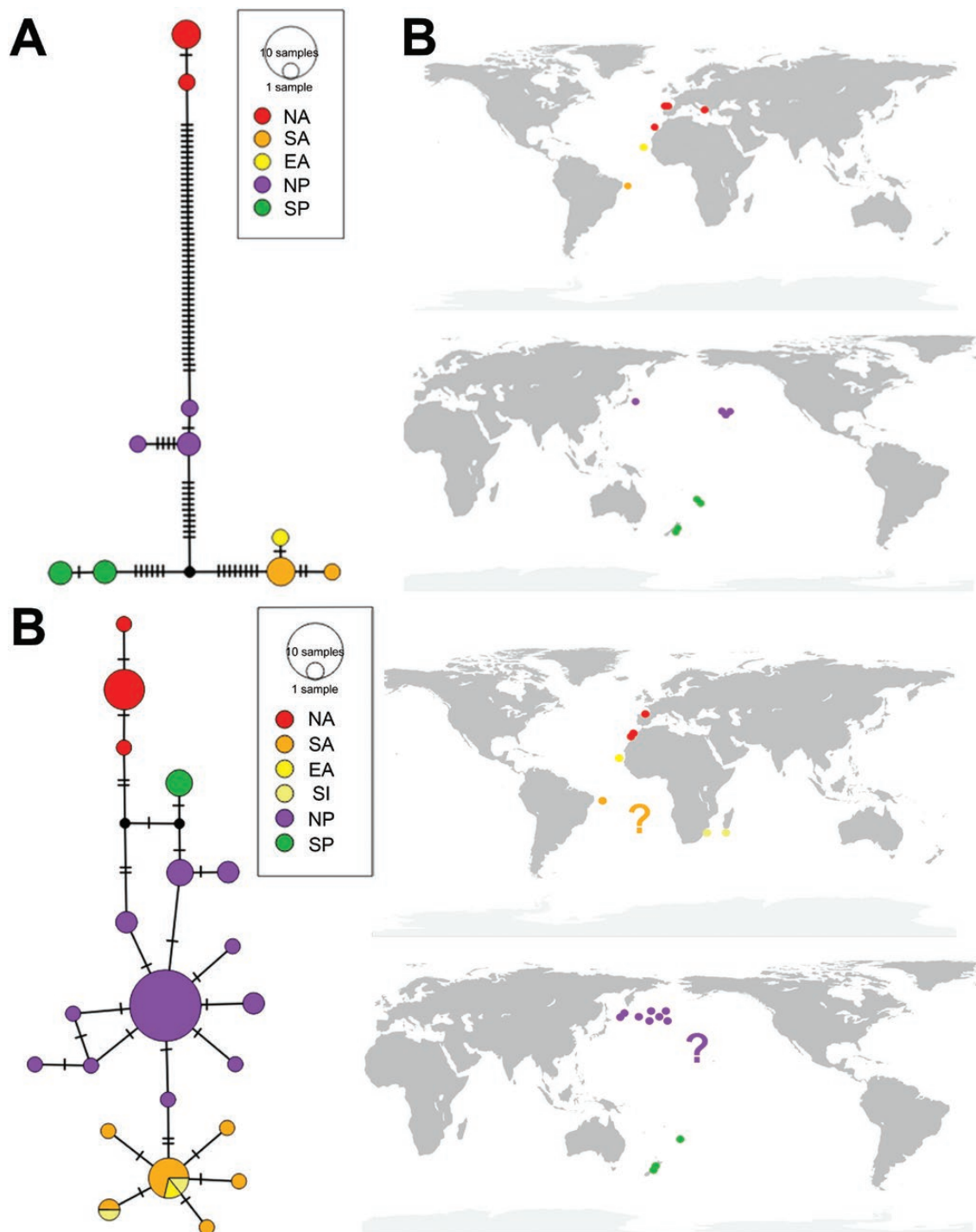


Figure 1. Haplotype statistical parsimony networks constructed by the TCS function of PopART. The geographical origins of the samples are indicated on the map. For GenBank records, the approximate geographical position was inferred when necessary. A, cytochrome *c* oxidase subunit I (*COI*). B, map depicting the localities sampled for *COI*. C, 16S rRNA (16S). D, map depicting the localities sampled for 16S. Abbreviations: EA, eastern tropical Atlantic; NA, North Atlantic; NP, North Pacific; SA, South Atlantic; SI, Indian; SP, South Pacific.

Table 2. Intraclade p -distances (expressed as percentages) among *Ommastrephes* groups for two mitochondrial gene regions [cytochrome c oxidase subunit I (COI) and 16S rRNA (16S)]

Gene region	Mean	Range	N
<i>COI</i>			
<i>Ommastrephes</i> group 1	0.1	0–0.3	5
<i>Ommastrephes</i> group 2	0.1	0–0.5	11
<i>Ommastrephes</i> group 3	0.1	0–0.2	5
<i>Ommastrephes</i> group 4	0.4	0–0.8	4
16S			
<i>Ommastrephes</i> group 1	0.1	0–0.4	10
<i>Ommastrephes</i> group 2	0.2	0–0.4	19
<i>Ommastrephes</i> group 3	0	0	3
<i>Ommastrephes</i> group 4	0.2	0–0.9	37

Table 3. Interclade mean p -distances (expressed as percentages) between *Ommastrephes* groups for two mitochondrial gene regions [cytochrome c oxidase subunit I (COI) and 16S rRNA (16S)]

Gene region			
<i>COI</i>			
<i>Ommastrephes</i> group 1	–	–	–
<i>Ommastrephes</i> group 2	8.8	–	–
<i>Ommastrephes</i> group 3	9.0	2.4	–
<i>Ommastrephes</i> group 4	7.8	3.4	3.1
16S			
<i>Ommastrephes</i> group 1	–	–	–
<i>Ommastrephes</i> group 2	1.9	–	–
<i>Ommastrephes</i> group 3	1.1	1.3	–
<i>Ommastrephes</i> group 4	1.3	0.8	0.7

minimal interspecific distances of ~1% in closely related freshwater mites (García-Jiménez *et al.*, 2017). The 16S p -distances are lower between *Ommastrephes* groups (Table 3), a phenomenon frequently reported for other animals in the literature (e.g. Hebert *et al.*, 2003; Rodríguez-Flores *et al.*, 2017). Although a small overlap between intra- and intergroup distances is found between 16S sequences (Tables 2 and 3), it is important to note that each geographical region has unique haplotypes that do not occur in other areas (Fig. 1B), which also supports the hypothesis of allopatric reproductive isolation. The 16S PTP analysis is able to isolate only *Ommastrephes* group 1, the most divergent species in the genus, as distinct from the other species (Fig. 2). Consequently, this indicates that 16S rRNA is too conserved to delimit species of *Ommastrephes*. The combined evidence presented here suggests that

each *Ommastrephes* group should be considered a single, geographically isolated species. This vision is reinforced by the fact that the phylogenetic analysis and most of the molecular species delimitation molecular methods recognize four groups consistent with the haplotype network analyses (Fig. 2).

Beyond molecular characters, differences known among specimens from different regions include their size structure (Zalygalin *et al.*, 1983; Nigmatullin *et al.*, 2003), spermatophore morphology (Nigmatullin *et al.*, 2003) and substrate-inhibitory traits of optic ganglia cholinesterases (Shevtsova *et al.*, 1979, Rozengart & Basova, 2005). The morphology of the copulatory organ (the hectocotylus) can also have a high importance for cephalopod taxonomy. The detailed morphology of the hectocotylized arm (including index of modified part length; number and size of suckers; and the type, number and size of teeth in the chitinous rings of the sucker) in mature males from different parts of the genus range (North Pacific, two males; South Pacific, eight males; South Atlantic, two males; and North Atlantic, three males) was studied during the USSR integrated target program ‘SQUID’ during the 1980s. No significant differences were observed among specimens from different areas (C.M.N, pers. obs.). *Ommastrephes* group 4, which occurs in the North Pacific, is distinguished from other congeners by the small maximal size of females at maturity (Roper *et al.*, 2010). It is important to indicate that maximal size at maturity does not generally represent a good taxonomic character for ommastrephid squids, because it is variable at the intraspecific level in most species. For instance, in the related species *D. gigas*, the smallest females mature at only 12% of the mantle length of the largest ones (Nigmatullin *et al.*, 2001), and this difference might occur inter-annually in members of the same geographical area (Hoving *et al.*, 2013, 2019; Fernández-Álvarez *et al.*, 2018b). North Atlantic *Ommastrephes* have larger spermatophores (≤ 53 mm, whereas other *Ommastrephes* species have a maximal length of 41 mm), which are distinguished from those of other species by the morphology of the cement body, sperm reservoir and posterior empty part (Nigmatullin *et al.*, 2003; Sabirov & Nigmatullin, 2012). Furthermore, these differences are more pronounced between *Ommastrephes* group 1 (North Atlantic *Ommastrephes*) and the other *Ommastrephes* species than they are among some other ommastrephid genera (Nigmatullin *et al.*, 2003). These morphological differences are also consistent with the fact that *Ommastrephes* group 1 is the most phylogenetically divergent of the groups in all our phylogenetic analyses (Figs 1, 2; Table 3) and has more diagnostic molecular characters (Table 4). Therefore, it appears that this species has had a longer evolutionary history isolated from the remaining congeneric species. Given

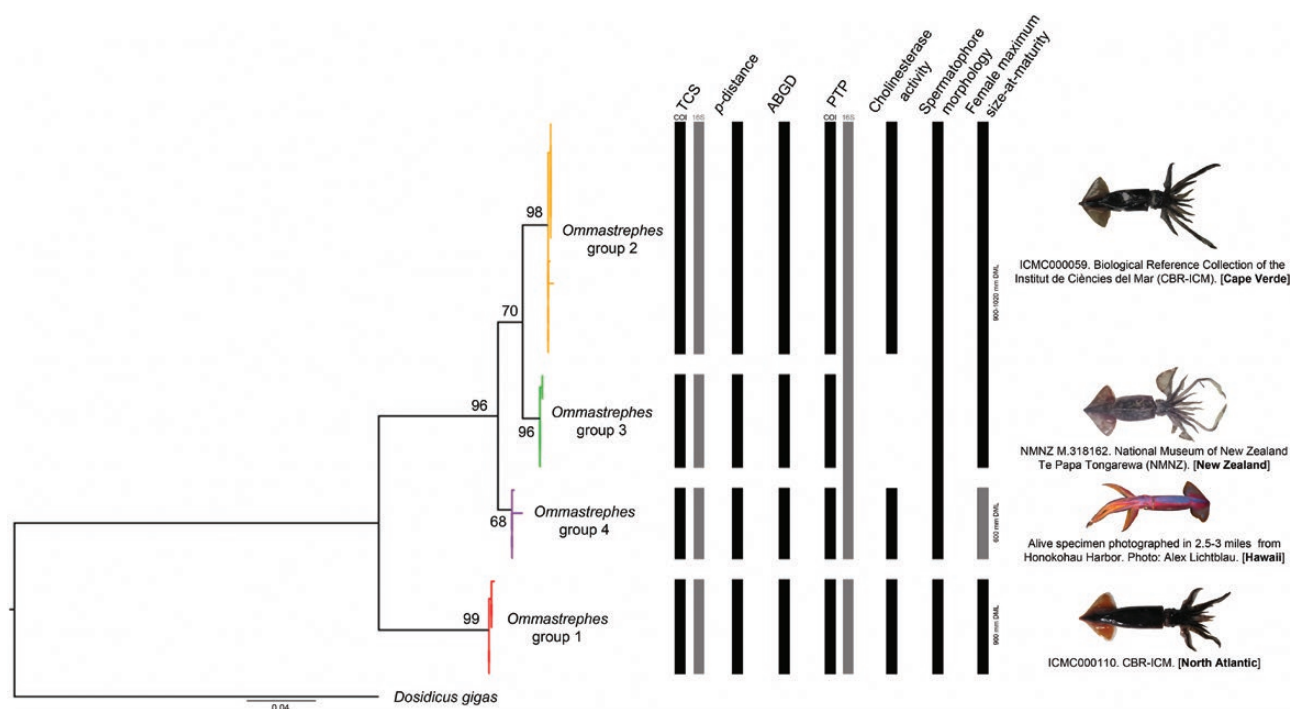


Figure 2. Summarized results from the molecular species delimitation analyses and the enzymatic and morphological information, represented on the maximum likelihood tree resulting from the analysis of the cytochrome *c* oxidase subunit I (*COI*) dataset. Values on the nodes represent the bootstrap values for *COI*. Black and grey bars to the right represent the hypothesized species groupings based on the molecular delimitation results of TCS, *p*-distances, ABGD and PTP for *COI*, and TCS and PTP for 16S rRNA (16S), in addition to the previously identified groups from the literature based on the differences in substrate and inhibitor specificity of cholinesterase activities of the optical ganglia (after Shevtsova *et al.*, 1979; Rozengart & Basova, 2005), the spermatophore morphology (after Nigmatullin *et al.*, 2003) and the maximal size at maturity of females (Roper *et al.*, 2010). It is important to note that Shevtsova *et al.* (1979) and Rozengart & Basova (2005) did not include any South Pacific individuals in their studies.

that morphological differences are known at least in the spermatophore between this species and the remaining ones, it could be considered a pseudocryptic species. As no important morphological differences have been found to distinguish the remaining species, they appear to be cryptic. Shevtsova *et al.* (1979) and Rozengart & Basova (2005) compared the differences in substrate- and inhibitor-specific cholinesterase activities of optical ganglia among *Ommastrephes* individuals from four geographical locations: the North Atlantic, the South Atlantic, the Great Australian Bight (south-eastern Indian Ocean) and the North Pacific. They found significant differences for these metabolic traits between specimens from all the studied geographical areas with the exception of the South Atlantic and south-western Indian Ocean *Ommastrephes* specimens. None of their specimens came from South Pacific waters, where *Ommastrephes* group 3 occurs (and thus was not represented in Fig. 2). The differences in metabolic traits are interpreted as another source of evidence to support the specific status of each *Ommastrephes* group.

Subadult and adult ommastrephid specimens are nektonic organisms able to perform large-scale horizontal oceanic migrations (Markaida *et al.*, 2005). Migrations related to feeding and reproductive grounds have been described for the North Pacific *Ommastrephes* (Ichii *et al.*, 2009). However, the first ontogenetic stages of ommastrephids are planktonic, representing one of the smallest cephalopod hatchlings recorded (mantle length of 1–2 mm; Villanueva *et al.*, 2016), and paralarval dispersion is likely to be limited by oceanic features, such as the main oceanic gyres and currents. In addition, hatching size is inversely related to cephalopod distributional ranges (Villanueva *et al.*, 2016). Consequently, the distributional range of *Ommastrephes* spp. seems to be shaped mainly by the Equatorial oceanic currents (Fig. 3) and surface water temperatures (Roper *et al.*, 2010). The boundary between *Ommastrephes* group 3 and 4 is likely to be formed by the Pacific Equatorial currents. The distributional boundary between Atlantic *Ommastrephes* groups 1 and 2 seems to be influenced by the Canary and Atlantic Equatorial currents, because Canary and Azores specimens belong

Table 4. Molecular diagnostic characters obtained from cytochrome *c* oxidase subunit I (*COI*)

Position	<i>Ommastrephes</i>				Outgroups					
	Group 1	Group 2	Group 3	Group 4	<i>Dosidicus gigas</i>	<i>Sthenoteuthis pteropus</i>	<i>Sthenoteuthis oualaniensis</i>	<i>Euclideanoteuthis luminosa</i>	<i>Hyaloteuthis pelagica</i>	
6	T	A	A	A	A	G	A	A	A	
30	A	G	A	A	A	T	A	A	A	
36	A	A	G	A	A	A	A	A	A	
48	G	T	T	T	A	A	A	A	A	
60	T	T	C	T	T	T	T	T	T	
81	A	T	T	T	C	T	T	T	T	
103	A	G	A	A	A	A	A	A	A	
153	G	A	A	A	A	A	A	A	A	
159	G	C	C	C	C	T	T	T	T	
177	C	A	A	A	A	A	G	A	A	
198	G	A	A	A	A	A	A	A	A	
228	G	C	C	C	T	T	T	T	T	
258	C	G	G	G	T	T	T	T	T	
273	G	A	A	A	A	A	A	C	A	
306	C	A	T	T	T	C	T	T	T	
334	G	A	A	A	A	A	A	A	A	
366	C	T	T	T	T	T	T	T	T	
429	G	A	A	A	A	A	A	A	A	
432	C	G	G	G	T	T	A	G	T	
450	A	A	G	A	A	A	A	A	A	
454	T	T	T	C	T	T	T	T	T	
493	C	T	C	C	C	C	C	C	C	
534	G	A	A	A	C	A	A	T	A	
573	G	T	T	T	A	T	A	A	A	

Diagnostic characters are shown in bold. The alignment is provided in [Supporting FASTA File S1](#) to name each nucleotide position unambiguously.

Table 5. Molecular diagnostic characters obtained from 16S rRNA (16S)

Position	<i>Ommastrephes</i>				Outgroups				
	Group 1	Group 2	Group 3	Group 4	<i>Dosidicus gigas</i>	<i>Sthenoteuthis oualaniensis</i>	<i>Euclideanoteuthis luminosa</i>	<i>Hyaloteuthis pelagica</i>	<i>Hyaloteuthis pelagica</i>
16	T	T	C	T	T	T	T	T	T
435	A	G	A	A	A	A	A	A	A

Diagnostic characters are shown in bold. The alignment is provided in [Supporting FASTA File S2](#) to name each nucleotide position unambiguously.

to group 1, whereas the specimen caught near Cape Verde belongs to group 2. These sampling localities are only ~1100–1600 km apart, whereas larger geographical distances (~3500–3600 km) between conspecifics have been confirmed for those *Ommastrephes* species with genetics. Therefore, the Canary and Atlantic Equatorial currents appear to represent the boundary to paralarval distribution between these two species.

There are important conservation, economic and food security (e.g. [Jiao *et al.*, 2018](#)) ramifications for the results of this study. Given that *Ommastrephes* is an important fishing resource exploited commercially in the North Pacific ([Arkhipkin *et al.*, 2015b](#)), it is important to define which species of this complex is being impacted by fishery activities. The North Pacific Ocean contains only *Ommastrephes* group 4 ([Figs 1, 3](#)).

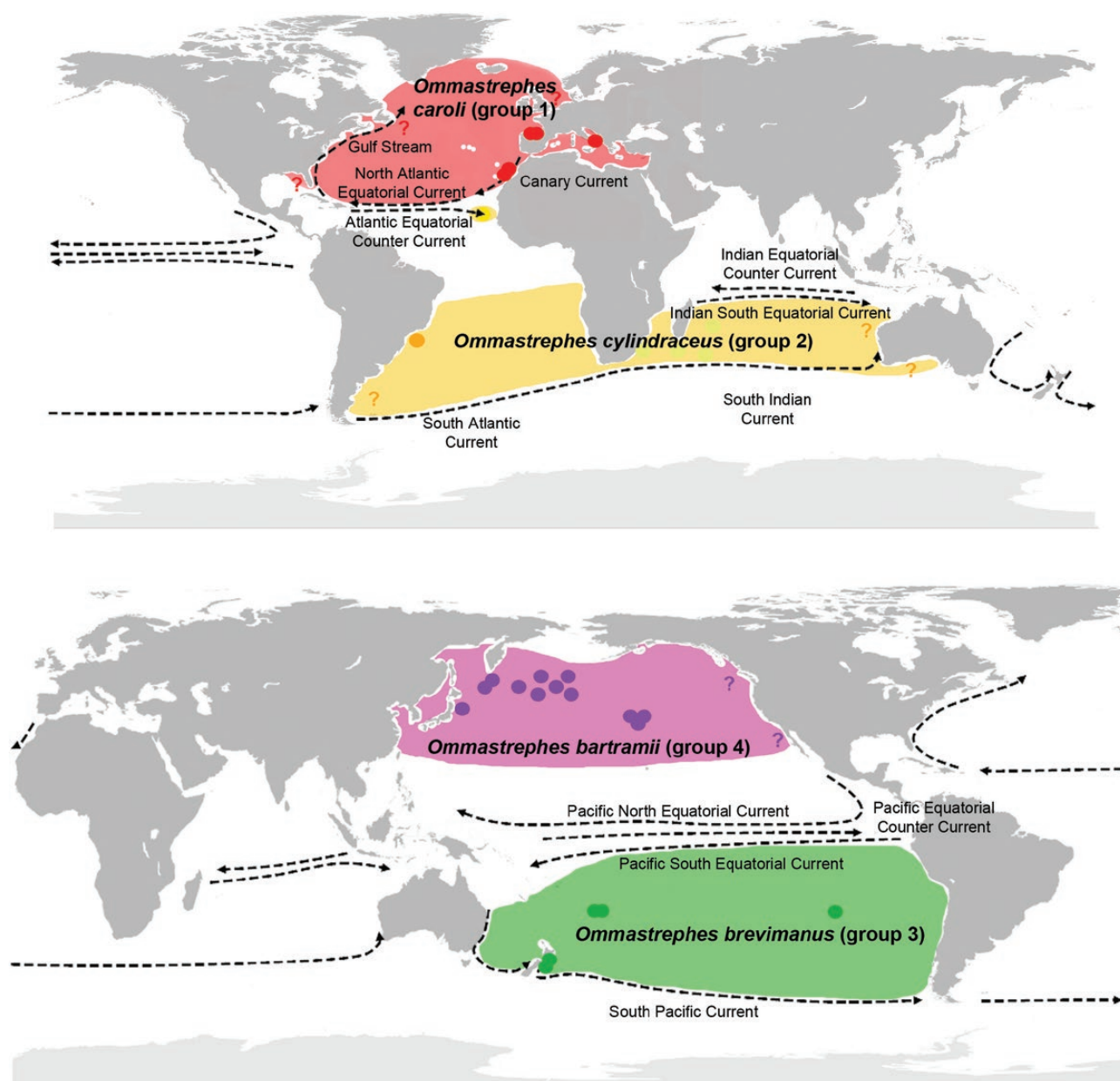


Figure 3. Schematic map of the distributional range of each species of the genus *Ommastrephes*, based on the distribution of the genus depicted by Roper *et al.* (2010) and the results of the present study. Sampled points for both molecular markers are depicted on the map. The oceanic currents that are likely to contribute to the reproductive isolation of each species are depicted. Parts of the distributional range of each species that are not yet confirmed with molecular data are indicated with a question mark.

Although the genus has a circumglobal distribution, it is not targeted commercially outside of the North Pacific, and in other regions it is caught only as bycatch (Battaglia *et al.*, 2010). Given that the operational unit for conservation and natural resource management is the species, the identification, definition and naming of each biological species from taxonomically complex groups is an increasingly important task.

UNTIDYING A GORDIAN KNOT: *OMMASTREPHESES* SPECIES TAXONOMY

Given that new cryptic species are being discovered at an increasing rate (e.g. Jörger & Schrold, 2013), currently many taxonomists agree that future taxonomic descriptions should be integrative (Dayrat, 2005), ideally covering a range of aspects for species delimitation (e.g. morphology, genetics, biogeography

and behaviour). Traditional cephalopod taxonomy involves the use of counts, measures and indices (Roper & Voss, 1983), which were inadequate for distinguishing *Ommastrephes* species (Roper *et al.*, 2010). For *Ommastrephes*, previous morphological works have only revealed important morphological differences in the spermatophore morphology of North Atlantic specimens in comparison to individuals from other regions (Nigmatullin *et al.*, 2003; Sabirov & Nigmatullin, 2012). Herein, molecular diagnostic characters have been integrated into the descriptions, and the geographical range of each species is reported based on the available molecular information. Although the addition of molecular characters is gaining support among researchers working in other animal groups (e.g. Jörger & Schrödl, 2013, 2014; Johnson *et al.*, 2014), as far as we know this is the first time that molecular characters have been included as diagnostic characters in cephalopod species descriptions, although molecular data have commonly been used for detecting new species or solving other taxonomic problems (Allcock *et al.*, 2015). It is important to note that a molecular character was used in the diagnosis of an octopod family previously (Strugnelli *et al.*, 2014: 227).

The phylogenetic analyses (Figs 1, 2; Tables 1–3) support four distinct species of *Ommastrephes* and reveal molecular diagnostic characters for each species (Tables 4 and 5). Therefore, we formally resurrect three previously used species names to split *O. bartramii* into four nominal species (see below). Several additional species names considered previously to be junior synonyms of *O. bartramii* have been researched and, where possible, are listed in synonymy with the appropriate species below. As a primary source of *O. bartramii* synonyms, the compilation of Sweeney & Young (2003) is used as a starting point, followed by a bibliographic review. For objectivity of scientific names, we designated neotypes for three of the species and, when possible, ethanol-fixed tissues were stored in the Biological Reference Collections of the Institut de Ciències del Mar (CBR-ICM; Spain) and National Museum of New Zealand Te Papa Tongarewa (NMNZ; New Zealand).

GENUS *OMMASTREPHE*S D'ORBIGNY, 1834 IN
1834–1847

Ommastrephes d'Orbigny, 1834 in 1834–1847: 45.

Synonyms

(?) *Cycria* Leach in Gray, 1849: 58. Listed as synonym of *Ommastrephes* [*fide* Hoyle (1910: 408)]. Type species with no type given [*fide* Hoyle (1910: 408)]

Lolimnites Risso, 1854: 41. [*fide* Adam (1942: 17)] Type species *Lolimnites meridionalis* Risso, 1854, by monotypy.

Ommastrephes Lovén, 1845: 122. Emendation of *Ommastrephes* d'Orbigny 1834 in 1834–1847 [*fide* Hoyle (1910: 411)].

Type species: *Loligo bartramii* Lesueur, 1821.

Diagnosis: The following diagnosis was adapted from the morphological description of Roper *et al.* (2010); additional paralarval characters have been added following the descriptions of Sweeney *et al.* (1992), Young & Hirota (1990), Sakurai *et al.* (1995) and Vijai *et al.* (2015), as reviewed by Fernández-Álvarez *et al.* (2017).

Maximal mantle length 1020 mm. Mantle wide; posterior end without pronounced pointed tail. Fins rhomboidal; slightly attenuate posteriorly. Fin length 40–50% and width 60–85% of mantle length; fin angle 46–65°. Funnel groove with foveola with five to eight, occasionally nine, longitudinal folds and two to five (usually three or four) distinct side pockets. Small, scattered, subcutaneous photogenic tissue embedded in tissue of mantle, head and ventral arms, without large dorsal mantle photophore or ocular or intestinal photophores. Long, broad, silvery or golden opalescent strip along ventral midline from anterior fin edge to mantle opening and similar ventral strip on ventral surface of head and ventral arms; relatively dense aggregations of small subcutaneous photogenic tissue under opalescent tissue. Arms with 24–35 pairs of arm suckers. Arm tips not attenuate; tips of trabeculae of protective membranes do not project beyond edge of membrane. Ventral protective membranes of arms III wide and in adult females expanded into large, triangular, membranous lobe; in males, right or left ventral arm hectocotylized, with tip lacking suckers. Tentacle suckers covering ~60% of tentacle length. Four to seven suckers with denticulate rings present on carpus proximal to first carpal knob. Carpal-locking apparatus on tentacular stalk with two to five knobs and two to four smooth-ringed suckers. Largest medial manus suckers with four enlarged, pointed teeth, one at each quadrant. Dactylus of tentacular club with four series of small suckers. Cone flags of gladius short, rhomboidal, with distinct radial creases. Greatest width of cone flags ~56% width of rachis. Marginal rigidity ribs of rachis doubled. Axial rigidity rib of rachis wide rounded-rectangular in cross-section. Lateral plates of gladius not adhered to dorsal surface of rachis but forming wide free folds over rachis. Stem of rachis short; width of stem slightly greater than its thickness. Cone short and laterally flattened. Rostrum absent. Thick alveola covered with tiny ribs and thorns. Monoflagellate spermatozoon. Hatchlings with skin sculpture; without ocular or visceral photophores. Two rows of pegs present in proboscis suckers; diameter of lateral proboscis suckers 200% that of central suckers and with unequal number of pegs. Three leaflets in the gills.

OMMASTREPHESES BARTRAMII (LESUEUR, 1821)

Loligo bartramii Lesueur, 1821: 90, pl. 7.

Type material: Academy of Natural Sciences (ANSP). Not extant [*vide* Voss (1962: 1); Lu *et al.* (1995: 312)].

Neotype: National Museum of Nature and Science, Tokyo, specimen NSMT-Mo 67507, mature male, 270 mm DML, collected by squid jigging at 41.95°N, 135.17°W on 8 September 2009.

Type locality: Not designated in the original description. Here it is designated, based on the neotype, as North Pacific waters (Table 1; Fig. 3) (see 'Remarks').

Synonyms

(?) *Loligo touchardii* Souleyet, 1852: 22, pl. 2, figs 6–13 [*vide* Pfeffer (1912: 466)] MNHN Syntype 7-3-724 [*vide* Lu *et al.* (1995: 326)]. Locality: Pacific Ocean.

(?) *Ommastrephes ensifer* Owen, 1881: 144, pl. 28. Type repository unresolved [Royal College of Surgeons, London, UK?]. Type locality not designated.

Diagnosis

Ommastrephes with a maximal mantle length of 600 mm and weight of 6 kg; maximal spermatophore length of 21–41 mm ($9.5 \pm 1.45\%$ DML), cement body of spermatophore 11%, sperm reservoir 44.7% and posterior empty end 22% of spermatophore length; cytochrome *c* oxidase subunit I diagnostic character: 454, C.

Name of the species in the phylogenetic analyses: *Ommastrephes* group 4.

Distribution: Temperate North Pacific, from the coasts of China (25°N) to Russia (60°N) in the west, and probably from Alaska (55°N) to the Gulf of California (20°N) in the east. The distribution has been confirmed using molecular tools for the majority of its range, excluding north-eastern Pacific waters (Fig. 3).

Remarks: *Ommastrephes bartramii* was described as *Loligo bartramii* by Lesueur (1821: 90–92, pl. VII) and was later transferred to the genus *Ommastrephes* by d'Orbigny (1834–1848). In his description, Lesueur did not provide any specific locality for the species, and the type specimen no longer exists (Voss, 1962: 1; Lu *et al.*, 1995: 312). The only reference to the origin of the material he examined is that they came 'from the collection of the academy, and that from the Philadelphia Museum' (Lesueur, 1821: 89). Without

any further accurate reference, it is possible that the material came from the Philadelphia shores and adjacent waters. However, Lesueur also participated in the Baudin Expedition (1800–1803; see Péron & Freycinet, 1816) from Le Havre (France) to Australia, and he might have collected specimens during this cruise, covering the distribution area of *Ommastrephes* groups 1, 2 and 3. Based on the available information, it is not possible to exclude any other specimens that were previously donated to the Philadelphia Museum from other localities. Therefore, the type locality data of the *O. bartramii* type material remains unresolved and uncertain.

Although the type locality remains uncertain, the name '*Ommastrephes bartramii*' has been widely used in the North Pacific, where the only commercial fishery for this squid occurs and where the majority of studies on this genus have been conducted. The International Code of Zoological Nomenclature (ICZN) precludes the substitution of a long-accepted name in its accustomed meaning in order to increase taxonomic stability (ICZN Article 32.2; International Commission on Zoological Nomenclature, 1999). The name *O. bartramii* referring to North Pacific individuals (i.e. *Ommastrephes* group 4) has been used in > 25 works authored by more than ten researchers in the last 50 years (e.g. Young & Hirota, 1990; Sakurai *et al.*, 1995; Ichii *et al.*, 2009, 2017; Vijai *et al.*, 2015; Budyansky *et al.*, 2017; Fang *et al.*, 2017; Feng *et al.*, 2017, 2018a, b, 2019; Igarashi *et al.*, 2017, 2018; McKinnell & Seki, 2017; Tang *et al.*, 2017; Wang *et al.*, 2017; Wen *et al.*, 2017; Yu *et al.*, 2017a, b, 2018, 2019; Hu *et al.*, 2018; Jiao *et al.*, 2018; Ding *et al.*, 2019; Zhang *et al.*, 2019), which is in agreement with the conditions described in the ICZN Article 23.9.1.2. Although *O. bartramii* is the name that has been used commonly for the remaining species in other parts of the distributional range of the genus (recent examples: Franjevic *et al.*, 2015 and Tsiamis *et al.*, 2015 for Mediterranean individuals; Villanueva & Sánchez, 1993 for the South Atlantic; and Guerra *et al.*, 2010 for the South Pacific), these species are far less studied, and consequently, the name is less commonly applied to them. Therefore, either considering the name *O. bartramii* invalid or designating a neotype from a location outside of the North Pacific would generate further taxonomic instability and create problems in tracking the current biological information on the species, instead of solving the taxonomy of the genus.

In order to fix a suitable type locality for the species and ensure the stability of the name, the specimen NSMT-Mo 67507 from the National Museum of Nature and Science (Tokyo) is **hereby designed as a neotype**. The neotype locality is north-east Pacific, 41.95°N, 135.17°W.

OMMASTREPHEs BREVIMANUS (GOULD, 1852)

Onychoteuthis brevimanus Gould, 1852: 483, fig. 596.

Type material: Not extant [*vide* Johnson (1964: 32)].

Neotype: National Museum of New Zealand Te Papa Tongarewa (NMNZ), New Zealand, specimen M.318162, female, 580 mm DML, beached in Princess Bay, Wellington, New Zealand on 24 May 2015. Ethanol-fixed tissues available through the accession number M.318162/1. The GenBank sequences MK995130 (COI) and MK991817 (16S) refer to the neotype.

Type locality: One hundred and twenty miles west of Tutuila, Samoa Islands (south-western Pacific). The neotype was collected in Princess Bay, Wellington, New Zealand. According with the ICZN Article 76.3, the neotype locality becomes the type locality of the species.

Synonyms

Ommastrephes caroli stenodactyla Rancurel, 1976: 81. [*vide* Dunning (1998: 426)].

Type material: Museum National d'Histoire Naturelle (MNHN), Laboratoire Biologie Invertébrés Marins et Malacologie, syntypes 1974, 1975, 1976, 1977 [*vide* Lu *et al.* (1995: 325)].

Type locality: Auameo, Ile des Pins, New Caledonia (south-western Pacific).

Diagnosis

Ommastrephes with a maximal mantle length of 1020 mm and weight of 35 kg; maximal spermatophore length 21–41 mm ($9.5 \pm 1.45\%$ DML), cement body of spermatophore 11%, sperm reservoir 44.7% and posterior empty end 22% of spermatophore length. Cytochrome *c* oxidase subunit I diagnostic characters: 36, G; 60, C; 450, G; 16S rRNA diagnostic character: 16, C.

Name of the species in the phylogenetic analyses: *Ommastrephes* group 3.

Distribution: Tropical and temperate South Pacific. Present in the Kermadec Islands, New Zealand (Braid & Bolstad, 2019).

OMMASTREPHEs CAROLI (FURTADO, 1887) [*NOMEN PROTECTUM*]

Ommastrephes caroli Furtado, 1887: 5, pls 1, 2.

Type material: Kobenhavns Universitet, Zoologisk Museum (ZMUC), syntypes (suckers only) [*vide* Kristensen & Knudsen (1983: 221)].

Type locality: 'Barre de Lisbonne', Portugal (North Atlantic Ocean).

Synonyms

Loligo pironneauii Souleyet, 1852: 20, pl. 2, figs 1–5 [*vide* Pfeffer (1912: 466)] MNHN. Syntype 2-4-402 (gladius only) [*vide* Lu *et al.* (1995: 322)]. *Locality:* 48°N, 22°W of Paris, France (North Atlantic Ocean) [*nomen oblitum*].

Lolimnites meridionalis Risso, 1854: 41, pl. 19, figs 1–3 [*vide* Adam (1942: 18)]. *Locality:* 'Regions profondes', (?) Nice, France (north-western Mediterranean Sea) [*nomen oblitum*].

(?) *Ommastrephes bartrami sinuosus* Lonnberg, 1896: 701. Zoologiska Museet, Uppsala Universitets (ZMUU), holotype 126 [*vide* Wallin (1991: 66)]. *Locality:* Teneriffe, Canary Islands, Spain (North Atlantic).

Diagnosis

Ommastrephes with a maximal mantle length of 900 mm and weight of 25 kg; maximal spermatophore length 21–54 mm ($11.15 \pm 3.5\%$ DML), cement body of spermatophore 9.8%, sperm reservoir 33% and posterior empty end 30.3% of spermatophore length. Cytochrome *c* oxidase subunit I diagnostic characters: 6, T; 48, G; 81, A; 153, G; 159, G; 177, C; 198, G; 228, G; 258, C; 273, G; 334, G; 366, C; 429, G; 432, C; 534, G; 573, G.

Name of the species in the phylogenetic analyses: *Ommastrephes* group 1.

Distribution: North Atlantic, confirmed with molecular tools from the Bay of Biscay (43°N) to Canary Islands (27°N), Azores (40°N) and the Mediterranean Sea (Fig. 3). Also known to occur in the north-eastern Atlantic from the Bay of Biscay, from Scandinavia (60°N) and in the north-western Atlantic from the Gulf of Mexico (24°N) to Nova Scotia (45°N).

Remarks: The name *O. caroli* has been used marginally to refer some North Atlantic *Ommastrephes* specimens during part of the 20th century (e.g. Rees, 1950; Lozano Soldevilla & Franquet Santaella, 1986). To the best of our knowledge, the remaining names that might be resurrected for *Ommastrephes* group 1 have not been used beyond their original descriptions. In accordance with ICZN Article 23.9.1.1, junior synonyms should be applied when the senior synonym or homonym has not been used as a valid name after 1899. It is important

to note that the conditions described in ICZN Article 23.9.1.2 also apply here, because *O. caroli* has been used to refer to members of this species in >25 works authored by more than ten authors in the last 50 years (Threlfall *et al.*, 1971; Young, 1972; Clarke & Lu, 1974; Clarke & Stevens, 1974; Holme, 1974; Roper & Young, 1975; Clarke *et al.*, 1976, 1979; Wormuth, 1976; Roper, 1977; Clarke, 1978; Muntz & Johnson, 1978; Pérez-Gándaras & Guerra, 1978; Arnold, 1979; Roper & Lu, 1979; Guerra & Pérez-Gándaras, 1983; Roper *et al.*, 1984; Guerra, 1985; Martins *et al.*, 1985; Guescini & Manfrin, 1986; Pérez-Gándaras, 1986; Lozano Soldevilla & Franquet Santaella, 1986; Clarke & Maddock, 1988; Mangold & Boletzky, 1988; Vecchione *et al.*, 1989; Vecchione & Roper, 1991; Gouveia, 1992; Clarke, 2003). Therefore, *O. caroli* is hereby designated as *nomen protectum* and conferred on *Ommastrephes* group 1, while *L. pironneauui* and *L. meridionalis* are both considered senior synonyms [*nomina oblita*]. Tissues of the individuals of *O. caroli* according to the sense of this article can be accessed at the Biological Reference Collections of the Institut de Ciències del Mar CBR-ICM, Barcelona, through the accession numbers ICMC000070, ICMC000110, ICMC000398 and ICMC000399.

OMMASTREPHESES CYLINDRACEUS D'ORBIGNY, 1835 IN
1834–1847

Loligo cylindracea d'Orbigny, 1835 in 1834–1847: 54, pl. 3, figs 3, 4.

Type material: MNHN type; specimen not extant [*vide* Lu *et al.* (1995: 314)].

Neotype: Biological Reference Collections of the Institut de Ciències del Mar CBR-ICM, Barcelona, specimen ICMC000400, immature subadult, 144 mm DML, collected by fish jigging at 25.87°S, 45.76°W on 18 December 2014. The GenBank sequences MK995138 (*COI*) and MK991824 (16S) refer to the neotype. Ethanol-fixed tissues from another specimen fished in the same batch are available under the accession code ICMC000401.

Type locality: Austral Atlantic, 35°S, 40°W off Paris, slightly south of Buenos Aires parallel of latitude, Argentina (South Atlantic). The neotype was collected off Ilha Comprida, São Paulo, Brazil. According to ICZN Article 76.3, the neotype locality becomes the type locality of the species.

Synonyms

Loligo cylindricus d'Orbigny, 1835 in 1834–1847: pl. 3, figs 3, 4.

Loligo vitreus Rang, 1837: 71, pl. 96.

Type material: MNHN type; specimen not extant [*vide* Lu *et al.* (1995: 327)].

Type locality: Equatorial coast of Africa (Equatorial Atlantic).

Diagnosis

Ommastrephes with a maximal mantle length of 900 mm and weight of 25 kg; maximal spermatophore length 21–41 mm (9.5 ± 1.45% DML), cement body of spermatophore 11%, sperm reservoir 44.7% and posterior empty end 22% of spermatophore length. Cytochrome *c* oxidase I diagnostic characters: 30, G; 103, G; 306, A; 493, T; 16S rRNA diagnostic character: 435, G.

Name of the species in the phylogenetic analyses: *Ommastrephes* group 2.

Distribution: Tropical and South Atlantic (from 14 to ~50°S) and tropical and south Indian (~10–35°S) waters. A significant part of the distributional range for this species was confirmed with *COI* (Fig. 3), but specimens were not available for genetic analysis from the eastern part of the Indian Ocean or from the southernmost part of the Atlantic Ocean. The absence of differences in substrate- and inhibitor-specific cholinesterase activities of optical ganglia between specimens sampled in the South Atlantic and south-eastern Indian waters reported by Shevtsova *et al.* (1979) and Rozengart & Basova (2005) supports the conspecificity of all *Ommastrephes* specimens within the distributional range depicted for *O. cylindracea* (Fig. 3). It is also noteworthy that Dunning (1998) described a discontinuous distributional range of *Ommastrephes* spp. at the tip of South America and the south-eastern tip of Australia and considered both populations reproductively isolated. The results provided here (Figs 1–3; Tables 2–5) support this point of view and ensure the recognition of *O. cylindracea* and *O. brevimanus* as different species.

The single specimen of this species analysed from Cape Verdean waters (18°N) merits further discussion. Zuev *et al.* (1976) sampled Equatorial Atlantic waters extensively without finding any *Ommastrephes* individuals. Therefore, it is commonly accepted that the genus *Ommastrephes* is not present in Equatorial Atlantic owing to the temperature (see Roper *et al.*, 2010). However, sequences obtained herein reveal that the Cape Verde individual belongs to *O. cylindracea* (Figs 1–3; Tables 2–5). This isolated spot from the remaining distributional range of the species can be explained by drift of specimens from the

Southern Hemisphere, along with the subsurface and intermediate waters of southern origin with the South Atlantic central water (100–500 m, 5–18 °C) and the Antarctic intermediate water (500–1200 m, 2–6 °C), which penetrate from the southern subtropical zone to the north-western coast of Africa up to 20–24 and 28–34°N, respectively (Aristegui *et al.*, 2009; Machini & Pelegri, 2009). Similar cases of distant migrations far outside the main distributional range of the species to the other hemisphere with deep waters are also known (Møller *et al.*, 2003; Arkhipkin *et al.*, 2010).

Unavailable *Ommastrephes* names:

Ommastrephes ayresii Gabb in Carpenter, 1864: 613, 664 [*nomen nudum*].

Ommastrephes californica Heath, 1908: 582 [*nomen nudum*].

Ommastrephes crassus Lafont, 1871: 275, pl. 16 [*nomen nudum*].

CONCLUSION

The long-standing problem of *Ommastrephes* taxonomy (Roper *et al.*, 2010) is here re-evaluated using two molecular markers and multiple molecular species delimitation methods in combination with metabolic and morphological knowledge in an integrative taxonomic approach. This study has revealed the presence of four species of *Ommastrephes* that occupy distinct geographical regions, all previously believed to be a single monotypic cosmopolitan species (*O. bartramii*). Although the type specimen for *O. bartramii* is no longer extant and the type locality unknown, we have designated a neotype for this species and applied this name to the well-studied and commercially exploited species in the North Pacific in accordance with ICZN regulations. Three other names were resurrected for the additional species recognized in the present study using all available morphological, metabolic and molecular data in an integrative approach, and neotypes were designated for each species. There are currently no known morphological characters that separate *O. bartramii* from *O. brevimanus* or *O. cylindraceus*, and they appear to represent cryptic species. *Ommastrephes caroli* represents a pseudocryptic species, because it exhibits morphological differences from the other species in this genus. Although our study included specimens from each species, the entire distributional area for each species has not yet been sampled, and our inferred species distributions should be used with caution until more detailed molecular information is available. We also used this information to hypothesize the oceanographic features that delimit the distribution

of each species. Given that only spermatophores showed important taxonomic differences for a single one of the recognized species (*Ommastrephes* group 1, defined here as *O. caroli*), molecular characters proved to be especially useful for the recognition of diagnostic differences between the species. The single species of the genus commercially exploited at present is *O. bartramii*, but it is important to note that the real distributional range of the species is far smaller than previously considered (e.g. Roper *et al.*, 2010). Thus, this knowledge is important for the proper fishery management of the species. Although every effort was made to obtain samples from the greatest possible geographical range of *Ommastrephes*, including requesting international collaboration during the 2015 Cephalopod International Advisory Council Conference (Hakodate, Japan; Fernández-Álvarez *et al.*, 2015b), which resulted in many participants contributing material, the entire distributional range for each *Ommastrephes* species was not covered. This is a direct consequence of the oceanic lifestyle of this genus coupled with the absence of directed fisheries in most of its distributional range, which makes its collection from some localities a fortuitous phenomenon. However, specimens were available for sequencing from the majority of the distributional range of *O. bartramii*, *O. brevimanus* and *O. cylindraceus*. The metabolic results of Shevtsova *et al.* (1979) and Rozengart & Basova (2005) suggest conspecificity of the South Atlantic and the south-eastern Indian Ocean specimens and were used herein to complement genetic data to delimit the distribution of *O. cylindraceus*. This study increases the number of accepted species of the family Ommastrephidae from 22 (Roper *et al.*, 2010) to 25, which represents a 13% increase in the known biodiversity of the family.

ACKNOWLEDGEMENTS

We are thankful to José Manuel Reyes-González (University of Barcelona, Spain) and Ángel Soria (RV *Hesperides*, Spain) for collecting and donating the individuals ICMC000070 and ICMC000059, respectively. Luis Laria (Coordinadora para el Estudio y Protección de las ESpecies MARinas [CEPESMA], Spain) kindly allowed the examination and sample collection of the specimens from El Parque de la Vida (Asturias). Francisco Olivas performed the curation of the morphological vouchers under the Biological Reference Collections (CBR-ICM). Our thanks also to Bruce Marshall (the National Museum of New Zealand Te Papa Tongarewa; NMNZ) and Peter Jackson for providing New Zealand specimens. Thanks for Dr Tsunemi Kubodera (National Museum of Nature and

Science, Tsukuba Research Institute, Japan) for his help in the search for a suitable individual as neotype for *O. bartramii*. We thank Alex Lichtblau (Inside Under Dive & Travel, Hawaii, HI, USA) for kindly sharing with us his *Ommastrephes bartramii* photograph for Figure 2. We are grateful to Annie Machordom and Ricardo García-Jiménez (MNCN-CSIC, Spain) for their kind advice with phylogenetic methods. Some of the sequences were obtained through AllGenetics (A Coruña, Spain). The specimens DE.2.1.5.4.1–DE.2.1.5.4.5 were collected by jigging during the 10th Indian Expedition to Southern Ocean/Antarctic waters during 2017–2018 conducted by the National Centre for Polar and Ocean Research (NCPOR), Goa, India. K.K.S. and N.R. are thankful to Dr K. S. Mohamed (Central Marine Fisheries Research Institute, India) for the encouragement. We are grateful to the two anonymous reviewers, whose thoughtful comments contributed to improving the initial manuscript. The specimen ICMC000059 was collected on board the RV *Hesperides* during the research project MAFIA (CTM2012-39587-C04-03), funded by the Spanish Ministry of Economy and Competitiveness (MINECO/FEDER/EU). F.Á.F.-Á. was supported by the MINECO grants BES-2013-063551 and EEBB-C-16-00694 and by an Irish Research Council–Government of Ireland Postdoctoral Fellowship Award (ref. GOIPD/2019/460). This study was funded by the research project AGL2012-39077 (MINECO/FEDER/EU).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site. The alignments of COI and 16S matrices are provided as additional Supporting FASTA files S1 and S2, respectively.