



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

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Global biodiversity of the genus *Ommastrephes* d'Orbigny, 1834 (Ommastrephidae: Cephalopoda): an allopatric cryptic species complex

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Abstract:	<p>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 that each occupies a smaller fraction of the original distribution 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. Prior to the present study, <i>Ommastrephes bartramii</i> was considered a monotypic cosmopolitan species with a discontinuous distribution. Here, mitochondrial sequences of individuals from nearly its entire distribution range were evaluated with morphology and 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 knowledge from the literature, were used to resurrect three formerly synonymized names and propose revised distribution ranges for each species. In addition, diagnostic characters from the molecular sequences were incorporated to the species description. Only one of the four newly recognized species is currently commercially exploited by fisheries; however, it now appears that the actual distribution range of this species is far more reduced than previously believed and this is essential for proper fisheries management.</p>

1
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3 **1 Abstract**
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6 2 Cryptic speciation among morphologically homogeneous species is a phenomenon increasingly reported
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8 3 in cosmopolitan marine invertebrates. This situation usually leads to the discovery of new species that
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12 5 of *species complexes* is essential because species are used as the unit of action for conservation, and
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14 6 natural resource management politics. Prior to the present study, *Ommastrephes bartramii* was considered
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16 7 a monotypic cosmopolitan species with a discontinuous distribution. Here, individuals from nearly its
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18 8 entire distribution range were evaluated with mitochondrial DNA (cytochrome *c* oxidase subunit I and
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20 9 16S rRNA). Four distinct species were consistently identified using four molecular species delimitation
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22 10 methods. These results, in combination with morphological and metabolic information from the literature,
23
24 11 were used to resurrect three formerly synonymized names (*Ommastrephes brevimanus*, *Ommastrephes*
25
26 12 *caroli* and *Ommastrephes cylindraceus*) and propose revised distribution ranges for each species. In
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28 13 addition, diagnostic characters from the molecular sequences were incorporated to the species description.
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30 14 Only one of the four newly recognized species (*Ommastrephes bartramii*) is currently commercially
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32 15 exploited by fisheries in the North Pacific; however, it now appears that the actual distribution range of
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34 16 this species is far smaller than previously believed, an essential consideration for effective fisheries
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36 17 management.

37 18 ADDITIONAL KEYWORDS: Cephalopoda - *Ommastrephes brevimanus* - *Ommastrephes caroli* -
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39 19 *Ommastrephes cylindraceus* - Phylogeny - Systematics - Taxonomy
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21 INTRODUCTION

22 Traditionally, species descriptions were based solely on morphological characters. However,
23 reliance on morphological characters alone can overlook species that evolved and developed
24 genetic barriers (e.g., habitat, life history, or recognition systems) without a parallel
25 morphological differentiation, leading to species complexes (Knowlton, 1993). Species
26 complexes can be either cryptic (i.e., there are not morphological differences) or pseudocryptic
27 (i.e., there are morphological differences, which might be overlooked or considered as
28 intraspecific variation due to mistaken or overconservative taxonomic practices). For marine
29 animals, this situation is quite common due to the long-standing general belief that the oceanic
30 realm is a continuum devoid of barriers for genetic exchange. As a result, many marine taxa
31 with relatively homogeneous morphology have been assigned to previously described species
32 from a distant place (e.g., Carrera-Parra *et al.*, 2011) or several similar species from distant
33 areas have been synonymized under a single cosmopolitan morphospecies, but in fact represent
34 different biological species (e.g., Valdés *et al.*, 2017). With a recent increase in the inclusion of
35 molecular tools in taxonomy, it was revealed that many “cosmopolitan” species actually
36 represent multiple morphologically similar species (e.g., Kawauchi & Giribet, 2010). This is a
37 direct consequence of physical barriers to dispersal in marine environments and several
38 biological and physiological factors that affect the dispersal capabilities in species.

39 Conservation and natural resource management are limited by taxonomic resolution. Recently
40 however, there appears to be an increase in the recognition of cryptic species of marine
41 invertebrates, which typically results in species that occupy a small portion of the original
42 distribution described for the previously cosmopolitan species (e.g., Bickford *et al.*, 2007, Calvo
43 *et al.*, 2009; Amor *et al.*, 2017). Because conservation and resource management politics work
44 at the species level, it is especially important to ascertain how many cryptic species are involved
45 in problematic taxa and describe and name the newly discovered species (Templado *et al.*,
46 2016). However, due to practical reasons or journal requirements (Jörger & Schrödl, 2013),
47 many researchers postpone formal description of discovered cryptic species and they remain

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3 48 unnamed and, therefore, excluded from conservation planning and natural resource
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5 49 management.
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8 50 Squids of the family Ommastrephidae Steenstrup, 1857 are considered the most economically
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10 51 and commercially important cephalopods worldwide (Roper *et al.*, 2010). Their abundance,
11
12 52 rapid growth and massive body size make them one of the most exploited invertebrate fishing
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14 53 resources (Arkhipkin *et al.*, 2015b). Ecologically, these oceanic squids are both important prey
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16 54 (Romeo *et al.*, 2012) and predators (Villanueva *et al.*, 2017), occupying a wide range of trophic
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18 55 levels in marine pelagic food webs (Coll *et al.*, 2013). They are characterized by a short life
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20 56 span, usually less than two years (Arkhipkin *et al.*, 2015a), and by a unique paralarval phase
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22 57 known as rhyngoteuthion (Roper *et al.*, 2010; Fernández-Álvarez *et al.*, 2017) with a
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24 58 detritivore diet (Fernández-Álvarez *et al.*, 2018a). The neon flying squid, *Ommastrephes*
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26 59 *bartramii* (Lesueur, 1821), is the second largest representative of the family, only exceeded in
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28 60 size by the Humboldt flying squid, *Dosidicus gigas* (d'Orbigny, 1835). The neon flying squid
29
30 61 can reach a maximum size of 1020 mm in dorsal mantle length (DML) and 35 kg in weight
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32 62 (Guerra *et al.*, 2010), but usually attain smaller sizes. *Ommastrephes* d'Orbigny, 1834 is
33
34 63 currently considered a monotypic genus with a cosmopolitan distribution, with three distinct
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36 64 populations defined by region (Nesis, 1987; Roper *et al.*, 2010): the North Atlantic, the
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38 65 Southern Hemisphere and the North Pacific. These undescribed populations were defined
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40 66 according to differences in the size structure (Zalygalin *et al.*, 1983), the spermatophore
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42 67 structure (Nigmatullin *et al.*, 2003) and by substrate-inhibitory traits of optic ganglia
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44 68 cholinesterases (Shevtsova *et al.*, 1979, Rozengart & Basova, 2005). These morphological and
45
46 69 metabolic differences have created some doubts regarding the taxonomic accuracy of
47
48 70 considering the genus *Ommastrephes* to be monotypic. Some literature before the 1990s
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50 71 considered at least two species to exist within the genus (e.g, Roper *et al.*, 1984; Lozano
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52 72 Soldevilla & Franquet Santaella, 1986; Clarke, 2003). The ocean basins inhabited by
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54 73 *Ommastrephes* are also fragmented (Roper *et al.*, 2010), containing geographic barriers that
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56 74 might lead to speciation events. This study therefore aimed to use molecular analyses of two
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3 75 mitochondrial markers in order to resolve this long-standing debate among the cephalopod
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5 76 research community.
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10 78 MATERIAL AND METHODS

11 79 SAMPLE COLLECTION

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14 80 *Ommastrephes* samples were obtained from local markets (specimen ICMC000070), from land
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17 81 strandings, or were collected by jigging during the Atlantic research cruises MAFIA (Olivar *et*
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19 82 *al.*, 2017) and BATHYPELAGIC. After collection, a small piece of the mantle was preserved in
20
21 83 96 % ethanol for molecular analysis. In some cases, a morphological voucher was preserved in
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23 84 4 % buffered seawater formalin and deposited in the following collections: the Biological
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25 85 Reference Collections of the Institut de Ciències del Mar (Barcelona, Spain) (CBR-ICM),
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27 86 Museu Oceanográfico of the Rio Grande Federal University (Brazil) (MORG), the Central
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29 87 Marine Fisheries Research Institute (Kerala, India) (CMFRI), and the National Museum of New
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31 88 Zealand Te Papa Tongarewa (NMNZ). Information on the locality and GenBank and collection
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33 89 accession numbers is summarized in Table 1.
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39 90 DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

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41 91 Total genomic DNA was extracted from ethanol-fixed tissue using the NZY Tissue gDNA
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43 92 isolation kit (NZYTech, Lisbon, Portugal), following the manufacturer's protocol and
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45 93 resuspended in a final volume of 100 μ L. A negative control that contained no tissue was
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47 94 included in every DNA extraction round to check for contamination. Sequences from the partial
48
49 95 mitochondrial cytochrome *c* oxidase subunit I (COI) gene were amplified using the primer pair
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51 96 LCO1490 and HCO2198 (Folmer *et al.*, 1994). The partial mitochondrial 16S rRNA (16S)
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53 97 fragment was amplified using the primer pair 16sbr-H-myt and 16sar-L-myt (Lydeard *et al.*,
54
55 98 1996). Standard PCRs were performed using the NZYTaq Green PCR Master Mix (NZYTech,
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57 99 Portugal) following the manufacturer's protocol in a total volume of 25 μ L, which included 0.5
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3 100 μM of each primer, 25 ng of template DNA and PCR-grade water up to 25 μL . PCRs consisted
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5 101 of an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for
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7 102 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
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9 103 a final extension of 5 min at 72 °C. The amplified products were sequenced using both forward
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11 104 and reverse PCR primers on an ABI 3730xl [sequencer](#). DNA sequence data were edited and
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13 105 aligned with Geneious 8.1.5 (<http://www.geneious.com>). Ommastrephid squids have duplicated
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15 106 regions of the mitochondrial genome, including the gene COI (Yokobori *et al.*, 2004; Staaf *et*
16
17 107 *al.*, 2010). Although it is assumed that concerted evolution mechanisms apply in ommastrephid
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19 108 mitochondria (Allcock *et al.*, 2015), several variable positions were found. The IUPAC
20
21 109 ambiguity codes were used to codify these nucleotide variable positions as in Fernández-
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23 110 Álvarez *et al.* (2015a).

27 111 *PHYLOGENETIC ANALYSIS*

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30 112 Sequences generated in the present study and available on GenBank from previous studies were
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32 113 used for the development of cytochrome c oxidase subunit I (COI) and 16S rRNA databases
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34 114 (Table 1). Sequences lacking locality data or with COI sequences with stop codons or indels
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36 115 were excluded from our analysis. The final alignment included 25 individuals for COI and 69
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38 116 individuals for 16S. Sequences were manually aligned using the software Bioedit v. 7.0.1 (Hall,
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40 117 1999). Sequences were trimmed to be the same length, resulting in 612 and 467 bp alignments
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42 118 for COI and 16S, respectively. For the 16S alignment, a single gap needed to be added to the
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44 119 sequence KC603489 due to the presence of a single nucleotide deletion.

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48 120 As a preliminary species delimitation analysis, the software TCS v. 1.21 (Clement *et al.*, 2000)
49
50 121 was used to construct the haplotype networks with a maximum connectivity limit of 95 % with
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52 122 the COI database. This analysis resulted in four separate networks which were named as
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54 123 *Ommastrephes* groups 1 to 4 to simplify the nomenclature (Table 1). This nomenclature was
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56 124 applied to both matrices. The TCS function of the software PopART (Leigh & Bryant, 2015)
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58 125 was used to represent the statistical parsimony networks. Uncorrected *p*-distances within each
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3 126 *Ommastrephes* group and between groups were calculated with MEGA6.06 (Tamura *et al.*,
4
5 127 2013) for both molecular markers. The online version of software Automatic Barcode Gap
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7 128 Discovery (ABGD, Puillandre *et al.*, 2012) was employed to check the distribution and size of a
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9 129 potential barcoding gap for both databases.

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12 130 The phylogenetic relationships of Ommastrephidae are not yet fully resolved. According to
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14 131 different authors, the sibling genus of *Ommastrephes* might be either *Dosidicus gigas* or
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16 132 *Sthenoteuthis* spp. (Lindgren *et al.*, 2012, Strugnell *et al.*, 2017, Pardo-Gandarillas *et al.*, 2018).
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18 133 Uncorrected *p*-distances of both COI and 16S showed a closer relation between *Ommastrephes*
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20 134 and *Dosidicus gigas* (Fernández-Álvarez, pers. obs.). This species was selected as outgroup for
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22 135 the phylogenetic analyses. Both gene regions were also analyzed using the Poisson Tree
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24 136 Processes (PTP) (Zhang *et al.*, 2013). The starting Maximum Likelihood (ML) trees were
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26 137 constructed with the online version of RaxML (<https://raxml-ng.vital-it.ch/#/>) using the GTR
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28 138 gamma model with bootstrap values calculated from 100 replicates. The obtained tree was
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30 139 visualized and converted to Newick format using FigTree v1.4.3 (Rambaut, 2006–2009) and
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32 140 submitted to the PTP portal (<http://species.h-its.org/ptp/>). The default parameters and 300,000
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34 141 MCMC (Markov chain Monte Carlo) generations were used.

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38 142 In this work, the unified species concept (De Queiroz, 2007) was applied. The concordance of
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40 143 results of molecular species delimitation methods was considered a confirmation of the
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42 144 reproductive isolation between groups and therefore the species status for each *Ommastrephes*
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44 145 group.

46 47 48 146 *DNA DIAGNOSTIC CHARACTERS*

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50 147 DNA sequences contain valuable diagnostic characters for species descriptions, especially when
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52 148 species complexes are involved. Here, COI and 16S rRNA were examined for diagnostic
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54 149 characters. Diagnostic molecular characters are nucleotides in a specific position and gene
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56 150 region that are the same in all individuals examined for a single species, and consistently
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58 151 distinct from all other known species (autoapomorphies). Only homogeneous characters were
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3 152 considered. Special care was taken to avoid the inclusion of plesiomorphic characters as
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5 153 diagnostic characters by the inclusion of the putative sister species of the genus (*Dosidicus*
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7 154 *gigas*, see above) and the remaining members of the subfamily Ommastrephinae Posselt, 1891,
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9 155 as outgroups (Table 1). For the presentation of the results and to ensure the reproducibility of
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11 156 this work, the general recommendations of Jörger & Schrödl (2013, 2014) were followed. To
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13 157 ensure transparency in our selection of diagnostic nucleotides, the alignments of COI and 16S
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15 158 matrices are provided as supplementary material.
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160 RESULTS

161 The haplotype parsimony statistical network analysis of COI identified four groups with
162 conspicuous geographical patterns (Fig. 1A). *Ommastrephes* group 1 included exclusively
163 North Atlantic individuals and 45 mutations separated it from the closest group. *Ommastrephes*
164 groups 2–4 were more closely related, with 15–20 mutations between them. *Ommastrephes*
165 group 2 is represented by individuals from Tropical and South Atlantic and South Indian waters,
166 while groups 3 and 4 occurred exclusively in the South and North Pacific, respectively. The
167 COI intragroup *p*-distances ranged from 0–0.8 % (Table 2), while intergroup *p*-distances were
168 2.4–9.0 % (Table 3). The ABGD analysis of COI identified four groups (prior maximal distance
169 $P = 0.001$) and a clear barcoding gap between intra- and intergroup distances. Although there is
170 a tendency to group the sequences by geographic origin, the statistical parsimony network
171 analysis of the 16S database (Fig. 1B) revealed a pattern not as clear as COI. The four
172 *Ommastrephes* networks were separated by 2–5 mutations. Intragroup and intergroup distances
173 were 0–0.9 and 0.7–1.9 %, respectively (Tables 2–3). Therefore, there was an overlap between
174 the maximum intraspecific distance and the minimum interspecific distance for 16S.
175 The ML analyses of COI revealed four clades consistent with the four *Ommastrephes* groups
176 identified in the haplotype parsimony analysis (Fig. 2). *Ommastrephes* groups 2 and 3 were
177 recovered as sister taxa, *Ommastrephes* group 4 was the sister group of this clade, and

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3 178 *Ommastrephes* group 1 was the sister group of the clade formed by the groups 2–4. Bootstrap
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5 179 values of each group were high (96–98 %) with the exception of *Ommastrephes* group 4 (68 %).
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7 180 The PTP analysis recovered four species, which were consistent with the four clades revealed in
8
9 181 the ML analyses. The ML analysis of 16S showed two well-supported clades formed by
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11 182 *Ommastrephes* group 1 and another clade formed by the remaining *Ommastrephes* sequences
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13 183 (data not shown). The PTP analysis for 16S recovered two species consistent with two clades
14
15 184 from the ML analysis. This indicates that 16S might be too conserved to resolve the taxonomy
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17 185 of this genus. Figure 2 summarizes the results of all the species molecular delimitation methods
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19 186 for COI (haplotype networks –TCS–, *p*-distance, ABGD and PTP) and the TCS and PTP
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21 187 analyses for 16S.
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25 188 For COI, a total of 23 diagnostic positions were identified (Table 4). *Ommastrephes* group 1 had
26
27 189 16 diagnostic positions, while *Ommastrephes* groups 2, 3 and 4 had 4, 3 and 1 diagnostic
28
29 190 positions, respectively. No diagnostic positions for 16S were recognized in *Ommastrephes*
30
31 191 groups 1 and 4, but one was identified for group 2 (435, G) and one for group 3 (16, C) (Table
32
33 192 5). It is important to note that diagnostic characters (as considered here) are not the only
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35 193 variable positions among species, since only homogeneous autoapomorphies were considered.
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195 **DISCUSSION**

196 *SPECIFIC BIODIVERSITY OF THE GENUS OMMASTREPHEs*

47 197 Previous empirical studies have shown that individuals assigned to a statistical parsimony
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49 198 network with a 95 % probability for COI correspond to species (Pons *et al.*, 2006; Hart &
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51 199 Sunday, 2007; Bond & Stockman, 2008, Kang *et al.*, 2015). Statistical parsimony network
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53 200 analysis of COI in the present study with 95 % confidence intervals identified four isolated
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55 201 groups with a recognizable geographic pattern: Northeast Atlantic samples belong to group 1;
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57 202 Eastern Tropical and South Atlantic together with South Indian samples belong to group 2;
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59 203 South Pacific samples belong to group 3 and Northwestern and Central North Pacific
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3 204 individuals belong to group 4 (Fig. 1). This pattern is also found in the statistical parsimony
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5 205 networks of 16S. The maximum intragroup COI p -distance was 0.8 % (Table 2), while
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7 206 intergroup distances ranged from 2.4 to 9.0 % (Table 3) suggesting the existence of a barcoding
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9 207 gap. This is supported by the recognition of four different groups with the ABGD analysis.
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11 208 Similar distances have been reported between several other cephalopods, such as octopuses
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13 209 (Allcock *et al.*, 2011) and bobtail squids (Gebhardt & Knebelsberger, 2015), and in other
14
15 210 invertebrates such as land planarians (Lago-Barcia *et al.*, 2015), crustaceans (Robles *et al.*,
16
17 211 2007) and annelids (Tomioka *et al.*, 2016), even including minimal interspecific distances of ~1
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19 212 % in closely related freshwater mites (García-Jiménez *et al.*, 2017). The 16S p -distances were
20
21 213 lower between *Ommastrephes* groups (Table 3), a phenomenon frequently reported for other
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23 214 animals in the literature (e.g., Hebert *et al.*, 2003; Rodríguez-Flores *et al.*, 2017). Although a
24
25 215 small overlap between intra- and intergroup distances was found between 16S sequences
26
27 216 (Tables 2–3), it is important to note that each geographic region had unique haplotypes that did
28
29 217 not occur in other areas (Fig. 1B), which also supports the hypothesis of allopatric reproductive
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31 218 isolation. The 16S PTP analysis was only able to isolate *Ommastrephes* group 1, the most
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33 219 divergent species in the genus, as distinct from the other species (Fig. 2). Consequently, this
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35 220 indicates that 16S rRNA is too conserved to delimit species of *Ommastrephes*. The combined
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37 221 evidence presented here suggests that each *Ommastrephes* group should be considered a single
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39 222 geographically isolated species. This vision is reinforced by the fact that the phylogenetic
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41 223 analysis and most of the molecular species delimitation molecular methods recognized four
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43 224 groups consistent with the haplotype network analyses (Fig. 2).
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48 225 Beyond molecular characters, differences known among specimens from different regions
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50 226 include their size structure (Zalygalin *et al.*, 1983; Nigmatullin *et al.*, 2003), spermatophore
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52 227 morphology (Nigmatullin *et al.*, 2003), and substrate-inhibitory traits of optic ganglia
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54 228 cholinesterases (Shevtsova *et al.*, 1979, Rozengart & Basova, 2005). The morphology of the
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56 229 copulatory organ – the hectocotylus – can also have a high importance for cephalopod
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58 230 taxonomy. The detailed morphology of the hectocotylized arm (including index of modified part
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3 231 length; number and size of suckers; and the type, number and size of teeth in the sucker's
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5 232 chitinous rings) in mature males from different parts of the genus range (North Pacific, 2 males;
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7 233 South Pacific, 8 males; South Atlantic, 2 males; and North Atlantic, 3 males) was studied during
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9 234 the USSR integrated target program "SQUID" during the 1980s. No significant differences were
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11 235 observed among specimens from different areas (Nigmatullin, pers. obs.). *Ommastrephes* group
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13 236 4, which occurs in the North Pacific, is distinguished from other congeners by the small
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15 237 maximum size of females at maturity (Roper *et al.*, 2010). It is important to indicate that
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17 238 maximum size-at-maturity does not generally represent a good taxonomic character for
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19 239 ommastrephid squids, since it is hugely variable at intraspecific level in most species. For
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21 240 instance, in the related species *D. gigas*, the smallest females mature at only 12 % of the mantle
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23 241 length of the largest ones (Nigmatullin *et al.*, 2001) and this difference might occur inter-
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25 242 annually in members of the same geographic area (Hoving *et al.*, 2013, 2019; Fernández-
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27 243 Álvarez *et al.*, 2018b). North Atlantic *Ommastrephes* have larger spermatophores (up to 53 mm,
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29 244 while other *Ommastrephes* species have a maximum length of 41 mm), which are distinguished
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31 245 from those of other species by the morphology of the cement body, sperm reservoir, and
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33 246 posterior empty part (Nigmatullin *et al.*, 2003; Sabirov & Nigmatullin, 2012). Furthermore,
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35 247 these differences are more pronounced between *Ommastrephes* group 1 (North Atlantic
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37 248 *Ommastrephes*) and the other *Ommastrephes* species than they are among some other
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39 249 ommastrephid genera (Nigmatullin *et al.*, 2003). These morphological differences are also
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41 250 consistent with the fact that *Ommastrephes* group 1 is the most phylogenetically divergent of
42
43 251 the groups in all our phylogenetic analyses (Figs 1 and 2, Table 3) and has more diagnostic
44
45 252 molecular characters (Table 4). Therefore, it appears that this species has had a longer
46
47 253 evolutionary history isolated from the remaining congeneric species. Since morphological
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49 254 differences are known at least in the spermatophore between this species and the remaining
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51 255 ones, it could be considered a pseudocryptic species. Since no important morphological
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53 256 differences have been found to date to distinguish the remaining species, they appear to be
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55 257 cryptic species. Shevtsova *et al.* (1979) and Rozengart & Basova (2005) compared the
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57 258 differences in substrate and inhibitor-specific cholinesterase activities of optical ganglia among
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3 259 *Ommastrephes* individuals from four geographic locations: the North Atlantic, the South
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5 260 Atlantic, the Great Australian Bight (Southeastern Indian Ocean), and the North Pacific. They
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7 261 found significant differences for these metabolic traits between specimens from all the studied
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9 262 geographic areas with the exception of South Atlantic and Southwestern Indian *Ommastrephes*
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11 263 specimens. None of their specimens came from South Pacific waters, where *Ommastrephes*
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13 264 group 3 occurs (and thus was not represented in Fig. 2). The metabolic trait differences are
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15 265 interpreted as another source of evidence to support the specific status of each *Ommastrephes*
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17 266 group.

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21 267 Subadult and adult ommastrephid specimens are nektonic organisms able to perform large-scale
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23 268 horizontal oceanic migrations (Markaida *et al.*, 2005). Migrations related to feeding and
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25 269 reproductive grounds have been described for North Pacific *Ommastrephes* (Ichii *et al.*, 2009).
26
27 270 However, the first ontogenetic stages of ommastrephids are planktonic, representing one of the
28
29 271 smallest cephalopod hatchlings recorded (1–2 mm mantle length, Villanueva *et al.*, 2016), and
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31 272 paralarval dispersion is very likely limited by oceanic features, such as the main oceanic gyres
32
33 273 and currents. In addition, hatching size is inversely related with cephalopod distribution ranges
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35 274 (Villanueva *et al.*, 2016). Consequently, the distribution range of *Ommastrephes* spp. seems to
36
37 275 be mainly shaped by the Equatorial oceanic currents (Fig. 3) and surface water temperatures
38
39 276 (Roper *et al.*, 2010). The boundary between *Ommastrephes* spp. 3 and 4 is likely formed by the
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41 277 Pacific Equatorial currents. The distribution boundary between Atlantic *Ommastrephes* groups 1
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43 278 and 2 seems to be influenced by the Canary and Atlantic Equatorial currents, since Canary and
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45 279 Azores specimens belong to group 1 while the specimen caught near Cape Verde belongs to the
46
47 280 group 2. These sampling localities are only ~1100–1600 km apart, while larger geographic
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49 281 distances (~3500–3600 km) between conspecifics have been confirmed for those *Ommastrephes*
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51 282 species with genetics. Therefore, the Canary and Atlantic Equatorial currents appear to represent
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53 283 the boundary to paralarval distribution between these two species.

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56
57 284 There are important conservation, economic and food security (e.g., Jiao *et al.*, 2018)
58
59 285 ramifications for the results of this study. Since *Ommastrephes* is an important fishing resource

1
2
3 286 commercially exploited in the North Pacific (Arkhipkin *et al.*, 2015b), it is important to define
4
5 287 which species within this complex is being impacted by fishery activities. The North Pacific
6
7 288 Ocean contains only *Ommastrephes* group 4 (Figs 1, 3). Although the genus has a circumglobal
8
9 289 distribution, it is not commercially targeted outside of the North Pacific, and in other regions it
10
11 290 is only caught as bycatch (Battaglia *et al.*, 2010). Since the operational unit for conservation and
12
13 291 natural resource management is the species, identifying, defining and naming each biological
14
15 292 species from taxonomically complex groups is an increasingly important task.
16
17
18
19

293

294 *UNTIDYING A GORDIAN KNOT: OMMASTREPHESES SPP. TAXONOMY*

295 Because new cryptic species are being discovered at an increasing rate (e.g., Jörger & Schrod,
296 2013), currently many taxonomists agree that future taxonomic descriptions should be
297 integrative (Dayrat, 2005), ideally covering a range of aspects for species delimitation (e.g.,
298 morphology, genetics, biogeography, and behavior). Traditional cephalopod taxonomy involves
299 the use of counts, measures, and indices (Roper & Voss, 1983), which were inadequate for
300 distinguishing *Ommastrephes* species (Roper *et al.*, 2010). For *Ommastrephes*, previous
301 morphological works have only revealed important morphological differences in the
302 spermatophore morphology of North Atlantic specimens in comparison with individuals from
303 other regions (Nigmatullin *et al.*, 2003; Sabirov & Nigmatullin, 2012). Herein, molecular
304 diagnostic characters have been integrated into the descriptions, and the geographical range of
305 each species is reported based on the available molecular information. Although adding
306 molecular characters is gaining support among researchers working in other animal groups (e.g.,
307 Jörger & Schrödl 2013, 2014; Johnson *et al.*, 2014), as far as we know this is the first time that
308 molecular characters have been included as diagnostic characters in cephalopod species
309 descriptions, although molecular data have commonly been used for detecting new species or
310 solving other taxonomic problems (Allcock *et al.*, 2015). It is important to note that a molecular

1
2
3 311 character was used in the diagnosis of an octopod family previously (Strugnell *et al.*, 2014:
4
5 312 227).

6
7
8 313 The phylogenetic analyses (Figs 1–2; Tables 1–3) support four distinct species of
9
10 314 *Ommastrephes*, and reveal molecular diagnostic characters for each species (Tables 4 and 5).
11
12 315 Therefore, we formally resurrect three previously used species names to split *O. bartramii* into
13
14 316 four nominal species (see below). Several additional species names previously considered to be
15
16 317 junior synonyms of *O. bartramii* have been researched and, where possible, are listed in
17
18 318 synonymy with the appropriate species below. As a primary source of *O. bartramii* synonyms,
19
20 319 the compilation of Sweeney & Young (2003) was used as a starting point, followed by a
21
22 320 bibliographic review. For objectivity of scientific names, we designated neotypes for three of
23
24 321 the species and, when possible, ethanol fixed tissues were stored in the Biological Reference
25
26 322 Collections of the Institut de Ciències del Mar (CBR-ICM, Spain) and National Museum of
27
28 323 New Zealand Te Papa Tongarewa (NMNZ, New Zealand).
29
30

31
32 324

33
34
35 325 **Genus *Ommastrephes* d'Orbigny, 1834** in 1834–1847: 45.

36
37
38 326 *Type Species: Loligo bartramii* Lesueur, 1821.

39
40
41 327 *Synonyms*

42
43
44 328 (?) *Cycria* Leach in Gray, 1849: 58. Listed as synonym of *Ommastrephes* [fide Hoyle (1910:
45
46 329 408)]. Type species with no type given [fide Hoyle (1910: 408)]

47
48
49 330 *Lolimnites* Risso, 1854: 41. [fide Adam (1942: 17)] Type species *Lolimnites meridionalis* Risso,
50
51 331 1854, by monotypy.

52
53
54 332 *Ommatostrephes* Loven, 1845: 122. Emendation of *Ommastrephes* D'Orbigny 1834 in 1834–
55
56 333 1847 [fide Hoyle (1910: 411)].
57
58
59
60

1
2
3 334 *Diagnosis:* The following diagnosis was adapted from the morphological description of Roper
4
5 335 *et al.* (2010); additional paralarval characters **have been** added following the descriptions of
6
7 336 Sweeney *et al.* (1992), Young & Hirota (1990), Sakurai *et al.* (1995) and Vijai *et al.* (2015), as
8
9 337 reviewed by Fernández-Álvarez *et al.* (2017).

11
12 338 Maximum mantle length 1020 mm; mantle wide, posterior end without pronounced pointed tail;
13
14 339 fins rhomboidal, slightly attenuate posteriorly, fin length 40–50 % and width 60–85 % of mantle
15
16 340 length, fin angle 46° to 65°; funnel groove with foveola with 5–8, occasionally 9, longitudinal
17
18 341 folds and 2–5 (usually 3 or 4) distinct side pockets; small, scattered, subcutaneous photogenic
19
20 342 tissue embedded in tissue of mantle, head and ventral arms, without large dorsal mantle
21
22 343 photophore nor ocular or intestinal photophores; long, broad, silvery or golden opalescent strip
23
24 344 along ventral midline from anterior fin edge to mantle opening and similar ventral strip on
25
26 345 ventral surface of head and ventral arms, relatively dense aggregations of small subcutaneous
27
28 346 photogenic tissue under opalescent tissue; arms with 24–35 pairs of arm suckers; arm tips not
29
30 347 attenuate; tips of trabeculae of protective membranes do not project beyond edge of membrane;
31
32 348 ventral protective membranes of arms III very wide and in adult females expanded into large,
33
34 349 triangular, membranous lobe; in males, right or left ventral arm hectocotylized, with tip lacking
35
36 350 suckers; tentacle suckers covering ~60 % of tentacle length; 4–7 suckers with denticulate rings
37
38 351 present on carpus proximal to first carpal knob; carpal-locking apparatus on tentacular stalk
39
40 352 with 2–5 knobs and 2–4 smooth-ringed suckers; largest medial manus suckers with 4 **enlarged**
41
42 353 pointed teeth, 1 at each quadrant; dactylus of tentacular club with 4 series of small suckers; cone
43
44 354 flags of gladius short, rhomboidal, with distinct radial creases, greatest width of cone flags
45
46 355 about 56 % width of rachis, marginal rigidity ribs of rachis doubled; axial rigidity rib of rachis
47
48 356 wide rounded-rectangular in cross-section, lateral plates of gladius not adhered to dorsal surface
49
50 357 of rachis but form wide free folds over rachis, stem of rachis short, width of stem slightly
51
52 358 greater than its thickness; cone short and laterally flattened, rostrum absent, thick alveola
53
54 359 covered with tiny ribs and thorns; monoflagellate spermatozoon; hatchlings with skin sculpture;
55
56 360 without ocular or visceral photophores; two rows of pegs present in proboscis suckers, diameter

1
2
3 361 of lateral proboscis suckers 200 % that of central suckers and with unequal number of pegs; 3
4
5 362 leaflets in the gills.
6
7

8 363 ***Ommastrephes bartramii* (Lesueur, 1821)**
9

10
11 364 *Loligo bartramii* Lesueur, 1821: 90, pl. 7.
12

13
14 365 *Type material*: Academy of Natural Sciences (ANSP). Not extant [fide Voss, 1962: 1; Lu et al.,
15
16 366 1995: 312].
17

18
19 367 *Neotype*: National Museum of Nature and Science, Tokyo, specimen NSMT-Mo 67507, mature
20
21 368 male, 270 mm DML, collected by squid jigging at 41.95°N, -135.17°E on 8th September 2009.
22

23
24 369 *Type locality*: Not designated in the original description. Here it is designated, based on the
25
26 370 neotype, as North Pacific waters (Table 1, Fig. 3) (see *Remarks*).
27

28
29 371 *Synonyms*
30

31
32 372 (?) *Loligo touchardii* Souleyet, 1852: 22, pl. 2 Figs 6–13 [fide Pfeffer (1912: 466)] MNHN
33
34 373 Syntype 7-3-724 [fide Lu et al. (1995: 326)]. Locality: Pacific Ocean.
35

36
37 374 (?) *Ommastrephes ensifer* Owen, 1881: 144, pl. 28. Type repository unresolved [Royal College
38
39 375 of Surgeon, London?]. Type locality not designated.
40

41
42 376 *Diagnosis*:
43

44
45 377 *Ommastrephes* with a maximum mantle length of 600 mm and weight of 6 kg; maximum
46
47 378 spermatophore length of 21–41 mm (9.5 ± 1.45 % DML), cement body of spermatophore 11 %,
48
49 379 sperm reservoir 44.7 % and posterior empty end 22 % of spermatophore length; cytochrome *c*
50
51 380 oxidase subunit I diagnostic character: 454, C.
52

53
54 381 *Name of the species in the phylogenetic analyses*: *Ommastrephes* group 4.
55

56
57 382 *Distribution*: Temperate North Pacific, from the coasts of China (25°N) to Russia (60°N) by the
58
59 383 west to probably from Alaska (55°N) to the Gulf of California (20°N) by the east. Distribution
60

1
2
3 384 confirmed using molecular tools for the majority of its range, excluding Northeastern Pacific
4
5 385 waters (Fig. 3).
6
7

8 386 *Remarks: Ommastrephes bartramii* was described as *Loligo bartramii* by Lesueur (1821: 90–92,
9
10 387 pl. VII) and later was transferred to the genus *Ommastrephes* by D'Orbigny (1834–1848). In his
11
12 388 description, Lesueur did not provide any specific locality for the species and the type specimen
13
14 389 no longer exists (Voss, 1962: 1; Lu *et al.*, 1995: 312). The only reference to the origin of the
15
16 390 material he examined is that they came “*from the collection of the academy, and that from the*
17
18 391 *Philadelphia Museum*” (Lesueur, 1821: 89). Without any further accurate reference, it is
19
20 392 possible that the material came from the Philadelphia shores and adjacent waters. However,
21
22 393 Lesueur also participated in the Baudin Expedition (1800–1803, see Péron & Freycinet, 1816)
23
24 394 from Le Havre (France) to Australia and he might have collected specimens during this cruise,
25
26 395 covering the distribution area of *Ommastrephes* groups 1, 2 and 3. Based on the available
27
28 396 information, it is not possible to exclude any other specimens that were previously donated to
29
30 397 the Philadelphia Museum from other localities. Therefore, the type locality data of the *O.*
31
32 398 *bartramii* type material remains unresolved and uncertain.
33
34
35

36 399 Although the type locality remains uncertain, the name ‘*Ommastrephes bartramii*’ has been
37
38 400 widely used in the North Pacific, where the only commercial fishery for this squid occurs and
39
40 401 where the majority of studies on this genus have been conducted. The International Code of
41
42 402 Zoological Nomenclature (ICZN) precludes the substitution of a long-accepted name in its
43
44 403 accustomed meaning in order to increase taxonomic stability (ICZN Article 32.2) (International
45
46 404 Commission on Zoological Nomenclature, 1999). The name *O. bartramii* referring to North
47
48 405 Pacific individuals (i.e., *Ommastrephes* group 4) has been used in more than 25 works authored
49
50 406 by more than 10 researchers in the last 50 years (e.g., Young & Hirota, 1990; Sakurai *et al.*,
51
52 407 1995; Ichii *et al.*, 2009, 2017; Vijai *et al.*, 2015; Budyansky *et al.*, 2017; Ding *et al.*, 2019; Fang
53
54 408 *et al.*, 2017; Feng *et al.*, 2017, 2018a, 2018b, 2019; Igarashi *et al.*, 2017, 2018; McKinnell &
55
56 409 Seki, 2017; Tang *et al.*, 2017; Hu *et al.*, 2018; Jiao *et al.*, 2018; Wang *et al.*, 2017; Wen *et al.*,
57
58 410 2017; Yu *et al.*, 2017a, 2017b, 2018, 2019; Zhang *et al.*, 2019), which is in agreement with the
59
60

1
2
3 411 conditions described in the ICZN Article 23.9.1.2. Although *O. bartramii* has been commonly
4
5 412 used to name the remaining species in other parts of the distribution range of the genus (recent
6
7 413 examples: Franjevic *et al.*, 2015 and Tsiamis *et al.*, 2015 for Mediterranean individuals;
8
9 414 Villanueva & Sánchez, 1993 for South Atlantic; and Guerra *et al.*, 2010 for South Pacific), these
10
11 415 species are far less studied and consequently the name is less commonly applied to them.
12
13 416 Therefore, either considering the name *O. bartramii* invalid, or designating a neotype from a
14
15 417 location outside of the North Pacific, would generate further taxonomic instability and create
16
17 418 problems in tracking the current biological information on the species, instead of solving the
18
19 419 taxonomy of the genus.

20
21
22
23 420 In order to fix a suitable type locality for the species and ensure the stability of the name, the
24
25 421 specimen NSMT-Mo 67507 from the National Museum of Nature and Science (Tokyo) is
26
27 422 hereby designed as a neotype. The neotype locality is Northeast Pacific, 41.95°N, -135.17°E.

28
29
30 423

31
32
33 424 ***Ommastrephes brevimanus* (Gould, 1852)**

34
35
36 425 *Onychoteuthis brevimanus* Gould, 1852: 483, Fig. 596.

37
38
39 426 *Type material*: Not extant [fide Johnson (1964: 32)].

40
41
42 427 *Neotype*: National Museum of New Zealand Te Papa Tongarewa (NMNZ), New Zealand,
43
44 428 specimen M.318162, female, 580 mm DML, beached in Princess Bay, Wellington, New
45
46 429 Zealand on 24th May 2015. Ethanol fixed tissues available through the Accession number
47
48 430 M.318162/1. The GenBank sequences MK995130 (COI) and MK991817 (16S) refer to the
49
50 431 neotype.

51
52
53 432 *Type locality*: 120 miles west of Tutuila, Samoa Islands (Southwestern Pacific). The neotype
54
55 433 was collected in Princess Bay, Wellington, New Zealand. According with the ICZN Article
56
57 434 76.3, the neotype locality becomes the type locality of the species.

58
59
60 435 *Synonyms*

1
2
3 436 *Ommastrephes caroli stenodactyla* Rancurel, 1976: 81. [fide Dunning (1998: 426)]. Type:
4
5 437 Museum National d'Histoire Naturelle (MNHN), Laboratoire Biologie Invertébrés Marins et
6
7 438 Malacologie, syntypes 1974, 1975, 1976, 1977 [fide Lu *et al.* (1995: 325)]. Type Locality:
8
9 439 Auameo, Ile des Pins, New Caledonia (Southwestern Pacific).

11
12 440 *Diagnosis:*

13
14
15 441 *Ommastrephes* with a maximum mantle length of 1020 mm and weight of 35 kg; maximum
16
17 442 spermatophore length 21–41 mm (9.5 ± 1.45 % ML), cement body of spermatophore 11 %,
18
19 443 sperm reservoir 44.7 % and posterior empty end 22 % of spermatophore length; cytochrome *c*
20
21 444 oxidase subunit I diagnostic characters: 36, G; 60, C; 450, G; 16S rRNA diagnostic character:
22
23 445 16, C.

24
25
26 446 *Name of the species in the phylogenetic analyses:* *Ommastrephes* group 3.

27
28
29 447 *Distribution:* Tropical and temperate South Pacific. Present in the Kermadec Islands, New
30
31 448 Zealand (Braid & Bolstad, 2019).

32
33
34
35 449
36
37 450 ***Ommastrephes caroli* (Furtado, 1887)** [nomen protectum]

38
39
40 451 *Ommatostrephes caroli* Furtado, 1887: 5, pls. 1–2.

41
42
43 452 *Type material:* Kobenhavns Universitet, Zoologisk Museum (ZMUC), syntypes (suckers only)
44
45 453 [fide Kristensen & Knudsen (1983: 221)].

46
47
48 454 *Type Locality:* “Barre de Lisbonne”, Portugal (North Atlantic Ocean).

49
50
51 455 *Synonyms*

52
53
54 456 *Loligo pironneauui* Souleyet, 1852: 20, pl. 2 Figs 1–5 [fide Pfeffer (1912: 466)] MNHN Syntype
55
56 457 2–4–402 (gladius only) [fide Lu *et al.* (1995: 322)]. Locality: 48°N, 22°W of Paris, France
57
58 458 (North Atlantic Ocean). [nomen oblitum]

1
2
3 459 *Lolimnites meridionalis* Risso, 1854: 41, pl. 19, Figs 1–3 [fide Adam (1942: 18)]. Locality:
4
5 460 "regions profondes", (?) Nice, France (Northwestern Mediterranean Sea). [nomen oblitum]
6
7

8 461 (?) *Ommastrephes bartrami sinuosus* Lonnberg, 1896: 701. Zoologiska Museet, Uppsala
9
10 462 Universitets (ZMUU), holotype 126 [fide Wallin (1991: 66)]. Locality: Teneriffe, Canary
11
12 463 Islands, Spain (North Atlantic).
13
14

15 464 *Diagnosis:*

16
17
18 465 *Ommastrephes* with a maximum mantle length of 900 mm and weight of 25 kg; maximum
19
20 466 spermatophore length 21–54 mm (11.15 ± 3.5 % ML), cement body of spermatophore 9.8 %,
21
22 467 sperm reservoir 33 % and posterior empty end 30.3 % of spermatophore length; cytochrome *c*
23
24 468 oxidase subunit I diagnostic characters: 6, T; 48, G; 81, A; 153, G; 159, G; 177, C; 198, G; 228,
25
26 469 G; 258, C; 273, G; 334, G; 366, C; 429, G; 432, C; 534, G; 573, G.
27
28

29 470 *Name of the species in the phylogenetic analyses:* *Ommastrephes* group 1.
30
31

32 471 *Distribution:* North Atlantic, confirmed with molecular tools from the Bay of Biscay (43°N) to
33
34 472 Canary Islands (27°N), Azores (40°N) and the Mediterranean Sea (Fig. 3). Also known to occur
35
36 473 in the Northeastern Atlantic from the Bay of Biscay from Scandinavia (60°N), and in the
37
38 474 Northwestern Atlantic from the Gulf of Mexico (24°N) to Nova Scotia (45°N).
39
40

41 475 *Remarks:* The name *O. caroli* has been marginally used to refer some North Atlantic
42
43 476 *Ommastrephes* specimens during part of the 20th Century (e.g., Rees, 1950; Lozano Soldevilla
44
45 477 & Franquet Santaella, 1986). To our best knowledge, the remaining names that might be
46
47 478 resurrected for *Ommastrephes* group 1 have not been used beyond their original descriptions. In
48
49 479 accordance with the ICZN Article 23.9.1.1, junior synonyms should be applied when the senior
50
51 480 synonym or homonym has not been used as a valid name after 1899. It is important to note that
52
53 481 the conditions described in the ICZN Article 23.9.1.2 also apply here, since *O. caroli* has been
54
55 482 used to refer to members of this species in more than 25 works authored by more than 10
56
57 483 authors in the last 50 years (Threlfall *et al.*, 1971; Young, 1972; Clarke & Lu, 1974; Clarke &
58
59
60

1
2
3 484 Stevens, 1974; Holme, 1974; Roper & Young, 1975; Clarke *et al.*, 1976, 1979; Wormuth, 1976;
4
5 485 Roper, 1977; Pérez-Gándaras & Guerra, 1978; Clarke, 1978; Muntz & Johnson, 1978; Roper &
6
7 486 Lu, 1979; Arnold, 1979; Guerra & Pérez-Gándaras, 1983; Roper *et al.*, 1984; Guerra, 1985;
8
9 487 Guescini & Manfrin, 1986; Pérez-Gándaras, 1986; Mangold & Boletzky, 1988; Clarke &
10
11 488 Maddock, 1988; Martins *et al.*, 1985; Lozano Soldevilla & Franquet Santaella, 1986; Vecchione
12
13 489 *et al.*, 1989; Vecchione & Roper, 1991; Gouveia, 1992; Clarke, 2003). Therefore, *O. caroli* is
14
15 490 hereby designated as *nomen protectum* and conferred on *Ommastrephes* group 1, while *L.*
16
17 491 *pironneauii* and *L. meridionalis* are both considered senior synonyms [*nomina oblita*]. Tissues
18
19 492 of the individuals of *O. caroli* according with the sense of this article can be accessed at the
20
21 493 Biological Reference Collections of the Institut de Ciències del Mar CBR-ICM, Barcelona,
22
23 494 through the Accession numbers ICMC000070, ICMC000110, ICMC000398 and ICMC000399.
24
25
26
27
28
29

30 496 ***Ommastrephes cylindraceus* D'Orbigny, 1835** *In* 1834–1847

31
32
33 497 *Loligo cylindracea* D'Orbigny, 1835 *In* 1834–1847: 54, pl. 3. Figs 3–4.

34
35
36 498 *Type material*: MNHN Type; specimen not extant [fide Lu *et al.* (1995: 314)].

37
38
39 499 *Neotype*: Biological Reference Collections of the Institut de Ciències del Mar CBR-ICM,
40
41 500 Barcelona, specimen ICMC000400, immature subadult, 144 mm DML, collected by fish jigging
42
43 501 at 25.87°S, 45° 45.76°W on 18th December 2014. The GenBank sequences MK995138 (COI)
44
45 502 and MK991824 (16S) refer to the neotype. Ethanol fixed tissues from another specimen fished
46
47 503 in the same batch are available under the Accession code ICMC000401.

48
49
50 504 *Type locality*: Austral Atlantic, 35°S, 40°W off Paris, slightly South of Buenos Aires parallel of
51
52 505 latitude, Argentina (South Atlantic). The neotype was collected off Ilha Comprida, São Paulo,
53
54 506 Brazil. According with the ICZN Article 76.3, the neotype locality becomes the type locality of
55
56 507 the species.

57
58
59 508 *Synonyms*:

1
2
3 509 *Loligo cylindricus* D'Orbigny, 1835 *In* 1834–1847: pl. 3, figs 3–4.
4
5

6 510 *Loligo vitreus* Rang, 1837: 71, pl. 96.
7
8

9 511 *Type material*: MNHN Type; specimen not extant [fide Lu *et al.* (1995: 327)].
10
11

12 512 *Type locality*: Equatorial coast of Africa (Equatorial Atlantic).
13
14

15 513 *Diagnosis*:

16
17 514 *Ommastrephes* with a maximum mantle length of 900 mm and weight of 25; maximum
18
19 515 spermatophore length 21–41 mm (9.5 ± 1.45 % ML), cement body of spermatophore 11 %,
20
21 516 sperm reservoir 44.7 % and posterior empty end 22 % of spermatophore length; cytochrome *c*
22
23 517 oxidase I diagnostic characters: 30, G; 103, G; 306, A; 493, T; 16S rRNA diagnostic characters:
24
25 518 435, G.
26
27
28

29 519 *Name of the species in the phylogenetic analyses*: *Ommastrephes* group 2.
30
31

32 520 *Distribution*: Tropical and South Atlantic (from 14°S to ~50°S) and Tropical and South Indian
33
34 521 (~10–35°S) waters. A significant part of the distribution range for this species is confirmed with
35
36 522 COI (Fig. 3); however, specimens were not available for genetic analysis from the eastern part
37
38 523 of the Indian Ocean or from the southernmost part of the Atlantic Ocean. The absence of
39
40 524 differences in substrate and inhibitor specific cholinesterase activities of optical ganglia between
41
42 525 specimens sampled in South Atlantic and Southeastern Indian waters reported by Shevtsova *et*
43
44 526 *al.* (1979) and Rozengart & Basova (2005) supports the conspecificity of all the *Ommastrephes*
45
46 527 specimens within the distribution range depicted for *O. cylindraceus* (Fig. 3). It is also
47
48 528 noteworthy that Dunning (1998) described a discontinuous distribution range of *Ommastrephes*
49
50 529 spp. at the tip of South America and the southeastern tip of Australia and considered both
51
52 530 populations reproductively isolated. The results provided here (Figs 1–3; Tables 2–5) support
53
54 531 this point of view and ensure the recognition of *O. cylindraceus* and *O. brevimanus* as different
55
56 532 species.
57
58
59
60

1
2
3 533 The single specimen of this species analyzed from Cape Verde waters (18°N) merits further
4
5 534 discussion. Zuev *et al.* (1976) extensively sampled Equatorial Atlantic waters without finding
6
7 535 any *Ommastrephes* individuals. Therefore, it is commonly accepted that the genus
8
9 536 *Ommastrephes* is not present in Equatorial Atlantic due to the temperature (see Roper *et al.*,
10
11 537 2010). However, sequences obtained herein reveal that the Cape Verde individual belongs to *O.*
12
13 538 *cylindraceus* (Figs 1–3; Tables 2–5). This isolated spot from the remaining distribution range of
14
15 539 the species can be explained by drift of specimens from the Southern Hemisphere, along with
16
17 540 the subsurface and intermediate waters of southern origin with the South Atlantic central water
18
19 541 (100–500 m, 5–18 °C) and the Antarctic Intermediate water (500–1200 m, 2–6 °C) which
20
21 542 penetrate from the southern subtropical zone to the northwestern coast of Africa up to 20–24°N
22
23 543 and 28–34°N respectively (Aristegui *et al.*, 2009; Machini & Pelegri, 2009). Similar cases of
24
25 544 distant migrations far outside the main distribution range of the species to the other hemisphere
26
27 545 with deep waters are also known (Møller *et al.*, 2003; Arkhipkin *et al.*, 2010).
28
29
30
31 546

32
33
34 547 Unavailable *Ommastrephes* names:

35
36
37 548 *Ommastrephes ayresii* Gabb *In* Carpenter, 1864: 613, 664. [nomen nudum]

38
39
40 549 *Ommastrephes californica* Heath, 1908: 582. [nomen nudum]

41
42
43 550 *Ommastrephes crassus* Lafont, 1871: 275, pl 16. [nomen nudum]

44
45
46 551

47 48 49 552 **CONCLUSION**

50
51
52 553 The long-standing problem of *Ommastrephes* taxonomy (Roper *et al.*, 2010) is here reevaluated
53
54 554 using two molecular markers and multiple molecular species delimitation methods in
55
56 555 combination with metabolic and morphological knowledge in an integrative taxonomic
57
58 556 approach. This study has revealed the presence of four species of *Ommastrephes* that occupy
59
60 557 distinct geographical regions, all previously believed to be a single monotypic cosmopolitan

1
2
3 558 species (*O. bartramii*). Although the type specimen for *O. bartramii* is no longer extant, and the
4
5 559 type locality unknown, we have designated a neotype for this species and applied this name to
6
7 560 the well-studied and commercially exploited species in the North Pacific in accordance with
8
9 561 ICZN regulations. Three other names were resurrected for the additional species recognized in
10
11 562 the present study using all available morphological, metabolic, and molecular data in an
12
13 563 integrative approach, and neotypes were designed for each species. There are currently no
14
15 564 known morphological characters that separate *O. bartramii* from *O. brevimanus* or *O.*
16
17 565 *cylindraceus*, and they appear to represent cryptic species. *O. caroli* represents a pseudocryptic
18
19 566 species because it has morphological differences from the other species in this genus. Although
20
21 567 our study included specimens from each species, the entire distribution area for each species has
22
23 568 not been sampled yet, and our inferred species distributions should be used with caution until
24
25 569 more detailed molecular information is available. We also used this information to hypothesize
26
27 570 the oceanographic features that delimit the distribution of each species. Since only
28
29 571 spermatophores showed important taxonomic differences for a single one of the recognized
30
31 572 species (*Ommastrephes* group 1, defined here as *O. caroli*), molecular characters proved to be
32
33 573 especially useful for the recognition of diagnostic differences between the species. The single
34
35 574 species of the genus commercially exploited at present is *O. bartramii*, but it is important to
36
37 575 note that the real distribution range of the species is far smaller than previously considered (e.g.,
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39 576 Roper *et al.*, 2010). Thus, this knowledge is important for the proper fishery management of the
40
41 577 species. Although every effort was made to obtain samples from the greatest possible
42
43 578 geographic range of *Ommastrephes*, including requesting international collaboration during the
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45 579 2015 Cephalopod International Advisory Council Conference (Hakodate, Japan) (Fernández-
46
47 580 Álvarez *et al.*, 2015b)—which resulted in many participants contributing material—, the entire
48
49 581 distribution range for each *Ommastrephes* species was not covered. This is a direct consequence
50
51 582 of the oceanic lifestyle of this genus coupled with the absence of directed fisheries in most of its
52
53 583 distribution range, which makes its collection from some localities a fortuitous phenomenon.
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55 584 However, specimens were available for sequencing from the majority of the distribution range
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57 585 of *O. bartramii*, *O. brevimanus*, and *O. cylindraceus*. The metabolic results of Shevtsova *et al.*

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3 586 (1979) and Rozengart & Basova (2005) suggest conspecificity of the South Atlantic and the
4
5 587 Southeastern Indian Ocean specimens and were used herein to complement genetic data to
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7 588 delimit the distribution of *O. cylindraceus*. This study increases the number of accepted species
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9 589 of the family Ommastrephidae from 22 (Roper *et al.*, 2010) to 25, which represents a 13 %
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11 590 increase of the known biodiversity of the family.
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591

592 **REFERENCES**

593 **Adam W. 1942.** Notes sur les Cephalopodes, XXI.- A propos d'une publication peu connue de
594 A. Risso, 1854. *Bulletin du Musee royal d'Histoire naturelle de Belgique* 18: 1–36.

595 **Allcock AL, Barratt I, Eléaume M, Linse K, Norman MD, Smith PJ, Steinke D, Stevens**
596 **DW, Strugnell JM. 2011.** Cryptic speciation and the circumpolarity debate: a case study on
597 endemic Southern Ocean octopuses using the coxI barcode of life. *Deep Sea Research II* 58:
598 242–249.

599 **Allcock AL, Lindgren A, Strugnell JM. 2015.** The contribution of molecular data to our
600 understanding of cephalopod evolution and systematics: a review. *Journal of Natural History*
601 49: 1373–1421.

602 **Alonso H, Granadeiro JP, Waap S, Xavier J, Symondson WOC, Ramos JA, Ca P. 2014.**
603 An holistic ecological analysis of the diet of Cory's shearwaters using prey morphological
604 characters and DNA barcoding. *Molecular Ecology* 23: 3719–3733.

605 **Amor MD, Norman MD, Roura A, Leite TS, Gleadall IA, Reid A, Perales-Raya C, Lu CC,**
606 **Silvey CJ, Vidal EAG, Hochberg FG, Zheng X, Strugnell JM. 2017.** Morphological
607 assessment of the *Octopus vulgaris* species complex evaluated in light of molecular-based
608 phylogenetic inferences. *Zoologica Scripta* 46: 275–288.

- 1
2
3 609 **Arístegui J, Barton ED, Álvarez-Salgado XA, Miguel P, Santos A, Figueiras FG, Kifani S,**
4
5 610 **Hernández-León S, Mason E, Machú E, Demarcq H. 2009.** Sub-regional ecosystem
6
7 611 variability in the Canary Current upwelling. *Progress in Oceanography* 83: 33–48.
8
9
10 612 **Arkhipkin A, Argüelles J, Shcherbich Z, Yamashiro C. 2015a.** Ambient temperature
11
12 613 influences adult size and life span in jumbo squid (*Dosidicus gigas*). *Canadian Journal of*
13
14 614 *Fisheries and Aquatic Sciences* 72: 400–409.
15
16
17 615 **Arkhipkin AI, Laptikhovsky VV, Brickle P. 2010.** An antipodal link between the North
18
19 616 Pacific and South Atlantic Oceans? *Deep Sea Research I* 57: 1009–1011.
20
21
22 617 **Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, Allcock L, Arguelles J,**
23
24 618 **Bower JR, Castillo G, Ceriola L, Chen C-S, Chen X, Diaz-Santana M, Downey N, Gonz-**
25
26 619 **alez AF, Granados Amores J, Green CP, Guerra A, Hendrickson LC, Ibañez C, Ito K,**
27
28 620 **Jereb P, Kato Y, Katugin ON, Kawano M, Kidokoro H, Kulik VV, Laptikhovsky VV,**
29
30 621 **Lipinski MR, Liu B, Mariategui L, Marin W, Medina A, Miki K, Miyahara K,**
31
32 622 **Moltschaniwskyj N, Moustahfid H, Nabhitabhata J, Nanjo N, Nigmatullin CM, Ohtani T,**
33
34 623 **Pecl G, Perez JAA, Piatkowski U, Saikliang P, Salinas-Zavala CA, Steer M, Tian Y, Ueta**
35
36 624 **Y, Vijai D, Wakabayashi T, Yamaguchi T, Yamashiro C, Yamashita N, Zeidberg LD.**
37
38 625 **2015b.** World squid fisheries. *Reviews in Fisheries Science & Aquaculture*, 23: 92–252.
39
40
41 626 **Arnold GP. 1979.** Squid. A review of their biology and fisheries. *Laboratory Leaflet* 48: 1–37.
42
43
44
45 627 **Battaglia P, Romeo, T, Consoli P, Scotti G, Andaloro F. 2010.** Characterization of the
46
47 628 artisanal fishery and its socio-economic aspects in the central Mediterranean Sea (Aeolian
48
49 629 Islands, Italy). *Fisheries Research* 102: 87–97.
50
51
52 630 **Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I.**
53
54 631 **2007.** Cryptic species as window on diversity and conservation. *Trends in Ecology and*
55
56 632 *Evolution* 22: 148–155.
57
58
59
60

- 1
2
3 633 **Bond J, Stockman A. 2008.** An integrative method for delimiting cohesion species: finding the
4
5 634 population–species interface in a group of Californian trapdoor spiders with extreme genetic
6
7 635 divergence and geographic structuring. *Systematic Biology* 57: 628–646.
8
9
10 636 **Bosc LAG. 1802.** *Histoire naturelle des vers contenant leur description et leurs moeurs; avec*
11
12 637 *figures dessinees d'apres nature.* Paris: Déterville.
13
14
15 638 **Braid HE, Bolstad KSR. 2019.** Cephalopod biodiversity of the Kermadec Islands: implications
16
17 639 for conservation and some future taxonomic priorities. *Invertebrate Systematics* 33: 402–425.
18
19
20 640 **Budyansky MV, Prants SV, Samko EV, Uleysky MY. 2017.** Identification and Lagrangian
21
22 641 analysis of oceanographic structures favorable for fishery of neon flying squid (*Ommastrephes*
23
24 642 *bartramii*) in the South Kuril area. *Oceanology* 57: 648–660.
25
26
27 643 **Calvo M, Templado J, Oliverio M, Machordom A. 2009.** Hidden Mediterranean biodiversity:
28
29 644 molecular evidence for a cryptic species complex within the reef-building gastropod
30
31 645 *Dendropoma petraeum* (Mollusca: Caenogastropoda). *Biological Journal of the Linnean Society*
32
33 646 96: 898–912.
34
35
36 647 **Carlini DB, Graves JE. 1999.** Phylogenetic analysis of cytochrome c oxidase I sequences to
37
38 648 determine higher-level relationships within the coleoid cephalopods. *Bulletin of Marine Science*
39
40 649 64: 57–76.
41
42
43
44 650 **Carpenter PP. 1864.** Supplementary report on the present state of our knowledge with regard
45
46 651 to the Mollusca of the West Coast of North America. *Report of the British Association for the*
47
48 652 *Advancement of Science* 33: 517–686.
49
50
51 653 **Carrasco SA, Meerhoff E, Yannicelly B, Ibáñez CM. 2018.** First records and descriptions of
52
53 654 early-life stages of cephalopods from Rapa Nui (Easter Island) and the nearby Apolo Seamount.
54
55 655 *Pacific Science* 73: 163–175.
56
57
58
59
60

- 1
2
3 656 **Carrera-Parra LF, Fauchald K, Gambi C. 2011.** Revision of the taxonomic status of *Lysidice*
4
5 657 (Polychaeta, Eunicidae) in the Western Caribbean Sea with observation on species reproductive
6
7 658 features and habitat preference. *Italian Journal of Zoology* 78: 1–14.
8
9
10 659 **Clarke MR. 1978.** The cephalopod statolith - an introduction to its form. *Journal of the Marine*
11
12 660 *Biological Association of the United Kingdom* 58: 701–712.
13
14
15 661 **Clarke MR. 2003.** Potential of statoliths for interpreting coleoid evolution: a brief review.
16
17 662 *Berliner Paläobiologische Abhandlungen* 3: 37–47.
18
19
20 663 **Clarke MR, Denton EJ, Gilpin-Brown JB. 1979.** On the use of ammonium for buoyancy in
21
22 664 squids. *Journal of the Marine Biological Association the United Kingdom* 59: 259–276.
23
24
25 665 **Clarke MR, Lu CC. 1974.** Vertical distribution of cephalopods at 30° N 23° W in the North
26
27 666 Atlantic. *Journal of the Marine Biological Association the United Kingdom* 54: 969–984.
28
29
30 667 **Clarke MR, MacLeod N, Paliza O. 1976.** Cephalopod remains from the stomachs of sperm
31
32 668 whales caught off Peru and Chile. *Journal of Zoology* 180: 477–493.
33
34
35 669 **Clarke MR, Maddock L. 1988.** Statoliths of fossil coleoid cephalopods. In: Wilbur KM, ed.
36
37 670 *The Mollusca. (12)*. London: Academic Press, 153–168.
38
39
40 671 **Clarke MR, Stevens JD. 1974.** Cephalopods, blue sharks and migration. *Journal of the Marine*
41
42 672 *Biological Association the United Kingdom* 54: 949–957.
43
44
45 673 **Clement M, Posada D, Crandall K. 2000.** TCS: a computer program to estimate gene
46
47 674 genealogies. *Molecular Ecology* 9: 1657–1660.
48
49
50 675 **Coll M, Navarro J, Olson RJ, Christensen V. 2013.** Assessing the trophic position and
51
52 676 ecological role of squids in marine ecosystems by means of food-web models. *Deep Sea*
53
54 677 *Research II* 95: 21–36.
55
56
57 678 **D'Orbigny A. 1834-1847.** Mollusques. *Voyage dans l'Amerique Meridionale*, 5:1–758.
58
59
60

- 1
2
3 679 **Dayrat B. 2005.** Towards integrative taxonomy. *Biological journal of the Linnean Society*, 85:
4
5 680 407–417.
6
7
8 681 **De Queiroz K. 2007.** Species concepts and species delimitation. *Systematic Biology*, 56: 879–
9
10 682 886.
11
12
13 683 **Ding Q, Cao J, Chen X. 2019.** Stock assessment of the western winter-spring cohort of
14
15 684 *Ommastrephes bartramii* in the Northwest Pacific Ocean using a Bayesian hierarchical DeLury
16
17 685 model based on daily natural mortality during 2005-2015. *Scientia Marina* 83: 155–166.
18
19
20 686 **Dunning M. 1998.** A review of the systematics, distribution and biology of the arrow squid
21
22 687 genera *Ommastrephes* Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Ornithoteuthis* Okada,
23
24 688 1927 (Cephalopoda, Ommastrephidae). In: Voss NA, Vecchione M, Toll RB, Sweeney MJ, eds.
25
26 689 *Systematics and Biogeography of Cephalopods*. Washington: Smithsonian University Press,
27
28 690 425–433.
29
30
31 691 **Fang Z, Chen XJ, Su H, Thompson K, Chen Y. 2017.** Evaluation of stock variation and
32
33 692 sexual dimorphism of beak shape of neon flying squid, *Ommastrephes bartramii*, based on
34
35 693 geometric morphometrics. *Hydrobiologia* 784: 367–380.
36
37
38 694 **Feng YJ, Chen XJ, Gao F, Liu Y. 2018a.** Impacts of changing scale on Getis-Ord G_i^*
39
40 695 hotspots of CPUE: a case study of the neon flying squid (*Ommastrephes bartramii*) in the
41
42 696 northwest Pacific Ocean. *Acta Oceanologica Sinica* 37: 67–76.
43
44
45 697 **Feng YJ, Chen XJ, Liu Y. 2017.** Detection of spatial hot spots and variation for the neon
46
47 698 flying squid *Ommastrephes bartramii* resources in the northwest Pacific Ocean. *Chinese*
48
49 699 *Journal of Oceanology and Limnology* 35: 921–935.
50
51
52 700 **Feng YJ, Cui L, Chen XJ, Chen LJ, Yang QQ. 2019.** Impacts of changing spatial scales on
53
54 701 CPUE-factor relationships of *Ommastrephes bartramii* in the northwest Pacific. *Fisheries*
55
56 702 *Oceanography* 28: 143–158.
57
58
59
60

- 1
2
3 703 **Feng YJ, Liu Y, Chen XJ. 2018b.** Modeling Monthly Spatial Distribution of *Ommastrephes*
4 *bartramii* CPUE in the Northwest Pacific and Its Spatially Nonstationary Relationships with the
5 704 Marine Environment. *Journal of Ocean University of China* 17: 647–658.
6
7 705
8
9
10 706 **Fernández-Álvarez FÁ, García-Jiménez R, Machordom A. 2015a.** *Carinina ochracea*
11 (Palaeonemertea: Tubulanidae) reaches its Southernmost distribution: new morphological and
12 707 molecular data. *Zoological Science* 32: 590–595.
13
14 708
15
16
17 709 **Fernández-Álvarez FÁ, Machordom A, García-Jiménez R, Salinas-Zavala CA, Villanueva**
18 **R. 2018a.** Predatory flying squids are detritivores during their early planktonic life. *Scientific*
19 710 *Reports* 8: 3440.
20
21 711
22
23
24 712 **Fernández-Álvarez FÁ, Martins CPP, Vidal EAG, Villanueva R. 2017.** Towards the
25 713 identification of the ommastrephid squid paralarvae (Mollusca: Cephalopoda): morphological
26 714 description of three species and a key to the north-east Atlantic species. *Zoological Journal of*
27 715 *the Linnean Society* 180: 268–287.
28
29
30
31
32
33
34 716 **Fernández-Álvarez FÁ, Sánchez P, Cuesta-Torralvo E, Escáñez A, Martins CPP, Vidal**
35 **EAG, Villanueva R. 2015b.** The genus *Ommastrephes* d'Orbigny, 1834: a single species or
36 717 more than one hidden behind a single name? Cephalopod International Advisory Council
37 718 Conference 2015. Hakodate, Japan, November 6–14. Book of Abstracts: 103.
38
39
40
41
42
43 720 **Fernández-Álvarez FÁ, Villanueva R, Hoving HJT, Gilly WF. 2018b.** The journey of squid
44 721 sperm. *Reviews in Fish Biology and Fisheries* 28: 191–199.
45
46
47
48 722 **Franjevic D, Sharamuca D, Katavic V, Rajevic N, Skaramuca B. 2015.** Genetic
49 723 Identification of a rare record of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae)
50 724 from the Eastern Adriatic Sea. *Folia Biologica* 63: 19–22.
51
52
53
54
55 725 **Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of
56 726 mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular*
57 727 *Marine Biology and Biotechnology* 3: 294–299.
58
59
60

- 1
2
3 728 **Furtado A. 1887.** Sur une nouvelle espèce de céphalopode appartenant au genre
4
5 729 *Ommatostrephes*. *Memorias da Academia Real das Ciencias de Lisboa* 6: 3–16.
6
7
8 730 **García-Jiménez R, Horreo JL, Valdecasas AG. 2017.** Minimal barcode distance between two
9
10 731 water mite species from Madeira Island: a cautionary tale. *Experimental and Applied Acarology*
11
12 732 72: 133–143.
13
14
15 733 **Gebhardt K, Knebelsberger T. 2015.** Identification of cephalopod species from the North and
16
17 734 Baltic Seas using morphology, COI and 18S rDNA sequences. *Helgoland Marine Research* 63:
18
19 735 259–271.
20
21
22 736 **Gould AA. 1852.** *Mollusca and Shells. United States Exploring Expedition, during the years*
23
24 737 *1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U. S. N. Vol. XII.* Boston:
25
26 738 Gould & Lincoln.
27
28
29 739 **Gouveia L. 1992.** Swordfish (*Xiphias gladius*, Linnaeus) fishing experiment in Madeira EEZ.
30
31 740 *Collective Volume of Scientific Papers ICCAT* 39: 477–483.
32
33
34 741 **Gray JE. 1849.** *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda*
35
36 742 *Antepedia*. London: Spottiswoodes & Shaw.
37
38
39 743 **Guerra A. 1985.** La pesca de cefalópodos mediante poteras automáticas. *Informes Técnicos del*
40
41 744 *Instituto de Investigaciones Pesqueras* 123: 3–123.
42
43
44 745 **Guerra A, Pérez-Gándaras G. 1983.** Las pesquerías mundiales de cefalópodos: situación
45
46 746 actual y perspectivas. *Informes Técnicos del instituto de investigaciones Pesqueras* 102–104: 3–
47
48 747 141.
49
50
51 748 **Guerra A, Pierce GJ, Santos MB, González AF, Hernández-Milian G, Porteiro C, Patiño**
52
53 749 **B. 2010.** Record of the largest specimen of neon flying squid *Ommastrephes bartramii*
54
55 750 (Cephalopoda: Ommastrephidae). *Iberus* 28: 61–66.
56
57
58
59
60

- 1
2
3 751 **Guescini A, Manfrin G. 1986.** Rinvenimento di Cefalopodi rari in Adriatico: *Abralia veranyi*
4
5 752 (Ruppell, 1844) e *Ommastrephes caroli* (Furtado, 1887). *Nova Thalassia* 3: 519–521.
6
7
8 753 **Hall TA. 1999.** BioEdit: a user-friendly biological sequence alignment editor and analysis
9
10 754 program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
11
12
13 755 **Hart MW, Sunday J. 2007.** Things fall apart: biological species form unconnected parsimony
14
15 756 networks. *Biological Letters* 3: 509–512.
16
17
18 757 **Heath H. 1908.** Additions to the museum- Recent Mollusca. *Proceedings of the Academy of*
19
20 758 *Natural Sciences, Philadelphia* 59: 582–583.
21
22
23 759 **Hebert PD, Cywinska A, Ball SL. 2003.** Biological identifications through DNA barcodes.
24
25 760 *Proceedings of the Royal Society of London B: Biological Sciences* 270: 313–321.
26
27
28 761 **Holme NA. 1974.** The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the
29
30 762 Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* 54: 481–
31
32 763 503.
33
34
35 764 **Hoving HJT, Fernández-Álvarez FÁ, Portner EJ, Gilly WF. 2019.** Same-sex sexual
36
37 765 behaviour in an oceanic squid, ommastrephid *Dosidicus gigas* (Humboldt squid). *Marine*
38
39 766 *Biology* 166: 33. <https://doi.org/10.1007/s00227-019-3476-6>
40
41
42 767 **Hoving HJT, Gilly WF, Markaida U, Benoit-Bird KJ, Brown ZW, Daniel P, Field JC,**
43
44 768 **Parassenti LZ, Liu B, Campos B. 2013.** Extreme plasticity in life-history strategy allows a
45
46 769 migratory predator (jumbo squid) to cope with a changing climate. *Global Change Biology* 19:
47
48 770 2089–2103.
49
50
51 771 **Hoyle WE. 1910.** A list of the generic names of Dibranchiate Cephalopoda with their type
52
53 772 species. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 32: 407–413.
54
55
56
57
58
59
60

- 1
2
3 773 **Hu GY, Fang Z, Liu BL, Chen XJ, Staples K, Chen Y. 2018.** Using different standardized
4
5 774 methods for species identification: a case study using beaks from three ommastrephid species.
6
7 775 *Journal of Ocean University of China* 17: 355–362.
8
9
10 776 **Ichii I, Mahapatra K, Sakai M, Okada Y. 2009.** Life history of the neon flying squid: effect
11
12 777 of the oceanographic regime in the North Pacific Ocean. *Marine Ecology Progress Series* 378:
13
14 778 1–11.
15
16
17 779 **Ichii T, Nishikawa H, Igarashi H, Okamura H, Mahapatra K, Sakai M, Wakabayashi T,**
18
19 780 **Inagake D, Okada Y. 2017.** Impacts of extensive driftnet fishery and late 1990s climate regime
20
21 781 shift on dominant epipelagic nekton in the Transition Region and Subtropical Frontal Zone:
22
23 782 Implications for fishery management. *Progress in Oceanography* 150: 35–47.
24
25
26 783 **Igarashi H, Ichii T, Sakai M, Ishikawa Y, Toyoda T, Masuda S, Sugiura N, Mahapatra K,**
27
28 784 **Awaji T. 2017.** Possible link between interannual variation of neon flying squid
29
30 785 (*Ommastrephes bartramii*) abundance in the North Pacific and the climate phase shift in
31
32 786 1998/1999. *Progress in Oceanography* 150: 20–34.
33
34
35
36 787 **Igarashi H, Saitoh, Ishikawa Y, Kamachi M, Usui N, Sakai M, Imamura Y. 2018.**
37
38 788 Identifying potential habitat distribution of the neon flying squid (*Ommastrephes bartramii*) off
39
40 789 the eastern coast of Japan in winter. *Fisheries Oceanography* 27: 16–27.
41
42
43 790 **International Commission on Zoological Nomenclature. 1999.** *International Code of*
44
45 791 *Zoological Nomenclature. 4th ed.* London: International Trust for Zoological Nomenclature.
46
47
48 792 **Jiao YN, Chen JD, Li W, Liu YJ, Xin CL, Yang LP. 2018.** Trace elements concentrations in
49
50 793 squids consumed in Shandong Province China and their associated risks to the human health.
51
52 794 *Marine Pollution Bulletin* 128: 267–274.
53
54
55 795 **Johnson RI. 1964.** The Recent Mollusca of Augustus Addison Gould. *United States National*
56
57 796 *Museum, Bulletin* 239: 1–182.
58
59
60

- 1
2
3 797 **Johnson SB, Warén A, Tunnicliffe V, Van Dover C, Wheat CG, Schultz TF, Vrijenhoek**
4
5 798 **RC. 2014.** Molecular taxonomy and naming of five cryptic species of *Alviniconcha* snails
6
7 799 (Gastropoda: Aabysochrysoidea) from hydrothermal vents. *Systematics and Biodiversity* 13:
8
9 800 278–295.
- 11
12 801 **Jörger KM, Schrödl M. 2013.** How to describe a cryptic species? Practical challenges of
13
14 802 molecular taxonomy. *Frontiers in Zoology* 10: 59.
- 16
17 803 **Jörger KM, Schrödl M. 2014.** How to use CAOS software for taxonomy? A quick guide to
18
19 804 extract diagnostic nucleotides or amino acids for species descriptions. *Spixiana* 37: 21–26.
- 21
22 805 **Kang X-X, Fernández-Álvarez FÁ, Alfaya J, Machordom A, Strand M, Sundberg P, Sun**
23
24 806 **S-C. 2015.** Species diversity of *Ramphogordius sanguineus/Lineus ruber* like nemerteans
25
26 807 (Nemertea: Heteronemertea) and geographic distribution of *R. sanguineus*. *Zoological Science*
27
28 808 32: 579–589.
- 30
31 809 **Kawauchi GY, Giribet G. 2010.** Are there true cosmopolitan sipunculan worms? A genetic
32
33 810 variation study within *Phascolosoma perlucens* (Sipuncula, Phascolosomatidae). *Marine*
34
35 811 *Biology* 157: 1417–1431.
- 37
38 812 **Knowlton N. 1993.** Sibling species in the sea. *Annual Review of Ecology and Systematics* 24:
39
40 813 189–216.
- 42
43 814 **Kristensen TK, Knudsen J. 1983.** A catalogue of the type specimens of Cephalopoda
44
45 815 (Mollusca) in the Zoological Museum, University of Copenhagen. *Steenstrupia* 9: 217–227.
- 47
48 816 **Kurosaka K, Yanagimoto T, Wakabayashi T, Shigenobu Y, Ochi Y, Inada H. 2012.**
49
50 817 Population genetic structure of the neon flying squid *Ommastrephes bartramii* inferred from
51
52 818 mitochondrial DNA sequence analysis. *Nippon Suisan Gakkaishi* 78: 212–219.
- 54
55 819 **Lafont A. 1871.** Note pour servir a la fauna de la Gironde contenant la liste des animaux marins
56
57 820 dont la presence à ete constatee a Arcochon pendant les annees 1869-1870. *Actes de la Societe*
58
59 821 *Linneenne Bordeaux* 28: 237–279.

- 1
2
3 822 **Lago-Barcia D, Fernández-Álvarez FÁ, Negrete L, Brusa F, Damborenea C, Grande C,**
4
5 823 **Noreña C. 2015.** Morphology and DNA barcodes reveal the presence of the non-native land
6
7 824 planarian *Obama marmorata* (Platyhelminthes, Geoplanidae) in Europe. *Invertebrate*
8
9 825 *Systematics* 29: 12–22.
- 11
12 826 **Leigh JW, Bryant D. 2015.** PopART: Full-feature software for haplotype network
13
14 827 construction. *Methods in Ecology and Evolution* 6: 1110–1116.
- 16
17 828 **Lesson RP. 1830–1831.** *Mollusques, Anellides et Vers.* In: *Bougainville B. Voyage autour du*
18
19 829 *monde sur la corvette de la Majeste, la Coquille, pendant les annees 1822–1825 sous le*
20
21 830 *commandement du capitaine Duperrey.* Paris: Arthus Bertrand.
- 23
24 831 **Lesueur CA. 1821.** Description of several new species of Cuttlefish. *Journal of the Academy of*
25
26 832 *Natural Sciences of Philadelphia* 2: 86–101.
- 28
29 833 **Lindgren AR, Pankey MS, Hochberg F, Oakley TH. 2012.** A multi-gene phylogeny of
30
31 834 Cephalopoda supports convergent morphological evolution in association with multiple habitat
32
33 835 shifts in the marine environment. *BMC Evolutionary Biology* 12: 129.
- 35
36 836 **Lönnberg E. 1896.** Two cephalopods from Teneriffe collected by A. Tullgren. *Ofversigt af*
37
38 837 *Kongl. Vetenskaps-Akademiens Forhandlingar* 53: 697–706.
- 40
41 838 **Loven S. 1845.** Malacologiska notiser. [Om nordiska Cephalopoder.]. *Ofversigt af Kongl.*
42
43 839 *Vetenskaps-Akademiens Forhandlingar* 2: 120–123.
- 45
46 840 **Lozano Soldevilla F, Franquet Santaella F. 1986.** Sobre la presencia de *Ommastrephes caroli*
47
48 841 (Furtado, 1887) (Cephalopoda: Ommastrephinae), en la costa del NE de la isla de Tenerife
49
50 842 (Canarias). *Vieraea* 161-162: 35–38.
- 52
53 843 **Lu CC, Boucher-Rodoni R, Tillier A. 1995.** Catalogue of types of recent Cephalopoda in the
54
55 844 Museum national d'Histoire Naturelle (France). *Bulletin du Museum national d'Histoire*
56
57 845 *naturelle, Paris (series 4)* 17: 307–343.
- 59
60

- 1
2
3 846 **Lydeard C, Mulvey M, Davis GM. 1996.** Molecular systematics and evolution of reproductive
4
5 847 traits of North American freshwater unionacean mussels (Mollusca: Bivalvia) as inferred from
6
7 848 16S rRNA gene sequences. *Philosophical Transactions of the Royal Society of London, Series B*
8
9 849 351: 1593–1603.
- 11
12 850 **Machini F, Pelegri JL. 2009.** Northward penetration of Antarctic intermediate water off
13
14 851 Northwest Africa. *Journal of Physical Oceanography* 39: 512–535.
- 16
17 852 **Mangold K, Boletzky Sv. 1988.** Mediterranean cephalopod fauna. In: Clarke MR, Trueman
18
19 853 ER, eds. *The Mollusca. Volume 12. Paleontology and neontology of cephalopods*. New York:
20
21 854 Academic Press, 315–330.
- 23
24 855 **Markaida U, Rosenthal J, Gilly W. 2005.** Tagging Studies on the jumbo Squid (*Dosidicus*
25
26 856 *gigas*) in the Gulf of California, Mexico. *Fishery Bulletin* 103: 219–226.
- 28
29 857 **Martins HR, Clarke MR, Reiner F, Santos SR. 1985.** A pygmy sperm whale, *Kogia*
30
31 858 *breviceps* (Blainville, 1838) (Cetacea: Odontoceti) stranded on Faial Island, Azores, with notes
32
33 859 on cephalopod beaks in stomach. *Ciencias Biológicas* 6: 63–69.
- 35
36 860 **McKinnell S, Seki MP. 2017.** Arcane epipelagic fishes of the subtropical North Pacific and
37
38 861 factors associated with their distribution. *Progress in Oceanography* 150: 48–61.
- 40
41 862 **Móller PR, Nielsen JG, Fossen I. 2003.** Patagonian toothfish found off Greenland. *Nature* 421:
42
43 863 599.
- 45
46 864 **Muntz WRA, Johnson MS. 1978.** Rhodopsins of oceanic decapods. *Vision Research* 5: 601–
47
48 865 602.
- 50
51 866 **Nesis KN. 1987.** *Cephalopods of the World; Squids, cuttlefishes, Octopuses, and Allies*.
52
53 867 Neptune City: T.F.H. Publications.
- 55
56 868 **Nigmatullin CM, Nesis KN, Arkhipkin AI. 2001.** A review of the biology of the jumbo squid
57
58 869 *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fisheries Research* 54: 9–19.

- 1
2
3 870 **Nigmatullin CM, Sabirov RM, Zalygalin VP. 2003.** Ontogenetic aspects of morphology, size,
4
5 871 structure and production of spermatophores in ommastrephid squids: An overview. *Berliner*
6
7 872 *Palaeobiologische Abhandlungen* 3: 225–240.
8
9
10 873 **Olivar MP, Hulley PA, Castellón A, Emelianov M, López C, Tuset VM, Contreras T, Molí**
11
12 874 **B. 2017.** Mesopelagic fishes across the tropical and equatorial Atlantic: Biogeographical and
13
14 875 vertical patterns. *Progress in Oceanography* 151: 116–137.
16
17 876 **Owen R. 1881.** Descriptions of some new and rare Cephalopoda (Part II). *Transactions of the*
18
19 877 *Zoological Society of London* 11: 131–170.
21
22 878 **Pardo-Gandarillas MC, Torres FI, Fuchs D, Ibáñez CM. 2018.** Updated molecular
23
24 879 phylogeny of the squid family Ommastrephidae: insights into the evolution of spawning
25
26 880 strategies. *Molecular Phylogenetics and Evolution* 120: 212–217.
28
29 881 **Pérez-Gándaras G. 1986.** Estudio de los Cefalópodos Ibéricos: sistemática y bionomía
30
31 882 mediante el estudio morfométrico comparado de sus mandíbulas. Unpublished D. Phil. Thesis,
32
33 883 Universidad Complutense de Madrid.
35
36 884 **Pérez-Gándaras G, Guerra, Á. 1978.** Nueva cita de *Architeuthis* (Cephalopoda: Teuthoidea):
37
38 885 Description y alimentación. *Investigación Pesquera* 42: 401–414.
39
40
41 886 **Péron F, Freycinet L. 1816.** *Voyage de Découvertes aux Terres Australes, exécuté sur les*
42
43 887 *corvettes Le Géographe, Le Naturaliste, et La Goëlette Le Casuarina, pendant les années 1800,*
44
45 888 *1801, 1802, 1803 et 1804; Historique: Tome Second.* Paris: De l'Imprimerie impériale.
47
48 889 **Pfeffer G. 1912.** Die Cephalopoden der Plankton-Expedition. Zugleich eine monographische
49
50 890 übersicht der Oegopsiden Cephalopoden. *Ergebnisse der Plankton-Expedition der Humboldt-*
51
52 891 *stiftung* 2: 1–815.
53
54
55 892 **Pons J, Barraclough TG, Gómez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S,**
56
57 893 **Sumlin WD, Vogler AP. 2006.** Sequence-based species delimitation for the DNA taxonomy of
58
59 894 undescribed insects. *Systematic Biology* 55: 595–609.
60

- 1
2
3 895 **Posselt HI. 1891.** *Todarodes sagittatus* (Lmk.) Stp., En anatomisk studie med Bemaerkinger
4
5 896 om Slaegtskabsforholdet mellem Ommatostrephfamiliens Genera. *Videnskabelige Meddelelser*
6
7 897 *fra den Naturhistoriske Forening I Kjobenhavn* 1890: 301–359.
8
9
10 898 **Puillandre N, Lambert A, Brouillet S, Achaz G. 2012.** ABGD, Automatic Barcode Gap
11
12 899 Discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877.
13
14
15 900 **Rambaut A. 2006-2009.** FigTree: tree figure drawing tool. Version 1.3.1, 2006–2009 [cited
16
17 901 2019 August 18]. Available from: <http://tree.bio.ed.ac.uk/software/figtree/>
18
19
20 902 **Rancurel P. 1976.** Presence dans le sud-ouest Pacifique du calmar grant *Ommastrephes caroli*
21
22 903 Furtado, 1887 (Cephalopoda - Oegopsida) et description du male. **Cahiers O.R.S.T.O.M.**
23
24 904 **(series Océanographique)** 14: 81–96.
25
26
27 905 **Rang MS. 1837.** Documents pour servir a l'histoire naturelle des cephalopodes crypyobranches.
28
29 906 *Magasin de Zoologie* 7: 1–77.
30
31
32 907 **Rees WJ. 1950.** On a giant squid *Ommastrephes caroli* Furtado stranded at Looe, Cornwall.
33
34 908 *Bulletin of the British Museum (Natural History)* 1: 31–41.
35
36
37 909 **Risso A. 1854.** *Mollusques Cephalopodes vivants observes dans les parage mediterraneen du*
38
39 910 *Comte de Nice*. Nice: Impr. Société Typographique.
40
41
42 911 **Robles R, Schubart CD, Conde JE, Carmona-Suárez C, Alvarez F, Villalobos JL, Felder**
43
44 912 **DL. 2007.** Molecular phylogeny of the American *Callinectes* Stimpson, 1860 (Brachyura:
45
46 913 Portunidae), based on two partial mitochondrial genes. *Marine Biology* 150: 1265–1274.
47
48
49 914 **Rodríguez-Flores PC, Machordom A, Macpherson E. 2017.** Three new species of squat
50
51 915 lobsters of the genus *Fennerogalatea* Baba, 1988 (Decapoda: Galatheidae) from the Pacific
52
53 916 Ocean. *Zootaxa* 4276: 46–60.
54
55
56
57
58
59
60

- 1
2
3 917 **Romeo T, Battaglia P, Pedà C, Perzia P, Consoli P, Esposito V, Andaloro F. 2012.** Pelagic
4
5 918 cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content
6
7 919 of large fish predators. *Helgoland Marine Research* 66: 295–306.
8
9
10 920 **Roper CFE. 1977.** The biogeography and numerical taxonomy of the oegopsid squid family
11
12 921 Ommastrephidae in the Pacific ocean. Bulletin of the Scripps Institution of Oceanography, vol.
13
14 922 23. John H. Wormuth. University of California Press, Berkeley, California, U.S.A. 1976. 90 p.
15
16 923 *Malacological Review* 10: 95–97.
17
18
19 924 **Roper CFE, Lu CC. 1979.** Rhynchoteuthion larvae of ommastrephid squids of the western
20
21 925 North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus*.
22
23 926 *Proceedings of the Biological Society of Washington* 91: 1039–1059.
24
25
26 927 **Roper CFE, Sweeney MJ, Nauen CE. 1984.** *FAO species catalogue. Vol. 3. Cephalopoda of*
27
28 928 *the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO*
29
30 929 *Fisheries Synopsis*. Rome: FAO.
31
32
33 930 **Roper CFE, Nigmatullin C, Jereb P. 2010.** Family Ommastrephidae. In: Jereb P, Roper CFE,
34
35 931 eds. 2010. *Cephalopods of the world. An annotated and illustrated catalogue of species known*
36
37 932 *to date. Vol. 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes.*
38
39 933 Rome: FAO, 269–347.
40
41
42 934 **Roper CFE, Young RE. 1975.** *Vertical distribution of pelagic cephalopods.* Washington DC:
43
44 935 Smithsonian University Press.
45
46
47 936 **Roper CFE, Voss GL. 1983.** Guidelines for taxonomic descriptions of cephalopod species.
48
49 937 *Memoirs of the National Museum Victoria, Melbourne, Australia* 44: 49–63.
50
51
52 938 **Rozengart EV, Basova NE. 2005.** Differences in substrate and inhibitor specificity of
53
54 939 cholinesterase activity of optical ganglia of the squid *Ommastrephes bartrami* (Les) as a
55
56 940 characteristic of isolation of populations from different areas of a disjunctive home range.
57
58 941 *Doklady Biochemistry and Biophysics* 400: 56–60.
59
60

- 1
2
3 942 **Sabirov RM, Nigmatullin CM. 2012.** Male reproductive system of the neon flying squid
4
5 943 *Ommastrephes bartramii* (Ommastrephidae): morpho-functional and geographical aspects.
6
7 944 Cephalopod International Advisory Council Symposium CIAC-2012, Florianopolis, Brazil, 27
8
9 945 October-November 2012. Book of abstract: 201.
10
11
12 946 **Sakurai Y, Young RE, Hirota J, Mangold K, Vecchione M, Clarke MR, Bower J. 1995.**
13
14 947 Artificial fertilization and development through hatching in the oceanic squids *Ommastrephes*
15
16 948 *bartramii* and *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae). *Veliger* 38: 185–
17
18 949 191.
19
20
21 950 **Sasaki M. 1915.** On three interesting new oegopsids from the Bay of Sagami. Journal of the
22
23 951 College of Agriculture, Tohoku Imperial University, Sapporo, 6: 131–150.
24
25
26 952 **Shevtsova SP, Nesis KN, Rozengart EV. 1979.** Differences in the properties of cholinesterases
27
28 953 in the visual ganglions of *Ommastrephes bartrami* (Les.) squids as an indicator of the isolation
29
30 954 of populations from various parts of a discontinuous range. *Okeanologiya* 19: 481–485.
31
32
33 955 **Souleyet FL. 1841-1852.** *Mollusques, volume 2. Voyage autour du monde execute pendant les*
34
35 956 *années 1836 et 1837 sur la corvette La Bonite. Zoologie par MM. Eydoux et Souleyet.*
36
37 957 Paris: Typographie lie Fiimin Didot Frères.
38
39
40
41 958 **Staa DJ, Ruiz-Cooley RI, Elliger C, Lebaric Z, Campos B, Markaida U, Gilly WF. 2010.**
42
43 959 Ommastrephid squids *Sthenoteuthis oualaniensis* and *Dosidicus gigas* in the eastern Pacific
44
45 960 show convergent biogeographic breaks but contrasting population structures. *Marine Ecology*
46
47 961 *Progress Series* 418: 165–178.
48
49
50 962 **Steenstrup J. 1855.** Kjaeber af en kolossal Blaeksprutte. *Oversigt over det Kongelige Danske*
51
52 963 *Videnskabernes Selskabs Forhandlinger* 1855: 199–200.
53
54
55 964 **Steenstrup J. 1857.** Oplysning om en ny Art af Blaeksprutter, *Dosidicus Eschrichtii*. *Oversigt*
56
57 965 *over det Kongelige Danske Videnskabernes Selskabs Forhandlinger* 1857: 11–14.
58
59
60

- 1
2
3 966 **Strugnell JM, Hall NE, Vecchione M, Fuchs D, Allcock AL. 2017.** Whole mitochondrial
4
5 967 genome of the Ram's Horn squid shines light on the phylogenetic position of the monotypic
6
7 968 order Spirulida (Haeckel, 1896). *Molecular Phylogenetics and Evolution* 109: 296–301.
8
9
10 969 **Strugnell JM, Norman MD, Vecchione M, Guzik M, Allcock AL. 2014.** The ink sac clouds
11
12 970 octopod evolutionary history. *Hydrobiologia* 725: 215–235.
13
14
15 971 **Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, Boletzky SV. 1992.** *'Larval' and*
16
17 972 *juvenile cephalopods: a manual for their identification.* Washington DC: Smithsonian
18
19 973 Institution Press.
20
21
22 974 **Sweeney MJ, Young RE. 2003.** Taxa associated with the Family Ommastrephidae Streenstrup,
23
24 975 1857. Tree of Life web project [cited 2019 August 18]. Available from:
25
26 976 http://tolweb.org/accessory/Ommastrephidae_Taxa?acc_id=2336
27
28
29 977 **Tamura K, Stecher G, Peterson D, Filipinski A, Kumar S. 2013.** MEGA6: Molecular
30
31 978 Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.
32
33
34 979 **Tang F, Zhang S, Cui X, Wang J, Du J. 2017.** Analysis of the typical radionuclides for neon
35
36 980 flying squid of the high seas fisheries in North Pacific Ocean and risk assessment in 2013.
37
38 981 *Yingyong Shengtai Xuebao* 28: 3071–3077.
39
40
41 982 **Templado J, Richter A, Calvo M. 2016.** Reef building Mediterranean vermetid gastropods:
42
43 983 disentangling the *Dendropoma petraeum* species complex. *Mediterranean Marine Science* 17:
44
45 984 13–31.
46
47
48 985 **Threlfall W, Lu CC, Aldrich FA. 1971.** *Tentacularia coryphaenae* Bosc, 1802, from 2 species
49
50 986 of ommastrephid squids. *Journal of Parasitology* 57: 926–927.
51
52
53 987 **Tomioka S, Kondoh T, Sato-Okoshi W, Ito K, Kakui K, Kajihara H. 2016.** Cosmopolitan or
54
55 988 cryptic species? A case study of *Capitella teleta* (Annelida: Capitellidae). *Zoological Science*
56
57 989 33: 545–554.
58
59
60

- 1
2
3 990 **Tsiamis K, Aydogan Ö, Bailly N, Balistreri P, Bariche M, Carden-Noad S, Corsini-Foka**
4
5 991 **M, Crocetta F, Davidov B, Dimitriadis C, Dragičević B, Drakulić, Dulčić MJ, Escánez A,**
6
7 992 **Fernández-Álvarez FÁ, Gerakaris V, Gerovasileiou V, Hoffman R, Izquierdo Gómez D,**
8
9 993 **Izquierdo-Muñoz A, Kondylatos G, Latsoudis P, Lipej L, Madiraca F, Mavrič B,**
10
11 994 **Parasporo M, Sourbès L, Taşkin E, Türker A, Yapici S. 2015.** New Mediterranean
12
13 995 Biodiversity Records (July 2015). *Mediterranean Marine Science* 16: 472–488.
14
15
16 996 **Valdés A, Breslau E, Padula V, Schrödl M, Camacho Y, Malaquias MA, Alexander J,**
17
18 997 **Bottomley M, Vital XG, Hooker Y, Gosliner TM. 2017.** Molecular and morphological
19
20 998 systematics of Dolabrifera Gray, 1847 (Mollusca: Gastropoda: Heterobranchia:
21
22 999 Aplysiomorpha). *Zoological Journal of the Linnean Society* 184: 31–65
23
24
25 1000 **Vecchione M, Roper CFE, Sweeney MJ. 1989.** Marine flora and fauna of the eastern United
26
27 1001 States. Mollusca: Cephalopoda. *NOAA Technical Report NMFS* 73: 1–23.
28
29
30 1002 **Vecchione M, Roper CFE. 1991.** Cephalopods observed from submersibles in the western
31
32 1003 North Atlantic. *Bulletin of Marine Science* 49: 433–445.
33
34
35 1004 **Vijai D, Sakai M, Sakurai Y. 2015.** Embryonic and paralarval development following artificial
36
37 1005 fertilization in the neon flying squid *Ommastrephes bartramii*. *Zoomorphology* 134: 417–430.
38
39
40 1006 **Villanueva R, Perricone V, Fiorito G. 2017.** Cephalopods as predators: A short journey
41
42 1007 among behavioral flexibilities, adaptations, and feeding habits. *Frontiers in Physiology* 8: 598.
43
44
45 1008 **Villanueva R, Sánchez P. 1993.** Cephalopods of the Benguela Current off Namibia: new
46
47 1009 additions and considerations on the genus *Lycoteuthis*. *Journal of Natural History* 27: 15–46.
48
49
50 1010 **Villanueva R, Vidal EAG, Fernández-Álvarez FÁ, Nabhitabhata J. 2016.** Early mode of life
51
52 1011 and hatchling size in cephalopod molluscs: influence on the species distributional ranges. *PLoS*
53
54 1012 *ONE* 11: e0165334.
55
56
57 1013 **Voss GL. 1962.** List of the types and species of cephalopods in the collections of the Academy
58
59 1014 of Natural Sciences of Philadelphia. *Notulae Naturae* 356: 1–7.
60

- 1
2
3 1015 **Wakabayashi T, Suzuki N, Sakai M, Ichii T, Chow S. 2006.** Identification of ommastrephid
4
5 1016 squid paralarvae collected in northern Hawaiian waters and phylogenetic implications for the
6
7 1017 family Ommastrephidae using mtDNA analysis. *Fisheries Science* 72: 494–502.
8
9
10 1018 **Wakabayashi T, Suzuki N, Sakai M, Ichii T, Chow S. 2012a.** Phylogenetic relationships
11
12 1019 among the family Ommastrephidae (Mollusca: Cephalopoda) inferred from two mitochondrial
13
14 1020 DNA gene sequences. *Marine Genomics* 7: 11–16.
15
16
17 1021 **Wakabayashi T, Wada S, Ochi Y, Ichii T, Sakai M. 2012b.** Genetic differentiation of the
18
19 1022 neon flying squid *Ommastrephes bartramii* between North Pacific and South Atlantic
20
21 1023 populations. *Nippon Suisan Gakkaishi* 78: 198–203 [In Japanese].
22
23
24 1024 **Wallin L. 1991.** *Catalogue of type specimens. 2. General Zoology.* Uppsala: Uppsala University
25
26 1025 Zoological Museum.
27
28
29 1026 **Wang JT, Chen XJ, Tanaka K, Cao J, Chen Y. 2017.** Environmental influences on
30
31 1027 commercial oceanic ommastrephid squids: a stock assessment perspective. *Scientia Marina* 81:
32
33 1028 37–47.
34
35
36 1029 **Wen J, Tinacci L, Acutis PL, Riina MV, Xu Y, Zeng L, Ying X, Chen Z, Guardone L,**
37
38 1030 **Chen D, Sun Y, Zhao J, Guidi A, Armani A. 2017.** An insight into the Chinese traditional
39
40 1031 seafood market: Species characterization of cephalopod products by DNA barcoding and
41
42 1032 phylogenetic analysis using COI and 16SrRNA genes. *Food Control* 82: 333–342.
43
44
45 1033 **Wormuth JH. 1976.** *The biological and numerical taxonomy of the oegopsid squid family*
46
47 1034 *Ommastrephidae in the Pacific Ocean.* Berkeley: University of California Press
48
49
50 1035 **Yokobori S, Fukuda N, Nakamura M, Aoyama T. 2004.** Long-term conservation of six
51
52 1036 duplicated structural genes in cephalopod mitochondrial genomes. *Molecular Biology and*
53
54 1037 *Evolution* 21: 2034–2046.
55
56
57 1038 **Young RE. 1972.** *The Systematics and areal distribution of the cephalopods from the seas off*
58
59 1039 *Southern California.* Washington DC: Smithsonian University Press.
60

- 1
2
3 1040 **Young RE, Hirota J. 1990.** Description of *Ommastrephes bartramii* (Cephalopoda:
4
5 1041 Ommastrephidae) paralarvae with evidence for spawning in Hawaiian waters. *Pacific Science*
6
7 1042 44: 71–80.
8
9
10 1043 **Yu W, Chen XJ, Chen C, Zhang Y. 2017a.** Impacts of oceanographic factors on interannual
11
12 1044 variability of the winter-spring cohort of neon flying squid abundance in the Northwest Pacific
13
14 1045 Ocean. *Acta Oceanologica Sinica* 36: 48–59.
15
16
17 1046 **Yu W, Chen XJ, Yi Q. 2017b.** Fishing Ground Distribution of Neon Flying Squid
18
19 1047 (*Ommastrephes bartramii*) in Relation to Oceanographic Conditions in the Northwest Pacific
20
21 1048 Ocean. *Journal of Ocean University of China* 16: 1157–1166.
22
23
24 1049 **Yu W, Chen X, Zhang Y. 2019.** Seasonal habitat patterns of jumbo flying squid *Dosidicus*
25
26 1050 *gigas* off Peruvian waters. *Journal of Marine Systems* 194: 41–51.
27
28
29 1051 **Yu W, Johansen MP, He JH, Men W, Lin LS. 2018.** Artificial radionuclides in neon flying
30
31 1052 squid from the northwestern Pacific in 2011 following the Fukushima accident. *Biogeosciences*
32
33 1053 15: 7235–7242,
34
35
36 1054 **Zalygalin VP, Nigmatullin CM, Sabirov RM. 1983.** Morphology and functioning of the male
37
38 1055 reproductive system of the squid *Ommastrephes bartramii* Lesueur. In: Starobogatov YI, Nesis
39
40 1056 KN, eds. *Taxonomy and Ecology of Cephalopods*. Leningrad: USSR Publication, 62–64 (In
41
42 1057 Russian).
43
44
45
46 1058 **Zhang J, Kapli P, Pavlidis P, Stamatakis A. 2013.** A general species delimitation method
47
48 1059 with applications to phylogenetic placements. *Bioinformatics* 29: 2869–2876.
49
50
51 1060 **Zhang KQ, Wei RB, Song R. 2019.** Extraction of Cathepsin D-Like Protease from neon flying
52
53 1061 squid (*Ommastrephes bartramii*) viscera and application in antioxidant hydrolysate production.
54
55 1062 *Biomolecules* 9: 228.
56
57
58 1063 **Zuev GV, Nesis KN, Nigmatullin CM. 1976.** Distribution of the genera *Ommastrephes*
59
60 1064 d’Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Todarodes* Steenstrup, 1880 (Cephalopoda:

- 1
2
3 1065 Oegopsida) in the Atlantic Ocean. *Bulletin of the Moscow Society of Natural Biology* 81: 53–63
4
5 1066 [In Russian].
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
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Table 1. Sample data of the ommastrephid squid individuals studied, including their accession numbers for GenBank and the morphological vouchers. Coordinates are included only when available. COI, cytochrome *c* oxidase subunit I; 16S, 16S rRNA.

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 ¹	MK995126		This work
	Gijón, Asturias, Spain. NE Atlantic.	1	Whole specimen: Parque de la Vida (La Mata, Asturias, Spain, http://www.parquedelavida.org) ² . Tissue snips: ICMC000398 ¹	MK995127	MK991813	This work
	Colunga, Asturias, Spain. NE Atlantic.	1	Whole specimen: Parque de la Vida (La Mata, Asturias, Spain, http://www.parquedelavida.org) ² . Tissue snips: ICMC000399 ¹	MK995128		This work
	40.12°N, 19.99°W. NE Atlantic.	1	ICMC000110 ¹	MK995129	MK991814	This work
	Luka Šipanska, Island of Šipan, Croatia. Mediterranean Sea.	1		KF212462		Franjevic <i>et al.</i> , 2015
	Selvagem Grande island, Portugal. NE Atlantic.	8			KC603479, KC603482- KC603484, KC603486- KC603489	Alonso <i>et al.</i> , 2014
<i>Ommastrephes</i> group 2	Cape Verde. 18.11°N, 20.20°W. E Tropical	1	ICMC000059 ¹	MF980596	MK991815	Fernández- Álvarez <i>et al.</i> (2018a), this

	Atlantic.					work
	Parana State,	4	ICMC000400 ¹ , MORG	MK995138–	MK991824–	This work
	Brazil. 25.86°S,		51418 ³	MK995141	MK991827	
	45.75°W. SW					
	Atlantic.					
	S Atlantic.	6			AB635411–	Wakabayashi
					AB635416	<i>et al.</i> , 2012b
	40.20°S, 58.41°E.	2	DE.2.1.5.4.2 and	MK995134–	MK991820–	This work
	SW Indian Ocean.		DE.2.1.5.4.3 ⁴	MK995135	MK991821	
	30.95°S, 57.52°E.	4	DE.2.1.5.4, DE.2.1.5.4.1,	MK995132–	MK991818–	This work
	SW Indian Ocean.		DE.2.1.5.4.4, DE.2.1.5.4.5 ⁴	MK995133,	MK991819,	
				MK995136–	MK991822–	
				MK995137	MK991823	
	34–36°N, 40–50°E.	2			AB635465–	Kurosaka <i>et</i>
	SW Indian Ocean.				AB635466	<i>al.</i> , 2012
<i>Ommastrephes</i>	Mangaia, Cook	2		HQ829183,	HQ829182	Unpublished
group 3	Islands (William F.			HQ829184		
	Gilly, pers.					
	comm.). Central S					
	Pacific.					
	Princess Bay,	1	NMNZ M.318162 ⁵	MK995130	MK991817	This work
	Wellington, New					
	Zealand. SW					
	Pacific.					
	Off Manukau	1	NMNZ M.318203 ⁵	MK995131	MK991816	This work
	Harbour entrance,					
	New Zealand. SW					
	Pacific.					
	Rapa Nui, Chile.	1		MH347315		Carrasco <i>et</i>
	SE Pacific.					<i>al.</i> 2018
<i>Ommastrephes</i>	Cruise Hokusei-	1		AF000057		Carlini <i>et al.</i> ,
group 4	Maru, NW Pacific.					1999
	Northern Hawaiian	2		AB199549,		Wakabayashi
	waters, Central N			AB199551		<i>et al.</i> , 2006
	Pacific.					
	Cruise Shunyo-	1		AB270941		Wakabayashi
	Maru, Northern					<i>et al.</i> , 2012a

Hawaiian waters,

Central N Pacific.**N Pacific.**

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AB635404–

Wakabayashi

AB635410

et al., 2012b

39–46°N, 163–

30

AB509422–

Kurosaka *et*173°W. **NW**

AB509451

al., 2012**Pacific and****Central N Pacific.**

<i>Dosidicus</i>	1	AB270944	AB270959	Wakabayashi
<i>gigas</i>				<i>et al.</i> , 2012a
(D'Orbigny, 1835)				
<i>Sthenoteuthis</i>	1	AB270942	AB270957	Wakabayashi
<i>pteropus</i>				<i>et al.</i> , 2012a
(Steenstrup, 1855)				
<i>Sthenoteuthis</i>	1	AB270943	AB270958	Wakabayashi
<i>oualaniensis</i>				<i>et al.</i> , 2012a
(Lesson, 1830–1831)				
<i>Eucleoteuthis</i>	1	AB270945	AB270960	Wakabayashi
<i>luminosa</i>				<i>et al.</i> , 2012a
(Sasaki, 1915)				
<i>Hyaloteuthis</i>	1	AB270947	AB270962	Wakabayashi
<i>pelagica</i>				<i>et al.</i> , 2012a
(Bosc, 1802)				

1070 ¹CBR-ICM, Barcelona, Spain.1071 ²No voucher accession number available.1072 ³Museu Oceanográfico de Rio Grande (Morg), Rio Grande, Brazil.1073 ⁴Central Marine Fisheries Research Institute (CMFRI), Kochi-682018, Kerala, India.1074 ⁵National Museum of New Zealand Te Papa Tongarewa (NMNZ), New Zealand.

1075

1076 **Table 2.** Intraclade *p*-distances (%) among *Ommastrephes* groups for two mitochondrial gene
 1077 regions (cytochrome *c* oxidase subunit I [COI] and 16S rRNA [16S]).

COI	Mean	Range	n
<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

1078

1079 **Table 3.** Interclade mean *p*-distances (%) between *Ommastrephes* groups for two mitochondrial
 1080 gene regions (cytochrome *c* oxidase subunit I [COI] and 16S rRNA [16S]).

COI			
<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

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1082 **Table 4.** Molecular diagnostic characters obtained from cytochrome *c* oxidase subunit I (COI).
 1083 Diagnostic characters are shaded. The alignment is provided as supplementary material to unambiguously
 1084 name each nucleotide position.

Position	<i>Ommastrephes</i>				Outgroups				
	Group	Group	Group	Group	<i>Dosidicus</i>	<i>Sthenoteuthis</i>	<i>Sthenoteuthis</i>	<i>Eucleoteuthis</i>	<i>Hyaloteuthis</i>
	1	2	3	4	<i>gigas</i>	<i>pteropus</i>	<i>oualaniensis</i>	<i>luminosa</i>	<i>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

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1086 **Table 5.** Molecular diagnostic characters obtained from 16S rRNA (16S). Diagnostic characters are
 1087 shaded. The alignment is provided as supplementary material to unambiguously name each nucleotide
 1088 position.

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

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3 1091 **Figure 1.** Haplotype statistical parsimony networks constructed by the TCS function of PopART. The
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5 1092 geographic point of the samples is indicated in the map. For GenBank records, the approximate
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7 1093 geographic position was inferred when necessary. (A) Cytochrome *c* oxidase subunit I (COI). (B) Map
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9 1094 depicting the localities sampled for COI. (C) 16S rRNA (16S). (D) Map depicting the localities sampled
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11 1095 for 16S. Abbreviations: NA, North Atlantic; SA, South Atlantic; EA, Eastern Tropical Atlantic; SI,
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13 1096 Indian; NP, North Pacific; SP, South Pacific.

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15 1097

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18 1098 **Figure 2.** Summarized results from the molecular species delimitation analyses and the enzymatic and
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20 1099 morphological information, represented on the maximum likelihood tree resulted from the analysis of the
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22 1100 cytochrome *c* oxidase subunit I (COI) dataset. Values on the nodes represent the bootstrap values for
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24 1101 COI. Black and grey bars to the right represent the hypothesized species groupings based on the
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26 1102 molecular delimitation results of TCS, *p*-distances, ABGD and PTP for COI, and TCS and PTP for 16S
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28 1103 rRNA (16S), as well as the previously identified groups from the literature based on the differences in
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30 1104 substrate and inhibitor specificity of cholinesterase activities of the optical ganglia (after Shevtsova *et al.*,
31
32 1105 1979 and Rozengart & Basova, 2005), the spermatophore morphology (after Nigmatullin *et al.*, 2003) and
33
34 1106 maximum size-at-maturity of females (Roper *et al.*, 2010). It is important to note that Shevtsova *et al.*
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36 1107 (1979) and Rozengart & Basova (2005) did not include any South Pacific individuals in their studies.

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38 1108

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41 1109 **Figure 3.** Schematic map of the distribution range of each species of the genus *Ommastrephes*, based on
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43 1110 the distribution of the genus depicted by Roper *et al.* (2010) and the results of this work. Sampled points
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45 1111 for both molecular markers are depicted on the map. The oceanic currents that probably contribute to the
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47 1112 reproductive isolation of each species are depicted. Parts of the distribution range of each species that still
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49 1113 are not confirmed with molecular data are indicated with a question mark.

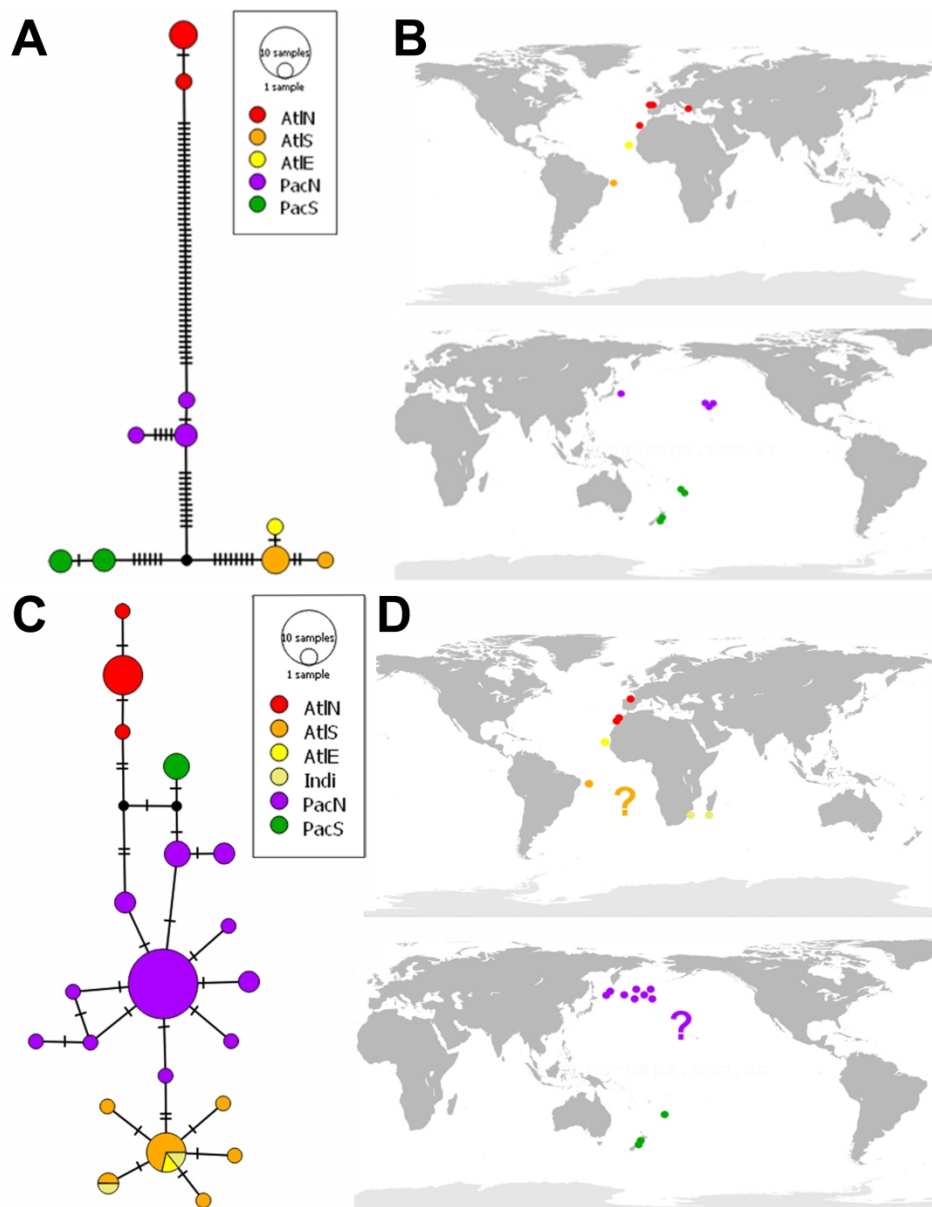


Figure 1. Haplotype statistical parsimony networks constructed by the TCS function of PopART. The geographic point of the samples is indicated in the map. For GenBank records, the approximate geographic position was inferred when necessary. (A) Cytochrome c oxidase subunit I (COI). (B) Map depicting the localities sampled for COI. (C) 16S rRNA (16S). (D) Map depicting the localities sampled for 16S. Abbreviations: NA, North Atlantic; SA, South Atlantic; EA, Eastern Tropical Atlantic; SI, Indian; NP, North Pacific; SP, South Pacific.

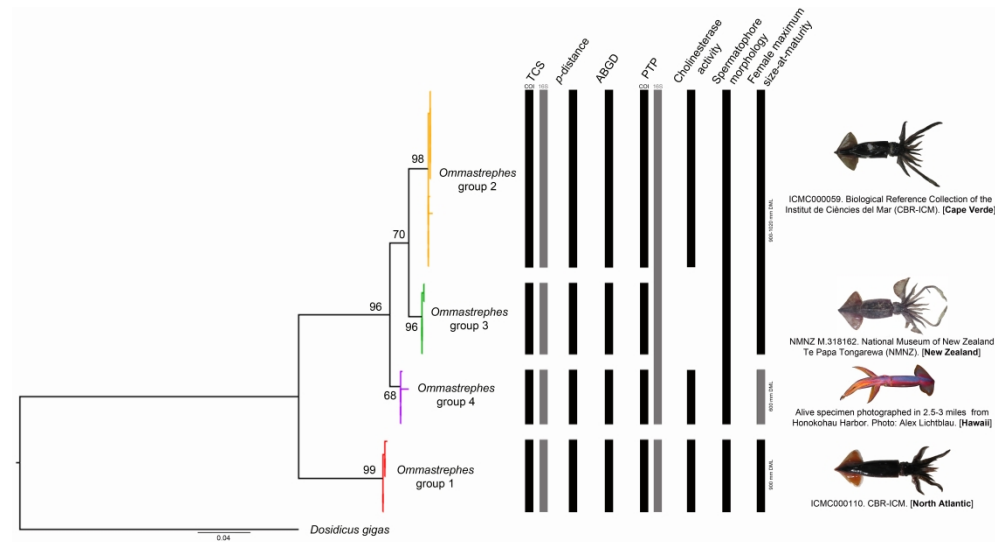


Figure 2. Summarized results from the molecular species delimitation analyses and the enzymatic and morphological information, represented on the maximum likelihood tree resulted from the analysis of the cytochrome c oxidase subunit I (COI) dataset. Values on the nodes represent the bootstrap values 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), as well as 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 and Rozengart & Basova, 2005), the spermatophore morphology (after Nigmatullin et al., 2003) and maximum 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 individual in their studies.

560x303mm (300 x 300 DPI)

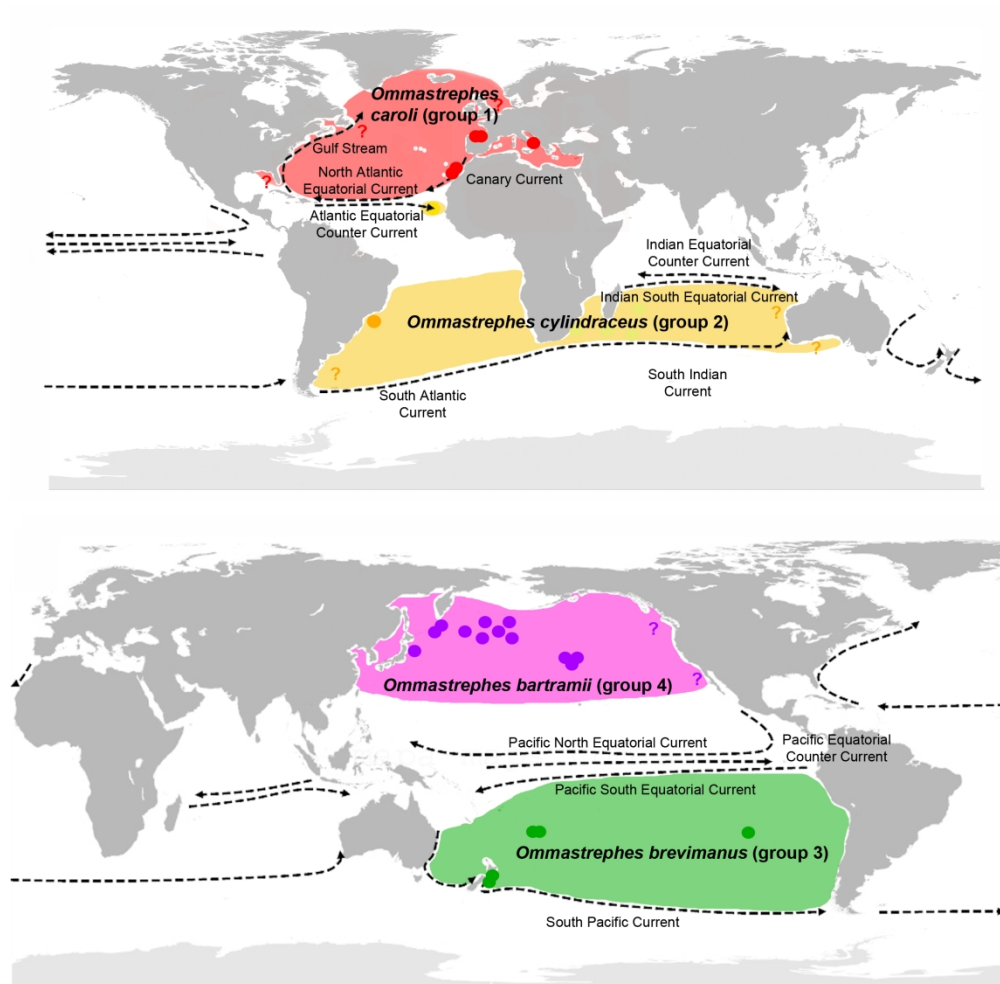


Figure 3. Schematic map of the distribution range of each species of the genus *Ommastrephes*, based on the distribution of the genus depicted by Roper et al. (2010) and the results of this work. Sampled points for both molecular markers are depicted on the map. The oceanic currents that probably contribute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