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REVIEW, CONCEPT, AND SYNTHESIS

Biodiversity of octopuses in the Americas

Roberto González-Gómez[1,2] · Otilio Avendaño[3] · Irene de los Angeles Barriga-Sosa[4] · Penélope Bastos[5] · Claudia Caamal-Monsreal[6] · Gabriela Castillo-Estrada[7] · Celso Cedillo-Robles[8] · Adam Daw[9] · Mariana Díaz-Santana-Iturrios[10,11] · Gabriela Galindo-Cortes[1] · Jürgen Guerrero-Kommritz[12] · Manuel Haimovici[13] · Christian M. Ibáñez[10] · María de Lourdes Jiménez-Badillo[1] · Paul Larson[14] · Tatiana Leite[15] · Françoise D. Lima[16] · Unai Markaida[17] · César Meiners-Mandujano[1] · Piedad S. Morillo-Velarde[1,2] · Nicolás Ortiz[18] · M. Cecilia Pardo-Gandarillas[10] · Ricardo Pliego-Cárdenas[4] · María Edith Ré[19] · Brian Siegel[20] · Brian Urbano[21] · Erica A. G. Vidal[22] · Ian G. Gleadall[23,24]

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Abstract
A comprehensive survey of the octopus fauna around the Americas is presented to facilitate and accelerate the assessment of a full understanding of American octopus biodiversity. Brief accounts are provided summarizing research efforts on octopus species taxonomy, diversity and distribution in different regions of North and South America. *Octopus americanus* and *O. insularis* are compared and clearly distinguished from each other and from the closely-related European species, *O. vulgaris*. The use of genus names *Paroctopus* and *Pinnoctopus* is clarified. Included is a discussion of the recent application of genus name *Paroctopus* to warm-temperate and tropical species of small size, along with a cautionary note about species identifications in the light of past errors in misassigning large-to-giant cold-water species to genus *Paroctopus*. Related to problems with identifying species of *Paroctopus*, there is an appended note concerning misidentifications and the importance of thorough species descriptions to obtain species information at the levels of both phenotype and genotype. A lectotype is formally designated for *Bathypolypus arcticus* (Prosch, 1849); and the status of so-called '*Octopus giganteus*' is reviewed briefly. A supplementary online database, AmeriCeph, provides basic information about all known octopus species of the Americas, including the institutional location of type material and the identification of voucher specimens and their depositories. DNA sequences registered in this database are not all fully compatible with barcoding standards. However, a subset of DNA sequences conforming to strict barcode identifications is provided in a second supplementary table, providing barcode sequences directly applicable also to improving standards of seafood traceability. This in turn contributes to building sustainability of exploited octopus fisheries stocks and identification of species suitable for aquaculture trials to meet the increasing commercial demand for octopus worldwide.

Keywords Biodiversity · Biogeography · *Bathypolypus arcticus* · *Octopus americanus* · *O. insularis* · *Paroctopus* · *Pinnoctopus* · Identification · Misapplication · Misidentification · Taxonomy · North America · Central America · South America · Seafood traceability

Introduction

When biodiversity (including 'genetic diversity') was first championed by E.O. Wilson, he pointed out its importance as one of the key problems of science as a whole (Wilson 1985). In recent years, biodiversity decline has been recognized as a threat to global stability more serious than climate change, with the potential to contribute to destabilizing the Earth system from its current state established approximately 11,700 years ago at the start of the Holocene Epoch (Steffen et al. 2015). To address the problems associated with declining biodiversity, biodiversity itself must be quantified, by counting the number of species, among other parameters. To do that, it is first necessary to distinguish each species. Only then can the size of the species population be estimated and assessments made of threats that could lead to potential population collapse, possible extinction

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(loss of biodiversity) and the consequent destabilization of the ecological system.

While acknowledging that the number of species (species richness) represents only one aspect of biological diversity (along with genetics, evenness, population size, etc.; Bermudez and Lindemann-Matthies 2020), it ‘is the only metric that has been reported often enough, and in a sufficiently standardized way, to allow general comparisons across different regions, habitats, taxa, or scales of space and time’ (Vellend 2017). Therefore, in here attempting to quantify and discuss the biodiversity of octopuses in the Americas, species richness is used as a significant proxy (cf. also other recent cephalopod studies: Judkins et al. 2010; Rosa et al. 2019; Boavida-Portugal et al. 2022; Oesterwind et al. 2022).

Biodiversity is not uniform but characterized by patches of endemism located in certain key areas where species numbers are much higher than the global mean: the so-called biodiversity hotspots. For many groups of marine animals these happen to coincide with coral reef ecosystems (Roberts et al. 2002), and around the equator where species turnover is highest (Chaudhary and Costello 2023). A recent global assessment of coastal cephalopods found that 44% of species (164) are benthic octopuses, and the major hotspot of octopus biodiversity was found to be in the seas of eastern Asia, apparently associated with warm current systems flowing northwards from the Central Indo-Pacific (Rosa et al. 2019). This coincides well with the broad study of global patterns and predictors for species richness of 13 taxonomic groups by Tittensor et al. (2010), who showed that the maximum marine coastal biodiversity is in the Western Pacific and that sea surface temperature is the major environmental factor associated with marine biodiversity hotspots. This is also a conclusion arrived at more than 170 years ago by d’Orbigny (1849), who compared the present (Holocene) faunal distributions with the apparently broader, more uniform distributions of Mesozoic fossil species, when cephalopods thrived throughout uniformly warm, shallow seas. He concluded that cephalopods seem to be adapted to warmer seas and that faunal distribution is under the influence of three factors: ocean currents, temperature, and land-mass orography, of which he considered temperature to have the greatest effect (d’Orbigny 1849).

Biodiversity threats may coincide with biodiversity hotspots and thereby affect a disproportionately large number of species (Tittensor et al. 2010). Threats such as exploitation, habitat destruction, pollution and climate change have large impacts in coastal areas of East Asia, Europe, North America and the Caribbean, and Tittensor et al. (2010) found weak but significant correlations between mean anthropogenic impacts and species richness, suggesting that the overlap of species hotspots and human impact may be important for marine management and conservation efforts across taxa. However, certainly for octopodids, there has been relatively little research on the fauna of the Americas, particularly the tropical Western Atlantic, which is a huge coastal extent including the southern Gulf of Mexico (GoM), the Caribbean, and more than half of the Atlantic coast of South America. In this regard, it is noted that coastline length is another important factor associated with biodiversity hotspots (Tittensor et al. 2010).

The Caribbean area is well-known as a marine biodiversity hotspot for various faunal groups (Briggs and Bowen 2013; Cowman and Bellwood 2013) and the creation of vicariant ‘geminate species’ has been emphasized for octopuses (Voight 1988), when the Atrato Seaway between North and South America was closed by the rise of the Panamanian isthmus (around 2.8 Mya; O’Dea et al. 2016), splitting the fauna into Pacific and Atlantic sub-populations. Certainly, several octopus species that inhabit both coastal sides of the isthmus are very closely related since apparently they share a common ancestor that was present before the closure of the Atrato Seaway (Nesis 1975a, b; Leite et al. 2008; Gleadall 2013; Ibáñez et al. 2016; Lima et al. 2020b; the ‘geminate species’ of Voight 1988). However, for many animal groups this did not always result in doubling of species by allopatry (one each side of the isthmus). For them, closure of the Atrato Seaway resulted in a paucity of species in the Atlantic, where the population died out, leaving only a ‘source’ population on the Pacific side (e.g., Landau et al. 2009), and a recent analysis found that Caribbean cephalopod diversity is relatively modest (Rosa et al. 2019).

The Caribbean Sea and southern GoM are part of the Tropical Northwestern Atlantic Province, a relatively compact area containing nine different ecoregions, which have been recognized based on the species distributions of different animal groups within this province (Spalding et al. 2007). The component endemic populations have probably formed during the last 20 My or so, through a combination of the changes and migrations occurring due to the rise of the Isthmus (e.g. Landau et al. 2009), periods of marked rising and falling of sea level (*cf.* Hallam and Wignall 1999), and faunal replacements resulting from extinction events at the end of the Pliocene and Pleistocene epochs, along with subsequent speciation (Vermeij 2005; LaViolette 2011; Pimiento et al. 2017; Melott et al. 2018). These include faunal disappearances, migrations and speciation in both North–South and East–West directions across the province (e.g., Vermeij 2005; Landau et al. 2009), resulting in a patchwork of paraprovinces, ecoregions and endemic species. It is therefore possible that the biodiversity of the endemic octopus populations may be markedly high in this province. However, the extent to which this may be true has yet to be determined, so one aim of the present review was to begin to assess identifications of the octopus species in the different ecoregions in and around the GoM and Caribbean.

When any group of organisms becomes the focus of more in-depth research, it soon becomes apparent that its taxonomy is more complex than at first realized. Octopuses are no exception. Until the latter part of the twentieth century, most octopus species were identified as belonging to genus *Octopus* but in recent decades the numbers of genera recognized and species identified have increased steadily (compare Roper et al. 1984 with the greatly updated account by Jereb et al. 2016). Tittensor et al. (2010) noted that their data contained a higher level of uncertainty for cephalopods because data available for their study account for only about 25% of known diversity, and were biased towards commercial species. Since that time, several new species of octopus have been described, increasing the total number of known octopus species in the Americas. Included among these recently described taxa are several new commercially important species within the genus *Octopus* sensu stricto (i.e., *Octopus* Cuvier sensu O'Shea 1999: e.g., Leite et al. 2008; Avendaño et al. 2020; Amor and Hart 2021; see Sect. "Distinguishing among species in the *Octopus vulgaris* complex"). The so-called 'common octopus', for example, was considered to be a single cosmopolitan species, *Octopus vulgaris* Cuvier 1797, even following the analysis of mitochondrial and nuclear DNA sequences from specimens sampled around the globe (Warnke et al 2004). However, further research has shown that in fact the global population is a complex of closely related species, which only recently are beginning to be distinguished and their ranges defined (Amor et al. 2017b, 2019; Gleadall 2016). At least two of the species recently distinguished from true *O. vulgaris* from the Mediterranean and East Atlantic are known to be found off the American Atlantic coasts (Leite et al. 2008; Amado et al. 2015; Lima et al. 2017). This means that within the last two decades the number of American species in the *O. vulgaris* complex is actually two more than previously realized, and not part of the Eastern Atlantic populations of the genuine *O. vulgaris* (Amor et al. 2017b, 2019).

Other aspects complicating octopus taxonomy include misidentifications and brief, uninformative descriptions, such as the early descriptions of *O. americanus* and species of *Argonauta* (see Sect. "Distinguishing among species in the *Octopus vulgaris* complex" and Sect. "Canada, United States of America and western Greenland"). Inadequate descriptions are still occurring, however, and these of course only hinder attempts to acquire an accurate assessment of octopus biodiversity.

Recognizing the problems with octopus identification in the literature, and noting the lack of any recent account of the American octopus fauna as a whole, the present study aims to provide a snapshot review of current knowledge of octopus species extant around the American continental masses. It began with discussions and sharing of knowledge among cephalopod scientists who attended two meetings in November, 2018: the first in Sisal at UNAM, Mexico, and the second in Florida, at CIAC 2018. The contributors to the present paper are mostly specialists from various countries around the Americas who have been conducting research on their local octopus fauna. As attempts are made to address issues such as climate change and the recent dramatic increase in effort to fish octopus stocks worldwide (Sauer et al. 2021), this review provides a timely update of our knowledge on octopus biodiversity in the Americas, which can serve as a reference for fisheries managers and others involved in various aspects of the biology, fisheries and conservation of octopuses. For instance, we include information on species that recently have begun to be targeted as prospective species for aquaculture trials (Rosas et al. 2014; Uriarte and Farías 2014; Zúñiga et al. 2014), so this contribution may help to ensure that the most appropriate species are being selected.

This review also includes brief historical accounts of the collection and description of octopus species throughout the Americas, among which are maps comparing the distribution of closely related octopus species groups. Finally, there is an analysis of the biogeographical features of octopus species in the Americas and then a discussion of different facets of American octopus biodiversity.

Species identification is often difficult and the taxonomy of most organisms is constantly changing in the light of new information and discoveries, so this review includes clarification of some of the most recent taxonomic changes. In the next section, there is an explanation of how to distinguish the two recently described American species closely related to *O. vulgaris*, with which they have long been confused, followed by a brief explanation of the broadening application of genus name *Paroctopus*. Another genus name, *Pinnoctopus*, is also beginning to be used more widely but requires more explanation, for which see Appendix 1. Four other appendixes are provided: Appendix 2 deals briefly with a nomenclatural technicality for *Bathypolypus arcticus*; Appendix 3 explains and confirms that the controversially named '*Octopus giganteus*' is not a cephalopod at all; Appendix 4 deals with the previously common, unfortunate misapplication of genus name *Paroctopus* to large, cold-water species; and Appendix 5 discusses problems and controversy in identifying American species of octopus, explaining the reasoning behind modern requirements for identification and the establishing of new animal species by complementary use of both 'traditional' (morphological) and 'molecular' (DNA sequencing) techniques.

Comments on selected species and species groups

Distinguishing among species in the *Octopus vulgaris* complex

The closely-related octopus species on the eastern and western sides of the Atlantic may be either amphi-Atlantic (one species distributed on both sides) or present as distinct western and eastern species. Until recently, most species have been classed in the former group and identified by their eastern Atlantic (European) name. Species in the '*O. vulgaris* complex' have been the first to be studied and the results include an intriguing mixture of the two possibilities: one of two newly recognized American species is now known to be distributed as far East as some of the islands off the coast of West Africa (hence its name *Octopus insularis*) but is not recognized as 'amphi-Atlantic'. Although their exact distributions are yet to be fully resolved, the main differences between the two American species of this complex are now clear and are summarized here: *Octopus insularis* was described by Leite et al (2008) based on specimens from Brazil; and *O. americanus* Froriep 1806, was redescribed by Avendaño et al. (2020), based on specimens from Mexico.

Octopus insularis is an example of a species misidentified for decades as an eastern Atlantic species (its congener, the European species *O. vulgaris*). In this regard, recently, Guerrero-Kommritz and Camelo-Guarin (2016) described an octopus from Colombian Caribbean waters as the new species *O. tayrona*. However, evidence is accumulating which, on balance, suggests that *O. tayrona* represents a local population of *O. insularis*. For instance, the body pattern and morphological data of the former are very similar to those of the adults and juveniles of the latter (see Leite et al. 2008; Leite and Mather 2008; González-Gómez et al. 2018). Moreover, DNA sequences from *O. tayrona* for the mitochondrial gene cytochrome c oxidase subunit I (COI) are identical to those of *O. insularis* (Ritschard et al. 2019; Puentes-Sayo et al. 2021), so they are here considered to be the same species, for which name *O. insularis* has priority. If there are other differences at the gene level that might distinguish a separate Colombian population (as a species or subspecies *O. tayrona*), that will require further research.

In her study on the littoral Octopoda of the western Atlantic, Pickford (1945) mentioned that specimens identified as *O. vulgaris* from Florida and North Carolina have arms that are four times longer than the mantle while those from Bermuda have markedly shorter arms. Moreover, she wrote: 'The occurrence of specimens with specially enlarged suckers is very sporadic in the west Atlantic, only two were observed in the present investigation, one from Florida […] and one from North Carolina […], both males. None of the Bermuda specimens, which include four males, have this feature'. Finally, she states: 'Adam (1937) found no specially enlarged suckers in a series of eight specimens from Bonaire although the four males seemed to have slightly larger normal suckers'. Based on the data presented by Pickford (1945), the mean normal sucker index for the male specimens from Bermuda and Bonaire was 12 and 13, respectively, which falls within the enlarged sucker index range value reported for *O. insularis* in the tropical south and northwestern Atlantic (eSDI 9–15; Leite et al. 2008; González-Gómez et al. 2018). In contrast, specimens from North Carolina and Florida had mean eSDI values of 19 and 20 respectively. According to these observations and the fact that *O. insularis* has already been identified in Bermuda, Turks and Caicos (O'Brien et al. 2021) and South Florida (Maloney et al. 2023), it seems that "*O. vulgaris*" specimens analyzed by Pickford from those areas were probably *O. insularis*. Further supporting these observations of the presence of two sympatric species, Robson (1929) had already suggested that the Bermudas might be the most northerly point of the range of '*O. vulgaris*' on the western side of the Atlantic, while also recognizing some morphological variation among the material examined, including some individuals of uncertain identification.

In considering the octopus fauna of the Americas, specimens taken to Europe and identified as *Octopus americanus* have been recorded since the mid-eighteenth century. The name is best known following a review of octopus species by Denys de Montfort (1802), which included the French phrase 'le poulpe américain' with reference to a description of two small specimens from the West Indies by Baker (1759). The Latinized name *Octopus americanus* was first coined by Seba (1758) (though not as a true binomial name in the Linnean sense), and later (apparently independently) by Froriep (1806) and Blainville (1826). Unfortunately, none of these authors described any features which might characterize the species; the specimens described by Seba (1758) and Baker (1759) are no longer extant.

In past accounts (e.g. Baker 1759; Denys de Montfort 1802; Froriep 1806; Blainville 1826), *O. americanus* has been described vaguely with reference to (and even synonymized with) the common octopus of Europe, *Octopus vulgaris*. However, *O. vulgaris* is now considered to be confined to the eastern side of the Atlantic (Gleadall 2016; Amor et al. 2017b). Voss and Toll (1998) suggested that if an *O. vulgaris*-like species in American waters were to be subsequently identified as a species different from *O. vulgaris* sensu Cuvier 1797, then the name *americanus* could be used to name it. Accordingly, the name '*Octopus americanus*' was finally stabilized by Avendaño et al. (2020) who redescribed it and designated a neotype from the northeastern corner of the Yucatan Peninsula, Mexico (which is near Cuba; *cf*. the brief description of *O. vulgaris* subspecies *americanus* by d'Orbigny 1845a).

Norman et al. (2016) considered that the western Atlantic coast included two taxa (apparently at species level) closely related to *O. vulgaris* (a species endemic to the Mediterranean and northeastern Atlantic), which they referred to as '*O. vulgaris* Type I' (more conventionally identified as *Octopus* aff. *vulgaris* sp. 1) in the Caribbean, GoM, and North

America; and '*O. vulgaris* Type II' (*Octopus* aff. *vulgaris* sp. 2) in the southwestern Atlantic. It has been confirmed that an *O. vulgaris*-like specimen from southern Brazil is morphologically and genetically different from *O. vulgaris* sensu stricto (Amor et al. 2017b, 2019). No features distinguishing the taxa affiliated to *O. vulgaris* sensu stricto were described by Norman et al. (2016).

Recent studies in Brazil and Mexico have shown that the two 'Types' proposed by Norman et al. (2016) were confounded because *O. vulgaris*-like specimens from the tropical western Central Atlantic and Brazil are genetically the same species (Lima et al. 2017; Avendaño et al. 2020). Since *O. americanus* had been historically recorded in different latitudes of the American Atlantic, including Cuba (d'Orbigny 1845a), and since specimens from localities attributed to *O. vulgaris* so-called types I and II apparently are genetically identical, Avendaño et al. (2020) decided to name this species *O. americanus*, a species distributed along much of the eastern American continent coast from Mar del Plata, Argentina, through Brazil, northeastern South America, the Caribbean and GoM to the eastern coast of the USA (Avendaño et al. 2020). Using an existing name for this genetically distinct species kills two birds with one stone: avoiding the possibility of generating another synonym; and finding a legitimate use for a name first introduced for a Western Central Atlantic species more than 200 years ago (Froriep 1806; Blainville 1826; d'Orbigny 1845a).

Octopus americanus is the main target species of the industrial octopus fishery in intermediate and colder waters in southern Brazil (Avila-da-Silva et al. 2014), and the Campeche Bank, GoM (Avendaño et al. 2020), while *O. insularis* has a greater importance to the artisanal and subsistence fishermen in tropical waters (Leite et al. 2009; González-Gómez et al. 2020; Lopes et al. 2021).

Morphological and genetic differences

Morphological and genetic differences between *O. insularis*, *O. americanus* and *O. vulgaris* have been clearly defined by several authors (e.g. Leite et al. 2008; González-Gómez et al. 2018; Avendaño et al. 2020). However, all three species show similar morphology and are difficult to distinguish (Amor et al. 2017b; Table 1). Two of the most notable morphological differences between *O. vulgaris* and *O. insularis* are the relatively shorter arms and smaller enlarged suckers of the latter; and very conspicuous enlarged suckers in mature male *O. vulgaris* (Mangold 1998), while those of *O. insularis* are only slightly enlarged (Leite et al. 2008; González-Gómez et al. 2018). Morphological differences (Table 1) have also been observed between sympatric *O. insularis* and *O. americanus* with the former having fewer suckers on the hectocotylized arm, deeper web, larger calamus and larger spermatophores (Leite et al. 2008); conspicuous enlarged suckers are also present in *O. americanus* captured off western Florida (González-Gómez pers obs). Characteristics such as the presence and position of enlarged suckers only in mature males, the index of the diameter of the enlarged suckers, the number of gill lamellae per demibranch, and the size of the egg in *O insularis* and *O. americanus* clearly differentiate these taxa from *O. vulgaris* (Leite et al. 2008; González-Gómez et al. 2018; Avendaño et al. 2020; Table 1). However, features of the ligula of *O. americanus* (e.g. LLI, CLI, and ligula shape) appear to have no differences with respect to *O. vulgaris*, and similarly to *O. sinensis* (Gleadall 2016).

Based on body pattern, clear differences are visible between *O. insularis* and *O. americanus* when they are inside the den, with *O. insularis* showing a distinct red-and-white reticulate pattern on the ventral surfaces of the arms and a dark bar across the eye (Leite and Mather 2008;

Table 1 Comparison of morphological and meristic characters of *Octopus insularis* (based on Leite et al. 2008; Lenz et al. 2015; González-Gómez et al. 2018), *O. americanus* (Avendaño et al. 2020) and *O. vulgaris* (Mangold 1998; Iglesias et al. 2000; Guerra et al. 2010; Gleadall 2016; Norman et al. 2016)

	Octopus insularis	*Octopus americanus*	*Octopus vulgaris*
Sucker count on normal arms	220–238	224–258	220–240
Sucker count on hectocotylus	96–142	138–158	162–192
Gill lamellae per demibranch	8–11	7–8	9–11
Enlarged suckers	Only males	Only males	Both sexes
Position of enlarged sucker field	15–18	13–16	13–18
Mantle arm index	3–4	4–5	4–5
Ligula length (% R3)	0.6–1.4	1.2–1.7	1.2–2.1
Calamus length (% ligula length)	40–60	45–57	47–52
Pseudophallus length (% ML)	15–16	14–22	15–21
Diameter of normal suckers (% ML)	8–14	10–10.8	12.5–13.5
Diameter of enlarged suckers (% ML)	8.87–15	13–15	18.2–21.1
Egg length (mm)	2.1	2.6	2.9
Total length (mm)	530	790	1000
Depth range	0–45 m	15 to ≥ 100	0–150 m

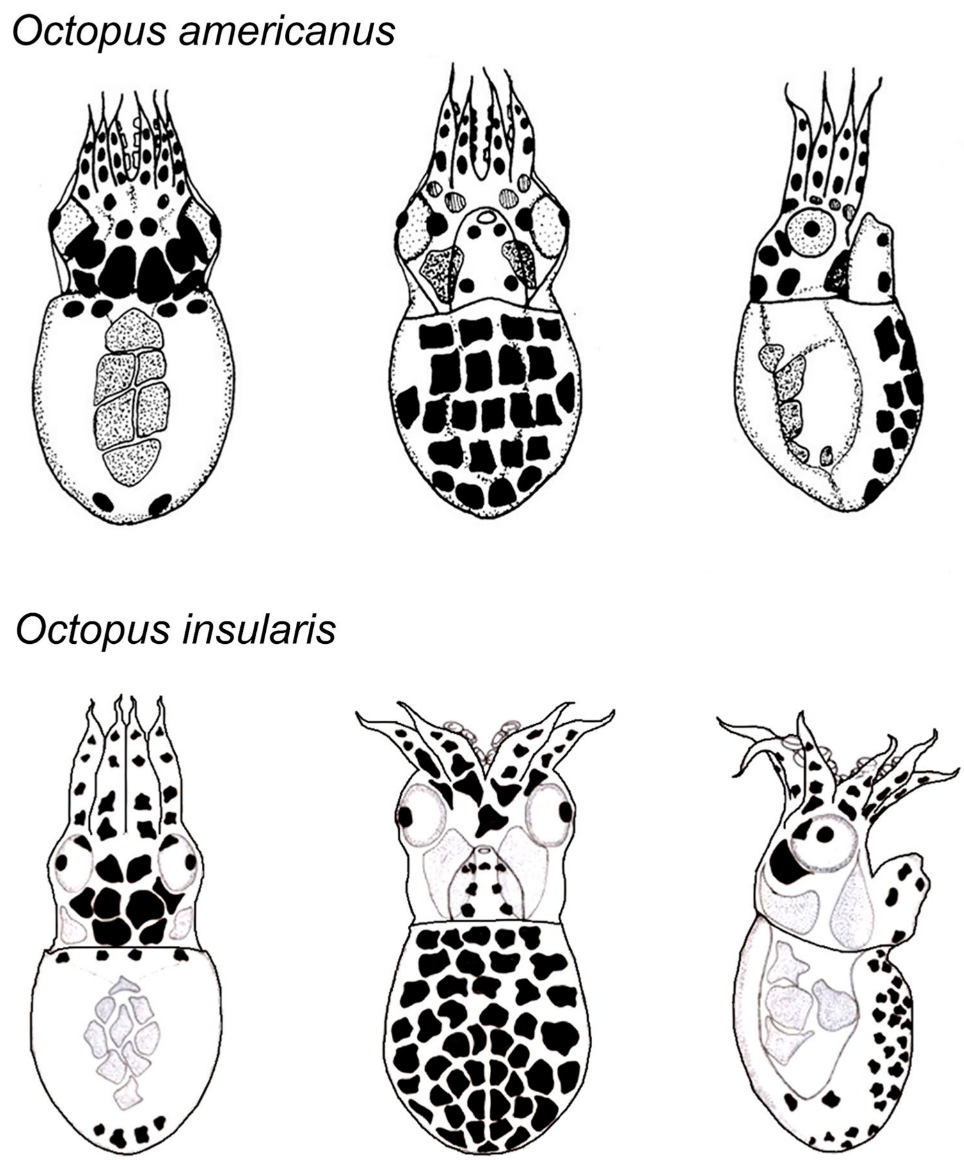

Fig. 1 Chromatophore patterns of newly-hatched paralarvae of *Octopus americanus* (upper row) and *O. insularis* (lower row) in three views: dorsal (left); ventral (centre); lateral (right). Scale bars = 1 mm. Images modified from Vidal et al. (2010) (upper row, originally identified as *O. vulgaris*), and Lenz et al. (2015) (lower row)

González-Gómez et al. 2018). *Octopus americanus* usually remains uniformly dark, with orange-coloured ventral arm surfaces and dark colour around the eyes (O'Brien et al. 2021).

Following the experimental rearing of both *O. insularis* and *O. americanus*, the differences between the paralarvae of these species are also clear, as summarized in Figs. 1, 2 and Table 2. Both *O. insularis* and *O. americanus* produce small eggs and planktonic paralarvae. Egg mean lengths and widths were found to be 2.6 ± 0.1 and 0.88 ± 0.07 for *O. americanus* (n = 30, Vidal et al. 2010) and 2.13 ± 0.06 mm and 0.82 ± 0.04 mm for *O. insularis* (n = 130, Lenz et al. 2015), respectively. Hatchlings have three suckers per arm in both species (Vidal et al. 2010; Maldonado et al. 2019).

The chromatophore number and pattern of these two species are distinctive, especially on the mantle, head and funnel (Figs. 2, 3): *O. americanus* paralarvae display a dorsal

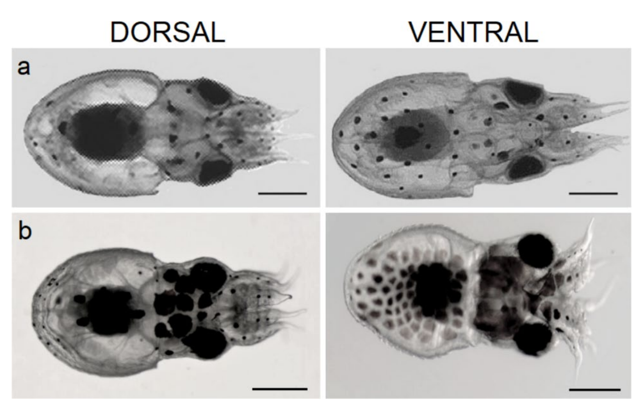

Fig. 2 Comparison of dorsal (left) and ventral (right) views of paralarvae of **a** *O. americanus* and **b** *O. insularis*. Scale bars: 0.5 mm. (Images in 'a' from Vidal et al. 2010, identified originally as *O. vulgaris*. In 'b', left image is original, right image from Lenz et al. 2015)

Table 2 Number of chromatophores and body dimensions of newly-hatched paralarvae of *O. americanus* and *O. insularis*

	O. americanus [a]		*O. insularis* [b]	
	Dorsal	Ventral	Dorsal	Ventral
Number of chromatophores				
Arms	4	4	3–4	4–5
Head	8–12	2–4	9–12	3
Eyes	1–4	1–2	2–4	2
Funnel	_	4–6	_	8
Mantle	11–20 (6–9 vs)	23–36	9–22 (6–12 vs)	32–56
Total number (dorsal + ventral)	56–77		84–112	
Body dimensions of living paralarvae in mm (means ± SD)				
Mantle length	2.21 ± 0.09		1.68 ± 0.13	
Mantle width	1.28 ± 0.05		0.98 ± 0.09	
Length of arm II	0.83 ± 0.05		0.66 ± 0.10	
Head width	0.96 ± 0.04		0.86 ± 0.06	
Eye diameter	0.34 ± 0.05		0.31 ± 0.04	
Total length	2.84 ± 0.20		2.34 ± 0.16	

vs visceral chromatophores

[a]From Vidal et al. (2010), as *O. vulgaris*

[b]From Lenz et al. (2015)

chromatophore pattern very similar to that of *O. vulgaris* Cuvier; while those of *O. insularis* show a very different, distinctive chromatophore pattern. From the dorsal aspect, the large chromatophores above the viscera are markedly dissimilar between the two species: larger in *O. americanus* in relation to *O. insularis* and noticeable whatever the state of expansion or contraction of the chromatophores in both species. There are 6–9 large chromatophores in *O. americanus* (Vidal et al. 2010); 6–12 smaller ones in *O. insularis* (Fig. 3). The dorsal head pattern is also different, with *O. insularis* often showing a larger number of smaller dark chromatophores. On the ventral mantle, *O. americanus* has a mean of 23 chromatophores distributed in five horizontal rows; whereas *O. insularis* has a mean of 40 chromatophores arranged in 9 rows, with the first 3 rows distributed horizontally and the others arranged in a spiral on the posterior region of the mantle. On the funnel, *O. americanus* has just 4 chromatophores, while *O. insularis* has eight (Lenz et al. 2015).

As shown in Figs. 1, 2 and Table 2, *O. insularis* paralarvae have many more chromatophores and when they are fully expanded, the dorsal head is completely dark, and in combination with the dark chromatophores on the viscera form a thick dark 'Y' shape over the dorsum. This fact gives the paralarvae a generally darker appearance in comparison with those of *O. americanus*.

Biogeographical distribution

Octopus insularis was initially described from the coast and oceanic islands of northeastern Brazil (Leite et al. 2008; Sales et al. 2013) and afterward recorded as far as St Helena and Ascension Island (Amor et al. 2017a, 2019), the Caribbean Sea (Lima et al. 2017, 2020a), the southwestern GoM (Flores-Valle et al. 2018; González-Gómez et al. 2018) and recently in the northern GoM, northwestern Yucatan peninsula (Alacranes Reef), the Bahamas, Cuba, Jamaica, the Dominican Republic, Turks and Caicos islands and Bermuda (O'Brien et al. 2021), south Florida (Maloney et al. 2023), and recently also in oceanic islands off Africa (Lima et al. 2023) (Fig. 3). *Octopus americanus* ranges from the north of Argentina to the northeast coast of the USA (Avendaño et al. 2020), thus, the distribution of both species is known to overlap, and it has been suggested that they might be occupying different niches related to temperature and depth in the western Atlantic, with *O. insularis* inhabiting shallower and warmer waters (Lima et al. 2017, 2020a; Borges et al. 2022). According to Amado et al. (2015), *O. insularis* has a higher tolerance to salinity oscillations, as demonstrated by experiments with artificial seawater preparations at different osmolalities. This may explain its presence in shallow reef waters and tide pools (Bouth et al. 2011), and also their proximity to river estuaries (Avendaño-Alvarez et al. 2017). Ecological and fishery data support these observations as *O. insularis* is commonly found in shallow waters (< 5 m) on reefs and rocky seabeds and is targeted by artisanal fishermen both

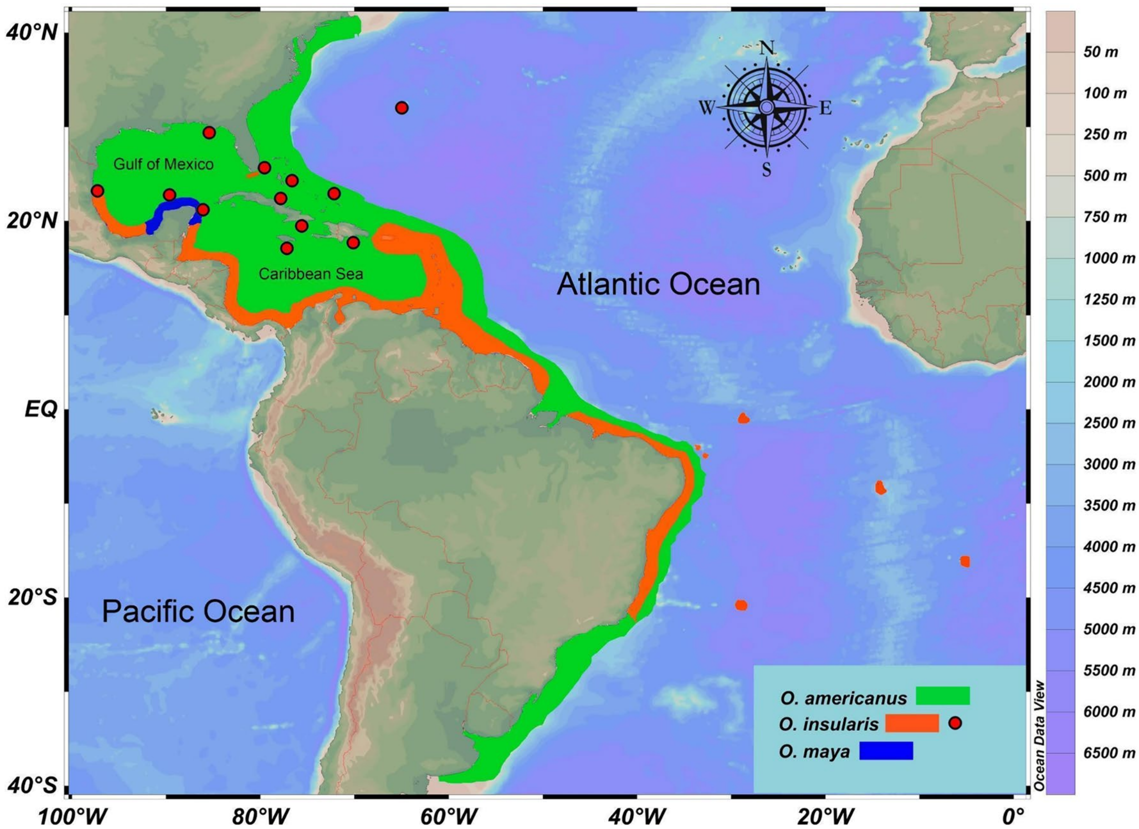

Fig. 3 Map showing the corroborated distribution (based on genetic and/or morphological confirmation of the species identification) of *O. americanus* (green), *O. insularis* (orange) and *O. maya* (blue). Red circles represent positive identifications of *O. insularis* made by the authors from georeferenced photographs contained in the public-access online database iNaturalist (iNaturalist 2023). See references in the text. Map generated with Ocean Data View ver. 4.7.10 (Schlitzer 2017)

in Brazil (Leite et al. 2009; Lima et al. 2014) and the GoM (González-Gómez et al. 2018). *Octopus americanus* is often captured at depths > 20 m, in the offshore large-scale fisheries of the northern GoM (Roper 1997; Avendaño et al. 2022), and also between 50 and 100 m in southern Brazil (Imoto et al. 2016).

In relation to temperature tolerance differences between the two species, *O. insularis* has been found in waters ranging from 23 °C at its southernmost distribution to up to 32 °C in tide pools in northeastern Brazil (Batista and Leite 2016). In addition, species distribution modelling based on thermal optimum and pejus for embryos of *O. maya*, *O. insularis*, and *O. americanus* showed that *O. insularis* has the potential to facilitate its geographical expansion under scenarios of global warming (Ángeles-González et al. 2020).

In contrast, *O. americanus* has been captured in research trawl cruises between 62 and 108 m depth at temperatures in the range 16.2–16.9 °C in southern Brazil and 14.1–16.0 °C in southeastern Brazil (Haimovici, pers obs) and by artisanal research trawl in shallow waters (< 15 m) at temperatures of 14.2–24.0 °C (Bastos, pers obs) and is found occasionally in estuarine areas in the temperature range 15.5–24.5 °C (Teixeira 2011; Bastos and Vieira 2018).

Expanding application of genus name *Paroctopus* Naef, 1923

Recent research on species related to *Octopus digueti* Perrier & Rochebrune 1894 (type species of genus *Paroctopus* Naef 1923), confirms that they are a group of small-bodied octopuses and recognizes their distribution throughout southern California, the Baja California Peninsula, the Sea of Cortez, and the eastern central Pacific; and, in the western Atlantic, particularly the GoM and Caribbean region (Voight 1991; Leite et al. 2021; Pliego-Cárdenas pers obs; Gleadall and Hutchinson pers obs; Fig. 4). The type species still requires redescription (Gleadall, Leite, Navarte, Pliego-Cárdenas and Storero, research in progress), since the earlier descriptions (Perrier and Rochebrune 1894; Rochebrune 1896) were insufficient by modern standards (cf. Appendix 5). However, a diagnosis of genus *Paroctopus* was recently expanded by Leite et al. (2021). Other species in this genus include *O.*

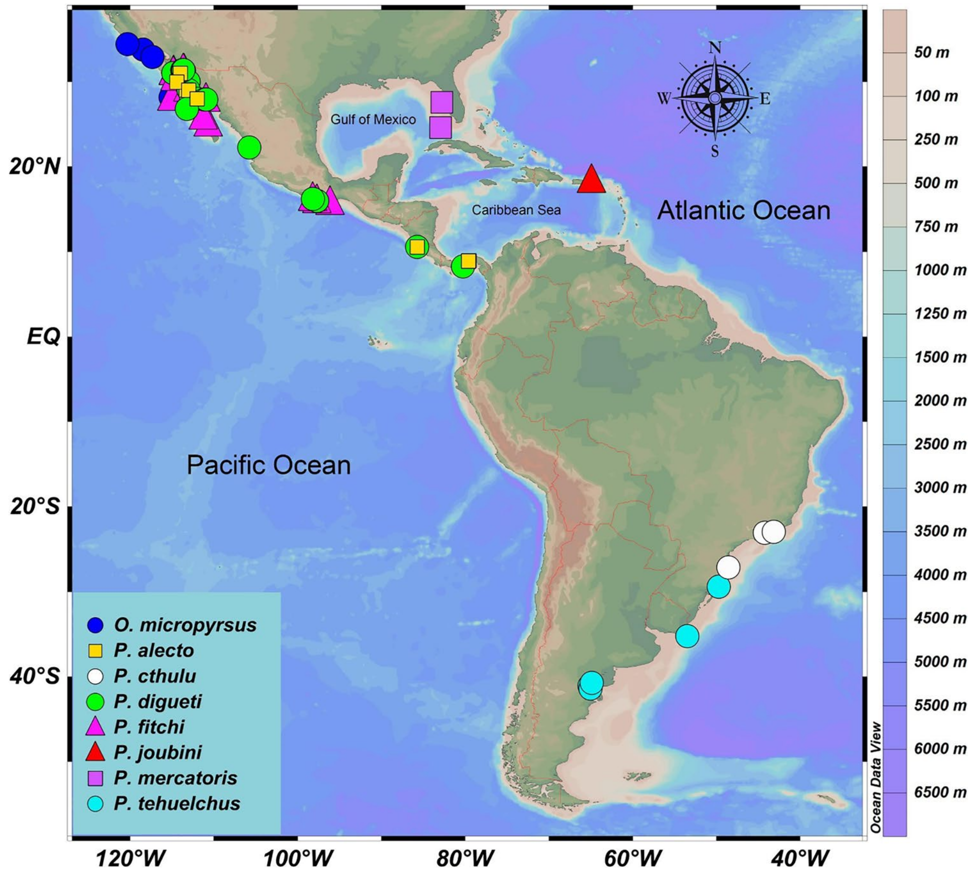

Fig. 4 Map showing the distribution of small species of octopus in the Americas: species here identified as species of *Paroctopus* (genus name abbreviated to '*P.*') and '*Octopus*' *micropyrsus*. See references in the text. (Data supplemented by database records from the Smithsonian National Museum of Natural History and the California Academy of Sciences). Map generated with Ocean Data View ver. 4.7.10 (Schlitzer 2017)

joubini Robson 1929; *O. mercatoris* Adam 1937; *O. alecto* Berry 1953; *Paroctopus cthulu* Leite, Lima, Lima and Haimovici in Leite et al. 2021; and probably *O. tehuelchus* d'Orbigny, 1834 (Haimovici and Andriguetto 1986; Scarabino 2003; Narvarte et al. 2006; Storero et al. 2012), and *O. fitchi* Berry 1953 (Leite et al. 2021). A recent analysis by Ibáñez et al. (2020: Fig. 3), using the COI and COIII genes from the study by Acosta-Jofré et al. (2012), with addition of the 16S rRNA gene, found the that latter two species belong to the same *Paroctopus* group (Ibáñez et al. 2020: 'Clade 4').

The first *Paroctopus* species of the South American Atlantic, *P. cthulu*, was described from the coast of Brazil (Leite et al. 2021; Table 3). A population was found using sea debris as refuges in the mainland and island coastal waters of Rio de Janeiro State, and other specimens were subsequently identified from Museum collections. The Western Atlantic group of small octopus species probably shared a common ancestor before the uplift of the Isthmus of Panama, evidence for which is their close relationship with *P. digueti* and *P. alecto* from the East Pacific (Lima et al. 2020b). *Paroctopus cthulu* may have arrived in the Southwest Atlantic via the shallow waters of the continental shelf linking South and Central America, before the effects of the Amazon river discharge into the Atlantic Ocean began around 10 million years ago (Mya) (Hoorn 1994), which became a low-salinity barrier for many marine species (Rocha 2003; Muss et al. 2007; Gleadall 2013). This event seems to have coincided with the divergence of *P. cthulu* and *P. joubini* (mean 9.4 Mya; Lima et al. 2020b).

Most of these small octopuses are known only from single specimens or from reports on laboratory culture studies and in situ observations where specimens were not preserved (Mather 1982; Hanlon 1983; Verrill 1884a, b; Haaker 1985; DeRusha et al. 1987; Forsythe and Toll 1992). Some characters distinguishing among these species are summarized in Table 3, although further research is required to clearly ascertain the composition and distribution of *Paroctopus* species in this region. For instance, according to Leite et al. (2021), species *O. alecto*, *O. fitchi* and *O. tehuelchus* should be assigned to genus *Paroctopus* based on shared characters and closely similar DNA sequences.

Paroctopus spp. 1, 2 and 3 refer to species commonly considered in the literature as '*Octopus joubini*' (*i.e.* '*Octopus*' aff. *joubini*): *Paroctopus* sp. 1 was cultured by Forsythe and Toll (1992) and referred to as '*Octopus* sp. X', and was considered to be either a synonym of *P. mercatoris* or an undescribed species; *Paroctopus* spp. 2 and 3 are species collected by Arocha and Urosa (1982). Although these authors recognized the presence of two species in their samples (based on two different egg sizes), they offer a single

Table 3 Comparison of locality, egg length, hatchling type (where known) and position and number of enlarged suckers for the small species '*Octopus*' *micropyrsus* in comparison with species identified as *Paroctopus*

Species	Locality	Egg (oocyte) length, in mm	Hatchling type	Arms (#1, 2, 3, 4) with enlarged suckers	Enlarged suckers position
'*O*'. *micropyrsus*	NEP, CA	10–12	Ho	1–3	5–6 or 7–8
P. alecto	SCor	2–2.5	Me	2 and 3	?
P. cthulu	WSA, Br	4.7–9	Me	1–3 including some females	9–10
P. digueti	SCor, BaCa	8 (6.5)	Ho	1–3 (males)	10–11
P. fitchi	SCor, BaCa	7–8	Me	All (both sexes)	8–9 or 7–9
P. joubini	NECar, VI	2.3–2.9 (2.5)	Me	2 and 3	6?
P. mercatoris	NEGoM, FL	?	Ho.?	1–3 (males)	5–7?
P. tehuelchus	WSA, Ar, Uy, Br	9–12	Ho	2 and 3 (males)	?
P. sp. 1	NEGoM, FL	6–8	Ho	?	?
P. sp. 2	SECar, Ve	7–8 (6)	Ho.?	?	?
P. sp. 3	SECar, Ve	(2.5–3.9)	Me.?	?	?
P. sp. 4	WNA, GA	?	?	1–3	6–7

Genus names: '*O*'., '*Octopus*' (? not sensu Cuvier 1797); *P*., *Paroctopus* Naef 1923. Genus designations based on Pliego-Cárdenas (unpublished research) and Leite et al. (2021). Specimens attributable to '*Octopus*' *joubini* have also been obtained from Belize and Costa Rica (Hochberg and Camacho-García 2009)

Ar Argentina, *BaCa* the Baja California peninsula, *Br* Brazil (Rio de Janeiro), *CA* California, *Car* Caribbean, *FL* Florida, *GA* Georgia, *GoM* Gulf of Mexico, *Ho.* Holobenthic, *Me.* Merobenthic, *NE* Northeast, *NEP* eastern N. Pacific, *SCor* Sea of Cortez (Gulf of California), *SE* Southeast, *Uy* Uruguay, *Ve* Venezuela, *VI* Virgin Islands, *WNA* western North Atlantic, *WSA* western South Atlantic

morphological description for '*O. joubini*', therefore, when they state that 'one or two enlarged suckers can be noted in the medial portion of each arm in mature males', it is unclear if they are referring to *Paroctopus* sp. 2 or 3. *Paroctopus* sp. 4 refers to a mature male specimen taken off the coast of Georgia, USA (Gleadall and Howard unpublished data) (Table 3). More recent work on the '*O. joubini*' group (e.g. Holloway et al. 2023) has yet to resolve the number of species involved (Appendix 4, Table 4, Events 20, 23, 26, 27, 31–33; Appendix 5).

Morphological similarities and phylogenetic analyses of either mitochondrial COIII or several concatenated gene sequences (Ibáñez et al. 2020) consistently show that species *Paroctopus digueti* is closely related to *P. fitchi*. In addition, recent phylogenetic analyses from 13 concatenated mitochondrial protein-coding genes (Magallón-Gayón et al. 2020) demonstrated large genetic distances (24–25%) for *P. fitchi* in relation to species of the genera *Octopus* and *Pinnoctopus*, supporting the identification of these small species of octopus as members of a genus distinct from *Octopus*. Other identifications in Table 3 are based on morphological similarities of octopuses identified as species of genus *Paroctopus*.

Recently, yet another small species has been reported from Curacao, Venezuela: *Octopus jeraldi* Pratt, Baldwin and Vecchione, 2020 (discussed further in Appendix 5). However, its affinities are unclear and further specimens are required before a confident identification is possible (at the levels of both genus and species); and comparisons have yet to be made between *O. jeraldi* and other specimens of small octopus from localities close by (e.g. the Venezuelan specimens of *Paroctopus* sp. 2 and 3, identified as species *joubini* by Arocha and Urosa 1982). See also Appendix 5.

Region-specific accounts of octopus collection in the Americas

Acquiring knowledge about octopus biodiversity began in earnest with the advent of scientific expeditions around the world. Much of the early activity began in Europe, and for octopuses in the Americas important expeditions were those both of institutions and individuals, beginning in the late eighteenth century (Molina 1788; d'Orbigny 1835–1843; Gay 1854; Rochebrune and Mabille 1889; Hoyle 1886), with expeditions mounted from the USA following later (Gould 1852; Verrill 1873, 1881a, b, 1884b; Dall 1884, 1908; Boone 1938; Voss 1955, 1968, 1971; Voss and Pearcy 1990).

The following account is mainly historical and organized according to the countries or regions of the coast where research has been done, is currently under way and/or where expertise is currently available, moving through the Americas from north to south. The species involved show considerable overlap, so information on the more speciose or abundant genera is collated within a series of maps showing their known distribution (Figs 3, 4, 5 and 6) and there is a brief statistical analysis summarizing the characteristics of the American octopus species and the ecoregions among which they are distributed (see Sect. "Biogeography" and Figs. 7 and 8). The Discussion further considers species distributions at different biogeographic levels and various aspects of octopus biodiversity.

Canada, United States of America and western Greenland

The octopus fauna off Canada, the USA and western Greenland was sampled fairly well during the latter decades of the nineteenth century and much of the twentieth century, resulting in descriptions of 70 species to date (actually 51 excluding 19 considered to be junior synonyms of other species), mainly by authors based in the USA. These descriptions were facilitated by systematic series of scientific survey cruises and investigations attended by a few key researchers: Addison Emery Verrill (a malacologist who surveyed the Atlantic coast; Coe 1929); Samuel Stillman Berry (on the Pacific coast, based in California; Sweeney and Roper 1984); and Gilbert Voss (mostly in southern Florida, the GoM and Caribbean; Sweeney and Roper 1992). These three authors described 14, 16 and 17 North American species, respectively (Verrill 1873, 1879, 1880, 1881a, b, 1882, 1883a, b, 1884a, 1885, 1897a, b, c; Berry 1911, 1912, 1913, 1920, 1949, 1952, 1953, 1954, 1955; Voss 1950, 1955, 1964, 1968, 1971, 1975, 1982; Voss and Solís-Ramírez 1966; Voss and Pearcy 1990). One other octopus species name attributed to Verrill was not a cephalopod (see Appendix 3).

Five other prolific researchers active earlier than Verrill, Berry and Voss were George Washington Tryon Jr (Ruschenberger 1888); Henry Augustus Pilsbry (Clench and Turner 1962); William More Gabb (a pioneer palaeontologist, particularly of the Cretaceous and Tertiary faunas of North America; Dall 1909; Coan and Bogan 1988); William Healey Dall (a malacologist and palaeontologist known mostly for his research in Alaska and the Aleutians; Bartsch et al. 1946; Woodring 1958); and Augustus Addison Gould (Wyman 1867; Wyman and Dall 1903; Johnson 1964), along with his colleague Joseph Pitty Couthouy (Gould 1852; Johnson 1946). However, although giants in their own particular fields, these earlier authors described few cephalopod species in North and Central America.

The first in a monumental series of Mollusca monographs by Tryon (1879) began with his impressive volume on the Cephalopoda. He described no new species but included an extensive listing and brief characterization of the known species of octopus (as well as other living and fossil Cephalopoda). However, his approach was global and he did not group species geographically but morphologically, according to arm proportions, so did not emphasize American cephalopods (and, at that time, few North American octopus species had been identified). Tryon's Mollusca monograph series was completed by Pilsbry who, also, did not describe any new cephalopods. Gabb (1863) described one new species, *Octopus punctatus* (discussed by Coan and Bogan 1988; see also comments by Dall 1866, 1873, 1884, and the end of Sect. "Expanding application of genus name *Paroctopus* Naef, 1923"). Three species of *Argonauta* were described by Dall (1869, 1872, 1889, 1908); one (from off South America) was described by Gould and Couthouy (in Gould 1852); and five more by Conrad (1854). All nine species of *Argonauta* were inadequately described (including six for which no type locality was specified) and are considered to be of doubtful validity, probably junior synonyms of other species (Finn 2013).

Expansion of the known distribution to North America of species described originally from non-American localities has added another 13 species, for a total of 83 North American species (64 when junior synonyms are removed). There have been two relevant major reviews and detailed redescriptions of some of the more commonly encountered Pacific species: *Octopus bimaculoides, O. micropyrsus, O. rubescens* and '*Octopus*' *dofleini* by Hochberg and Fields (1980); and '*Benthoctopus*' *leioderma*, '*B.*' *robustus*, *Graneledone pacifica*, *O. rubescens*, '*Octopus*' *californicus* and *Enteroctopus dofleini* by Hochberg (1998). Apart from these, there have been few updates of North American species beyond their original descriptions (e.g. Bower et al. 2024), although species summaries and updated distribution maps have been published for the North Pacific (Conners and Jorgensen 2007; Jorgensen 2009) and the central Western Atlantic (eastern US, Gulf of Mexico and the Caribbean: Vecchione 2002; Judkins 2009; Pratt et al. 2021, 2023). Textbook accounts (e.g. Smith et al. 1961) and lists generally have been superficial and incomplete, such as that for the USA and Canada by Turgeon et al. (1988), which included nine Atlantic species, eight Pacific species and four species from both oceans, the latter including *Tremoctopus violaceus* (although recently specimens from the Pacific have been identified as *T. gracilis*; Jiménez-Badillo et al. 2021), *Octopus [Pinnoctopus] macropus* and *O. vulgaris* (both of which are species endemic to the eastern Atlantic, now not considered present in the Americas). Vecchione et al. (1989) and Vecchione (2002) listed 26 Atlantic species: 16 from or near the northern coast and 10 species from off the Carolinas and further south.

No new species have been described from Canada, faunal lists of which are encountered in the literature only rarely (e.g., Taylor 1895; Whiteaves 1901; La Roque 1953). Whiteaves (1901) provided a useful account of specimens collected in Canadian waters resulting from expeditions mounted by other countries, among which were just five octopods, all described by Verrill and all (except the cirrate

Stauroteuthis syrtensis) now identified as just two species of genus *Bathypolypus*: *B. arcticus* and *B. bairdii* (of which the other three are currently identified as synonyms: '*O.*' *piscatorum,* '*O.*' *obesus* and '*O.*' *lentus*). Berry (1925) reported on specimens collected during the Canadian Arctic Expedition (1913–1918) but the only cephalopod material was in the form of illustrated (but unidentified) beaks from the stomach contents of two seals. The species from Canadian waters that has received the most attention is the giant Pacific octopus (e.g., Hartwick et al. 1978; Hartwick and Barriga 1997). A new species of giant octopus from Alaska, the frilled giant Pacific octopus, awaits formal description (Hollenbeck and Scheel 2017).

Gulf of Mexico and Caribbean Sea

The biodiversity of octopuses along the Atlantic coasts of the Americas has long been confounded by Eurocentric identifications of species which largely have been assumed to have an amphi-Atlantic distribution. However, although there are some amphi-Atlantic species, new studies and observations are gradually making clear that (i) many species from this region are closely related to those found in European waters but they are in fact different, undescribed species; and (ii) as with other animals in this region, there is probably more octopus endemism associated with recent geological history than has been detected so far, particularly with regard to faunal provinces and paraprovinces around Florida, in the GoM and the Caribbean (see *cf.*, for example, Petuch 1982; Lee and Foighil 2005; Vermeij 2005; Spalding et al. 2007; Pimiento et al. 2017; Lima et al. 2020b).

A number of fisheries surveys for cephalopods have been conducted in the waters of the GoM and Caribbean but certainly for octopuses there seem to have been relatively few surveys of littoral and sublittoral species, so the octopus fauna of this region occupying such niches as coral rubble and rock crevices is poorly known. Descriptions of single specimens in widely distributed parts of the region have been recorded in the past, but in view of the sparse data from such a low number of specimens it is unclear whether these represent different endemics or species that are widely distributed in the region. Within the northern regions of the GoM the majority of information comes from observations around Florida. The first review of octopus species in this region was that of Voss (1956) who catalogued the cephalopods of Florida, including 14 species from the Order Octopodida, all collected from the GoM or the GoM/Atlantic convergence in the Straits of Florida. The most recent surveys in the region, along with studies of specimen collections in various museums, have been reported by Judkins (2009) and Judkins et al. (2009, 2010, 2017), who found a total of 22 octopod species in the GoM.

There is little information on the details of distribution of octopuses within the GoM. Many of the shallow-water species for which there is some information on distribution are generally reported as having northern or eastern distributions within the GoM (Nesis 1975b; Vecchione 2002; Judkins et al. 2009; Jereb et al. 2016) but this may be due to the high sampling effort in these regions. Many species may be more widely distributed than previously thought. For instance, the species *Pinnoctopus* aff. *furvus* (Jesus et al. 2021), *O. hummelincki* and *O. briareus*, which are often reported to be found around southern Florida, have also been observed off the Texas coast (Flower Gardens National Marine Sanctuary) as well as in the southwestern section of the GoM and the Caribbean Sea (González-Gómez pers obs). *Amphioctopus burryi* (Voss 1950) is an amphi-Atlantic species that has been collected from several localities embracing nearly the whole GoM, tropical western and eastern Atlantic (Voss 1951; Hanlon and Hixon 1980), including the Veracruz Reef System (Cedillo-Robles pers obs) and the reefs of Campeche Bank (Markaida pers obs). Two species of relatively limited geographic distribution within the GoM are *O. maya* and *Paroctopus mercatoris*. Off the Mexican coast of the GoM, most studies have been devoted to the former as it is the most exploited species in the area (e.g., Voss and Solís-Ramírez 1966; Solís 1967; Baeza-Rojano et al. 2013; Gamboa-Álvarez et al. 2015). *Octopus maya* is endemic to the shallow waters of the Campeche Bank, off the Yucatan peninsula, where it is highly abundant and practically excludes any other octopus species (Rosas et al. 2014), while the distribution of *P. mercatoris* is not well known within the GoM, being recorded to date only along the Florida coast (Forsythe and Toll 1992). As *P. mercatoris* was previously identified as *O. joubini*, historical records of its distribution are difficult to validate (Forsythe and Toll 1992; Holloway et al. 2023).

Besides the studies on *O. maya*, there has been some research on *O. americanus* (Avendaño et al. 2022) and *O. insularis* (often referred to previously as *O. vulgaris*) within the Mexican region of the GoM. Several aspects of the biology and ecology of *O. insularis* have been addressed, including its fishery (Mota Rodríguez 2004; Jiménez Badillo and Castro Gaspar 2007), some experiments on its culture in captivity (Méndez-Aguilar et al. 2007), estimations of age and growth (Díaz Álvarez 2011) and its feeding ecology (Rosas-Luis et al. 2019). However, studies on shallow-water octopods of the southern GoM are scarce, mostly in Spanish, and have not been published widely (confined to bachelor and master theses). Mancha Yáñez and Moreno Galdeano (1986) identified and described *O. insularis* (as *O. vulgaris*) and *Macrotritopus* aff. *defilippi* captured by free diving in shallow waters from Lobos Island, in Veracruz, based on the keys developed by Voss (1968) and Roper (1978). Later, Hernández-Tabares (1993) examined the commercial catches of the artisanal fishery operating in the Veracruz Reef System and identified four species: *O. insularis* (as *O. vulgaris*), *Pinnoctopus* [aff.] *furvus* (as *O. macropus*), *O. maya*, and *O. hummelincki*, based on just a few morphometric measurements (e.g. mantle and total length, weight, ligula index and number of gill lamellae) and the existing literature.

The most recent taxonomic studies in the area have revealed that misidentifications are common among commercially-targeted species. Attention is currently focused on *O. insularis*, the common octopus in shallow waters and coral reefs in the area, which had been previously misidentified as *O. vulgaris* both in the GoM and Caribbean Sea (Lima et al. 2017; Flores-Valle et al. 2018; González-Gómez et al. 2018). Although the distribution of *O. insularis* in the northern GoM is not yet fully clarified, there are some morphologically-similar adult specimens from off Tamaulipas, Mexico, in the Colección de Peces e Invertebrados Marinos y Estuarinos (Cedillo-Robles pers obs) and photographs from the iNaturalist database confirm its presence in that area as well as in Bay County, Florida (Fig. 3; González-Gómez pers obs). Given the existence of a well-established population of *O. insularis* in the Veracruz Reef System (González-Gómez et al. 2018), the presence of its paralarvae in the eastern Yucatan peninsula (Castillo-Estrada et al. 2020) as well as off the Tamaulipas coast (Santana-Cisneros et al. 2021), and the genetic confirmation of adult specimens in the coastal waters of the Florida Keys (Maloney et al. 2023), these identifications seem well-supported. In line with recent reports on octopus misidentifications, it may be wise to consider revising identifications where GoM specimens have been identified by species names with type localities in far-removed parts of the Atlantic Ocean (such as the East or Southwest).

Regarding deep-sea taxa, following a survey of bathyal incirrate octopods using videos taken by ROVs as well as museum records, Pratt et al. (2021) found the following species inhabiting the GoM and Caribbean Sea: *Bathypolypus bairdii*, *Graneledone verrucosa*, *Muusoctopus januarii*, *M. oregonae*, *Pteroctopus tetracirrhus*, *Scaeurgus unicirrhus* and *Tetracheledone spinicirrus*. Among these, *M. januarii* and *P. tetracirrhus* were the most frequently observed species in the region. Besides these taxa, the pelagic *Tremoctopus violaceus* has recently been recorded in the Veracruz Reef system, thus representing the most westerly record of the species and its first known occurrence in the southwestern GoM (Jiménez-Badillo et al. 2021). Other pelagic taxa present in the GoM and Caribbean Sea include: *Argonauta argo*, *A. hians*, *Bolitaena pygmaea*, *Haliphron atlanticus*, *Japetella diaphana*, *Vitreledonella richardi*, *Vampyroteuthis infernalis* (Vecchione 2002; Jereb et al. 2016; Judkins et al. 2017).

Mexican Pacific and Sea of Cortez (Gulf of California)

The taxonomic descriptions of most octopods from the Mexican Pacific, including the Gulf of California, were originally posted as preliminary (e.g., Berry 1953) and there have been few updates since, except for those of Hochberg (1980, 1998) who redescribed two species from the area. Norman and Hochberg (2005) provided a list of nominal species of the family Octopodidae with reassignment to different genera, including 11 species of the genus *Octopus* from the Mexican Pacific, provisionally attributing seven of these taxa to the genus.

The early accounts of the cephalopod fauna in the Mexican Pacific and Gulf of California summarized in Roper et al. (1995) were followed by the identification of *O. hubbsorum* Berry 1953, as the main species supporting the octopus fisheries in the area (Aguilar and Godínez-Domínguez 1997; López-Uriarte et al. 2005; Pliego-Cárdenas et al. 2011; Domínguez-Contreras et al. 2013) and more studies focused on further taxonomic identifications (Alejo-Plata 2002; Granados-Amores 2008; De Silva-Dávila et al. 2013, 2018; Alejo-Plata et al. 2014, 2019; Urbano et al. 2014; Pliego-Cárdenas 2015; García-Guillén et al. 2018; Urbano and Hendrickx 2018; Díaz-Santana-Iturrios et al. 2019; Valdez-Cibrián et al. 2020) as well as by novel citizen science projects (e.g. the Facebook public group 'Avistamiento de Cefalópodos México', González-Gómez pers obs). Derived from these studies, the octopus fauna of the Mexican Pacific is now known to comprise 12 formally-described species (Barriga-Sosa et al. 2018) and at least three undescribed species (Cedillo-Robles and Pliego-Cárdenas pers obs). However, as in other regions, there are unresolved taxonomic issues that require attention, mostly concerning synonymy (e.g. *Octopus mimus*, *O. hubbsorum*, and *O. oculifer*); appropriate generic assignations for species currently included within genus *Octopus* (e.g. '*Octopus*' *alecto,* '*O.*' *penicillifer,* '*O.*' *rubescens*; Jereb et al. 2016) and species redescriptions (e.g. *Pinnoctopus* aff. *macropus*).

Regarding the deep-sea and pelagic octopods of this area, most information comes from studies of the diet of fishes (Markaida and Hochberg 2005; Torres-Rojas et al. 2010; Alejo-Plata et al. 2019), mammals (Tripp-Valdez et al. 2010; Pablo-Rodríguez et al. 2016), or other cephalopods (Alejo-Plata et al. 2009; Markaida and Sosa-Nishizaki 2003, 2010), with *Argonauta* spp. emerging as the dominant taxa. However, during recent years, greater direct sampling efforts using research vessels, mainly in the Gulf of California, have recorded various species, both paralarvae and adults, including at least five *Argonauta* spp., *Japetella diaphana*, *Octopus veligero*, *Opisthoteuthis californiana*, *Graneledone boreopacifica*, *Muusoctopus leioderma* and *M. robustus* (Urbano et al. 2014; García-Guillén et al. 2018; Urbano and

Hendrickx 2018). In addition, several specimens of *Tremoctopus violaceus* have been reported stranded or close to the shore by the local community in the Gulf of California (Díaz-Santana-Iturrios pers obs). Specimens of some of these taxa are housed in Mexican biological collections: Colección de Peces e Invertebrados Marinos y Estuarinos (Instituto Politécnico Nacional), Colección Malacológica Antonio García Cubas, Colección Regional de Invertebrados Marinos and Colección Nacional de Moluscos (Universidad Nacional Autónoma de México), including a total of around 500 voucher specimens of octopuses from the Mexican Pacific, the Gulf of California and the GoM. Currently, no type specimens are included but the available collections now provide support for extended distribution boundaries for various species, such as the Pacific species *Euaxoctopus panamensis* (Salcedo-Vargas and Jaime-Rivera 1999).

The distribution limits of some species as well as their taxonomic status are still uncertain, such as the so-called 'Larger Pacific Striped Octopus' (LPSO), which is well-known but frequently misidentified as '*O.*' *chierchiae* (Rodaniche 1984, 1992; Caldwell et al. 2015). A similar issue exists in regard to *O. mimus*, concerning its distribution and its synonymy with *O. hubbsorum* (Pardo-Gandarillas pers obs). Recently, genetic analyses have confirmed the high genetic similarity between both taxa (Pliego-Cárdenas et al. 2014, 2016, 2020), thus, although mapped separately (see Fig. 5), they are here referred to provisionally as the '*O. mimus-hubbsorum* complex'. Also, Alejo-Plata et al. (2014) reported the presence of '*Octopus macropus*' in the Gulf of Tehuantepec, Mexican Pacific, but the study lacks any description for comparison and the original species, *Pinnoctopus macropus* (Risso 1826) is distributed solely in the Mediterranean Sea and eastern Atlantic Ocean (Norman et al. 2016) so this Pacific species is presumably a new species of *Pinnoctopus*.

Colombia

The first catalogue of Mollusca from the Colombian Caribbean listed 17 cephalopod species (including taxa from orders Spirulida, Myopsida, Oegopsida and Octopoda) including nine octopods in Superfamily Octopodoidea (Diaz and Puyana 1994), followed shortly by a guide to the Mollusca of the Caribbean (Pointier and Lamy 1998) and a revision of the Cephalopoda (including orders Spirulida, Sepiida, Myopsida, Oegopsida and Octopoda) in Colombian Caribbean waters (Díaz et al. 2000). Gracia et al. (2002) published the first list of cephalopods from the continental slope above 940 m which included four octopods: *Opisthoteuthis agassizii*, *Amphioctopus burryi*, *Muusoctopus januarii* and

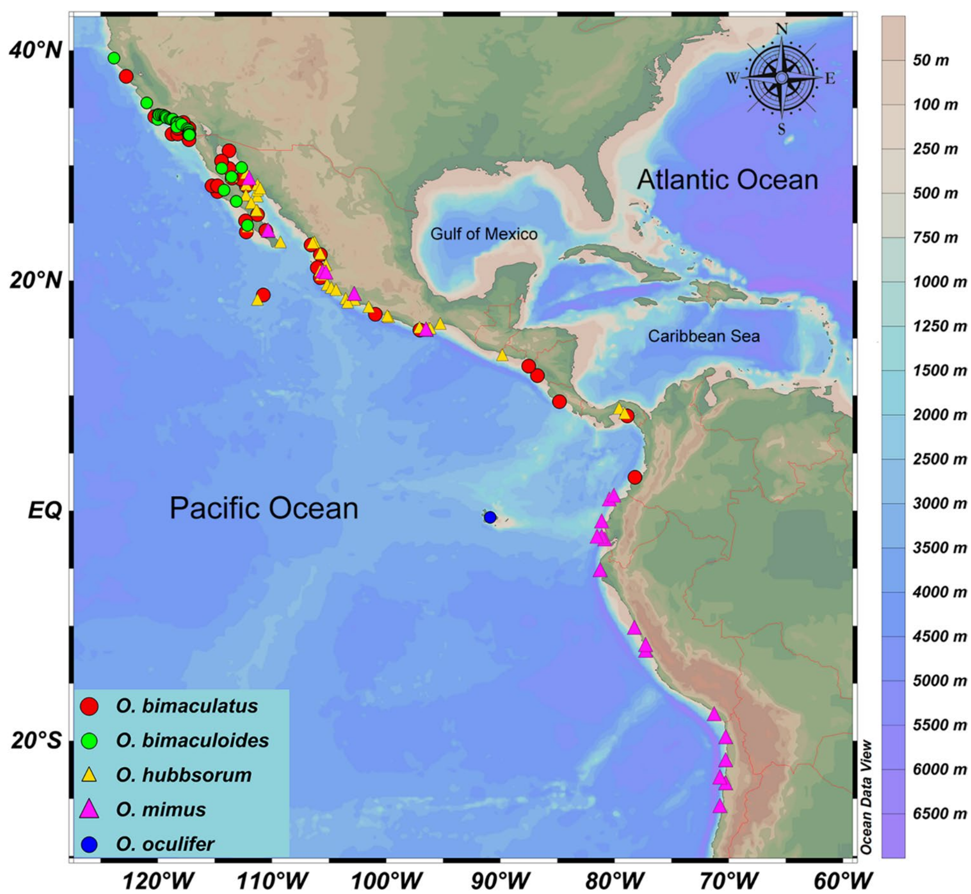

Fig. 5 Distribution of large, morphologically-similar shallow-water octopus species along the eastern Pacific coast of the Americas. See references in the text. (Data supplemented by observations rated as "good points" in SeaLifeBase (Palomares and Pauly 2019) and by database records from the Smithsonian National Museum of Natural History, the California Academy of Sciences and the Colección de Peces e Invertebrados Marinos y Estuarinos, México). Map generated with Ocean Data View ver. 4.7.10 (Schlitzer 2017)

Muusoctopus oregonae; and Judkins et al. (2010) published the first estimation of cephalopod richness in the Caribbean, suggesting the presence of around 20 species in the southern Caribbean. In 2021 the last catalogue of cephalopods from the Colombian Caribbean was published listing 48 confirmed species from which 18 are from Order Octopoda (Guerrero-Kommritz 2021).

In 2012, a research program on Caribbean cephalopods was started by Guerrero-Kommritz in the Tayrona Sector (about 10% of the Caribbean coast of Colombia) where 15 octopus species (belonging to family Octopodidae) were identified, nine of them new, of which three have been formally described: *Octopus tayrona* (junior name for *O. insularis*), *O. taganga* and *Macrotritopus beatrixi* (Guerrero-Kommritz and Camelo-Guarin 2016; Guerrero-Kommritz et al. 2016; Guerrero-Kommritz and Rodriguez-Bermudez 2018); descriptions of the remaining species in the genera *Pinnoctopus* (as *Callistoctopus*) and *Amphioctopus*, and one new genus are in preparation (J. Guerrero-Kommritz, unpublished research).

Octopuses (Order Octopoda) of the Pacific coast of Colombia have received much less attention, but it is known that all the species present in the Gulf of Panama reported by Voss (1971) are present in the Choco region, with voucher specimens deposited in the Makuriva Invemar collection (Guerrero-Kommritz pers obs). Included are at least six new species and two new genera, among which are several small rocky-shore species with adults of ML < 20 mm. The area is devoid of coral reefs and has a very high abundance of plankton (Guerrero-Kommritz pers obs). Collections of cephalopods (including Decapodiformes and Octopodiformes) in Colombia are housed in the Museo de Historia Natural Marina de Colombia Makuriwa at the Invemar Institute in Santa Marta (MHNMC), in the Instituto de Ciencias de Colombia, and in the Museo de la Salle, in Bogota.

Pacific coastal region of Central America and northwestern South America

There have been few studies of the octopus fauna in this region, so it is relatively poorly known compared to other regions. Caldwell et al. (2015) recently reported on a very interesting species, the only truly social species of octopus known. It was first identified in the last century on the Pacific coast of Panama (Rodaniche, unpublished data; see the account by Caldwell et al. 2015). A taxonomic description of this species is pending, so currently it has no scientific name and is here referred to as the "Larger Pacific Striped Octopus (LPSO)" after Caldwell et al. (2015). It appears to be related to *Octopus chierchiae* Jatta 1889, and *O. zonatus* Voss, 1968, which are found on the Pacific and Atlantic sides, respectively, of tropical America.

The LPSO appears to have a tropical distribution, having been reported from Magdalena Bay, Baja Sur, Mexico, and the coasts of Guatemala, Nicaragua, Panama, and the northern Pacific coast of Colombia (G. Hinojosa Arango, pers comm, in Caldwell et al. 2015). It is here reported for the first time from two localities on the coast of the Ecuador Province of Santa Elena (San Pablo beach, and Barandua; Oscar Carreño, pers comm).

On the littoral to sublittoral coast of Esmeraldas, northern Ecuador, there is also an undescribed species of octopus with a distinctive blue ocellus. It is a small species collected only sporadically in the intertidal zone, which may explain why this species has been overlooked by scientists in the past. No ocellate octopus species have been described from the tropical eastern Pacific. *Octopus bimaculatus* and *O. bimaculoides* from the US (Ambrose 1982) and Mexican Californian coasts and Gulf of California (Armendáriz-Villegas et al. 2014) have clear affinities with temperate waters, and *O. oculifer* (Hoyle 1904) is restricted to the Galapagos Islands (Edgar et al. 2004) (Fig. 5).

In the original description of *O. bimaculatus*, Verrill (1883b) mentioned that 'Numerous small specimens were obtained at Panama and on the coast of San Salvador…'. Alejo-Plata et al. (2012) analyzed paralarvae and juveniles of *O. bimaculatus* apparently from Oaxaca, but identification of paralarvae is difficult, so these records are open to question and may in fact represent a small undescribed species, at least in part (cf. also Pickford 1945). Specimens of *O. bimaculatus* identified in various museum collections also include some from localities in Central America and northern Colombia (see Fig. 3 of Alejo-Plata et al. 2012).

Brazil

The first lists of cephalopods from Brazilian waters were based on specimens collected by naturalists in the nineteenth century, such as d'Orbigny (1835–1843, 1835–1848), followed by the U.S. Exploring Expedition (Gould 1852) and the Challenger (Hoyle 1885b, 1886), Vettor Pisani (Jatta 1889, 1898), Plankton (Pfeffer 1912), Terra Nova (Massy 1916) and Mercator (Adam 1937) expeditions. The corresponding specimens are in various museum collections as reviewed by, for example, Tryon (1879), Robson (1929, 1932) and Pickford (1945, 1955).

Cephalopod taxonomic research in Brazil began to develop in the early 1980's. Haimovici (1985) listed 26 species of cephalopods, of which 14 were octopods, based mostly on the literature reviewed by Voss (1964) and Roper et al. (1984). Haimovici et al. (1994) expanded this list to 19 octopods (including the newly described *Eledone gaucha* Haimovici, 1988), based on information from bottom trawl surveys along the continental shelf and upper slope of Southern Brazil and research on collections in Brazilian museums and research institutes (Haimovici and Perez 1992; Perez and Haimovici 1991, 1993).

In the ensuing years, Central and Northeastern Brazil were included with specimens collected in bottom trawl surveys (Haimovici et al. 2007, 2008), predator stomach contents (Santos and Haimovici 2002), pelagic surveys (Haimovici et al. 2002), onboard collection by fisheries observers (Perez et al. 2004), and diving in shallow waters of the oceanic islands along Northeastern Brazil (Leite and Haimovici 2006). Additionally, Nesis (1999) provided an account of early stages of cephalopods from the Southwest Atlantic, including first-hand information on their worldwide distribution. Haimovici et al. (2009) described 26 octopod species, including three cirrate species from the continental slope of Central Brazil: *Opisthoteuthis agassizii* Verrill, 1883; *Cirrothauma magna* (Hoyle 1885a); and *Cirroteuthis* cf. *muelleri* Eschricht, 1836 (Haimovici et al. 2007). They also included the new species *Octopus insularis* Leite and Haimovici, 2008, a shallow water species found on the tropical coast and Brazilian oceanic islands (Leite et al. 2008; Lima et al. 2017; see discussion of this species above). In a recent effort to identify the molluscan biodiversity in Brazil, Machado et al. (2023) included contributions from several recent cephalopod studies (e.g. Vaske 2006, 2011; Leite et al. 2021; Costa et al. 2015; Luna-Sales et al. 2019), which increased the total number of octopods to 31 species for the Brazilian coast.

Gene barcoding has facilitated the identification of benthic octopus species in the stomach contents of several predators (Luna Sales et al. 2019), and recognition of cryptic species (Leite et al. 2008; Sales et al. 2014; Lima et al. 2017, 2020a, b). Studies on the population genetics within their distribution range have been carried out for *O. americanus* (Moreira et al. 2011) and also for *O. insularis* (Lima et al. 2022; Bein et al. 2023).

The number of octopod species recorded in Brazilian waters has almost doubled during the last four decades. Most of the new records are from recognized range expansions of previously described species but also included the following newly-described benthic octopuses (mostly endemic to the Southwest Atlantic): *Vosseledone charrua* Palacio, 1978; *Eledone gaucha* Haimovici, 1988; *Graneledone yamana* Guerrero Kommritz, 2000; *Octopus insularis* Leite and Haimovici, 2008; *Lepidoctopus joaquini* Haimovici and Sales (in Luna Sales et al. 2019) and *Paroctopus cthulu* Leite et al., 2021.

Other taxa present in Brazil that were previously identified as species occurring in other parts of the world include *Pinnoctopus furvus* (Jesus et al. 2021), *Macrotritopus* aff. *defilippi* (Verany, 1851) and *Octopus hummelincki* Adam, 1936. A new species resembling *O. hummelincki* Adam (but much smaller in size) has also been genetically identified in Brazilian waters (Lima et al. 2020b), however, it still lacks a formal taxonomic description. Specimens of *Graneledone* and *Muusoctopus* have been collected along the continental slope of Central Brazil (Haimovici et al. 2007).

Formerly only one species of genus *Scaeurgus* had been identified in this region: *S. unicirrhus* (Delle Chiaje in d'Orbigny, 1841). However, there is a second, undescribed species, present on the continental slope of northeastern Brazil, which is genetically distinct, with fewer suckers and fewer outer lamellae in the gills than *S. unicirrhus* (Leite and Haimovici pers obs).

Octopod specimens from this region are housed mainly in the Museu de Zoologia da Universidade de São Paulo (MZUSP), with collections also deposited in several Brazilian university facilities such as the Museu Oceanográfico "Prof. Eliézer de C. Rios" (MORG). A paratype of *Vosseledone charrua* Palacios, 1978, and the holotypes of *Eledone gaucha*, *Octopus insularis*, *Paroctopus cthulu* and *Lepidoctopus joaquini* are housed in MORG. Unfortunately, all specimens (including types and many undescribed taxa) deposited at the Museu Nacional do Rio de Janeiro (MNRJ) were lost during a major fire in 2018.

Southeastern Pacific region

Octopus systematics in the southeastern Pacific coast of South America started in the 19th Century with the expedition reports of d'Orbigny (1835–1843) and Gould (1852) describing new species in the region (Ibáñez et al. 2010). Subsequent research identified more species (Odhner 1922; Thore 1959; Rocha 1997; Guerra et al. 1999; Ibáñez et al. 2006, 2009), several of which have been redescribed during the last 20 years (Guerra et al. 1999; Ibáñez et al. 2008, 2012, 2016). Research on octopus systematics, biology and ecology increased during the late 1980s and early 1990s when octopus exploitation began in northern Chile and Peru, marketed as the European species *O. vulgaris* (Ibáñez et al. 2010). The study of Guerra et al. (1999) identified the common species from northern Chile and Peru as *O. mimus* Gould, 1852, a conclusion subsequently verified by molecular data (Söller et al. 2000; Warnke et al. 2000, 2004; Acosta-Jofré et al. 2012).

Octopus catches in the Southeast Pacific are mainly concentrated in Chile and Peru. In Peru and northern Chile (and also in Ecuador), the only commercially-exploited octopus species is *O. mimus* (Pliego-Cárdenas et al. 2016; Sauer et al. 2021), whilst in southern Chile, *E. megalocyathus* (Couthouy in Gould, 1852) is the targeted species. Other benthic octopus species such as *Muusoctopus eicomar* (Vega, 2009), *M. longibrachus longibrachus* (Ibáñez, Sepúlveda & Chong, 2006) (Fig. 6) and *Graneledone* sp. are common as by-catch in the crustacean fisheries in Chile and Peru (Ibáñez et al. 2006, 2011, 2012, 2016; Cardoso

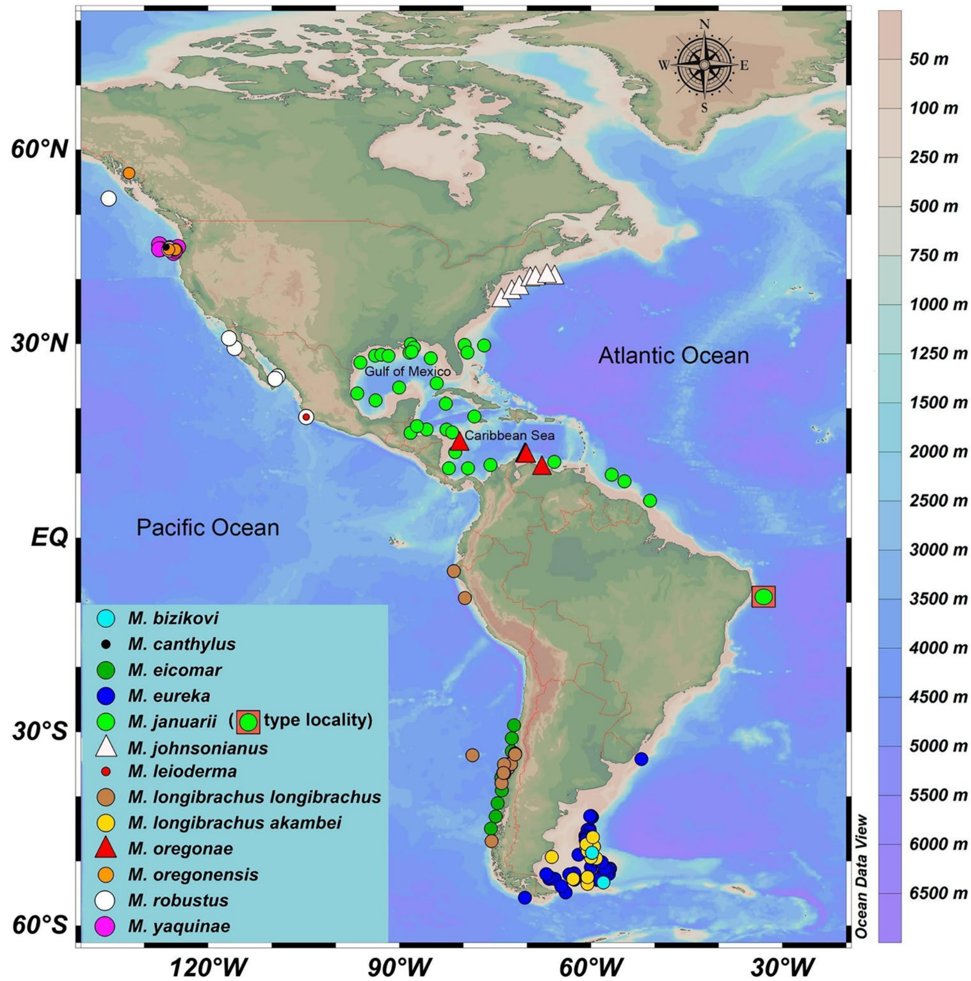

Fig. 6 Distribution of species of *Muusoctopus* Gleadall, 2004, around the Americas. See references in the text. (Data supplemented by database records from the Smithsonian National Museum of Natural History and the California Academy of Sciences). Map generated with Ocean Data View ver. 4.7.10 (Schlitzer 2017)

and Hochberg 2014). Artisanal fishermen occasionally catch the small-sized octopus *Robsonella fontaniana* (d'Orbigny, 1834) but, to date, this species does not represent a commercial resource (Osorio et al. 1979; Ibáñez et al. 2008). Recently, *E. megalocyathus* and *M. eureka*, have been genetically identified and reported as caught by the king crab fishery along the Beagle Channel in southern Chile (Pliego-Cárdenas et al. 2022). In addition to continental species from Chile, Peru and Ecuador, *O. mimus* and a species similar to *O.* aff *vulgaris* have been identified by DNA sequence comparisons obtained from the oceanic islands of the Juan Fernández Archipelago (33° S, 78° W; ~ 600 km from continental Chile; Amor et al. 2017b; Pardo-Gandarillas, pers obs). In regard to cirrates, *Opisthoteuthis bruuni* (Voss, 1982) is the only species recorded from Peru and Chile (Pardo-Gandarillas et al. 2021).

Octopus collections from this region are housed principally in the Museo Nacional de Historia Natural at Santiago, Chile (MNHNCL), with collections also deposited at Chilean university facilities, including the Museo Zoológico de la Universidad de Concepción, Concepción (MZUC); Sala de Colecciones Biológicas de la Universidad Católica del Norte, Coquimbo (SCBUCN); and Colección de Flora y Fauna, Profesor Patricio Sánchez de la Pontificia Universidad Católica de Chile, Santiago (SSUC). These institutions contain the holotype and paratypes of *M. longibrachus longibrachus* (MNHNCL & MZUC) and the neotype of *M. eicomar* (MNHNCL).

Argentina

As in other parts of South America, octopus systematics in the southwest Atlantic began with the expeditions and publications of d'Orbigny (1835–1843, 1835–1848) and Gould (1852). The first cephalopod revision lists for Argentine waters were provided by Carcelles (1944, 1950) and Carcelles and Williamson (1951). Thereafter, octopus taxonomic research was carried out in the early 1960s by Castellanos (1967, 1970) and Castellanos and Menni (1969a, b). These studies were taken up by Ré (1980) who redescribed *Enteroctopus megalocyathus* and summarized the morphological attributes of octopus species frequently found in Argentinean coastal areas: *E. megalocyathus, Robsonella fontaniana* (d'Orbigny, 1834), *Paroctopus* *tehuelchus* (d'Orbigny, 1834), and *Eledone massyae* Voss, 1964 (Ré 1998). Among these, *P. tehuelchus* and *E. megalocyathus,* are harvested by small-scale fisheries in intertidal and subtidal coastal environments in different coastal sectors (Iribarne 1991; Ré 1998; Storero et al. 2010; Ortiz et al. 2011; Ortiz and Ré, 2019), while *Eledone massyae* and *R. fontaniana* are caught as bycatch in fish and crustacean trawling fisheries. *Robsonella fontaniana* is frequently misidentified by fishermen as *P. tehuelchus* or as a juvenile stage of *E. megalocyathus* (Ré and Taylor 1981; Ré 1998; Ortiz and Ré 2011).

Recent studies of octopus taxonomy in this area have been focused on the identification and description of the early stages of *E. megalocyathus* (Ortiz et al. 2006), *R. fontaniana* (Ortiz and Ré 2011), and *P. tehuelchus* (Braga et al. 2021). Note that *E. megalocyathus* (originally as *Octopus megalocyathus*, type locality Orange Harbour, Tierra del Fuego, Argentina) is NOT the type species of genus *Enteroctopus* (as stated by Hochberg 1998, who described it as 'type species of genus *Enteroctopus* by virtual monotypy'). The type species of *Enteroctopus* is *Enteroctopus membranaceus*, as designated by Hoyle 1910, even though it is a *nomen dubium* (ICZN 1999 Art. 67.1.2, 69.1). Also, the original description of the species is headed '*Octopus megalocyathus* (Couthouy, MS) (Gould)' and Gould states: 'The description is mostly made from notes by Mr. Couthouy, whose name I adopt.' Therefore, the correct authorship (ICZN Art. 50.1.1) is: *E. megalocyathus* (Couthouy in Gould, 1852).

In the latest catalogue of cephalopod species found off Argentina, Brunetti (2010) listed nearly 90 species of cephalopods comprising 34 families, including the unique *Vampyroteuthis infernalis* and 10 families of octopuses: Opisthoteuthidae and Cirroctopodidae (in the Order Cirroctopodida); and (in the Order Octopodida) Amphitretidae, Argonautidae, Bolitaenidae, Octopodidae, Enteroctopodidae, Ocythoidae, Tremoctopodidae and Vitreledonellidae. The specimens were identified from the Argentine continental shelf, continental slope and the adjacent oceanic region, between 34 and 55ºS, based on specimens registered during research cruises and the activities of commercial vessels, bibliographic reports, and specimens housed in the Cephalopod Reference Collection of INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero). Recent research on the Argentinian octopus fauna is augmenting the data available in the report by Brunetti (2010), which did not specify capture localities. In addition, some species in this list are now considered to be synonyms of other species and require revision. These include: *O. lobensis* Castellanos and Menni, 1969, a junior synonym of *P. tehuelchus* as shown by Pujals (1984); *Cirroctopus antarcticus* (Kubodera and Okutani, 1986), a possible junior synonym of *C. glacialis* (Robson, 1930) according to O'Shea (1999); *Benthoctopus magellanicus* Robson, 1930, a synonym of *Muusoctopus eureka* (Robson 1929) as determined by Gleadall et al. (2010); *O. pentherinus* Rochebrune and Mabille, 1889, considered to be a *nomen dubium* by Gleadall et al. (2010); and one unidentified species of Family Vitreledonellidae (Brunetti 2010).

Except perhaps for sampling around the South Georgia Islands, available information on the octopus species associated with the deep water environment to the east of the Argentine continental shelf is scarce and is known only from samples obtained from a small number of research surveys. Gleadall et al. (2010) analyzed samples obtained between 46 and 54 °S and between 200 and 1000 m isobaths and found three octopus species of the genus *Muusoctopus* (Fig. 6). Among them were two previously unknown species for the region: *M. longibrachus akambei* and *M. bizikovi* Gleadall et al. 2010. Guerra et al. (2011) explored the Patagonian upper and middle slope of the continental shelf, between 44 and 48ºS and down to 1500 m depth, recognizing five octopus species including three specimens of *Graneledone antarctica* Voss, 1976, which represents an expansion of its previously known distribution.

Compiling records from investigations carried out in Argentine coastal waters and outside the Argentinean continental shelf up to Lat 55° S, nearly 30 octopus species have been identified. Among them, *G. antarctica*, *G. macrotyla* and *Thaumeledone gunteri* Robson, 1930, are typically found in deep Antarctic and subantarctic waters (Collins and Rodhouse 2006) but were found far north (44° S and 48° S) in deep waters (> 770 m) off the outer Patagonian shelf and the upper and middle slope (Guerra et al. 2011). As suggested for *G. macrotyla,* expansion of these Antarctic species northwards into the southwestern Atlantic is presumably facilitated by the northward flow of cold subantarctic waters along the Patagonian shelf and slope transported by the Malvinas (Falkland) Current (Guerra et al. 2012).

Octopus collections in Argentina are housed in the Molluscan Collection of the Museo de La Plata (MLP-Ma), the National Collection of Invertebrates of Museo Argentino de Ciencias Naturales (MACN-In), the General Invertebrate Collection of the Instituto de Biología de Organismos Marinos (CNP-INV) and the INIDEP Cephalopod Reference Collection. Considering the MLP-Ma, MACN-In and CNP-INV collections, there are nearly 233 records of octopus obtained in Argentine waters, all of them from the families Argonautidae, Enteroctopodidae and Octopodidae, but only 33 specimens have been identified to species level, so further research and revision of the taxonomic status of the octopus specimens housed in Argentinian collections is needed.

Biogeography

A database was built considering the 62 species of coastal (benthic) octopods of the Americas to determine their geographical ranges. The species richness was estimated for each ecoregion following the classification of Spalding et al. (2007). To classify biogeographic units, a non-metric Multidimensional Scaling (nMDS) was performed (Clarke 1993) in PAST v3.18 (Hammer et al. 2001) using presence–absence data through Jaccard similarities. Differences among biogeographic units (provinces) were evaluated with one-way PERMANOVA using 10,000 permutations (Anderson 2001).

The maximum benthic octopod richness was found in temperate and tropical latitudes on both sides of the Americas (11–13 species), and decreased towards the poles (1–4 species). This latitudinal gradient in cephalopod species richness has also been observed in previous studies and attributed to oceanographic conditions, shelf area and extent of coral habitat (Rosa et al. 2008; Ibáñez et al. 2019). West of the continent, the highest values were observed in the warm temperate Northeast Pacific, mainly related to the presence of several *Octopus* spp. and *Paroctopus* spp. In contrast, in the Atlantic Ocean, high values were detected in both northern and southern hemispheres within the tropical ecoregions (Fig. 7) with the presence of numerous reef-associated taxa such as *O. briareus, O. insularis* and *O. hummelincki*. The high species richness in these tropical areas of the Atlantic has been attributed to the closure of the Atrato Seaway at the Isthmus of Panama which possibly led to the isolation of cephalopod populations and then to allopatric speciation (Gleadall 2013; Rosa et al. 2019).

Figure 7 reveals that ecoregions of similar temperature and latitude present a similar species richness. Fourteen groups were detected according to the nMDS analysis, which present significant differences in species composition (PERMANOVA Jaccard, $F = 6.599$, $p < 0.00001$). On this basis, fourteen biogeographic units are defined, ranked provisionally as provinces according to Spalding et al. (2007), illustrated in Fig. 8, the ordination in which shows three principal groups: the Arctic and northwestern Atlantic provinces (Group 1); Warm Temperate and Tropical Atlantic provinces (Group 2); and Pacific and Magellanic provinces (Group 3). The coastal biogeographic provinces of Nesis (1982, 1985, 2003) match some of these results, although all the studies by Nesis were based on coastal cephalopods (all groups, both pelagic and benthic), while the present analysis considers only benthic octopuses. It is worth noting that these large biogeographic groups reflect the broad distribution of several octopus species along and off the coasts of America (e.g., *Enteroctopus dofleini*, *Graneledone pacifica*, *Octopus insularis*, *O. briareus*, *O. mimus*, *O. rubescens*, and *Robsonella fontaniana*).

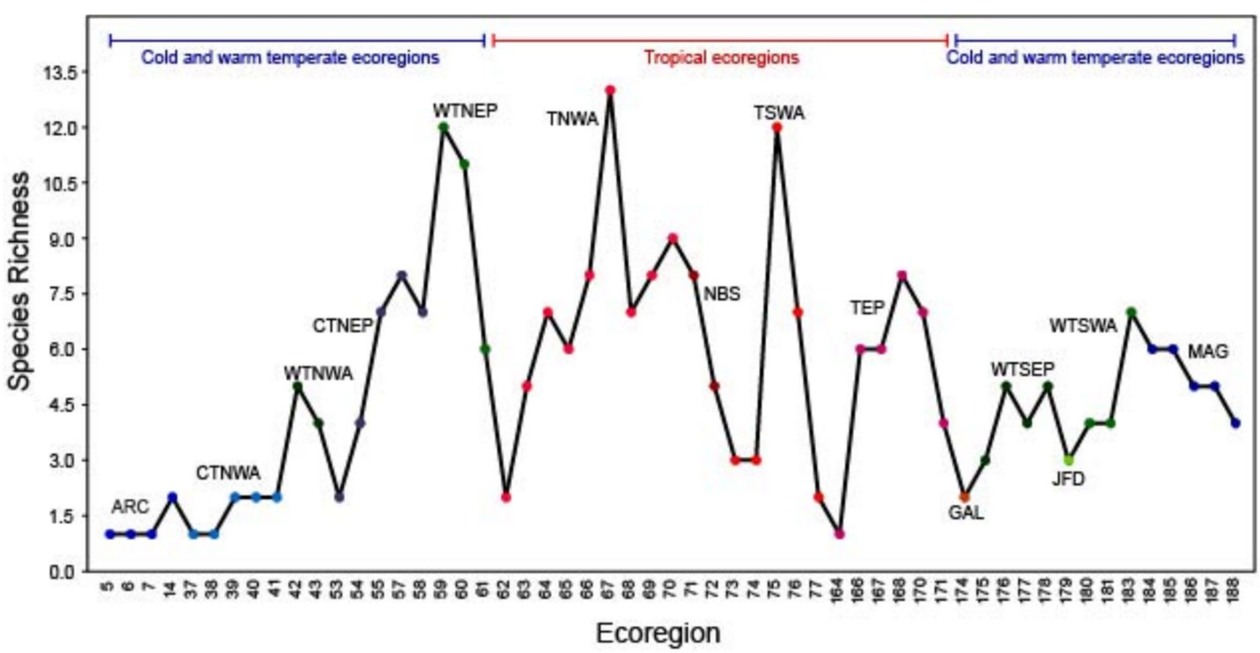

Fig. 7 Benthic octopus species richness (number of species) for each ecoregion (numbers) of America following Spalding et al. (2007). Province abbreviations (left to right): *ARC* Arctic, *CTNWA* cold temperate northwestern Atlantic, *WTNWA* warm temperate northwestern Atlantic, *CTNEP* cold temperate northeastern Pacific, *WTNEP* warm temperate northeastern Pacific, *TNWA* tropical northwestern Atlantic, *NBS* North Brazil Shelf, *TSWA* tropical southwestern Atlantic, *TEP* tropical eastern Pacific, *GAL* galapagos, *WTSEP* warm temperate southeastern Pacific, *JFD* Juan Fernández and Desventuradas, *WTSWA* warm temperate southwestern Atlantic, *MAG* magellanic

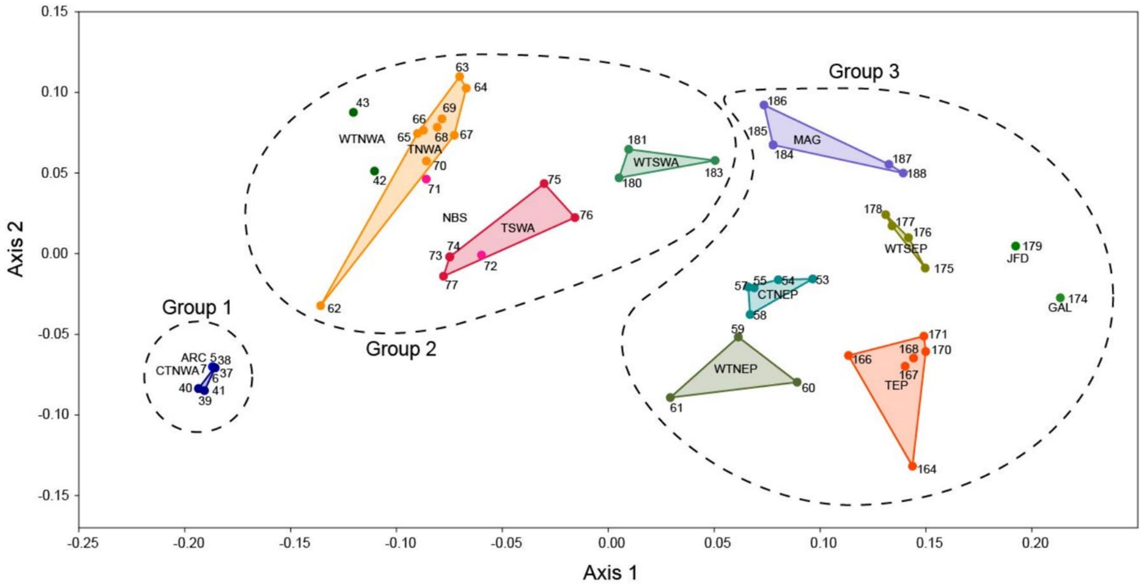

Fig. 8 Nonmetric multidimensional scaling (nMDS) ordination of benthic octopus species richness and ecoregions (numbers) of America following Spalding et al. (2007). Abbreviations of provinces as in Fig. 7. See text for further explanation and interpretation

AmeriCeph: species database of octopus biodiversity in the Americas

A database named AmeriCeph is provided as Supplementary Table TS1. This was compiled by the authors as a summary of the identifications and reference specimens of octopus species found around the Americas. It refers to type material as well as voucher material identified in various institutional collections around the world, with collecting localities listed by country. This is intended to provide a resource to facilitate local species identifications and rapid recognition of undescribed species, in the anticipation of accelerating the publication of new species descriptions and thereby improving the assessment of the octopus biodiversity around the Americas. While it contains reference to some DNA sequences in databases such as GenBank, many of the species require further investigation to confirm the identification of the specimens from which DNA samples were taken. A second database (Supplementary Table TS2) provides a resource of confident identifications for DNA samples conforming to the strict criteria of Strohm et al. (2016), with the aim of improving the accuracy of cephalopod seafood tracking (cf. Gleadall et al. 2024) as well as providing a resource to improve phylogenetic assessments of the relationships among octopus species and genera.

Discussion

The generally typical benthic habits, prey and life of octopuses, and wide differences in familiarity with different species, are not conducive to making any useful comments on functional diversity. However, species richness of the octopus populations around the Americas is apparent from the accounts and distribution maps, as also is the biodiversity distribution across geographical scales. The distribution of species of *Paroctopus* appears to show a high degree of endemism, but it is clear that the distribution of individual species is very poorly understood, with relatively few specimens collected and identified for each species, and as yet very few species have been described in detail morphologically along with representative DNA sequences.

The information brought to light by this study for the distribution of *Muusoctopus* species is interesting (Fig. 6). Being bathybenthic organisms living in a relatively uniform cold water habitat, apparently they are not associated with particular biogeographic regions. Rather, their distribution appears to support the hypothesis of their ancestral origins in the North Pacific (Gleadall 2013) and, during speciation and further migration, a general southerly movement along the seabed of the western American continental slopes, spreading out into the Atlantic either via the Atrato Seaway (ancestors of *M. januarii*), before its closure around 2.8 Mya, or after travelling around Cape Horn (ancestors of *M. johnsonianus*/*M. oregonae*) and then spreading north into the Atlantic to join their relative, *M. januarii* (see Toll

1981 and Hoyle 1885a, b). In the American coastal regions the latter is distributed along the continental slope from the eastern coast of Florida, through the GoM and Caribbean to northeastern South America (Fig. 6; cf. also the amphi-Atlantic distribution recognized by Gleadall 2013). The amphi-Atlantic distribution of species *M. johnsonianus*/*M. oregonae* (which includes the Mid-Atlantic Ridge; Vecchione 2004; Strugnell et al. 2011; Gleadall 2013) appears to include also the eastern American continental slope, at least between Nova Scotia and Cape Hatteras (Fig. 6).

The distribution pattern of *O. americanus* and *O. insularis* (the two American species of the *Octopus vulgaris* complex) is also worth noting. Both have a very broad distribution, apparently straddling several of the provinces as defined by Spalding et al. (2007). Briggs and Bowen (2013) realigned the marine biogeographic provinces, eliminating the distinction between tropical and warm-temperate regions, and their Western Atlantic province coincides well with the coastal distribution of *O. americanus* in Fig. 3, which includes both the northern and southern warm temperate provinces. However, *O. insularis* is confined to the Western Tropical Atlantic realm as defined by Spalding et al. (2007). It will be interesting to investigate these two species further to elucidate the causes behind the differences in their distribution. A possible hint is available from a study based in the NW Atlantic coast of the US: Pappalardo et al. (2015) found that species distributions of some 1800 species of marine invertebrates were strongly influenced by currents but also the duration of pelagic larvae, particularly for species normally living deeper than 20 m.

Concerning species richness, the results of this study in general indicate that benthic octopus diversity shows a latitudinal gradient around the Americas, decreasing from tropical to cold ecoregions. A recent survey on global patterns of coastal cephalopod species richness found similar results (Rosa et al. 2019). However, the present study considers several taxa not included in that work, including certain *Muusoctopus* spp., *Graneledone* spp., and some recently described species such as *Lepidoctopus joaquini, Octopus taganga*, *Macrotritopus beatrixi*, and *Paroctopus cthulu*, which augment assessments of the biodiversity of this part of the world. We hope that the expertise harnessed for this paper will help to boost collaborative studies beyond national borders in order to better approach topics in both basic research and applications to fisheries and aquaculture.

Temperature is known to strongly influence the reproduction and growth of octopus species, and this has been shown for several species of the Americas including: *O. maya* in Mexican waters (see Rosas et al. 2014; Angeles-Gonzalez et al. 2017); *P. tehuelchus* in the SW Atlantic (Klaich et al. 2006; Braga et al. 2021); *E. megalocyathus* in Patagonian waters (Ortiz et al. 2011; Uriarte et al. 2016) and *O. insularis* in the western Atlantic (Lima et al. 2020a). However, for many species there is no clear trend other than range expansion, so reported fluctuations in their catches are difficult to interpret. Regarding *P. tehuelchus*, for example, its fishery is still developing in some Patagonian coastal areas (Iribarne 1991) and currently there are no official records of fishery landings.

According to Rosa et al. (2019), the greater species richness of the benthic cephalopod forms compared to the pelagic ones reflects the importance of seabed heterogeneity as a speciation driving force (*cf.* also d'Orbigny 1849). Therefore, adjustments to our understanding of octopus diversity and biogeography are likely to improve as further sampling is conducted. It is also important to find out more about possible drivers, in addition to temperature, influencing the distribution and abundance of octopuses to better comprehend effects such as climate change on their physiology and life cycle and to contribute to the assessment and management of octopus fishery stocks. For example, it has been shown that the extent of spatial distribution of a species is closely correlated with hatchling size and developmental mode: species that produce small planktonic hatchlings tend to have broader distributional ranges than species with large, benthic juvenile hatchlings, which are often endemics (Villanueva et al. 2016).

Due to scarce information about the biodiversity of octopuses, as well as their general morphological similarity and the lack of taxonomic expertise in many areas, adult specimens of some species (such as *P. tehuelchus* and *Paroctopus* spp.) may be misidentified as juveniles of larger species (such as *O. americanus*), resulting in inaccuracies which find their way into official fishery statistics. An integrative approach to identifying octopuses, including DNA sequencing, morphometric analyses, body pattern descriptions and ecological studies, is necessary to achieve effective and sustainable octopus fishery exploitation and management (cf. Gleadall et al. 2024) and also to inform the development of techniques for octopus aquaculture.

Progress in identifying octopuses, along with the detected presence of many undescribed species, highlights the need for further research to reach a more comprehensive assessment of the full biodiversity of octopuses in the Americas. On the way to meeting this need, collaborative taxonomic (systematic), genetic and morphometric studies comparing octopuses in both European and American waters are in progress, fostered by the improved international collaboration achieved through the efforts of the authors of the present paper, including compilation of the AmeriCeph database.

Appendixes: Octopus taxonomy issues and updates

Appendix 1: Usage of genus name *Pinnoctopus* d'Orbigny, 1845

In discussing species related to *Octopus macropus* Risso, 1826, the genus name used in the present paper is *Pinnoctopus* d'Orbigny, 1845b. In a peer-reviewed monograph on the octopuses of New Zealand, O'Shea (1999) included a thorough review of the '*Octopus macropus* group' of Robson (1929), concluding that the appropriate genus name to use for this group is *Pinnoctopus*. The study by O'Shea also included a redescription of the type species of *Pinnoctopus*, *Octopus cordiformis* Quoy & Gaimard, 1832, and designation of a neotype from the type locality to stabilize both the genus and species names (cf. ICZN Art. 75.3). More recently, the eggs and paralarval stage of *P. cordiformis* have been described by Carrasco (2014).

Norman and Hochberg (2005) confounded *P. cordiformis* with *Enteroctopus zealandicus* (Benham 1944), accusing O'Shea of the very same error despite the fact that the distribution of *E. zealandicus* does not include the type locality of *P. cordiformis* (so they are not synonymous). Further, a redescription of (and neotype designation for) *E. zealandicus* was provided by O'Shea (1999), who had therefore clarified the genus and species names for both species. Norman and Hochberg (2005) chose to dismiss *P. cordiformis* as an 'unresolved' species, ignoring the validity (and priority) of O'Shea's revision and neotype designation and instead of *Pinnoctopus* used the genus name *Callistoctopus* Taki, 1964, for species in the '*Octopus macropus* group', identifying *P. cordiformis* as a member of a different genus using one of its junior synonyms, *Macroctopus maorum* (Hutton, 1880) (cf. O'Shea 1999).

Recently, other authors, too, have followed Norman and Hochberg (2005), choosing to disregard O'Shea's important contribution and to use *Callistoctopus* as the genus name for this group of octopuses, which apparently is based on the synonymy of *Callistoctopus arakawai* Taki, 1964, and *Octopus ornatus* Gould, 1852, proposed by Voss (1981). However, use of *Callistoctopus* as the senior generic synonym for this group of octopuses is clearly untenable because, even if the genus name *Pinnoctopus* were found to be inappropriate, the next available genus name is not *Callistoctopus* but *Eledonenta* Rochebrune, 1884 (cf. Norman 1993). In this review, therefore, the priority and validity of *Pinnoctopus* is recognized and it is used as the appropriate genus name for the '*Octopus macropus* group' of octopus species, with genus names *Callistoctopus* and *Eledonenta* identified as junior synonyms of *Pinnoctopus*, as clarified by O'Shea (1999).

Further supporting the seniority of genus name *Pinnoctopus*, the morphology of the type species, *P. cordiformis*, places it clearly within the '*Octopus macropus* group' (O'Shea 1999). *Pinnoctopus cordiformis,* according to both d'Orbigny (1845b) and O'Shea (1999), is a valid species name, and the thorough discussion and diagrams by Benham (1943) support this identification. In addition, a recent publication on molecular phylogeny of New Zealand octopuses (Ibáñez et al. 2020) confirmed the validity of *P. cordiformis* and showed that three species identified as species of genus *Callistoctopus* are closely associated with *Pinnoctopus cordiformis*. The species in this group have a number of distinctive morphological features in common, including arm length formula and the morphology of the ligula, pseudophallus and stylets (Gleadall pers. obs; González-Gómez pers obs).

Appendix 2: *Bathypolypus arcticus* (Prosch, 1849): ratification of the lectotype designation intended by Muus (2002)

Lectotypes designated after 1999 must 'contain an express statement of deliberate designation (merely citing a specimen as "lectotype" is insufficient)' according to the Code (ICZN 1999 Art. 74.7.3; ICZN 2003, Declaration 44). In the original description, Prosch (1849) did not designate any types of *B. arcticus* (originally as *Octopus arcticus*) but Muus (2002) noted that the specimens used by Prosch (1849) were recognized and labelled during curation around 1930, and that Kristensen and Knudsen (1983) had referred to these as a holotype and paratypes. However, since types were not designated originally, the recognized types are syntypes, not a holotype and paratypes. Muus (2002) recognized this and referred to the so-called holotype as the lectotype but he did not provide the obligatory statement of deliberate designation. To rectify this, the subsequently registered specimen ZMUC CEP-13 (a male, DML 42 mm; loc. off Greenland, coll. 26.viii.1841) is here designated as the lectotype of *Bathypolypus arcticus* (Prosch, 1849) in order to stabilize the species name in view of potential confusion with closely related species such as *B. bairdii* (Verrill, 1873) and *B. pugniger* Muus, 2002.

Appendix 3: The controversy over so-called *Octopus giganteus* Verrill, 1897

The taxonomic literature concerned with octopus names formally attributed to Verrill also includes many references to a tissue specimen (USNM 149380) still extant in the Smithsonian Institution (see Verrill 1897b) which was identified as a species of octopus. This was an identification error which, although realized soon after by Verrill himself, caused confusion and controversy that was not finally laid to rest until a century later.

The piece of tissue had been sent to Verrill (1897a), who at first described the animal from which it came as *Octopus giganteus* but soon after retracted this identification (Verrill 1897c), strongly suspecting it to be part of a decaying whale. However, almost a century later, Johnson (1989) cited Gennaro (1971) and Mackal (1986) as confirming that the specimen in USNM (sent by collector Dr Webb to Verrill) is a giant species of octopus, in agreement with Wood (1971a), who also cited a confirmatory communication from a renowned teuthologist, the late F.A. Aldrich (Wood 1971b). Johnson (1998) eventually retracted this identification following studies by Pierce and others who used rigorous electron microscopy, protein analysis (Pierce et al. 1995) and DNA analysis (Pierce et al. 2004) to demonstrate that the specimen is indeed part of a cetacean. This is in agreement with Verrill (1897c) himself and F.A. Lucas (Curator of Comparative Anatomy at the Smithsonian at the turn of the nineteenth-twentieth century), who is cited as stating that: 'The substance looks like blubber, and smells like blubber and it is blubber, nothing more or less' (Wood 1971b). For other references in the literature to this controversy (recording arguments both for and against the validity of *O. giganteus*) see the reviews by Pierce et al. (1995, 2004) and Johnson (1998).

Appendix 4: Misapplication of genus name *Paroctopus* to large, cold-water species

Identifications concerning genus *Paroctopus* are now understood to be applicable only to a group of small species but (since 1929 until relatively recently) this genus name has been applied also to some of the largest octopus species known to science, including several cold-water species found only in Japanese waters. Tracing the source of these misidentifications reveals errors and assumptions stretching back into the nineteenth century, resulting mostly from a failure to publish sufficiently detailed descriptions, measurements and illustrations. For many species of octopus this is still a major, unfulfilled requirement. Almost half of the identifications listed in Table 4 (a chronology of 33 events) contributed to the confusion. One exception was a reasonable species description provided by Verrill (1883b: Table 4, Event 7), who included detailed measurements and clear illustrations of a specimen of the giant Pacific octopus (GPO) in the Gulf of Georgia, near Vancouver, although his identification used the species name *Octopus punctatus* Gabb, 1863, for which the original description was brief and inadequate (Table 4, Event 3). The type locality of *O. punctatus* (San Francisco) is a known region of overlap between the southern distributions of northern octopus species (including the GPO), and the northern extent of the distribution of southern species (including *O. bimaculoides*). The original type specimen was destroyed in the San Francisco fire of 1906, so even today the identity of *O. punctatus* as a valid species is uncertain: it is a *nomen dubium*.

Hoyle (1885a, b) described many new species from the Challenger Expeditions, among which was a large Japanese species, *Octopus hongkongensis*. Shortly after, Hoyle explained that (after seeing the description by Verrill 1883b: Table 4, Event 7), he identified *O. hongkongensis* as a synonym of *O. punctatus* Gabb (Hoyle 1886: Table 4, Event 5), stating his belief that the GPOs should all be identified as *O. punctatus*. In the following century, Berry (1912: Event 11) read the dictionary entry on 'Poulpe' by Blainville (1826: Event 2) and identified *O. punctatus* Gabb as a homonym of '*O. punctatus*' Say, 1819, *fide* Blainville (1826). Therefore, as the next available name, he used Hoyle's identification and began to identify the GPOs as *O. hongkongensis*. However, Blainville was discussing *Ocythoe punctata* Say, 1819 (a misidentification of an American species of *Argonauta*; Table 4, Event 1), so *Octopus punctatus* Gabb is an available name (which, therefore, could have been retained by Berry 1912). Shortly after, Berry considered that Hoyle (1886) was mistaken about the identity of the American GPO and discontinued using *O. hongkongensis*; but if *O. punctatus* was (as he believed) a junior homonym and could not be used, the GPO needed a new species name, so he described a GPO specimen from Alaska as new species *O. apollyon* (Berry 1913: Table 4, Event 12).

Naef (1923) described genus *Paroctopus* based only upon the character of possessing 'large' eggs (Table 4, Event 13), although to this day a description of the type species, *P. digueti*, still requires further refinement to enable unambiguous comparisons with other closely related species. Robson (1929: Table 4, Event 15) saw an illustration of the eggs of '*O. punctatus*' by Tryon (1879: Event 4) and assumed that they were 'large' eggs, although there is no scale bar nor other indication of the size of the eggs, so equally the illustration may be of 'small' eggs greatly enlarged. Therefore, from the brief description of *O. punctatus* ('the common poulpe of the California coast') provided by Tryon, of a specimen of moderate size with a distribution from 'Alaska to Lower California', the specimen could have been one of at least three species: a small GPO with 'small' eggs; or a moderately sized specimen of either *O. bimaculatus* (with 'small' eggs) or *O. bimaculoides* (with 'large' eggs; cf. Table 4, Event 22). A specimen labelled '*O. punctatus*' in Tryon's collection was identified by G. Voss (Table 4, Event 30) as *O. bimaculatus* or *O. bimaculoides* (egg size was not mentioned). From this, it is considered that Robson's observation (Table 4, Event 15) may have been an erroneous association of the GPO (as species '*Octopus*' *apollyon*; see Event 12) with *O. bimaculoides* (as *O. punctatus*).

Table 4 Events associated with identifications using genus name *Paroctopus* Naef, 1923

Event	AA*	Original identification	Suggested valid identification	Author(s)	Year
1. Original species description loc. N. America Atlantic coast, deposited at the Acad. Nat. Sci. Philadelphia	!	*Ocythoe punctata*	*Argonauta punctata* (Say)	Say	1819
2. Dictionary entry 'Poulpe' under subheading of genus *Ocythoe*, including comparisons with *Argonauta*	–	'*O. punctatus*'	'*O.*' = *Ocythoe* (= *Argonauta*: see above)	Blainville	1826
3. Original species description loc. San Francisco (see entry in Table TS1)	–	*Octopus punctatus*	cf. *Enteroctopus dofleini* or *Octopus bimaculoides*	Gabb	1863
4. Description of California specimen, ML c.89 mm, arm lengths 235–274 mm	–	*Octopus punctatus*	cf. *E. dofleini, O. bimaculatus, O. bimaculoides*	Tryon	1879
5. Octopus punctatus (? *E. dofleini,* Alaska) misidentified as *O. hongkongensis* (Japan)	!	*Octopus hongkongensis*	cf. *O. punctatus*, *E. ?dofleini*	Hoyle	1886
6. Caribbean specimen identification as southern S. American *O. tehuelchus* (probably genus *Paroctopus*)	–	*Octopus tehuelchus*	*Paroctopus joubini* (Robson 1929)	Hoyle	1886
7. Extensive redescription with figures (E. dofleini?). The only locality mentioned is the Gulf of Georgia [Salish Sea, Vancouver Island]	+	*Octopus punctatus*	*Enteroctopus ?dofleini*	Verrill	1883
8. Original description loc. Baha California; compared with local *O. punctatus* (= *O. bimaculoides*?)	–	*Octopus digueti*	*O. digueti*	Perrier & Rochebrune	1894
9. Redescription of *O. digueti*; compared with local *O. punctatus* (= *O. bimaculoides*?)	–	*Octopus digueti*	*O. digueti*	Rochebrune	1896
10. Original description of Japanese giant Pacific octopus (GPO)	–	*Polypus dofleini*	*Enteroctopus dofleini*	Wülker	1910
11. *Ocythoe punctata* Say (*fide* Blainville 1826) mistaken for a homonym of *Octopus punctatus* Gabb	!	*Octopus hongkongensis*	*O. punctatus*, cf. *E. dofleini*	Berry	1912
12. First valid description of species *apollyon* loc. Gulf of Alaska, Kodiak Is., Uyak Bay	–	*Polypus apollyon*	?*E. dofleini*	Berry	1913
13. Original description of genus *Paroctopus* established. Type species *O. digueti* Perrier & Rochebrune 1894	–	*Octopus digueti*	*Paroctopus digueti*	Naef	1923
14. Hoyle's *O. tehuelchus* from St. Thomas (E. of Puerto Rico)	–	*Octopus joubini*	*Paroctopus joubini*	Robson	1929
15. Remarks on genus *Paroctopus*, recognizing *O. apollyon* as possessing 'large' eggs based on Tryon (1879)	!	*Paroctopus apollyon*	*Octopus punctatus* Gabb eggs Pl. 19 Fig. 3	Robson	1929
16. Remarks on genus *Paroctopus*, synonymizing *O. apollyon* and *O. punctatus*	!	*Paroctopus apollyon*	*Octopus punctatus* Gabb	Robson	1929
17. Comparison of *Paroctopus apollyon* and *Paroctopus hongkongensis*	!	*Paroctopus hongkongensis*	'*Octopus*' *hongkongensis* Hoyle (holotype only)	Robson	1929
18. Inclusion of species '*Octopus*' *conispadiceus* (NE Pacific) in genus *Paroctopus*	!	*Paroctopus conispadiceus*	'*Octopus*' *conispadiceus* (Sasaki 1917)	Robson	1929
19. Inclusion of species '*Octopus*' *yendoi* (NE Pacific) in genus *Paroctopus*	!	*Paroctopus yendoi*	'*Octopus*' *yendoi* (Sasaki 1917)	Robson	1929
20. Identification of (warm temperate) Florida specimens as (tropical E. Caribbean) *Paroctopus joubini*	!	*Paroctopus joubini*	?*Paroctopus* sp., 9 lots off W. Florida	Pickford	1945
21. Identification of *Octopus briareus* as a species of *Paroctopus*	!	*Paroctopus briareus*	'*Octopus*' *briareus*, 8 lots off Florida & Curaçao	Pickford	1945

Table 4 (continued)

Event	AA*	Original identification	Suggested valid identification	Author(s)	Year
22. Distinction of *O. bimaculoides* (a large-egged species) from *O. bimaculatus* Verrill, 1883 (a small-egged species)	+	*Octopus bimaculoides*	*Octopus bimaculoides*	Pickford & McCon-naughey	1949
23. *Paroctopus* as an invalid genus name, based on comparison of *O. bimaculatus* and *O. bimaculoides*	!	*Octopus joubini*	(sensu Robson 1929) *Paroctopus joubini*	Pickford & McCon-naughey	1949
24. Identification of three subspecies of '*Octopus*' *dofleini*: *O.d. dofleini*, *O.d. apollyon* and *O.d. martini*	–	*Octopus dofleini apollyon*	cf. *Polypus apollyon* Berry	Pickford	1964
25. Application of genus name *Paroctopus* to the giant Pacific octopus of Japan	!	*Paroctopus dofleini dofleini*	*Enteroctopus dofleini*	Taki	1965
26. Assumption (not confirmed) of just 2 species in GoM and Caribbean: one small-egged (Western GoM)	?	*Octopus joubini*	*Paroctopus* cf. *joubini*	Forsythe & Toll	1992
27. Assumption (not confirmed) of just 2 species in GoM and Caribbean: one large-egged (GoM & Atlantic)	?	*Octopus* sp. X	*Paroctopus* sp. cf. *mercatoris* (Adam 1937)	Forsythe & Toll	1992
28. GPO species *Enteroctopus zealandicus* disassociated from *Paroctopus*	+	*Paroctopus dofleini*	*Enteroctopus dofleini*	O'Shea	1999
29. Key to (*Paroctopus*) group in Central W. Atlantic (GoM and Caribbean) based on Pickford, Forsythe & Toll	?	*Octopus joubini* group	1 large-egged + 1 small-egged species hypothesis	Vecchione	2002
30. Philadelphia Academy of Natural Sciences: one of the specimens possibly described by Tryon (1879)	?	*Octopus punctatus*	*O. bimaculatus* (or *O. bimaculoides*)	G. Voss (N. Voss)	Undated[a]
31. New species named but desciption is deficient. Closest COI sequence is stated to be '*Octopus joubini*'	?	*Octopus jeraldi*	?*Paroctopus* sp.	Pratt et al	2020
32. Identification of species based on two specimens 'washed up on Sanibel Island' (W. Florida, GoM). Egg size?	?	*Octopus mercatoris*	?*Paroctopus* sp. A (ID confirmation required)	Holloway et al.	2023
33. Based on Vecchione (2002) and two-species hypothesis for W. Florida specimens only. Nothing on egg size	?	*Octopus joubini*	?*Paroctopus* sp. B (ID confirmation required)	Holloway et al.	2023

Key to event assessments: !, error; ?, requires confirmation and a full description; –, not bad, but descriptions insufficient for confident identification; +, good description

GoM Gulf of Mexico, *AA, Arbitrary assessment

[a]Notes of G Voss (late 1950s?) communicated to IG Gleadall by N Voss in 2004

Robson (1929) was rightly sceptical of such a simplistic character as 'large eggs' to define a genus but at that time there were few species of large-egged octopus known to science and in the end he applied genus *Paroctopus* to several large-egged Japanese species (Table 4, Events 17–19) which had just been described by Sasaki (1929). By the time of the publication of the illustrated Japanese encyclopædia of animals, to which Taki (1965) contributed the section on Cephalopoda, the identity of the GPO had been associated with '*Octopus*' *hongkongensis* and '*Octopus*' *punctatus* sensu Berry 1912; and then between the latter and Japanese species '*Octopus*' *dofleini* Wülker, 1910 (Table 4, Event 10). A year earlier than Taki's contribution to the encyclopædia, '*O.*' *hongkongensis* was identified as a species different from the GPO and Pickford (1964) had concluded that there were three GPO subspecies: *O. dofleini dofleini*, *O. d. apollyon* and *O. d. martini* (Table 4, Event 24). Since Robson's monograph of 1929, however, several large species had been identified as species of *Paroctopus*, including Berry's *O. apollyon*. Because there were three closely related subspecies somewhat different from other octopus species groups (such as *Octopus* Cuvier), including subspecies *apollyon*, it was perhaps not unreasonable at that time for Taki to conclude (based on the information available to him) that the appropriate species name for the Japanese GPO should be *Paroctopus dofleini dofleini* (Taki 1965: Table 4, Event 25). Since this encyclopædia was a major 3-volume zoological work describing some 7,500 species, it naturally became a major source of reference, so Taki's identification long continued to be used for the Japanese GPO (e.g. Nagasawa et al. 1993) until the detailed study by O'Shea (1999: Table 4, Event 28) identified all the cold-water giant species using genus name *Enteroctopus* (cf. also Hochberg 1998).

In addition to misapplication of genus name *Paroctopus* to species of large octopus such as the GPOs and other species of Enteroctopodidae, problems of misidentification continue to plague our understanding of species identifications assigned to this genus in the GoM and Caribbean, as outlined in the following Appendix 5.

Appendix 5: Accurate description of species richness and diversity: awareness of mismatches between phenotype and genotype and guarding against misidentification

The use of DNA sequences has gained in importance in taxonomy and systematics over the last two decades as sequencing techniques have improved (for mitochondrial genes in particular), complementing development of the molecular clock concept of evolution (Zuckerkandl and Pauling 1962, 1965; Bromham and Penny 2003; Carroll 2008; Ho 2008). However, when considering species divergence, it should not be forgotten that the evolutionary changes happening at the level of DNA sequences occur by stochastic increments, altering individual nucleotide sequences which at first may not result in any changes at the amino-acid level; while detectable phenotypic changes to the organism are sporadic, far less frequent events (e.g. Schleifer and Ludwig 1994). Particularly for closely-related species, this means that differences at the level of a given gene may not correspond with differences in phenotype.

When comparing any two species, then, there are three possibilities that must be borne in mind. (1) Differences may be obvious both in genotype (the DNA sequence of a particular gene) and in the phenotype (morphology) of specimens of the two species: an ideal occurrence for constructing phylogenies. (2) There may be a difference between DNA sequences but without apparent morphological difference, when the two species would be considered 'cryptic' (phenotypically indistinguishable). (3) There may be a difference in morphology but no apparent difference in the DNA sequence for a particular target gene: that is, for two species that have undergone recent divergence, differences in morphology have occurred due to changes elsewhere in the genome but not in the particular target gene sequence used to determine phylogenetic relationships. A fourth possibility is that morphological changes can be brought about by environmental factors such as temperature and food availability. This is well documented in loliginid squids (the effects on which include manifestations such as development of males of two different size classes, behaviour and reproductive tactics; e.g. Pang et al. 2022). However, such effects have not been reported for octopuses, although apparent differences in form can occur as allometric growth of the arms versus the body progresses (e.g. Gleadall 2016).

Occurrences of the third possibility have been detected recently among species in genus *Octopus*. In one example, Reid and Wilson (2015) compared cytochrome oxidase III nucleotide sequences and concluded that specimens currently attributed to *O. sinensis* and *O. jollyorum* represent a single species, while Gleadall (2016) observed clear morphological differences between males of the two species and therefore considered them to be different. In another example, Amor et al. (2019) concluded from whole genome data that an undescribed species in the region of the South African coast (yet to be characterized morphologically and given a species name) is different from *O. vulgaris* sensu stricto, despite the two species having indistinguishable mitochondrial genomes.

If phenotype and genotype are not always congruent, then, it is obvious that for all species it is important to have information on both. In many animal groups, telling species apart phenotypically can be difficult, which is why there are detailed requirements to describe each species as fully as possible, including various internal anatomical and external morphological features, so that subsequently they can be recognized by careful inspection (or at least by morphological and meristic measurements). For octopuses, this requires access to a type series (collection of reference specimens) including sexually mature males and females: males of one species are often easier to distinguish from those of another using male sexual characters; and for females, in addition to morphological appearance, the size and appearance of the eggs and hatchlings are useful distinguishing characters.

There are still many species for which no DNA sequences are available, so they are known only by their morphology. Therefore, when novel DNA sequences (as yet unrecorded in a sequence database such as GenBank) are obtained, but without robust morphological data, it is impossible to know whether these sequences represent a new species or are from a species already described, though only by its morphology. To cover both possibilities, it is obvious that new DNA sequence information must be accompanied by an unambiguous identification entailing a thorough description of the physical morphological attributes of the specimens from which the new sequences have been sampled: it is of no use to a fisherman or research biologist to know that there are 15 different species available in local waters if it is not possible to distinguish them without sampling and sequencing every specimen; and research would not progress very well without understanding the identity and physical attributes of a particular target species.

Techniques of environmental DNA (eDNA) sampling can detect several different species simultaneously (Willette et al. 2021; Gleadall et al. 2024) and for some research purposes it is sufficient to report on the taxonomic affinities and number of species present. However, having sequences but knowing little or nothing about the physical appearance of the animals is of limited use (for example, a list of sequences can contribute little to decisions on fisheries management), and may lead to duplication and consequent mis-estimation of species numbers and abundance. So, for taxonomic descriptions of species, it is important to acquire and record both DNA sequence information and detailed, unambiguous physical descriptions of several representative specimens. Lack of such rigorous morphological descriptions was (and still is) the cause of the great deal of confusion over species identifications using genus name *Paroctopus* (see also Appendix 4). Despite knowing this, however, superficial species descriptions continue to find their way into the literature, associated with additions to DNA sequence databases allocated to species names that are unverified and likely to be misidentifications. Such sequence contributions are heralded as clarifying species identifications (see, for example, Holloway et al. 2023) when they are achieving just the opposite.

The short description of Venezuelan species *Octopus jeraldi* Pratt, Baldwin and Vecchione, 2020, mentioned in the main text is an example where the phenotype and genotype information available would not be sufficient to address the issues mentioned in the second paragraph of this appendix. The only two specimens of *O. jeraldi* available are a juvenile and an immature female, so the morphological and meristic features of both male and female adult specimens are unavailable for comparisons. There is no description of any morphological features (either internal or external) that might be used subsequently to attempt identification of newly acquired specimens. It is particularly unfortunate that characters from mature males are unavailable, and the egg size and mode of development of the hatchlings are unknown: do they develop as direct benthic juveniles, or via an indirect planktonic paralarval stage? Also, it is not clear to which genus this species belongs: the genus assignation proposed is *Octopus* but the closest match to the DNA sequence obtained was stated to be *Octopus joubini* (which, if conspecific with the true *O. joubini*, suggests that the appropriate genus name could be *Paroctopus*; see main text discussion of genus *Paroctopus*). However, the phylogenetic analysis presented does not provide any further evidence for this conclusion, with the most closely related species labelled as a mysterious ‘Cephalopoda 1’. Since the specimens available are immature, the normal adult size is also uncertain (such as ML around 30 mm for some species of *Paroctopus*; or well in excess of 100 mm, as with many species of *Octopus* and *Pinnoctopus*).

In one of the most recent studies, Holloway et al. (2023) collected 30 specimens off the western coast of Florida; two specimens ‘collected after being washed ashore on Sanibel Island’ [near Fort Myers]; and two specimens (identified originally as ‘*O. joubini*’) were later identified as ‘*O. vulgaris* sensu stricto’ and included on their map of localities. The 30 specimens were identified as *O. joubini* based on ‘morphological identification’ with reference to Vecchione (2002), who discussed only the ‘*O. joubini* group’ as extant in the GoM and Caribbean region and did not provide any species descriptions for this group. Indeed, it was impossible for Vecchione to provide any truly informative species descriptions because the 3 type specimens available for the two named species (*O. joubini* and *O. mercatoris*) do not provide sufficient morphological information to enable competent species descriptions sufficient to make clear distinctions among closely related species. Based on these two species (one with its type locality in the NE Caribbean, the other off SW Florida), and with reference to two northern (western and eastern) GoM species raised in the laboratory by Forsythe and Toll (1992), Vecchione (2002) suggested the presence of just two species throughout the entire GoM and Caribbean region: one 'large-egged' and the other 'small-egged.' This may well be a false inference, though, applying a binary assumption based on the findings of the classic study of the Pacific sibling species *O. bimaculatus* and *O. bimaculoides* by Pickford and McConnaughey (1949). Experience with other animal groups in this region (e.g. Briggs and Bowen 2013; Cowman and Bellwood 2013) suggests that it is likely to be populated by more than just two closely similar *Paroctopus* species.

The morphological identification by Holloway et al. (2023) was apparently based on mean arm length, web depth and diameter of suckers #1 (at the mouth) and mid-way along one arm: a minimal character set offering little information for distinguishing among species, especially those in the same genus. Characters known to be useful were not investigated, such as: enlarged suckers (number, position, and occurrence on particular arms); sucker counts (especially those of the modified third right arm of males); or size of oocytes or laid eggs (cf. Leite et al. 2008, 2021; Gleadall et al. 2010; Gleadall 2016). There was no comment on the identification of the two (apparently anomalous) specimens of '*O. vulgaris* sensu stricto', particularly to explain their presence when *O. vulgaris* is considered to be absent from the western Atlantic and there are at least two other possible identifications that seem very much more likely (*O. americanus* or *O. insularis*). In short, this study by Holloway et al. (2023) contributed little towards resolving the distribution of species in this region; rather it increased the confusion by adding more DNA sequences associated with species identifications of questionable accuracy (certainly for *O. vulgaris*; and probably also for '*O. joubini*', since the extent of its distribution has yet to be investigated, in addition to a thorough morphological description so that subsequently it may be identified with confidence).

An example of a much more detailed account of a small American species of octopus is the 23-page description of *Paroctopus cthulu* by Leite et al. (2021), based on 12 specimens with detailed measurements, images, illustrations and DNA sequence analyses showing clear affinities with other species identified as belonging to the genus *Paroctopus*. In the future, any requirement to resolve issues pertaining to points (2) or (3) in the second paragraph of this appendix should be possible based on the information available from the original description by Leite et al. (2021). Attempts to resolve such issues for *O. jeraldi*, however, will require that the species be redescribed based on newly obtained specimens confirmed as belonging to the same species. Similarly, in trying to distinguish among the (clearly morphologically similar) species of *Paroctopus* in the central Western Atlantic, the data provided by Holloway et al. (2023) will require further, more detailed study (especially more comprehensive sampling throughout the GoM and Caribbean region and detailed morphological descriptions) in order to contribute to an accurate understanding of octopus diversity in the region.

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Author contributions IGG, RGG and UM conceived this review and the AmeriCeph Database following a Workshop on the Biodiversity and Taxonomy of Cephalopods from the Gulf of Mexico and the Caribbean Sea, organized by IGG and UM and hosted by Prof. Carlos Rosas Vázquez at the *Cephalopod Biodiversity, Taxonomy and Aquaculture Workshops, Sisal, Yucatán, México, 5–7 Nov., 2018*; and a Breakout Session on the Biodiversity and Taxonomy of Cephalopods from the Gulf of Mexico and Caribbean Sea, organized by IGG and RGG at the *Cephalopod International Advisory Council Workshops and Symposium, St. Petersburg, 10–16 Nov., 2018*. All authors made substantial contributions to the AmeriCeph Database; to drafting the review and revising it critically for important intellectual content and relevance; approved the version to be published; and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Data availability Supplementary Table TS1 is the AmeriCeph database generated for this study, Supplementary Table TS2 is a table of metadata for DNA sequences available for barcoding to the standards laid out by Strohm et al. (2016) for expert-identified species. Both tables are available online at Harvard Dataverse: https://doi.org/10.7910/DVN/JUVZLE.

Declarations

Competing interests IGG is Executive Director of AiCeph LLC and Consultant to Hotland plc, Tokyo (a fast-food franchise company specializing in octopus products). CMI is Associate Editor of the Marine Evolutionary Biology, Biogeography and Species Diversity section of Frontiers in Marine Science. The remaining authors declare that there are no competing interests.

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Authors and Affiliations

Roberto González-Gómez[1,2] · Otilio Avendaño[3] · Irene de los Angeles Barriga-Sosa[4] · Penélope Bastos[5] · Claudia Caamal-Monsreal[6] · Gabriela Castillo-Estrada[7] · Celso Cedillo-Robles[8] · Adam Daw[9] · Mariana Díaz-Santana-Iturrios[10,11] · Gabriela Galindo-Cortes[1] · Jürgen Guerrero-Kommritz[12] · Manuel Haimovici[13] · Christian M. Ibáñez[10] · María de Lourdes Jiménez-Badillo[1] · Paul Larson[14] · Tatiana Leite[15] · Françoise D. Lima[16] · Unai Markaida[17] · César Meiners-Mandujano[1] · Piedad S. Morillo-Velarde[1,2] · Nicolás Ortiz[18] · M. Cecilia Pardo-Gandarillas[10] · Ricardo Pliego-Cárdenas[4] · María Edith Ré[19] · Brian Siegel[20] · Brian Urbano[21] · Erica A. G. Vidal[22] · Ian G. Gleadall[23,24]

✉ Ian G. Gleadall
enoctopus@yahoo.co.uk

Roberto González-Gómez
gonzalezgomezroberto@gmail.com

Otilio Avendaño
ottoavend@gmail.com

Irene de los Angeles Barriga-Sosa
irabaso29@gmail.com

Penélope Bastos
penelopebastos@gmail.com

Claudia Caamal-Monsreal
cpcm@ciencias.unam.mx

Gabriela Castillo-Estrada
gacastilloes@gmail.com

Celso Cedillo-Robles
celsocedillo93@gmail.com

Adam Daw
larviculture@gmail.com

Mariana Díaz-Santana-Iturrios
marianadiazsani@gmail.com

Gabriela Galindo-Cortes
ggalindo06@gmail.com

Jürgen Guerrero-Kommritz
greledone@hotmail.com

Manuel Haimovici
manuelhaimovici@gmail.com

Christian M. Ibáñez
ibanez.christian@gmail.com

María de Lourdes Jiménez-Badillo
ljimenez@uv.mx

Paul Larson
Paul.Larson@MyFWC.com

Tatiana Leite
tati.polvo@gmail.com

Françoise D. Lima
francoisedl@yahoo.com.br

Unai Markaida
umarkaida@ecosur.mx

César Meiners-Mandujano
cmeiners@uv.mx

Piedad S. Morillo-Velarde
piedad_smv@hotmail.com

Nicolás Ortiz
nicortizcnp@gmail.com

M. Cecilia Pardo-Gandarillas
pardogandarillas@gmail.com

Ricardo Pliego-Cárdenas
rip_rojo@hotmail.com

María Edith Ré
marilucnp@gmail.com

Brian Siegel
briansiegel@mote.org

Brian Urbano
maclen55@yahoo.com

Erica A. G. Vidal
ericavidal2000@yahoo.com.br

[1] Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Boca del Río, Veracruz, Mexico

[2] Present Address: Centro Oceanográfico de Murcia (IEO-CSIC), San Pedro del Pinatar, Murcia, Spain

[3] Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Sisal, Yucatán, Mexico

[4] Planta Experimental de Producción Acuícola, Departamento de Hidrobiología, Universidad Autónoma Metropolitana unidad Iztapalapa, Mexico City, Mexico

[5] Aquaculture Department, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil

[6] Unidad Multidisciplinaria de Docencia e Investigación Sisal (UMDI-Sisal), Facultad de Ciencias, Universidad Nacional Autónoma de México, Sisal, Yucatán, México

[7] Posgrado de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico City, México

[8] Universidad Autónoma de Yucatán, Mérida, Yucatán, Mexico

[9] U.S. Fish and Wildlife Service, Uvalde National Fish Hatchery, Uvalde, TX, USA

[10] Departamento de Ecología y Biodiversidad, Facultad de Ciencias de la Vida, Universidad Andres Bello, Santiago, Chile

[11] Present Address: Cientinela del Mar, A.C., La Paz, Baja California Sur, Mexico

[12] FUNDABAS Foundation, Bogotá, Colombia

[13] Universidade Federal do Rio Grande-FURG, Rio Grande, Brazil

[14] Fish and Wildlife Research Institute (FWRI), St. Petersburg, FL, USA

[15] Department of Ecology and Zoology, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil

[16] Laboratório de Ictiologia Sistemática e Evolutiva, Departamento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Lagoa Nova, Natal, RN, Brazil

[17] Laboratorio de Pesquerías Artesanales, El Colegio de la Frontera Sur (CONACyT), Lerma , Campeche, Mexico

[18] Laboratorio de Cefalópodos, Instituto de Biología de Organismos Marinos (IBIOMAR) CCT CONICET-CENPAT, Universidad Tecnológica Nacional-Facultad Regional Chubut, Puerto Madryn, Chubut, Argentina

[19] Puerto Madryn, Chubut, Argentina

[20] MOTE Marine Laboratory & Aquarium, Sarasota, FL, USA

[21] Posgrado en Ciencias Biológicas, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico

[22] Centro de Estudos do Mar, Universidade Federal do Paraná (UFPR), Pontal do Paraná, PR, Brazil

[23] Graduate School of Agricultural Science, Tohoku University, Aobayama Campus, Aramaki, Aobayama, Sendai, Japan

[24] Present Address: AiCeph LLC, Sendai, Japan