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Traditional Knowledge Aids Description When Resolving the Taxonomic Status of Unsettled Species Using Classical and Molecular Taxonomy: The Case of the Shallow-Water Octopus *Callistoctopus furvus* (Gould, 1852) From the Western Atlantic Ocean

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Shallow-water marine invertebrate fauna is diverse in tropical latitudes but generally poorly known. This is in part due the remoteness of many of these regions, and a lack of locally trained taxonomists. In such cases, the ethnoknowledge (i.e., information acquired from the sociocultural references of a given social group) of traditional human populations may be a valuable tool to elucidate gaps in the occurrence of some taxa. In this study, we used a combined approach of ethnoknowledge, classic taxonomy and molecular techniques to describe and diagnose an unsettled species of shallow-water octopus of the genus *Callistoctopus*. A neotype for the Brazilian eastern octopus *Callistoctopus furvus* (Gould, 1852) is described along with some ecological notes. Octopuses were collected between April and May 2018 during field trips guided by artisanal octopus fishers of Bahia State (Brazil). A linear discriminant analysis showed that the morphology of *C. furvus* overlapped poorly with *Callistoctopus* sp. from the Caribbean and Macaronesia (Madeira Archipelago) as well as with *Callistoctopus macropus stricto sensu* from Mediterranean Sea. Analysis of mitochondrial large ribosomal subunit (rrnL, also known as 16S) gene and cytochrome C oxidase I (COI) showed that *C. furvus* differs genetically from European *C. macropus* and the other species in the genus. In general, *C. furvus* differs from other Atlantic/Mediterranean *Callistoctopus* species in having a slender body shape and longer mantle lengths. As in other species of the genus, *C. furvus* is nocturnal and inhabits sandy bottoms, seagrass beds and/or low-profile reefs. Interestingly, *C. furvus* burrows itself into the sand as a defense mechanism. In conclusion, we showed the support of ethnoknowledge for integrative biodiversity assessments in poorly surveyed remote areas in the western tropical Atlantic.

Keywords: Octopoda, cryptic species, neotype, ethnoknowledge, western Atlantic Ocean, Brazil

INTRODUCTION

Modern taxonomy has benefited greatly from advances in molecular techniques and tools in the last few decades (Radulovici et al., 2010; White and Last, 2012). At the same time, traditional taxonomy–that based in meticulous and methodical descriptions of morphology, color patterns and other characters–have experienced an unjustified and unfair decline in prestige (Wheeler, 2004; Wheeler et al., 2004; Agnarsson and Kuntner, 2007; Chen et al., 2011). Traditionally less valued than these two taxonomic schools, is the use of traditional folk knowledge, or ethnoknowledge, which is a precious but underappreciated tool that can allow us to improve and complement our taxonomic knowledge, particularly in remote or isolated geographic areas (see Alves and Souto, 2015, for a comprehensive review).

Shallow-water marine invertebrate fauna is believed to be diverse in tropical latitudes, but this biodiversity remains generally poorly known (Briggs and Bowen, 2013). This is in part due the remoteness of many of these regions, and a generalized lack of locally trained taxonomists. As expected, knowledge on tropical shallow-water octopus fauna remains rudimentary (Voight, 1998; Leite et al., 2008; Lima et al., 2020), particularly in the southwestern Atlantic Ocean, including the South American mainland and oceanic islands (Voss and Toll, 1998). Among these poorly known octopuses, the genus *Callistoctopus* comprises a speciose monophyletic group supported by both morphological and genetic analyses (Norman and Hochberg, 2005; Kaneko et al., 2011). This genus likely includes many cryptic species and occurs in tropical and temperate waters of the Atlantic, Indian and Pacific Oceans (Norman, 2000; Norman et al., 2016). Typically, live *Callistoctopus* are brick red or bright red in color with white spots or blotches forming distinctive patterns on the body (Norman, 2000).

The white-spotted octopus *Callistoctopus macropus* (Risso, 1826) is cited to be present in the western Atlantic waters (including the Brazilian coast) and has long been considered an amphi-Atlantic species (Voight, 1998; Haimovici et al., 2009). However, this species is restricted to the Mediterranean Sea and northeastern Atlantic Ocean down to Senegal, and therefore considered an eastern Atlantic species (Norman et al., 2016). Brazilian occurrences were based on a lot deposited at the University of São Paulo Zoology Museum, comprising specimens collected in the shallow-waters off Bahia state (∼15°S) (Perez and Haimovici, 1991), plus data from a cephalopod biogeography study that was conducted in the late 1970s (Palacio, 1977). Two newer lots (one from the same region and another from Fernando de Noronha Island) were deposited at the University of Rio Grande Oceanographic Museum (Leite and Haimovici, 2006). Leite et al. (2008) urged a critical revision on the taxonomic status of "Brazilian" *C. macropus*, and recent genetic analysis suggest that the western Atlantic *Callistoctopus* is distinct form *C. macropus stricto sensu* (Ritschard et al., 2019; Lima et al., 2020).

The American malacologist August Addison Gould (1805–1866) established *Callistoctopus furvus* as a distinct species from *C. macropus* some 168 years ago. He acquired the specimen at a fish market in Rio de Janeiro (Brazil) and, according to his original description, "Its proportions are much like those of *Octopus macropus*, Risso, but is coloration is very different." Thus, the taxonomic validity of *C. furvus* remained disputed (*taxon inquirendum*) for a long time, and the species was treated as a junior synonym of *C. macropus* (WoRMS Editorial Board, 2020). To complicate things further, the holotype is missing, and the original description has been considered too ambiguous to allow for reliable taxonomic identification (Voss and Toll, 1998). During recent morphological and genetic studies on shallow-water octopuses off the Mexican and Colombian Caribbean coasts, samples representing this genus have been variably named as *C.* cf. *macropus* (Flores-Valle et al., 2018), *C. furvus* (Cedillo-Robles and Pliego-Cardenas, 2018), or as an undefined species of *Callistoctopus* requiring description (Ritschard et al., 2019).

Molecular techniques and tools have been widely applied to elucidate cephalopod systematics and biogeography, allowing for the identification of distinct genetic linages, full descriptions of new species and genera, and the revision and more accurate delimitation of distribution ranges (Cheng et al., 2014; Sales et al., 2014, 2019; Amor et al., 2016, 2017; González-Gómez et al., 2018). Such molecular studies have also been used to validate genetic linages, or to clarify the taxonomic status of unsettled species (Söller et al., 2000; Sales et al., 2013; Anderson and Marian, 2020; Costa et al., 2021). For instance, Anderson and Marian (2020) established the grass squid *Pickfordiateuthis pulchella* as a genetically valid species with affinities to the new world genera *Doryteuthis* and *Lolliguncula*, whereas the subsequent papers of Sales et al. (2014, 2017) revised the accepted distribution range of these two loliginids, showing the influence of past biogeographic barriers and events on the emergence of specific genetic linages. Costa et al. (2021) has proven the molecular validity of *Lolliguncula argus* Brackoniecki and Roper (1985), suggesting that the recent speciation between *L. argus* and *Lolliguncula diomedeae* is associated to oceanic environmental changes associated with past glaciation, deep sea cooling and tropical upwelling.

Considering (1) the increasing body of evidence on the validity of *C. furvus* as a species and, (2) the fact that the missing holotype was collected in Brazil, we used an integrated, multidisciplinary taxonomic approach (as recommended by Dayrat, 2005) to designate a neotype for the species. Our methods combine traditional taxonomy and molecular techniques with ethnoknowledge to provide a comprehensive description of *C. furvus*, an updated distribution range, and notes on its ecology, as a contribution to the difficult taxonomy of the *C. macropus*-group complex.

MATERIALS AND METHODS

Ethnoecological Survey

Based on earlier results (i.e., Martins et al., 2011; Jesus et al., 2015) that indicated the existence of an "unusual" shallow-water octopus off Bahia State, an ethnoknowledge-based survey was designed to establish a baseline on the occurrence of *Callistoctopus* in Brazilian waters. Data-collection took place from March 2018 to August 2019 at 17 locations on the Brazilian coast (**Figure 1**). To maximize the likelihood of finding specimens, surveyed locations encompassed localities nested within seven marine protected areas (MPAs) with different limits of use and protection, plus two non-protected locations (**Table 1**). Participants included octopus fishers, spearfishers and commercial SCUBA divers contacted via fishing associations, fishing colonies, and diving schools. Permission to conduct interviews was granted by the study participants and approved by the UESC Human Ethics committee (clearance number # 2.593.218).

Participants were personally interviewed either during fishing trips, or elsewhere (households, cooperatives, markets, restaurants, etc.) We used the direct observation technique with the fishers during fishing trips (Minayo, 2016) to investigate *Callistoctopus* occurrence, identification, and ecological characteristics. Some participants also voluntarily shared photos and video clips before, during and after interviews, and those visual records were used to substantiate the geographic distribution of *Callistoctopus* (Jesus et al., 2020).

A semi-structured questionnaire was used for interviews with the participants (**Supplementary File 1**). Questions sought to obtain information about *Callistoctopus* fishing and ecology. Fishing-related questions included information on fishing period (day/night), fishing duration (in hours), fishing frequency, type of gear used and tide level, plus data on consumption and marketing. The ecological component of the survey included questions on *Callistoctopus* frequency of occurrence, color pattern, behavior and the co-occurrence of other octopus species on the fishing grounds. SCUBA divers and spearfishers were also questioned about the most frequent depths of *Callistoctopus* sightings.

For practical purposes, we only use the name *C. furvus* for ethnoecological data gathered close to or on the neotype locality (see below). For results based on sights reported during interviews elsewhere, octopuses are referred to as *Callistoctopus*.

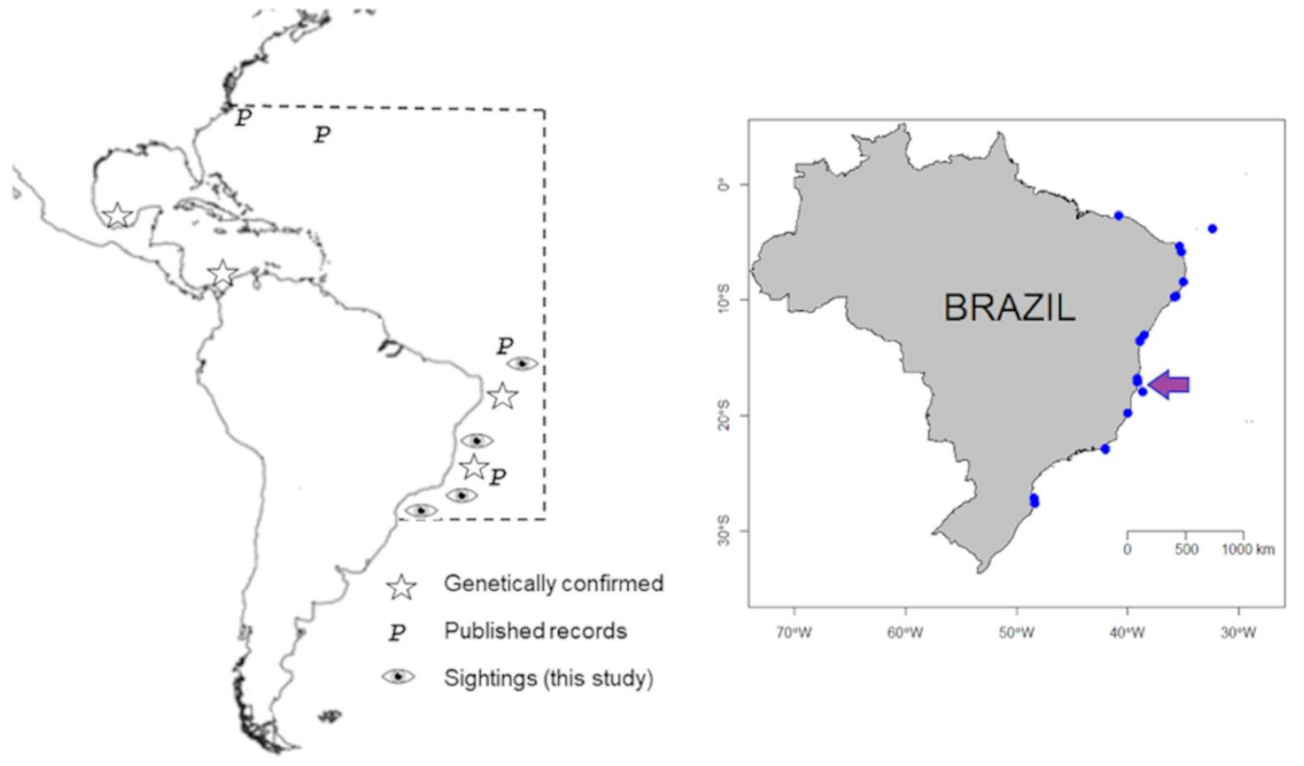

FIGURE 1 | *Callistoctopus furvus*. Left: putative occurrence area on the western Atlantic (boxed). Right: surveyed area, including neotype and voucher specimens site locations (arrowed). Blue dots refer to localities where personal interviews were conducted.

TABLE 1 | Summary of *Callistoctopus* ethnobiological survey areas, including protected and unprotected locations.

Location	Environmental management regime (SNUC/IUCN class)	Number of interviews	Was *Callistocopus* reported?	Vernacular name
Jericoacoara (2.7°S)	not protected	10	No	–
Fernando de Noronha (4°S)	MPA (National Marine Park/II)	15	Yes	–
Natal (5.8°S)	not protected	10	No	–
Costa dos Corais (8°S)	MPA (Environmental Protection Area/V)	16	Yes	–
Tinharé-Boipeba (13.5°S)	MPA (Environmental Protection Area/V)	30	Yes	Sand octopus
Corumbau (16.5°S)	MPA (Marine Extractive Reserve/VI)	36	Yes	Eastern octopus
Abrolhos Archipelago (18°S)	MPA (National Marine Park/II)	35	Yes	–
Arraial do Cabo (22°S)	MPA (Marine Extractive Reserve/VI)	20	Yes	Cheetah octopus
Reserva Marinha do Arvoredo (27.5°S)	MPA (Marine Biological Reserve/Ia)	15	Yes	–
Total		187		

MPA = Marine Protected Area; SNUC = Brazilian National Conservation Unit System; IUCN classes: Ia – Strict Nature Reserve, II – National Park, V – Protected Landscape/Seascape, VI – Protected area with sustainable use of natural resources. Locations are geographically listed from north to south.

Collection Sites, Sampling and Laboratory Procedures

Samples were acquired during guided fishing trips with artisanal fishers at Morro de São Paulo (13°24′24″S 38°54′09″W) (Bahia State, Brazil), carried out between 12 and 15 April 2018 (**Figure 1**). Octopuses were collected at night (07:00 to 11:00 PM) on the mosaic of sandy bottoms/seagrass beds among reef flats. Fishing was conducted by foot at low tide, and the octopuses were captured either by hand or hooks and stored in plastic buckets. Live animals were photographed and filmed *in situ* to record color and body patterns and the behavior. Samples were frozen on site and airfreighted several days later to the laboratory elsewhere for measurement and genetic analysis. Authorization to take samples was granted by the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) (SISBIO clearance number # 60468-2).

On arrival, samples were thawed at room temperature, and fresh octopuses were weighed to the nearest gram. Beaks and radula were extracted from the buccal mass and stored in a mixture of 70% ethanol and glycerin to prevent dehydration. Tissue samples were taken from the inner side of the mantle and stored in 5 ml Eppendorf flasks with absolute ethanol for genetic analyses (see below). Fresh octopuses were fixed in 10% buffered formalin solution for 72 h and then transferred to 70% ethanol. Each specimen was identified with a numbered plastic tag.

Morphometric measurements (millimeters), counts, illustrations and indices were obtained from the ethanol-preserved specimens following Roper and Voss (1983); Norman et al. (1997) and Huffard and Hochberg (2005). Sucker counts were totaled for each arm (Huffard and Hochberg, 2005). Abbreviations for depositories, measurements, counts and indices are given in **Table 2**. Maturity stage was assigned following the dissection of ventral mantle according to Norman (1993) three-point macroscopic scale: immature (sex indeterminate or reproductive organs minute), submature (reproductive organs distinct but poorly developed) and mature (distinct developed spermatophores or eggs).

Shape Variation Analysis

To test our hypothesis of a distinct species for Brazilian *Callistoctopus* on a morphological basis, we followed the methodology employed by Voight (1998) to analyze morphologic

TABLE 2 | Abbreviation for depositories, formulas, counts, indices and weight measurements used in the present study.

Depositories	
MZUSP	University of São Paulo Zoology Museum
NHMUK	Natural History Museum, London
Formulas	
AF (arm formula)	Arm numbers ordered from longest to shortest
WF (web formula)	Web sectors ordered from deepest to shallowest
Counts	
GC (gill count)	Number of gill lamellae per outer demibranch
SC (sucker count)	Number of suckers on normal arms
SCh (sucker count hectocotylized arm)	Number of suckers on hectocotylized arm of males
Indices	
MWI (mantle width index)	Mantle width ÷ ML
HWIw (head width index)	Head width ÷ mantle width
GLI (gill length index)	Gill length ÷ ML
FLI (funnel length index)	Funnel length ÷ ML
FFLI (free funnel length index)	Free funnel length ÷ funnel length
AMI (arm mantle index)	Arm length ÷ ML
AWI (arm width index)	Arm width ÷ ML
HAMI (hectocotylized arm mantle index)	Hectocotylized arm length ÷ ML
OAI (opposite arm index)	Hectocotylized arm length ÷ normal third arm length
LLI (ligula length index)	Ligula length ÷ hectocotylized arm length
CLI (calamus length index)	Calamus length ÷ ligula length
SDIn (sucker diameter index for normal suckers)*	Normal sucker diameter ÷ DML
WDI (web depth index)	Depth of deepest web ÷ length of longest arm
Weight	
TWw (total wet weight)	

**SDIn are reported for dorsal and ventral arms separately.*

variation in shallow-water octopuses. In short, we ran a Principal Component Analysis (PCA) using standard measurements made on the octopuses. According to the author, body size variability is captured by the first Principal Component (PC1), whereas the second (PC2) and third (PC3) Principal Components account for shape variability. Plots of specimen scores on PC2 and PC3 allowed visual comparison of shape differences.

Following the PCA analyses, we used a size-free Linear Discriminant Analysis (LDA) to maximally separate groups defined *a priori*. We removed the body size influence by using the residuals resulting from the regression between each morphological character measured against the PC1 loadings as input data. Groups were considered significantly different if they did not overlap on discriminant plots (Voight, 1998).

Morphological data of Atlantic/Mediterranean *Callistoctopus* groups included the neotype, voucher specimens and animals not selected for the taxonomic description (n = 13), octopuses from the Caribbean (Barbados, n = 1, and Haiti, n = 3), Mediterranean Sea (Italy, n = 2, France, n = 1, and "Mediterranean," n = 1), and Macaronesia (Madeira Archipelago, n = 8). Details on the specimens used are given in **Supplementary Table 1**. Since complete datasets for each standard measurement were not available for all individuals, we used only the total length (TL), dorsal mantle length (DML), mantle width (MW), and head width (HW) in this analysis. Data were normalized (zero mean and unit standard deviation) prior to analysis (Allcock et al., 2008).

Genetic Analysis

We used six tissue samples for genetic procedures. Samples were kept in a freezer at −4°C until the extraction of the DNA. The genomic DNA was extracted with a Wizard Genomic DNA Purification kit (Madison, WI, United States), using the mouse-tail protocol. The fragments of mitochondrial 16S rDNA and Cytochrome Oxidase I (COI) gene were amplified by PCR following Sales et al. (2013), including the same primers for the markers 16S (Palumbi et al., 1991) and COI (Folmer et al., 1994). To sequence the fragments, the PCRs were first purified using the ExoSAP-IT enzyme (Amersham Pharmacia Biotech Inc.), and the sequencing reactions were done with a BigDye Terminator kit (Applied Biosystems) before being processed on an ABI 3500 automatic sequencer (Applied Biosystems).

The sequences of the two markers analyzed here were aligned in Geneious 9.0 (Kearse et al., 2012), using the MUSCLE tool (Edgar, 2004) in default mode. The automatically aligned sequences were inspected visually to verify possible incongruities. We utilized three data sets for the present study: A-16S (544 pb), B-COI (588 bp) and C-16S + COI (1132 bp). Additional sequences of *Callistoctopus* species were obtained from GenBank. We used *Grimpella thaumastocheir* Robson (1928) as an outgroup for our analysis (**Supplementary Table 2**). Given that some sequences were just available for one of the markers, we completed all unknown sequences with N for the concatenate database.

The best evolutionary model for each data set was selected using ModelTest 2 (Darriba et al., 2012). We used the AIC criteria to determine the model for subsequent Maximum Likelihood (ML) analyses and BIC criteria for subsequent Bayesian Inference (BI) analyses. Phylogenetic trees (ML and BI) were obtained from PhyML 3.0 (Guidon et al., 2010) and Mr. Bayes v. 3.2 (Ronquist et al., 2012), respectively. For the ML tree, branch support values were obtained using 1000 bootstrap pseudo-replicates (Felsenstein, 1985). The BI trees were based on MCMC (Markov Chain Monte Carlo) sampling, with four simultaneous runs of 10 million generations, each consisting of four chains (one cold and three hot). Bayesian posterior probabilities were defined using a 60% consensus rule, random seeds, and sampling every 1000 generations, with 25% of the first trees sampled in each MCMC run discarded as burn-in. The log-likelihood files generated by each run were then visualized in Tracer v. 1.4 (Rambaut and Drummond, 2007) and only runs with ESS values equal to or higher than 200 for all marginal parameters.

RESULTS

Distribution and Notes on Ethnoecology

One hundred and eighty-seven interviews were carried out during this study, covering nearly 24° of latitude on the Brazilian coast. Most surveyed areas were located on the Brazilian northeastern and eastern coasts (2.7–19°S), and only two on the southeastern and south coasts (22–27°S) (**Table 1**). Among the surveyed areas, *Callistoctopus* was not reported/recognized in only two locations. The northernmost and easternmost record came from the Fernando de Noronha National Park (4°S; an oceanic island) and the southernmost was near Arvoredo Biological Reserve (27.5°S). Interestingly, the two localities where *Callistoctopus* was not recorded/recognized are located in the region where this octopus has been previously frequently reported (**Table 1**).

According to SCUBA divers and spearfishers, whenever spotted underwater, *Callistoctopus* is readily recognized as a slender, long armed red/orange octopus with distinctive white spots. Reported underwater observations of live specimens in the wild occurred mostly between 8 and 15 meters, but the deepest bathymetric limit for these octopuses remains unknown. Shore-based artisanal octopus fishers, on the other hand, could not answer questions regarding *Callistoctopus* bathymetric distribution, as they only interact with these octopuses on reef flats/seagrass beds/sandy bottoms during low tide.

Octopus fishers at Morro de São Paulo (13°S) report that at least four aspects can easily tell *C. furvus* apart from *Octopus insularis* (a sympatric species exploited in the same fishing grounds; Jesus et al., 2015). These include: (1) capture time (*C. furvus* nocturnal vs. *O. insularis* diurnal), (2) color pattern (brick red color body in *C. furvus*), (3) total body length and thickness of the arms (smaller and slender in *C. furvus*) and (4) escape strategy. As regarding the latter, fishers' accounts indicated that *C. furvus* buries itself in the sand to escape from predators, while *O. insularis* takes refuge in holes and crevices on the reef. Because of this observation, fishers name *C. furvus* as the "sand octopus" whereas *O. insularis* is called the "stone octopus."

Morro de São Paulo fishers capture *C. furvus* exclusively at night during low tides, describing that the species is more abundant during new moon nights. They capture octopuses that traverse shallow pools among reef flats, or areas of exposed reef, using an iron rod and a bucket, or sometimes without any fishing gear (i.e., by hand). *C. furvus* has no commercial value and, whenever caught, is either used as bait for subsistence fishing, or as food in the fisher's households. In contrast, fishers interviewed at Porto Seguro (16°S) had less information on the species, because they rarely catch *C. furvus*, as their fishing operations take place during the day, targeting the sympatric *O. insularis*.

Systematic Description

Family Octopodidae d'Orbigny, 1840
Subfamily Octopodinae d'Orbigny, 1840
Genus *Callistoctopus* Taki, 1964.
Synonym: "*macropus* species-group" *sensu* Norman (1993, 2000).

Callistoctopus furvus (Gould, 1852).

Common Names

Brazilian eastern octopus (English), Polvo-de-leste (Brazilian Portuguese).

Material Examined

All specimens from Morro de São Paulo (13°24′24″S 38°54′09″W, Bahia State, Brazil). Neotype, here designed, submature male (ML 97 mm), MZUSP 152154, April 2018, M.D. Jesus.

Other Material Examined

All samples collected with the neotype at the same location and date by M.D. Jesus. 1 submature male (ML 113 mm), MZUSP 152155; 1 submature male (ML 111 mm), NHMUK 20200275; 1 submature female (ML 135 mm), MZUSP 152156; 1 submature female (ML 110 mm), MZUSP 152157; 1 submature female (ML 98 mm), NHMUK 20200276; 1 submature female (ML 94 mm), NHMUK 20200277, 1 immature female (ML 85 mm), NHMUK 20200278 1 immature female (ML 80 mm), MZUSP 152158.

Amended Diagnosis

Taki (1964) established the genus *Callistoctopus* to accommodate two new species from Japanese waters. According to the author, *Callistoctopus* is very similar to *Octopus* Cuvier, 1797, but differs from the latter by including large and robust octopuses with reduced ink sacs and a characteristic color pattern. However, apart from the color, the remaining characters are not reliable for *Callistoctopus* species identification (Voss, 1981). The genus *Callistoctopus* includes medium to large benthic octopuses (mantle to 190 mm and total weight up to 4.2 kg). Mantle muscular, ovoid to elongate cylindrical in shape, lacking a skin ridge around the lateral margin. Arms muscular, long (5–8 × mantle length), bearing two rows of suckers with no augmented suckers in either sex. Dorsal arms longest. Hectocotylized arm (third right arm) in males is remarkably shorter than the opposite arm. A well-developed, deeply grooved cylindrical ligula present, along with a calamus. Interbrachial web shallow to moderate, with dorsal webs deepest. Multicuspid radula with nine elements, namely seven rows of teeth plus two marginal plates. Skin smooth or with scattered low papillae. Conspicuous primary papillae present over each eye. Live animals brick red to bright red in color, with white spots, blotches or bars forming distinctive patterns over the whole body surface. Large funnel organ W- or U-shaped. Ink sac and anal flaps present. Gills with 10–15 lamellae per outer demibranch. Octopuses of this genus are typically nocturnal, inhabiting reefs, seagrass beds and soft bottoms from the intertidal zone up to 200 m. Diet consists of crustaceans and shelled mollusks.

Description

The following description is based on three males (all submature) and six females (four submature and two immature). Counts, measurements and indexes for this material are given in **Tables 3**, **4**. Indices are included in the text as ranges in parentheses. Since we found no mature individuals, egg and spermatophore descriptions are not reported. Notwithstanding, dissection of ovaries of submature females yielded high numbers of tiny oocytes, implying that mature eggs would certainly be small.

Preserved animals pinkish gray in color on the dorsal side and creamy-colored on the ventral side, with a smooth skin texture. The typical white spots of live animals remain in preserved specimens as darkish spots. Body with a remarkably slender outline. Medium to large species (**Figure 2**). Submature males to at least 110 mm ML, submature females to at least 135 mm ML, TL up to 1335 mm and fresh weight up to 530 g. Saccular mantle with thin, muscular wall, widest medially (MWI 44.4–62.7), tapering to a blunt point in the posterior end. Lateral mantle skin ridge absent. Head typically narrower (HWI 34.6–72.5) than the mantle. Eyes not prominent. Stylets absent. Funnel tubular, moderately long (FLI 34.6–46.0), broad-based, with a large U-shaped funnel organ (**Figure 2**). Gills with 10 to 11 lamellae per demibranch.

Arms long, unequal in length, longest arms typically 4.6 to 9 times mantle length. Dorsal arms longest (typically AF 1 > 2 > 3 > 4). Arms narrow (AMI 11.7–20.4) tapering evenly along length. Normal arm tips very fine, long and delicate. Dorsal arms thicker than ventral arms. Two rows of suckers on each arm. Sucker counts, normal arms 138–380 per intact arm in immature and submature animals (males: 138–340; females: 228–380), 126–168 on hectocotylized arms of submature males. Suckers smaller (SDI 6.7–8.0) on ventral arms and larger on dorsal arms (SDI 8.1–11.2), none especially enlarged in either sex. Web very shallow (WI 2.5–6.6). Web formula variable, but dorsal webs (A and B) typically deepest, and web E generally the shallowest (33–64% as deep as the deepest web). Web may reach between 1/3 and 1/4 of arm length in live animals (**Figure 3**). Third right arm of males hectocotylized, relatively shorter than opposite arm (OAI 55.7–58.4). Ligula medium-sized (LLI 6.3–9.6), with a long calamus (CLI 29.6–49.4). Ligula blunt, roughly cylindrical and deeply grooved (**Figure 2**).

Beaks and radula are depicted in **Figure 4**. The narrow hooded upper beak has a distinct but rather short, slightly hooked pointed rostrum, and an obtuse jaw angle. Lower beak with a short and sharp rostrum, obtuse jaw angle, hood

TABLE 3 | *Callistoctopus furvus* measurements (mm), counts and indices for preserved males (neotype and voucher specimens).

Depository and Collection number	MZUSP 152154 Neotype	MZUSP 152155	NHMUK 20200275
Maturity	submature	submature	Submature
TWw (g)	212.4	522.4	313.9
ML	97	113	111
TL	665	783	795
MW	49	68	61
HW	26	23	45
FL	44	39	44
FFL	34	33	40
WD A	41	25	43
WD B	36	36	26
WD C	21	30	40
WD D	10	24	32
WD E	33	18	19
WF	A.B.E.C.D	B.C.A.D.E	A.C.D.B.E
AL 1	603	569	*
AL 2	618	691	724
AL 3	542	*	538
AL 4	433	569	437
Hc	302	610	314
AW	13	19	23
AF	2.1.3.4	–	–
SDn (ventral)	7	9	9
SDn (dorsal)	10	12	11
SC 1	256	278	–
SC 2	138	280	324
SC 3	318	–	340
SC 4	212	234	300
Hc	168	153	126
G (count)	10	10	11
GL	35	42	44
LL	9.3	8.1	8.7
CL	3.1	2.4	4.3
MWI	51.1	59.8	55.6
HWIw	51.9	34.6	72.5
GLI	36.5	36.7	40.0
FLI	46.0	34.6	36.2
FFLI	76.0	83.3	81.7
AMI 1	622	504	8
AMI 2	637	612	655
AMI 3	559	–	487
AMI 4	446	472	395
HAMI	311	540	283
OAI	55.7	–	58.4
AWI	13.8	16.9	20.4
WDI	6.6	5.2	6.0
SDIn (ventral)	6.9	7.9	8.0
SDIn (dorsal)	10.3	10.6	9.9
LLI	9.6	1.3	7.8
CLI	33.4	29.6	49.4

**Damaged.*

narrow, wings broadly spread with flaring lateral walls, split in the posterior half. Radula with seven teeth in each transverse row. Rhachidian teeth long, broad-based with three cusps on each side, basal cusps largest, decreasing in size distally. First lateral tooth short, cusp absent. Second lateral larger than first, broad-based and triangular, with concave margins and a single cusp point toward the midline. First marginal teeth curved, scythe-like, nearly as long as second laterals, with tooth directed toward midline. Marginal plates flat, almost rectangular and slightly curved.

Color, Skin Sculpture and Body Patterns of Live Animals

These octopuses are typically brick red in color, with numerous white spots forming distinct patterns on dorsal mantle, head, and arms, most often associated to a smooth skin texture over the whole body (**Figures 3A,B**). A slightly similar color pattern, but with numerous small white dots scattered on the whole body, but denser on the arm's bases and extended webs, was associated to a rugose skin texture (**Figure 3C**) and sometimes to knobbed white spots on the mantle (**Figure 3D**). A distinctive pattern included green-grayish color over the mantle concealing its white spots, plus dark brick red arms with evident white spots and a dense white dotted network. This color pattern was associated with a strikingly rugose texture over the whole body and distinct rounded and flat skin papillae on the mantle (**Figure 3E**). On several specimens, the white spots on the mantle were barely noticeable, and they were almost uniformly red in color across the whole body, except for rows of knobbed white spots on the arms. In these situations, the body skin texture is rugose, and raised flattish papillae are present on the upper half of the arms (**Figure 3F**). Another color pattern worthy of note was a gray coloration over a flattened body shape that allowed the animal to blend with the substrate (see **Supplementary Movie 1**).

Morphological Comparison Between Atlantic and Mediterranean *Callistoctopus* spp.

Principal Component Analysis results showed that the three axes explained over 99% of the total morphological variance. The size-related first principal axis had equal contributions of ML and MW component loadings, accounted for nearly 92.49% of the total variance. Shape variation, as explained by the second and third axes, had the HW (5.37%) and MW (1.62%) as the most important loadings for the explained variance (**Table 3**). *Callistoctopus* of all geographic origins overlapped in shape, but it is worthwhile to note that Brazilian representatives tended to show narrower heads and mantles, and Mediterranean animals had the broadest heads among all samples analyzed. Interestingly, Caribbean and Macaronesian *Callistoctopus* overlapped strongly in terms of shape (**Figure 5A**).

Size-free LDA results reflected the PCA outputs showed some degree of overlap, although the centroid for most groups were clearly well separated. Brazilian *Callistoctopus* had the longest ML and shortest TL, and the narrowest HW and MW, overlapping poorly with Mediterranean specimens, and completely separated from Caribbean and Macaronesian animals. Again, these two latter groups had the highest degree of overlap, clearly split from Mediterranean and Brazilian specimens. Mediterranean octopuses were considerably shorter in ML than

TABLE 4 | *Callistoctopus furvus* measurements (mm), counts and indices for preserved females (voucher specimens).

Depository and Collection Number	**MZUSP 152156**	**MZUSP 152157**	**NHMUK 20200276**	**NHMUK 20200277**	**NHMUK 20200278**	**MZUSP 152158**
Maturity	submature	submature	submature	submature	immature	immature
TWw (g)	465.4	178.6	212.4	193.8	78.9	76.6
ML	135	110	98	94	85	80
TL	1335	629	574	665	494	540
MW	60	69	53	44	38	36
HW	30	24	30	20	29	19
FL	48	41	34	36	35	nm
FFL	37	35	25	24	29	nm
WD A	22	39	25	34	30	22
WD B	28	34	36	27	26	20
WD C	31	21	20	17	15	14
WD D	24	30	18	18	19	18
WD E	19	20	12	13	17	14
WF	C.B.D.A.E	B.A.D.C.E	B.A.C.D.E	A.B.D.C.E	A.B.D.E.C	A.B.D.C = E
AL 1	1220	587	470	612	414	469
AL 2	536	566	574	484	375	413
AL 3	485	566	448	340	371	368
AL 4	524	433	348	440	255	297
AW	21	20	16	11	16	9
AF	1.2.4.3	1.2 = 3.4	2.1.3.4	1.2.4.3	1.2.3.4	1.2.3.4
SDn (ventral)	9	9	7	8	6	4
SDn (dorsal)	11	12	11	nm	9	nm
SC 1	240	228	314	304	242	258
SC 2	264	293	326	380	244	284
SC 3	282	302	268	240	286	306
SC 4	260	253	296	342	176	206
G (count)	10	10	11	10	10	10
GL	43	39	28	38	33	27
MWI	44.4	62.7	54.1	46.8	44.7	45.0
HWIw	50.0	34.8	56.6	45.5	76.3	52.8
GLI	31.9	35.5	28.6	40.4	38.8	33.8
FLI	35.6	37.3	34.7	38.3	41.2	49.8
FFLI	77.1	85.4	73.5	66.7	82.9	59.3
AMI 1	904	534	480	651	487	323
AMI 2	397	515	586	515	441	355
AMI 3	359	515	457	362	436	383
AMI 4	388	394	355	468	300	258
AWI	15.6	18.2	16.3	11.7	18.8	11.3
WDI	2.5	6.6	6.3	5.6	7.2	4.7
SDIn (ventral)	6.7	8.2	7.1	8.5	7.1	5.0
SDIn (dorsal)	8.1	10.9	11.2	–	10.6	–

nm = not measured.

their counterparts elsewhere, and had the largest dimensions for all the remaining measures taken in our analysis (**Figure 5B**).

Callistoctopus furvus vs. *C. macropus stricto sensu*

Historically, *C. furvus* has been misidentified as *C. macropus* (i.e., Voss and Toll, 1998). Thus, it was most instructive to compare basic indexes of male and female octopuses of both species (**Table 5**). Of note, it is clear that *C. furvus* mantle and head are narrower and the funnel is shorter than those of *C. macropus*. It is also remarkable that *C. macropus* suckers are proportionally larger, and the dimensions of suckers on dorsal and ventral arms are not as marked as in *C. furvus* (in fact, those differences in sucker dimensions were even not noted on arms of *C. macropus* females). Unfortunately, we had just one *C. macropus* male for comparison. Nonetheless, we found that the hectocotylus length was about half of the length of the opposite arm in *C. macropus*, but slightly longer in *C. furvus* material. In contrast, the ligula and calamus indexes were considerably larger in *C. macropus*.

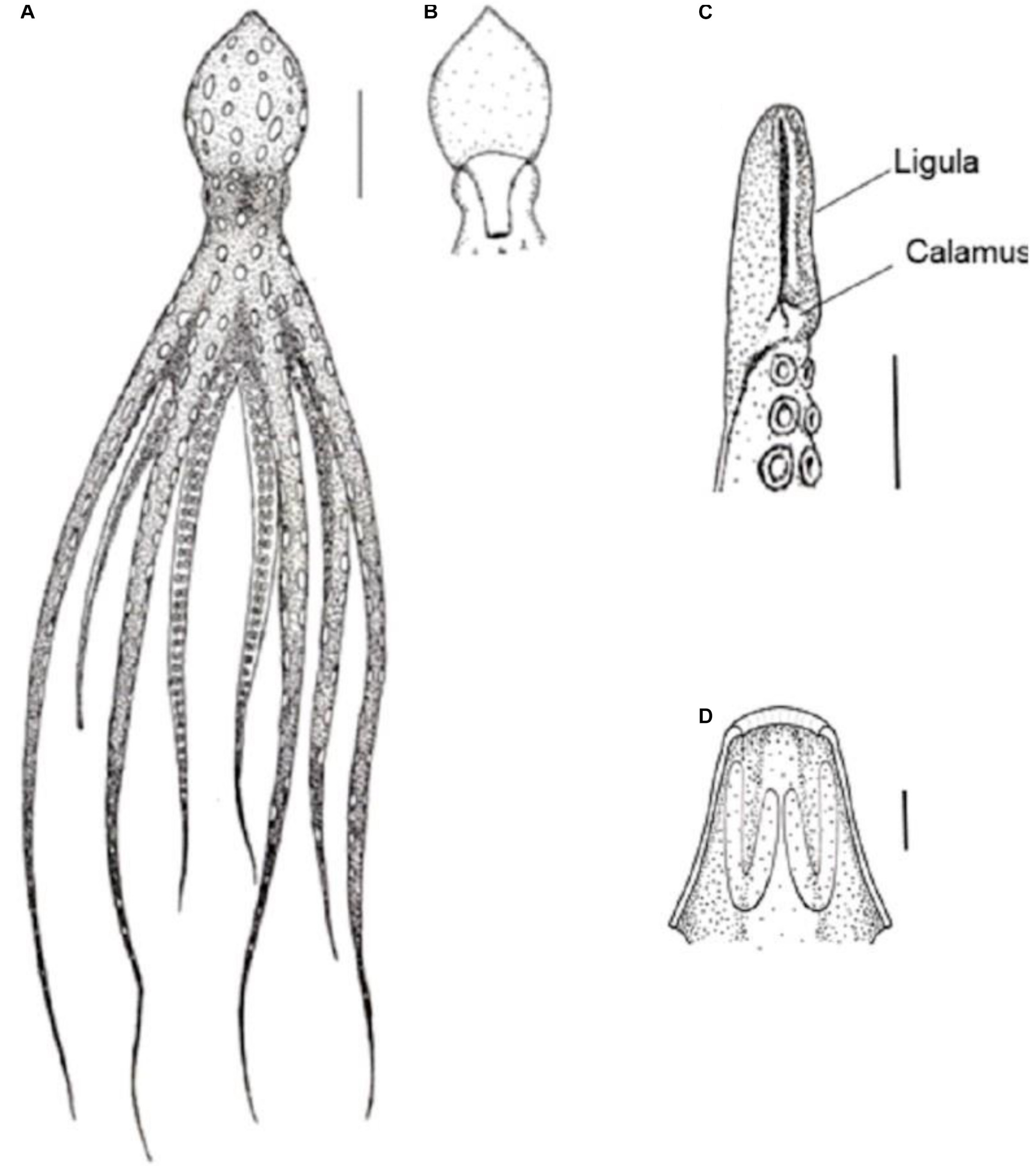

FIGURE 2 | *Callistoctopus furvus*. **(A–C)** Neotype (95 mm ML MZUSP 152154); **(D)** Voucher specimen (85 mm ML NHMUK 20200278). **(A)** Dorsal view. **(B)** Ventral view (mantle). **(C)** Copulatory organ (ligula and calamus) on tip of right third arm. **(D)** Funnel organ on dorsal surface of funnel. Scale bars: **(A,B)** = 50 mm, **(C)** = 5 mm, **(D)** = 10 mm.

Finally, it is also worth noting that, despite similar coloration in live animals (brick red) and smooth skin texture in both species, the single, large supraocular papilla often reported in *C. macropus* was not present in *C. furvus*.

Callistoctopus furvus Neotype/Voucher Specimens vs. Gould (1852) Original Description

Other authors have reported that Gould's original description of *C. furvus* was not sufficiently detailed to allow for a clear separation from the morphologically similar *C. macropus* (e.g., Voss and Toll, 1998). A general comparison between our and Gould's original description is given in **Table 6**. Overall, the slender, elongated body shape, smooth skin, relatively long funnel, narrow head, long arms and short webs reported in Gould's description conform to the general morphology in our neotype and voucher specimens. However, we also found two noticeable differences, namely: (i) the absence of three distinct cirri on each eye as reported by Gould (not present in our samples; either in preserved or fresh specimens; in fact, it was not discernible even in live

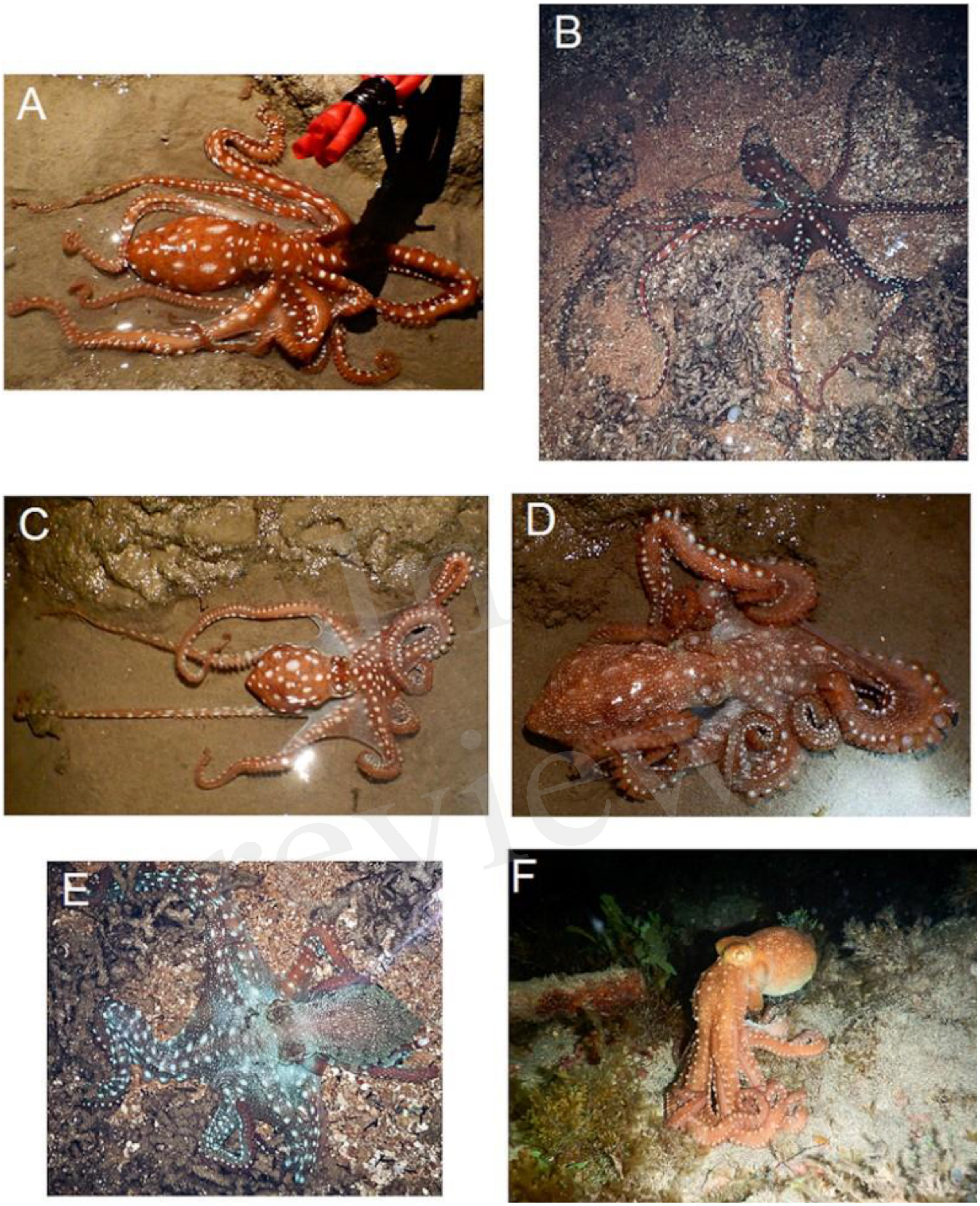

FIGURE 3 | *Callistoctopus furvus*. Examples of color patterns of living specimens recorded (except F) at Morro de São Paulo (Bahia State). **(A,B)** Typically brick red color with white spots associated to smooth skin. **(C)** Red brick color associated to smooth skin with numerous minuscule white spots dotting the superior half of arms and the expanded web. **(D)** Brick red pattern dotted with numerous minuscule with spots associated to a knobbed texture of the larger white spots. **(E)** Green-grayish associated with a rugose texture over the whole body and maximally extended rounded and flat dorsal mantle papillae. **(F)** Uniformly red color associated to distinguishable rows of knobbed white spots on the arms (Abrolhos, Bahia State).

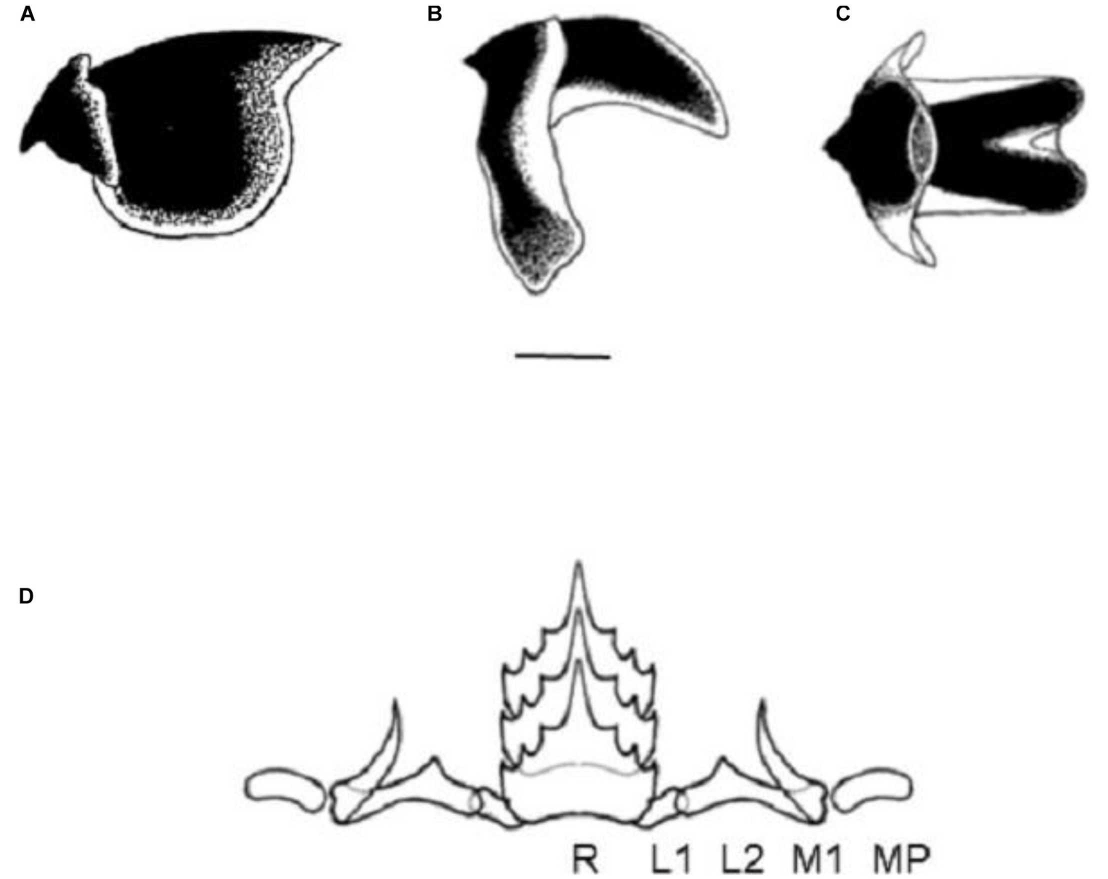

FIGURE 4 | *Callistoctopus furvus*. **(A–D)** Neotype (95 mm ML MZUSP 152154). **(A)** Upper beak, lateral view of. **(B)** Lower beak, lateral. **(C)** Lower beak, tripod orientation. **(D)** Radula. Abbreviations: L1, first lateral tooth; L2, second lateral tooth; M1, first marginal tooth; MP, marginal plate; R, Rachidian tooth. Scale bars **(A–C)**: 5 mm.

animals; see **Figure 3**) and (ii) differing colorations (varying from dark to ash to ash-mottled in Gould's description) (**Table 7**).

Molecular Results

The ML and BI evolutionary models for the concatenated database recovered extremely similar topologies, with strong statistical support. Thus, for the sake of simplicity, we only present the BI topology (**Figure 6**). The *Callistoctopus* lineage present in the western Atlantic Ocean (Brazil, Colombia and Mexico) comprises a genetically well-supported clade (ML = 93%, BI = 1). This indicates that *C. furvus* is evolutionarily distinct from *C. macropus*, with the two linages clustered as sister species.

Callistoctopus ornatus was recovered as the closest species to *C. furvus* and *C. macropus* clade (ML = 100%, BI = 1). The two *Callistoctopus minor* linages recovered were closely related to *Callistoctopus aspilosomatis* (ML = 89%, BI = 0.92). The position of *Callistoctopus luteus* could not be defined within our phylogeny, probably due to the absence of other species of the genus in our database. Nonetheless, this species was found to be phylogenetically valid and monophyletic (ML = 100%, BI = 1) (**Figure 6**).

DISCUSSION

Overview

To the best of our knowledge, this is the first octopus neotype described with the aid of fishers' traditional knowledge. Previous ethnoecological surveys indicated that artisanal octopus fishers exploited an "unusual" shallow-water octopus species (e.g., Martins et al., 2011; Jesus et al., 2015), and served as a baseline for our taxonomic study. Thus, our collaborative approach highlights the importance and usefulness of coupling ethnoknowledge with traditional and molecular taxonomy for producing and refining biodiversity assessments. Neotype designation is often necessary and desirable, particularly in octopuses with missing type specimens belonging to widespread and "catchall" species names such as "*vulgaris*," "*macropus*," and "*defilippi*," for which superficial morphological similarities often lead to misidentification (Norman and Hochberg, 2005; Gleadall, 2016).

The taxonomic status of the western Atlantic *Callistoctopus* has long been problematic and, along with *C. furvus*, at least two other described species [i.e., *Callistoctopus bermudensis* (Hoyle, 1885) and *Callistoctopus chromatus* (Heilprin, 1888)]

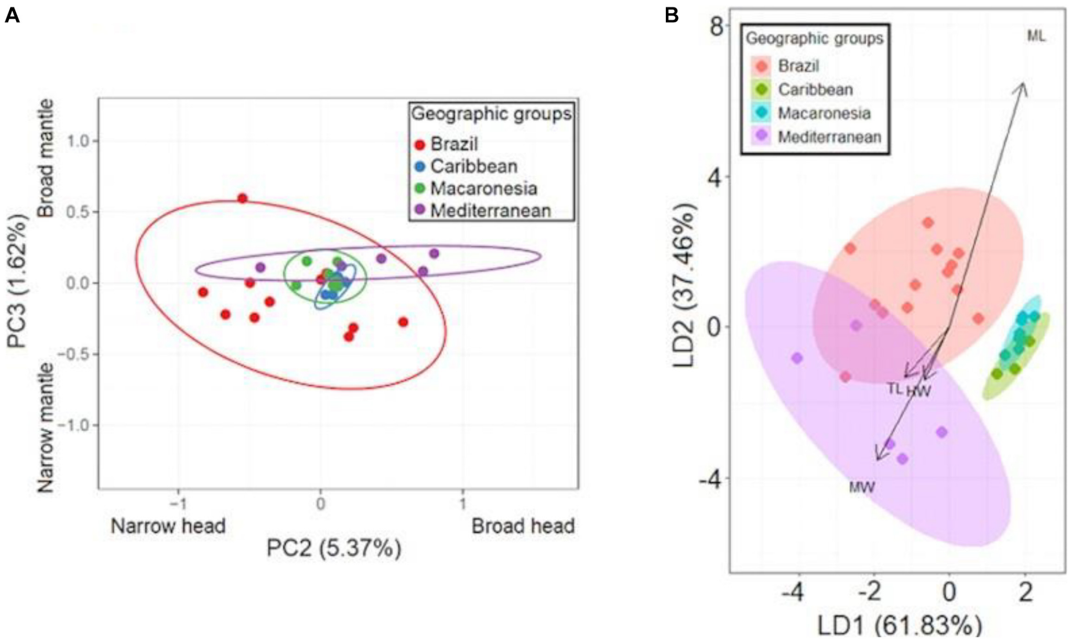

FIGURE 5 | Morphological variation between regional populations of *Callistoctopus*, including *C. furvus* and *C. macropus*. **(A)** Plot of individual scores of PC2 vs. PC3 depicting shape variation among geographic samples. **(B)** Size-free LDA plot depicting the degree of morphological separation among geographic samples. Prediction ellipses in both plots are such that with probability 0.95, a new observation from the same group will fall inside the ellipse.

were initially recognized in the region but later synonymized within *C. macropus* (Voss and Toll, 1998). However, earlier authors did not have access to modern multivariate statistics and molecular tools that allowed us to recognize *C. furvus* as a valid species distinct from *C. macropus*, a conclusion also supported by genetic studies of tropical western Atlantic shallow-water octopus fauna recently conducted by Ritschard et al. (2019) and Lima et al. (2020).

Ethnoknowledge and *Callistoctopus furvus*

Systematic classification was one of the main goals of scientists in the 19th century, and at that time, taxonomists relied heavily on morphological/morphometric data along with other characters (color, behavior, etc.) to describe and classify species (Mayr, 1971). Like trained "classical" taxonomists, traditional fishers systematically record morphological, chromatic and behavioral characters and habitats to recognize their target species (Begossi and Figueiredo, 1995; Johannes et al., 2000; Carvalho et al., 2009), and octopuses are no exception. In our study, it was shown that artisanal octopus fishers, spearfishers and SCUBA divers alike use accumulated sets of perceived characteristics to identify and name sympatric octopuses.

TABLE 5 | Character loadings on the principal components analysis applied for morphological variation of *Callistoctopus* spp. in Brazil, the Caribbean, Macaronesia and Mediterranean Sea.

Character	PC1	PC2	PC3
ML	−0.51	0.25	−0.13
TL	−0.50	0.54	0.56
MW	−0.51	−0.02	−0.74
HW	−0.48	−0.80	0.35
Variance explained	92.49%	5.37%	1.62%

In the region of Porto Seguro (16°S, Bahia State), where the ethnoecological aspects of *C. furvus* were firstly addressed (e.g., Martins et al., 2011; Jesus et al., 2015), octopus fishers associate the occurrence of the species to strong and persistent easterly winds, using the name "eastern octopus" to identify the species. The species is deemed rare amongst local fishers. However, this is most likely because fishers work during daylight hours, and the species is nocturnal. Thus, the infrequent encounters with *C. furvus*–often in early mornings–may represent the last individuals foraging at low tide before seeking daylight refuge in the reef (Jesus et al., 2015).

According to Marques (1991), the identification process takes place through an information set, where specific morphological characteristics are added up to more general characters, as the shape and/or coloration of the animal, through analogies with other animals. In the region of Cabo Frio (22°S, Rio de Janeiro State), *Callistoctopus* is called the "cheetah octopus" by SCUBA divers, based on similarity to the color pattern of the white-spotted "cheetah stingray" (*Aetobatus narinari*). Interestingly, *Callistoctopus* had no vernacular names in six out of nine of our surveyed locations.

At Morro de São Paulo (13°S, Bahia State), fishers' adopted ecological criteria refer mainly to the usual habitat or substrate to name two exploited sympatric octopus species. "Sand octopus"

TABLE 6 | Comparison of basic measurement indices for male and female *Callistoctopus furvus* and Mediterranean *C. macropus stricto sensu* (male: 62 mm ML, Villefranche-sur-Mer, France, NHMUK 1952.4.1.43; females: 30 mm ML, Naples, Italy, NHMUK Reg TBC; 47 mm ML, Zoological Station Naples, Italy, NHMUK 1898.5.21.344; and 153 mm ML, "Mediterranean," NHMUK 1908.12.22.20).

Index	Males		Females	
	***C. furvus* (*n* = 3)**	***C. macropus* (*n* = 1)**	***C. furvus* (*n* = 6)**	***C. macropus* (*n* = 3)**
ML range	97–113	62	80–135	31–153
MWI	56 ± 4.4	71	50 ± 7.4	77 ± 16.4
HWIw	53 ± 19.0	73	53 ± 13.8	62 ± 2.4
AMI 1	563 ± 83.4	D	563 ± 197.6	545 ± 152.2
AMI 2	635 ± 21.6	567	468 ± 85.9	584 ± 329.7
AMI 3	523 ± 50.9	607	419 ± 61.8	531 ± 269.4
AMI 4	438 ± 39.2	*	361 ± 74.3	507 ± 233.8
HAMI	297 ± 19.8	298	–	–
OAI	57 ± 1.9	53	–	–
WDI max	6 ± 1.0	9	5 ± 1.7	4 ± 0.5
WDI min	2 ± 1.0	8	3 ± 0.8	3 ± 0.2
FLI	39 ± 6.2	42	39 ± 5.5	46 ± 10.6
LLI	8 ± 1.7	15	–	–
CLI	37 ± 10.5	15	–	–
GLI	38 ± 2.0	31	35 ± 4.4	43 ± 13.6
G (count) range	10–11	10–11	10–11	9–11
SDIn (ventral)	8 ± 0.6	10.3	7 ± 1.2	10 ± 2.1[†]
SDIn (dorsal)	11 ± 1.0	11.9	10 ± 1.4	
SC (N)	138–340	251–269	228–380	97–308
SC (hectocotylus)	126–168	119	–	–

[†] *Ventral and dorsal sucker diameter was not remarkably different in C. macropus females.*

**Damaged arm.*

TABLE 7 | Comparison of some selected characters between *Callistoctoctopus furvus* new (present study) and original (Gould, 1852) description.

Character	Neotype and voucher specimens	Gould's original description (1852, "*Octopus furvus*," p. 476)
Overall body shape	Slender, elongated	"Body elongated (...)"
Mantle	Elongated and saccular	"(. . .) pyriform (. . .)"
Skin texture	Smooth in preserved specimens, may be transiently wrinkled and sculptured in live animals, which may also show completely smooth skin	(.) smooth or faintly wrinkled (...)
Head	Narrower than mantle	"Head long (. . .)"
Eyes	Not prominent	"Eyes not prominent (. . .)"
Funnel	Broad based, relatively long, almost reaching to the base of the arms	"Tube broad at base (...) slender and cylindrical, truncate at tip, reaching to the origin of the arms"
Arm length	Long, slender and unequal	"Arms very long and slender, and nearly equal in length"
Web depth	Short in preserved animals, extending between 1/3 and 1/4 of arm length in live animals	"The umbrella is small (. . .) not extending far along the sides of the arms"
Supraocular cirri	None	"(. . .) three cirrhi (...)"
Color	Live specimens: color variable, but most commonly brick red with withe spots on the dorsal side of mantle, head and arms. Preserved specimens: dorsal surface pinkish gray with darkish spots replacing the white spots of the live animal	"The ground color is ochreous, but constantly varies, sometimes (...) nearly black, or mottled with ash-color, or entirely ash-colored (...). The under side is paler, and shaded with orange-colored dots"

(*C. furvus*) and "stone octopus" (*O. insularis*) are the names that indicate the usual habitat of each octopus species. Behavioral perceived characteristics were another set of information used for systematization. Fishers correctly recognize the stone octopus as a diurnal species, and the sand octopus as nocturnal (Jesus et al., 2015). They also had a clear perception that frightened stone octopuses seek refuge in existing holes and crevices on the reef environment where it is commonly found (Batista and Leite, 2016), whereas sand octopuses burrows themselves into the sand as an escape response from predators or immediate danger.

Burrowing behavior (i.e., active movement through soft substrates; Dorgan, 2015) is found in very few cephalopod species (Hanlon and Messenger, 2018) and, as far as we known, it has never been described for any *Callistoctopus* species. In addition, it seems that it is only the third instance in which burrowing behavior is reported for western Atlantic shallow-water octopuses (this was firstly reported in southern Caribbean for *Amphioctopus burryi* and *Macrotritopus beatrixi*; see Guerrero-Kommritz and Rodriguez-Bermudez, 2019). Whether *C. furvus* burrows itself by displacing sediments using sweeping movements of the arms and suckers, or by sediment-fluidization akin to quicksand formation (the two recognized burrowing mechanisms in octopuses; Montana et al., 2015), is currently unknown.

Thus, fishers at Morro de São Paulo correctly identified habitat use and behaviors that allow direct competition avoidance and therefore the coexistence of these two sympatric octopuses in the same environment. This method of distinction is clearly as valid, reliable and accurate as scientifically based surveys. For instance, Bennice et al. (2019), using *in situ* observations, marking locations of octopus-occupied dens, and photoquadrats, observed that the use of different types of substrate allow fine-scale habitat partitioning between *Macrotritopus defilippi* (associated to sandy bottoms) and *Octopus vulgaris* (now *Octopus americanus*; Avendaño et al., 2020) (associated to hard substrate) in a shallow-water lagoon on the Florida coast.

Distribution and Taxonomic Remarks

Our data points to a wide latitudinal range for the genus *Callistoctopus* along the Brazilian coast, with records spanning from Fernando de Noronha National Park (4°S) to the Arvoredo Biological Reserve (27.5°S). Thus, in accordance with previous studies (i.e., Haimovici and Perez, 1991; Leite and Haimovici, 2006; Haimovici et al., 2009; Martins et al., 2011; Jesus et al., 2015, 2020) our data indicate that these octopuses occur on both nearshore and oceanic island waters off Brazil. Despite the lack of morphological and genetic confirmation for most of our

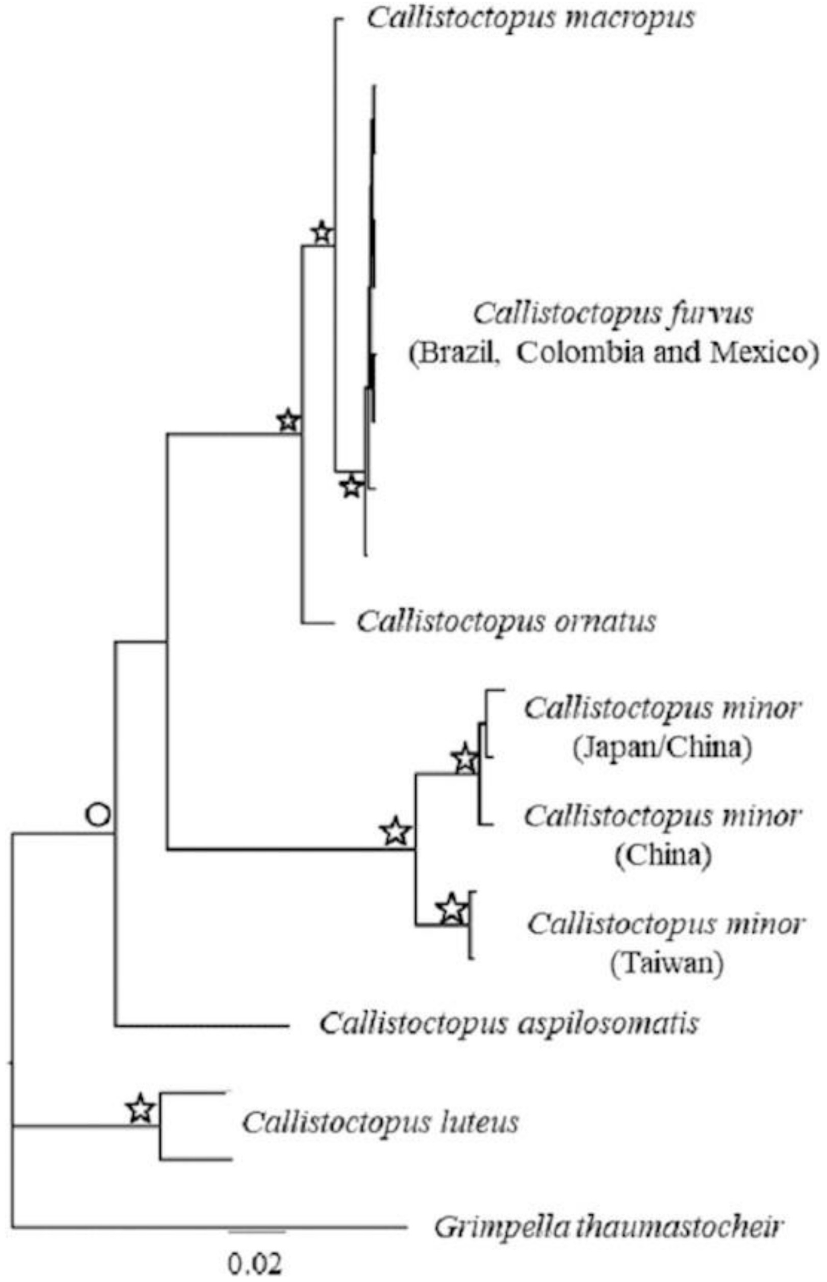

FIGURE 6 | Bayesian consensus phylogenetic tree of *Callistoctopus* species based on two molecular markers (16S + COI). Star denotes support values between 95% (0.95) and 100 (1) for Maximum Likelihood (ML) and Bayesian Inference (BI), respectively. Circles, denotes support values between 85% ML (0.85 BI) and 90% ML (0.9 BI).

records (largely based on interviews and photographic records) in the surveyed area, the high dispersal potential of small-egged *C. furvus* (see below) suggests that most–if not all–recorded octopuses may belong to the same species.

On the continental scale, combining genetic studies in southern Caribbean (Ritschard et al., 2019) and northeastern Brazil (Lima et al., 2020 and our results), plus published occurrences in the western Atlantic (Hanlon, 1988; Voss and Toll, 1998; Cedillo-Robles and Pliego-Cardenas, 2018; Flores-Valle et al., 2018) results in a broad, cross-hemisphere distribution range for the species on the western Atlantic Ocean, including the Caribbean Sea (∼19°N–28°S). However, Schwartz (1992) reported the occurrence of "*Octopus macropus*" off North Carolina (34°N; United States), implying that *C. furvus* northernmost range limit may extend farther north than the Gulf of Mexico (**Figure 1**).

The precise bathymetric horizon for *C. furvus* off the Brazilian coast is poorly established. Accounts of *Callistoctopus* reported by SCUBA divers and spearfishers alike are relatively rare along the entire studied area, which may be due to the shallow-water and nocturnal habits of these octopuses (Norman, 2000), as both recreational and professional/fishing dives are often conducted during daylight hours in deeper (>10 m) waters. The same is true for northwestern Atlantic records, as published accounts invariably describe *C. furvus* as a shallow-water species (e.g., Ritschard et al., 2019).

Callistoctopus-like octopuses are most commonly recognized by traditional fishers in northeast and eastern Brazilian shores, and apparently less further south on the Brazilian coast. This may partially be explained by the presence of easily accessible intertidal reef flats at these latitudes, the typical *Callistoctopus* habitat (Norman, 2000), where traditional fishers often exploit shellfish at low tide using a number of fishing techniques (e.g., Hauzer et al., 2013; Pratchett et al., 2020). On the other hand, similar shallow-water environments are virtually absent on the southeastern Brazilian coast, which may partially account for the lower awareness of this species by local fishers in this region. In fact, southern *Callistoctopus* records were reported exclusively by SCUBA divers (Jesus et al., 2020).

The present study is the first to direct molecular research specifically to the genus *Callistoctopus* in the western Atlantic. Thus far, the taxonomic status of *Callistoctopus* in this region remained dubious, as previous reviews based purely on morphology indicated the presence of *C. macropus* on both sides of the Atlantic (Voight, 1998; Voss and Toll, 1998; Leite and Haimovici, 2006; Haimovici et al., 2009). However, Gould (1852) stressed that the southwestern Atlantic *Callistoctopus* differed from eastern Atlantic/Mediterranean *C. macropus* in color and arm formula. Our results not only support this morphological differentiation, but also validate *C. furvus* as the genetic lineage of the genus in the western Atlantic Ocean.

The genetic homogeneity between specimens from Brazil and the Caribbean/Gulf of Mexico can possibly be explained by the high dispersal potential of *C. furvus* as the species is small-egged, and their paralarvae may be transported over long distances by the action of ocean currents (Villanueva et al., 2016). It has long been thought that the presence of the low salinity Amazon–Orinoco plume (AOP) in the North Brazil Shelf may act as a barrier to larval dispersal and population connectivity between the Caribbean and Brazilian biogeographic provinces (Muller-Karger et al., 1988; Floeter et al., 2008). However, recent studies indicated that the AOP does not represent a barrier for both squid and octopus species (Lima et al., 2017; Sales et al., 2017; Flores-Valle et al., 2018; González-Gómez et al., 2018; Pratt et al., 2020). The same is also true for some fish, crustaceans and fire coral species (Luiz et al., 2012; Laurenzano et al., 2013; Souza et al., 2017; Buranelli et al., 2019).

Shape Variation in Atlantic and Mediterranean *Callistoctopus*

Allcock et al. (2008) criticized the use of multivariate analysis of morphological datasets in coleoid cephalopods as, according to their results, this methodology does not provide good enough discrimination at species level. Notwithstanding, these authors suggest that multivariate analysis may be useful at the generic level. At least in our case, multivariate analysis yielded excellent shape discrimination among *Callistoctopus* sampled at several locations in the Atlantic Ocean and Mediterranean Sea. Similar results using multivariate analysis allowed for the identification of subtle morphological differences between *O. insularis* sampled off Vera Cruz (19°N, Mexico) and Brazil, despite the lack of genetic differences (i.e., González-Gómez et al., 2018).

The poor morphological overlap among different geographic samples found in our discriminant analysis reinforces the distinction of *Callistoctopus*-like octopuses between the eastern and western Atlantic. Brazilian *C. furvus* differs morphologically from Mediterranean Sea *C. macropus* by the overall slender shape (i.e., relatively narrower head and MWs), shorter TLs, and longer mantle lengths. Since Mexican and southern Caribbean specimens (sequences produced by Flores-Valle et al., 2018; Ritschard et al., 2019) were identified as *C. furvus* belonging to the same linage as the Brazilian octopuses, the shape separation may be due to phenotypic variability, as also seen in the case of subtle morphological differences between Mexican and Brazilian *O. insularis* (González-Gómez et al., 2018).

The morphological overlap between Caribbean and Macaronesian *Callistoctopus* warrants further investigation, since these octopuses inhabit very distinct oceanographic environments (i.e., the tropical waters of the Caribbean and warm temperate waters of Macaronesia). Although reliable lineage assignments require (currently lacking) genetic studies, we hypothesize that Macaronesian *Callistoctopus* may potentially belong to the western Atlantic clade. While the pelagic larval duration in *C. furvus* is still unknown, the eastward, fast-flowing Gulf Stream (average core velocity of $\sim 1\ \mathrm{m\ s^{-1}}$; Rossby et al., 2014) and its associated filaments and meanders (Caldeira and Reis, 2017) may maintain larval connectivity between the Caribbean and Macaronesian Islands. A similar mechanism (i.e., long-distance transport by fast-flowing ocean currents) seems to connect *O. insularis* between the Brazilian mainland and the mid-Atlantic islands of Ascension and St Helena (Amor et al., 2017).

Phylogenetic Relationships

Our results suggest a close phylogenetic affinity among *C. furvus*, *C. macropus*, and *C. ornatus*, where each of those constitutes well-supported phylogenetic lineages. In addition, the three species share behavioral and morphological similarities (Lima et al., 2020). The recently estimated time divergence between *C. macropus* and *C. furvus* (identified as '*Callistoctopus* sp.' in Lima et al., 2020) indicates that the two lineages probably separated some ~ 5 MYA, when the Panama seaway played an important role in the colonization of the western Atlantic Ocean from the western Pacific Ocean (Lima et al., 2020). However, their results had low statistical support, suggesting that the addition of more species of the genus would improve the reconstruction of the dispersion route of the common ancestor of the two species. Taking into account the diversity of species in the genus (greater in Asia and Oceania, smaller in Africa, Europe and in the Americas), it is likely the ancestor of the two species also followed a similar route from the Pacific toward the Atlantic, as other neritic cephalopod species (e.g., Anderson, 2000; Ulloa et al., 2017).

In our phylogenetic reconstructions, the position of *C. luteus* was not well defined, probably due to the lack of sequences from other species of the genus. The position of this species was also found to be unclear in previous studies (Kaneko et al., 2011; Acosta-Jofré et al., 2012). Increasing the taxonomic and geographic coverage of sequences for a target group should improve the internal phylogenetic resolution, yielding more accurate indications about the evolution of a given group (Sales et al., 2014; Anderson and Marian, 2020).

Reconciling Contemporary and Original *Callistoctopus furvus* Descriptions

The taxonomic status of *C. furvus* remained controversial for many decades. This may be not only due the morphological, behavioral and chromatic resemblance with eastern Atlantic *C. macropus*, but also because the holotype was missing (Voss and Toll, 1998). In addition, *Callistoctopus* records in the western Atlantic Ocean have been relatively infrequent (e.g., Haimovici et al., 2009), and Gould's original description was not sufficiently detailed enough to allow for reliable identification to species level. Increasing recent research efforts on western Atlantic shallow-water octopus fauna, undoubtedly driven and boosted by the development, diffusion and popularization of molecular tools (Radulovici et al., 2010; White and Last, 2012), renewed the interest of regional teuthologists in these species (e.g., Flores-Valle et al., 2018; Ritschard et al., 2019; Lima et al., 2020).

On a morphological basis, the most controversial difference between our neotype description and Gould's original work is the alleged existence of three distinct cirri on each eye in *C. furvus*. No supraocular cirri were observed in preserved, fresh or even in live specimens analyzed in this study. In addition, the sole contemporary *C. furvus* drawing found (i.e., Cedillo-Robles and Pliego-Cardenas, 2018) also show no cirri on the eyes. Unfortunately, this dispute will remain open, at least in the short term, as the most recently published accounts (e.g., Leite and Haimovici, 2006; Flores-Valle et al., 2018, Lima et al., 2020 and others) do not describe the morphology in sufficient detail for useful comparisons. Nonetheless, distinct morphotypes in genetically homogeneous species populations (either sympatric or allopatric) have been reported in marine mollusks (Saad et al., 2014), including cephalopods (van der Vyver et al., 2016; González-Gómez et al., 2018). This suggests that the lack of supraocular cirri in our specimens may be the result of phenotypic variability. It is also reasonable to assume that the different coloration described by Gould could well be an artifact caused by the preservation methods used by the author in the mid-19th century.

CONCLUSION

In summary, in line with contemporary best practices in taxonomy (see Dayrat, 2005), we have redescribed and designated a neotype for *C. furvus* using an integrative approach, combining scientifically orthodox methods for diagnosis with ethnoknowledge gathered from traditional fishers. This work highlights the reliability of information furnished by traditional people that are scientifically untrained but nonetheless seasoned observers of their surrounding nature (e.g., Ogar et al., 2020). Undoubtedly, this kind of collaborative approach may be useful in the case of cryptic invertebrates such as octopuses, particularly in remote coastal locations such as those studied here. Thus, our integrative taxonomic approach supports biodiversity assessments in poorly surveyed and/or difficult-to-access coastal regions, and may help in the development of management plans of small-scale fisheries and marine conservation areas (Johannes et al., 2000; Hauzer et al., 2013; Carvalho et al., 2009).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary Material**.

ETHICS STATEMENT

Ethical review and approval was not required for this animal study, in accordance with the local legislation and institutional requirements. Brazilian law on ethics in the use of animals in research ("Lei n° 11.794, de 8 de outubro de 2008" – an online version of this law, in Portuguese, can be accessed at https://www.planalto.gov.br/ccivil_03/_ato2007-2010/2008/lei/l11794.htm) does not consider invertebrates among the organisms that require consideration in protocols, recommendations and regulations in their use. According to Section 02 of the referred law: "The provisions of this Law apply to animals of classified species as phylum Chordata, subphylum Vertebrata, subject to environmental legislation."

AUTHOR CONTRIBUTIONS

MDJ, AS, RSM, and JBLS contributed to conception and design of the study. MDJ collected the biological samples. JBLS, JSR, and TASC conducted the genetic analyses. RSM, MDJ, and JDA carried out the morphological measurements. RSM and JBLS performed the statistical analysis. RSM wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.595244/full#supplementary-material

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