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Recognizing *Panulirus meripurpuratus* sp. nov. (Decapoda: Palinuridae) in Brazil—Systematic and biogeographic overview of *Panulirus* species in the Atlantic Ocean

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Abstract

Genetic analysis divides *Panulirus argus* into two different species, physically separated by the Amazon-Orinoco plume since the Last Glacial Maximum. *Panulirus argus* sensu stricto is distributed north of this biogeographic barrier and the second species to the south, occurring in Brazil. The *Panulirus* species in the Atlantic Ocean are being overfished and the standing stocks are unknown and still not considered endangered or threatened due to a deficiency of precise abundance data. The lack of data makes it impossible to undertake an effective conservation and management policy. In order to assist in the future management and conservation of the Spiny Lobster in the Atlantic Ocean and particularly for the indigenous species from Brazilian waters, this study formally recognizes and describes a new species, *Panulirus meripurpuratus* sp. nov., for what was previously known as *P. argus* in Brazilian waters, and differentiates it from *Panulirus argus* from North American waters and the Caribbean Sea. The work also presents an overview of the biogeographic distribution of the species and presents two identification keys to Atlantic species, one based on morphology and the other on live colouration.

Key words: Crustacea, Spiny lobster, Brazilian *P. argus*, identification key, threatened species, conservation

Introduction

Spiny lobsters (Decapoda: Achelata: Palinuridae) are considered one of the most important fishery resources in the world. They support some of the most economically lucrative global fisheries, valued at billions of U.S. dollars on an annual basis for the last decade (Cervigón *et al.* 1992; Ivo & Pereira 1996; Silva & Fontelles-Filho 2011; Phillips 2013). The family Palinuridae Latreille, 1802 presents 12 genera, with the most speciose being *Panulirus* White, 1847 with 24 species/subspecies, followed by *Jasus* Parker, 1883 and *Palinurus* White, 1847, each with six species (De Grave *et al.* 2009; Chan 2010; Phillips 2013; Briones-Fourzán 2014). Species of the genus *Panulirus* present the greatest biomass in shallow waters at 0–50 m depth, in warm waters ranging from 20 to 30°C at the latitudes between 0° to approximately 30°. The species of *Jasus* and *Palinurus* occur in colder waters of <20°C at higher latitudes >30° including species in deeper waters ranging between 100–500 m deep (George & Main 1967).

In the Atlantic Ocean, prior to the recent genetic analysis (Sarver *et al.* 1998), five different species of *Panulirus* were described based on morphological differences, *P. argus* (Latreille, 1804); *P. echinatus* Smith, 1869; *P. guttatus* (Latreille, 1804); *P. laevicauda* (Latreille, 1817); and *P. regius* De Brito Capello, 1864 (Holthuis 1991; Melo 1999; Williams 1986, 1984). The genetic analysis of Sarver *et al.* (1998) divided *P. argus* into two subspecies: *Panulirus argus westonii* for the form from Brazilian waters and *Panulirus argus argus* for the form from Caribbean and North Americas waters. Subsequently, Naro-Maciel *et al.* (2011) and Tourinho *et al.* (2012) considered the two subspecies as different cryptic species, with two distinct lineages. In proposing the name *Panulirus argus westonii*, however, Sarver *et al.* (1998) did not meet requirements of the International Code of Zoological Nomenclature, including the absence of any form of diagnosis or description. Thus, *Panulirus argus westonii* is a *nomen nudum* and so the Brazilian species remained formally undescribed.

It should be noted that the species under review in this study presents differences in both colour pattern and morphology. Coloration as an identifying feature of a decapod species is of limited value in some taxa but of great value others, such as the ornamental genus of *Stenopus* (Saito *et al.* 2009) and among many species of lobsters (Williams 1986; Holthuis 1991). In the western Atlantic, including Brazil, *P. "argus"* is the most economically valuable lobster with the highest added economic value per unit effort within the decapod fishery; as a result it is heavily exploited (Cervigón *et al.* 1992; Silva & Fontelles-Filho 2011; Butler *et al.* 2013). The IUCN Red List of threatened species has identified the standing stock of *P. argus* as being in a state of constant decline from being over-exploited. However the species is still not considered endangered or threatened due to a deficiency of data in relation to its abundance index (Butler *et al.* 2013).

In order to assist in the future management and conservation of *Panulirus* in the Atlantic Ocean and particularly for the indigenous species from Brazilian Waters, this study formally described a new species *Panulirus meripurpuratus* sp. nov. and differentiates it from *Panulirus argus* from North American and Caribbean waters. The work also presents a review of the biogeographic distribution of the species and presents two identification keys to the Atlantic *Panulirus* species, one based on morphology and the other on live colouration.

Systematics

Infraorder Achelata Scholtz & Richter, 1995

Family Palinuridae Latreille, 1802

Panulirus meripurpuratus n. sp

(Figs. 1–3, 4B, 5)

Panulirus argus.—Fontelles-Filho & Ivo 1980: 25–32.—Ivo & Pereira 1996: 7–94.—Melo 1999: 436, fig. 294.—Silva & Fontelles-Filho 2011: 19, 22–94.—Teschima *et al.* 2012: 5.—Faria-Junior *et al.* 2013: 29, fig 2.—Gaeta *et al.* 2015: 2, fig 4.
Panulirus argus westonii.—Sarver *et al.* 1998: 185.—Sarver *et al.* 2000: 871.—George 2006: 1289.—Chan 2010: 159. [Nomen nudum].

Type material. *Holotype*. Offshore area around Pau Amarelo Beach, Pernambuco ($7^{\circ}54'15.6"S$, $034^{\circ}49'14.3"W$), 04 November 2015, sampled by traps (*covo*), obtained from local fisherman, male, CL = 178 mm, (Oceanographic Museum Petrônio Alves Coelho in Pernambuco—MOUFPE 15564).

Paratypes. 7 specimens obtained from local fisherman, sampled by traps (*covo*), offshore around Pau Amarelo beach Pernambuco ($7^{\circ}54'15.6"S$, $034^{\circ}49'14.3"W$), 04 November 2015: 2 males (#3 CL = 92 mm, #5 CL = 112 mm) and 5 females (#1 CL = 72 mm, #2 CL = 132 mm, #4 CL = 78 mm, #6 CL = 81 mm, #7 CL = 87 mm) (MOUFPE 15562).

Type-locality. Pernambuco state, northeastern coast of Brazil.

Etymology. From Latin *Meri* (plural of merus) + *purpuratus* (purple). Based on the main colour pattern in the meri of pereiopods that differentiates this species from the Caribbean *P. argus*.

Description of male holotype (Figs 1, 2 B–E). Carapace 1.4 times longer than wide, slightly shorter than abdomen length; covered with sharp anteriorly directed spines; very large spines (horns) above orbits, laterally compressed, directed anterodorsally, posteriorly with small spines; 2 transverse rows of 4 gastric spines; cervical groove distinct, other regions demarcated by shallow groove, with almost imperceptible divisions between cardiac, branchial and intestinal regions (Fig. 1).

Abdomen smooth; somites 2–5 with shallow and incomplete transverse groove, without bristles, distinctly interrupted medially, especially on somites 3–4 (Fig. 2E); maximum width of abdomen 4.8 times less than total body length. Male pleopods 2–5 leaf shaped, without endopods.

Telson and uropods hard proximally and membranous distally; hard part of exopod with line of 7 small spines distally; hard part of endopod with 3+1 spines distally.

Antennular plate broad, bearing 2 pairs of large spines arranged in a square, with 2 anterior larger spines in the limit of antennular plate and 2 smaller spines posteriorly in the middle of antennular plate (Fig. 2B). Antennulae nearly 0.8 times total body length; outer flagellum setose distally and shorter and thicker than inner (Fig. 1). Distal article of antennular peduncle exceeding antennal peduncle and over reaching first pereiopods (Figs. 1); second and

third articles equal in length, half length of first article. Antennae very large, heavy, exceeding body length; peduncle reaching the distal limit of second antennular peduncle article; peduncle with numerous strong spines; ventral surface of first article smooth, with only 1 distomedial spine; flagellum stout, stiff, line of setae along inner margin and ringed with spines at intervals (Fig. 1).

Third maxilliped with exopod (Figs. 2D); reaching carpi of first pereiopod; exopod with multi-articulate flagellum reaching 2/3 length of merus of endopod; first segment of exopod half length of flagellum (Figs. 1, 2D). Exopod of second maxilliped with multi-articulate flagellum reaching beyond endopod; first segment of exopod slightly shorter than flagellum (Fig. 2C).

Pereiopods unequal in size; pereiopod 2 longest, followed by pereiopods 3, 4, 5 and 1; dactylus about half length of propodus, covered with bristles; merus with dorsodistal and outer distoventral spines; carpi with longitudinal dorsolateral grooves. Pereiopods 3–5 ending with superior spines. Pereiopod 1 slightly exceeding the end of antennal peduncle, reaching the end of second antennular article and reaching 1/3 length of propodus of pereiopod 2. Pereiopod 1 little longer than carapace length; propodus with ventral bristles. Pereiopod 2 about 1.4 times longer than carapace.

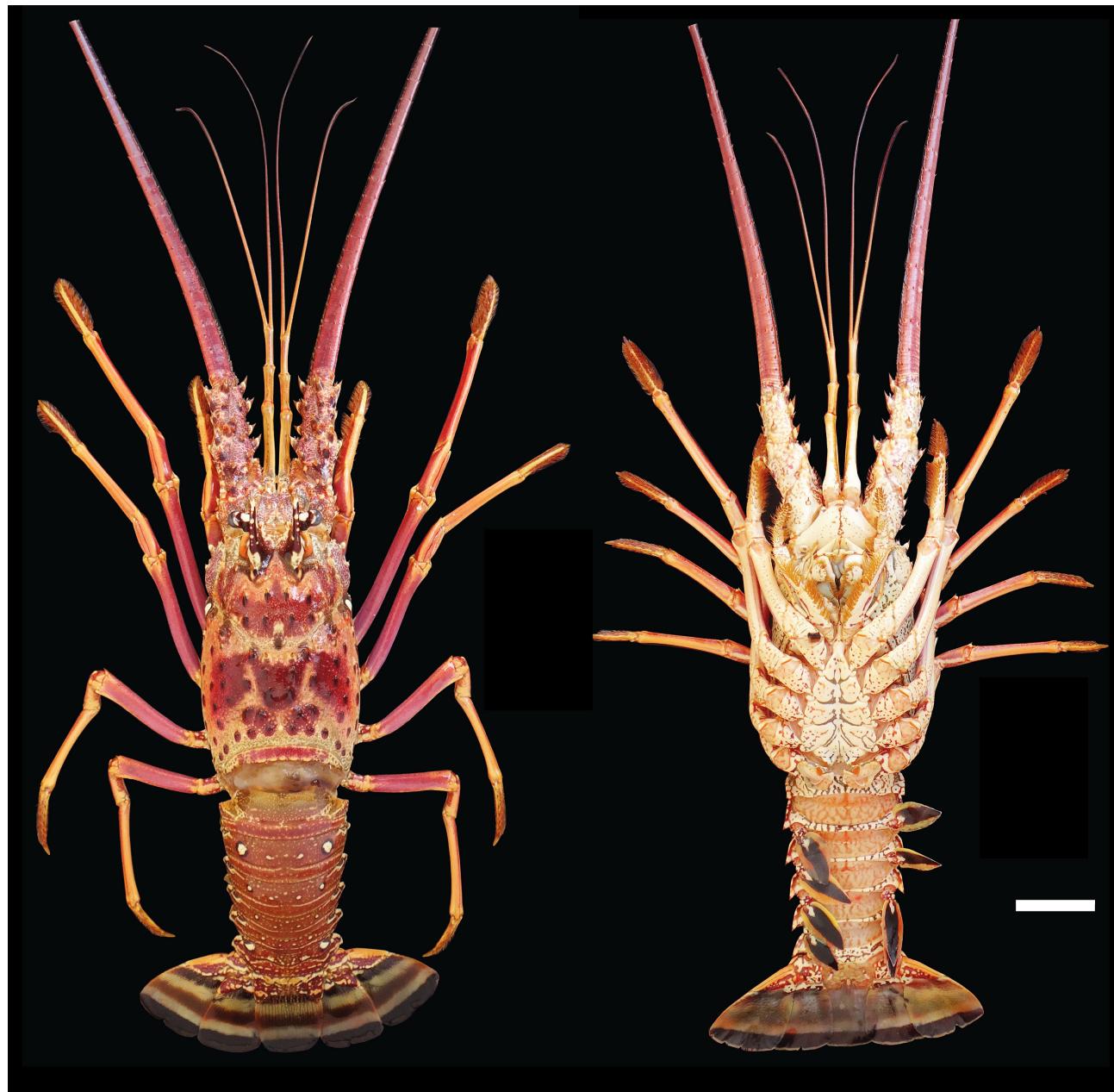


FIGURE 1. Holotype of *Panulirus meripurpuratus* sp. nov. captured in Pernambuco—Brazil. Scales: 5cm. Photographic credits: Jesser Fidelis.

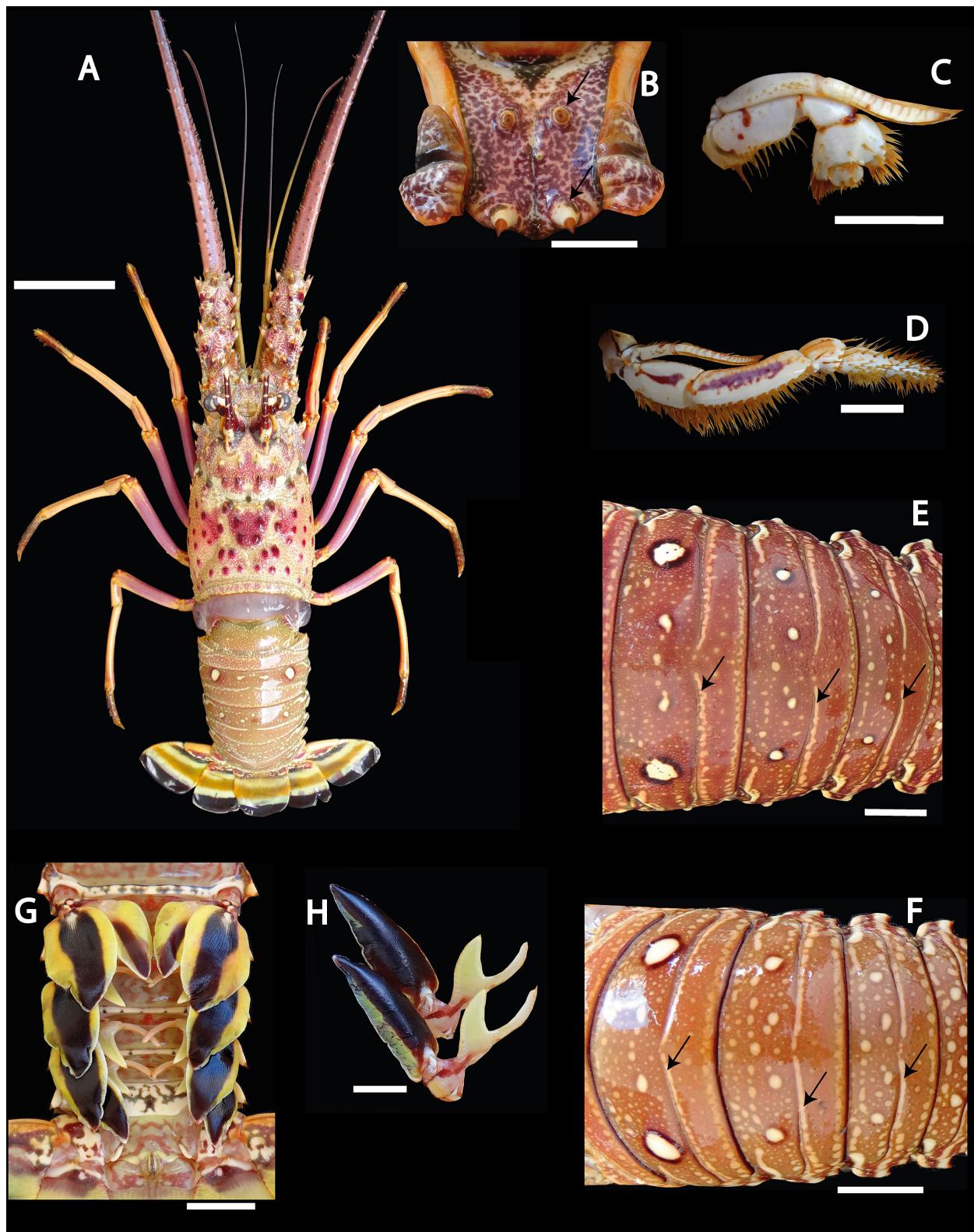


FIGURE 2. Details of *Panulirus meripurpuratus* sp. nov. A, the male paratype #3 (CL = 92 mm) with lighter colour; B, antenniferous plate of holotype highlighting the four spines in square; C, lateral view of the right second maxillipeds of holotype; D, lateral view of the right third maxillipeds of holotype; E, abdominal somites 2–4 of holotype highlighting the end of the groove in each somite; F, abdominal somites 2–4 of female paratype #6 (CL = 81 mm) highlighting the end of the separated groove even with spotted line in transverse groove merged; G, abdomen of female paratype #4 (CL = 78 mm) highlighting the pleopods with endopod and exopod; H, details of pleopods with endopod and exopod of female paratype #6 (CL = 81 mm). Scales: A = 5 cm; B–G = 2 cm; H = 1 cm. Photographic Credits: Jesser Fidelis.

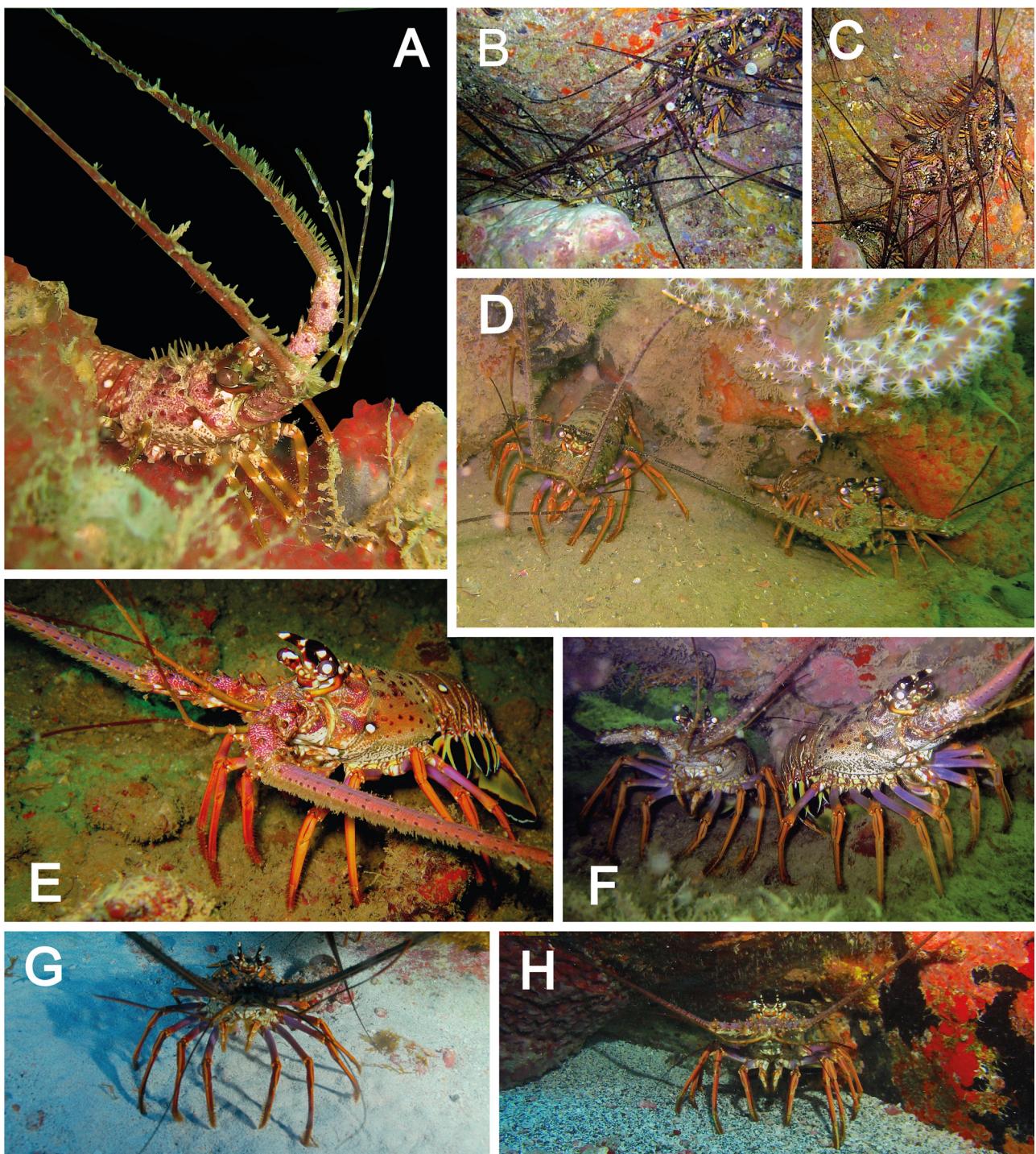


FIGURE 3. *Panulirus meripurpuratus* sp. nov. photographed at night in-situ in different habitats according to life stage. A, puerulus alone on reef fringe (reef surface) at shallow coastal reefs; B–C, juveniles upside down in groups in cavity in the caves at shallow reefs; D, F, large juveniles or pre-adults in the interface between soft substrate and reef in shallow coastal reefs; E, pre-adults foraging in the bottom among the reef structures, G–H, adults in deep zones in soft bottom and near the reefs. Images: specimens from Salvador-BA photographed by Claudio Sampaio (A, D–F); specimen from Fernando de Noronha-PE photographed by Bruno Welter Giraldes (B, C); specimens from Fernando de Noronha-PE photographed by Ronaldo Guillen (G–H).

Colour of male holotype (Figs 1, 2E). Antennal flagella purple. Mosaic of small purple dashes on antennal peduncle, antennular plate and anterolateral surface of carapace. Antennules orange-greenish. Supraorbital horns and ocular peduncle black and white. Body and pereiopods colourful dorsally, with inferior part whitish with reticulated sparse dashes.

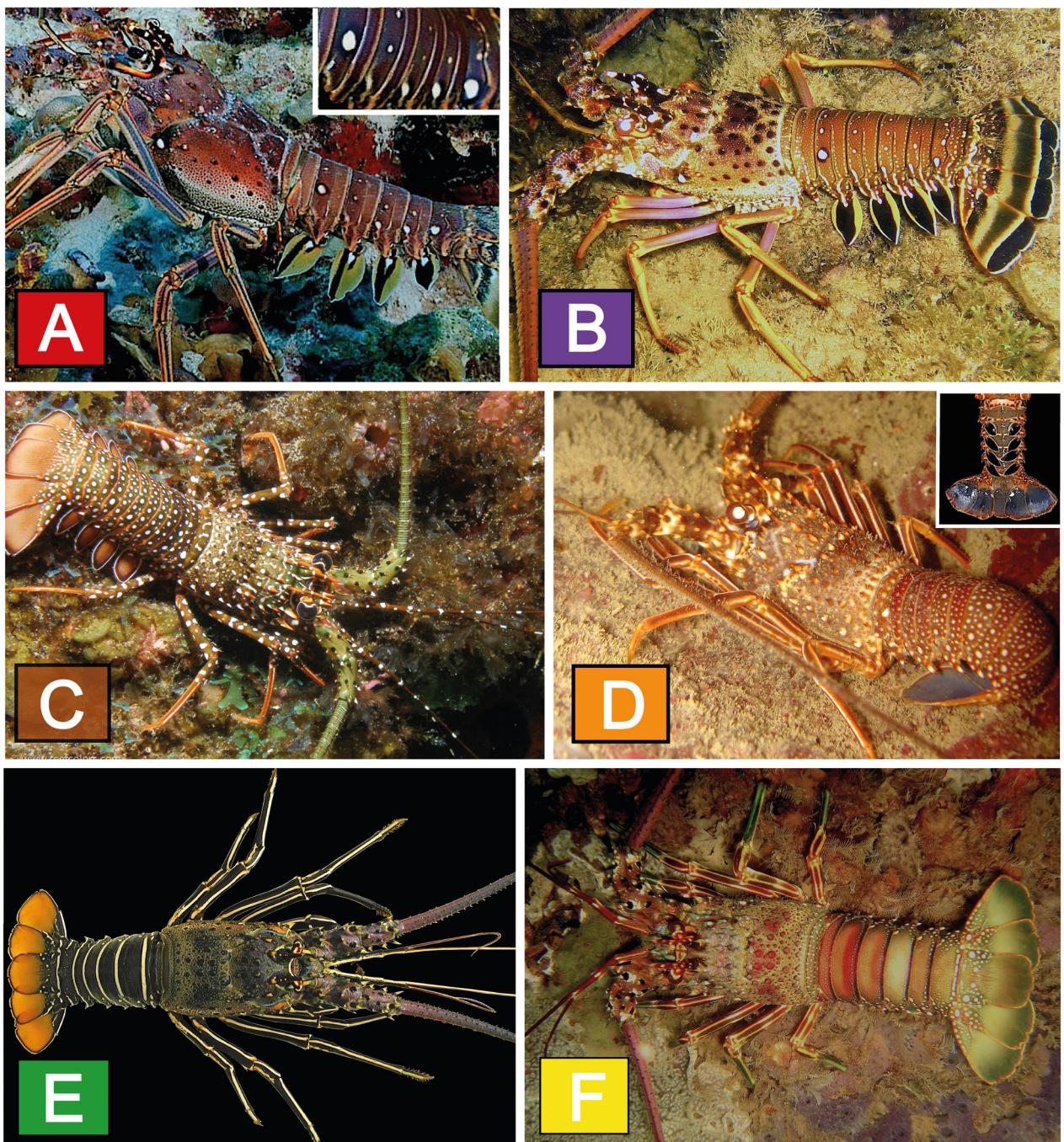


FIGURE 4. Species of *Panulirus* from the Atlantic Ocean. A, *P. argus* (Latreille, 1804) in Cuba; B, *P. meripurpuratus* sp. nov. in Bahia, Brazil; C, *P. guttatus* (Latreille, 1804) in Cuba; D, *P. echinatus* Smith, 1869 in Pernambuco, Brazil; E, *P. regius* De Brito Capello, 1864 in Cape Verde; F, *P. laevicauda* (Latreille, 1817) in Bahia, Brazil. The colours of the textbox correspond to the colour in the distribution map in Fig 5. Photographic Credits: Wolfram Sander (A, C); Claudio Sampaio (B, F); Bruno W. Giraldes (D); Rui Freitas (E).

Carapace with light red gastric region; base of spines dark red; cardiac region red with darker red tones on last four rounded spines; intestinal region red near cardiac region, with four darker red rounded spines on each side; branchial region with gradient of red, darker only posterodorsally near cardiac region (lighter anteriorly) and lighter laterally, with only rounded spines with darker colours; posterior margin of carapace with dashed line of dark red rounded spines; very light mosaic of granules laterally and posteriorly in carapace.

Meri of pereiopods purple without lines; carpi, propodus and dactylus with predominant orange yellowish colour; longitudinal purple line only in the grooves on each side of carpi; propodus without lines.

Abdomen light reddish brown; line of very small white spots (not continuous line) along posterior region of

each abdominal somite; grooves at somites 2–5 posteriorly lined by very small white spots; abdominal somite 2 with two large, irregular, white eyespots with black margin, one on each lateral, and with two irregular white spots centrally; abdominal somite 6 also with two large, irregular, white eyespots with black margin, one on each lateral and further areas irregularly white spotted; abdominal somites 3–5 with line of four small white eyespots with black margin dorsally and further areas irregularly white spotted.

Membranous part of tail fan (telson and uropods) greenish with two black transverse bands distally and proximally, and brownish band centrally. Protopod and hard part of uropods and telson with same colour pattern as abdomen but with larger white dashes. Pleopods black medially with yellow-greenish margin.

Variation in Paratypes. In some specimens the antennular plates presented 1–4 additional spines between the main four spines. Paratype males present the same morphological proportions as the holotype. In one male specimen, the antennae are 1.7 times the total length of body.

In females, the third antennular article does exceed the antennal peduncle and still proximally 0.8 times the total length of body. The first pereiopod is shorter and in most specimens does not reach the end of the antennal peduncle. The second pereiopod is proportionally shorter than in males at 1.02–1.07 times carapace length. The fifth pereiopod of females is distally subchelate. The antennae are 1.5–1.7 times the total length of body (few specimens with complete antennae for comparisons). The exopod of maxilliped 2 is almost same size as flagellum or 0.8 shorter. The carapace is 1.6–1.8 times longer than wide and 0.8–0.9 times shorter than abdomen length; maximum width of the abdomen is 3.8–4.3 times less than the total body length. The female pleopods on the abdominal somite 2 have a leaf-shaped endopod similar to exopod but slightly smaller; pleopods 3–5 with bifid endopods (Fig. 2G, H).

Thus, sexual dimorphism is evident in reproductive males, which present a larger cephalothorax, longer antennular peduncle and longer pereiopod 2 used in mating. Reproductive females have a larger abdomen and laminar endopods of pleopod 2; abdominal somites 3–5 with bifurcated endopods modified for carrying eggs; and the fifth pereiopod with a sub-chela for grooming.

Colour variation was not related to sexual dimorphism. Some adult males and females present a paler carapace and abdomen (Fig. 2A); as well as more purplish than red on the dorsal regions and more greenish antennules and abdomen (Fig. 2A). The spotted line on the transverse groove of the abdominal somites is sometimes merged, but the grooves remain separated (Fig. 2F).

Speciation. The differentiation between *P. argus* from the Caribbean sea and *P. meripurpuratus* from Brazil, according to genetic analysis occurred between 8.4 and 26.1 My (George 2006; Sarver *et al.* 1998, 2000; Tourinho *et al.* 2012). During this period at the beginning of late Miocene (around 10 My) with the Last Glacial Maximum, a great change took place in the western Atlantic Ocean with the beginning of the outflow of the Amazon-Orinoco River (Campbell Jr *et al.* 2006). This created a massive physical barrier of low salinity water isolating biological populations and enabling allopatric speciation and vicariance. Indeed, the Amazon-Orinoco River plume is currently the most prominent biogeographic barrier in the western Atlantic Ocean, separating two tropical eco-regions with great differences in biodiversity composition (Spalding *et al.* 2007; Floeter *et al.* 2008; Rocha *et al.* 2008). This biogeographic barrier is reported as the main factor leading to allopatric speciation (Sarver *et al.* 1998, 2000; Tourinho *et al.* 2012) separating *P. argus* and *P. meripurpuratus* into genetically different populations. Isolating *P. argus* to the region north of the Amazon river plume and *P. meripurpuratus* to the south in Brazilian waters.

Distribution. From Pará (2°S) to Santa Catarina (27°S) on the Brazilian coast, including the oceanic island of São Pedro and the São Paulo Archipelago, Fernando de Noronha and Rocas Atoll (Melo 1999; Silva & Fonteles-Filho 2011; Teschima *et al.* 2012; Gaeta *et al.* 2015). Freitas & Castro (2005) reported *P. argus* (but with the characteristics of *P. meripurpuratus*) from Cape Verde; however Tourinho *et al.* (2012) reported an uncertainty about these populations and suggested that the species presence was instead due to anthropogenic transport. Sarver *et al.* (2000) described the presence of *P. meripurpuratus* (as the Brazilian form of *P. argus*) in Caribbean Waters was also uncertain of the provenance of local populations.

Biology. (Based on Ivo & Pereira 1996; George 2006; Silva & Fonteles-Filho 2011; Butler *et al.* 2013; Giraldes *et al.* 2015a; b; as *P. argus* in Brazil). *Panulirus meripurpuratus* presents two distinct migration behaviours: the trophic migration in the first three or four months of the year, with random displacement parallel to the coast searching for sites with high food concentration; and the reproductive (ontogeny) migration through deeper areas in the first and second trimesters searching for favourable sites for reproduction. Like other lobsters

reproduction occurs by front position mating, with male depositing the sperm mass on the sternum of the female. Fertilized eggs are attached to the exopod of pleopods of the female. Planktonic larvae stay for 12 months in the water mass where they assume a benthic position and become a puerulus; in the next 12 month the puerulus stage remains in shallow water for 1–2 years of life during which it becomes a juvenile; the juveniles stay in coastal reefs for 3 years during which they become adults in a pre-reproductive stage and migrate to deeper water for reproduction. This species presents a long life cycle of approximately 18.5 years. Adults are found in reproductive condition every month in tropical regions; however, the greatest reproductive intensity occurs from January to April. The average length of females at the first stage of sexual maturity is estimated at 20.5 cm in total length (7.5 cm for carapace length and 13.0 cm for tail length). The species presents a high fecundity with an average of 29,4175 eggs per female and 630 eggs/g of adult female; larger females produce more eggs and also incubate a greater number of eggs than smaller females. The sex ratio in the adult population supposedly is higher for males due to a numerical predominance of captured males reported in fishing stock description. The diet consists mainly of molluscs and crustaceans and as secondary food, echinoderms, algae and corals. Feeding habits are based on nightly foraging. The recruitment is dependent on the number and size of females. The natural recruitment ratio of new specimens into the population for this species in Brazil is uncertain, as biological data has traditionally been provided by analysis conducted by the fishing industry. It is important to report that the recruitment of this species happens in shallow coastal reefs and as suggested by Giraldes *et al.* (2012, 2015a, b), it is possible to monitor this large lobster in coastal areas using nocturnal underwater visual cense and obtain information about species recruitment using low impact methods.

Habitat. (Based in Ivo & Pereira 1996; Rocha *et al.* 1997; Melo 1999; George 2006; Silva & Fonteles-Filho 2011; Giraldes *et al.* 2012, 2015a; b; as *P. argus* in Brazil).

Panulirus meripurpuratus is usually found on reefs and coralline algae, sponges or other objects which afford protection or places of concealment; from low-tide mark to depths of about 50 m; increasing the abundance perpendicular to coast, with a maximum abundance at around 41–50 m. There are different habitats according to the life stage. Post larvae, puerulus and early stage juveniles live on outer reef habitats in coastal shallow reefs, associated with sessile benthic organisms and fouling, such as algae (Fig. 3A). Juveniles inhabit shallow coastal reefs (around 0–15 meters) but small juveniles are found on the roof of caves inside cavities (Figs. 3B, C) and large juveniles (or young adults in a pre-reproductive stage just before the ontogenetic migration) are found in cavities at the interface between the soft bottom and the reef/rock; at this time it is usually observed at night walking on the bottom near the reef structure (Figs. 3D–F). Adults are found in deeper water around 20–50 m after the reproductive migration; observed by day and at night usually in soft bottom near a sheltered area (Figs. 3G, H). During migration, it is found in groups on soft bottom habitats walking through deeper reefs. The main description for *P. meripurpuratus* associated habitat is based on reports from commercial fishing activity and by nocturnal scuba diving observations.

Fishing history. (Based on Ivo & Pereira 1996; Rocha *et al.* 1997; Silva & Fonteles-Filho 2011; Giraldes *et al.* 2015b; as *P. argus* in Brazil).

The fishing of *P. meripurpuratus* as a target species in Brazil started around 1950, with the aim to export frozen lobster tails as they commanded a high market price. In Brazil, the species was fished intensely from Pará to Espírito Santo state an area of around 74.607 km². The fishing methodologies centre around three types of techniques: traps (*covo* or *cangalha*), anchored bottom gillnets (*caçoeira*) and diving (free diving or compressor diving); of the three fishing methods the trap is presently the only legalized technique nowadays. The Northern sub-region comprises the coast of the states of Amapá, Pará and Maranhão and despite the large marine area the population of this species presents a low density due to the strong influence of fresh water plumes from the Amazon and Orinoco rivers. This has caused a reduction in the fishing catchment area, which has pushed lobster fishing activities into deep-water sites offshore. The large continental shelf area of the Northern Northeast sub-region from Piauí to Rio Grande do Norte state, has a habitat of calcareous algae and rocks and delivers the highest recorded landings for this species in Brazil. The East Northeast sub-region, from Rio Grande do Norte to Espírito Santo state supports a large number of coralline reefs and a high abundance and diversity of demersal fish of economic value to the fishing industry. This region has the lowest catch per unit effort within the commercial lobster fishing industry and the lowest recorded landings of lobsters of the three sub-regions. There is no commercial fishing activity between Espírito Santo and Santa Catarina State. Historically the most intense fishing activity takes place between the Northern Northeast and East Northeast sub-regions, with Ceará and Pernambuco

state accounting for about 80% of the total catch for the export market. Since the 1960s the region has recorded a drastic reduction in landings for this species. In the past advances in fishing technology have shown false increases in population numbers with increases in catch not a true representation of a standing stock but attributed to improvements in fishing methodologies. A pattern in increased landings can also be seen when the market value of a target species increases fishing effort also increases leading in-turn to increased landings. This can sometimes be wrongly interpreted as a recovery in stock. Unfortunately due to the constant increase in the fishing effort and the increase in size of the fishing fleet the stock abundance of this species is in a state of constant decline. Clearly the management and oversight strategies to control and limit the capture of this species by the Brazilian government have not been rigorous enough to address the overfishing scenario. A major concern about the management of this species was highlighted by Giraldes *et al.* (2015b) when particular emphasis was focused on the importance of protecting the natural nursery regions of the shallow coastal reef ecosystem (<15m).

Remarks. *Panulirus argus* (Latreille, 1804) remains the name for the species indigenous to the Caribbean Sea. The original description by Latreille (1084: 393 as *Palinurus argus*) is very limited and could apply to both *P. argus* and *P. meripurpuratus*. Images, pictures and descriptions for *P. argus* reported in references such as Crawford & Smidt (1922: 291, figs. 265–271), Williams (1984: 170, fig. 120), Williams (1986: fig. 44, fig. 79b–c), Holthuis (1991: fig. 249, 257) and Cervigón *et al.* (1992: 143 pl. II, fig 13) are based mainly on specimens from regions north of the Amazon-Orinoco river barrier. It was on examination of these references that differences between the specimens of *P. meripurpuratus* and *P. argus* were first discovered.

The characteristics used to differentiate *P. argus* and *P. meripurpuratus* have been used as part of the key identification presented below. *P. argus* presents carapace with deep grooves well defining all regions, with very distinct divisions among cardiac, branchial and intestinal regions; while the carapace in *P. meripurpuratus* presents only distinct cervical groove, with shallow groove dividing the regions, faintly perceptible divisions between cardiac, branchial and intestinal regions. Abdominal somites 2–5 in *P. argus* with deep transverse groove often faint medially (not distinctly interrupted); and in *P. meripurpuratus* abdominal somites 2–5 present shallow and incomplete transverse groove, interrupted medially, especially on somite 3. The conspicuous spots are observed in both species but they are isolated in the abdomen of *P. argus* presenting only the scattered spots; while in the abdomen of *P. meripurpuratus* the conspicuous scattered spots are mixed with several small spots. The abdomen is darker, with solid colour in *P. argus* and in *P. meripurpuratus* it is lighter and spotted. In the grooves and at the end of each abdominal somite, *P. argus* present continuous light line and *P. meripurpuratus* present small white spots in line. Carapace of *P. argus* has an intense and solid dark red colour dorsally, extending onto lateral surfaces; while the carapace of *P. meripurpuratus* has a light background with pale red (sometimes almost pink), with darker areas mainly in cardiac region and on dorso-posterior area of branchial region (near the cardiac) and only the base of spines are dark red, forming conspicuous dark spots in the light background. Pereiopods are striped longitudinally in *P. argus*, including meri and propodus; and in *P. meripurpuratus* the pereiopods are mostly without stripes (present only on carpi), with peculiar conspicuous and solid purple colour on meri, with orange/brown shades at propodus and dactylus. Pleopods in *P. argus* are yellow-green with a longitudinal black line medially with sickle shape; in *P. meripurpuratus* its pleopods present only a lateral border green or yellowish with a large black area in centre (not only a black sickle shape line).

The distribution of *Panulirus argus* (Latreille, 1804) is now restricted to northern localities from North Carolina (35°N) to Venezuela (8°N) including the Caribbean Sea, West Indies, Gulf of Mexico and Bermudas—localities north of the biogeographic barrier of the Amazon River plume (Williams, 1986; Holthuis, 1991; Sarver *et al.* 2000; Tourinho *et al.* 2012). At localities south of the Amazon River plume on the Brazilian marine domain (from 2°S to 27°S) *P. meripurpuratus* is the representative species (see distribution section above). It was highlighted that neither *P. argus* nor *P. meripurpuratus* were reported between the parallels of 8°N and 2°S, the area which is influenced by the Amazon-Orinoco River (Sarver *et al.* 2000; Tourinho *et al.* 2012). It can therefore be regarded as a physical barrier blocking the gene flow and isolating the two populations. Sarver *et al.* (2000) reported that there was no recorded specimen of the Caribbean *P. argus* in Brazilian waters and that the presence of *P. meripurpuratus* upward of the biogeographic barrier is uncertain. However, after the formal description of *P. meripurpuratus* presented in this study, it is now possible to confirm whether the two species populations remain in isolation or co-habit within a specific region. It should also be noted that the number of Atlantic Ocean *Panulirus* species has increased to six species.

Key to Atlantic *Panulirus*—based on morphology

(Adapted from Abele & Kim 1986; Williams 1986; Holthuis 1991; Melo 1999)

1. Antennular plate bearing one pair of strong spines. 2
- Antennular plate bearing 2 pairs of large spines arranged in a square 3
2. Abdominal somites 3–5 with complete transverse groove; anterior margin of side plates of somites 2–5 bearing very small teeth. Fully spotted carapace, meri of pereiopods and antennules *P. guttatus*
- Abdominal somites 3–5 with incomplete transverse groove (interrupted in the middle). Carapace, meri of pereiopods and antennules not spotted. Meri of pereiopods striped. *P. echinatus*
3. No transverse groove on abdominal somites 2–5; spotted only on lateral margin of the abdominal somites *P. laevicauda*
- Abdominal somite 2–5 with transverse groove and with bands or spots on upper surface 4
4. No exopod on third maxilliped. Supraorbital horns short, not reaching the anterior spines on antennular plate. Abdominal somites with conspicuous transverse bands. Pereiopods with continuous longitudinal lines dorsally *P. regius*
- Third maxilliped with exopod. Supraorbital horns long, overtaking the anterior spines on antennular plate. Abdominal somites with conspicuous ocellated spot on either side of each somite, largest on somites 2 and 6. When present, longitudinal lines on pereiopods are not continuous and dorsal 5
5. Carapace with deep grooves well defining all regions; very distinct divisions among cardiac, branchial and intestinal regions. Abdominal somites 2–5 with deep transverse groove often faint I medially (not distinctly interrupted); presenting only the scattered spots (not full spotted) and a continuous light line at the end of each somite *P. argus*
- Carapace with shallow groove dividing the regions; only cervical groove distinct; and faintly perceptible divisions between cardiac, branchial and intestinal regions. Abdominal somites 2–5 with shallow and incomplete transverse groove, interrupted medially, especially on somite 3; several small spots mixed among the scattered spots; small white spots lining the grooves and posterior margin of each somite *P. meripurpuratus*

Key to Atlantic *Panulirus*—based on colour in life

(Adapted from Williams 1986; Holthuis 1991)

1. Membranous part of telson and uropods uniformly coloured, without bands. Supraorbital horns and ocular peduncle with shades of yellow, orange, brown or green, (not only black and white). Abdomen or full spotted, or with white transverse bands or only white spotted laterally; no conspicuous larger ocellated spot on somites 2 and 6 2
- Membranous part of telson and uropods transversely banded. Supraorbital horns and ocular peduncle with a conspicuous black and white colour. Abdominal somites with conspicuous ocellated yellow/white spot on either side of each segment, largest on somites 2 and 6; somites 2–6 with two small spots central-dorsally 5
2. Abdomen fully spotted white, including dorsally. Pereiopods with brown or orange propodus 3
- Abdomen without spots dorsally; when present spots are concentrated on the lateral surfaces. Pereiopods with green propodus 4
3. Abdomen, carapace, antennulae and meri of pereiopods white spotted. Carapace, abdomen and antennae greenish. Spines on carapace and grooves of abdomen orange. Propodus and dactylus of pereiopods orange, not spotted. Membranous part of tail fan orange-yellow or reddish. Pleopods same colour as tail fan, with thin white border *P. guttatus* (Fig. 4C)
- Only abdomen white spotted. Pereiopods with longitudinal light stripes in shades of white or yellowish. Carapace, abdomen and antennae brownish. Membranous part of telson and uropods dark blue. Pleopods black or dark blue with thin white border *P. echinatus* (Fig. 4D)
4. Carapace with red details dorsally; supraorbital horns yellow with black/brown spots. Antennules not striped. Pereiopods with stripes (not continuous) and intense green propodus and dactylus. Abdominal somites only white spotted laterally. Abdominal somites 1–3 red-brown and 4–6 greenish. Pleopods green, white spotted and with yellow border. Membranous part of tail fan in shades of green (darker at extremities) *P. laevicauda* (Fig. 4F)
- Bluish or olive green. Carapace without red colouration dorsally. Supraorbital horns dark green dorsally (with yellow tip) and white ventrally. Pereiopods and antennules with continuous longitudinal yellow/white stripe. Abdomen green (with no brownish segments) with a conspicuous transverse white band on each somite. Membranous part of tail fan orange-yellow *P. regius* (Fig. 4E)
5. Carapace dark red dorsally, extending onto laterally surfaces. Pereiopods striped longitudinally (including meri and propodus) with different shades and colours. Abdomen darker, with solid colour presenting only as the peculiar spots and a continuous light line in the end of each somite. Pleopods yellow-green with a longitudinal black sickle shape line medially *P. argus* (Fig. 4A)
- Pale red on carapace, with darker areas only in cardiac region and on dorso-posterior area of branchial region (near the cardiac); base of spines with dark red colour, conspicuous against the light background. Pereiopods mostly without stripes (present only on carpi), with peculiar conspicuous purple colour on meri; propodus and dactylus orange/brown. Abdomen lighter with several small spots beyond the same peculiar spots as *P. argus*; abdominal somites with line of small white spots on grooves and posterior margin of each somite. Pleopods with large black area in centre, with lateral border green or yellowish *P. meripurpuratus* (Fig. 4B)

Biogeographic overview of *Panulirus* species in the Atlantic Ocean

All species from the genus *Panulirus* as described by George & Main (1967) are characterized by living in shallow water with the greatest biomass between 0–50 m deep and limited geographic distribution between 0° to about 30° degrees of latitude. In other words they are tropical and subtropical species, inhabiting shallow warm waters mainly at temperatures between 20 and 30°C. George (2006) describes two evolutionary patterns in distribution of *Panulirus* spiny lobsters: 1) coastal species that keep the entire life cycle in shallow waters between 0–20 m, in Atlantic Ocean *P. echinatus* and *P. guttatus*; and 2) species that migrate to deeper waters between 20–50 m in an ontogenetic migration, in Atlantic Ocean *P. argus*, *P. meripurpuratus*, *P. laevicauda* and *P. regius*.

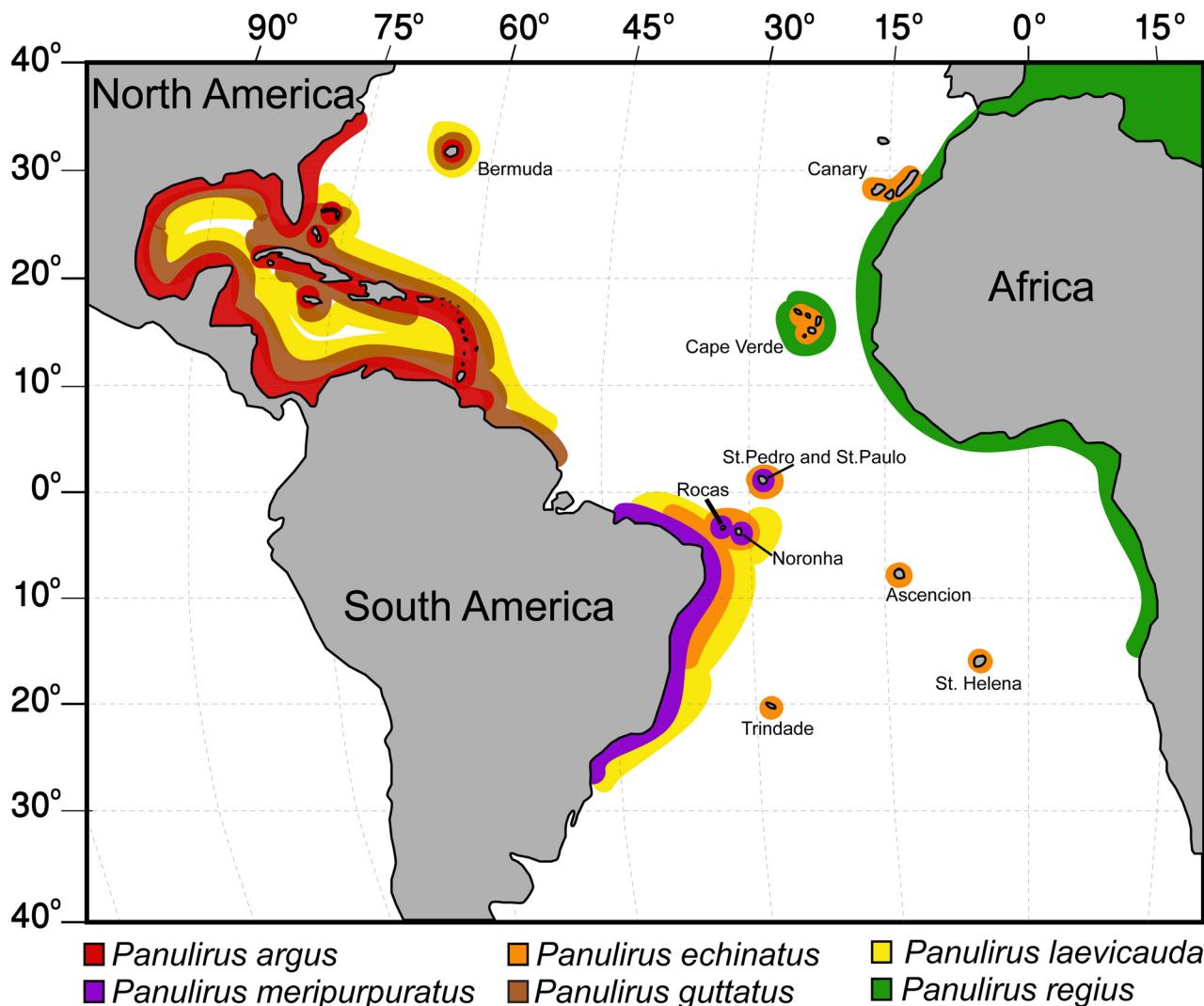


FIGURE 5. Map of the Atlantic Ocean with details of the American Continent (North and South), Africa and Oceanic Islands; and the distribution of the species within genus *Panulirus*: [red] *P. argus*; [purple] *P. meripurpuratus*; [brown] *P. guttatus*; [orange] *P. echinatus*; [green] *P. regius*; and [yellow] *P. laevicauda*.

The actual distribution of *Panulirus* species in Atlantic Ocean (Fig. 5), are as follows:

Panulirus argus: North Carolina (35°N) to Venezuela (8°N) including the Caribbean Sea (discussed here).

Panulirus meripurpuratus: native to Brazil, from distributed from Pará (2°S) to Santa Catarina state (27°S) (described here); with an uncertain population recorded in Cabo Verde e Caribe-Florida (cited above).

Panulirus echinatus: native to Brazil; distributed on the extreme north eastern coast of Brazil from Ceará (3°S) to Bahia (17°S) and the Central Atlantic Islands at St. Pedro and St. Paulo Archipelago, Fernando de Noronha, Rocas Atoll, Trindade, Cape Verde, Canary, Ascension and Saint Helena (Vianna, 1986; Holthuis, 1991; Pinheiro *et al.* 2003; Coelho *et al.* 2007).

Panulirus guttatus: found in coastal waters from the Bahamas and South Florida, (25°N) to Suriname (5°N) including Bermuda (32°N), Belize, Panama, the Caribbean Arc (Cuba to Trinidad), Curacao, Bonaire, and Los Roques (Holthuis, 1991).

Panulirus laevicauda: widely distributed, from the Bahamas and Florida, (25°N) to Guyanas (6°N) including Bermuda (32°N), Yucatan, Caribbean Sea, Gulf of Mexico, Central America, Antilles (Absent between 5°N and 2°S), starting again in Brazil from Maranhão (2°S) to Santa Catarina (27°S) including Fernando de Noronha and Rocas Atoll (Holthuis, 1991; Melo, 1999; Coelho *et al.* 2007; Teschima *et al.* 2012; Gaeta *et al.* 2015).

Panulirus regius: is the only indigenous species from the eastern Atlantic, from 35°N to 15°S; common from Cape Juby (Morocco) to southern Angola in Africa; including Cape Verde, Western Mediterranean (east coast of Spain, south coast of France) and Black Sea (Williams 1986; Holthuis 1991).

Discussion

The biogeographic division of the spiny lobster species presented here highlights some co-occurrences per region. In the northwestern Atlantic above the biogeographic barrier of the Amazon-Orinoco plume, *P. guttatus* co-occurs with *P. argus* and *P. laevicauda*. In Brazil, below the Amazon-Orinoco barrier *P. echinatus* co-occurs with *P. meripurpuratus* and *P. laevicauda*. In the oceanic islands of Cape Verde, *P. regius* and *P. echinatus* occur. In Trindade, Martin Vaz, Ascension, Saint Helena and the Canary Islands, only *P. echinatus* dominates. Similar territorial domains have been recorded of the coast of Africa with only *P. regius*. Successful co-occurrence aggressive species like *Panulirus* need to avoid competition and must present different behaviour, feeding and habitat preferences (Connell 1980). Indeed several strategies already have been reported, such as spending the entire benthic cycle in shallow water or adults stage moving to deeper regions (George 2006); different habitat niches within the same reef outcrop (Lozano-Álvarez *et al.* 2007); different aggregation behaviour as anti-predator strategies (Lozano-Álvarez *et al.* 2007); different recruitment time in the year; different diet (Silva & Fonteles-Filho 2011); and possibly a different time of day for foraging. The avoidance of competition and predation even within the same species is important for spiny lobsters during their different life stages, such as reported for juvenile of *P. argus* (Cruz *et al.* 2006). Similarly, as reported for *P. meripurpuratus* in this study in the habitat description, this species uses different habitats according to life stage. More studies *in situ* are necessary, however, to understand the mechanisms used by each species to avoid intra- and interspecific competition in a co-occurrence situation.

The virtual absence of an ecological index for several lobster species such as *P. argus* (see Butler *et al.* 2013) makes it impossible to undertake an effective conservation and management policy for lobsters in the Atlantic Ocean. The implementation of a low impact monitoring methodology such as nocturnal Underwater Visual Censuses suggested by Giraldes *et al.* (2015a, b) is urgently required to obtain the necessary ecological data about these large lobsters in coastal areas. The use of Underwater Visual Censuses has proved successful in obtaining ecological indexes for decapod species including spiny lobsters (Faria Júnior *et al.* 2007; Lozano-Álvarez *et al.* 2007; Rios-Lara *et al.* 2007; Bertelsen *et al.* 2009; Teschima *et al.* 2012; Giraldes *et al.* 2012, 2015a, 2015b). These in-situ studies can provide important ecological information which will aid the protection of threatened lobster species such as; intensity and seasonality of recruitment, differences in populations between sites, foraging habits, feeding behaviour, seasonal changes, spatial distribution, lunar influence, anthropogenic influence, niche differentiations, among others. Therefore, the identification key based in colour patterns presented here will be useful for in-situ studies that will undoubtedly provide crucial data for the conservation of these lobster species in the Atlantic Ocean.

The greatest contribution to conservation of Brazilian lobsters documented in this study is the description of *P. meripurpuratus*, recognizing it as being biogeographically separated from *P. argus*. This is important as the current population models used on stock management are constructed with information based on *P. argus* sensu stricto (Butler *et al.* 2013), thereby misrepresenting the true standing stocks of *P. meripurpuratus*. This is a matter of concern as *P. meripurpuratus* is currently over-exploited in Brazil with stocks in constant decline (Silva & Fonteles-Filho 2011). Naming this species and recognizing it as native species to Brazil could also have the potential to improve management efforts by the Brazilian government and scientific community in creating more adequate legislation and more effective management strategies. These include: protecting the species during the period of

reproduction and spawning at strategic regions, ensuring the recruitment of new specimens, as well as protecting the shallow coastal reefs that act as the lobster's natural nurseries.

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