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Brittle stars from the Saint Peter and Saint Paul Archipelago: morphological and molecular data

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Morphological and molecular data on brittle stars from the Saint Peter and Saint Paul Archipelago, a very small isolated group of islets situated between South America and Africa, are hereby presented. We found no endemic ophiuroids. Instead, the five species, Amphipholis squamata, Ophiactis lymani, Ophiactis savignyi, Ophiocomella ophiactoides *and* Ophiothrix *(*Ophiothrix*)* angulata*, are either cosmopolitan or derived from the equatorial western Atlantic region. Results indicated a western Atlantic colonization and highlighted the existence of cryptic species in the genus* Ophiactis.

Keywords: oceanic islands, equatorial Atlantic Ocean, ophiuroids, mitochondrial sequences, phylogeography

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INTRODUCTION

The Saint Peter and Saint Paul Archipelago (SPSPA) (00°55′N 29°21′W) is a group of very small islets located on the mid-Atlantic ridge, 1010 km from the Cape of Calcanhar, on the north-eastern coast of Brazil and 1824 km from Africa. The SPSPA is a unique setting in the Atlantic Ocean, as the islands were formed by a geological uplift of the seafloor rather than through volcanic activity and have only a thin layer of sedimentary covering (Campos *et al.*, 2009). Due to its very small size and isolation, the SPSPA is of historical and biogeographical interest (Edwards & Lubbock, 1983a, b). It was visited by Charles Darwin during the Beagle Expedition in the first half of the 19th Century, followed by the H.M.S. *Challenger* some decades later. Over the next hundred years, only sporadic scientific reports have come to light. Several manuscripts appeared as a result of the Cambridge Expedition (1979) (Edwards & Lubbock, 1983a, and references therein) and investigations at SPSPA were intensified after the implementation of the Brazilian scientific station in 1998. Since then, there has been a great increase in knowledge of the biodiversity and ecology from SPSPA (Hazin, 2009 and references therein).

Brittle stars, a very common group in benthic communities, live in a great variety of habitats, from sea shores to the deep ocean, in soft sediments or on rocks and in association with corals, sponges, algae and thermal seeps (Hendler *et al.*, 1995; Stöhr *et al.*, 2012). With a total of 2138 described species and subspecies (Stöhr *et al.*, 2014), they comprise the most diverse class of echinoderms, a group that also includes sea urchins, sea cucumbers, sea stars and sea lilies. O'Hara *et al.* (2014) published the most complete phylogeny yet of brittle stars using molecular and fossil data. They used all extant echinoderms classes and confirmed the hypothesis that brittle stars are a sister group of sea stars with a mid-Permian origin. Species that have been recorded from the Brazilian coast constitute about 6% of those known worldwide (Barboza & Borges, 2012). Records from the north-eastern coast and their oceanic islands, such as the Fernando de Noronha Archipelago, are evidence of a tropical fauna that shares most of the species from the Caribbean Sea, revealing the great affinity between the two regions. Bearing in mind the scarcity of records on the diversity and ecology of echinoderms from SPSPA, this article is a contribution towards bridging this gap, by increasing the number of brittle star records, with the inclusion of diagnoses and images and the provision of mitochondrial DNA sequences.

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MATERIAL AND METHODS

Study area

SPSPA comprises four larger islets plus several minor rocks, rising 4000 m from the ocean depths (Figure 1). The emerged area of the archipelago is about 13,000 m², 420 m across at the greatest breadth. The maximum height is 18 m. Belmonte, the largest islet, together with Saint Paul, Saint Peter and Barão de Teffé, constitute a horseshoe-shaped cove 100 m long, 50 m wide and with a maximum depth of around 15–18 m (Figure 1). We sampled the four distinctive sublittoral zones recognized by Edwards & Lubbock (1983a):

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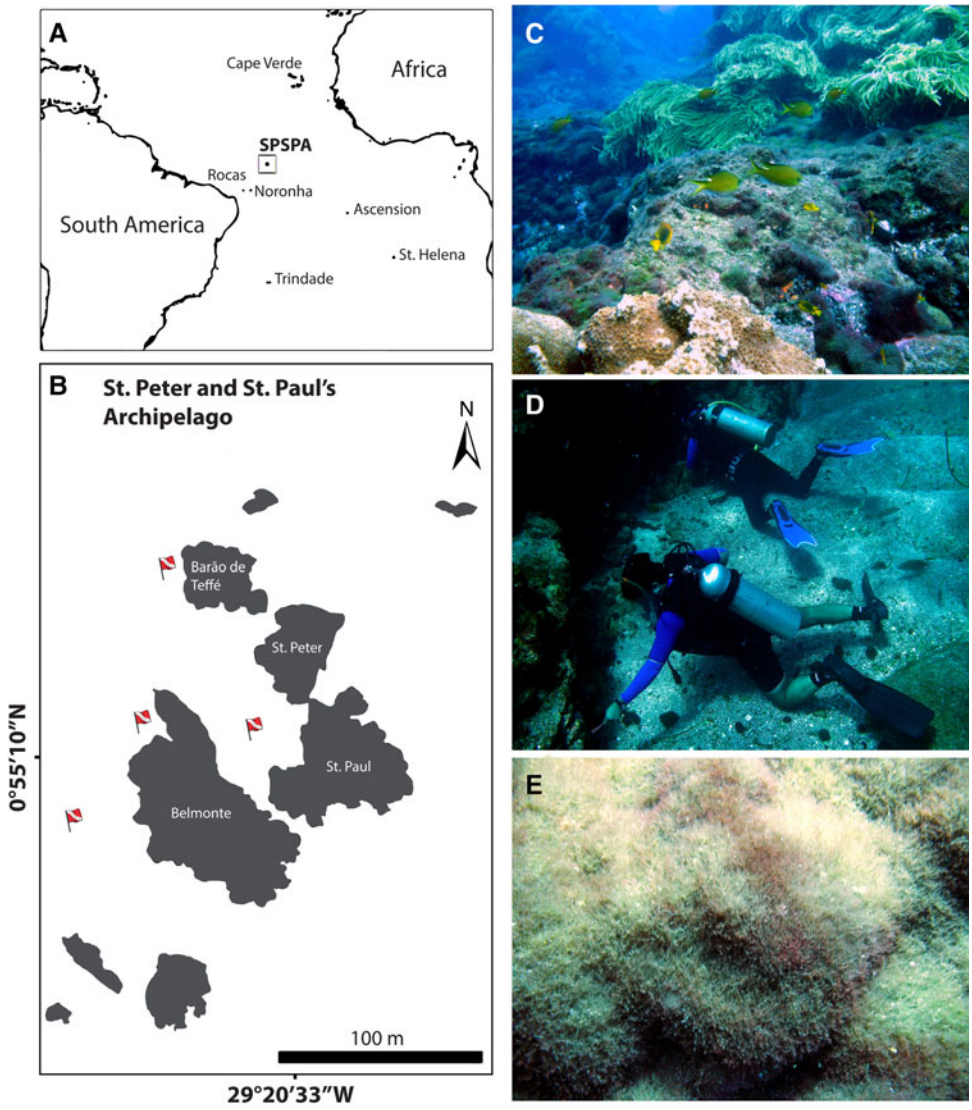


Fig. 1. Location of Saint Peter and Saint Paul's Archipelago (A), dive points distribution (B) and details of sampling sites (C–E).

(1) the *Palythoa* zone (3–8 m), dominated by *Palythoa caribaeum* (Duchassaing & Michelotti, 1860) with the presence of the green alga *Caulerpa racemosa* (Forsskål) J. Agardh, 1873 in the more sheltered areas. The brown alga *Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809a, sponges and hydroids dominate the substrates where *P. caribaeum* is absent; (2) the *Caulerpa racemosa* zone, formed by dense carpets at depths between 3 and 8 m and then between 30 and 6 m, and absent in unstable substrates; (3) the sub-*Caulerpa* zone, which occupies depths deeper than 30–36 m, where *Caulerpa* is replaced by *D. dichotoma*, *Ceratodictyon planicaule* (W.R. Taylor) M.J. Wynne, 2011, *Bryopsis pennata* J.V. Lamouroux, 1809b, crustose lithothamnia, bryozoans, *Antipathes* black corals and sponges; (4) the zones of patches of unstable substrates that occur at depths between 3 and 25 m. This substrate is mainly formed by coarse sand, rubble and rocks (Figure 1D).

The oceanographic regime of the Archipelago is dominated by the influence of the South Equatorial Current (SEC) and the Atlantic Equatorial Undercurrent (UEC) (Araujo & Cintra, 2009). The SEC, the prevailing surface current of the region, flows westward providing connections with east Atlantic waters (Briggs, 1974). As a branch derived from the North Brazilian Current, the UEC flows eastwards at subsurface depths between 60 and 100 m and reaches speeds higher than 100 cm seg^{-1} (Macedo *et al.*, 2009). Thus, despite a westward-prevailing current system, SPSPA is also influenced by western Atlantic waters.

Sampling procedures

Field sampling was conducted by scuba diving during the months of June 2011 and July 2013, in the areas indicated in Figure 1B. Samples of alga-turf, tubes of the polychaete *Chaetopterus* and sponges scraped from rock surfaces were collected at depths between 3 and 30 m. All the material was placed in plastic bags for further sieving. Samples of soft sediments were also collected and subsequently washed through a 0.5 mm mesh. All brittle star individuals were preserved in a 95% alcohol solution. All specimens were deposited at the collection of the National Museum of Rio de Janeiro.

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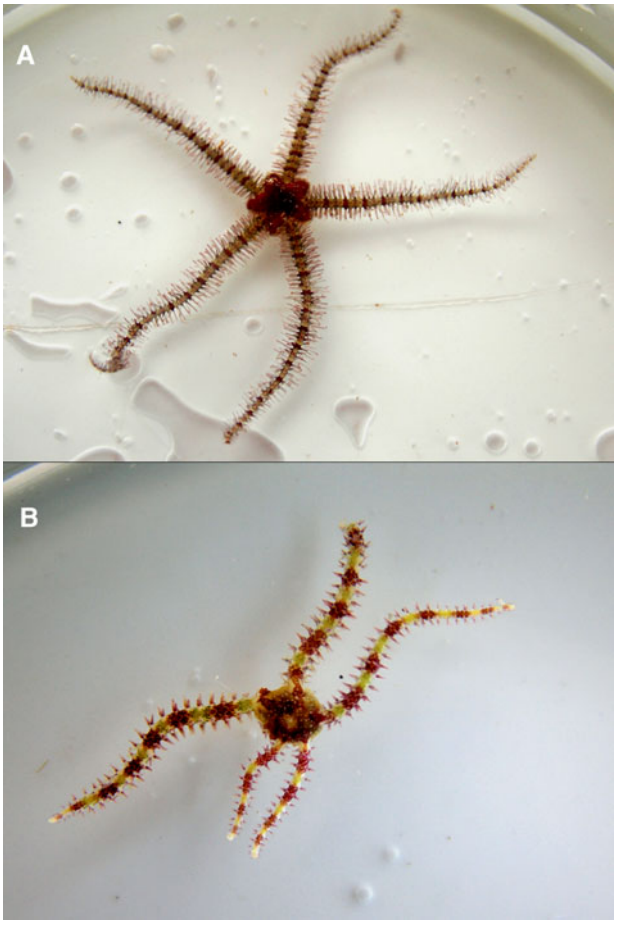


Fig. 2. Living individuals of *Ophiothrix (Ophiothrix) angulata* (A) and *Ophiocomella ophiactoides* (B). Disk diameters are: 5 mm (A), 3.5 mm (B).

Molecular data

Tissue of brittle star arms was used for DNA extraction, according to the NaOH protocol (Floyd *et al.*, 2002). Fragments of COI were amplified using the forward primer COIf (5′-CCTGCAGGAGGAGGAGAYCC-3′) and the reverse primer COIa (5′-AGTATAAGCGTCTGGGTAG TC-3′) (Palumbi *et al.*, 1991). Fragments of 16S were amplified using a contig of the forward primers 16SarL (5′-CGCCT GTTTATCAAAAACAT-3′) and 16SF2 (5′-GTTTCGGTTTA CCAAAAACAT-3′), and reverse primers 16SAN-R (5′-GCT TACGCCGGTCTGAACTCAG-3′) and 16SR2 (5′-AGGTT TTTCTGATCCAACATCG-3′) (Palumbi *et al.*, 1991; Le Gac *et al.*, 2004; Zanol *et al.*, 2010). PCRs were carried out at a total volume of 25 µL, with an annealing temperature of 45°C (COI) and 50°C (16S). Bidirectional sequencing was performed using the same amplification primers. Sequence data were aligned through Muscle using Mega 6.0 (Tamura *et al.*, 2013). For 16S fragments the unalignable bits were removed using GBlocks within SeaView v.4.3.5 (Gouy *et al.*, 2010) applying all the less stringent selection options. Sequences were submitted to GenBank (accession numbers: KP128035-42) and to BOLDSYSTEMS (Brazilian Barcode of Life database [BrBOL]).

To source out to which clade our specimens belong we used GenBank sequences from the brittle star genera *Amphipholis*, *Amphiura*, *Ophiactis*, *Ophionereis*, *Ophiopholis*, *Ophiothrix*, *Macrophiothrix*, *Ophiocoma*, *Ophiopeza* and the sea star *Luidia clathrata* (Say, 1825) (accession numbers: AF331527-30, AF331533, AF331534, AF331536, AF331537, AF331539-73, AF331591, AF331592, AF331594, AF331595, AF331600, AF331601, AF331603-16, AF331629, AF331632, AF331634-36, AF480892-480905, EU583176, EU583205, NC013876, AY652509, KC760129, DQ297108, AY652511-13, AY365182, AY365179, AY365169, AY365176, AY365153-55, AY365161, AY365147, AY365158, AY365143, AY365165, AY365170, AY365174, KF662941-42, DQ297102, KC760098, HM473899, DQ297096). Maximum-likelihood (ML) trees were obtained using the program Mega 6.0 (Tamura *et al.*, 2013) using GTR + G + I (16S) and T92 + G + I (COI) models of evolution and 1000 pseudo-replicates to calculate bootstrap values.

RESULTS

A total of 108 individuals of five species representing four families were sampled: Ophiotrichidae, *Ophiothrix* (*Ophiothrix*) *angulata* (Say, 1825) (N = 1); Ophiocomidae, *Ophiocomella ophiactoides* (H.L. Clark, 1900) (N = 3); Amphiuridae, *Amphipholis squamata* (Delle Chiaje, 1828) (N = 43); Ophiactidae, *Ophiactis lymani* Ljungman, 1872 (N = 89); and *Ophiactis savignyi* (Müller & Troschel, 1842) (N = 6).

Taxonomic account

SYSTEMATICS

Order OPHIURIDA Müller & Troschel, 1840
Family OPHIOTRICHIDAE Ljungman, 1867
Ophiothrix (*Ophiothrix*) *angulata* Say, 1825
(Figures 2A, 3A–E)

MATERIAL EXAMINED

One individual (0.91°N 29.34°W, 5 m, July 2013). Disk diameter: 5 mm.

DIAGNOSIS

A living individual is presented in Figure 2A. Disk bears long spines with bifid and trifid tips (Figure 3A, B). The spines also cover the radial shields, but less densely. Oral shields wider than long. Adoral shields wing-like and separated at the proximal edge (Figure 3C). A clump of oral papillae at the tip of each jaw (Figure 3C). Dorsal arm plates longer than wide, the convex distal edge slightly lobed (Figure 3D). Ventral plates longer than wide with a median depression on distal edge (Figure 3E). Seven to eight very thorny arm spines. Dorsal ones are three segments in length, decreasing ventrally. One very small tentacle scale. The ground colour is violet. Arms have regular transverse violet banding pattern that extend to the spines. The distal edge of the dorsal arm plates is white. These plates also have irregular white spots. A longitudinal stripe on the upper side of the arm is wanting.

DISTRIBUTION

West coast of Mexico, Florida, Gulf of Mexico and the Caribbean, between 0 and 540 m (Hendler *et al.*, 1995; Miloslavich *et al.*, 2010; Stöhr *et al.*, 2014). Recorded along the entire Brazilian coast (Barboza & Borges, 2012 and references therein).

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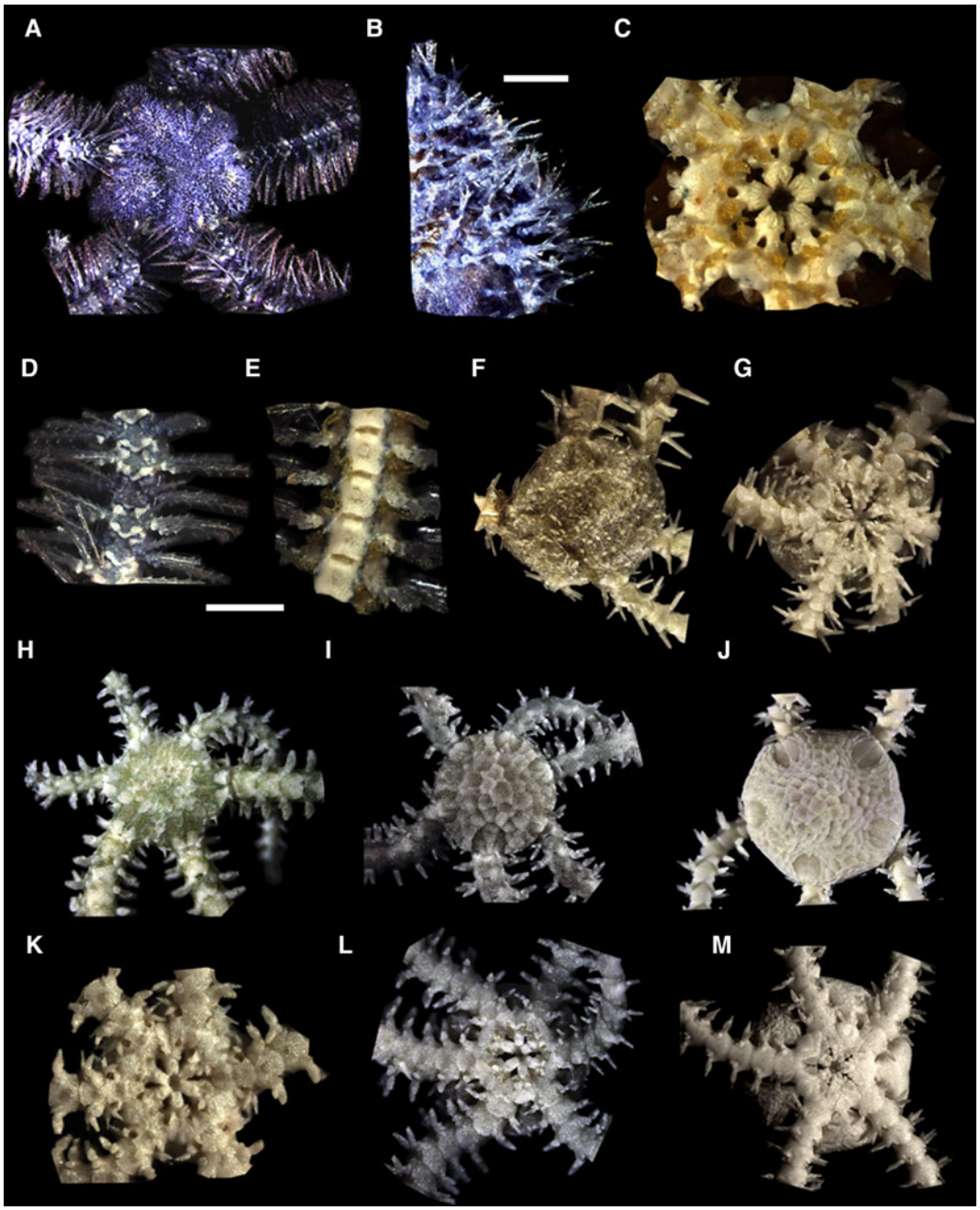


Fig. 3. *Ophiothrix (Ophiothrix) angulata*: dorsal view (A), details from the spines of the disk (B), ventral view (C), dorsal view of the arms (D), ventral view of the arms (E). *Ophiocomella ophiactoides*: dorsal view (F), ventral view (G). *Ophiactis savignyi*: dorsal view (H), ventral view (K). *Ophiactis lymani*: dorsal view (I), ventral view (L). *Amphipholis squamata*: dorsal view (J), ventral view (M). Disk diameters are: 5 mm (A and C), 3.5 mm (F–G), 2.8 mm (H–K), 2.3 mm (I–L) and 2.8 mm (J–M). Scale bars: B, 0.2 mm, D and E, 1.25 mm.

REMARKS

Ophiothrix (*Ophiothrix*) *angulata* has a great diversity in all characters used to distinguish the *Ophiothrix* species (Clark, 1918). From a typical form *sensu* Clark (1918), our specimen differs by lacking a white longitudinal stripe on the upper side of the arms and flattened or smoothed upper arm spines. In this study, it was sampled and associated with *Chaetopterus* polychaete tubes.

Order OPHIURIDA Müller & Troschel, 1840
Family OPHIOCOMIDAE Ljungman, 1867
Ophiocomella ophiactoides H.L. Clark, 1900
(Figures 2B, 3F–G)

MATERIAL EXAMINED

Four individuals (0.91°N 29.34°W, 5–15 m, July 2013). Disk diameter: 1.5–3.5 mm.

DIAGNOSIS

A living individual is presented in Figure 2B (one broken arm). Hexamerous, fissiparous species. Disk dorsally covered with scales bearing conical spines (Figure 3F). Only the tips of the radial shields are visible. Each jaw, longer than wide, bears two apical and three lateral papillae (Figure 3G). Oral shields slightly longer than wide with a distal lobe. Adoral shields long, with flaring distal edge (Figure 3G). Dorsal

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arm plates longer than wide with a convex distal edge. Ventral plates longer than wide with truncated edge. Three or four conical spines and one tentacle scale.

DISTRIBUTION

A shallow water species recorded from the west coast of Mexico, Gulf of Mexico and the Caribbean (Hendler *et al.*, 1995; Miloslavich *et al.*, 2010; Stöhr *et al.*, 2014). In Brazil, it has been recorded from the Vitoria–Trindade Seamount Chain to the north-east coast (Barboza & Borges, 2012 and references therein).

REMARKS

Ophiocomella ophiactoides is a common brittle star from north-eastern Brazil. In this study it was sampled associated with algae (absent on *Caulerpa* turfs).

Order Ophiurida Müller & Troschel, 1840
Family Ophiactidae Matsumoto, 1915
Ophiactis savignyi (Müller & Troschel, 1842)
(Figure 3H–K)

MATERIAL EXAMINED

Five individuals (0.91°N 29.34°W, 15 m, June 2011); one individual (0.91°N 29.34°W, 8 m, July 2013). Disk diameter: 1–3 mm.

DIAGNOSIS

Hexamerous brittle star. Disk with conical spines at the distal edge and between the pairs of radial shields (Figure 3H). The latter are contiguous lengthwise over at least half of the internal edges. Oral shields with rounded edges as wide as long. Each jaw bears a rectangular tooth at the tip (Figure 3K). The number of lateral oral papillae can vary from no papillae, to one, two or three. Variability can occur in a single individual (Figure 3K). Dorsal arm plates as wide as long. Ventral plates with a slightly convex distal edge. Four to five thorny arm-spines. One tentacle scale.

DISTRIBUTION

Cosmopolitan species from tropical and temperate waters between depths of 0 and 550 m (Roy & Sponer, 2002; Pawson *et al.*, 2009). Recorded along the entire Brazilian coast (Barboza & Borges, 2012 and references therein). Suspected to be a species complex.

REMARKS

Clark (1918) reported individuals with none, one or two papillae. This variability was also pointed out by Tommasi (1970). Here, as mentioned by Clark (1918), small specimens have less fan-shaped dorsal arm plates and coarser dorsal disk scales. In this study individuals were sampled associated with algae (absent on *Caulerpa* turfs). Most presented evidence of regeneration.

Order Ophiurida Müller & Troschel, 1840
Family Ophiactidae Matsumoto, 1915
Ophiactis lymani Ljungman, 1872
(Figure 3I–L)

MATERIAL EXAMINED

24 individuals(0.91°N 29.34°W, 5–30 m, June 2011); 65 individuals (0.91°N 29.34°W, 5–20 m, July 2013). Disk diameter: 0.5–2.5 mm.

DIAGNOSIS

Hexamerous species. Disk covered above (Figure 3I) and below (Figure 3L) with scales. Radial shields separated proximally and in contact at distal edge. Oral shields rhombic. Adoral shields distally enlarged and separated at proximal edge. A distinctive rectangular tooth at the tip of each jaw. One lateral oral papilla (Figure 3L). Fan-shaped dorsal arm-plates, wider than long on proximal segments and as wide as long on distal ones. Ventral plates pentagonal. Three conical, minutely thorny arm-spines. One tentacle scale.

DISTRIBUTION

Caribbean Sea and South Atlantic, between depths of 0 and 600 m (Tommasi, 1970; Monteiro, 1987; Miloslavich *et al.*, 2010; Stöhr *et al.*, 2014). Recorded along the entire Brazilian coast (Barboza & Borges, 2012 and references therein).

REMARKS

Ophiactis lymani is a very common brittle stars species from the western Atlantic that can be distinguished from *Ophiactis savignyi* by: (1) the shape of the dorsal scales of the disk; (2) the more fan-shaped dorsal arm plates; (3) the morphology of the arm spines. In this study *Ophiactis lymani* was primarily sampled associated with algae (absent on *Caulerpa* turfs). Almost all the individuals were regenerating parts of the arms or the disk.

Order Ophiurida Müller & Troschel, 1840
Family Amphiuridae Ljungman, 1867
Amphipholis squamata (Delle Chiaje, 1828)
(Figure 3J–M)

MATERIAL EXAMINED

Five individuals (0.91°N 29.34°W, 5–30 m, June 2011); 38 individuals (0.91°N 29.34°W, 5–20 m, July 2013). Disk diameter: 1–3 mm.

DIAGNOSIS

Both sides of the disc covered with plates. Radial shields internally united (Figure 3J). Oral shields rhombic (Figure 3M). Longer than wide wing-like adoral shields meet inter-radially. Two apical papillae. Two lateral oral papillae, the distal one enlarged (Figure 3M). Dorsal arm-plates with rounded distal edges. Ventral arm-plates pentagonal. Three to four conical and minutely thorny arm-spines. Two small tentacle scales.

DISTRIBUTION

Cosmopolitan species of tropical and temperate waters between depths of 0 and 1.200 m (Paterson, 1985; Boissin *et al.*, 2008; Stöhr *et al.*, 2014). Recorded along the entire Brazilian coast (Barboza & Borges, 2012 and references therein). Suspected to be a species complex.

REMARKS

Due to the size of the examined specimens there are no visible primary plates on the disc as an adult. In this study

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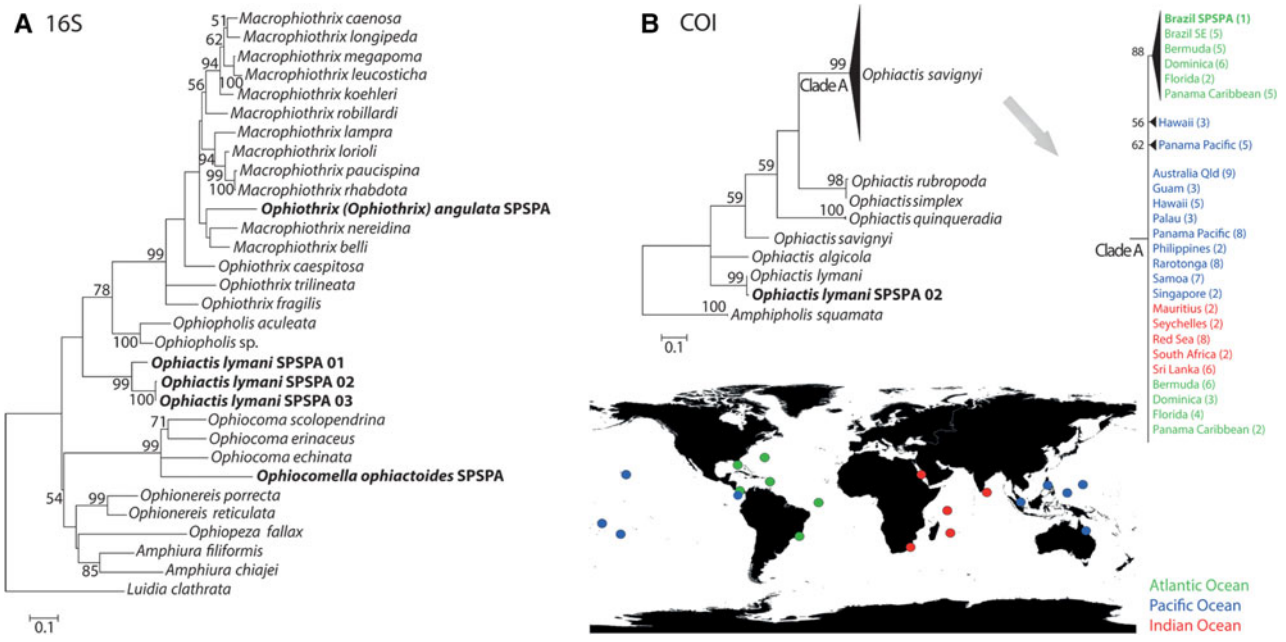


Fig. 4. Maximum-likelihood trees of the 16S (A) and COI (B) mitochondrial fragments. Parentheses indicate the number of sequences from each location. Values associated with nodes are bootstrap support (1000 replicates) using GTR + G + I (16S) and T92 + G + I (COI) models. Figure at the bottom right represents the localities of sequences (COI) from *Ophiactis savignyi*.

Amphipholis squamata, a common brittle star in SPSPA, was sampled associated with algae (absent for *Caulerpa* turfs) and in soft substrates.

Molecular results

Sequences were obtained for four of the five species, 16S: *Ophiothrix* (*Ophiothrix*) *angulata* (1; 433 bp), *Ophiocomella ophiactoides* (1; 433 bp), *Ophiactis lymani* (3; 433 bp); COI *Ophiactis savignyi* (1; 301 bp), *Ophiactis lymani* (1; 227 bp) and *Ophiocomella ophiactoides* (1; 409 bp). *Ophiactis lymani* formed a single clade with high support in the 16S and COI trees (Figure 4). However, we got a high molecular divergence (p-distance = 8.5) between sequences of the 16S tree (Figure 4A). Our sequence of *Ophiactis savignyi* was included in a clade formed by western Atlantic sequences from the Caribbean, Florida and Brazil (Figure 4B). The *Ophiactis savignyi* species complex was formed by multiple lineages with molecular divergence, ranging from 0.0 to 5.4%. In the 16S tree, *Ophiothrix* (*Ophiothrix*) *angulata* was included in the clade of Ophiotrichidae sequences. Our 16S sequence of *Ophiocomella ophiactoides* formed the sister group of the genus *Ophiocoma* with high molecular support (Figure 4A). In the COI tree, the resulting topology was a long branch without support inside the *Ophiactis* clade (data not presented).

DISCUSSION

This article is instrumental in updating the records of brittle stars from SPSPA, since only *Ophiactis savignyi* had been previously recorded (Edwards & Lubbock, 1983a) and in adding new sequences to Genbank that could surrogate future phylogeography investigations. The very low brittle star diversity is probably due to islets isolations and a small area of shallow waters (<50 m) of less than 0.5 km² (Edwards & Lubbock, 1983b), thereby resulting in reduced habitat heterogeneity.

It is noteworthy that, in contrast to the endemism expected to be found at oceanic islands (MacArthur & Wilson, 1967), and as observed for the reef fishes (Feitoza *et al.*, 2003), molluscs (Oliveira *et al.*, 2009) and sponges (Moraes *et al.*, 2006) from SPSPA, all the brittle stars recorded in this study have a global or wide-geographic distribution. However, molecular results showed that we must take care with these results and diversity could be underestimated. *Ophiactis savignyi*, a complex of species recorded in tropical waters worldwide, has been extensively studied (Clark, 1946; Roy & Sponer, 2002). Commonly found in the fouling communities of harbours and ship hulls, over time this wide distribution has probably been enhanced by anthropogenic influence (Hendler *et al.*, 1999; Paulay *et al.*, 2002; Roy & Sponer, 2002; Hendler & Brugneaux, 2013). Considering a within-species molecular p-distance ranging from 0 to 2.2% baseline for brittle-star COI-sequence divergence (Ward *et al.*, 2008), our results revisited the existence of multiple cryptic lineages of *Ophiactis savignyi*. However, the minimum pairwise distance of 0.0% from SPSPA sequence and available western Atlantic sequences contradicts the idea of endemic genetic lineage in SPSPA. On the other hand, one sequence of *Ophiactis lymani* diverged by 8.5% from the clade formed by the other two, revealing the existence of two lineages. *Ophiactis lymani* is a very common amphi-Atlantic brittle star and elucidation requires further molecular analyses. *Amphipholis squamata* is another example of a complex of species recorded worldwide and commonly found on corals, sponges, algal turf and bryozoan colonies (Boissin *et al.*, 2008). *Amphipholis squamata* predominates in the scarce soft substrate of SPSPA, probably by taking advantage of the absence of other common species of coarse sand and rubble, such as species of the genera *Ophiophragmus* and *Microphiopholis*.

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Despite the fact that our 16S tree is congruent in resolving the position of species sequences in relation to family and genera levels, it is not a probable phylogenetic reconstruction of the families' relationships – that is a subject beyond the scope of our study. The position of Ophiocomidae has a low bootstrap support, Amphiuridae is probably not a sister taxon of Ophionereididae and the position of the long branch of *Ophiopeza* (Ophiodermatidae) is also probably wrong (see Smith *et al.*, 1995; O'Hara *et al.*, 2014). The relationship between Ophiactidae and Ophiotrichidae is well supported by other studies (Smith *et al.*, 1995; O'Hara *et al.*, 2014). The relationship between *Ophiopholis* (Ophiactidae) and Ophiotrichidae was got by Smith *et al.* (1995) and our results indicated that *Ophiopholis* is closer with Ophiotrichidae than Ophiactidae.

Whilst *A. squamata* and *Ophiactis savignyi* are cosmopolitan species that occur in the eastern Atlantic, the other three are common brittle stars from the Caribbean, the Gulf of Mexico and north-eastern Brazil. More than 70% of the benthic species of SPSPA included in the analysis of Edwards & Lubbock (1983b) are exclusively from the western Atlantic. According to them, the transportation of larvae and small organisms from Brazil to SPSPA can passively occur over a period of three to five weeks, time enough for planktonic echinoderm larvae to reach the rocks. For example, the late ophiopluteus stage of *Ophiactis savignyi* is reached in about 21 days (Mortensen, 1931). Furthermore, if the proper environmental conditions are not encountered, metamorphosis can be delayed for several more days (Thorson, 1950). Chesher (1966) suggested that the transportation of echinoid larvae by the UEC from the west to east Atlantic, a trip that would take at least 43 days, 70 at the most, is enough to maintain genetic flow between populations. Our molecular results support the idea of a western Atlantic colonization. The Fernando de Noronha Archipelago, 627 km to the west, is the closest source of potential colonists via UEC. Colonization by juveniles and adults associated with drifting algae is also a very plausible hypothesis (Winston, 2012).

The transportation of immigrants from the east Atlantic by the SEC, the prevailing surface current, must be considered for the sea urchin *Eucidaris clavata* Mortensen, 1928 and the sea cucumber *Holothuria* (*Halodeima*) *manningi* Pawson, 1978, two further echinoderm species from SPSPA that also occur at Ascension Island, 1940 km off in the south-east Atlantic (Edwards & Lubbock, 1983b). Another hypothesis could be the multiple colonization of SPSPA, which seems to have occurred with the fireworm *Eurythoe complanata* Pallas, 1766 (Barroso *et al.*, 2010). Edwards & Lubbock (1983b) suggested that for many species, arrival is only occasional, as exemplified by the single young individual of *Eucidaris clavata* collected by the Cambridge Expedition. After more than 40 diving-hours, we also found only two individuals. *Eucidaris clavata* was also seen by other research divers in the past (unpublished data). This shows that even species found at very low densities can commonly reach the rocks and the SPSPA may serve as stepping stones for larval dispersal across the Atlantic. Even so, simple arrival is insufficient to colonize a site. At this point, it is important to highlight that three (*Ophiactis lymani*, *Ophiactis savignyi*, *Ophiocomella ophiactoides*) of the five species of brittle stars recorded in SPSPA are fissiparous, possibly an important mechanism for enhancing population density by cloning individuals.

Fishing boats and vessels have been visiting SPSPA or the surrounding waters for a long time and occasional arrival events mediated by anthropogenic vectors cannot be discharged. However, against this hypothesis, *Ophiothela mirabilis* Verrill, 1867, a native Pacific species that invaded the Atlantic Ocean during the last decades through the probable association with ship hulls and today occurs along almost the entire Brazilian coast (Hendler *et al.*, 2012), is completely absent in SPSPA.

The records of brittle stars from SPSPA, a rather poor fauna in a small isolated oceanic archipelago, are updated. The list is composed of cosmopolitan species and those with a wide geographic distribution, commonly found along the Brazilian and Caribbean coasts. There are indications that, similar to *Ophiactis savignyi*, the common amphi-Atlantic brittle star *Ophiactis lymani* comprises a species complex, but this topic requires future molecular investigations. Data pointed to a prevailing western Atlantic colonization of SPSPA.

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REFERENCES

Agardh J.G. (1873) Till algernes systematik. Nya bidrag. *Lunds Universitets Års-Skrift, Afdelningen for Mathematik och Naturvetenskap* 9, 1–71.

Araújo M. and Cintra M. (2009) Modelagem matemática da circulação oceânica da região equatorial. In Hazin F.H.V. (ed.) *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília: Secretaria da Comissão Interministerial para os Recursos do Mar, pp. 106–113.

Barboza C.A.M. and Borges M. (2012) A check list of the extant species of ophiuroids from Brazilian waters. *Zootaxa* 3447, 1–21.

Barroso R., Klautau K., Solé-Cava A.M. and Paiva P.C. (2010) *Eurythoe complanata* (Polychaeta: Amphinomidae), the 'cosmopolitan' fireworm, consists of at least three cryptic species. *Marine Biology* 157, 69–80.

Boissin E., Féral J.P. and Chenuil A. (2008) Defining reproductively isolated units in a cryptic and syntopic species complex using mitochondrial and nuclear markers: the brooding brittle star, *Amphipholis squamata* (Ophiuroidea). *Molecular Ecology* 17, 1732–1744.

Briggs J.C. (1974) *Marine Zoogeography*, 1st edn. New York: MacGraw-Hill Book Co.

Campos T.F.C., Petta R.A., Theye T., Sichel S.E., Simões L.S.A., Srivastava N.K., Motoki A., Neto J.V. and Andrade F.G.G. (2009) Posição ímpar do Arquipélago São Pedro São Paulo na diversidade

https://doi.org/10.1017/S1755267214001511 Published online by Cambridge University Press

geológica da Terra. In Hazin F.H.V. (ed.) *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília: Secretaria da Comissão Interministerial para os Recursos do Mar, pp. 54–63.

Clark H.L. (1900) The echinoderms of Porto Rico. *Bulletin of the U.S. Fisheries Commission* 20, 232–263.

Clark H.L. (1918) Brittle-stars, new and old. *Bulletin of the Museum of Comparative Zoology at Harvard College* LXII, 266–338.

Clark H.L. (1946) *The echinoderm fauna of Australia: its composition and its origins*. Washington: Carnegie Institute of Washington Publication.

Chesher R.H. (1966) The R/V Pillsbury deep-sea biological expedition to the Gulf of Guinea, 1964–65, 10: report on the Echinoidea collected by the R/V Pillsbury in the Gulf of Guinea. *Studies in Tropical Oceanography, Institute of Marine Sciences (University of Miami)* 4, 209–223.

Delle Chiaje S. (1828) *Memorie sulla storia e anotomia degli animali senza vertebre del regno di Napoli*. Napoli: Fratelli Fernandes (Vol. 1) and Società Tipografica (Vol. 2–4).

Duchassaing P. and Michelotti J. (1860) Mémoire sur les coralliaires des Antilles. *Mémoires de l'Academie des Sciences de Turin* 19, 279–365.

Edwards A. and Lubbock R. (1983a) The ecology of Saint Paul's rocks (Equatorial Atlantic). *Journal of Zoology, London* 200, 51–69.

Edwards A. and Lubbock R. (1983b) Marine zoogeography of Saint Paul's rocks. *Journal of Biogeography* 10, 65–72.

Feitoza B.M., Rocha L.A., Luiz-Júnior O.J., Floeter S.R. and Gasparini J.L. (2003) Reef fishes of St. Paul's rocks: new records and notes on biology and zoogeography. *Aquatic Journal of Ichthyology and Aquatic Biology* 7, 62–82.

Floyd R., Abebe E., Papert A. and Blaxter M. (2002) Molecular barcodes for soil nematode identification. *Molecular Ecology* 11, 839–850.

Gouy M., Guindon S., Gascuel O. (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27, 221–224.

Hazin F.H.V. (2009) *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*, 1st edn. Brasília: Secretaria da Comissão Interministerial para os Recursos do Mar.

Hendler G. and Brugneaux S. (2013) New records of brittle stars from French Guiana: *Ophiactis savignyi* and the alien species *Ophiothela mirabilis* (Echinodermata: Ophiuroidea). *Marine Biodiversity Records* 6, 1–5.

Hendler G., Baldwin C.C., Smith D.G. and Thacker C.E. (1999) Planktonic dispersal of juvenile brittle stars (Echinodermata: Ophiuroidea) on a Caribbean reef. *Bulletin of Marine Science* 65, 283–288.

Hendler G., Migotto A.E., Ventura C.R.R. and Wilk L. (2012) Epizoic *Ophiothela* brittle stars have invaded the Atlantic. *Coral Reefs* 31, 1005.

Hendler G., Miller J.E., Pawson D.L. and Kier P.M. (1995) *Sea stars, sea urchins and allies: echinoderms of Florida and the Caribbean*, 1st edn. Washington: Smithsonian Institution Press.

Lamouroux J.V.F. (1809a) Exposition des caractères du genre Dictyota, et tableau des espèces qu'il renferem. *Journal de Botanique Desvaux* 2, 38–44.

Lamouroux J.V.F. (1809b) Observations sur la physiologie des algues marines, et description de cinq nouveaux genres de cette famille. *Nouveau Bulletin des Sciences, par la Société Philomathique de Paris* 1, 330–333.

Le Gac M., Féral J.P., Poulin E., Veyret M. and Chenuil A. (2004) Identification of allopatric clades in the cosmopolitan ophiuroid species complex *Amphipholis squamata* (Echinodermata). The end of a paradox? *Marine Ecology Progress Series* 278, 171–178.

Ljungman A. (1867) Ophiuroidea viventia huc usque cognita enumerat. *Öfversigt af Kongliga Vetenskaps-Akademiens Forhandlingar* 23, 303–336.

Ljungman A.V. (1872) Förteckning öfver uti Vestindien af Dr A. Goës samt under korvetten Josefinas expedition i Atlantiska Oceanen samlade Ophiurider. *Öfversigt af Kungliga Vetenskapsakademiens Förhandlingar 1871* 28, 615–658.

MacArthur R.H. and Wilson E.O. (1967) *The theory of island biogeography*, 1st edn. Princeton, NJ: Princeton University Press.

Macedo S.J., Montes M.J.F. and Costa K.M.P. (2009) Hidrologia. In Hazin F.H.V. (ed.) *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília: Secretaria da Comissão Interministerial para os Recursos do Mar, pp. 101–106.

Matsumoto H. (1915) A new classification of the Ophiuroidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 67, 43–92.

Monteiro A.M.G. (1987) *Ophiuroidea (Echinodermata) da região de Ubatuba (SP) – aspectos morfológicos e ecológicos*. Phd thesis, Universidade de São Paulo, São Paulo, Brazil.

Moraes F., Ventura M., Klautau M., Hajdu E. and Muricy G. (2006) Biodiversidade de esponjas das ilhas oceânicas brasileiras. In Alves R. and Castro J. (eds) *Ilhas Oceânicas Brasileiras – da pesquisa ao manejo*. Brasília: Ministério do Meio Ambiente, pp. 147–178.

Mortensen T. (1928) A monograph of the Echinoidea. 1, Cidaroidea. Copenhagen and London: C.A. Reitzel and Oxford University Press.

Mortensen T. (1931) Contributions to the study of the development and larval forms of Echinoderms I–II. *Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afdeling*, Series 9, 4, 1–39.

Miloslavich P., Díaz J.M., Klein E., Alvarado J.J., Díaz C., Gobin J., Escobar-Briones E., Cruz-Motta J.J., Weil E., Cortés J., Bastidas A.C., Robertson R., Zapata F., Martín A., Castillo J., Kazandjian A., Ortiz M. and Hernández C.E. (2010) Marine biodiversity in the Caribbean: regional estimates and distribution patterns. *PLoS ONE* 5, e11916, doi: 10.1371/journal.pone.0011916.

Müller J. and Troschell F.H. (1840) *System der Asteriden. 1. Asteriae. 2. Ophiuridae*. Braunschweig: Friedrich Vieweg & Sohn Verlag.

Müller J.H. and Troschel F.H. (1842) *System der Asteriden*. Braunschweig: Friedrich Vieweg & Sohn Verlag.

O'Hara T.D., Hugall A.F., Thuy B. and Moussalli A. (2014) Phylogenomic resolution of the class ophiuroidea unlocks a global microfossil record. *Current Biology* 24, 1874–1879.

Oliveira P.S., Martins-Silva M.J., Barros J.C.N., Swoboda I., Francisco J.A., Schneider M., Batista J.C.L., Aquino P.P.U., Vianna G. and Coutinho M.F. (2009) Malacofauna. In Hazin F.H.V. (ed.) *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília: Ministério do Meio Ambiente, pp. 106–113.

Pallas P.S. (1766) *Miscellanea zoologica quibus novae imprimis atque obscurae Animalium species describuntur et observationibus iconibusque illustrantur*. Hagae: Petrum Van Cleef.

Palumbi S., Martin A., Romano S., McMillan W.O., Stice L. and Grabowski G. (1991) *The simple fool's guide to PCR*, ver. 2.0. Honolulu: University of Hawaii.

Paulay G., Kirkendale L., Lambert G. and Meyer C. (2002) Anthropogenic biotic interchange in a coral reef ecosystem: a case study from Guam. *Pacific Science* 56, 403–422.

Paterson G.L.J. (1985) The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History), Zoology Series* 49, 1–162.

Pawson D.L. (1978) The echinoderm fauna from Ascension Island, South Atlantic Ocean. *Smithsonian Contribution to the Marine Sciences, Occasional Publications*, no. 2, 31 pp.

https://doi.org/10.1017/S1755267214001511 Published online by Cambridge University Press

Pawson D.L., Vance D., Messing C.G., Solis-Marin F.A. and Mah C.L. (2009) Echinodermata of the Gulf of Mexico. In Felder D.L. and Camp D.K. (eds) *Gulf of Mexico, origin, waters, and biota. 1. Biodiversity*. Texas: A&M University Press, pp. 1177–1204.

Roy M.S. and Sponer R. (2002) Evidence of a human-mediated invasion of the tropical Western Atlantic by the 'world's most common brittle star'. *Proceedings of the Royal Society of London B* 269, 1017–1023.

Say T. (1825) On the species of the Linnaean genus *Asterias* inhabiting the coast of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 5, 141–154.

Smith A.B., Paterson G.L.J. and Lafay B. (1995) Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. *Zoological Journal of the Linnean Society* 114, 213–243.

Stöhr S., O'Hara T.D. and Thuy B. (2012) Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS ONE* 7, 1–14.

Stöhr S., O'Hara T.D. and Thuy B. (2014) *World Ophiuroidea database*. Available at: http://www.marinespecies.org/ophiuroidea (accessed 10 July 2014).

Tamura K., Stecher G., Peterson D., Filipski A. and Kumar S. (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30, 2725–2729.

Tommasi L.R. (1970) Os ofiuróides recentes do Brasil e de regiões vizinhas. *Contribuições Avulsas do Instituto Oceanográfico da Universidade de São Paulo, Série Oceanografia Biológica* 20, 1–146.

Thorson G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society* 25, 1–45.

Ward R.D., Holmes B.H. and O'Hara T.D. (2008) DNA barcoding discriminates echinoderm species. *Molecular Ecology Resources* 8, 1202–1211.

Winston J.E. (2012) Dispersal in marine organisms without a pelagic larval phase. *Integrative and Comparative Biology* 52, 447–457.

Wynne M.J. (2011) A checklist of benthic marine algae of the tropical and subtropical western Atlantic: third revision. *Nova Hedwigia Beihefte* 140, 7–166.

Verrill A.E. (1867) Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. No. 2. Notes on the Echinoderms of Panama and the West Coast of America with descriptions of new genera and species. *Transactions Connecticut Academy Arts & Sciences* 1, 251–322.

and

Zanol J., Halanych K.M., Struck T.H. and Fauchald K. (2010) Phylogeny of the bristle worm family Eunicidae (Eunicida, Annelida) and the phylogenetic utility of non-congruent 16S, COI and 18S in combined analyses. *Molecular Phylogenetics and Evolution* 55, 660–676.

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