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Overview of the biodiversity and distribution of the Class Homoscleromorpha in the Tropical Western Atlantic

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In this study we revise the current knowledge on the biodiversity and distribution of the Class Homoscleromorpha in the Tropical Western Atlantic (TWA). Twenty-seven species are currently recognized in the TWA, belonging to the genera Oscarella *(*O. nathaliae*),* Plakortis *(*P. angulospiculatus, P. dariae, P. edwardsi, P. halichondrioides, P. insularis, P. microrhabdifera, P. myrae, P. petrupaulensis, P. potiguarensis, P. simplex, P. spinalis, P. zyggompha*),* Plakinastrella *(*P. globularis, P. microspiculifera, P. onkodes, P. stinapa*),* Plakina *(*P. coerulea, P. elisa, P. jamaicensis, P. monolopha, P. tetralopha, P. trilopha, P. versatilis*),* Corticium *(*C. diamantense, C. quadripartitum*) and* Tetralophophora *(*T. mesoamericana*). Three of these 'species' are cosmopolitan and in fact represent complexes of cryptic species:* Plakina monolopha, P. trilopha *and* Plakortis simplex. *All other 24 species reported are TWA endemics. Only four species are found both in the Caribbean and in Brazil:* Plakortis angulospiculatus, P. halichondrioides, Plakinastrella microspiculifera *and* P. onkodes, *but these may also be species complexes. Seven species are Brazilian endemics:* Plakina coerulea, Plakinastrella globularis, Plakortis insularis, P. microrhabdifera, P. petrupaulensis, P. potiguarensis *and* P. spinalis. *Thirteen species are restricted to the Tropical North-western Atlantic:* Corticium diamantense, C. quadripartitum, Oscarella nathaliae, Plakina elisa, P. jamaicensis, P. tetralopha, P. versatilis, Plakortis dariae, P. edwardsi, P. myrae, P. zyggompha, Plakinastrella stinapa *and* Tetralophophora mesoamericana. *The Greater Antilles is the richest ecoregion, with 12 species reported. Only the Guianan ecoregion has no records of Homoscleromorpha. Several undescribed species of* Oscarella *and* Plakina *are also known from the TWA. We estimate that the biodiversity of Homoscleromorpha in the TWA is at least twice as high than currently known.*

Keywords: Homoscleromorpha, Porifera, biodiversity, distribution, Tropical Western Atlantic

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INTRODUCTION

The Class Homoscleromorpha Bergquist, 1978 is the smallest class of sponges, with 103 species classified in a single order (Homosclerophorida Dendy, 1905) and two families (Oscarellidae von Lendenfeld, 1887 and Plakinidae Schulze, 1880; cf. van Soest *et al.*, 2015). Only one genus is currently accepted in family Oscarellidae: *Oscarella* Vosmaer, 1884, without skeleton. Another aspiculate genus, *Pseudocorticium* Boury-Esnault *et al.*, 1995, was recently synonymized to *Oscarella* by Gazave *et al.* (2013). Six genera are valid in family Plakinidae: *Plakortis* Schulze, 1880, *Plakinastrella* Schulze, 1880, *Plakina* Schulze, 1880, *Corticium* Schmidt, 1862, *Placinolopha* Topsent, 1897 and *Tetralophophora* Rützler *et al.*, 2014, all with a skeleton composed of siliceous spicules (diods, triods, smooth calthrops, lophose calthrops, candelabra and microrhabds; Díaz & van Soest, 1994; Muricy & Díaz, 2002; Gazave *et al.*, 2010, 2013; Rützler *et al.*, 2014).

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In recent years, the Homoscleromorpha has gained special attention due to its relevant position at the basis of the metazoan phylogenetic tree. The presence of a basement membrane made of type IV collagen is considered a synapomorphy of the Eumetazoa and Homoscleromorpha that is not shared with other sponges (Boute *et al.*, 1996). Their cinctoblastula larvae is similar to a presumed step on metazoan evolution (Nielsen, 2008; Ereskovsky *et al.*, 2009a). Like all eumetazoans but unlike most other sponges, the spermatozoans of homosclerophorids have an acrosome; furthermore, and also in contrast to other sponges, the spermatogenesis is asynchronous inside spermatocysts (Ereskovsky *et al.*, 2009a). Recently, phylogenetic studies with different molecular markers suggested that the Homoscleromorpha should be separated from other sponges at class or even at phylum level (Borchiellini *et al.*, 2004; Erpenbeck & Wörheide, 2007; Phillippe *et al.*, 2009; Gazave *et al.*, 2012; Nielsen, 2012).

The class Homoscleromorpha is cosmopolitan, occurring from the equator to the poles and from the intertidal to the deep sea. However, despite its importance, little is known about its diversity and distribution in most regions of the world. Only in the Mediterranean Sea has the group been recently revised, with 23 species currently accepted

(Ereskovsky *et al.*, 2009b; Pérez *et al.*, 2011; Pansini *et al.*, 2011). In this paper we investigate all records of Homoscleromorpha species from the Tropical Western Atlantic (TWA) and present an overview of their taxonomy, biodiversity and distribution to put in evidence taxonomic problems, distribution patterns and diversity hotspots of Homoscleromorpha in the TWA.

MATERIALS AND METHODS

The Tropical Western Atlantic was divided by Spalding *et al.* (2007) into 16 ecoregions and three provinces: Tropical North-western Atlantic, North Brazil Shelf, and Tropical South-western Atlantic. We followed this division and also included in our study area the Warm Temperate North-west Atlantic Province, with Carolinian and Northern Gulf of Mexico ecoregions (Figure 1). Based on a literature survey, the distribution of each species was mapped and compared with these ecoregions.

RESULTS AND DISCUSSION

Biodiversity and taxonomy

Twenty-seven species of Homoscleromorpha are currently recognized in the Tropical Western Atlantic, including one of the family Oscarellidae (*Oscarella nathaliae*) and 26 plakinids: two *Corticium*, seven *Plakina*, four *Plakinastrella*, 12 *Plakortis* and one *Tetralophophora* (Table 1). This number represents 26.2% of the total of 103 species currently known worldwide (van Soest *et al.*, 2015), and is slightly higher than the 23 species listed from the Mediterranean (Ereskovsky *et al.*, 2009b; Pansini *et al.*, 2011; Pérez *et al.*, 2011).

The most specious genus of Homoscleromorpha in the TWA is *Plakortis* with 12 species, followed by *Plakina* (7 spp.) and *Plakinastrella* (4 spp.). This pattern contrasts with that of the Mediterranean, where *Plakina* and *Oscarella* dominate with 11 and seven species, respectively. Only one species of *Plakortis, P. simplex* Schulze, 1880, was reported so far from the Mediterranean (Ereskovsky *et al.*, 2009b), in strong contrast with its high species richness in the TWA. This may be related to a general preference of *Plakortis* spp. for coral reefs or rocky coast environments in tropical waters. The genus *Plakortis* is also very common and diverse in the tropical Indo-Australian region (Muricy, 2011).

Twelve new species and one new genus of Homoscleromorpha have been described from the TWA in the last two years, 2013–2014. Such recent descriptions illustrate well the growing interest in the diversity and biology of the class. These descriptions are quite detailed, usually including colour underwater photographs of living specimens, SEM pictures of spicules, and information on skeletal architecture in both the choanosome and the ectosome (Cedro *et al.*, 2013; Domingos *et al.*, 2013; Ereskovsky *et al.*, 2014; Rützler *et al.*, 2014; van Soest *et al.*, 2014). Older descriptions, however, are often much less complete and frequently raise doubts on the identity of several records of Homoscleromorpha in the region. It is thus difficult to recognize species such as *Plakinastrella onkodes* Uliczka, 1929, *Plakortis angulospiculatus* (Carter, 1879), *Plakortis halichondrioides* (Wilson, 1902), *Plakortis simplex, Plakortis zyggompha* (de Laubenfels, 1934), *Corticium*

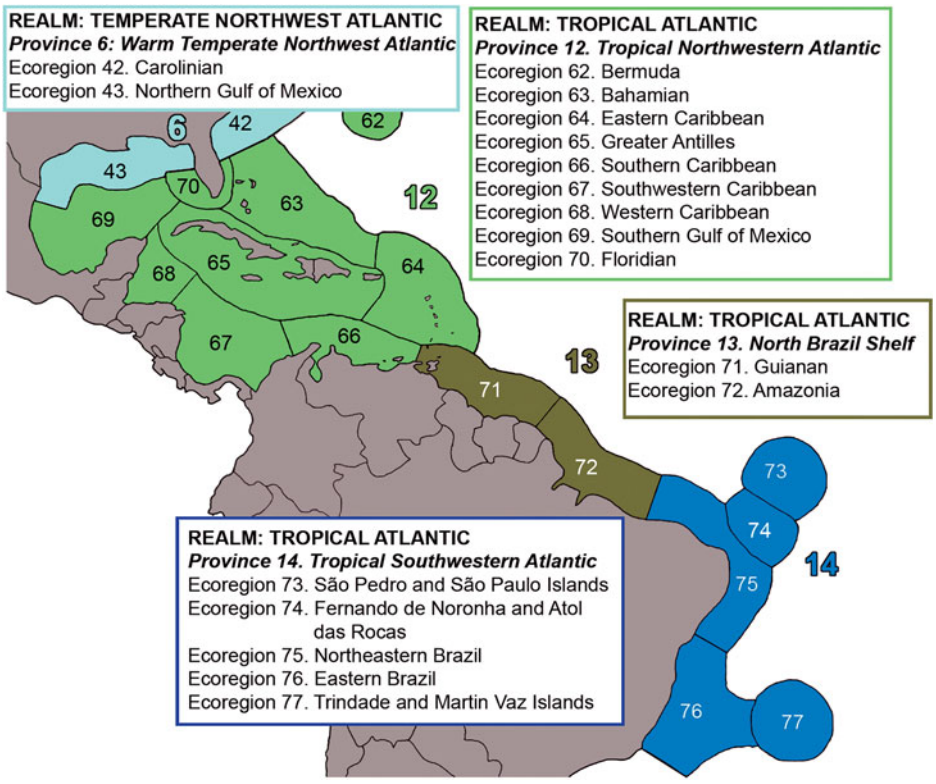

Fig. 1. Study area, according to the division of the Western Atlantic Ocean in realms, provinces and ecoregions of Spalding *et al.* (2007).

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Table 1. Checklist of currently accepted species of Homoscleromorpha from the Tropical Western Atlantic.

Corticium diamantense Ereskovsky, Lavrov & Willenz, 2014[1]
Corticium quadripartitum Topsent, 1923[2, 27, 39]
Oscarella nathaliae Ereskovsky, Lavrov & Willenz, 2014[1]
Plakina coerulea Cedro, Hajdu & Correia, 2013[3]
Plakina elisa (de Laubenfels, 1936b)[4, 6]
Plakina jamaicensis Lehnert & van Soest, 1998[1, 5, 6, 15, 22]
Plakina monolopha Schulze, 1880[6, 35]
Plakina tetralopha (Hechtel, 1965)[5, 6, 7, 27]
Plakina trilopha Schulze, 1880[8, 18, 31, 42]
Plakina versatilis (Schmidt, 1880)[2, 6, 9, 27, 43]
Plakinastrella globularis Domingos, Moraes & Muricy, 2013[10]
Plakinastrella microspiculifera Moraes & Muricy, 2003[5, 11, 18, 29, 30, 31, 33, 34, 44, 45]
Plakinastrella onkodes Ulizcka, 1929[5, 6, 11–18, 22, 24, 27, 29, 31, 39]
Plakinastrella stinapa van Soest, Meesters & Becking, 2014[40]
Plakortis angulospiculatus (Carter, 1879)[4–8, 11, 14, 16, 18–34, 39, 42, 43, 46]
Plakortis dariae Ereskovsky, Lavrov & Willenz, 2014[1]
Plakortis edwardsi Ereskovsky, Lavrov & Willenz, 2014[1]
Plakortis halichondrioides (Wilson, 1902)[5, 6, 14–16, 18, 22, 27, 36, 37, 47]
Plakortis insularis Moraes & Muricy, 2003[11, 18, 30, 33, 44, 45]
Plakortis microrhabdifera Moraes & Muricy, 2003[11, 18, 34]
Plakortis myrae Ereskovsky, Lavrov & Willenz, 2014[1]
Plakortis petrupaulensis Domingos, Moraes & Muricy, 2013[10]
Plakortis potiguarensis Domingos, Moraes & Muricy, 2013[10, 34]
Plakortis simplex Schuze, 1880[6–8, 11, 13, 14, 20, 29, 31, 41, 42]
Plakortis spinalis Domingos, Moraes & Muricy, 2013[10]
Plakortis zyggompha (de Laubenfels, 1934)[5–7, 11, 14, 21, 27, 38, 39, 41, 46]
Tetralophophora mesoamericana Rützler, Piantoni, van Soest & Diaz, 2014[39]

References of all articles reporting the species from the TWA are numbered within parentheses and listed below.
References: (1) Ereskovsky *et al.* (2014); (2) Topsent (1923); (3) Cedro *et al.* (2013); (4) de Laubenfels (1936*b*); (5) Lehnert & van Soest (1998); (6) Miloslavich *et al.* (2010); (7) Hechtel (1965); (8) Boury-Esnault (1973); (9) Schmidt (1880); (10) Domingos *et al.* (2013); (11) Moraes & Muricy (2003); (12) Uliczka (1929); (13) Pulitzer-Finali (1986); (14) Zea (1987); (15) Rützler *et al.* (2000); (16) Díaz (2005); (17) Mothes *et al.* (2006); (18) Muricy *et al.* (2011); (19) Carter (1879); (20) Alcolado (1976); (21) Alcolado (2002); (22) Diaz & Rützler (2009); (23) van Soest (1981); (24) Wintermann-Kilian & Kilian (1984); (25) Kobluk & van Soest (1989); (26) Alvarez *et al.* (1990); (27) Díaz & van Soest (1994); (28) Kossuga *et al.* (2008); (29) Mothes & Bastian (1993); (30) Muricy & Moraes (1998); (31) Santos *et al.* (2002); (32) Epifanio *et al.* (2005); (33) Moraes *et al.* (2006); (34) Muricy *et al.* (2008); (35) Arndt (1927); (36) Wilson (1902); (37) Collette & Rützler (1977); (38) de Laubenfels (1934); (39) Rützler *et al.* (2014); (40) van Soest *et al.* (2014); (41) de Laubenfels (1950a); (42) Hechtel (1976); (43) Rützler *et al.* (2009); (44) Moraes (2011); (45) Moraes *et al.* (2003); (46) de Laubenfels (1936a); (47) Karlson & Osman (2012).

quadripartitum Topsent, 1923, *Plakina elisa* (de Laubenfels, 1936) and *Plakina versatilis* (Schmidt, 1880). These species need taxonomic revision. This taxonomic uncertainty, especially in the genera *Plakortis* and *Plakinastrella*, is currently a major problem in the estimation of the biodiversity of Homoscleromorpha in the TWA.

Distribution patterns

Three species of Homoscleromorpha reported from the TWA are allegedly cosmopolitan: *Plakina monolopha* Schulze, 1880, *P. trilopha* Schulze, 1880 and *Plakortis simplex* (Table 2, Figure 2), all originally described from the Mediterranean. They have been reported in the TWA with short or without descriptions (e.g. Boury-Esnault, 1973; Pulitzer-Finali, 1986; Miloslavich *et al.*, 2010). These records represent complexes of cryptic species and the TWA populations probably deserve new species names. The distribution of *Plakina monolopha* and *P. trilopha* within the study area is much more restricted than that of the *Plakortis simplex* complex, which occurs in five ecoregions (Figure 2).

All other 24 species reported are TWA endemics. Within the TWA, only four species are widely distributed, occurring both in the Tropical North-western Atlantic and in the North Brazil Shelf or in the Tropical South-western Atlantic provinces: *Plakinastrella onkodes, Plakinastrella microspiculifera* Moraes & Muricy, 2003, *Plakortis angulospiculatus* and *Plakortis halichondrioides*. These species also occurred in a large number of ecoregions, from 5–12 (Figure 3). As discussed above, however, this apparently wide distribution may be the result of misidentifications or different interpretations of each species' concept, in general due to insufficient descriptions. One example is the concept of *Plakinastrella onkodes*, originally described as a light brown (in alcohol), massive sponge with small oscules (maximum 5 mm in diameter) on the sides of several small, irregular lobes (Uliczka, 1929). In more recent years, however, this species has been often described as light or dark brown, with a single or few tubes topped by a large apical oscule, or light grey and thick encrusting (Figure 4). Such taxonomic problems may have artificially increased by many thousands of kilometres and in three more provinces the estimated range of this (or these) species. *Plakortis angulospiculatus* and *P. halichondrioides* also have been described with wide morphological and ecological variations by different authors (e.g. Carter, 1879; Wilson, 1902; Zea, 1987; Díaz & van Soest, 1994; Lehnert & van Soest, 1998;

Table 2. Worldwide records of the three allegedly cosmopolitan species of Homoscleromorpha reported from the Tropical Western Atlantic: *Plakina monolopha, P. trilopha* and *Plakortis simplex*.

Realm/region of collection	*Plakina monolopha*	*Plakina trilopha*	*Plakortis simplex*	References
Temperate Northern Atlantic				
Adriatic Sea	+	+	+	van Soest *et al.* (2015)
Aegean Sea	+	+	+	van Soest *et al.* (2015)
Levantine Sea			+	van Soest *et al.* (2015)
Greece	+	+	+	van Soest *et al.* (2015)
Sardenha, Italy	+		+	Melone (1965)
Naples, Italy	+	+	+	van Soest *et al.* (2015)
Monaco	+	+	+	van Soest *et al.* (2015)
Port-Cros, S France		+		van Soest *et al.* (2015)

Continued

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Table 2. Continued

Realm/region of collection	*Plakina monolopha*	*Plakina trilopha*	*Plakortis simplex*	References
Banyuls, S France	+	+	+	van Soest *et al.* (2015)
Blanes, S Spain		+		van Soest *et al.* (2015)
Bandol, S France		+		van Soest *et al.* (2015)
Algeria			+	van Soest *et al.* (2015)
Tunisia	+			van Soest *et al.* (2015)
Alboran Sea	+	+		van Soest *et al.* (2015)
Azores			+	van Soest *et al.* (2015)
Canary Is.	+	+		van Soest *et al.* (2015)
Galicia, W Spain	+			Durán & Solórzano (1982); Solórzano (1991)
Roscoff, N France			+	van Soest *et al.* (2015)
United Kingdom	+		+[1]	van Soest *et al.* (2015)
Ireland	+			van Soest & Weinberg (1980)
Norway			+	van Soest *et al.* (2015)
Temperate Northern Pacific				
Japan	+		+	Koltun (1971); Hoshino (1981)
Tropical Atlantic				
Cape Verde	+[1]		+[1]	van Soest (1993); van Soest *et al.* (2015)
Senegal			+	van Soest *et al.* (2015)
Bermuda			+	van Soest *et al.* (2015)
Cayman Is.			+[1]	van Soest *et al.* (2015)
Puerto Rico			+	Pulitzer-Finali (1986)
Dominican Republic			+	Pulitzer-Finali (1986)
Cuba			+[1]	Alcolado (1976); van Soest *et al.* (2015)
Jamaica			+[1]	Pulitzer-Finali (1986); van Soest *et al.* (2015)
Mexico			+[1]	van Soest *et al.* (2015)
Belize			+[1]	van Soest *et al.* (2015)
Panama			+[1]	van Soest *et al.* (2015)
Bonaire			+[1]	van Soest *et al.* (2015)
Curaçao	+[1]		+[1]	van Soest *et al.* (2015)
NE Brazil		+		Boury-Esnault (1973), Muricy *et al.* (2011)
Western Indo-Pacific				
Gulf of Mannar	+			Thomas (1970)
Seychelles			+[1]	Thomas (1973); van Soest *et al.* (2015)
Kenya			+[1]	van Soest *et al.* (2015)
Mozambique			+[1]	van Soest *et al.* (2015)
Madagascar	+[1]			van Soest *et al.* (2015)
Central Indo-Pacific				
Ambon, Indonesia			+[1]	van Soest *et al.* (2015)
Aru Is., Indonesia			+	Hentschel (1912)
Philippines		+	+	Lévi & Lévi (1989)
Eastern Indo-Pacific				
Hawaii	+		+	de Laubenfels (1950b, 1951); Bergquist (1977)
Temperate South America				
Chile		+		Desqueyroux (1972)
Falkland Is.		+		Burton (1932)
Tristan da Cunha	+			Burton (1932)
Temperate Australasia				
N New Zealand	+[1]	+[1]		van Soest *et al.* (2015)
Southern Ocean				
South Georgia Is.		+		Burton (1932)
Kerguelen Is.		+		Boury-Esnault & van Beveren (1982)
Antarctica	+[1,2]	+[1,2]		Topsent (1917); Burton (1932); Koltun (1976); van Soest *et al.* (2015)

Realms according to Spalding *et al.* (2007).
[1]Record considered inaccurate by van Soest *et al.* (2015).
[2]Variety *antarctica*.

Moraes & Muricy, 2003; Figure 5), and their distribution could in fact be much more restricted than currently thought.

Most species (20/27, or approximately 74%) have narrow distributions, being restricted to 1–3 ecoregions in a single biogeographic province: 13 in the Tropical North-western Atlantic (*Corticium diamantense, C. quadripartitum, O. nathaliae, Plakina elisa, P. jamaicensis, P. tetralopha, P. versatilis, Plakortis dariae, P. edwardsi, P. myrae, P. zyggompha,*

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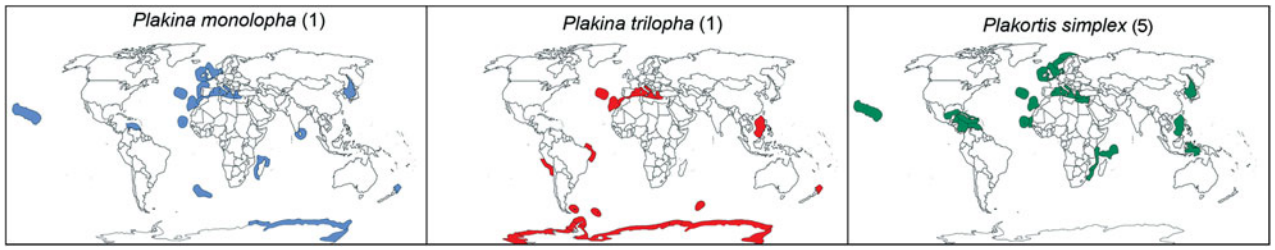

Fig. 2. Distribution of allegedly cosmopolitan Homoscleromorpha species that occur in the TWA. Numbers within parentheses represent the total of ecoregions in which the species occurs within the TWA. Data from Table 2. See Figure 1 for the names of provinces and ecoregions in the TWA.

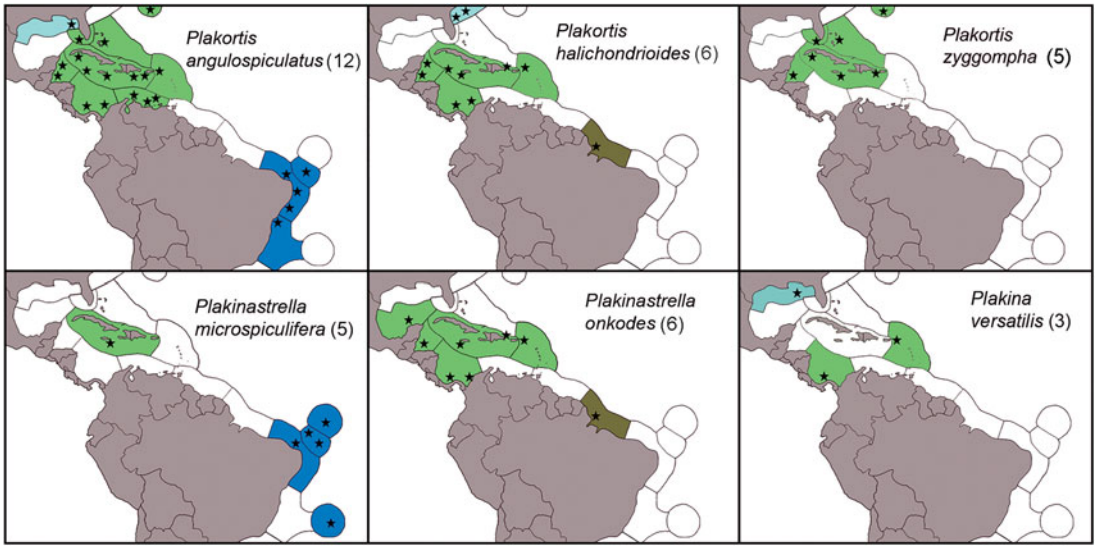

Fig. 3. Distribution of Homoscleromorpha species that occur in two or more biogeographic provinces in the TWA: widely distributed species or complexes of cryptic species with more restricted distributions. Numbers within parentheses represent the total of ecoregions in which the species occurs. See Figure 1 for the names of provinces and ecoregions.

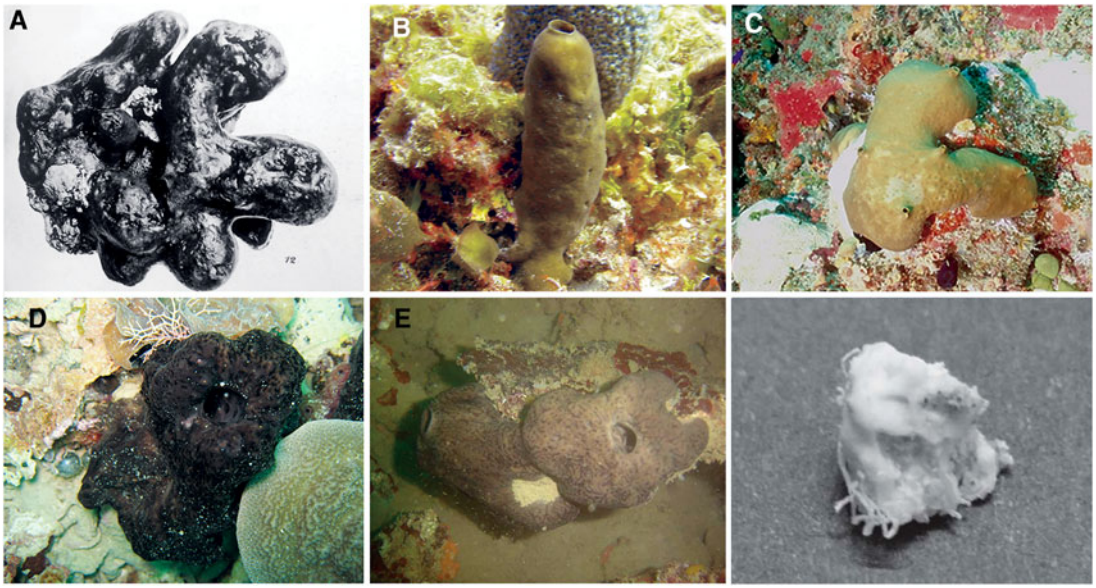

Fig. 4. Morphological variation of *Plakinastrella onkodes*: (A) the holotype is irregularly lobate, bright light brown in alcohol, with small oscules (reproduced from Uliczka, 1929); (B–F) examples of the current concepts of *P. onkodes*: (B) greenish-brown, tubular specimen from the Bahamas (photo from Zea *et al.*, 2014; http://www.spongeguide.org); (C) light brown, massively encrusting specimen from the Caribbean (photo Charles and Anne Sheppard; http://coralpedia.bio.warwick.ac.uk); (D) lobate, dark brown specimen from the Caribbean (photo Chris Freeman; http://porifera.lifedesks.org); (E) lobate, greyish brown specimen from Bocas del Toro, Panama (photo Renata Goodridge; http://biogeodb.stri.si.edu/bocas_database); (F) whitish specimen from Amapá State, N Brazil (reproduced from Mothes *et al.*, 2006).

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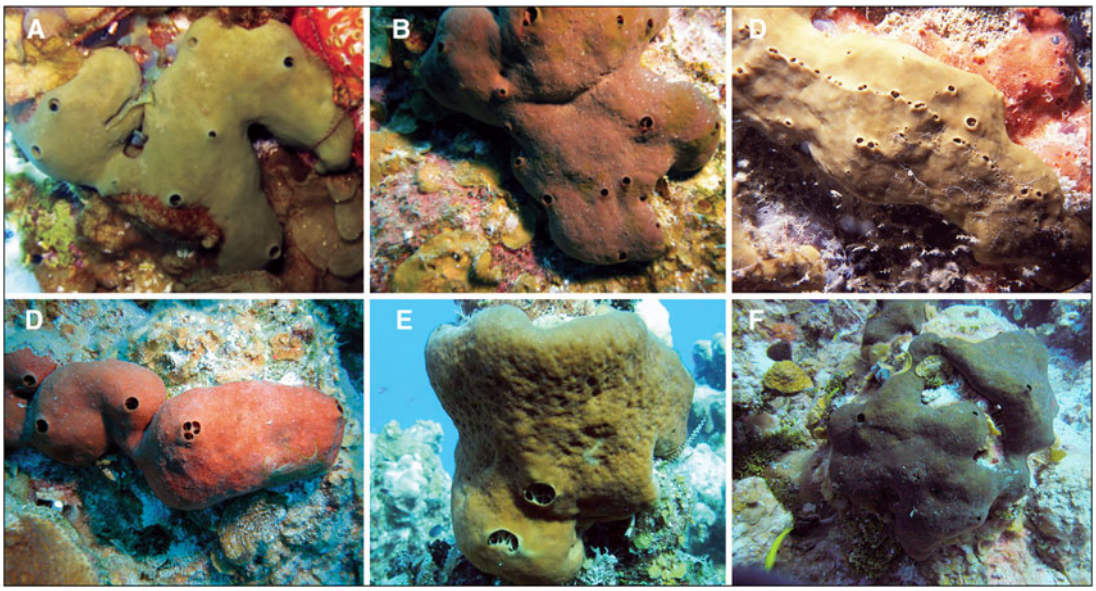

Fig. 5. *In situ* photographs of *Plakortis* spp. from the TWA showing morphological variation. (A–C) *P. angulospiculatus*: (A–B) specimens from the Bahamas (photographs from Zea *et al.*, 2014; http://www.spongeguide.org); (C) specimen from Potiguar Basin, NE Brazil (photo Fernando Moraes; http://www.poriferabrasil.mn.ufrj.br); (D–F) *P. halichondrioides*: specimens from the Bahamas (photographs from Zea *et al.*, 2014; http://www.spongeguide.org). High variation in external morphology suggests possible cryptic speciation.

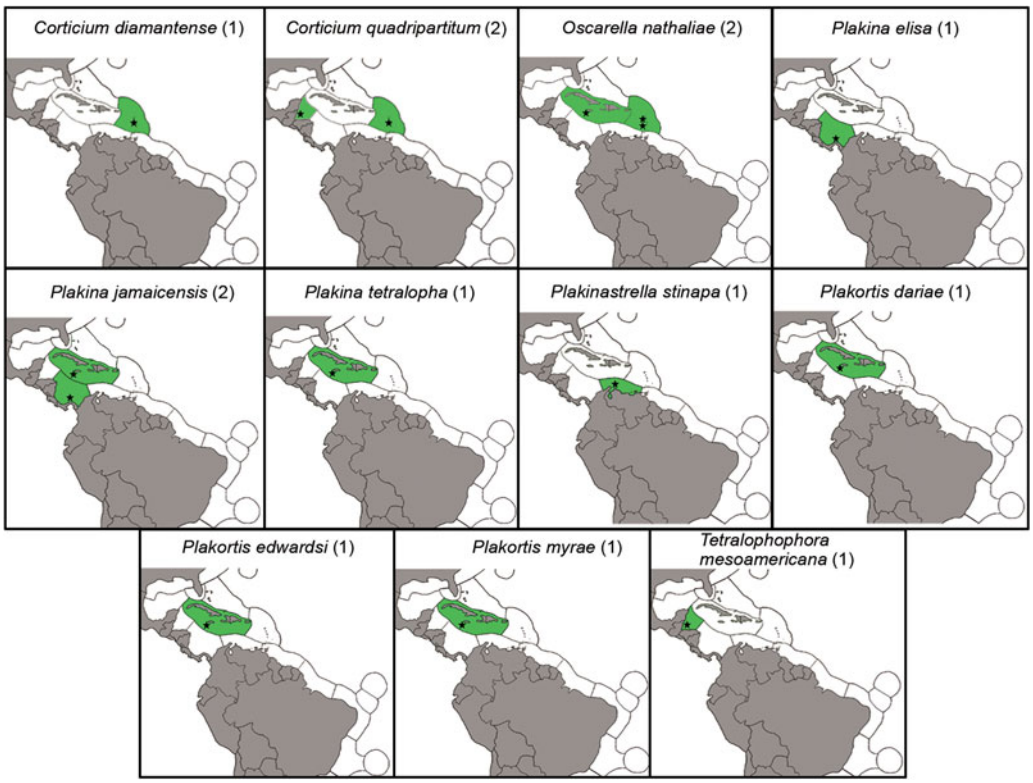

Fig. 6. Distribution of species restricted to the Tropical North-western Atlantic province ('Caribbean endemics'). Numbers within parentheses represent the total of ecoregions in which the species occur. See Figure 1 for the names of provinces and ecoregions.

Plakinastrella stinapa, Tetralophophora mesoamericana; Figure 6), and seven in the Tropical South-western Atlantic (*Plakina coerulea, Plakinastrella globularis, Plakortis insularis, P. microrhabdifera, P. potiguarensis, P. spinalis, P. petrupaulensis*; Figure 7). This pattern probably reflects a low dispersal ability of the cinctoblastula larvae, rather than an artifact due to insufficient collections.

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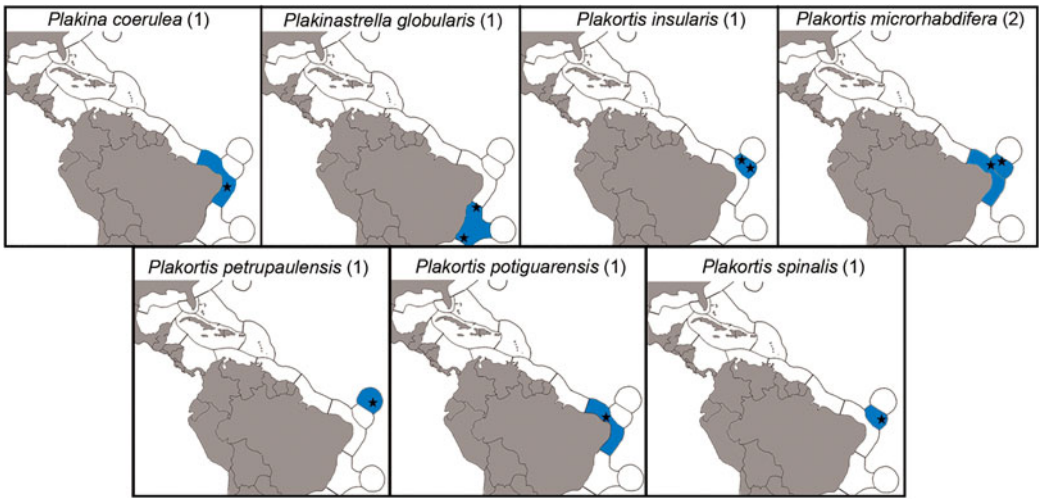

Fig. 7. Distribution of species restricted to the Tropical Southwestern Atlantic province ('Brazilian endemics'). Numbers within parentheses represent the total of ecorregions in which the species occur. See Figure 1 for the names of provinces and ecoregions.

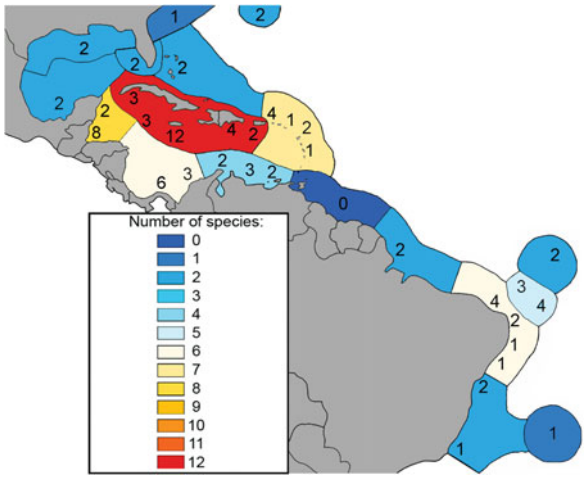

Fig. 8. Species richness of Homoscleromorpha in different localities (numbers) and ecoregions (colour code) in the Tropical Western Atlantic. See Figure 1 for the names of provinces and ecoregions.

Biodiversity hotspots

The areas with the highest number of species recorded are Jamaica (12 spp.), Belize (8 spp.) and Panama (6 spp.) in the Caribbean, and Fernando de Noronha Archipelago and Potiguar Basin in Brazil (4 spp. each; Figure 8). On the other hand, five other areas had only one or two records (South Carolina, Bermuda, off the mouth of the Amazon River, Abrolhos Reefs, Trindade Island), and only the Guiana ecoregion has no record of homoscleromorphs so far (Figure 8).

This pattern may be explained by the sum of several factors: (1) subjective taxonomic decisions leading to over-splitting of species and high apparent diversity (possibly the case of Jamaica); (2) subjective 'lumping' of populations that belong in fact to complexes of cryptic species, leading to a lower estimation of biodiversity (e.g. *Plakortis simplex, P. angulospiculatus, Plakinastrella onkodes*); (3) unequal sampling effort in different places (e.g. higher in Jamaica,

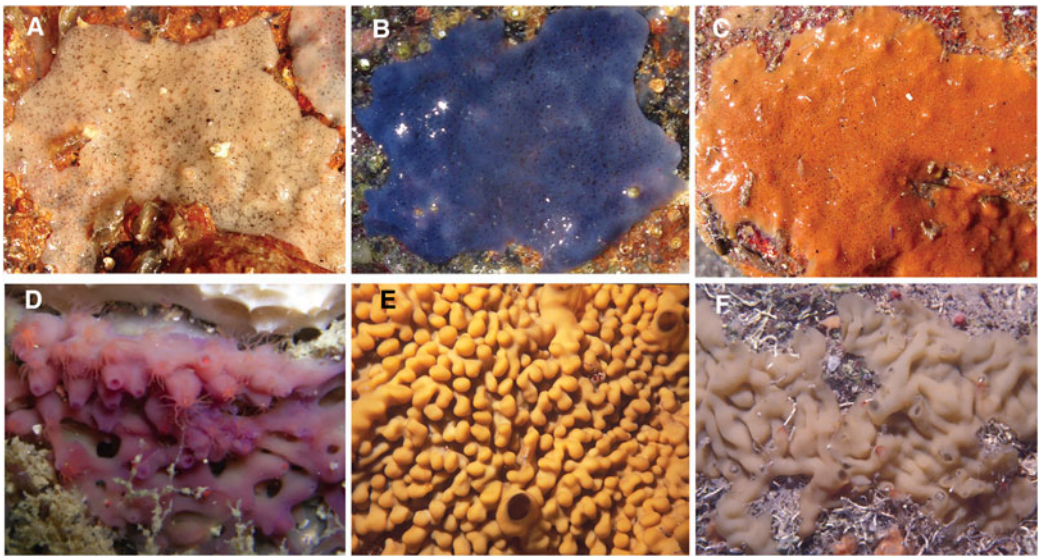

Fig. 9. *In situ* photographs of undescribed species of *Plakina* and *Oscarella* from the Tropical Western Atlantic. (A–C) *Plakina* spp. from Cabo Frio, SE Brazil; (D–F) *Oscarella* spp. from: (D) Cabo Frio, SE Brazil; (E) Cuba and (F) Fernando de Noronha, NE Brazil.

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Panama, Curaçao and Belize; lower in Abrolhos Reefs, Trindade Island and the Guianas); (4) real differences in species richness due to biogeographic, historical or ecological factors (this may be the case of the Guianas and Amazonian ecoregions, with high sediment input from the Amazonas and Orinoco rivers and relatively few hard substrates for sponge colonization). In the last hypothesis, the Guianas and Amazonian ecoregions could be effective barriers separating North-western and South-western Tropical Atlantic populations of Homoscleromorpha species and leading to allopatric speciation, increasing the diversity of the class in the Tropical Western Atlantic realm. More objective, integrative taxonomic approaches (e.g. Boury-Esnault *et al.*, 2013; Cruz-Barraza *et al.*, 2014; Ereskovsky *et al.*, 2014; Ruiz *et al.*, 2014), and increasing sampling efforts in poorly explored areas such as the Guianas and Abrolhos Reefs will help to make more precise estimations of the biodiversity and biogeography of Homoscleromorpha. The exploration of submarine caves and other sciaphilic habitats should also lead to a large number of species discovered, since most species of *Oscarella, Plakina* and *Corticium* are highly sciaphilic (Solé Cava *et al.*, 1992; Muricy *et al.*, 1996, 1998; Ereskovsky *et al.*, 2009b; Gerovasileiou & Voultsiadou, 2012). Species of *Plakinastrella* and *Plakortis*, however, are often exposed to sunlight and wave action in reef environments (e.g. Zea, 1987; Moraes & Muricy, 2003), so these habitats should not be neglected as well.

Despite all the taxonomic problems and the need of more collections, several undescribed species of *Oscarella, Plakina, Plakinastrella* and *Plakortis* are known from Brazil and from the Caribbean (Figure 9; Muricy *et al.*, 2011). We therefore estimate that the true biodiversity of Homoscleromorpha in the TWA is at least twice as high as the 27 species currently known.

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