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Taxonomic revision of the southwestern Atlantic Madracis and the description of Madracis fragilis n. sp. (Scleractinia: Pocilloporidae), a new coral species from Brazil

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SUMMARY: The genus *Madracis* has been known in Brazil from four deep water species, namely *M. mirabilis*, *M. asperula*, *M. brueggemanni*, and *M. pharensis*, and one zooxanthellate species from shallow water environments, *M. decactis*. Delicate fragments of a small branching colony of an undescribed *Madracis* were collected at 73 m depth, northern Salvador (Bahia State). Although resembling the congeners *M. asperula* and *M. brueggemanni*, the new species has distinct features including reduced branch thickness, smaller diameter of corallite and columella structure and pattern of coenosteum ornamentation. Because of the worldwide focus on reef-building corals, knowledge of azooxanthellate scleractinians remains scarce. In addition to contributing to the inventory of Brazilian coral fauna, the occurrence of a new species of *Madracis* provides further evidence of the high diversity of deep-water coral communities in the tropical South Atlantic.

Keywords: biodiversity, systematics, morphology, azooxanthellate coral, deep sea, South Atlantic.

RESUMEN: REVISIÓN TAXONÓMICA DEL GÉNERO *MADRACIS* EN EL ATLÁNTICO SUDOCCIDENTAL Y DESCRICIÓN DE *MADRACIS FRAGILIS* N. SP. (SCLERACTINIA: POCILLOPORIDAE), UNA NUEVA ESPECIE DE CORAL BRASILEÑA. – En Brasil el género *Madracis* había sido conocido hasta ahora por cuatro especies de mar profundo, *M. mirabilis*, *M. asperula*, *M. brueggemanni*, y *M. pharensis*, y una especie zooxantelada de aguas poco profundas, *M. decactis*. Delicados fragmentos de una pequeña colonia ramificada de una especie no descrita de *Madracis* fueron recolectadas a una profundidad de 73 m al norte de Salvador (Estado de Bahia). A pesar de su afinidad a los congéneres *M. asperula* y *M. brueggemanni*, la nueva especie tiene características diferentes incluyendo el reducido espesor de las ramas, el pequeño diámetro del coralito, la estructura de la *columela* y la ornamentación del *coenosteum*. Debido al énfasis mundial en corales constructores de arrecifes, el conocimiento de escleractínidos azooxantelados es todavía limitado. El descubrimiento de una nueva especie de *Madracis*, además de contribuir al inventario de la fauna coralina del Brasil, añade evidencia de la alta diversidad de las comunidades coralinas del Atlántico Sur Tropical.

Palabras clave: biodiversidad, sistemática, morfología, corales azooxantelados, mar profundo, Atlántico Sur.

INTRODUCTION

The genus *Madracis* is primarily represented by azooxanthellate colonial species from deep-water environments. Varying from fragile branching or dense ramose coralla to massive columnar, nodular or encrusting forms, *Madracis* is expected to be a well-defined group commonly with cryptic habits (Veron, 2000). Some taxonomical controversies involving the description of *Madracis* have been attributed to Milne-Edwards and Haime (1849) during simultaneous designation of the referred genus and *Axhelia*. Following Cairns (1979), Locke *et al.* (2007) provided a concise historical summary of

conflicting nomenclature between Madracis and Axhelia, which affected the designation of type species and species authority until Vaughan and Wells (1943) placed Axhelia myriaster and Axhelia asperula within Madracis, with Axhelia being definitively regarded as a junior synonym. Although Madracis is closely related to the Pocilloporidae, morphological data concerning the columella structure have supported the inclusion of Madracis in the family Astrocoeniidae (Veron, 2000). According to Veron et al. (1996), 'Pocilloporidae and Astrocoeniidae both have Triassic origins and probably diverged from other extant Scleractinia near or before the evolution of skeletogenesis'. However, because of the sexual similarities between Madracis and pocilloporids, the replacement has been argued to be doubtful (see Vermeij et al., 2004). In fact, Kerr's (2005) supertree analysis concatenating molecular (ITS1 and 2,5.8S) and morphological data available from the literature pointed out a close relationship between Madracis and Pocilloporidae, but he placed the genus within the clade Astrocoeniidae at the base of the robusta group (sensu Romano and Palumbi, 1996). The 'conflict' remains apparently unsolved, and similarly to other highly controversial genera (e.g. Acropora, Montastraea, see Fukami et al., 2004), Madracis' species definition has challenged taxonomy and the evolutionary concept. Phylogenetically, the genus may comprise mono-, para- and polyphyletic species, which are likely to hybridise, complying with Veron's (1995) model of reticulate speciation (Diekmann, et al. 2001; Vermeij et al., 2004; Kerr, 2005). Following this pathway, the zooxanthellate M. carmabi Vermeij, Diekmann and Bak, 2003 has been proposed to be a hybrid, resulted from the interbreeding of M. decactis (Lyman, 1859) and M. formosa Wells, 1973. From a morphological standpoint, Locke et al. (2007) pointed to another taxonomical issue by suggesting that the shallow-water M. auretenra Locke et al., 2007 has been misidentified as M. mirabilis (Duchassaing and Michelotti, 1860), the latter an 'invalid species' considered to be a junior synonym of *M. myriaster* (Milne Edwards and Haime, 1849). Actually, concerning 'the history of the synonymy of M. myriaster', Cairns (1979) previously emphasised the need of a new name for M. mirabilis.

Providing a key to *Madracis* identification, Wells (1973) recognised seven Atlantic species (up to 100 m): *M. asperula* Milne Edwards and Haime, 1849, *M. myriaster* (Milne Edwards and Haime, 1849), *M. decactis* (Lyman, 1859), *M. mirabilis* (Duchassaing

and Michelotti, 1860) (M. auretenra sensu Locke et al., 2007), M. pharensis (Heller, 1868), M. brueggemanni (Ridley, 1881) and M. formosa Wells, 1973. Including the hybrid *M. carmabi* and the recently described M. auretenra, six species occur on Caribbean reefs: M. decactis, M. pharensis, M. senaria Wells, 1974 and M. formosa. Differing partially in composition and number of species, in Brazil the genus is represented by M. asperula, M. decactis, M. brueggemanni, and M. pharensis. The common M. decactis has a highly variable bathymetric distribution, being found from shallow-water environments (from 3 to 30 m) to deep-water coral communities (Laborel, 1970; Cairns, 2000). Madracis asperula and M. pharensis were both reported by Laborel (1967) on the Bahia coast, up to 30 m, the former also being mentioned by Fernandes and Young (1986) on the Rio de Janeiro coast at 24 to 98 m depth.

Concerning influence of abiotic factors, variation in light may regulate morphology and distributional pattern of coral species. Indeed, light availability has been attested to affect colony shape of M. decactis and M. pharensis, and due to their distinct strategies the species have been considered as different 'ecotypes' (Fenner, 1993; Vermeij and Bak, 2002). Madracis auretenra (M. mirabilis sensu Wells, 1973) has also been documented responding to physical gradients (Fenner, 1993; Bruno and Edmunds, 1997, 1998; Sebens et al., 1997). However, M. auretenra and M. senaria have been recognised as 'true' or monophyletic genetic species, whereas, because of the absence of striking genetic differentiation, M. pharensis and M. decactis together with M. formosa and M. carmabi form 'species complexes' (Diekmann et al., 2001; Vermeij and Bak, 2002; Vermeij et al., 2004).

Despite the ecological importance of the Brazilian Province and the expressive distinctness of the geological architecture and biological assemblage of Brazilian reefs, information on coral communities located in this area is scarce and somewhat restricted to shallow-water environments (Laborel, 1970; Neves et al., 2002). Recent studies have provided significant changes in the inventory of zooxanthellate species, and in knowledge of population structure (Neves, 2004; Neves et al., 2006; Neves et al., 2008). Under a similar perspective, deep-water coral assemblages have been poorly explored and few species have been reported in Brazil (Cairns, 2000). Most studies concentrated on the southern platform, along the south-southeastern coast, have provided considerable perspective on new occurrences, including new species and genera (Kitahara and Cairns, 2005; Kitahara, 2006).

Therefore, in addition to improving the number of scleractinian species known worldwide, upgrading the azooxanthellate coral inventory of the South Atlantic, this study provides a comparative taxonomical analysis between M. fragilis n. sp. and all previously reported congeners in Brazil (M. asperula, M. decactis, M. brueggemanni, and M. pharensis). The description of a new branching Madracis in the Bahia State also reinforces the impressive marine diversity of the northeast coast, helping to assess the faunistic composition of the Brazilian Province.

MATERIALS AND METHODS

Samples of *M. fragilis* were unexpectedly obtained during logistical experiments of the 'Biskaia Bat' fishing boat along the coast of Bahia State. Colony fragments were removed from trap-cages tested for capturing commercial demersal fishes and crustaceans on the upper limit of the continental slope known as 'Paredes de Itapuã' (12°59'771''S, 38°15'807''W), off Itapuã beach (nearly 11 km off the coast), northern Salvador, Bahia State, at 73 m depth (Fig. 1). Material was fixed in 90% alcohol. In the laboratory, fragments were selected and bleached in a solution of 2% sodium hydrochloride overnight. After complete tissue removal, skeletons were rinsed in fresh water and dried for morphometric analysis and identification. The taxonomical approach (including relevant structures and terms) was partially



FIG. 1. - Area of collections of Madracis fragilis n. sp. (black star) in Bahia State, northeastern Brazil.

based upon criteria adopted by Locke et al. (2007), Cairns (2000), Veron (2000) and Wells (1973) for Madracis. A total of 100 corallites were analysed. Measurements were developed under a Nikon SMZ 1000 stereomicroscope with an eyepiece micrometer and a Nikon Coolpix 995 digital camera attached. Tip and basal skeleton fragments were mounted on aluminum pin stubs, previously covered with a double-sided sticky tape, sputter-coated with 35 nm of gold in a Shimadzu IC-50 ion coater, and examined through a Shimadzu Superscan SS-550. Type-species and paratypes were deposited at the Cnidaria Collection of the 'Museu de Zoologia da Universidade Federal da Bahia', acronym: UFBA/CNI.

RESULTS

SCLERACTINIA Bourne, 1900 POCILLOPORIDAE Gray, 1842 Madracis Milne-Edwards and Haime, 1849

Axhelia Milne-Edwards and Haime, 1849. Comptes rendus, XXIX, p. 69. Madracis Milne-Edwards and Haime, 1849. Comptes rendus,

- XXIX, p. 70.
- Axhelia Milne-Edwards and Haime, 1850. Ann. Sci. Nat., XIII, p. 91

Axohelia Milne-Edwards and Haime, 1857. Hist. Corall, II, p. 126 Reussia Duchassaing and Michelotti, 1860. Mém. Corall, p. 63. Pentalophora Kent, 1871. Proc. Zool. Soc. London, p. 283

- Madracis Duncan, 1884. Linn. Soc. London J., XVIII, p. 45. Madracis Vaughan, 1900. US Geol. Surv. Mon., XXXIX, p. 128. Axhelia Vaughan, 1901. US Fish Comm. Bull., II, p. 294.
- Madracis Verrill, 1902. Conn. Acad. Arts Sci. Trans., XI, p. 108.

Stylopsammia Oppenheim, 1930. N. Jahrb. Geol. Paläont., LXIX, p. 320.

Type species. Madracis asperula Milne-Edwards and Haime, 1850, Recent, Madeira (according to Wells, 1973: unnumbered types in British Museum of Natural History).

Diagnosis (after Cairns, 1979, 2000; Veron, 2000). Massive or ramose colonies formed by extratentacular budding; corallites plocoid with 6, 8, 9 or 10 septa and well-developed costae; primary septa fused with a styliform columella, usually bearing paliform lobes; S2 often absent or rudimentary; coenosteum solid, costate or spinose.

Madracis fragilis n. sp. (Fig. 2)

Holotype. Dry parts of a single specimen, including two bifurcating fragments, the largest one 3.0 cm in height, 7.5 cm in width, MZUFBA/CNI 473, collected Apr 2004 by C. Sampaio.



FIG. 2. – *Madracis fragilis* n. sp. A-H, holotype (dry specimen):A, slender branches; B, bifurcation of the primary axis; C, anastomosis in the tertiary branch; D, E, corallite uniformly circular on the branch tip with 8 primary septa (predominant arrangement); E, detail of septa projecting upwards through the theca. F-H, SEM images of corallites: F, octameral corallite from branch tip; G, H, basal corallite: central columellar papilla and spines. I-J, paratype (fixed specimen): I. corallum base infested by tubes of serpulid worms; J, plocoid corallites regularly spaced (not crowded) along the branch. Scale bars: A–C, I, J = 1.0 cm; D, E = 1.0 mm; F-H = 500 μm.

Type locality. Off Itapuã beach, Salvador (Bahia State). 12°59'771''S, 38°15'807''W. Depth 73 m.

Paratypes. Three fragments of alcohol fixed colony from the same type-species locality and depth, represented by its distal and basal parts (the latter infested by serpulids), MZUFBA/CNI 617, collected Apr 2004 by C. Sampaio.

Description. Colony very fragile with slender, delicate three dimensional branches (primary branch segments varying from about 3.2 to 6.5 cm in length); branch anastomosis rare (observed in tertiary branches); distal branches slim and homogeneous in thickness (2.0-2.2 mm); tertiary branch tips thinner (1.0-1.2 mm) sometimes sharp-edged; me-

dian and basal branch segments varying from 2.0 to 2.8 in diameter. Corallum tissue pale beige. Budding extramural. Corallites regularly circular, plocoid, ranging from 0.6 to 1.4 mm in diameter (X= 0.85, SD= 0.25), not crowded, separated regularly from each other by a distance of 0.7 to 1.0 mm (X= 0.82, SD= 0.11). Calices contain predominantly 8 exsert septa (occasionally 9, rarely 10), distributed in a single cycle (S1) fused to columellar platform. Septa vertical, projecting upwards through the theca margin. Septa margins irregularly dentate with coarse spines uniformly distributed along lateral faces. S2 absent. No paliform lobes. Columella varying from

0.3 to 0.6 mm (X= 0.4, SD= 0.06) in diameter, with a central styliform papilla (papillar surface finely granular). Coenosteum striate with fine spinules and short tubercles distributed around the corallite and linearly along low ridges.

DISCUSSION

A summary of diagnostic characteristics of South Atlantic Madracis is provided in Table 1. Following all descriptions, Madracis fragilis is a distinct species, differing from the congeners in branch thickness, diameter of corallite and columella, columella structure, and pattern of coenosteum ornamentation. Despite the intracolonial variation of the number of septa, 77.8% of the corallites examined had 8 septa whereas 14.8% and 7.4% had 9 and 10 septa, respectively. A similar condition may be observed in M. brueggemanni: most corallites contain 8 septa, but occasionally they contain 6, 7, 9, 10 or even 11 septa-these usually distributed in a single cycle (S1). Nevertheless, according to Cairns (2000: p. 39), 'those with less than 8 septa being more common than those with more'. Indeed, other diagnostic characters support the species identities: M. brueggemanni has small paliform lobes that form a crown encircling the columella-in contrast, M. fragilis n. sp. has no paliform lobes as well as no corallite with fewer than 8 septa. With a well-defined decameral septal arrangement, M. asperula, another branching colony, may occasionally exhibit corallites with 8 exsert septa. In this circumstance, other traits such as the corallite size, rudimentary S2 (reduced to spines), septa margins (smooth), and the small paliform lobes, may readily distinguish M. asperula from M. fragilis n. sp.

The occurrence of an octameral septal arrangement has constrained the identification of Atlantic *Madracis*. As for most scleractinian species complexes, septal number may be an unreliable character if considered exclusively. Ecological requirements related to habitat preferences have been used to separate the species and their morphotypes (Laborel, 1974). In this context, intergrading forms of *M. decactis*, comprising those that are more or less photophilous, and also differing in skeletal calcification, have been found in a graded light exposure—colonies developing in full sunlight, and others living in darker places (Laborel, 1974; Cairns, 2000). Depth and environment illumination may influence tissue pigmentation. Although inconspicuous among scleractinians (it is not consistent as a taxonomical attribute, because it may be highly variable intraspecifically), in a few particular cases polyp/tissue colour may contribute to recognition of the species in their natural habitat. Thus, according to Fenner (1993), the tissue of *M. mirabilis* is always light yellow, M. decactis may vary from dark-green to yellow-green, while M. pharensis, with the most variable palette, is concomitantly cream in colour with pink polyps in dark caves (at 20 m) or in shades of brown and green in shallower habitats. The intracolonial colour pattern of the three species was also described, revealing a gradual variation between illuminated and shaded areas of a single colony. Because of the few specimens originally analysed, some supposedly well-established characteristics for M. decactis as uniform septa (see Milne -Edwards and Haime, 1849) and the absence of costae (see Duncan, 1884) were subsequently refuted or restricted. Actually, in the late 19th century, Gregory (1895) observed a rudimentary set of septa (reduced S2) and costae in specimens from Barbados being designated as *M. decactis* variant forms. Invariably, some species with extended bathymetric distribution may be facultative zooxanthellate (or 'apozooxanthellate' sensu Stanley and Cairns, 1988), a condition regularly observed among Madracis species (e.g. M. asperula, M. decactis, M. pharensis). Being apparently restricted to deep-water environment, M. fragilis n. sp. has no zooxanthellae (corallum tissue being pale beige in situ), and levels of intercolonial variation are expected to be low among azooxanthellate species. Therefore, even representing one of the most conspicuous Brazilian species (with variant forms from deep-waters), the chances of misidentifying M. decactis as M. fragilis n. sp. are low. In addition to all the characteristics listed in Table 1, M. decactis (as M. asperula and M. pharensis) also has smooth septal margins. In the field, M. decactis and M. pharensis are interrelated because the corallum morphology (encrusting, nodular) is very different from that of the slender, ramose species. As emphasised by Vermeij and Bak (2002), these two species show noticeable morphological and genetic (see Diekmann et al., 2001) similarities, which make it doubtful to maintain them as distinct species. In fact, branch thickness and distance among corallites may primarily support the identification of *M. asperula*, *M. mirabilis*, *M. brueggemanni* and *M. fragilis* n. sp. Based on branch thickness, Wells (1973) described

TABLE 1 Corallum and corallite diagnostic characters for the identification of southwestern Atlantic Madracis (including M. fragilis n. sp.).						
Data summary based on Wells (1973), Fenner (1993), Cairns (2000), Veron (2000) and Locke et al. (2007). Within parenthesis (*) all possible						
variable values.						

Character/Species	M. asperula	M. decactis	M. brueggemanni	M. pharensis	<i>M. fragilis</i> n. sp.
Corallite form	plocoid, circular to elongate (branch tips), relatively closely spaced	plocoid to subcerioid, circular to polygonal, closely packed	plocoid, circular to elliptical (branch tips), well spaced	cerioid, circular to polygonal, closely packed	plocoid, mostly circular, slightly elliptical on branch tips
Colony form	branched to nodular, delicate	submassive, nodular, large-branched, laminar or encrusting	small, sparsely branched in three dimensions	stoloniferous chains of encrusting corallites, nodular growths, cylindrical to clavate in shape (not a true branch)	branched, delicate
Branch anastomosis	rare	absent	rare	absent	rare
Branch thickness	1.4-1.7 mm (3 mm, 5-6 mm)*	14-28 mm	3.0-4.0 mm	2.5-3.5 mm	2.0-2.8 mm
Corallite size	1.3-2.2 mm	1.0-1.5 mm	0.85-1.4 mm	1.5-2.3 mm	0.6-1.4 mm
Septa number	10 (8)*	10 (9,11)*	8 (6,7,9,10,11)*	12 (S1=6, S2=6)*	8 (9,10)*
S2	absent or rudimentary	absent or rudimentary	absent or rudimentary	present $(S2=6)$	absent
Paliform lobes	small, bordering the columella	none	small, forming a crown encircling the columella	well developed, forming a crown encircling the columella	none
Columella structure	solid, massive with a compressed styliform rod	solid, styliform	small (0.17 mm), with a compressed styliform rod	massive, pointed style, finely granular	solid platform (0.3-0.6 mm) with a central styliform papilla
Coenosteum ornamentation	fine spination arranged linearly	smooth or with fine spines (which may form a ridge between corallites)	spination similar in arrangement to <i>M. asperula</i> but spines are larger	fine spinules (surrounding the corallites)	striate with fine spinules and short tubercles distributed linearly along low ridges

the Caribbean *M. formosa* from Ridley (1881) specimens of Axhelia (Madracis) brueggemanni, the new species comprising those with thick, blunt branches while M. brueggemanni is represented by the one with slender, twiglike branches. However, data on branch thickness may be inconspicuous in the literature. As pointed out by Locke et al. (2007), the deep-water M. asperula 'has extremely slender branches'. Depending upon the branch segment measured during the analyses, great discrepancies may be found. Considering Milne-Edwards and Haime's (1949) original diagnosis, M. asperula would have the largest branches of about 5-6 mm. Regarding the same species, additional descriptions have suggested 3 mm (slender and attenuate—Wells, 1973), 1.4-1.7 mm (slender distal branches, Cairns, 2000) and 1.7 mm (J.M. Locke based upon USNM specimens 99046, 99048 and 45507). Furthermore, Bruno and Edmunds (1997, 1998) attested high levels of phenotypic plasticity for several skeletal traits in M. auretenra (M. mirabilis sensu Wells, 1973), including branch tip diameter, branch density and branch spacing as well. Basically, M. asperula could be suggested as one of the most fragile and delicate of all ramose *Madracis*, despite the irrefutably slim aspect of *M. fragilis* n. sp. branches. Nevertheless, other characteristics including septa with smooth margins, small paliform lobes and higher cycles reduced to spines would ensure undoubted distinction of *M. asperula* from *M. fragilis* n. sp.

The taxonomic status of M. auretenra remained for a long time controversial. The description originally provided by Vaughan (1919) as 'M. mirabilis' did not match Wells (1973), mainly in respect to branch thickness. According to Vaughan (1919: p. 345), the specimen from Limon (Costa Rica), had '2 mm in diameter at the lower end, and 3 mm in diameter just below trifurcation at the upper end'. There is a huge distance between 2-3 mm and the 6-10 mm pointed out by Wells (1973) for the same species. The conflict seemed purely based on morphological incongruence. Cairns (1979: p. 28) examined the holotype of 'M. mirabilis' from the Museo ed Instituto di Zoologia Sistematica (Torino, Italy) confirming that the striate specimen was in fact M. myriaster, and arguing that '... the common, shallowwater, nonstriate species, known today as M. mirabilis sensu Wells, 1973 requires a new name.' In a

personal communication Dr. S. Cairns has also stated 'Nonetheless, the name mirabilis was used by Wells to refer to another species with 6 mm branch tips. It is a true and distinct species, but the name mirabilis cannot be used for it. Thus Locke and collaborators suggested the new name aurentenra'. Indeed, Locke et al. (2007: p. 217) supporting the description of M. auretenra, have concisely summarised this entire circumstantial dilemma, requesting special attention for the puzzling situation of 'undescribed species' attributed to 'M. mirabilis'.

Despite the nomenclatural misunderstanding involving Caribbean species, branch aspect and diameter are clearly distinctive characters for Brazilian Madracis. Ongoing morphometric analyses of Madracis samples collected from several sites along the coast of Bahia State (basically from shallowwater areas) have suggested remarkable variation in corallum and corallite structures of the colonies, most forms being encrusting or submassive, slightly nodular, with cerioid corallites (each bearing 10 smooth septa) and no apparent coenosteum-a transitional unbranched pattern between the common M. decactis and M. pharensis f. luciphila (sensu Fenner, 1993). The material has not yet been identified but none of these specimens may be confounded with M. fragilis n. sp. It is not clear how abundant branching Madracis forms may be along the Brazilian coast, because there is no concise information on the distributional range or colonial cover of the species in deeper environments. In the literature, M. decactis is the only Brazilian pocilloporid supported by biological data (Castro and Pires, 2006), and all other aspects remain unpublished. Further efforts are necessary to clarify relevant aspects related to the diversity and structure of this complex genus with highly variable biological and evolutionary strategies. Finally, Madracis fragilis n. sp. may be endemic to Brazil, even restricted to Bahia State, supporting the species richness of the southwestern Atlantic and the tropical Brazilian Province.

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REFERENCES

- Bruno, J.F. and P.J. Edmunds. 1997. Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. *Ecology*, 78(7): 2177-2190.
- Bruno, J.F. and P.J. Edmunds. 1998. Metabolic consequences of phenotypic plasticity in the coral Madracis mirabilis (Duchassaing and Michelotti): the effect of morphology and water flow on aggregate respiration. J. Exp. Mar. Biol. Ecol., 229: 187-195.
- Cairns, S.D. 1979. The deep-water Scleractinia of the Caribbean Sea and adjacent waters. Stud. Faun. Curaçao Carib. Is., 180: 341
- Cairns, S.D. 2000. A revision of the shallow-water azooxanthellate Scleractinia of the Western Atlantic. In: L.J. van der Steen (ed.), Publications Foundation for Scientific Research in the Caribbean Region, n. 143. Stud. Nat. Hist. Carib. Reg., 75: 240.
- Castro, B.T. and D.O. Pires. 2006. Reproductive biology of Madracis decactis (Lyman, 1859) (Cnidaria, Scleractinia) from southern Bahia reefs. Arq. Mus. Nac., 64: 19-27. Diekmann, O.E., R.P.M. Bak, W.T. Stam and J.L. Olsen. – 2001.
- Molecular genetic evidence for probable reticulate speciation in the genus Madracis from a Caribbean fringing reef slope. Mar. Biol., 139: 221-233
- Duncan, P.M. 1884. A revision of the families and genera of the Sclerodermic Zoantharia, Ed. and H, or Madreporaria (M. Rugosa excepted). J. Linn. 18(104-105): 204.
- Fenner, D.P. 1993. Species distinctions among several Caribbean
- stony corals. *Bull. Mar. Sci.*, 53(3): 1099-1116. Fernandes, A.C.S. and P.S. Young. 1986. Corais coletados durante a 'Operação Geomar X' em junho de 1978 (Coelenterata, Anthozoa, Scleractinia). An. VII Cong. Bras. Zool., 66: 23-31.
- Fukami, H., A.F. Budd, D. R. Levitan, J. Jara, R. Kersanach and N. Knowlton. - 2004. Geographic differences in species boundaries among members of the Montastraea annularis complex based on molecular and morphological markers. Evolution, 58(2): 324-337.
- Gregory, J.W. 1895. Contributions to the paleontology and physical geology of the West Indies. Quat. J. Geol. Soc., 51(203): 255-328
- Kerr, A.M. 2005. Molecular and morphological supertree of stony

corals (Anthozoa: Scleractinia) using matrix representation parsimony. Biol. Rev., 80: 543-558.

- Kitahara, M.V. 2006. Novas ocorrências de corais azooxantelados (Anthozoa, Scleractinia) na plataforma e talude continental do sul do Brasil (25-34°S). *Biotemas*, 19(3): 55-63. Kitahara, M.V. and S.D. Cairns. – 2005. *Monohedotrochus capitolii*,
- a new genus and species of solitary azooxanthellate coral (Scleractinia, Caryophillidae) from southern Brazil. Zool. Meded., 79(3): 117-123.
- Laborel, J. 1967. Les peuplements de Madréporaires des côtes tropicales du Brésil. Faculté des Sciences de l'Université d'Aix-Marseille. Ph.D. thesis, part I, Univ. d'Aix-Marseille.
- Laborel, J. 1970. Madréporaires et hydrocoralliaires récifaux des côtes brésiliennes. Systématique, écologie, répartition verticale et géographique. Ann. Inst. Oceanogr., 47: 15-229.
- Laborel, J. 1974. West African reef corals an hypothesis on their origin. *Proc.* 2nd *Int. Coral Reef Symp.*, 1: 425-443. Locke, J.M., E. Weil and K.A. Coates. – 2007. A newly documented
- species of Madracis (Scleractinia: Pocilloporidae) from the Caribbean. Proc. Biol. Soc. Wash., 120(2): 214-226.
- Milne Edwards, H. and J. Haime. 1849. Recherches sur les polypiers. Ann. Sci. Nat., B, 12: 95-197.
- Neves, E.G. 2004. Complexo Siderastrea: espécies distintas? Significado da variabiliade do gênero Siderastrea de Blainville 1830 (Anthozoa, Scleractinia) no Brasil. Ph.D. thesis. Univ. de São Paulo.
- Neves, E.G., F.L. da Silveira, R. Johnsson and L.L. Longo. 2002. Shallow-water scleractinian corals and zoanthids from reefs of Coroa Grande, Pernambuco State, Brazil. Biociências, 10(2): 127-145.
- Neves, E.G., R. Johnsson, C. Sampaio and M. Pichon. 2006. The occurrence of Scolymia cubensis in Brazil: revising the problem of the Caribbean solitary mussids. Zootaxa, 1366: 45-54
- Neves, E.G., S.C.S. Andrade, F.L. da Silveira and V.N. Solferini. 2008. Genetic variation and population structuring in two brooding coral species (Siderastrea stellata and Siderastrea radians) from Brazil. Genetica, 132: 243-254.
- Ridley, S.O. 1881. Account of the zoological collections made during the survey of H.M.S. Alert in the Straits of Magellan and on the coast of Patagonia. X. Coelenterata. Proc. Zool. Soc.

Lon., 1881: 101-107.

- Romano, S.L. and S.R. Palumbi. 1996. Evolution of scleractinian corals inferred from molecular systematics. Science, 271: 640-642.
- Sebens, K.P., J. Witting and B. Helmuth. 1997. Effects of water flow and branch spacing on particle capture by the reef coral Madracis mirabilis (Duchassaing and Michelotti). J. Exp. Mar. Biol. Ecol., 211: 1-28.
- Stanley Jr., J.D. and S.D. Cairns. 1988. Constructional azooxanthellate coral communities: an overview with implications for the fossil record. Palaios, 3: 233-242.
- Vaughan, T.W. 1919. Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and recent coral reefs. Smithson. Inst. Bull., 103: 189-524.
- Vaughan, T.W. and J.W. Wells. 1943. Revision of the suborders, families and genera of the Scleractinia. Geo. Soc. Am., spec. pap., 44: 363.
- Vermeij, M.J.A. and R.P.M. Bak. 2002. How are coral populations structured by light? Marine light regimes and the distribution of Madracis. Mar. Ecol. Prog. Ser., 233: 105-116.
- Vermeij, M.J.A., E. Sampayo, K. Bröker and R.P.M. Bak. 2004. The reproductive biology of closely related coral species: gametogenesis in Madracis from the southern Caribbean. Coral Reefs, 23(2): 206-214.
- Veron, J.E.N. 1995. Corals in Space and Time. The Biogeography and Evolution of the Scleractinia. University of New South Wales Press, Sydney.
- Veron, J.E.N. 2000. Corals of the World. Vol. 2. Australian Institute of Marine Science, Townsville.
- Veron, J.E.N., D.M. Odorico, C.A. Chen and D.J. Miller. 1996. Reassessing evolutionary relationships of scleractinian corals. *Coral Reefs*, 15: 1-9. Wells, J.W. – 1973. New and old scleractinian corals from Jamaica.
- Bull. Mar. Sci., 23(1): 16-55.

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