

BIOGEOGRAPHY OF THREE CARIBBEAN CORALS (SCLERACTINIA) AND THE INVASION OF *TUBASTRAEA* *COCCINEA* INTO THE GULF OF MEXICO

Douglas Fenner

ABSTRACT

Tubastraea coccinea and *Mycetophyllia reesi* were found to have ranges that extend throughout the Caribbean, as do most zooxanthellate scleractinian corals found there. *Leptoseris caillieti* has not yet been found in some areas, but is a rarely reported coral. *T. coccinea* has not previously been reported from the Gulf of Mexico, but is now known from seven oil platforms in the northern Gulf of Mexico off the Texas coast, first being sighted in 1991. It has also been seen on four oil platforms in Louisiana, and it is known from oil platforms in the Southern Gulf of Mexico off Campeche and the western Gulf of Mexico off of Tuxpan, Mexico where it was first seen about 1977. Since it is not known from the Gulf of Mexico other than on oil platforms, this represents a rapid range expansion following oil platform placements. The range expansion into the Gulf of Mexico is likely due to a preference of this species for artificial substrates, which may be rapidly colonized.

Most Caribbean stony reef corals have ranges throughout the Caribbean (Glynn, 1973; Liddel and Ohlhorst, 1988; de Weerd, 1990; Fenner, 1993a, 1999; Johnson et al., 1995; Paulay, 1997), though only some of those corals extend outside the Caribbean into the waters of western Florida (Grimm and Hopkins, 1977; Hopkins et al., 1977), the Texas Flower Banks (Tresslar, 1974; Bright et al., 1984; Rezak et al., 1985), the SW Gulf of Mexico (Tunnell, 1988; Gutierrez et al., 1993), Bermuda (Laborel, 1966; Sterrer and Schoepfer-Sterrer, 1986), Brazil (Laborel, 1967, 1969) or the eastern Atlantic (Laborel, 1974). Within the Caribbean, only *Millepora squarrosa* has been documented to be endemic to a restricted area (de Weerd, 1990; Fenner, 1993b), while *Millepora striata* is a rare coral that is difficult to recognize and which has only been found in part of the Caribbean (Fenner, 1999). The ranges and distributions of several stony corals remain poorly known in the Western Atlantic, due to sparse records of their occurrences. Three of these species [*Tubastraea coccinea*, *Mycetophyllia reesi* and *Leptoseris caillieti* (= *Agaricia caillieti*)] have sparse published records that suggest that they extend to only part of the Caribbean (e.g., Cairns, 2000), and thus have a potential to be endemic to a restricted area in the Caribbean. However, the ranges of these species have not been studied systematically to date. This study used published records, museum collections and new collections, photos and field reports to study the distributions of these three species of stony corals.

METHODS

Species presence data were derived from published reports, and from personal communications primarily concerning the easily identified *T. coccinea*, which is distinctive in both color and colony shape. Most personal communications were from marine biologists, and were verified by examination of specimens and/or photos, as indicated in Table 2. The collections of museums with significant Caribbean coral collections were searched for the three species, including the Smithsonian Institution (USNM), Yale Peabody Museum (YPM), Harvard Museum of Comparative Zoology (HMCZ), La Parguera Marine Laboratory Museum (LPM), the University of Miami (RSMAS), the

California Academy of Sciences (CAS), the Dieckman collection (Belize City, Belize), and a catalog of the Scripps collection (Luke, 1998). Although the names *Tubastraea aurea* and *T. tenuilamellosa* have been used for the Caribbean species, current taxonomic work indicates that it is *T. coccinea* (Cairns, 1994, 2000), and there is no indication that there is more than one species in the Western Atlantic.

RESULTS

The locations given in published reports of the three corals are presented in Table 1. New reports of these corals are presented in Table 2, including museum records. New reports are for corals found on reefs, with the exception of several reports of *T. coccinea* found on man-made objects. *T. coccinea* was found on shipwrecks in S-SE Chinchorro Banks, Mexico (wreck of FALSTAFF, and also on the reef of NW Chinchorro Banks); La Boca, Santa Lucia, Cuba; Tortola Is, British Virgin Islands (wreck of RHONE); and Parc Nacional San Estiban, Venezuela. It was also found on pier pilings at Fredrickstad, St. Croix, U.S. Virgin Islands and NW Puerto Rico, and it was found inside the fuselages of sunken airplanes at Cozumel, Mexico and Long Cay, South Caicos, Turks and Caicos Islands. Table 3 presents details of the oil platforms in the Gulf of Mexico where *T. coccinea* has been found. Figure 1 presents a map of the known locations of *T. coccinea* in the Western Atlantic, Figure 2 presents the same for *M. reesi*, and Figure 3 for *L. cailleti*.

DISCUSSION

Two of the three species of stony coral studied here (*M. reesi* and *T. coccinea*) have ranges that are here documented to extend throughout the Caribbean, including the Bahamas and Florida. The third species, *L. cailleti*, has not yet been found in the Northwest Caribbean, Cuba, Florida or the Bahamas. *L. cailleti* is a very small, light brown zooxanthellate coral (Dinesen, 1980; P. Colin, pers. comm., C. Bouchon, pers. comm., Veron 2000 (Colin photo); but Macintyre et al., 1991 considered it to be ahermatypic) restricted to depths greater than about 33 m, and thus is rarely seen by divers. It is known primarily from dredged specimens. Dredging would seem likely to be sufficient to find it in Florida. Sufficient dredging has been carried out in the northwest Caribbean for about 43 species of azooxanthellate Scleractinia and Stylasterina to be reported from depths below 30 m in the Mexican Caribbean (Cairns, 1979, 1986; Horta-Puga and Carricart-Ganivet, 1993). This might suggest that the lack of a report of this species from these areas may not be due to inadequate searching. However, collections in most areas where it is known and in most museums consist of only a few specimens. Sampling in the northwestern Caribbean may simply be insufficient for it to have been found there yet. *M. squarrosa* remains the only stony coral well documented to have a range that includes only part of the Caribbean (de Weerd, 1990; Fenner, 1993b).

T. coccinea has never been reported from the Gulf of Mexico other than on oil platforms, though reefs have been studied in the S.W. Gulf of Mexico (Tunnell, 1988; Gutierrez et al., 1993), Texas Flower Banks (Tresslar, 1974; Bright et al., 1984; Rezak et al., 1985), and Florida Middle Ground (Grimm and Hopkins, 1977; Hopkins et al., 1977). *T. coccinea* has never been found on the Texas Flower Gardens, even though they receive about 20,000 dives per year (S. Gittings, pers. comm.), but it has been found on several oil platforms which are much less frequently dived, including some very close to the Flower Gardens.

Table 1. Published reports of the distribution of *Tubastraea coccinea* (Tc), *Mycetophyllia reesi* (Mr), and *Leptoseris cailetti* (Lc). A minus indicates that the paper did not include the species in a list of species for that location; a blank indicates that the paper did not present a species list and the species was not included in the paper topic.

| Location | Present +, absent - | | | Reference |
|--------------------|---------------------|----|----|---|
| | Tc | Mr | Lc | |
| Bahamas: | | + | | Colin (1978) |
| Grand Bahama | + | | | Frink (1994) |
| Bimini | - | - | - | Squires (1958) |
| Sapona wreck | + | | | Szmant et al. (1990) |
| Exuma | - | - | - | Chiappone and Sullivan (1991); Sullivan and Chiappone (1992); Chiappone et al. (1997) |
| Turks and Caicos | - | - | - | Sullivan et al. (1994); Chiappone et al. (1996) |
| | + | - | - | Steiner (1999) |
| Silver Bank | + | | | Cairns (2000) |
| Dominican Republic | | | + | Dinesen (1980) |
| | - | - | - | Williams et al. (1983) |
| Puerto Rico | + | - | - | Boschma (1953); Almy and Carrion-Torres (1963); Colin (1978) |
| | | | + | Dinesen (1980) |
| St. Thomas | | | + | Dinesen (1980) |
| St. Croix | + | - | - | Adey et al. (1977), Rogers et al. (1984) |
| St. John | + | | | Cairns (2000) |
| Anagada | + | - | - | Dunne and Brown (1979) |
| Saba | + | - | - | Roos (1971); Bak (1975); Edmunds et al. (1990) |
| St. Barthelemy | + | | | Bouchon and Laborel (1990) |
| St. Martin | + | | | Bak (1975); Bouchon and Laborel (1990) |
| St. Eustatius | + | | | Bak (1975) |
| Anguilla | + | | | Bouchon and Laborel (1990) |
| Guadeloupe | + | - | + | Bouchon and Laborel (1990) |
| Dominica | | | + | Dinesen (1980) |
| Martinique | - | - | + | Bouchon and Laborel (1986) |
| St. Lucia | - | - | - | Roberts (1972); Fenner (1998) |
| Barbados | - | - | - | Lewis (1960); Ott (1975) |
| | | | + | Macintyre et al. (1991) |
| St. Vincent | - | - | - | Adams (1968) |
| | | | + | Dinesen (1980) |
| Grenadines | - | - | - | Lewis (1975) |
| Tobago | - | - | - | Laydoo (1990) |

Table 1. Continued

| Location | Present +, absent - | | | Reference |
|------------------|---------------------|----|----|---|
| | Tc | Mr | Lc | |
| Trinidad | - | - | - | Hubbard and Wells (1986); Kenny (1989) |
| Venezuela: | | | | |
| Gulf of Cariaco | + | - | - | Olivares (1971); Antonius (1980) |
| Bahá de Mochima | + | - | - | Pauls (1982) |
| Aruba | + | - | + | Roos (1971); Bak (1975); Dinesen (1980) |
| Bonaire | + | - | - | Roos (1971); Scatterday (1974); Bak (1975); Van Veghel (1997); Cairns (2000) |
| Curaçao | + | + | - | Boschma (1953); Roos (1964, 1971); Bak (1975, 1977); Cairns (2000) |
| Colombia | + | - | - | Geyer (1969); Pfaff (1969); Erhardt and Meinel (1975); Werding (1979) |
| | + | + | - | Prahl and Erhardt (1985, 1988) |
| | + | | | Cairns (2000) |
| Isla Providencia | + | - | - | Geister (1975, 1992); Prahl and Erhardt (1985, 1988) |
| Isla San Andrés | - | - | - | Geister (1975) |
| Panama | + | | | Porter (1972); Robertson and Glynn (1977) |
| | | + | - | Dahl et al. (1974); Holst and Guzman (1993) |
| Costa Rica | - | - | - | Cortes et al. (1984); Cortes and Guzman (1985); Cortes (1992) |
| Nicaragua | - | - | - | Jameson (1998) |
| Honduras: Roatan | - | - | - | Halas and Jaap (1982); Fenner (1993a) |
| Swan Islands | - | - | - | Tortora and Keith (1980) |
| Belize | | + | | James and Ginsburg (1979) |
| | - | - | - | Cairns (1982) |
| | + | + | - | Fenner (1999) |
| Mexico: | - | - | - | Beltran-Torres and Carricart-Ganivet (1999) |
| Sian Ka'an | - | - | - | Gutierrez et al. (1993); Jordan-Dahlgren et al. (1994) |
| Akumal | - | - | - | Munoz-Chagin and Cruz-Aguero (1993) |
| Chinchorro | - | - | - | Jordan and Martin (1987) |
| Cozumel | - | - | - | Fenner (1988); Jordan (1988); Muckelbauer (1990); Fenner (1999) |
| Puerto Morelos | - | - | - | Jordan (1979); Jordan et al. (1981); Castanares and Soto (1982) |
| Isla Contoy | - | - | - | Reyes-Castro et al. (1989) |
| Grand Cayman | - | + | - | Ghiold and Smith (1990) |
| | + | + | + | Roberts (1994) |

Table 1. Continued

| Location | Present +, absent - | | | Reference |
|---------------------|---------------------|----|----|---|
| | Tc | Mr | Lc | |
| Little Cayman | - | + | - | Fenner (1993a); Miller (1993) |
| Cayman Brac | - | + | - | Miller (1993) |
| | - | - | - | Fenner (1993a) |
| Jamaica | + | + | - | Goreau (1959); Goreau and Wells (1967); Wells (1973); Wells and Lang (1973); Stievenart (1975); Cairns (2000) |
| Cuba: | - | - | - | Duarte Bello (1961) |
| | | + | | Kühlmann (1974) |
| Eastern | + | - | - | Zlatarski and Estallela (1982) |
| Western | - | + | - | Zlatarski and Estallela (1982) |
| Florida | - | - | - | Grimm and Hopkins (1977); Hopkins et al. (1977); Davis (1982); Jaap (1979); Wheaton and Jaap (1988); Levy et al. (1996) |
| North Atlantic: | | | | |
| Bermuda | - | - | - | Laborel (1966); Sterrer and Schoepfer-Sterrer (1986) |
| Gulf of Mexico: | | | | |
| Texas | - | - | - | Tresslar (1974); Bright, et al. (1984); Bright, et al. (1991) |
| S.W. Gulf of Mexico | - | - | - | Tunnell (1988); Gutierrez et al. (1993) |
| South Atlantic: | | | | |
| Brazil | - | - | - | Laborel (1967, 1969) |
| East Atlantic: | | | | |
| West Africa | +? | - | - | Laborel (1974) |

T. coccinea has been found on oil platforms in the Gulf of Mexico only a few years after their placement in the Gulf, while it has never been reported on the Flower Gardens, which have been there for thousands of years. There can be little doubt that the recently observed settlement of *T. coccinea* on Mexican, Texas and Louisiana oil platforms does indeed represent a major recent range expansion of that species. It parallels the discovery of the azooxanthellate coral *Lophelia pertusa* on North Sea oil rigs, which represents a range extension of that species into the North Sea (Bell and Smith, 1999).

T. coccinea has frequently been reported on shipwrecks and pilings, and here is also reported on sunken airplanes. Such artificial surfaces appear to provide superior habitat for this species, and it could be considered a fouling organism as well as a reef species. The expansion of *T. coccinea* into the Gulf is very likely due to the appearance of highly favorable new habitat in the Gulf in the form of oil platforms.

Table 2. New data on locations of *Tubastraea coccinea* (Tc), *Mycetophyllia reesi* (Mr), and *Leptoseris caillieti* (Lc), and data from museum collections. Names of researchers indicate personal communications. Abbreviations: Smithsonian Museum (USNM), Yale Peabody Museum (YPM), La Parguera Marine Laboratory Museum (LPM), Rosenstiel School of Marine and Atmospheric Science, University of Miami (RSMAS), California Academy of Sciences (CAS), and Harvard Museum of Comparative Zoology (HMCZ). s = sample, p = photograph, + = observation.

| | Tc | Mr | Lc |
|---------------------|----|----|------------------|
| Bahamas: | | | |
| Little Bahama Bank: | | | |
| SW Walker's Cay | + | | S. Viada |
| Bimini: | | | |
| Chicken & Hen Reef | p | | P. Humann |
| Lee Stocking: | | p | D. Danaher |
| Perry Reef | + | | E. Weil |
| Aklins Island | | s | RSMAS |
| Turk Is. | | | s RSMAS |
| Haiti | | | s USNM |
| Dominican Republic | + | + | E. Weil |
| | | | s USNM |
| Mono Is. | + | | R. P. van Dam |
| Puerto Rico | s | | A. Szmant, RSMAS |
| | | | s LPM, USNM |
| | + | + | E. Weil |
| St. Thomas | | | s USNM, YPM |
| | | | s B. Kojis |
| St. John | s | | CAS, C. Rogers |
| British Virgin Is. | s | s | C. Petrovic |
| Saba Bank | + | | M. Vermeij |
| Dominica | | | s USNM |
| Barbados | | + | T. Tomasick |
| | | | s USNM, HMCZ |
| Grenadines | | | s USNM |
| Venezuela: | | | |
| Isla Orchila | | | s RSMAS |
| Paraguaná Penn. | | | s USNM, RSMAS |
| Los Roques Is. | p | + | + |
| P.N. Morrocoy | + | | E. Weil |
| P.N. San Esteban | + | | C. Bastidas |

Table 2. Continued

| | Tc | Mr | Lc | |
|--------------------|----|----|----|---------------------------------------|
| Curaçao | s | | | RSMAS |
| Colombia islands: | | | | |
| San Andrés | + | | | S. Zea |
| Roncador | + | + | | S. Zea |
| Serrana | + | | | S. Zea |
| | | s | s | USNM, RSMAS |
| Honduras: Roatan | | p | | P. Humann |
| | p | | | P. Schroder |
| Belize | s | s | | Dieckman collection ¹ |
| Chinchoro Banks | + | | | E. Jordan |
| Cozumel, Mexico | p | | | J. Castello |
| Cuba: | | | | |
| Santa Lucía | + | | | H. Minor |
| Isle of Youth | + | | | D. Danaher |
| | | + | | A. Szmant |
| Gulf of Mexico: | | | | |
| Tuxpan oil rigs | + | | | J. Castello |
| Campeche oil rigs | + | | | J. Castello |
| Texas oil rigs | + | | | S. Gittings, C. Brewer, E. Hickerson, |
| | sp | | | J. Wiseman, S. Viada |
| Louisiana oil rigs | p+ | | | D. Stanley, J. Wiseman, S. Viada |

¹ Collection of Rev. L. E. Dieckman, St. John's College, Box 548 Belize City, Belize.

There are several possible modes of dispersal of *T. coccinea* into the Gulf of Mexico. Ships could have carried it, and indeed two early reports in the Caribbean were of colonies on boat hulls (Boschma, 1953; Roos, 1971). However, ships from the Caribbean are not allowed to tie up at Texas or Louisiana oil rigs (S. Gittings, pers. comm.). It could have been carried on floating rafts of pumice or wood (Jokiel, 1990). Or planula larvae could have been carried from the Caribbean directly to Texas on the loop current (Gittings, et al. 1992), or along the continental shelf, perhaps using the approximately 3800 oil platforms (Dokken, 1993) as 'stepping stones' as suggested for fish (Pattengill, et al. 1997). The planulae of corals of the genus *Tubastraea* have been observed to swim and remain competent to settle for up to 100 d (Richmond, pers. comm.), suggesting extensive dispersal abilities. Or attached adult colonies may have been carried on mobile 'jack-up' oil platforms, which are periodically moved from Venezuelan oil fields to the Gulf of Mexico. Any or several of these mechanisms of dispersal may have occurred; direct evidence of the mode of dispersal is currently lacking.

Cairns (1994) has suggested that *T. coccinea* may have been dispersed through the Caribbean by transport on ship hulls. He also suggested (Cairns, 2000) that it may have been carried on ship hulls from the Pacific where the same morphospecies is found, through

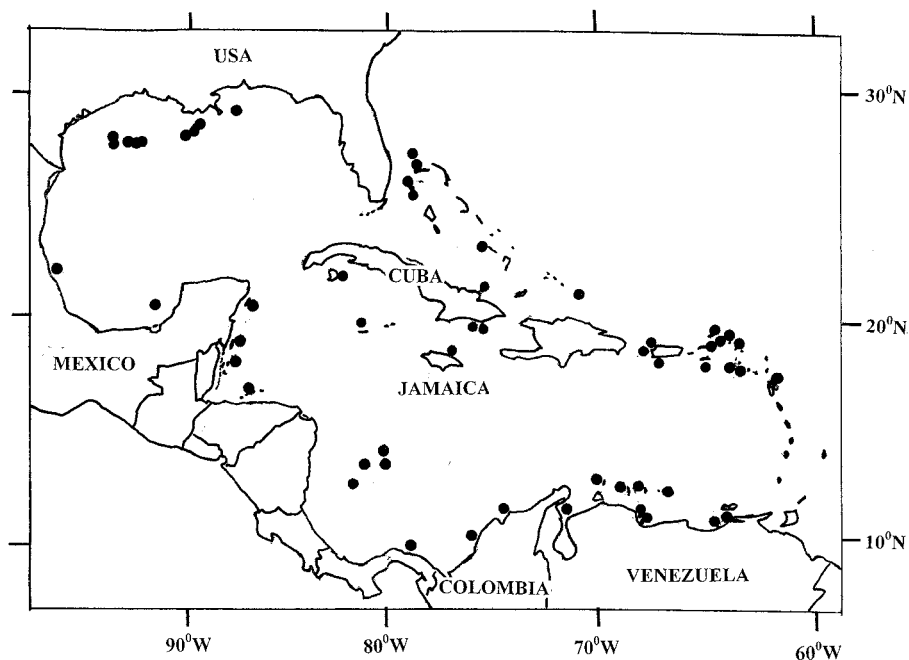


Figure 1. Map of locations from which *Tubastraea coccinea* has been reported in the Western Atlantic.

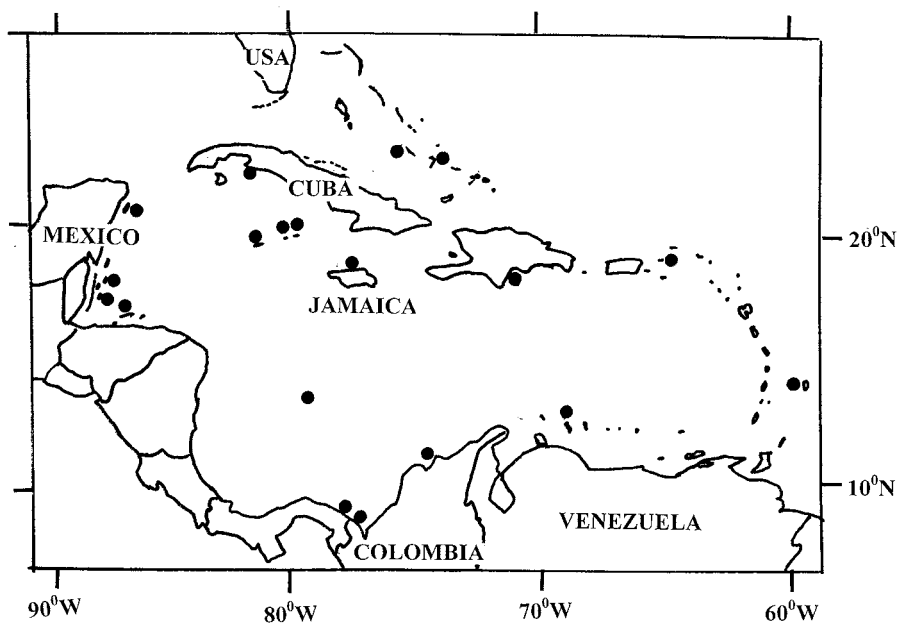


Figure 2. Map of locations from which *Mycetophyllia reesi* has been reported in the Western Atlantic.

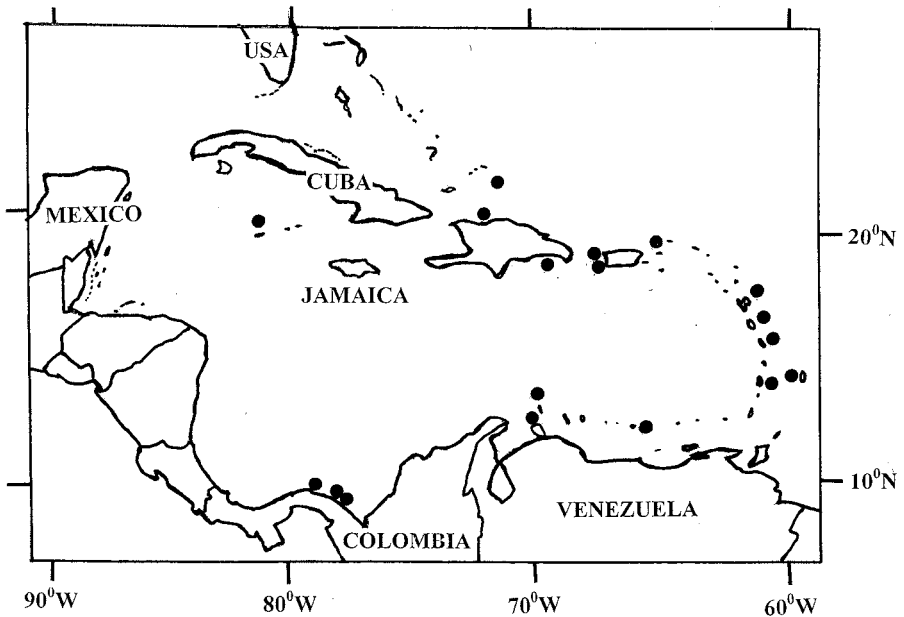


Figure 3. Map of locations from which *Leptoseris cailleti* has been reported in the Western Atlantic.

the Panama Canal and introduced into the Caribbean where it subsequently spread. Similarly, Zibrowius (1974) has suggested that the coral *Oculina patagonica* may have been carried by ships from Atlantic South America to the Mediterranean. Direct evidence to support these hypotheses remains to be found, though *T. coccinea* has not been found among Caribbean fossils (Cairns, in press). Dispersal of *T. coccinea* is very likely to include planular dispersal, since that is the most likely route for the colonization of sunken airplanes.

ACKNOWLEDGMENTS

Conversations with S. Gittings concerning the colonization of Texas oil platforms by *Tubastraea* sp. are gratefully acknowledged. The author thanks P. Young and H. Zibrowius for suggesting transport on mobile platforms, S. Viada for finding information on mobile oil platforms, and also thanks J. Castello, D. Stanley, S. Viada, S. Steiner, C. Petrovic, C. Bastidas, H. Minor, E. Jordan-Dahlgren, L. Harris, R. H. Richmond, E. Weil and B. Tewes for details concerning their observations. Those who generously shared the information contained in Table 2 and who are cited there are also gratefully acknowledged. The author thanks S. Cairns, H. Zibrowius and two anonymous reviewers for helpful comments on the manuscript.

Table 3. *Tubastraea coccinea* on oil platforms.

| Platform name | Location | First sighting | Verification | Reporter |
|-------------------------|---------------------------------------|----------------|-----------------|------------------------|
| High Island A389 | Texas 27.900534°N 93.577224°W | 1991 | visual | S. Gittings and Beaver |
| Anadarko 376A | Texas 27.96168°N 93.67089°W | 1994 | visual | S. Gittings and Beaver |
| East Breaks 165 | Texas 27.818735°N 94.322836°W | 1994 | visual | S. Gittings and Beaver |
| Matagord Island 526 | Texas 28°18'27"N 96°13'41"W | 1999 | sample photo | J. Wiseman |
| High Island 356A | Texas 28°02.48'N 93°45.55'W | 1994 | photo | S. Viada |
| High IslandA 245 | Texas 28.5520°N 93.6020°W | 2000 | sample | J. Wiseman |
| High IslandA 570A | Texas 27°7'2.35"N 94°02'43"W | 2000 | sample | J. Wiseman |
| Grand Isle 94 | Louisiana 28°32.33'N 90°05.52'W | | visual | D. Stanley |
| Green Canyon 18 | Louisiana 27°56.48'N 91°02.28'W | | visual | D. Stanley |
| Main Pass 265A | Louisiana 29.3466°N 88.2161°W | | photo | J. Wiseman |
| Mississippi Canyon 280A | Louisiana 28°39.46'N 89°09.28'W | 1994 | photo | S. Viada |
| Atum-1 | Tuxpan, Mexico | 1977 | visual | J. Castello |
| Atum-2 | Campeche, Mexico | 1985 | visual | J. Castello |

LITERATURE CITED

- Adams, R. D. 1968. The leeward reefs of St. Vincent, West Indies. *J. Geol.* 76: 587–595.
- Adey, W., W. Gladfelter, J. Ogden and R. Dill. 1977. Field guidebook to the reefs and reef communities of St. Croix, Virgin Islands. *Field Guidebooks, 3rd Int'l. Coral Reef Symp.* 52 p.
- Almy, C. and C. Carrion-Torres. 1963. Shallow-water stony corals of Puerto Rico. *Carib. J. Sci.* 3: 133–162.
- Antonius, A. 1980. Occurrence and distribution of stony corals in the Gulf of Cariaco, Venezuela. *Int. Rev. ges. Hydrobiol.* 65: 321–338.

- Bak, R. P. M. 1975. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. *Bijd. tot Dierk.* 45: 181–190.
- _____. 1977. Coral reefs and their zonation in Netherlands Antilles. Pages 3–16 in S. H. Frost, P. M. Weiss and J. B. Saunders, eds. *Reefs and related carbonates - ecology and sedimentology*. Amer. Assoc. Petrol. Geol., Tulsa, Okla.
- Bell, N. and J. Smith. 1999. Coral growing on North Sea oil rigs. *Nature* 402: 601.
- Beltran-Torres, A. and J. P. Carricart-Ganivet. 1999. Lista revisada y clave para los corales pétreos zooxantelados (Hydrozoa: Millepora; Anthozoa: Scleractinia) del Atlántico mexicano. *Rev. Biol. Trop.* 47: 813–829.
- Boschma, H. 1953. On specimens of the coral genus *Tubastraea*, with notes on phenomena of fission. *Stud. Fauna Curacao* 4: 109–119.
- Bouchon, C. and J. Laborel. 1986. Les peuplements coralliens des côtes de la Martinique. *Ann. Inst. Océanogr.* 62: 199–237.
- _____. and _____. 1990. Coral assemblages of the Grand Cul-de-Sac Marin in Guadeloupe. *Ann. Inst. Océanogr.* 66: 19–36.
- Bright, T. J., G. P. Draemer, G. A. Minnery and S. T. Viada. 1984. Hermatypes of the Flower Garden Banks, Northwestern Gulf of Mexico: a comparison to other Western Atlantic Reefs. *Bull. Mar. Sci.* 34: 461–476.
- _____, S. R. Gittings and R. Zingula. 1991. Occurrence of Atlantic reef corals on offshore platforms in the Northwestern Gulf of Mexico. *Northeast Gulf Sci.* 12: 55–60.
- Cairns, S. D. 1979. The deep-water Scleractinia of the Caribbean Sea and adjacent waters. *Stud. Fauna Curacao* 57: 1–341.
- _____. 1982. Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. *Smithson. Contrib. Mar. Sci.* 12: 271–302.
- _____. 1986. A revision of the Northwest Atlantic Stylasteridae (Coelenterata: Hydrozoa). *Smithson. Contrib. Zool.* 418: 1–131.
- _____. 1994. Scleractinia of the temperate North Pacific. *Smithson. Contrib. Zool.* 557: 1–150.
- _____. 2000. A revision of the shallow-water azooxanthellate Scleractinia of the Western Atlantic. *Stud. Nat. Hist. Carib.* 75: 1–240.
- _____. (in press). Stratigraphic distribution of Neogene azooxanthellate corals (Scleractinia, Stylasteridae). In *The Neogene of the Isthmus of Panama: A paleobiotic survey of the Caribbean coast*. Paleontological Research Institute.
- Castañeres, L. G. and L. A. Soto. 1982. Estudios sobre corales escleractinios hermatípicos de la costa noreste de la península de Yucatán, México. Parte I: Sinopsis taxinómica de 38 especies (Cnidaria, Anthozoa, Scleractinia). *An. Inst. Cienc. del Mar. y Limnol. Univ. Nal. Auton. México* 9(1): 295–344.
- Chiappone, M. and K. M. Sullivan. 1991. A comparison of line transect versus linear percentage sampling for evaluating stony coral (Scleractinia and Milleporina) community similarity and area coverage on reefs of the central Bahamas. *Coral Reefs* 10: 139–154.
- _____, _____ and C. Lott. 1996. Hermatypic scleractinian corals of the south-eastern Bahamas: a comparison to Western Atlantic reef systems. *Carib. J. Sci.* 32: 1–13.
- _____, _____ and R. Sluka. 1997. Reef invertebrates of the Exuma Cays: Part 1 – Corals. *Bahamas J. Sci.* 4: 30–36.
- Colin, P. L. 1978. *Caribbean reef invertebrates and plants*. T. F. H. Publications, Neptune City, New Jersey. 512 p.
- Cortés, J. 1992. Los arrecifes coralinos del Refugio Nacional de Vida Silvestre Gandoca- Mazanillo, Limón, Costa Rica. *Rev. Biol. Trop.* 40: 325–333.
- _____. and H. M. Guzmán. 1985. Organismos de los arrecifes coralinos de Costa Rica III. Descripción y distribución geográfica de corales escleractinios (Cnidaria: Anthozoa: Scleractinia) de la costa Caribe. *Brenesia* 24: 63–124.

- _____, M. M. Muirillo, H. Guzmán and P. O. Baumgartner. 1984. Organismos de los arrecifes coralinos de Costa Rica I. Lista de corales pétreos (Cnidaria: Hydrozoa, Scleractinia) de la costa Atlántica de Costa Rica. *Brenesia* 22: 57–59.
- Dahl, A.L., J. G. Macintyre and A. Antonius. 1974. A comparative survey of coral reef research sites. *Atoll Res. Bull.* 172: 37–120.
- Davis, G. E. 1982. A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bull. Mar. Sci.* 32: 608–623.
- Dinesen, Z. 1980. A revision of the coral genus *Leptoseris* (Scleractinia: Fungiina: Agariciidae). *Mem. Qd. Mus.* 20: 181–235.
- Dokken, Q. 1993. Flower Gardens ocean research project: using offshore platforms as research stations. *Mar. Tech. Soc. J.* 27(2): 45–50.
- Duarte Bello, P. P. 1961. Corales de los arrecifes cubanos. *Acuario Nacional, Ser. Educ.* 2: 1–85.
- Dunne, R. P. and B. E. Brown. 1979. Some aspects of the ecology of reefs surrounding Anegada, British Virgin Islands. *Atoll Res. Bull.* 236: 1–80.
- Edmunds, P. J., D. A. Roberts and R. Singer. 1990. Reefs of the northeastern Caribbean. I. Scleractinian populations. *Bull. Mar. Sci.* 46: 780–789.
- Erhardt, H. and W. Meinel. 1975. Die scleractinen Korallen der Insel Ceycen, Islas San Bernardo, vor der Kolumbianischen Atlantikküste. *Philippia* II, 4: 236–247.
- Fenner, D. P. 1988. Some leeward reefs and corals of Cozumel, Mexico. *Bull. Mar. Sci.* 42: 133–144.
- _____. 1993a. Some reefs and corals of Roatan (Honduras), Cayman Brac, and Little Cayman. *Atoll Res. Bull.* 388: 1–30.
- _____. 1993b. Species distinctions among several Caribbean stony corals. *Bull. Mar. Sci.* 53: 1099–1116.
- Fenner, D. 1998. Reef topography and coral diversity of Anse Galet Reef, St. Lucia. *Carib. Mar. Stud.* 6: 19–26.
- _____. 1999. New observations on the stony coral (Scleractinia, Milleporidae, Styliasteridae) species of Belize (Central America) and Cozumel (Mexico). *Bull. Mar. Sci.* 64: 143–154.
- Frink, S. 1994. UNEXSO's adventure dives. *Skin Diver* 43(7): 129–132.
- Geister, J. 1975. Riffbau und geologische Entwicklungsgeschichte der Insel San Andres (westliches Karibisches Meer, Kolumbien). *Stuttgarter Beitr. Naturk. Ser. B.* 15: 1–203.
- _____. 1992. Modern reef development and Cenozoic evolution of an oceanic island/reef complex: Isla de Providencia (Western Caribbean Sea, Colombia). *Facies* 27: 1–70.
- Geyer, O. F. 1969. Vorläufige liste der scleractinen Korallen der Bahía de Concha bei Santa Marta, Kolumbien. *Mitt. Inst. Colombo-Aleman Invest. Cient.* 3: 25–28.
- Ghiold, J. and S. H. Smith. 1990. Bleaching and recovery of deep-water, reef-dwelling invertebrates in the Cayman Islands, BWI. *Carib. J. Sci.* 26: 52–61.
- Gittings, S. R., G. S. Boland, K. J. P. Deslarzes, C. L. Combs, B. S. Holland and T. J. Bright. 1992. Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, Northwest Gulf of Mexico. *Bull. Mar. Sci.* 51: 420–428.
- Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. Pages 271–324 in O. A. Jones and R. Endean, eds. *Biology and geology of coral reefs, vol. II: Biology 1*. Academic Press, New York.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40: 67–90.
- _____. and J. W. Wells. 1967. The shallow-water Scleractinia of Jamaica: Revised list of species and their vertical distribution range. *Bull. Mar. Sci.* 17: 442–453.
- Grimm, D. E. and T. S. Hopkins. 1977. Preliminary characterization of the octocorallian and scleractinian diversity at the Florida Middle Ground. *Proc. 3rd Int'l. Coral Reef Symp.* 1: 135–141.
- Gutiérrez, D., C. Garcia-Saez, M. Lara and C. Padilla. 1993. Comparación de arrecifes coralinos: Veracruz y Quintana Roo. Pages 785–806 in S. I. Salazar-Vallejo and N. E. González, eds.

- Biodiversidad marina y costera de México. Comisión Nac. Con. Aprov. Biodiv. and Centro Invest. Q. Roo, Chetumal, México.
- Halas, J. and W. Jaap. 1982. Roatan environmental control plan marine environment study. Follow up studies for the Honduran government. 23 p.
- Holst, I. and H. M. Guzmán. 1993. Lista de corales hermatípicos (Anthozoa: Scleractinia; Hydrozoa: Milleporina) a ambos lados del istmo de Panamá. *Rev. Biol. Trop.* 41: 871–875.
- Hopkins, T.S., D. R. Blizzard, S. A. Brawley, S. A. Earle, D. E. Grimm, D. K. Gilbert, R. G. Johnson, E. H. Livingston, C. H. Lutz, J. K. Shaw and B. B. Shaw. 1977. A preliminary characterization of the biotic components of composite strip transects on the Florida Middlegrounds, Northeastern Gulf of Mexico. *Proc. 3rd Int'l. Coral Reef Symp.* 1: 31–37
- Horta-Puga, G. and J. P. Carricart-Ganivet. 1993. Corales pétreos recientes (Millepora, Stylasterina y Scleractinia) de México. Pages 66–80 in S. I. Salazar-Vallejo and N. E. Gonzalez, eds. Biodiversidad marina y costera de México. Com. Nal. Biodiversidad Y CIQRO, México.
- Hubbard, R. H. and J. W. Wells. 1986. Ahermatypic shallow - water scleractinian corals of Trinidad. *Stud. Fauna Curacao* 68: 121–147.
- Jaap, W. C. 1979. The ecology of the South Florida coral reefs: a community profile. U.S. Fish. Wild. Serv. 138 p.
- James, N. P. and R. N. Ginsburg. 1979. The seaward margin of Belize Barrier and Atoll Reefs. Blackwell Scientific Publ, Oxford. 191 p.
- Jameson, S. C. 1998. Rapid ecological assessment of the Cayos Miskitos Marine Reserve with notes on the stony corals off Nicaragua. *Atoll Res. Bull.* 457: 1–15.
- Johnson, K. G., A. F. Budd and T. A. Stemann. 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. *Paleobiology* 21: 52–73.
- Jokiel, P. L. 1990. Long-distance dispersal by rafting: re-emergence of an old hypothesis. *Endeavour* 14: 66–73.
- Jordan, E. 1979. Estructura y composición de arrecifes coralinos en la región norteste de la península de Yucatán, México. *An. Inst. Cienc. del Mar. y Limnol. Univ. Nal. Auton. México* 6(1): 69–85.
- _____. 1988. Arrecifes profundos en la Isla de Cozumel, México. *An. Inst. Cienc. del Mar. y Limnol. Univ. Nal. Auton. México* 15(2): 195–208.
- _____ and E. Martín. 1987. Chinchorro: morphology and composition of a Caribbean atoll. *Atoll Res. Bull.* 310: 1–20.
- _____, M. Merino, O. Moreno and E. Martín. 1981. Community structure of coral reefs in the Mexican Caribbean. *Proc. 4th Int'l. Coral Reef Symp.* 2: 303–308.
- Jordan-Dahlgren, E., E. Martín-Chávez, M. Sánchez-Sequea and A. Gonzalez de la Parra. 1994. The Sian Ka'an Biosphere Reserve coral reef system, Yucatan Peninsula, Mexico. *Atoll Res. Bull.* 423: 1–19.
- Kenny, J. S. 1989. Hermatypic scleractinian corals of Trinidad. *Stud. Fauna Curacao* 123: 83–100.
- Kühlmann, D. H. H. 1974. Die Korallenriffe Kubas III. Riegelriff und Korallenterrasse, zwei verwandte Erscheinungen des bankriffes. *Int. Revue ges. Hydrobiol.* 59: 305–325.
- Laborel, J. 1966. Contribution à l'étude des madreporaires des Bermudes (systématique et répartition). *Bull. Mus. Nat. D'Hist. Nat. 2nd Série* 38: 281–300.
- _____. 1967. A revised list of Brazilian scleractinian corals and description of a new species. *Postilla* 107: 1–14.
- _____. 1969. Madreporaires et hydrocoralliaires récifaux des côtes brésiliennes. *Res. Scient. Camp. Calypso* 9: 171–229.
- _____. 1974. West African reef corals an hypothesis on their origin. *Proc. 2nd Int'l. Coral Reef Symp.* 1: 425–443.
- Laydo, R. S. 1990. The shallow-water scleractinians (stony corals) of Tobago, West Indies. *Carib. Mar. Stud.* 1: 1–36.

- Levy, J. M., M. Chiappone and K. M. Sullivan. 1996. Invertebrate infauna and epifauna of the Florida Keys and Florida Bay, vol. 5: Site Characterisation for the Florida Keys National Marine Sanctuary. Pres. Farley Court Publ., Zenda, Wisconsin. 166 p.
- Lewis, J. B. 1960. The coral reefs and coral communities of Barbados, WI. *Canad. J. Zool.* 38: 1133–1145.
- _____. 1975. A preliminary description of the coral reefs of the Tobago Cays, Grenadines, West Indies. *Atoll Res. Bull.* 178: 1–9.
- Liddel, W. D. and S. L. Ohlhorst. 1988. Comparison of Western Atlantic coral reef communities. *Proc. 6th Int'l. Coral Reef Symp.* 3: 281–286.
- Luke, S. 1998. Catalog of the benthic invertebrate collections of the Scripps Institution of Oceanography: Coelenterata. *Scripps Inst. Oceanogr.* 58 p.
- Macintyre, I. G., K. Rutzler, J. N. Norris, K. P. Smith, S. D. Cairns, K. E. Bucher and R. S. Steneck. 1991. An early Holocene reef in western Atlantic: submersible investigations of a deep relict reef off the west coast of Barbados, WI. *Coral Reefs* 10: 167–174.
- Miller, J. 1993. The quantitative assessment of reef communities and potential sport diver effects on selected sites on Cayman Brac and Little Cayman. Report Sister Island Tourism Assoc. 35 p.
- Muckelbauer, G. 1990. The shelf of Cozumel, Mexico: topography and organisms. *Facies* 23: 185–240.
- Muñoz-Chagín, R. F. and G. de la Cruz-Agüero. 1993. Corales del arrecife de Akumal, Quintana Roo. Pages 761–771 in S. I. Salazar-Vallejo and N. E. González, eds. Biodiversidad marina y costera de México. Comisión Nac. Con. Aprov. Biodiv. and Centro Invest. Q. Roo, Chetumal, México.
- Olivares, M. A. 1971. Estudio taxonómico de algunos madreporarios del Golfo de Cariaco, Sucre, Venezuela. *Bol. Inst. Oceanogr. Univ. Oriente* 10: 73–78.
- Ott, B. 1975. Community patterns on a submerged barrier reef at Barbados, West Indies. *Int. Revue ges. Hydrobiol.* 60: 719–736.
- Pattengill, C. V., B. X. Semmens and S. R. Gittings. 1997. Reef fish trophic structure at the Flower Gardens and Stetson Bank, NW Gulf of Mexico. 8th Int'l. Coral Reef Symp. 1: 1023–1028.
- Paulay, G. 1997. Diversity and distribution of reef organisms. Pages 298–353 in C. Birkeland, ed. *Life and death of coral reefs*. Chapman Hall, New York.
- Pauls, S. M. 1982. Estructura de las comunidades coralinas de la Bahía de Mochima, Venezuela. MSc Thesis, Univ. de Oriente, Cumana, Venezuela. 124 p.
- Pfaff, R. 1969. Las Scleractinia y Milleporina de las Islas del Rosario. *Mitt. Inst. Colombo-Aleman Invest. Cient.* 3: 17–24.
- Prahl, H., von and H. Erhardt. 1985. Colombia, corales y arrecifes coralinos. Univ. del Valle, Bogota, Colombia. 295 p.
- _____. and _____. 1988. Lista anotada de corales ahermatipicos de Colombia. Pages 539–556 *In* Memorias del VI Seminario Nacional de Ciencias del Mar, Bogota, Colombia.
- Porter, J. W. 1972. Ecology and species diversity of coral reefs on opposite sides of the isthmus of Panama. *Bull. Biol. Soc. Wash.* 2: 89–116.
- Reyes-Castro, J., R. Saenz-Morales and G. Horta-Puga. 1989. Corales pétreos de Isla Contoy y Arrecife del Cabezo, Q. Roo, Mexico. *Revista Zool. Mex.* 1: 1–9.
- Rezak, R., T. J. Bright and D. W. McGrail. 1985. Reefs and banks of the northwestern Gulf of Mexico: their geological, biological, and physical dynamics. John Wiley, New York. 259 p.
- Roberts, H. H. 1972. Coral reefs of St. Lucia, West Indies. *Carib. J. Sci.* 12: 179–190.
- _____. 1994. Reefs and lagoons of Grand Cayman. Pages 75–104 in M. A. Brunt and J. E. Davies, eds. *The Cayman Islands: natural history and biogeography*. Kluwer Acad. Publ., Netherlands.
- Robertson, D. R. and P. W. Glynn 1977. Field guidebook to the reefs of San Blas Islands, Panama. *Field Guidebooks, 3rd Int'l. Coral Reefs. Symp.* 15 p.
- Rogers, C. S., H. C. Fitz, M. Gilnack, J. Beets and J. Hardin. 1984. Scleractinian coral recruitment patterns at Salt River Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* 3: 69–76.

- Roos, P. J. 1964. The distribution of reef corals in Curacao. *Stud Fauna Curacao* 20: 1–51.
- _____. 1971. The shallow-water stony corals of the Netherlands Antilles. *Stud. Fauna Curacao* 37: 1–108.
- Scatterday, J. W. 1974. Reefs and associated coral assemblages off Bonaire, Netherlands Antilles, and their bearing on Pleistocene and recent reef models. *Proc. 2nd Int'l. Coral Reef Symp.* 2: 85–106.
- Squires, D. F. 1958. Stony corals from the vicinity of Bimini, Bahamas, British West Indies. *Bull. Am. Mus. Nat. Hist.* 115: 215–262.
- Sterrer, W. and C. Schoepfer-Sterrer, eds. 1986. *Marine fauna and flora of Bermuda*. John Wiley, New York. 742 p.
- Stievenart, J. 1975. Famille de Mussidae: 1 Mise en evidence des relations symbiontes-coraux chez les genres *Mycetophyllia* et *Mussa*. *Ann. Soc. R. Zoo. Belg.* 105: 229–253.
- Steiner, S. C. C. 1999. Species presence and distribution of Scleractinia (Cnidaria: Anthozoa) from South Caicos, Turks and Caicos Islands. *Bull. Mar. Sci.* 65: 861–871.
- Sullivan, K. M. and M. Chiappone. 1992. A comparison of belt quadrat and species presence/absence sampling of stony coral (Scleractinia and Milleporina) and sponges for evaluating species patterning on patch reefs of the central Bahamas. *Bull. Mar. Sci.* 50: 464–488.
- _____, _____ and C. Lott. 1994. Abundance patterns of stony corals on platform margin reefs of the Caicos Bank. *Bahamas J. Sci.* 1: 2–11.
- Szmant, A. M., L. M. Ferrer and L. M. Fitzgerald. 1990. Nitrogen excretion and O:N ratios in reef corals: evidence for conservation of nitrogen. *Mar. Biol.* 104: 119–127.
- Tortora, L. R. and D. E. Keith. 1980. Scleractinian corals of the Swan Islands, Honduras. *Carib. J. Sci.* 16: 65–72.
- Tresslar, R. C. 1974. Corals. Pages 115–139 in T. J. Bright and L. H. Pequegnat, eds. *Biota of the West Flower Garden Bank*. Gulf Publ. Co., Houston, Texas.
- Tunnell, J. W. Jr. 1988. Regional comparison of southwestern Gulf of Mexico to Caribbean Sea coral reefs. *Proc. 6th Int'l. Coral Reef Symp.* 3: 303–308.
- Van Veghel, M. J. L. 1997. A field guide to the reefs of Curacao and Bonaire. *Proc. 8th Int'l. Coral Reef Symp.* 1: 223–234.
- Veron, J. E. N. 2000. *Corals of the World*. V. 1-3. Aust. Inst. Mar. Sci., Townsville.
- Weerdt, W. H. de. 1990. Discontinuous distribution of the tropical west Atlantic hydrocoral *Millepora squarrosa*. *Beaufor.* 41: 195–203.
- Wells, J. W. 1973. New and old scleractinian corals from the West Indies. *Bull. Mar. Sci.* 23: 16–54.
- _____, _____ and J. C. Lang. 1973. Systematic list of Jamaican shallow-water Scleractinia. *Bull. Mar. Sci.* 23: 55–58.
- Werding, B. 1979. Situacion sistematica de algunos corales de las Islas del Rosario y nuevos reportes. *An. Inst. Inv. Mar- Punta Betin.* 11: 25–26.
- Wheaton, J. L. and W. C. Jaap. 1988. Corals and other prominent benthic Cnidaria. *Fla. Ma. Res. Publ.* 43: 1–25.
- Williams, E. H. Jr., I. Clavijo, J. J. Kimmel, P. L. Colin, C. D. Carela, A. T. Bardales, R. A. Armstrong, L. B. Williams, R. H. Boulon and J. R. Garcia. 1983. A checklist of marine plants and animals of the south coast of the Dominican Republic. *Carib. J. Sci.* 19: 39–52.
- Zibrowius, H. 1974. *Oculina patagonica*, scleractiniaire hermatypique introduit en Mediterranee. *Helgolander Merresunters.* 26: 153–173.
- Zlatarski, V. and N. Estalella. 1982. *Les Scléactiniaires de Cuba*. Editions de l'Académie bulgare des Sciences, Sofia. 472 p.

DATE SUBMITTED: June 1, 1999.

DATE ACCEPTED: February 6, 2001.

ADDRESS: *Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810, Australia.*
 E-mail: <d.fenner@aims.gov.au>.