
2016

Documentation of Extensive Root Systems of *Thalassia* Seagrass Along the Banks of Pigeon Creek, San Salvador Island, Bahamas

Bosiljka Glumac
Smith College, bglumac@smith.edu

H. Allen Curran
Smith College, acurran@smith.edu

Follow this and additional works at: https://scholarworks.smith.edu/geo_facpubs



Part of the [Geology Commons](#)

Recommended Citation

Glumac, Bosiljka and Curran, H. Allen, "Documentation of Extensive Root Systems of *Thalassia* Seagrass Along the Banks of Pigeon Creek, San Salvador Island, Bahamas" (2016). Geosciences: Faculty Publications, Smith College, Northampton, MA.
https://scholarworks.smith.edu/geo_facpubs/95

This Conference Proceeding has been accepted for inclusion in Geosciences: Faculty Publications by an authorized administrator of Smith ScholarWorks. For more information, please contact scholarworks@smith.edu

PROCEEDINGS OF THE 16th SYMPOSIUM ON THE GEOLOGY OF THE BAHAMAS AND OTHER CARBONATE REGIONS

June 14-18, 2012



Edited by
Bosiljka Glumac and Michael Savarese



Gerace Research Centre
San Salvador, Bahamas
2016

**DOCUMENTATION OF EXTENSIVE ROOT SYSTEMS
OF *THALASSIA* SEAGRASS ALONG THE BANKS
OF PIGEON CREEK, SAN SALVADOR ISLAND,
BAHAMAS**

**Bosiljka Glumac & H. Allen Curran
Department of Geosciences
Smith College
Northampton, Massachusetts 01063, USA**



REPRINTED FROM:

**Bosiljka Glumac & Michael Savarese (eds.), 2016, *Proceedings of the 16th Symposium
on the Geology of the Bahamas and Other Carbonate Regions:*
San Salvador, Gerace Research Centre, p. 168-175.**

(Cover photo: San Salvador coastline by Erin Rothfus)

DOCUMENTATION OF EXTENSIVE ROOT SYSTEMS OF *THALASSIA* SEAGRASS ALONG THE BANKS OF PIGEON CREEK, SAN SALVADOR ISLAND, BAHAMAS

Bosiljka Glumac* and H. Allen Curran

Department of Geosciences, Smith College, Northampton, Massachusetts 01063

ABSTRACT. Tidal channel margin collapse, possibly in part during Hurricane Irene in August 2011, has exposed elaborate and extensive root systems of *Thalassia testudinum* (turtle grass) along the banks of Pigeon Creek in the southeastern part of San Salvador Island, Bahamas. Observations of collapsed blocks and relatively fresh exposures along steep channel walls were made in January of 2012 during ebb flow conditions near the mouth of the south arm of Pigeon Creek.

Shallow subtidal banks of Pigeon Creek are densely populated by *Thalassia* seagrass, which plays a major role in trapping and stabilizing sediment in this relatively high-energy environment characterized by strong tidal currents. Fresh exposures of the bank margin revealed the dominance of vertical (or orthotropic) rhizomes in the root system of *Thalassia* at this locality. Individual vertical, cylindrical rhizomes extend to about 80 cm below the sediment surface and reach up to 2 cm in diameter. In between these closely spaced, robust rhizomes are less prominent horizontal (plagiotropic) rhizomes, and a very dense and complex network of *Thalassia* roots. Individual roots can be up to several millimeters in diameter and extend from the central rhizome for up to 15 cm or more, forming a thick and extensive root system known as a rhizome and root mat or mesh.

Extensive *Thalassia* root systems may have high potential to produce traces in deposits formed in shallow subtidal carbonate settings characterized by prolific growth of this seagrass. Fossilized root casts or rhizoliths of seagrasses, however, have rarely been documented from the geological record. It is possible that taphonomic modifications can substantially alter, obscure or even completely obliterate the characteristic features of these root systems. This could preclude their positive identification as plant-related trace fossils. Instead the presence of seagrasses could be overlooked or their traces generally classified as structures related to bioturbation. Documentation of well-exposed modern examples can aid future ichnological interpretations and contribute important information on ecology and root-system morphology of seagrasses. Indeed, marine botanists have called for further studies of relatively poorly documented rhizome systems of different species of seagrasses in a variety of substrates and depositional settings.

*Corresponding author. E-mail: bglumac@smith.edu

INTRODUCTION AND STUDY AREA

The role of seagrasses in baffling sediment has been studied and debated by sedimentary geologists for many decades (e.g., Ginsburg and Lowenstam, 1958; Scoffin, 1970; Zieman, 1972; Wanless, 1981; Almasi et al., 1987; Bosence, 1995; among numerous others). Although the effects of substrate stabilization by seagrass rhizomes have been closely considered in these studies, documentation of the morphology and

preservation potential of seagrass root systems in geological literature remains scanty. These underground systems consist of roots for anchoring (e.g., *Thalassia* seagrass has unbranched roots with massive root hairs for penetrating various types of substrate), and of herbaceous, cylindrical rhizomes (i.e., underground stems) for mechanical support. The above ground parts of seagrasses are comprised of shoots with several leaves that have a basal sheath for protection and development, and distal blades

for photosynthesis and transpiration (Kuo and den Hartog, 2006).

The purpose of this study is to document one example of well-exposed seagrass root systems from Pigeon Creek in the southeastern part of San Salvador Island, Bahamas (Figure 1). Shallow subtidal banks of Pigeon Creek are densely populated by seagrass *Thalassia testudinum* (turtle grass), which plays a major role in trapping and stabilizing sediment in this relatively high-energy environment characterized by strong tidal currents (tidal range typically about 90 cm = 3 ft.; Mitchell, 1989). Tidal channel margin collapse, possibly in part during Hurricane Irene in August 2011, exposed elaborate and extensive *Thalassia* root systems, which were observed in January of 2012 during relatively high ebb flow conditions near the mouth of the southern

arm of Pigeon Creek (Figure 1). We present a preliminary investigation of the *Thalassia* root systems in this area, and a discussion of their preservation potential and general paucity of documented examples of seagrass-related bioturbation and/or rhizolith formation in the geological record. The main objective of this work is to draw attention to these extensive root systems, which could aid in future ichnological and sedimentological interpretations.

OBSERVATIONS

Underwater observations focused on the relatively fresh exposures of collapsed blocks and steep walls along Pigeon Creek tidal channel margins (Figure 2). These observations revealed dense growth of *Thalassia* along the surface of

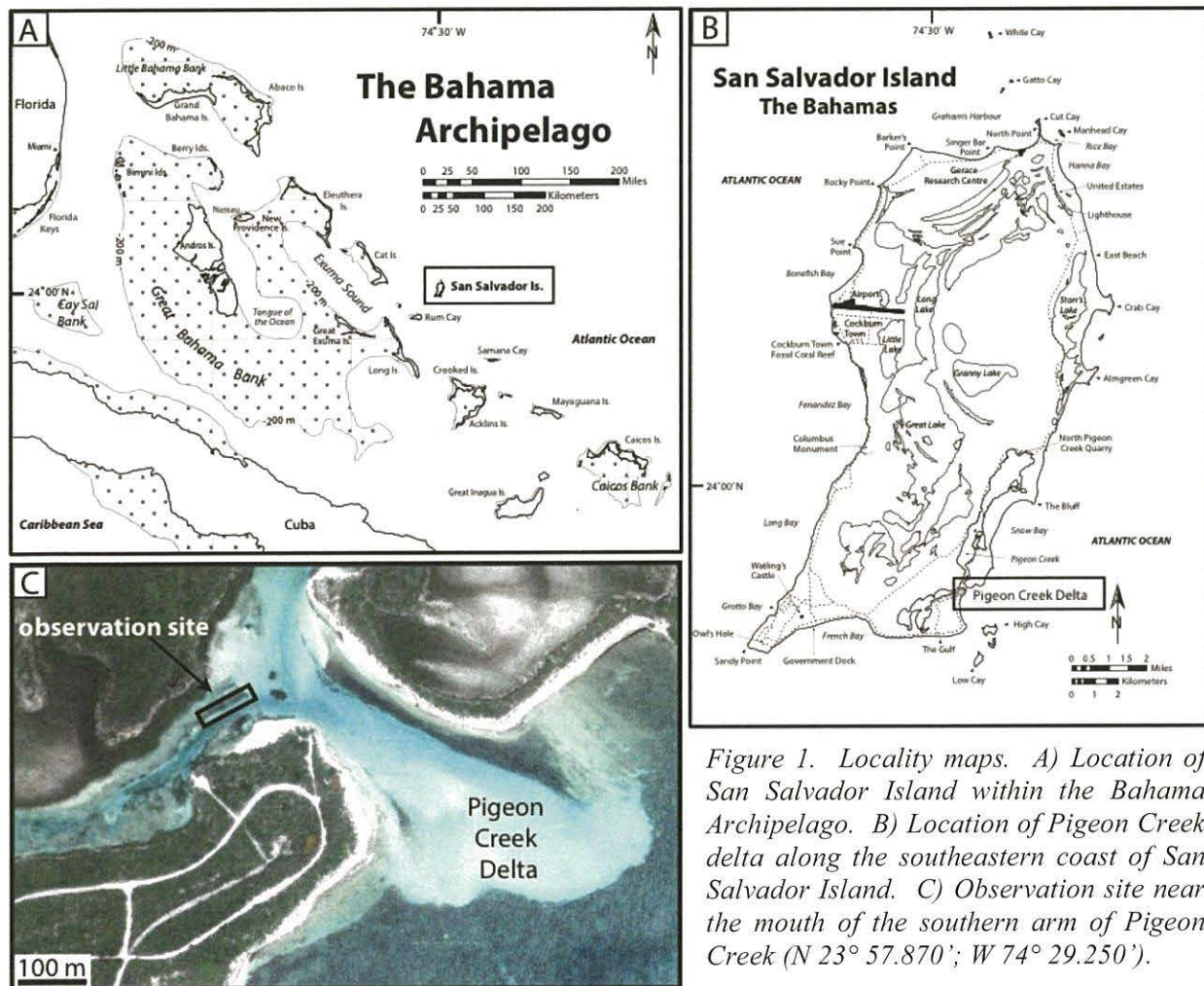


Figure 1. Locality maps. A) Location of San Salvador Island within the Bahama Archipelago. B) Location of Pigeon Creek delta along the southeastern coast of San Salvador Island. C) Observation site near the mouth of the southern arm of Pigeon Creek ($N 23^{\circ} 57.870'$; $W 74^{\circ} 29.250'$).

shallow subtidal banks (water depth reaching about 1.5 meters) in this area. Collapsed blocks and steep walls of the tidal channel exposed the dense and extensive *Thalassia* root systems (Figures 2A & B). Our observations also revealed the dominance of vertical (orthotropic) rhizomes in the root system of *Thalassia* at this locality (Figures 2C & D). Individual vertical cylindrical rhizomes extend to 80 cm below the sediment surface and reach up to 2 cm in diameter. In between, the robust vertical rhizomes are less prominent horizontal (plagiotropic) rhizomes, and a very dense and complex network of *Thalassia* roots (Figures 2E & F). Individual roots are up to about 3 millimeters in diameter, and they extend from the central rhizome for up to 15 cm (possibly longer) forming a thick and extensive root system commonly termed a rhizome and root mat or mesh (Kuo and den Hartog, 2006).

During our fieldwork we also recovered several entire plants with their root systems intact (Figure 3A). Parts of plants above the sediment surface are characterized by several relatively short leaves or leaf blades with common fish bite marks (Figure 3B). Examination of the recovered specimens supported our underwater observations of the root system consisting of a robust central rhizome and numerous thinner individual roots (Figure 3C).

Our observations did not closely focus on the nature and composition of sediment intercalated between the seagrasses and their root systems. Carbonate sediment on the surface of the bank consisted of unlithified skeletal, peloidal and oolitic sand (see also Mitchell, 1989). Sand between the underground seagrass rhizomes was of the same composition but also had some micritic matrix. Even though subjected to strong tidal currents, the exposed rhizomes were coated with sediment (Figure 2) suggesting effective trapping and baffling of sediment in and around root systems and potential early lithification, although the sediment completely washed off during the process of specimen collection (Figure

3). Strong tidal currents and murky waters precluded additional detailed observations.

DISCUSSION

Biology and ecology, including taxonomy, morphology and anatomy of seagrasses has been extensively documented in biological and marine science literature (e.g., den Hartog, 1970; Brasier, 1975; Burrell and Schubel, 1977; Hemminga and Duarte, 2000; Green and Short, 2003; Larkum et al., 1989, 2006). Although some of this literature focuses on or includes information on the morphology of seagrass root systems (e.g., Tomlinson, 1969; Hemminga, 1998; Kuo and den Hartog, 2006), discussions of root-sediment interactions do not usually go beyond recognizing the important role that seagrass root systems play in stabilization of sediment. Thus, seagrass researchers have recommended further detailed studies on the structure of the underground rhizome-root systems of various seagrass species in a range of different environmental settings (Kuo and den Hartog, 2006). Although seagrasses can be abundant in shallow marine ecosystems of tropical and subtropical coastal waters (for example, *Thalassia testudinum* occurs in western Atlantic between 9°S and 32°N, and is most common in water depths of 1–2 m, although it may be found as deep as 10 m; van Tussenbroek et al., 2006, and references therein), their subsurface root systems are not readily exposed and available for detailed examination.

Noel P. James photographed dense rhizome and root systems of *Thalassia* exposed off Eleuthera island, Bahamas, following a hurricane (Froede, 2002; Figure 6A). On San Salvador extensive *Thalassia* root systems, similar to those documented here from Pigeon Creek, have been previously noted in Blackwood Bay along the southern coast of the island, in the eastern portion of French Bay embayment (Pace et al., 1989). Blackwood Bay is a medium to low energy, shallow (0-2 m water depth at low tide) Holocene

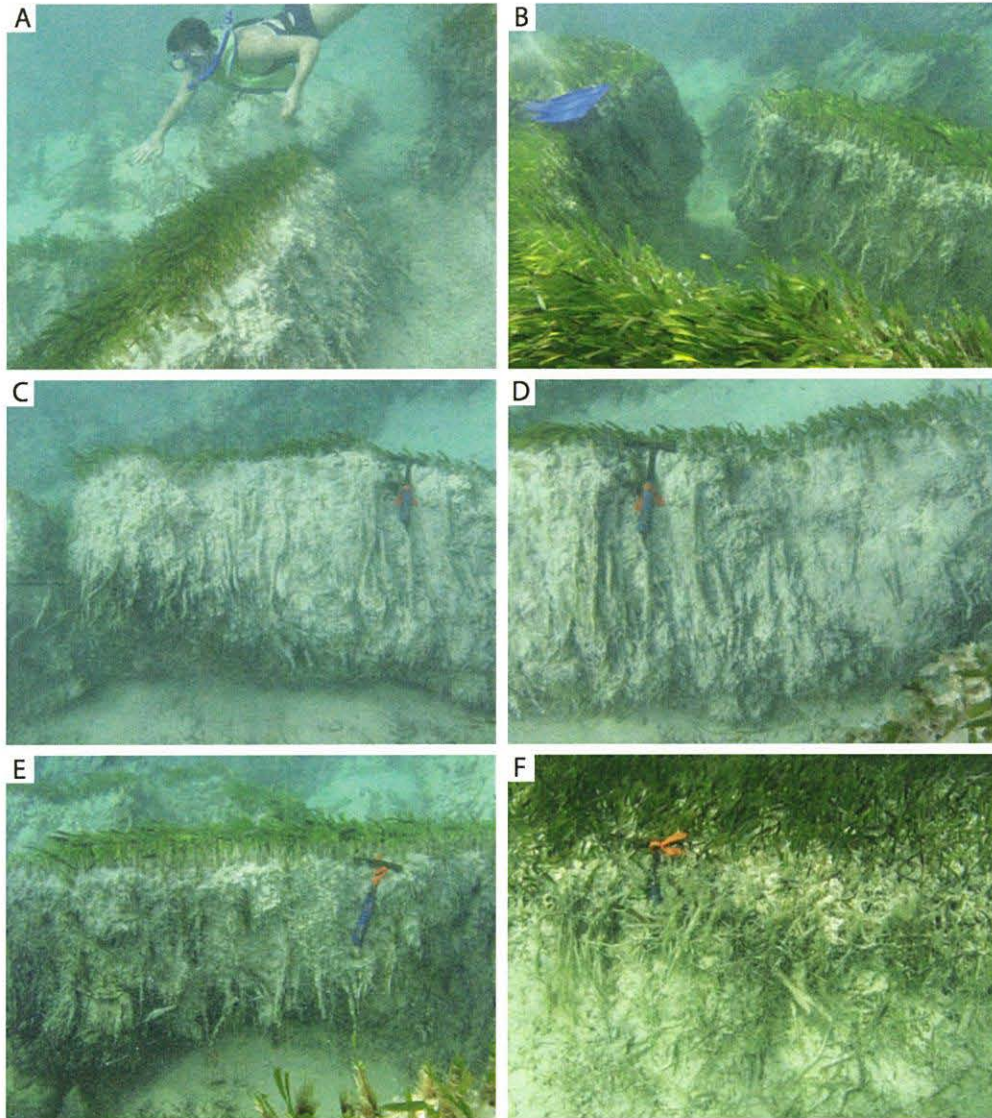


Figure 2. Underwater observations at the Pigeon Creek study site. A) Collapsed block of sediment, held together by a dense seagrass *Thalassia testudinum* root system along edge of the tidal channel (view to the WSW). B) Another view of collapsed blocks along steep margins of the tidal channel (view to the ENE). Note dense growth of *Thalassia* seagrass in shallow water along the banks of the channel and the freshly exposed dense *Thalassia* root system. Flipper for scale = 22 cm wide. C and D) Close-up views of a collapsed block illustrating dominance of vertical rhizomes in the *Thalassia* root system. Hammer for scale = 26 cm long. E) Close-up photo of a collapsed block showing an extensive *Thalassia* root system consisting of horizontal and vertical rhizomes and a dense network of thin roots. A strong tidal current was running, as noted to the left of the photograph and by the abundance of suspended sediment in murky water of the channel. F) Close-up photo of the tidal channel bank margin showing dense growth of *Thalassia* grasses and presence of horizontal rhizomes in the shallow portion of the root system. Hammer for scale.

platform-margin carbonate lagoon shielded from high wave energy by a boulder-rampart platform edge to the south (Pace et al., 1989). Here *Thalassia* grass traps and binds sediment creating

an extensive meadow with sediment accumulation of up to 2 m. Coring of this sediment revealed preserved *Thalassia* rhizomes in deposits younger than 3800 years (Pace et al., 1989). Storm



Figure 3. Photographs of recovered specimens of *Thalassia testudinum* from the study site in Pigeon Creek. Scale in cms. A) Entire specimens. B) Detail of top portions of specimens showing the short seagrass blades with common fish bite marks. C) Close-up photo of robust central cylindrical rhizome and dense network of thin *Thalassia* roots.

currents have eroded the meadow, producing *Thalassia* mounds with steep cliffs and breaking apart large blocks of sediment held together by a dense network of *Thalassia* rhizomes. Pace et al. (1989) also noted that during an intense storm in December of 1986 some of these blocks were torn from the *Thalassia* mounds and deposited in a surrounding sandy depression in water depth of 1.7 m. Analogous processes of strong tidal current cliff undercutting, aided by occasional strong storm-driven wave currents, is proposed here for the formation of breakdown blocks in the Pigeon

Creek area (Figure 2).

Similar to Pace et al. (1989), Bosence (1995) observed common *Thalassia* rhizomes and roots in a core through a “grass-bed” wackestone at depths of 2 to 2.5 meters below the surface of a recent mud-mound in Florida Bay. Comparable features interpreted as seagrass rhizomes with thin vertical rootlets of *Thalassia testudinum* extending 2-4 meters into the underlying substrate were documented by Wanless et al. (1995) and Tedesco and Wanless (1995) from shallow cores through skeletal mudstone to wackestone deposits of modern carbonate mudbanks in south Florida.

Seagrass rhizomes, together with roots and leaf sheath remains and surrounding sediment, may form extensive and dense mats. As the decomposition of the seagrass organic material is relatively slow (leaf sheath remains in the mat can persist for more than 4600 years; Kuo and den Hartog, 2006; and references therein) these mats can reach considerable thickness. In an example from Indonesia (Brouns, 1985), the mats were of comparable thickness to those documented here from the Pigeon Creek tidal channel. In a similar depositional setting – the tidal channel of the eastern margins of Shark Bay, Australia – an about 3 m deep cut exposed a *Posidonia* seagrass rhizome and root mat (Davies 1970). *Posidonia* in the Mediterranean Sea commonly grows on mats whose thickness can locally exceed 4 to 5 meters (Kuo and den Hartog, 2006; and references therein).

Such thick and extensive *Thalassia* root systems may have real potential to leave traces in deposits formed in shallow subtidal carbonate settings characterized by prolific growth of seagrasses. Fossilized remains of seagrasses, however, are very rare and commonly fragmented and incomplete (van der Ham et al., 2007), and some of the described seagrass fossils may not even represent seagrasses (den Hartog and Kuo, 2006). Consequently, the origin and evolution of seagrasses are not well understood (Larkum and den Hartog, 1989; Kuo and den Hartog, 2000; den

Hartog and Kuo, 2006). Judging from the relatively few confirmed fossils, it appears that seagrasses probably evolved during the Late Cretaceous at an early stage in the evolution of angiosperms. The oldest seagrass fossil record is from the Campanian and Maastrichtian of Germany, Belgium and the Netherlands (van der Ham et al., 2007 and reference therein, but see also den Hartog and Kuo, 2006 for uncertainties with identifying some of these Cretaceous fossils). Some of the notable younger, confirmed Cenozoic examples include seagrass remains from the Eocene of the Paris Basin (den Hartog, 1970; Larkum and den Hartog, 1989), Florida (including the oldest remains of *Thalassia testudinum*; Lumbert et al., 1984; Ivany et al., 1990), and Pliocene of Greece (Moissette et al., 2007). Most of these examples represent well-preserved fossils of seagrass leaves. Fossilized roots or rhizoliths of seagrasses, however, have only rarely been documented from the geological record.

Froede (2002) described 1000-2000 years old rhizoliths exposed within the intertidal zone of Key Biscayne, Florida, and interpreted them as root casts of *Thalassia testudinum*. These features had previously been interpreted as fossilized roots of a black mangrove (*Avicennia germinans*) thicket (Hoffmeister and Multer, 1965). Thus, the origin of these features remains controversial as their interpretation has important implications for late Holocene sea-level history and the possibility for a higher than present sea-level position.

Probably the best example of seagrass rhizoliths include the preservation of connected *Posidonia* horizontal and vertical rhizomes, several decimeter long and about 1 cm in diameter, in growth position within coarse siliciclastic and calcareous Pliocene deposits in Greece (Moissette et al., 2007). Despite their *in situ* position and preservation of surficial details, these rhizomes are substantially less well preserved relative to the associated leaves.

It is highly likely that taphonomic modifications substantially alter, obscure or

completely obliterate the characteristic features of seagrass root systems. This could preclude their positive identification as plant-related fossils and traces. Instead, the presence of seagrasses could be overlooked or their traces generally classified as biogenic sedimentary structures related to bioturbation. Records of well-exposed modern examples, such as this one from Pigeon Creek on San Salvador, may aid future paleontological interpretations and contribute important information on the relatively poorly documented seagrass underground rhizome-root systems.

CONCLUSIONS

1) Fresh exposures created by tidal channel margin collapse near the mouth of the southern arm of Pigeon Creek (southeastern San Salvador Island, Bahamas) revealed a thick and extensive root system (i.e., rhizome and root mat or mesh) of *Thalassia testudinum* (turtle seagrass), with individual vertical cylindrical rhizomes extending to about 80 cm below the sediment surface and reaching up to 2 cm in diameter. In between these closely spaced, robust, vertical rhizomes are less prominent horizontal rhizomes and a very dense and complex network of thin *Thalassia* roots.

2) Fossilized roots or rhizoliths of seagrasses have only rarely been documented from the geological record although the extensive *Thalassia* root systems would appear to have high potential to leave traces in deposits from shallow subtidal carbonate environments.

3) Taphonomic modifications seem to effectively alter, obscure or completely obliterate seagrass root systems, resulting in the inability to positively identify them as plant-related structures. Consequently, the presence of seagrasses could easily be overlooked in the geological record, and their traces may instead be classified as biogenic sedimentary structures generally related to bioturbation.

4) Documentation of impressive, well-

exposed modern examples of seagrass root systems, such as this one from Pigeon Creek, aims at drawing attention to these relatively poorly described features and can facilitate their future paleontological and sedimentological interpretations.

ACKNOWLEDGMENTS

Funding for this research was provided by the Department of Geosciences at Smith College. Paula Burgi, Sarah Brisson and Tony Caldanaro

(all Smith College) assisted in the field and David Griffing (Hartwick College) allowed the use of his waterproof GPS unit. Gerace Research Centre (GRC) provided accommodations on San Salvador. GRC Director Tom Rothfus and staff members Rochelle Hanna and Velda Knowles are thanked for organizing the 16th Symposium on the Geology of the Bahamas and Other Carbonate Regions. Thanks also to Michael Savarese (Florida Gulf Coast University) for co-chairing the Symposium and co-editing this Proceedings volume.

REFERENCES

- Almasi, M.N., Hoskin, C.M., Reed, J.K., and Mijo, J., 1987, Effects of natural and artificial *Thalassia* on rates of sedimentation: *Journal of Sedimentary Petrology*, v. 57, p. 901-906.
- Bosence, D.W.J., 1995, Anatomy of a Recent biodetrital mud-mound, Florida Bay, USA, in Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., and Pratt, B.R., eds., *Carbonate Mud-Mounds - Their Origin and Evolution: International Association of Sedimentologists Special Publication 23*, Blackwell, Oxford, p. 475-493.
- Brasier, M.D., 1975, An outline history of seagrass communities: *Palaeontology*, v. 18, p. 681-702.
- Brouns, J.J.W.M., 1985, A preliminary study of the seagrass *Thalassodendron ciliatum* (Forssk.) den Hartog from eastern Indonesia. Biological results of the Snellius II Expedition: *Aquatic Botany*, v. 23, p. 249-260.
- Burrell, D.C., and Schubel, J.R., 1977, Seagrass ecosystem oceanography, in McRoy, C.P., and Helfferich, C., eds., *Seagrass ecosystems: A scientific perspective*: Marcel Dekker, New York, p. 195-232.
- Davies, G.R., 1970, Carbonate bank sedimentation, eastern Shark Bay, Western Australia: in Logan, B.W., Davies, G.R., Read, J.F., and Cebulski, D.E., eds., *Carbonate Sedimentation and Environments, Shark Bay, Western Australia: American Association of Petroleum Geologists Memoir 13*, p. 85-168.
- den Hartog, C., 1970, Origin, evolution, and geographical distribution of the seagrasses: *Verhandelingen-Koninklijke Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde*, v. 59, p. 12-38.
- den Hartog, C., and Kuo, J., 2006, Taxonomy and biogeography of seagrasses, in Larkum, W.D. Orth, R.J., and Duarte, C.M., eds., *Seagrasses: Biology, Ecology and Conservation*: Springer, Dordrecht, The Netherlands, p. 1-23.
- Froede, C.R., Jr., 2002, Rhizolith evidence in support of a late Holocene sea-level highstand at least 0.5 m higher than present at Key Biscayne, Florida: *Geology*, v. 30, p. 203-206.
- Ginsburg, R.N., and Lowenstam, H.A., 1958, The influence of marine bottom communities on the depositional environment of sediments: *Journal of Geology*, v. 66, p. 310-318.
- Green, E.P., and Short, F.T., eds., 2003. *World Atlas of Seagrasses*: University of California Press, Berkeley, 298 p.
- Hemminga, M.A., 1998, The root/rhizome system of seagrasses: An asset and a burden: *Journal of Sea Research*, v. 39, p. 183-196.
- Hemminga, M.A., and Duarte, C., 2000, *Seagrass Ecology*: Cambridge University Press, Cambridge, 298 p.
- Hoffmeister, J.E., and Multer, H.G., 1965, Fossil mangrove reef of Key Biscayne, Florida: *Geological Society of America Bulletin*, v. 76, p. 845-852.
- Ivany, L.C., Portell, R.W., and Jones, D.S., 1990, Animal-plant relationships and paleobiogeography of

- an Eocene seagrass community from Florida: PALAIOS, v. 5, p. 244-258.
- Kuo, J., and den Hartog, C., 2000, Seagrasses: A profile of an ecological group: *Biologia Marina Mediterranea*, v. 7, p. 3-17.
- Kuo, J., and den Hartog, C., 2006, Seagrass morphology, anatomy, and ultrastructure, in Larkum, W.D., Orth, R.J., and Duarte, C.M., eds., *Seagrasses: Biology, Ecology and Conservation*: Springer, p. 51-87.
- Larkum, A.W.D., and den Hartog, C., 1989, Evolution and biogeography of seagrasses, in Larkum, A.W.D., McComb, A.J., Shepherd, S.A., eds., *Biology of Seagrasses*: Elsevier, Amsterdam, p. 112-156.
- Larkum, A.W.D., McComb, A.J., Shepherd, S.A., eds., 1989, *Biology of Seagrasses*: Elsevier, Amsterdam, 841 p.
- Larkum, A.W.D., Orth, R.J., and Duarte, C.M., eds., 2006: *Seagrasses: Biology, Ecology and Conservation*: Springer, Dordrecht, The Netherlands, 708 p.
- Lumbert, S.H., den Hartog, C., Phillips, R.C., and Olsen, F.S., 1984, The occurrence of fossil seagrasses in the Avon Park Formation (Late Middle Eocene), Levy County, Florida (USA): *Aquatic Botany*, v. 20, p. 121-129.
- Mitchell, S. W., 1989, Sedimentology of Pigeon Creek, San Salvador Island, Bahamas, in Curran, H.A., ed., *Proceedings of the 3rd Symposium on the Geology of the Bahamas*: Ft. Lauderdale, Florida, CCFL Bahamian Field Station, p. 215-230.
- Moissette, P., Koskeridou, E., Cornée, J-J., Guillocheau, F., and Lécuyer, C., 2007, Spectacular preservation of seagrasses and seagrass-associated communities from the Pliocene of Rhodes, Greece: PALAIOS, v. 22, p. 200-211.
- Pace, W., Mylroie, J.E., and Carew, J.L., 1989, Sedimentology of a Holocene platform-margin carbonate lagoon: Blackwood Bay, San Salvador island, Bahamas, in Mylroie, J.E., ed., *Proceedings of the 4th Symposium on the Geology of the Bahamas*: San Salvador, The Bahamian Field Station, p. 253-265.
- Scoffin, T.P., 1970, The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini lagoon, Bahamas: *Journal of Sedimentary Petrology*, v. 40, p. 249-273.
- Tedesco, L.P., and Wanless, H.R., 1995, Growth and burrow-transformation of carbonate banks: comparison of modern skeletal banks of south Florida and Pennsylvanian phylloid banks of southeastern Kansas, USA, in Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., and Pratt, B.R., eds., *Carbonate Mud-Mounds - Their Origin and Evolution*: International Association of Sedimentologists Special Publication 23, Blackwell, Oxford, p. 495-521.
- Tomlinson, P.B., 1969, On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae). II. Anatomy and development of the root in relation to function: *Bulletin of Marine Science*, v. 19, p. 57-71.
- van der Ham, R.W.J.M., van Konijnenburg-van Cittert, J.H.A., and Indeherberge, L., 2007, Seagrass foliage from the Maastrichtian type area (Maastrichtian, Danian, NE Belgium, SE Netherlands): *Review of Palaeobotany and Palynology*, v. 144, p. 301-321.
- van Tussenbroek, B.I., Vonk, J.A., Stapel, J., Erftemeijer, P.L.A., Middelburg, J.J., and Zieman, J.C., 2006, *The Biology of Thalassia: Paradigms and Recent Advances in Research*, in Larkum, W.D., Orth, R.J., and Duarte, C.M., eds., *Seagrasses: Biology, Ecology and Conservation*: Springer, Dordrecht, The Netherlands, p. 409-439.
- Wanless, H.R., 1981, Fining-upwards sedimentary sequences generated in sea-grass beds: *Journal of Sedimentary Petrology*, v. 51, p. 445-454.
- Wanless, H.R., Cottrell, D.J., Tagett, M.G., Tedesco, L.P., and Warzeski, E.R., Jr., 1995, Origin and growth of carbonate banks in south Florida, in Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., and Pratt, B.R., eds., *Carbonate Mud-Mounds - Their Origin and Evolution*: International Association of Sedimentologists Special Publication 23, Blackwell, Oxford, p. 439-473.
- Zieman, J.C., 1972, Origin of circular beds of *Thalassia* (Spermatophyta: Hydrocharitaceae) in south Biscayne Bay, Florida and their relationship to mangrove hammocks: *Bulletin of Marine Science*, v. 22, p. 559-574.