Bollettino della Società Paleontologica Italiana, 59 (3), 2020, 349-354. Modena

Lineages of *Acropora* (staghorn) corals in the Oligocene to Miocene of Florida and SW Georgia (USA)

Carden C. Wallace*, Roger W. Portell & Paul R. Muir

C.C. Wallace, Biodiversity and Geosciences Program, Queensland Museum, Brisbane, Queensland 4101, Australia; carden.wallace@qm.qld.gov.au
*corresponding author
R.W. Portell, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA; portell@flmnh.ufl.edu
P.R. Muir, Biodiversity Section, Queensland Museum, Townsville 4811, Australia; paul.muir@qm.qld.gov.au

KEY WORDS - Acroporidae, Suwannee Limestone, Arcadia Formation (Tampa Member), coral reefs, climate change, Atlantic corals.

ABSTRACT - The staghorn coral genus Acropora *is the most diverse living genus of reef-building corals. From earliest records around the K-Pg event, the genus has a geo-history of strongly persistent morphological lineages, dating from 49 Mya to present and extending across the Eocene of England and Europe, Oligocene to early Miocene of Europe, Oligocene to present in the western Atlantic, and late Paleogene to present reef-bearing areas in the Indo-Pacific. Because of these records and the usually well-preserved* Acropora *fossils, it is regarded as an exemplar for studying modern diversity and distribution of reef corals and predicting their response to future climate change. Here we examine previously undocumented diversity of* Acropora *species groups present in Oligocene and Miocene (Suwannee Limestone and Tampa Member of the Arcadia Formation, respectively) deposits in Florida and southern Georgia, USA. We find evidence of both species-group lineages from the European region and novel, probably unique Atlantic lineages. Of 11 extant species-group lineages first present in the Eocene to Miocene of the European region, seven are present in this American material, including the* cervicornis *group, never recorded in the Indo-Pacific and now extant only in the western Atlantic. Two as yet undescribed species in the samples and the known species* Acropora tampaensis *Weisbord, 1973 could not be matched within the 19 species groups recognised in extant* Acropora*, and these may be lineages uniquely developed and lost in the Americas. The two species in the* cervicornis *species group, both now categorised as critically endangered, are the only surviving representatives of the family Acroporidae, which was previously represented by five genera in the western Atlantic.* Acropora *species from Florida and Georgia reefs clearly played a substantive role in the continuation and diversification of* Acropora *species groups during the Oligocene-Miocene in the western Atlantic and it is possible that this contributed to the success of the genus in the Indo-Pacific, as well as* cervicornis *group as a critical environmental feature of western Atlantic reefs.*

INTRODUCTION

The reef-building coral genus *Acropora* (phylum Cnidaria, order Scleractinia, family Acroporidae), with more than 150 recognised living species (Wallace, 1999; Veron, 2000; Wallace et al., 2012), has come to dominate coral diversity and even influence the architecture of modern coral reefs. With a rich and accessible fossil history (e.g., Baron-Szabo, 2006; Wallace & Rosen, 2006; Wallace, 2008; Wallace & Bosellini, 2014; Santodomingo et al., 2015), generally stable skeletal biomineralisation (Stolarski et al., 2016), and 19 (previously 20: see Wallace et al., 2007) morphologically recognisable species groups (Wallace, 1999), it has been seen as an exemplar for the study of diversification and change on coral reefs. Its species are also particularly vulnerable to some environmental impacts associated with elevated sea surface temperatures and other types of change on coral reefs (e.g., Bruckner & Hourigan, 2002; Vollmer & Palumbi, 2007; Aronson et al., 2008a, b; Faith & Richards, 2012; Renema et al., 2016). However, many have been found to extend into mesophotic (and thus somewhat protected) reef zones as well as shallow reef fronts (Muir & Wallace, 2016; Muir et al., 2018a, b; Turak & DeVantier, 2019).

A finding of representatives of nine of the 19 (previously 20) modern *Acropora* species groups in the Eocene (49-33.9 Mya) of England and France (Wallace & Rosen, 2006), was taken as evidence that pre-existing diversity contributed to modern high diversity of *Acropora* in the Indo-Pacific region, in a contradiction of the previous premise that modern *Acropora* diversity sprang from a single Pliocene ancestor (Stehli & Wells, 1971; Potts, 1985; Veron, 1995; Fukami et al., 2000). These species groups: *humilis* (as *humilis I* and *II*), *cervicornis*, *muricata*, *robusta*, *aspera*, *florida*, *hyacinthus*, and *latistella* were subsequently matched up with ten species (some new, others previously described), and another species was tentatively matched with the *elegans* group (Wallace, 2008), which can now be validated. A subsequent study of Oligocene (23.0-33.9 Mya) and early Miocene (16.0-23.0 Mya) fossils from continental Europe (Wallace & Bosellini, 2014) found new and continuing species from all these groups except *elegans*, plus two additional groups *horrida* and *rudis*. That study concluded that conditions in the western Tethys region during the Oligocene and early Miocene were compatible with survival and range expansion of Eocene species and species turnover or origination of new species within lineages (Wallace & Bosellini, 2014).

In the western Atlantic Ocean region (Caribbean and the Americas) a "cosmopolitan pan-Tethyan fauna" was recognised in the coral fossil record from the Late Cretaceous to end-Eocene (Edinger & Risk, 1994; Budd, 2000). The family Acroporidae shows this pattern, with genera *Astreopora*, *Alveopora*, *Acropora*, and the now globally extinct *Dendracis*, all previously present in the western Atlantic as well as elsewhere in the Tethyan seaway (Wallace, 2012). This period was followed by

ISSN 0375-7633 doi:10.4435/BSPI.2020.15

Locality	Estimated age (Mya)	Biostratigraphical age	References
Tampa Member of the Arcadia Formation, Tampa Bay, Hillsborough County, Florida	22.3 - 26 Mya	Miocene (Aquitanian) to Oligocene (Chattian) W 11541, W 15166	Brewster-Wingard et al., 1997
Little Horseshoe Bend, Flint River, Decatur County, Georgia	27.8 - 33.9 Mya	Oligocene (Rupelian)	Dall, 1916
Terramar 01, Polk County, Socrum Quadrangle, Florida	33.6 - 34.1 Mya	Oligocene (Rupelian) to Eocene (Priabonian)	Herbert & Portell, 2002 (references therein)

Tab. 1 - Localities from which the *Acropora* fossils in this study were collected. Sources of ages and/or coral facies are from references indicated.

the Oligocene/early Miocene turnover period (OMT) characterised by loss of species and genera in many families including Acroporidae and leading to a "more distinctive Caribbean fauna" (Johnson & Kirby, 2006). By the end of the OMT only *Acropora* remained of the Atlantic Acroporidae, although it was briefly joined by its sister genus *Isopora* in the Neogene (Budd & Wallace, 2008; Wallace & Budd, 2009). Living *Acropora* is represented by the two extant species of the *cervicornis* group, *A. cervicornis* and *A. palmata*, and an F1 hybrid, currently accepted as *A. prolifera* (Lamarck, 1816) (see Wallace, 1999, p. 178-179; Vollmer & Palumbi, 2002; Anguila-Perera & Hernánde-Lander, 2018; Nylander-Asplin, 2018; Hoeksema & Cairns, 2020). While the histories of other genera of Acroporidae are well-documented (Budd et al., 1994, 1995) the origination and turnover of many species of *Acropora* in the western Atlantic remain to be detailed from fossil material deposited in museums. This paper documents a small part of this record, by looking at the species group status of fossils from Oligocene and Miocene deposits in Florida and Georgia, USA.

Geological setting

The basement conformation of the Florida Platform includes land that was rifted from the African Plate during the Triassic breakup of Pangea and sutured onto the North American continent (Scott, 2001, 2011; Smith, 2015; Upchurch et al., 2019). In the Cretaceous to mid Eocene, most of Florida was separated from the rest of North America by the Suwannee Straits, a swift marine current running from the Gulf of Mexico to the Atlantic Ocean (Fig. 1; Scott, 2011). Following this, tectonic activity and erosion of the Appalachian Mountains caused siliciclastic sediments and carbonates to fill the channel, forming the Gulf Trough (Smith, 2015; Upchurch et al., 2019). The flow of materials continued southwards, forming the Suwannee Limestone, named by Cooke & Mansfield (1936), which now underlies a portion of southern Georgia and most of modern Florida. It encompasses the early Oligocene (Rupelian, 27.8-33.9 Mya) and is thought to straddle the Eocene/Oligocene boundary (Herbert & Portell, 2002).

The Suwannee Limestone is exposed in river banks and at Little Horse Shoe Bend on the Flint River, Decatur County, Georgia (Dall, 1916) or accessed by mining, e.g., as at the FLMNH Terramar 01 site in Polk County, Florida (Herbert & Portell, 2002). In the region of Tampa Bay, Hillsborough County, Florida, the Suwannee Limestone is overlain by a younger deposit, the Tampa Member of the Arcadia Formation, which is late Oligocene (Chattian) to mid Aquitanian (early Miocene) (22.3-26 Mya) (Brewster-Wingard et al., 1997). These three locations provided our samples (Tab. 1, Fig. 1).

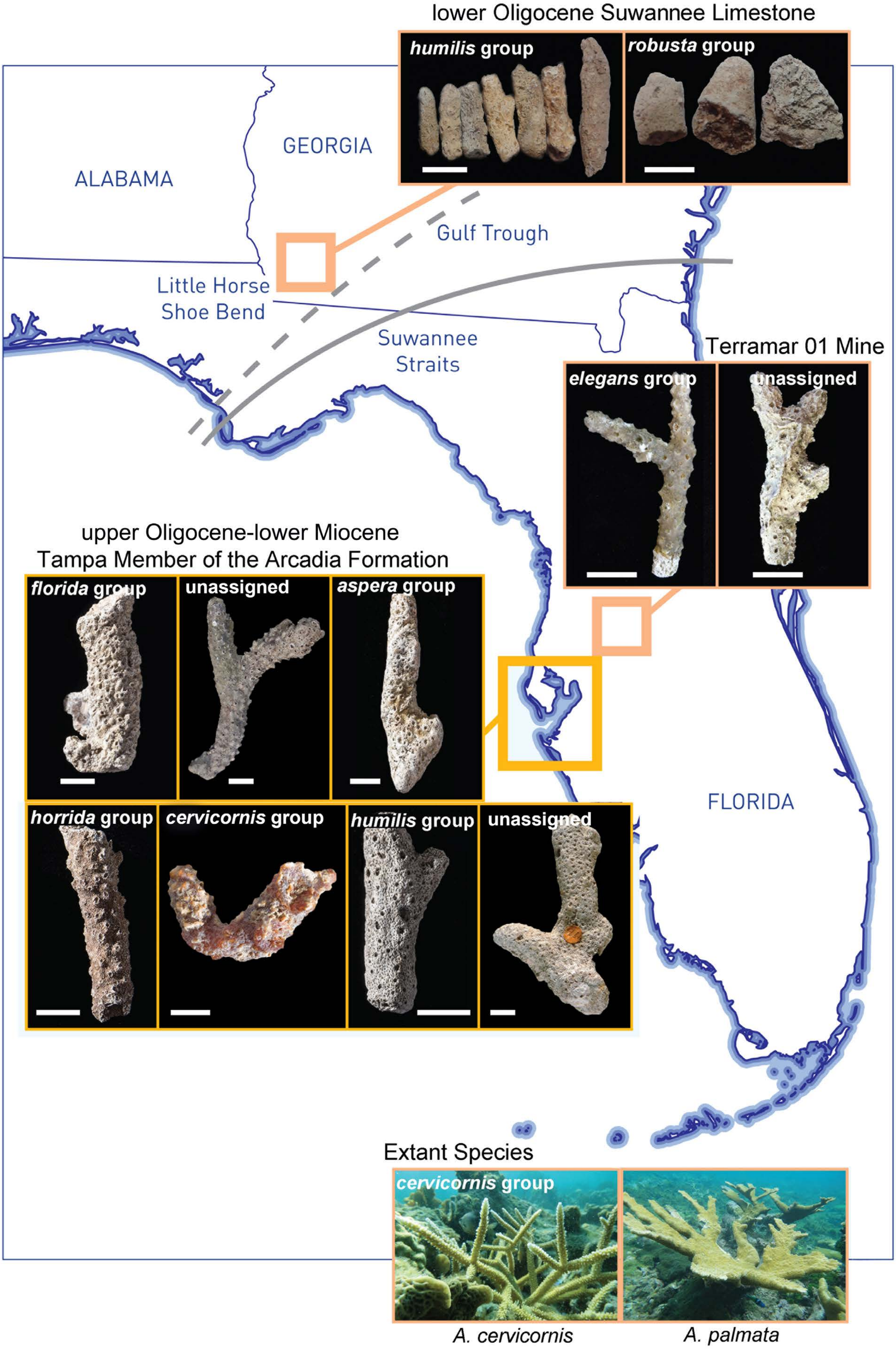
MATERIAL AND METHODS

Specimens were examined at the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville, USA, the National Museum of Natural History (USNM), Smithsonian Institution, Washington DC, and at Queensland Museum, Brisbane, using a binocular dissecting microscope with eyepiece micrometer. We examined fossil fragments from 12 specimen lots, collected at the localities (Tab. 1, Fig. 1) from mid-nineteenth century to present. The fragments were studied for discernible skeletal characters at species-group level, as outlined in Wallace & Rosen (2006: Methods and tab. 2) and subsequent fossil studies (Wallace, 2008; Santodomingo et al., 2015).

RESULTS AND DISCUSSION

Eleven forms with characters consistent with separate species were found, two from Georgia and nine from Florida (illustrated in Fig. 1 by locality). One was *Acropora tampaensis* Weisbord, 1973, with the others interpreted as new to science. Eight of the as yet undescribed species were attributed to seven of the species groups, assumed to be lineages, recognised in modern *Acropora* (Wallace, 1999; Wallace et al., 2012): *humilis*, *cervicornis*, *robusta*, *aspera*, *florida*, *elegans* and *horrida* groups (Fig. 1), leaving the affinities of the other three

Fig. 1 - (color online) Map of Florida and southern Georgia, indicating features and locations mentioned in the text. Images of species identified to species group are superimposed and arranged according to collecting location in: Suwannee Limestone (top and centre right hand images) and Tampa Member of the Arcadia Formation (left hand images). Two extant Atlantic Ocean species from the *cervicornis* group are shown alive and in situ in the San Blas Islands on the bottom right. All scale bars are 10 mm.


lower Oligocene Suwannee Limestone
humilis group
robusta group
GEORGIA
ALABAMA
Gulf Trough
Little Horse
Shoe Bend
Suwannee
Straits
Terramar 01 Mine
elegans group
unassigned
upper Oligocene-lower Miocene
Tampa Member of the Arcadia Formation
florida group
unassigned
aspera group
horrida group
cervicornis group
humilis group
unassigned
FLORIDA
Extant Species
cervicornis group
A. cervicornis
A. palmata

Period	Epoch	Age	Mya	*latistella*	*humilis**	*cervicornis**	*muricata*	*florida**	*hyacinthus*	*aspera**	*horrida**	*robusta**	*elegans**	*rudis*
Neogene	Miocene	Burdigalian	16.0-20.4	Europe[2]				Europe[2]			Europe[2]			
		Aquitanian	20.4-23.0	Europe[2]	Florida[1]	Florida[1]		Florida[1] Europe[2]		Florida[1] Europe[2]	Florida[1]	Europe[2]		
Paleogene	Oligocene	Chattian	23.0-28.1	Europe[2]	Europe[2]	Europe[2]		Florida[1]	Europe[2]	Florida[1] Europe[2]		Europe[2]		Europe[2]
		Rupelian	28.1-33.9		Georgia[1] Europe[2]	Europe[2]					Florida[1]	Georgia[1]	Florida[1]	
	Eocene	Priabonian	33.9-37.8		England, France[3]	Europe[2,3]		England[3]			Florida[1]	England[3]	Florida[1]	
		Bartonian	37.8-41.2	France[3]	England, France[3]	Europe[2] France[3]	France[3]	England[3]	France[3]	France[3]				
		Lutetian	41.2-47.8	France[3]		France[3]				France[3]			France[3]	

Fig. 2 - Occurrence of identified *Acropora* species groups (columns) from the strata (rows) studied in: the Oligocene and Miocene of USA (superscript 1 = this paper), compared with the Oligocene and Miocene of continental Europe (superscript 2 = Wallace & Bosellini, 2014) and the Eocene of England and/or France (superscript 3 = Wallace & Rosen, 2006 + Wallace, 2008). Strata represented as in the Geologic Time Scale (Walker et al., 2012). Europe records include France, Italy, Spain and Slovenia. Each record is for one or two species in the species group indicated. Asterisk = species group found in this study.

species (including *A. tampaensis*) undetermined. Tab. 2 lists the main characteristics by which these species groups were determined from the fossil fragments.

Fig. 2 compares the age of the species-group distributions in Florida and Georgia with known species-group presence in the *Acropora* fossil record from the western Tethys. The identified Atlantic lineages also occur in the Eocene, Oligocene and early Miocene of Europe, with the exception of *horrida* group, which has only a late Miocene record in Europe to date (Wallace & Rosen, 2006; Wallace, 2008; Wallace & Bosellini, 2014). All the groups except *cervicornis* group are also represented in the Miocene or younger of Indonesia in the central Indo-Pacific (Santodomingo et al., 2015). At this stage of interpretation, up to three unnamed species groups can be hypothesised to be uniquely American. A more complete description of the fossil material in this study is in preparation and this will describe the new species and further examine their lineages.

All Florida and Georgia records of *Acropora* lineages identified in this study, except *horrida* group, postdate their appearance in the western Tethys region. The presence of these species groups in northern America indicates that, from early diversification in the Eocene of England and Europe (Wallace & Rosen, 2006; Wallace, 2008), followed by range extension, species longevity and turnover in the European Oligo-Miocene (Wallace & Bosellini, 2014), the *Acropora* lineages were able to extend into the Atlantic and leave a diverse species record in mainland USA. This is a clear indication that *Acropora* played a role in the cosmopolitan pan-Tethyan fauna of the western Atlantic to end-Eocene (Budd et al., 1994). The possibility that it also played a role in "the development of a more distinctive western Atlantic fauna by diversification during the Oligo-Miocene" (Johnson & Kirby, 2006, p. 283) may be hypothesised from the survival of the *cervicornis* group and presence of up to three novel species groups.

The diversity of species groups derived from the western Tethys in the Oligo-Miocene of the Atlantic is indicative of the presence of suitable conditions for *Acropora* survival in a variety of habitat types. The unique geological and biological features involved in the development of reefs in the region and the deposition of the fossil-bearing Suwannee Limestone and Arcadia Formation are described in many publications (e.g., Mansfield, 1937; Scott, 2001, 2011; Smith, 2015; Upchurch et al., 2019 and numerous others). Few of the species groups recorded here have been seen to date in the Caribbean fossil fauna (Budd et al., 1994; Budd, 2000; Wallace, 2012), so it is possible that this USA fauna played a unique role, perhaps in parallel to that played out in the Caribbean, and that this contributed to the maintenance and extension of many *Acropora* lineages into the Indo-Pacific.

Four other sister genera of *Acropora* in the family Acroporidae: *Astreopora*, *Alveopora*, *Isopora* and *Dendracis* (now extinct worldwide) are also present in the fossil record of the western Atlantic region (Wallace, 2012), but extinct there today, making *A. cervicornis* and *A. palmata* and their F1 hybrid (the *cervicornis* group) the only remaining representatives of the family. These species are known for their rapid growth and

Species group	Main visible characteristics
humilis	Radial corallites short, thickened tubular with dimidiate openings, evenly sized or two sizes. Coenosteum throughout reticulate with laterally flattened spinules, sometimes reticulo-costate. Colonies corymbose or digitate, branch diameter axial dominated.
cervicornis	Radial corallites approximately tubo-nariform, evenly sized. Coenosteum reticulate between, costate on radial corallites, with laterally flattened spinules more or less in lines (costae). Colony shape various, branch diameter axial dominated.
robusta	Radial corallites dimorphic, one form long tubular with dimidiate opening, the other subimmersed. Coenosteum reticulate between, costate on radial corallites. Colonies sub-arborescent, branch diameter axial dominated.
aspera	Radial corallites labellate, upper wall absent, lower wall developed into a flaring lip, evenly sized or two sizes. Coenosteum open reticulate with few simple spinules between radial corallites, costate on radial corallites. Colonies corymbose or arborescent, branch diameter axial dominated.
florida	Radial corallites appressed tubular with thickened lip-like lower wall and round openings, evenly sized. Coenosteum between radial corallites reticulate and simple, with few simple spinules, on radial corallites costate or reticulo-costate. Colonies based on simple hispidose branching, branch diameter 50/50 axial: radial.
elegans	Radial corallites tubular or appressed tubular, evenly sized, sometimes alternate- sympodially arranged on the branch. Coenosteum throughout formed by elaborate spinules, densely to moderately densely arranged. Colonies with light structure, mostly horizontal branching and sparsely arranged branches, branch diameter axial: radial domination various.
horrida	Radial corallites simple tubular with round openings, evenly sized. Coenosteum throughout with simple to moderately elaborated spinules, parts of coenosteum fused. Colonies arborescent to hispidose, branch diameter 50/50 axial: radial.

Tab. 2 - Main characteristics of the seven modern *Acropora* species groups that could be recognised in the fossil fragments examined and allow comparison with material from other fossil studies, in particular Wallace (2008), Wallace & Bosellini (2014), Santodomingo et al. (2015).

contribution to reef front structure. The *cervicornis* group is not represented elsewhere in the world after the Miocene, and never recorded from the Indo-Pacific. Current evidence suggests that this species group has a lineage of up to 45.8 million years, making its critically endangered status a serious threat to future phylogenetic diversity and habitat integrity of the reef ecosystems of the western Atlantic. *Acropora* species from the fossil record of Florida and Georgia reefs clearly played a substantive role in the diversification of *Acropora* during the Oligocene-Miocene in the western Atlantic and it is possible that this contributed to the success of the genus in the Indo-Pacific, as well as to the establishment of the surviving *cervicornis* group as a critical environmental feature of western Atlantic reefs.

ACKNOWLEDGEMENTS

From the USNM we thank S. Cairns and T. Waller for advice and assistance and T. Coffer for loan preparation, from FLMNH we thank staff and postgraduates for assistance. Drs G. Alvarez and S. Calsada are thanked for access to Spanish specimens. From the Queensland Museum we thank A. Rozefelds and K. Spring, and P. Waddington, fossil photographs. Live coral images kindly provided by A. Rickert. R. Bullard is thanked for Fig. 1 and A. Welsh for assistance with Fig.2.

REFERENCES

Aguilar-Perera A. & Hernández-Landa R.C. (2018). Occurrence of large thickets of *Acropora prolifera* (Scleractinia: Acroporidae) in the southern Gulf of Mexico. *Marine Biodiversity*, 48: 2203-2205.

Aronson R., Bruckner A., Moore J., Precht B. & Weil E. (2008a). *Acropora cervicornis*. *The IUCN Red List of Threatened Species 2008*: e.T133381A3716457.

Aronson R., Bruckner A., Moore J., Precht B. & Weil E. (2008b). *Acropora palmata*. *The IUCN Red List of Threatened Species* 2008: e.T133006A3536699.

Baron-Szabo R.C. (2006). Corals of the K/T boundary: Scleractinian corals of the suborders Astrocoeniina, Faviina, Rhipidogyrina and Amphiastaena. *Journal of Systematic Palaeontology*, 4: 1-108.

Brewster-Wingard G.L., Scott T.M., Edwards L.E., Weedman S.D. & Simmons K.R. (1997). Reinterpretation of the peninsular Florida Oligocene: an integrated stratigraphic approach. *Sedimentary Geology*, 108: 207-228.

Bruckner A.W. & Hourigan T.F. (2002). Proactive management for conservation of *Acropora cervicornis* and *Acropora palmata*: Application of the US Endangered Species Act. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia 23-27 October 2000, 2: 661-665.

Budd A.F. (2000). Diversity and extinction in the Cenozoic history of Caribbean reefs. *Coral Reefs*, 1: 25-35.

Budd A.F., Johnson K.G. & Edwards J.C. (1995). Caribbean reef coral assemblages during the early to middle Miocene: An example from the Anguilla Formation. *Coral Reefs*, 14: 109-117.

Budd A.F., Stemann T. & Johnson K. (1994). Stratigraphic distributions of genera and species of Neogene to Recent Caribbean reef corals. *Journal of Paleontology*, 68: 951-997.

Budd A.F. & Wallace C.C. (2008). First record of the Indo-Pacific reef coral genus *Isopora* in the Caribbean region: Two new species from the Neogene of Curaçao, Netherlands Antilles. *Palaeontology*, 5: 1187-1401.

Cooke C.W. & Mansfield W.C. (1936). Suwannee Limestone of Florida (abstract): *Geological Society of America Proceedings*, 1935: 71-72.

Dall W.H. (1916). A contribution to the invertebrate fauna of the Oligocene beds of Flint River, Georgia. *Proceedings of the U.S. National Museum*, 51: 486-524.

Edinger E.N. & Risk M.J. (1994). Oligocene-Miocene extinction and geographic restriction of Caribbean corals: Roles of turbidity, temperature, and nutrients. *Palaios,* 9: 576-598.

Faith D.P. & Richards Z.T. (2012). Climate change impacts on the tree of life: Changes in phylogenetic diversity illustrated for *Acropora* corals. *Biology*, 1: 906-932.

Fukami H., Omori M. & Hatta M. (2000). Phylogenetic relationships in the coral family Acroporidae, reassessed by inference from the mitochondrial genes. *Zoological Science*, 17: 689-696.

Herbert G.S. & Portell R.W. (2002). A new species of *Antiliosa* (Muricidae: Neogastropoda) from the upper Eocene/lower Oligocene Suwannee Limestone of Florida. *The Veliger*, 45: 303-308.

Hoeksema B.W. & Cairns S. (2020). World List of Scleractinia. *Acropora prolifera* (Lamarck, 1816). Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=288235 on 2020-03-23

Johnson K.G. & Kirby M.X. (2006). The Emperador Limestone rediscovered: Early Miocene corals from the Culebra Formation, Panama. *Journal of Paleontology*, 80: 283-293.

Lamarck J.B.P.A. de M. de (1816). Histoire naturelle des animaux sans vertebres. Paris, 2: 1-568.

Mansfield W.C. (1937). Mollusks of the Tampa and Suwannee limestones of Florida. *Florida Geological Survey Geological Bulletin*, 15: 1-334.

Muir P.R., Pichon M., Squire L. Jr. & Wallace C.C. (2018b). *Acropora tenella*, a zooxanthellate coral extending to 110 m depth in the northern Coral Sea. *Marine Biodiversity*, 49: 1-6.

Muir P.R. & Wallace C.C. (2016). A rare 'deep-water' coral assemblage in a shallow lagoon in Micronesia. *Marine Biodiversity*, 46: 543-544.

Muir P.R., Wallace C.C., Pichon M. & Bongaerts P. (2018a). High species richness and lineage diversity of reef corals in the mesophotic zone. *Proceedings Royal Society B*, 285: 20181987.

Nylander-Asplin H.F. (2018). Population dynamics and genotypic richness of the Threatened *Acropora* spp. and their hybrid in the U.S. Virgin Islands. Master's thesis. Nova Southeastern University. Retrieved from NSUWorks. 47 pp.

Potts D.C. (1985). Sea-level fluctuations and speciation in Scleractinia. In Hamelin V. & Salvat B. (eds), Proceedings 5th International Coral Reef Congress. Volume 4. International Society of Reef Studies, Tahiti: 127-132.

Renema W., Pandolfi J.M., Kiessling W., Bosellini F.R., Klaus J.S., Korpanty C., Rosen B.R., Santodomingo N., Wallace C.C., Webster J.M. & Johnson K.G. (2016). Are coral reefs victims of their own past success? *Science Advances*: e1500850 22.

Santodomingo N., Wallace C.C. & Johnson K.G. (2015). Fossils reveal a high diversity of the staghorn coral genera *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Neogene of Indonesia. *Zoological Journal of the Linnean Society*, 175: 677-763.

Scott T.M. (2001). Text to accompany the Geological Map of Florida. Open-file Report 80, Florida Geological Survey, Tallahassee, Florida: 1-28.

Scott T.M. (2011). Geology of the Florida Platform – Pre-Mesozoic to Recent. *In* Buster N.A. & Holmes C.W. (eds), Gulf of Mexico: Origins, water, and biota, Vol. 3 Geology, Texas A&M University Press, College Station, TX, Chapter 2: 17-31.

Smith K. (2015). A study of the lithological and petrographical changes across the Eocene-Oligocene transition of the Ocala and Suwannee formations in northern Florida and southern Georgia. 51 pp. The Florida State University, ProQuest Dissertations Publishing: 1600084.

Stehli F.G. & Wells J.W. (1971). Diversity and age patterns in hermatypic corals. *Systematic Zoology*, 20: 115-126.

Stolarski J., Bosellini F.R., Wallace C.C., Gothmann A.M., Mazur M., Domart-Coulon I., Gutner-Hoch E., Neuser R.D., Levy O., Shemesh A. & Meibom A. (2016). A unique coral biomineralization pattern has resisted 40 million years of major ocean chemistry change. *Scientific Reports,* 6: 27579.

Turak E. & DeVantier L. (2019). Reef-building corals of the upper mesophotic zone of the central Indo-West Pacific. *In* Loya Y. et al. (eds), Mesophotic Coral Ecosystems, Coral Reefs of the World 12, Springer Nature Switzerland AG 2019: 621-651.

Upchurch S.B., Scott T.M., Alfieri M.C., Fratesi B. & Dobecki T.L. (2019). The Karst Systems of Florida. *In* Geologic framework of Florida: 59-91.

Veron J.E.N. (1995). Corals in space and time: Biogeography and evolution of the Scleractinia. 321 pp. University of New South Wales Press, Sydney.

Veron J.E.N. (2000). *Corals of the World*. Townsville, Australia. Three volumes. 1382 pp. Australian Institute of Marine Science, Melbourne.

Vollmer S.V. & Palumbi S.R. (2002). Hybridization and the evolution of reef coral diversity. *Science*, 296: 2023-2025.

Vollmer S.V. & Palumbi S.R. (2007). Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: Implications for the recovery of endangered reefs. *Journal of Heredity*, 98: 40-50.

Walker J.D., Geissman J.W., Bowring S.A. & Babcock L.E., Compilers (2012). Geological Time Scale V. 4.0: Geological Society of America.

Wallace C.C. (1999). Staghorn Corals of the World. 421 pp. PMID: 25506965. CSIRO Publishing, Melbourne.

Wallace C.C. (2008). New species and records from the Eocene of England and France support early diversification of the coral genus *Acropora*. *Journal of Paleontology*, 82: 313-328.

Wallace C.C. (2012). Acroporidae of the Caribbean. *Geologica Belgica*, 15: 388-393.

Wallace C.C. & Bosellini F.R. (2014). *Acropora* (Scleractinia) from the Oligocene and Miocene of Europe: Species longevity, origination and turnover following the Eocene–Oligocene transition. *Journal of Systematic Palaeontology*, 13: 447-469.

Wallace, C.C. & Budd A.F. (2009). Mirror-image fossils reveal colony form of extinct Curaçao *Isopora. Coral Reefs*, 28: 715.

Wallace C.C., Chen C.A.C., Fukami H. & Muir P.R. (2007). Recognition of separate genera within *Acropora* based on new morphological, reproductive and genetic evidence from *A. togianensis,* and elevation of the subgenus *Isopora* Studer, 1878 to genus (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs*, 26: 231-239.

Wallace C.C., Done B. & Muir P.R. (2012). Revision and catalogue of worldwide staghorn corals *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Museum of Tropical Queensland. *Memoirs of the Queensland Museum Nature*, 57: 1-255.

Wallace C.C. & Rosen B.R. (2006). Diverse staghorn corals (*Acropora*) in high-latitude Eocene assemblages: Implications for the evolution of modern diversity patterns of reef corals. *Proceedings of the Royal Society B*, 273: 975-982.

Weisbord N.E. (1973). New and little-known fossil corals from the Tampa Formation of Florida. *Florida Bureau of Geology, Geological Bulletin*, 56: 1-147.

Manuscript received 15 December 2019
Revised manuscript accepted 30 June 2020
Published online 1 September 2020
Guest Editor Francesca R. Bosellini