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Is the trace fossil *Macaronichnus* an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts

Luis I. Quiroz, Luis A. Buatois, M. Gabriela Mángano, Carlos A. Jaramillo and Nubia Santiago

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Notes

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Luis I. Quiroz[1,2], Luis A. Buatois[1], M. Gabriela Mángano[1], Carlos A. Jaramillo[2], and Nubia Santiago[3]
[1]Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada
[2]Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Republic of Panama
[3]División Oriente, Gerencia de Exploración, PDVSA, Edificio PDVSA, Nivel Plaza, Modulo A, Ofc-54, Puerto La Cruz 6023, Venezuela

ABSTRACT

The trace fossil *Macaronichnus* is reported for the first time from low-latitude, tropical settings based on its occurrence in nearshore deposits in the Upper Oligocene–Lower Miocene Naricual Formation and in the Middle to Upper Miocene Urumaco Formation in northern Venezuela. *Macaronichnus* is an intrastratal trace fossil attributed to the deposit-feeding of worms in high-energy, sandy shallow-marine environments. The majority of its occurrences are from Mesozoic to Cenozoic high- to intermediate-latitude shorelines. The opheliid polychaetes *Ophelia limacina* and *Euzonus mucronata* make structures identical to those described from the fossil record in modern intertidal and shallow subtidal sediments of northwestern United States, western Canada, and Japan. *Macaronichnus* shows a geographical and environmental distribution in the fossil record similar to that of its modern producers and has been proposed as an indicator of high to intermediate latitudes. Accordingly, its presence in the Neogene of Venezuela is highly anomalous and seems to challenge its paleoclimatic value. However, this occurrence may be related to seasonal coastal upwelling of nutrient-rich cold waters. Such oceanographic conditions were prevalent in the northern coast of South America, at least from the Late Oligocene to the Early Pliocene prior to the final closure of the strait of Panama. This study underscores the value of *Macaronichnus* because its presence in the tropics may indicate upwelling conditions, providing high-resolution information in paleoceanographic reconstructions.

INTRODUCTION

The ichnogenus *Macaronichnus* is an intrastratal trace fossil in high-energy, sandy shallow- to marginal-marine deposits that range in age from the Permian to the Holocene (Bromley, 1996; Clifton and Thompson, 1978). *Macaronichnus* is interpreted as a grazing trace (Pascichnia) produced by deposit-feeding worms, commonly in foreshore and shallow subtidal deposits (Clifton and Thompson, 1978; Pemberton et al., 2001). Structures identical to those described from the fossil record are produced by the opheliid polychaetes *Ophelia limacina* in Willapa Bay, northwestern United States (Clifton and Thompson, 1978), and *Euzonus mucronata* in Vancouver Island, Canada (Pemberton et al., 2001), and Japan (Seike, 2008).

The majority of occurrences of *Macaronichnus* are from Mesozoic to Cenozoic high- to intermediate-latitude shorelines (e.g., Pemberton et al., 2001; de Gibert et al., 2006; Carmona et al., 2008; Bromley et al., 2009). The distribution of its known opheliid producers is constrained by latitude and water temperature, being restricted to temperate to subarctic waters (McConnaughey and Fox, 1949; Bellan and Dauvin, 1991). Accordingly, *Macaronichnus* has been suggested as an indicator of high- to intermediate-latitude coastal environments (Pemberton et al., 2006).

In this paper, *Macaronichnus* is recorded for the first time in low latitudes, based on its occurrence in nearshore deposits of two Neogene units of northern Venezuela: the Upper Oligocene–Lower Miocene Naricual Formation and the Middle to Upper Miocene Urumaco Formation (Fig. 1). In addition, we have compiled all previously documented occurrences of *Macaronichnus* (n = 50) and provide compelling evidence of its recurrence in high to intermediate latitudes, outlining its paleoclimatic value (see Appendix DR1 the GSA Data Repository[1]). To explain the apparent paradox of *Macaronichnus* in tropical settings, we underscore the role of upwelling and emphasize the importance of this ichnogenus as a high-resolution paleoceanographic tool, opening a new field of research in ichnology.

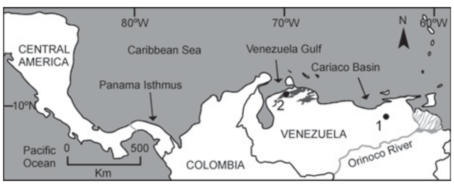

Figure 1. Location map. 1—El Furrial Field; 2—Urumaco Formation outcrops.

[1]GSA Data Repository item 2010174, Appendix DR1 (comprehensive compilation of all documented occurrences of *Macaronichnus* in the stratigraphic record) and Appendix DR2 (sedimentologic logs for the *Macaronichnus*-bearing deposits in the Naricual and Urumaco Formations), is available online at www.geosociety.org/pubs/ft2010.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

GEOLOGIC SETTING AND OCCURRENCE OF *MACARONICHNUS*

The specimens of *Macaronichnus segregatis* come from cores of the Upper Oligocene–Lower Miocene Naricual Formation and outcrops of the Middle to Upper Miocene Urumaco Formation. The Naricual Formation is exposed as a series of west-east–trending outcrops in the Anzoátegui state of northern Venezuela, but is known in the subsurface also. This formation consists of ~2000 m of coarse- to very fine-grained sandstone, siltstone, and coal (Hedberg, 1950). The Naricual Formation was mostly deposited in a widespread coastal plain, in which deltaic progradation alternated with formation of estuarine systems during transgression. The specimens described occur in cores of the El Furrial Field (Eastern Venezuela Basin) and are present in medium- to fine-grained sandstone with either trough cross-stratification, low-angle cross-stratification, or parallel stratification (swash-zone stratification) (Fig. 2A). The *Macaronichnus* beds occur at or near the top of parasequences reflecting either strandplain or deltaic progradation, and characterize the foreshore or the most proximal positions of delta front mouth bars (bathymetrically equivalent to the upper shoreface and foreshore of wave-dominated strandplains) (see Appendix DR2). The beds are overlain in most cases by transgressive deposits and, more rarely, by distributary-channel deposits.

The Urumaco Formation is exposed along the Urumaco River, in the Falcon state of northwestern Venezuela. The 1800-m-thick Urumaco Formation consists of an intercalation of medium- to fine-grained sandstone, organic-rich mudstone, coal, shale, and fossiliferous sandstone and packstone. It was deposited mainly in a prograding delta-strandplain complex. *Macaronichnus segregatis* occurs in medium-grained sandstone with horizontal to low-angle cross-bedding (Fig. 3A) interpreted as foreshore deposits, and, less commonly, in trough cross-stratified fine- to medium-grained sandstone formed by the migration of

Figure 2. ***Macaronichnus segregatis*** **in cores of the Naricual Formation, Eastern Venezuela Basin. A: General view of foreshore deposits showing low-angle cross-stratification and localized high density of** ***M. segregatis*****. B: View of** ***M. segregatis*****.**

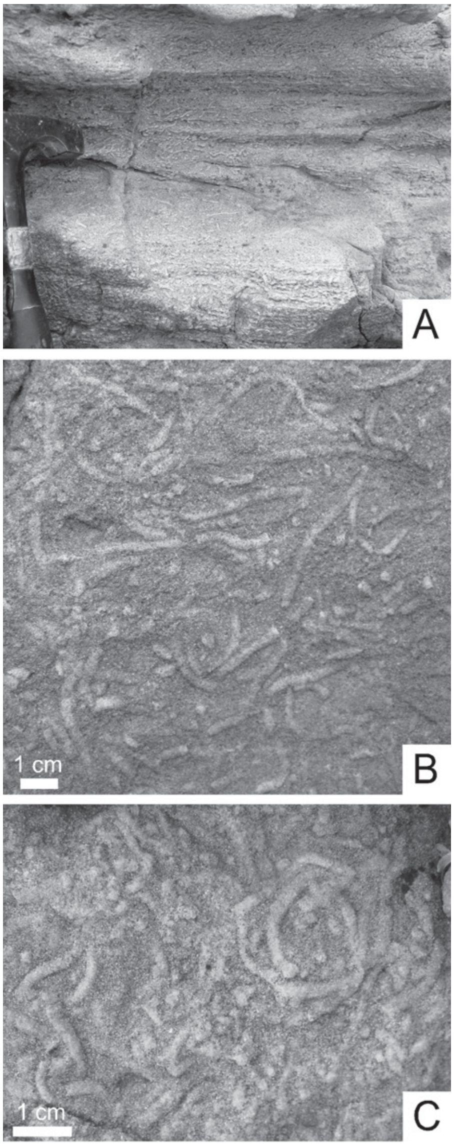

Figure 3. ***Macaronichnus segregatis*** **in outcrops of the Urumaco Formation, northwestern Venezuela. A: General view of foreshore deposits with low-angle cross-stratification and pervasive bioturbation by** ***M. segregatis*****. B: Close-up of** ***M. segregatis*****. C: Detail of the light-colored sand infill and the dark-colored surrounding mantle.**

a three-dimensional dune complex in the upper shoreface (see Appendix DR2).

Macaronichnus segregatis consists of densely packed, small cylindrical unbranched trace fossils, 2–3 mm in diameter, straight to slightly sinuous (Figs. 2A, 2B, 3B and 3C). They are preserved as endichnia and oriented parallel to the stratification. The trace fossils are actively filled by light-colored sand contrasting with the dark-colored surrounding mantle (Fig. 3C).

PALEOCLIMATIC SIGNIFICANCE OF *MACARONICHNUS*

Macaronichnus is attributed to the deposit-feeding of opheliid polychaetes who fed upon epigranular bacteria around sand grains and inhabited up to several meters below the sediment-water interface due to strong infiltration that produced well-oxygenated and nutrient-rich environments within the sediment (Pemberton et al., 2001). To date, *Macaronichnus* has only been recorded in shallow-marine deposits of high to intermediate latitudes (see Appendix DR1). Although most of the reported occurrences of *Macaronichnus* are from the Mesozoic to Cenozoic of the Northern Hemisphere (e.g., Pemberton et al., 2001; Bromley et al., 2009), this ichnogenus is also known from Cenozoic high to intermediate latitudes in the Southern Hemisphere (e.g., de Gibert et al., 2006; Carmona et al., 2008). Interestingly, *Macaronichnus* is absent in Paleocene to Lower Eocene rocks, most likely as a result of overall high temperatures and the expansion of subtropical belts (Zachos et al., 2001; Hollis et al., 2009). In addition, the few Middle to Upper Eocene occurrences are from high latitudes (e.g., Olivero et al., 2008), signaling the transition to colder climates. Notably, some of the oldest records of *Macaronichnus* are from Permian cold-water deposits of Australia (e.g., Bann et al., 2004).

Geographic and environmental distribution of *Macaronichnus* in the fossil record mimics that of its opheliid polychaete producers, which are mostly restricted to substrates within a relatively narrow range of particle size (Dales, 1952). *Euzonus mucronata* lives in dense populations in the sand beaches along the west coast of North America, from Baja California to Vancouver Island in British Columbia (McConnaughey and Fox, 1949), as well as in Japan (Seike, 2008). This species has been observed producing incipient *Macaronichnus* at Long Beach of Vancouver Island (Pemberton et al., 2001), and in the Pacific coast of central Japan (Seike, 2008). *Ophelia limacina* makes similar structures in the modern intertidal and shallow subtidal sediments of Willapa Bay, Washington (Clifton and Thompson, 1978). This species has a wider distribution, being found in seven regions of the Northern Hemisphere in subarctic to temperate waters, in the Pacific and Atlantic Oceans (Bellan and Dauvin, 1991). Other species of opheliid polychaetes are abundant in sandy beaches of the Southern Hemisphere, including *Euzonus furciferus* from Chile (Clarke and Peña, 1988) to southernmost Brazil (Gianuca, 1983) and *Euzonus otagoensis* in New Zealand (Probert, 1976). In each of these areas, *Macaronichnus* is known in Upper Miocene to Holocene deposits (de Gibert et al., 2006; Encinas et al., 2008; Gregory et al., 2008). *Euzonus* is not known in sandy beaches north of 30°S in South America (Jaramillo, 1994; Souza and Borzone, 2007).

DISCUSSION: *MACARONICHNUS* AS A PALEOCEANOGRAPHIC TOOL

The occurrence of *Macaronichnus* in Neogene deposits from Venezuela is an anomaly that challenges the value of this ichnogenus as a paleoclimatic indicator. However, this occurrence is herein explained by coastal upwelling of nutrient-rich cold waters. Upwelling has been widespread through the Caribbean before the final closure of the Panama Isthmus in the Late Pliocene, which created a marine barrier that profoundly changed ocean circulation (Vermeij, 1978; Keigwin, 1982; Petuch, 1981; Jackson et al., 1993; Teranes et al., 1996; Todd et al., 2002; O'Dea et al., 2007). A striking contrast resulted between the relatively warm, more saline, nutrient-poor Caribbean and the more seasonal, less saline and more productive eastern Pacific (Jackson and D'Croz, 1997). The change in oceanic circulation and the declining planktonic productivity in the Caribbean led to a restructuring of shallow-marine communities, from suspension-feeder-dominated communities to more carbonate-rich, phototrophic-based communities (Todd et al., 2002; O'Dea et al., 2007). As a consequence, a massive turnover in Caribbean mollusks (Jackson et al., 1993; Vermeij, 1978; Petuch, 1981) and a more gradual change in coral diversity and reef structure took place (Budd et al., 1996).

Distribution of benthic foraminifera along Panama and western Colombia indicates an Early Miocene to Early Pliocene open seaway consisting of a complex island-arc archipelago in southern Central America (Collins et al., 1996) and well-aerated deep and open oceanic conditions with free active water circulation between central Panama and western Colombia (Duque-Caro, 1990). The net water mass transport through the Central America seaway was directed from the Pacific Ocean into the Atlantic Ocean (Schneider and Schmittner, 2006). Isotopic profiles of $\delta^{18}O$ from venerid bivalves in Middle to Upper Miocene deposits on the Caribbean side of Panama record seasonal variations in salinity and temperature due to upwelling conditions (Teranes et al., 1996). Mixing of Pacific and Caribbean waters occurred until the Late Miocene, when the differences in carbon isotopic composition ($\delta^{13}C$) of benthic foraminifera from the deep sea in the Caribbean and Pacific started to increase, reaching modern values in the Late Pliocene (Keigwin, 1982).

In Venezuela, upwelling has been documented in the Upper Miocene–Lower Pliocene Cubagua Formation, based on an extremely rich fish assemblage and the exceptional co-occurrence of deep- and shallow-water taxa (Aguilera and de Aguilera, 2001). Bivalves in the Lower Miocene Chaguarmas Formation, a lateral equivalent of the Naricual Formation, are typical of inner-shelf turbid temperate waters, with abundant organic matter (Macsotay and Wesselingh, 2004), also suggesting upwelling. Further evidence is provided by high total organic carbon values (up to 3 wt%) in cores from the Naricual Formation in El Furrial Field, typical of modern upwelling areas of Peru, Africa, and the Arabian Sea (Ten Haven et al., 1992).

Extensive evidence of upwelling in the Urumaco Formation is revealed by marine fossil invertebrates and vertebrates. Díaz de Gamero and Linares (1989) reported *Crassostrea cahobasensis*, a fast-growing oyster typical of areas with high planktonic productivity, which became extinct in the Late Pliocene (Kirby and Jackson, 2004). Fossil teeth of the giant white shark *Carcharodon megalodon* and cetacean fragments are abundant in the Urumaco Formation (Linares, 2004; Aguilera, 2004; Aguilera et al., 2008). This extinct shark preferred relatively cold waters and is widespread in Neogene deposits of the western Atlantic in connection with upwelling (Purdy, 1996). High primary productivity was necessary to maintain the largest macropredatory shark to ever live (Gottfried et al., 1996).

Today upwelling is restricted to certain areas of the Caribbean along the northern coast of Venezuela and Colombia, such as the Venezuela Gulf (Vermeij, 1978; Petuch, 1981) and the Cariaco Basin (Hughen et al., 1996). These areas experience anomalous primary productivity compared to the rest of the Caribbean waters (Jackson and D'Croz, 1997). No opheliid polychaetes are known from modern Venezuelan shorelines (Bone and Klein, 2000; Díaz and Liñero-Arana, 2000, 2003). We predict that further exploration of foreshore siliciclastic deposits along high-energy shorelines in areas affected by upwelling will reveal the presence of some group of fast-burrowing polychaetes capable of producing *Macaronichnus*.

CONCLUSIONS

The occurrence of *Macaronichnus* in Oligocene–Miocene nearshore deposits in Venezuela is highly anomalous because all other documented occurrences are from high and intermediate latitudes. The presence of *Macaronichnus* in tropical shallow-marine deposits is linked to coastal upwelling that causes strong seasonality of cold water and replenishes the surface waters with nutrients. Such oceanographic conditions were prevalent in the northern coast of South America, at least from the Late Oligocene to the Early Pliocene, before the final closure of the strait of Panama. This evidence further expands the value of *Macaronichnus* not only in paleoclimatology as previously noted, but also in paleoceanography, because its presence in tropical coastal deposits is indicative of upwelling conditions, providing high-resolution information that may be particularly useful in the absence of body fossils.

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REFERENCES CITED

Aguilera, O.A., 2004, Tesoros paleontológicos de Venezuela: Urumaco, patrimonio natural de la humanidad: Caracas, Venezuela, Editorial Arte, 148 p.

Aguilera, O.A., and de Aguilera, D., 2001, An exceptional coastal upwelling fish assemblage in the Caribbean Neogene: Journal of Paleontology, v. 73, p. 732–742, doi: 10.1666/0022-3360(2001)075<0732:AECUFA>2.0.CO;2.

Aguilera, O.A., García, L., and Cozzuol, M.A., 2008, Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguaná Formation: Paläontologische Zeitschrift, v. 82, p. 204–208.

Bann, K., Fielding, C.R., MacEachern, J.A., and Tye, S.C., 2004, Differentiation of estuarine and offshore marine deposits using integrated ichnology and sedimentology: Permian Pebbly Beach Formation, Sydney Basin, Australia, *in* McIlroy, D., ed., The application of ichnology to palaeoenvironmental and stratigraphic analysis: The Geological Society of London Special Publication 228, p. 179–210.

Bellan, G., and Dauvin, J.C., 1991, Phenetic and biogeographic relationship in *Ophelia* (Polychaeta, Opheliidea): Bulletin of Marine Science, v. 48, p. 544–558.

Bone, D., and Klein, E., 2000, Temporal variations in a tropical soft-bottom community, Venezuela: Journal of Coastal Research, v. 16, p. 278–286.

Bromley, R.G., 1996, Trace fossils: Biology, taphonomy and applications (2nd edition): London, Chapman Hall, 361 p.

Bromley, R.G., Uchman, A., Milàn, J., and Hansen, K.S., 2009, Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: Reconstruction of paleoshoreline orientation: Ichnos, v. 16, p. 103–117, doi: 10.1080/10420940802470987.

Budd, A.F., Johnson, K.G., and Stemann, T.A., 1996, Plio–Pleistocene turnover and extinctions in the Caribbean reef-coral fauna, *in* Jackson, J.B.C., et al., eds., Evolution and environment in tropical America: Chicago, Illinois, University of Chicago Press, p. 168–204.

Carmona, N.B., Buatois, L.A., Mángano, M.G., and Bromley, R.G., 2008, Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: Animal-substrate interactions and the Modern Evolutionary Fauna: Ameghiniana, v. 45, p. 93–122.

Clarke, M., and Peña, R., 1988, Zonación de la macroinfauna en una playa de arena del Norte de Chile: Estudios Oceanológicos, v. 7, p. 17–31.

Clifton, H.E., and Thompson, J.K., 1978, *Macaronichnus segregatis*: A feeding structure of shallow marine polychaetes: Journal of Sedimentary Petrology, v. 48, p. 1293–1302.

Collins, L.S., Coates, A.G., Berggren, W.A., Aubry, M.P., and Zhang, J., 1996, The late Miocene Panama isthmian strait: Geology, v. 24, p. 687–690, doi: 10.1130/0091-7613(1996)024<0687:TLMPIS>2.3.CO;2.

Dales, R.P., 1952, The larval development and ecology of *Thoracophelia mucronata (*Treadwell): Biological Bulletin, v. 102, p. 232–242, doi: 10.2307/1538371.

de Gibert, J.M., de, Netto, R., Tognoli, F., and Grangeiro, M., 2006, Commensal worm traces and possible juvenile thalassinidean burrows associated with *Ophiomorpha nodosa*, Pleistocene, southern Brazil: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 230, p. 70–84.

Díaz, O., and Liñero-Arana, I., 2000, Poliquetos asociados a substratos artificiales sumergidos en la costa nororiental de Venezuela I: Terebellidae: Boletín del Instituto Oceanográfico de Venezuela, v. 39, p. 56–70.

Díaz, O., and Liñero-Arana, I., 2003, Nuevos registros de Trichobranchidae (Annelida: Polychaeta) para Venezuela: Boletín del Centro de Investigaciones Biológicas, v. 37, p. 182–190.

Díaz de Gamero, M.L., and Linares, O.J., 1989, Estratigrafía y paleontología de la Formación Urumaco, del Mioceno tardío de Falcón noroccidental: Actas VII Congreso Geológico de Venezuela, v. 1, p. 419–439.

Duque-Caro, H., 1990, Neogene stratigraphy, paleoceanography and paleobiology in northwest South America and the evolution of the Panama seaway: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 77, p. 203–234, doi: 10.1016/0031-0182(90)90178-A.

Encinas, A., Finger, K.L., Nielsen, S.N., Lavenu, A., Buatois, L.A., Peterson, D.E., and Le Roux, J.P., 2008, Rapid and major coastal subsidence during the late Miocene in south-central Chile: Journal of South American Earth Sciences, v. 25, p. 157–175, doi: 10.1016/j.jsames.2007.07.001.

Gianuca, N., 1983, A preliminary account of the ecology of sandy beaches in southern Brazil, *in* McLachlan, A., and Erasmus, T., eds., Sandy beaches as ecosystems: The Hague, Netherlands, Dr. W. Junk Publishers, p. 413–419.

Gottfried, M.D., Compagno, L.J.V., and Bowman, S.C., 1996, Size and skeletal anatomy of the giant "megatooth" shark *Carcharodon megalodon*, *in* Kinklei, A.P., and Ainley, D.G., eds., Great white sharks: The biology of *Carcharodon carcharias*: San Diego, California, Academy Press, p. 55–66.

Gregory, M., Campbell, K.A., Hudson, S.I., and Nichol, S.I., 2008, Trace fossil profiles in a prograding system of interglacial beach ridges: One Tree Point, Northland, New Zealand [abs.]: Second International Congress on Ichnology, Krakow, Poland, 29 August–8 September 2008p. 48–49.

Hedberg, H.D., 1950, Geology of the Eastern Venezuela Basin (Anzoátegui-Monagas-Sucre-eastern Guárico portion): Geological Society of America Bulletin, v. 61, p. 1173–1215, doi: 10.1130/0016-7606(1950)61[1173:GOTEVB]2.0.CO;2.

Hollis, C.J., Handley, L., Crouch, E.M., Morgans, H.E.G., Baker, J.A., Creech, J., Collins, K.S., Gibbs, S.J., Huber, M., Schouten, S., Zachos, S.J., and Pancost, R.D., 2009, Tropical sea temperatures in the high-latitude South Pacific during the Eocene: Geology, v. 37, p. 99–102.

Hughen, K.A., Overpeck, J.T., Peterson, L.C., and Anderson, R.F., 1996, The nature of varved sedimentation in the Cariaco Basin, Venezuela, and its palaeoclimatic significance, *in* Kemp, A.E.S., ed., Palaeoclimatology and palaeoceanography from laminated sediments: The Geological Society of London Special Publication 116, p. 171–183.

Jackson, J.B.C., and D'Croz, L., 1997, The ocean divided, *in* Coates, A.G., ed., Central America: A natural and cultural history: New Haven, Yale University Press, p. 38–71.

Jackson, J.B.C., Jung, P., Coates, A.G., and Collins, L.S., 1993, Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama: Science, v. 260, p. 1624–1626, doi: 10.1126/science.260.5114.1624.

Jaramillo, E., 1994, Patterns of species richness in sandy beaches of South America: South African Journal of Zoology, v. 29, p. 227–234.

Keigwin, L.D., 1982, Isotope paleoceanography of the Caribbean and east Pacific: Role of Panama uplift in late Neogene time: Science, v. 217, p. 350–353, doi: 10.1126/science.217.4557.350.

Kirby, M.X., and Jackson, J.B.C., 2004, Extinction of a fast-growing oyster and changing ocean circulation in Pliocene tropical America: Geology, v. 32, p. 1025–1028, doi: 10.1130/G21039.1.

Linares, O.J., 2004, Bioestratigrafía de las faunas de mamíferos de las formaciones Socorro, Urumaco y Codore (Mioceno Medio-Plioceno Temprano, de la región de Urumaco, Falcon, Venezuela: Paleobiología Neotropical, v. 1, p. 1–26.

Macsotay, O., and Wesselingh, F.P., 2004, Malacofauna de edad Mioceno temprano en las formaciones Quebradon y Chaguaramas, de las sub-cuenca de Guarico, Venezuela: Boletín de Geología, v. 20, p. 73–90.

McConnaughey, B.H., and Fox, D.L., 1949, The anatomy and biology of the marine polychaete *Thoracophelia mucronata* (Treadwell) Opheliidae: University of California Publications in Zoology, v. 47, p. 319–340.

O'Dea, A., Jackson, J.B.C., Fortunato, H., Smith, J.T., D'Croz, L., Johnson, K.G., and Todd, J.A., 2007, Environmental change preceded Caribbean extinction by 2 million years: Proceedings of the National Academy of Sciences of the United States of America, v. 104, p. 5501–5506, doi: 10.1073/pnas.0610947104.

Olivero, E.B., Torres, P., López, M.I., and Buatois, L.A., 2008, Variaciones faciales y arquitecturas complejas en depósitos marinos someros de la Formación Leticia, Eoceno, Andes Fueguinos [abs.]: XII Reunión Argentina de Sedimentología, Buenos Aires, 3–6 June 2008, p. 128.

Pemberton, S.G., Spila, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D., and Sinclair, I.K., 2001, Ichnology and sedimentology of shallow to marginal marine systems: Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin: Geological Association of Canada, Short Course Notes 15, 343 p.

Pemberton, S.G., MacEachern, J.A., Bann, K.L., and Gingras, M.K., 2006, High-latitude versus low-latitude: Capturing the elusive signal using trace fossil suites from the ancient record [abs.]: American Association of Petroleum Geologists 2006 Annual Convention, Houston, Texas, 9–12 April 2006, p. 84.

Petuch, E.J., 1981, A relict Neogene caenogastropod fauna from northern South America: Malacologia, v. 20, p. 308–309.

Probert, P.K., 1976, New species of *Euzonus* (Polychaeta: Opheliidae) from a New Zealand sandy beach: New Zealand Journal of Marine and Freshwater Research, v. 10, p. 375–379.

Purdy, R.W., 1996, Paleoecology of fossil white shark, *in* Kinklei, A.P., and Ainley, D.G., eds., Great white sharks: The biology of *Carcharodon carcharias*: San Diego, California, Academy Press, p. 67–78.

Schneider, B., and Schmittner, A., 2006, Simulating the impact of the Panamanian seaway closure on ocean circulation, marine productivity and nutrient cycling: Earth and Planetary Science Letters, v. 246, p. 367–380, doi: 10.1016/j.epsl.2006.04.028.

Seike, K., 2008, Burrowing behaviour inferred from feeding traces of the opheliid polychaete *Euzonus* sp. as response to beach morphodynamics: Marine Biology, v. 153, p. 1199–1206, doi: 10.1007/s00227-007-0893-8.

Souza, J.R.B., and Borzone, C.A., 2007, Population dynamics and secondary production of *Euzonus furciferus* Ehelers (Polychaeta, Opheliidae) in an exposed sandy beach of southern Brazil: Revista Brasileira de Zoologia, v. 24, p. 1139–1144.

Ten Haven, H.L., Eglinton, G., Farrimond, P., Kohnen, M.E.L., Poynter, J.G., Rullkötter, J., and Welte, D.H., 1992, Variations in the content and composition of organic matter in sediments underlying active upwelling regimes: A study from ODP Legs 108, 112, 117, *in* Summerhayes, C.P., et al., eds., Upwelling systems: Evolution since the Early Miocene: The Geological Society of London Special Publication 64, p. 229–246.

Teranes, F.L., Geary, D.H., and Bemis, B.E., 1996, The oxygen isotopic record of seasonality in Neogene bivalves from Central American Isthmus, *in* Jackson, J.B.C., et al., eds., Evolution and environment in tropical America: Chicago, Illinois, University of Chicago Press, p. 105–129.

Todd, J.A., Jackson, J.B.C., Johnson, K.G., Fortunato, H.M., Heitz, A., Alvarez, M., and Jung, P., 2002, The ecology of extinction: Molluscan feeding and faunal turnover in the Caribbean Neogene: Royal Society of London Proceedings, ser. B, v. 269, p. 571–577.

Vermeij, G.J., 1978, Biogeography and adaptation: Patterns of marine life: Cambridge, Massachusetts, and London, UK, Harvard University Press, 332 p.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: Science, v. 292, p. 686–693, doi: 10.1126/science.1059412.

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