



Morphological reassessment and molecular assessment of *Sargassum* (Fucales: Phaeophyceae) species from the Gulf of California, Mexico

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Abstract

Systematic molecular studies have not been performed on ecologically important brown algae (*Sargassum*) in the Gulf of California, Mexico, where 42 specific and infraspecific names have been recorded within this genus. We conducted phylogenetic analyses of nuclear ribosomal ITS and mitochondrial *cox1* and *cox3* sequences, along with detailed morphological observations of *Sargassum* collected in the Gulf of California. We confirmed the presence of six species, five previously described—*S. herporhizum*, *S. horridum*, *S. johnstonii*, *S. lapazeanum*, and *S. sinicola*, as well as the newly described *Sargassum ulixei* sp. nov. which is characterized by terete primary axes arising from the stipe, lanceolate to elliptical sessile ecostate blades with smooth margins, cryptostomata, ellipsoidal vesicles with a short mucron, and cylindrical to ellipsoidal receptacles. The individual analyses and subsequent phylogenetic analysis recognized two groups previously described by Dawson, one as *Sargassum* and other as *Horridum*. Our studies suggest that the Gulf of California is a region with endemic *Sargassum* species, and is clearly distinguished from the Pacific side of Baja California, where recently introduced species are common. Based on phylogenetic relationships, we propose two geographical origins for the *Sargassum* from the Gulf of California: a first group originating from the proto-Gulf, related to species from the northern hemisphere (including five species); and a second group, containing *S. sinicola*, introduced when the southern end opened at a later stage.

Keywords: Gulf of California, molecular markers, morphology, phylogeny, *Sargassum*, new species, new synonyms

Introduction

In the Gulf of California, originated in the early Late Miocene (Ledesma-Vázquez 2002, Ledesma-Vázquez & Carreño 2010), *Sargassum* species produce a large amounts of biomass (Norris 2010). Their ecological organization resembles that of a forest because they produce a canopy that acts as a habitat for diverse assemblages of epiphytic algae/microinvertebrates and understory algae, invertebrates, and fish (Soto-Mardones *et al.* 1999, Brusca *et al.* 2005, Enriquez-Andrade *et al.* 2005). *Sargassum* forests are reproductive and nursery areas of fishery-related species (Aburto-Oropeza *et al.* 2008) and endangered species such as the green turtle *Chelonia mydas*. Thus, these are critical habitats for coastal management and species conservation (Witherington *et al.* 2012).

Historically, some names applied to the *Sargassum* species from the Gulf of California were proposed by Setchell and Gardner (1924) who described 15 new species, and Setchell (1937) who described three more. Dawson (1944) reviewed the taxonomy of the genus and proposed a reduction to ten species (as well as one form) based on morphological features, and proposed two new species. Dawson (1944) also organized supraspecific taxonomic categories due to the difficulty in identification to the species level, as informal “groups” *Johnstonii* Dawson (1944: 239), *Lapazeanum* Dawson (1944: 241), *Sinicola* Dawson (1944: 245), and *Herporhizum* Dawson (1944: 249). Later, Taylor (1945) reported six species, including *Sargassum brandegeei* Setchell & Gardner (1924: 736), *Sasrgassum howellii* Setchell (1937: 132), *Sargassum pacificum* Bory de Saint-Vincent (1828: 123) and *Sargassum liebmannii* Agardh (1847: 8) for Maria Islands, without comparing all these species to others from the region.

patterns and formed new currents that flow along the east Pacific coast (Kessler 2006, Kirby *et al.* 2008). Once the taxonomy and phylogeny of *Sargassum* from the Gulf of California are clear, we will be able to infer their relationships with Mexican Pacific and Central American Pacific *Sargassum* species using morphological and molecular data in order to understand distributions, phylogeny relationships and the diversity of the genus.

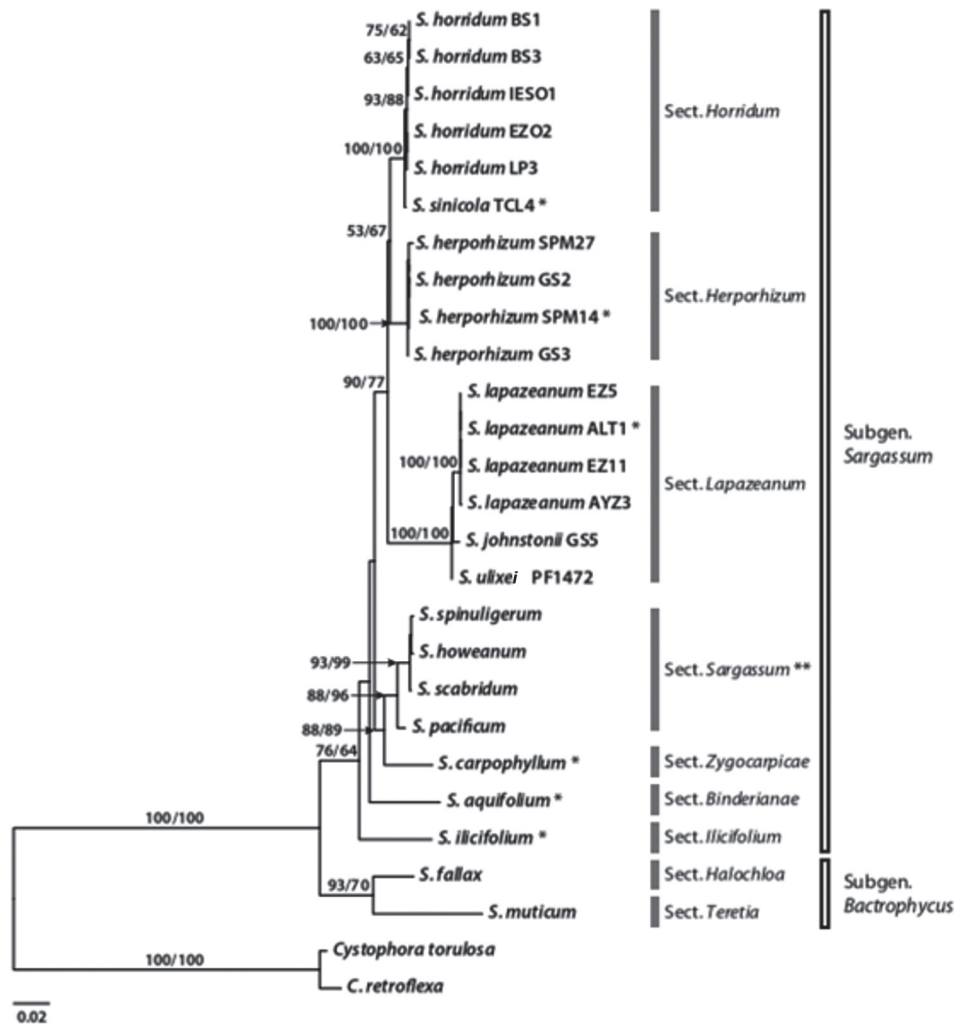


FIGURE 9. Maximum likelihood concatenated tree of *Sargassum* inferred from ITS2+cox1+cox3 sequences. Bootstrap values are indicated for ML/MP when over 50%. An asterisk indicates the type of each section, while two asterisks denote the type of each subgenus.

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References

Aburto-Oropeza, O., Erisman, B., Valdez-Ornelas, V. & Danemann, G. (2008) Commercially important Serranid fishes from the Gulf of California: Ecology, fisheries and conservation. *Ciencia y Conservación* 1: 4–43.

- Abbott, I.A., Tseng, C.K. & Baoren, L. (1986) Clarification of some subgeneric nomenclature in *Sargassum* subgenus *Sargassum*. In: Abbott, I.A. (Ed.) *Taxonomy of economic seaweeds. With reference to some Pacific and Caribbean Species*. California Sea Grant College Program, La Jolla, pp. 55–64.
- Agardh, J. (1847) Nya alger från Mexico. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm* 4: 5–17.
- Agardh, J. (1873) Till algerne systematik. Nya Bidrag. *Lunds Universitets Ars-Skrift, Afdelningen Fr Matematik Och Naturvetenskap* 9: 1–71.
- Andrade-Sorcía, G. & Riosmena-Rodríguez, R. (2011) Vegetative and reproductive anatomy of *Sargassum lapazeanum* (Fucales: Sargassaceae) in the south-western Gulf of California, Mexico. *Algae* 26(4): 327–331.
<http://dx.doi.org/10.4490/algae.2011.26.4.327>
- Andrade-Sorcía, G., Riosmena-Rodríguez, R. & Paúl-Chávez, L. (2008) Variabilidad Morfológica y Morfométrica de *Sargassum lapazeanum* (Sargassaceae: Phaeophyta) en el Suroeste del Golfo de California. *INSULA* 37: 68–80.
<http://dx.doi.org/10.5007/2178-4574.2008v37p67>
- Ang, P.O. Jr. (2006) Phenology of *Sargassum* spp. in Tung Ping Chau Marine Park, Hong Kong SAR, China. *Journal of Applied Phycology* 18: 629–636.
<http://dx.doi.org/10.1007/s10811-006-9071-5>
- Areschoug, J.E. (1854) Phyceae novae et minus cognitae in maribus extraeuropaeis collectae. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, series 3* 1: 329–372.
<http://dx.doi.org/10.5962/bhl.title.68745>
- Boo, G.H., Lindstrom, S.C., Klochkova, N.G., Yotsukura, N., Yang, E.C., Kim, H.G., Waaland, J.R., Cho, G.Y., Miller, K.A. & Boo S.M. (2011) Taxonomy and biogeography of the genus *Agarum* (Laminariales, Phaeophyceae) based on nuclear, mitochondrial, and plastid gene sequences. *Taxon* 60: 831–840.
- Bory de St. Vincent, J.B. (1828) Botanique, Cryptogamie. In: Duperrey, L.I. (Ed.) *Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, la Coquille, pendant les années 1822, 1823, 1824, et 1825*. Bertrand, Paris, pp. 97–200.
<http://dx.doi.org/10.5962/bhl.title.9464>
- Brusca, R.C., Findley, L.T., Hastings, P.A., Hendrickx, M.E., Cosio, J.T. & Heiden, A.M.V.D. (2005) *Macrofaunal diversity in the Gulf of California*. In: Cartron, J.L., Ceballos, G. & Felger, R.S. (Eds.) *Biodiversity, ecosystems, and conservation in northern Mexico*. Oxford University Press, New York, pp. 179–202.
- Brusca, R.C. & Hendrickx, M.E. (2010) Invertebrate Biodiversity and Conservation in the Gulf of California. In: Brusca, R.C. (Ed.) *The Gulf of California. Biodiversity and Conservation*. The University of Arizona Press, Arizona, pp. 72–95.
- Cheang, C.C., Chu, K.H., Fujita, D., Yoshida, G., Hiraoka, M., Critchley, A., Choi, H.G., Duan, D., Serisawa, Y. & Ang Jr., P.O. (2010) Low genetic variability of *Sargassum muticum* (Phaeophyceae) revealed by a global analysis of native and introduced populations. *Journal of Phycology* 46: 1063–1074.
<http://dx.doi.org/10.1111/j.1529-8817.2010.00901.x>
- Cho, S.M., Lee S.M., Ko, Y.D., Mattio, L. & Boo, S.M. (2012) Molecular systematic reassessment of *Sargassum* (Fucales, Phaeophyceae) in Korea using four gene regions. *Botanica Marina* 55: 473–484.
<http://dx.doi.org/10.1515/bot-2012-0109>
- Chu, S.H., Zhang, Q.S., Liu, S.K., Tang, Y.Z., Zhang, S.B., Lu, Z.C. & Yu, Y.Q. (2012a) Tolerance of *Sargassum thunbergii* germlings to thermal, osmotic and desiccation stress. *Aquatic Botany* 96: 1–6.
<http://dx.doi.org/10.1016/j.aquabot.2011.09.002>
- Chu, S.H., Zhang, Q.S., Tang, Y.Z., Zhang, S.B., Lu, Z.C. & Yu, Y.Q. (2012b) High tolerance to fluctuating salinity allows *Sargassum thunbergii* germlings to survive and grow in artificial habitat of full immersion in intertidal zone. *Journal of Experimental Marine Biology and Ecology* 412: 66–71.
<http://dx.doi.org/10.1016/j.jembe.2011.10.025>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
<http://dx.doi.org/10.1038/nmeth.2109>
- Dawson, E.Y. (1944) The marine algae of the Gulf of California. *Allan Hancock Pacific Expeditions* 3: 237–250.
- Dawson, E.Y. (1960) New records of marine algae from Pacific Mexico and Central America. *Pacific Naturalist* 1: 31–52.
- Dawson, M.N., Waples, R.S. & Bernardi, G. (2006) Phylogeography. In: Allen, L.G., Pondella, D.J. & Horn, M.H. (Eds.) *The ecology of marine fishes: California and adjacent waters*. University of California Press, Berkeley, pp. 26–54.
- Dixon, R.R.M., Huisman, J.M., Buchanan, J., Gurgel, C.F.D. & Spencer, P. (2012) A morphological and molecular study of austral *Sargassum* (Fucales, Phaeophyceae) supports the recognition of *Phyllotricha* at genus level, with further additions to the genus *Sargassopsis*. *Journal of Phycology* 47: 1–11.
- Douady, C.J., Delsuc, F., Boucher, Y., Doolittle, W.F. & Douzery, E.J.P. (2003) Comparison of Bayesian and Maximum Likelihood

Bootstrap Measures of Phylogenetic Reliability. *Molecular Biology and Evolution* 20: 248–254.

<http://dx.doi.org/10.1093/molbev/msg042>

- Enriquez-Andrade, R., Anaya-Reyna, G., Barrera-Guevara, J.C., Carvajal-Moreno, M.D.L.A., Martínez-Delgado, M.E., Vaca-Rodríguez, J. & Valdés-Casillas, C. (2005) An analysis of critical areas for biodiversity conservation in the Gulf of California region. *Ocean & Coastal Management* 48: 31–50.
<http://dx.doi.org/10.1016/j.ocecoaman.2004.11.002>
- Endo, H., Nishigaki, T., Yamamoto, K. & Takeno, K. (2013) Age- and size-based morphological comparison between the brown alga *Sargassum macrocarpum* (Heterokonta; Fucales) from different depths at an exposed coast in northern Kyoto, Japan. *Journal of Applied Phycology* 25: 1815–1822.
<http://dx.doi.org/10.1007/s10811-013-0002-y>
- Espinoza-Ávalos, J. (1993) Macroalgas marinas del Golfo de California. In: Salazar-Vallejo, S.I. & González, N.E. (Eds.) *Biodiversidad Marina y Costera de México*. Comisión Nacional para la Biodiversidad y CIQRO, México, pp. 328–356.
- Espinoza, J. & Rodríguez, H. (1987) Seasonal phenology and reciprocal transplantation of *Sargassum sinicola* Setchell et Gardner in the southern Gulf of California. *Journal of experimental Marine Biology and Ecology* 110: 183–195.
[http://dx.doi.org/10.1016/0022-0981\(87\)90027-X](http://dx.doi.org/10.1016/0022-0981(87)90027-X)
- Fagerberg, W.R. & Dawes, C.J. (1976) Studies on *Sargassum*. I. A light microscopic examination of the wound regeneration in mature stipes of *S. filipendula*. *American Journal of Botany* 63: 110–119.
<http://dx.doi.org/10.2307/2441673>
- Fensholt, D.E. (1955) An emendation of the genus *Cystophyllum* (Fucales). *American Journal of Botany* 42: 305–322.
<http://dx.doi.org/10.2307/2438568>
- Fernández-García, C., Riosmena-Rodríguez, R., Wysor, B., Tejada, O.L. & Cortés, J. (2011) Checklist of the Pacific marine macroalgae of Central America. *Botanica Marina* 54: 53–73.
<http://dx.doi.org/10.1515/bot.2011.001>
- Goldberg, N.A. & Huisman, J.M. (2004) *Sargassum kendrickii* (Fucales, Phaeophyceae), a new species of subgenus *Phyllotrichia* from southern Australia. *Botanica Marina* 47: 424–430.
<http://dx.doi.org/10.1515/BOT.2004.059>
- Grunow, A. (1916) Additamenta ad cognitionem Sargassorum. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 66: 136–185
- Hastings, P.A. Findley, L.T. & Van den Heiden, A.M. (2010) Fishes of the Gulf of California. In: Brusca, R.C. (Ed.) *The Gulf of California. Biodiversity and Conservation*. The University of Arizona Press, Tucson, pp. 96–118.
- Grunow, A. (1916) Additamenta ad cognitionem Sargassorum. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 66: 136–185.
- Kessler, W.S. (2006) The circulation of the eastern tropical Pacific: A review. *Progress in Oceanography* 69: 181–217.
<http://dx.doi.org/10.1016/j.pocean.2006.03.009>
- Kirby, M.X., Jones, D.S. & MacFadden, B.J. (2008) Lower Miocene stratigraphy along the Panama Canal and Its bearing on the Central American Peninsula. *PLoS ONE* 3: 1–14.
<http://dx.doi.org/10.1201/b12219-13>
- Kuntze, O. (1880) Revision von *Sargassum* und das sogenannte Sargasso-Meer. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 1: 191–239.
- Lane, C.E., Lindstrom, S.C. & Saunders, G.W. (2007) A molecular assessment of northeast Pacific *Alaria* species (Laminariales, Phaeophyceae) with reference to the utility of DNA barcoding. *Molecular Phylogenetics and Evolution* 44: 634–648.
<http://dx.doi.org/10.1016/j.ympev.2007.03.016>
- Lavín, M.F. & Marinone, S.G. (2003) An overview of the physical oceanography of the Gulf of California. In: Velasco Fuentes, O.U., Sheinbaum, J. & Ochoa de la Torre, J.L. (Eds.) *Nonlinear processes in geophysical fluid dynamics*. Kluwer Academic, Dordrecht, pp. 173–204.
http://dx.doi.org/10.1007/978-94-010-0074-1_11
- Ledesma-Vázquez, J. (2002) A gap in the Pliocene invasion of seawater to the Gulf of California. *Revista Mexicana de Ciencias Geológicas*. 19: 145–51.
- Ledesma-Vázquez, J. & Carreño, L. (2010) Origin, age, and geological evolution of the Gulf of California. In: Brusca, R. (Ed.) *The Gulf of California, Biodiversity and conservation*. The University of Arizona Press, Tucson, pp. 7–23.
- Lüning, K. (1990) *Seaweeds: their environment, biogeography, and ecophysiology*. Wiley, New York, 527 pp.
- Lucas, A.H.S. (1935) The marine algae of Lord Howe Island. *Proceedings of the Linnean Society of New South Wales* 60: 194–232
- Mattio, L. & Payri, C.E. (2009) Taxonomic revision of *Sargassum* species (Fucales, Phaeophyceae) from New Caledonia based on morphological and molecular analyses. *Journal of Phycology* 45: 1374–1388.

<http://dx.doi.org/10.1111/j.1529-8817.2009.00760.x>

- Mattio, L. & Payri, C.E. (2011) 190 years of *Sargassum* taxonomy, facing the advent of DNA phylogenies. *Botanical Review* 77: 31–70.
<http://dx.doi.org/10.1007/s12229-010-9060-x>
- Mattio, L., Payri, C.E. & Stiger, V. (2008) Taxonomic revision of *Sargassum* (Fucales, Phaeophyceae) from French Polynesia based on morphological and molecular analyses. *Journal of Phycology* 44: 1541–1555.
<http://dx.doi.org/10.1111/j.1529-8817.2008.00597.x>
- Mattio, L., Payri, C.E. & Verlaque, M. (2009) Taxonomic revision and geographic distribution of the subgenus *Sargassum* (Fucales, Phaeophyceae) in the Western and Central Pacific islands based on morphological and molecular analyses. *Journal of Phycology* 45: 1213–1227.
<http://dx.doi.org/10.1111/j.1529-8817.2009.00737.x>
- Mattio, L., Payri, C.E., Verlaque, M. & De Reviere, B. (2010) Taxonomic revision of *Sargassum* sect. *Acanthocarpicae* (Fucales, Phaeophyceae). *Taxon* 9: 896–904.
- Marmorino, G.O., Miller, W.D., Smith, G.B. & Bowles, J.H. (2014) Airborne imagery of a disintegrating *Sargassum* drift line. *Deep-Sea Research I* 58: 316–321.
<http://dx.doi.org/10.1016/j.dsr.2011.01.001>
- McCourt, R.M. (1983) *Zonation and phenology of three species of Sargassum in the intertidal zone of the northern Gulf of California*. Ph. D. Thesis, The University of Arizona, Tucson, 144 pp.
- McCourt, R.M. (1984) Seasonal Patterns of Abundance, Distributions, and Phenology in Relation to Growth Strategies of three *Sargassum* Species. *Journal of Experimental Marine Biology and Ecology* 57: 131–141.
[http://dx.doi.org/10.1016/0022-0981\(84\)90082-0](http://dx.doi.org/10.1016/0022-0981(84)90082-0)
- Norris, J.N. (2010) Marine algae of the North Gulf of California: Chlorophyta and Phaeophyceae. *Smithsonian Contributions to Botany* 94: 1–276.
<http://dx.doi.org/10.5479/si.0081024X.94.276>
- Paúl-Chávez, L. (2005) *Taxonomía y dinámica poblacional de Sargassum horridum para el suroeste del Golfo de California: implicaciones en manejo*. Ph. D. Thesis. CICIMAR-IPN, Mexico, 105 pp.
- Paúl-Chávez, L. & Riosmena-Rodríguez, R. (2000) Floristic and biogeographical trends in seaweed assemblages from a subtropical insular island complex in the Gulf of California. *Pacific Science* 54: 137–147.
- Perez, F. (2004) *Serial Cloner v.2.6.0*. Software SerialBasics.
- Phillips, N. (1995) Biogeography of *Sargassum* (Phaeophyta) in the Pacific basin. In: Abbott, I.A. (Ed.) *Taxonomy of economic seaweeds with reference to some Pacific and western Atlantic species. Vol. 5*. California Sea Grant College Program, La Jolla, pp. 107–145.
- Phillips, N. & Fredericq, S. (2000) Biogeographic and phylogenetic investigation of the pantropical genus *Sargassum* (Fucales, Phaeophyceae) with respect to Gulf of Mexico species. *Gulf of Mexico Science* 2: 77–87.
- Phillips, N.E., Smith, C.M. & Morden, C.W. (2005) Testing systematic concepts of *Sargassum* (Fucales, Phaeophyceae) using portions of the *rbcLS* operon. *Phycological Research* 53: 1–10.
<http://dx.doi.org/10.1111/j.1440-1835.2005.tb00353.x>
- Rambaut, A. (2002) Se-AL: Sequence alignment editor, Version 2.0a11, available at <http://tree.bio.ed.ac.uk/software/seal%20/>
- Rao, A.S. & Rao, M.U. (2002) Seasonal growth pattern in *Sargassum polycystum* C. Agardh (Phaeophyta, Fucales) occurring at Visakhapatnam, east coast of India. *Indian Journal of Marine Sciences* 31: 26–32.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- Sánchez-Rodríguez, I. (1995) *Fenología de Sargassum sinicola (Setchell y Gardner) en Bahía Magdalena, B.C.S., México*. Ph. D. Thesis, Instituto Politécnico Nacional. Centro Interdisciplinario de Ciencias Marinas, La Paz, B.C.S., 84 pp.
- Sánchez-Rodríguez, I., Fajardo-León, M.C. & Oliveiro-Pantoja, C. (1989) Estudio florístico estacional de las algas. *Investigaciones marinas CICIMAR* 4: 35–48.
- Setchell, W.A. (1937) The Templeton Crocker Expedition of the California Academy of Sciences, 1932, No. 34: Report on the *Sargassums*. *Proceedings of the California Academy of Science USA* 22: 127–58.
- Setchell, W.A. & Gardner, N.L. (1924) The Marine Algae, in Expedition of the California Academy of Sciences to the Gulf of California in 1921. *Proceedings of the California Academy of Sciences Series 4* 12(29): 695–949.
- Shimabujuro, H., Terada, R., Noro, T. & Yoshida, T. (2008) Taxonomic study of two *Sargassum* species (Fucales, Phaeophyceae) from the Ryuju Islands, southern Japan: *Sargassum ryukyense* sp. nov. and *Sargassum pinnatifidum* Harvey. *Botanica Marina* 51: 26–33.
<http://dx.doi.org/10.1515/BOT.2008.002>
- Silva, P.C. (1992) Geographic patterns of diversity in benthic marine algae. *Pacific Science* 46: 429–437.
- Simons, E. B. (1906) A morphological study of *Sargassum filipendula*. *Botanical Gazette* 41(3): 161–182.
<http://dx.doi.org/10.1086/328760>
- Sonder, G. (1845) Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae, collegit L. Priess, Ph. Dr.

Botanische Zeitung 3: 49–57.

- Soto-Mardones, L., Marinone, S.G. & Parés-Sierra, A. (1999) Variabilidad espaciotemporal de la temperatura superficial del mar en el Golfo de California. *Ciencias Marinas* 25: 1–30.
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stiger, V., Horiguchi, T., Yoshida, T., Coleman, A.W., & Masuda, M. (2000) Phylogenetic relationships of *Sargassum* (Sargassaceae, Phaeophyceae) with reference to a taxonomic revision of the section *Phyllocystae* based on ITS-2 nrDNA sequences. *Phycological Research* 48: 251–260.
<http://dx.doi.org/10.1046/j.1440-1835.2000.00210.x>
- Stiger, V., Horiguchi, T., Yoshida, T., Coleman, A.W. & Masuda, M. (2003) Phylogenetic relationships within the genus *Sargassum* (Fucales, Phaeophyceae), inferred from ITS-2 nrDNA, with an emphasis on the taxonomic subdivision of the genus. *Phycological Research* 51: 1–10.
<http://dx.doi.org/10.1046/j.1440-1835.2003.00287.x>
- Stock, J.M. & Hodges, K.V. (1989) Pre-Pliocen extension around the Gulf of California and the Transfer of Baja California to the Pacific Plate. *Tectonics* 8: 99–115.
<http://dx.doi.org/10.1029/TC008i001p00099>
- Swofford, D.L. (2002) *PAUP*: phylogenetic analysis using parsimony (and other methods)*, Version 4.0b10. Sinauer Associates, Sunderland.
- Taylor, W.R. (1945) Pacific marine algae of the Allan Hancock Expeditions to the Galápagos Islands. *Allan Hancock Pacific Expeditions* 12: 1–528.
- Witherington, B., Shigetomo, H. & Hardy, R. (2012) Young sea turtles of the pelagic *Sargassum*-dominated drift community: habitat use, population density, and threats. *Marine Ecology Progress Series* 463: 1–22.
<http://dx.doi.org/10.3354/meps09970>
- Yamasaki, M., Aono, M., Ogawa, N., Tanaka, K., Imoto, Z. & Nakamura, Y. (2014) Drifting algae and fish: Implications of tropical *Sargassum* invasion due to ocean warming in western Japan. *Estuarine, Coastal and Shelf Science* 147: 32–41.
<http://dx.doi.org/10.1016/j.ecss.2014.05.018>
- Yoshida, T., Stiger, V. & Horiguchi, T. (2000) *Sargassum boreale* sp. nov. (Fucales, Phaeophyceae) from Hokkaido, Japan. *Phycology Research* 48: 125–131.
<http://dx.doi.org/10.1046/j.1440-1835.2000.00197.x>