

Molecular parataxonomy as taxon description: examples from recently named Zoanthidea (Cnidaria: Anthozoa) with revision based on serial histology of microanatomy

TIMOTHY D. SWAIN^{1,2,3} & LAURA M. SWAIN²

¹Department of Civil and Environmental Engineering, Northwestern University, 2145 Sheridan Road, Evanston, Illinois, 60208, USA

²Biodiversity Synthesis Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois, 60605, USA

³Corresponding author. E-mail: tswain@fieldmuseum.org

Abstract

Current taxonomic practices require corroboration from multiple lines of evidence to provide sufficient rigor for species discovery and description. However, many recently named taxa (species–families) are defined by nucleotide sequence with little or no description of the features that traditionally define higher taxa and link nucleotide-based information to the existing taxonomic system. Without knowledge of form, it may be impossible to identify conspecifics, congeners, and confamilials of new taxa among the hundreds of specimens and described species for which nucleotide sequencing is not now, and may never be, available. Additionally, some nucleotide sequences are invariant or inconsistently differentiated between congeners; severely limiting the utility of nucleotide-based taxon definitions. Here we use serial histology of paratypes to reveal the microanatomy of internal structures and revise the definitions of the Zoanthidea taxa *Corallizoanthus tsukaharai* Reimer, *Antipathozoanthus hickmani* Reimer & Fujii, *Parazoanthus darwini* Reimer & Fujii, *Terrazoanthus onoi* Reimer & Fujii, *Terrazoanthus sinnigeri* Reimer & Fujii, *Microzoanthus kagerou* Fujii & Reimer, and *Zoanthus kuroshio* Reimer & Ono; examination of *Mesozoanthus lilkweminensis* Reimer & Sinniger failed to produce interpretable sections. The results described here, with individual measurements documented in Morphbank (collection 829724) and Encyclopedia of Life (by taxon name), indicate a notably rich diversity of form for an order that is often characterized as depauperate in morphological diversity. One prominent example is a novel marginal muscle structure (cyclically transitional) that is not observable without serial sections. These findings may renew interest in morphological characters and provide the foundation for revision of Zoanthidea higher taxa, particularly now that phylogenetic relationships for these taxa can be inferred.

Key words: Coelenterata, DNA barcoding, DNA taxonomy, molecular parataxonomy, symbiosis

Resumen

Las corrientes prácticas taxonómicas requieren de la corroboración de múltiples fuentes de información para proveer con suficiente rigurosidad el descubrimiento y la descripción de especies. Sin embargo, muchos de los taxones (especie–familia) actualmente nombrados han sido definidos mediante la secuencia de nucleótidos con incompleta o la no descripción de características que tradicionalmente definen los taxones superiores y que pueden conectar la información basada en los nucleótidos con el sistema de taxonomía existente. Sin el conocimiento de forma, podría ser imposible identificar la misma especie, género y familia de taxones nuevos entre cientos de especímenes y de especies descritas, y cuya secuenciación de nucleótidos no existen, o jamás estarán disponibles. Además, algunas secuencias de nucleótidos son idénticas, o inconsistentemente diferenciadas entre géneros; limitando severamente la utilización de la definición de taxones basada en los nucleótidos. Para el propósito de esta investigación, examinamos la histología en series de los paratípos que revelan la microanatomía de las estructuras internas y revisamos las definiciones de los taxones de Zoanthidea *Corallizoanthus tsukaharai* Reimer, *Antipathozoanthus hickmani* Reimer & Fujii, *Parazoanthus darwini* Reimer & Fujii, *Terrazoanthus onoi* Reimer & Fujii, *Terrazoanthus sinnigeri* Reimer & Fujii, *Microzoanthus kagerou* Fujii & Reimer, *Zoanthus kuroshio* Reimer & Ono; y al practicar el exámen a *Mesozoanthus lilkweminensis* Reimer & Sinniger fallamos en producir secciones histológicas que pudieron ser interpretadas. Los resultados que se describen aquí, con medidas individuales se documentan en Morphbank (colección 829724) y en la Encyclopedia of Life (buscar por el

Acknowledgements

We are grateful to S. Cairns, A. Collins, T. Coffer, and G. Keel of the USNM for permission to subsample specimens and assistance with loans. The Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution and K. Feldheim provided acids and antidotes, and working space to use them, with support from the Pritzker Foundation; R. Bieler provided access to his histology lab and expendables, and the assistance of M. Pryzdia. P. Sierwald and S. Ware provided access and expertise in the FMNH Collaborative Insect and Invertebrate Lab. The Biodiversity Synthesis Center and M. Westneat provided support and authorization for specimen loans. This work was supported in part by NSF CBET-0937987, Northwestern University, L. Marcelino, and V. Backman. L.O. Swain provided the abstract translation and A.K. Swain assisted with image analysis. Special thanks to Metra for providing the library-like environment of the Quiet Car, where most of this text was written.

References

- Carlgren, O.H. (1913) Zoantharia. *The Danish Ingolf-Expedition*, 5, 1–62.
- Carlgren, O.H. (1951) The actinian fauna of the Gulf of California. *Proceedings of the United States National Museum*, 101, 415–449.
<http://dx.doi.org/10.5479/si.00963801.101-3282.415>
- Carreiro-Silva, M., Braga-Henriques, A., Sampaio, I., de Matos, V., Porteiro, F.M. & Ocaña, O. (2011) *Isozoanthus primnoidus*, a new species of zoanthid (Cnidaria: Zoantharia) associated with the gorgonian *Callogorgia verticillata* (Cnidaria: Alcyonacea). *ICES Journal of Marine Science*, 68, 408–415.
<http://dx.doi.org/10.1093/icesjms/fsq073>
- Cerrano, C., Danovaro, R., Gambi, C., Pusceddu, A., Riva, A. & Schiaparelli, S. (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodiversity and Conservation*, 19, 153–167.
<http://dx.doi.org/10.1007/s10531-009-9712-5>
- Collins, R.A. & Cruickshank, R.H. (2013) The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*, 13, 969–975.
<http://dx.doi.org/10.1111/1755-0998.12046>
- Cutress, C.E. & Pequegnat, W.E. (1960) Three new species of Zoantharia from California. *Pacific Science*, 14, 89–100.
- DeSalle, R., Egan, M.G. & Siddall, M. (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 1905–1916.
<http://dx.doi.org/10.1098/rstb.2005.1722>
- Delage, Y. & Hérouard, E. (1901) Zoanthidés. – Zoanthidae. In: *Trait de Zoologie concrète. Tome II – 2me partie. Les Coelenterés*. C. Reinwald, Paris, pp. 654–667.
- Duerden, J.E. (1898) Jamaican Actiniaria. Part I. – Zoa. *Scientific Transactions of the Royal Dublin Society*, 6, 329–384.
- Fujii, T. & Reimer, J.D. (2011) Phylogeny of the highly divergent zoanthid family Microzoanthidae (Anthozoa, Hexacorallia) from the Pacific. *Zoologica Scripta*, 40, 418–443.
<http://dx.doi.org/10.1111/j.1463-6409.2011.00479.x>
- Haddon, A.C. & Shackleton, A.M. (1891) A Revision of the British Actini. Part II: The Zoa. *Scientific Transactions of the Royal Dublin Society*, 4, 609–672.
- Holland, B.S., Dawson, M.N., Crow, G.L. & Hofmann, D.K. (2004) Global phylogeography of *Cassiopea* (Scyphozoa: Rhizostomeae): molecular evidence for cryptic species and multiple invasions of the Hawaiian Islands. *Marine Biology*, 145, 1119–1128.
<http://dx.doi.org/10.1007/s00227-004-1409-4>
- Knowlton, N. (2000) Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia*, 420, 73–90.
- Lamarck, J.B.P. (1801) Zoa. Zoantha. In: *Système des animaux vertébrés, ou Tableau général des classes, des ordres et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et leur organisation, et suivant l'arrangement établis dans les galeries du Muséum d'Hist. Naturelle, parmi leur dépouilles conservées; Précédé du discours d'ouverture du Cours de Zoologie, donn dans le Muséum National d'Histoire Naturelle l'an 8 de la République. Vol. 1*. Déterville, Paris, pp. 363.
- McMurrich, J.P. (1904) The Actiniae of the Plate Collection. *Zoologische Jahrbücher*, 6, 215–306.
- Ocaña, O. & Brito, A. (2004) A review of Gerardiidae (Anthozoa: Zoantharia) from the Macaronesian islands and the Mediterranean Sea with the description of a new species. *Revista de la Academia Canaria de Ciencias*, 15, 159–189.
- Ocaña, O., Brito, A., González, G. & Herrera, R. (2007) Additions in relation to Gerardiidae from the Macaronesian waters and the Mediterranean Sea (Anthozoa: Zoantharia). *Vieraea*, 35, 163–168.
- Ocaña, O., Brito, A., Núñez, J. & Bacallado, J.J. (1995) Redescriptión de *Gerardia savaglia* (Bertoloni, 1819) (Anthozoa: Zoantharia: Gerardiidae). *Vieraea*, 24, 153–164.
- Pax, F. (1910) Studien an westindischen Actinien. *Zoologische Jahrbücher*, 2, 157–330.

- Philipp, N.A. & Fautin, D.G. (2009) Three new species of shallow water, yellow zoanthids (Hexacorallia: Zoanthidea: Epizoanthidae) from southern California, USA, and southern Australia. *Zootaxa*, 2058, 53–61.
- Reimer, J.D. & Fujii, T. (2010) Four new species and one new genus of zoanthids (Cnidaria, Hexacorallia) from the Galápagos Islands. *ZooKeys*, 42, 1–36.
<http://dx.doi.org/10.3897/zookeys.42.378>
- Reimer, J.D., Hirano, S., Fujiwara, Y., Sinniger, F. & Maruyama, T. (2007) Morphological and molecular characterization of *Abyssanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a northwest Pacific methane cold seep. *Invertebrate Systematics*, 21, 255–262.
<http://dx.doi.org/10.1071/is06008>
- Reimer, J.D., Nonaka, M., Sinniger, F. & Iwase, F. (2008a) Morphological and molecular characterization of a new genus and new species of parazoanthid (Anthozoa: Hexacorallia: Zoantharia) associated with Japanese Red Coral. *Coral Reefs*, 27, 935–949.
<http://dx.doi.org/10.1007/s00338-008-0389-0>
- Reimer, J.D., Ono, S., Iwama, A., Takishita, K., Tsukahara, J. & Maruyama, T. (2006) Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan, with descriptions of two new species. *Zoological Science*, 23, 261–275.
<http://dx.doi.org/10.2108/zsj.23.261>
- Reimer, J.D., Sinniger, F. & Hickman, C.P. (2008b) Zoanthid diversity (Anthozoa: Hexacorallia) in the Galapagos Islands: a molecular examination. *Coral Reefs*, 27, 641–654.
<http://dx.doi.org/10.1007/s00338-008-0376-5>
- Rodríguez, E., Barbeitos, M., Daly, M., Gusmão, L.C. & Häussermann, V. (2012) Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). *Cladistics*, 28, 375–392.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00391.x>
- Ryland, J.S. & Lancaster, J.E. (2003) Revision of methods for separating species of *Protopalythoa* (Hexacorallia : Zoanthidea) in the tropical West Pacific. *Invertebrate Systematics*, 17, 407–428.
<http://dx.doi.org/10.1071/is02008>
- Sinniger, F. & Häussermann, V. (2009) Zoanthids (Cnidaria: Hexacorallia: Zoantharia) from shallow waters of the southern Chilean fjord region, with descriptions of a new genus and two new species. *Organisms, Diversity & Evolution*, 9, 23–36.
<http://dx.doi.org/10.1016/j.ode.2008.10.003>
- Sinniger, F., Montoya-Burgos, J.I., Chevaldonn, P. & Pawłowski, J. (2005) Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on the mitochondrial ribosome genes. *Marine Biology*, 147, 1121–1128.
<http://dx.doi.org/10.1007/s00227-005-0016-3>
- Sinniger, F., Reimer, J.D. & Pawłowski, J. (2008) Potential of DNA sequences to identify zoanthids (Cnidaria: Zoantharia). *Zoological Science*, 25, 1253–1260.
<http://dx.doi.org/10.2108/zsj.25.1253>
- Sinniger, F., Reimer, J.D. & Pawłowski, J. (2010) The Parazoanthidae (Hexacorallia: Zoantharia) DNA taxonomy: description of two new genera. *Marine Biodiversity*, 40, 57–70.
<http://dx.doi.org/10.1007/s12526-009-0034-3>
- Stampar, S.N., Maronna, M.M., Vermeij, M.J.A., Silveira, F.L.d. & Morandini, A.C. (2012) Evolutionary diversification of banded tube-dwelling anemones (Cnidaria; Ceriantharia; Isarachnanthus) in the Atlantic Ocean. *PLoS ONE*, 7, e41091.
<http://dx.doi.org/10.1371/journal.pone.0041091>
- Swain, T.D. (2009a) *Isozoanthus antumbrosus*, a new species of zoanthid (Cnidaria: Anthozoa: Zoanthidea) symbiotic with Hydrozoa from the Caribbean, with a key to hydroid and sponge-symbiotic zoanthid species. *Zootaxa*, 2051, 41–48.
- Swain, T.D. (2009b) Phylogeny-based species delimitations and the evolution of host associations in symbiotic zoanthids (Anthozoa, Zoanthidea) of the wider Caribbean region. *Zoological Journal of the Linnean Society*, 156, 223–238.
<http://dx.doi.org/10.1111/j.1096-3642.2008.00513.x>
- Swain, T.D. (2010) Evolutionary transitions in symbioses: dramatic reductions in bathymetric and geographic ranges of Zoanthidea coincide with loss of symbioses with invertebrates. *Molecular Ecology*, 19, 2587–2598.
<http://dx.doi.org/10.1111/j.1365-294x.2010.04672.x>
- Swain, T.D. (2012) Context-dependent effects of symbiosis: Zoanthidea colonization generally improves Demospongiae condition in native habitats. *Marine Biology*, 159, 1429–1438.
<http://dx.doi.org/10.1007/s00227-012-1919-4>
- Swain, T.D. & Wulff, J.L. (2007) Diversity and specificity of Caribbean sponge-zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher-order systematics. *Biological Journal of the Linnean Society*, 92, 695–711.
<http://dx.doi.org/10.1111/j.1095-8312.2007.00861.x>
- Vogler, A.P. & Monaghan, M.T. (2007) Recent advances in DNA taxonomy. *Journal of zoological systematics and evolutionary research*, 45, 1–10.
<http://dx.doi.org/10.1111/j.1439-0469.2006.00384.x>
- Wood, R.L. (1957) *Identification and microanatomical study of a new species of Epizoanthus (Zoanthidea)*. Ph.D. dissertation, University of Washington, 82 pp.