BioOne COMPLETE

Phylogeny and Phylogeography of the Geoduck Panopea (Bivalvia: Hiatellidae)

Authors: Leyva-Valencia, Ignacio, Cruz-Hernández, Pedro, Álvarez-Castañeda, Sergio T., Rojas-Posadas, Delia I., Correa-Ramírez, Miguel M., et al.

Source: Journal of Shellfish Research, 34(1) : 11-20

Published By: National Shellfisheries Association

URL: https://doi.org/10.2983/035.034.0104

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Shellfish Research, Vol. 34, No. 1, 11–20, 2015.

PHYLOGENY AND PHYLOGEOGRAPHY OF THE GEODUCK *PANOPEA* (BIVALVIA: HIATELLIDAE)

IGNACIO LEYVA-VALENCIA,[1] PEDRO CRUZ-HERNÁNDEZ,[1] SERGIO T. ÁLVAREZ-CASTAÑEDA,[1]* DELIA I. ROJAS-POSADAS,[1] MIGUEL M. CORREA-RAMÍREZ,[2] BRENT VADOPALAS[3] AND DANIEL B. LLUCH-COTA[1]

[1]*Centro de Investigaciones Biológicas del Noroeste, Instituto Politécnico Nacional No. 195, Col. Playa Palo de Santa Rita Sur, Apdo. Postal 128, La Paz, B.C.S. 23096, México;* [2]*Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango, Instituto Politécnico Nacional, Calle Sigma 119 Fracc. 20 de Noviembre II Durango, Durango 34220, México;* [3]*School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98105*

ABSTRACT Geoducks (*Panopea* spp.) are recognized as one of the longest-lived and largest burrowing bivalves. Five extant species support commercial fisheries in different countries, yet their phylogenetic relationships are unclear. Phylogenetic analyses using cytochrome oxidase c subunit I, 28S, and 18S partial sequences on five *Panopea* spp. were performed to understand existing biogeography and to unravel taxonomic uncertainties in the genus. The cytochrome oxidase c subunit I sequences revealed two major clades. The first clade included *Panopea zelandica* as a sister taxon of *Panopea globosa*; the second clade included *Panopea abbreviata*, *Panopea generosa*, and *Panopea japonica*. Contrary to expectations, geographically proximate species (*P. generosa* and *P. globosa*) belong to different lineages, and geographically distant species (*P. generosa* and *P. japonica*) showed lower genetic distance at nuclear loci, suggesting that *P. generosa* could be related to the common ancestor of *P. japonica.* Divergence values for mitochondrial DNA, however, indicated that *P. japonica* might be regarded as a distinct species. Analyses using both nuclear genes suggest that the ancestral species of *P. globosa* may have been broadly distributed through the Pacific coast to South America.

KEY WORDS: *Panopea*, geoduck, phylogeny, phylogeography, evolution, molecular markers

INTRODUCTION

Clams of the genus *Panopea* comprise the largest and longest-lived of all deep-burrowing bivalves; *Panopea generosa* can live up to 168 y (Bureau et al. 2002). Specimens are found in intertidal and subtidal marine and estuarine waters, typically buried ~1 m below the substratum surface in sandy or mud sediments (Feldman et al. 2004). The genus *Panopea* is characterized as having a hinge with one small cardinal tooth in each valve (Cox et al. 1969), and a fully fused siphon and mantle. Other taxonomic traits, such as the shape and depth of the pallial sinus are variable among species (Yonge 1971). The genus *Panopea* was a cosmopolitan genus during the Triassic, and approximately 150 fossil species have been described. Currently only about 10 living species are found in worldwide temperate to subtropical seas and only five species are the subject of commercial fishing activities (Yonge 1971) (Table 1, Fig. 1).

The taxonomy, phylogeny, evolutionary history, and speciation processes of these clams are poorly defined. For example, *Panopea generosa* was incorrectly synonymized with the extinct *Panopea abrupta* for almost 25 y (Vadopalas et al. 2010). The clam *Panopea japonica* from Japan and South Korea has been variously considered as a synonym species of *P. generosa*—one of the 85 bivalve species distributed on the American and Asian sides of the Pacific Ocean, or as closely related species (Coan et al. 2000). Similarly, because of the geographic proximity (~700 km) *Panopea globosa* was described as a variety of *P. generosa*, endemic to the northern Gulf of California (Dall 1898). In addition, the speciation of *P. globosa* was thought to be associated with the formation of the Gulf of California (Hertlein & Emerson 1956). Fossils of the Latrania Formation, however, indicate that *P. globosa* lived in the Imperial Sea, California, during the late Miocene (Scott Rugh, Brian F. Smith and Associates, pers. comm., 2011). In addition, geometric morphometric and genetic analyses reveal the presence of *P. globosa* on the western shore of the Baja Peninsula (Bahia Magdalena) in the Pacific Ocean (Leyva-Valencia 2012, Leyva-Valencia et al. 2012, Suárez-Moo et al. 2012). The fossil *Panopea taeniata,* found near Bahia Magdalena and described by Dall (1918), was also long considered a subspecies of *P. generosa*. Recent morphometric analyses, however, revealed that *P. taeniata* is a fossil morphotype of *P. globosa*, changing our understanding of the ancient biogeography of *P. globosa* from the Miocene to the Pleistocene along California and the Baja California Peninsula (Leyva-Valencia et al. 2013).

The biogeographic history of the *Panopea* genus in the southern circum-Pacific is likewise incomplete. Two extant species of *Panopea* occur in New Zealand; *Panopea zelandica* is distinguished from *Panopea smithae* by morphological differences such as a more shallow pallial sinus and a more squarely truncated posterior end, and inhabiting shallower depths (Beu & Maxwell 1990), and fossils of *Panopea worthingtoni* have been found in Cretaceous sediments in both New Zealand and Antarctica. Fossils of Antarctic *Panopea philippii* and *Panopea andreae* have a close morphological affinity with the extant South American species *Panopea abbreviata* (Zinsmeister 1984, Studencka 1991). These observations suggest a close relationship among *Panopea* spp. from New Zealand, Antarctica, and South America.

Phylogenetic studies that include the genus *Panopea* are scarce (Adamkewicz et al. 1997, Taylor et al. 2007). A recent

*Corresponding author. E-mail: sticul@cibnor.mx
DOI: 10.2983/035.034.0104

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1.

Living species of *Panopea* recognized around the world.

Species	Authority	Distribution range	Citation
Panopea glycimeris	von Born, 1778	Northwestern Spain; Mediterranean Sea to South Africa	Kensley (1974), Rolán (1983), Scotti et al. 2011
Panopea australis	Sowerby, 1833	Southern and eastern Australia	Grove (2011)
Panopea zelandica	Quoy and Gaimard, 1835	New Zealand	Breen et al. (1991)
Panopea smithae	Powell, 1950	New Zealand	Breen et al. (1991)
Panopea abbreviata	Valenciennes, 1839	Southwestern Argentina	Morsán & Ciocco (2004)
Panopea japonica	Adams, 1850	Japan Sea	Coan et al. (2000)
Panopea bitruncata	Conrad, 1872	North Carolina to the Gulf of Mexico	Robertson (1963), John Slapcinsky (FLMNH pers. comm.)
Panopea generosa	Gould, 1850	Southern Alaska to Mexico	Goodwin & Pease (1989), Coan et al. (2000), Cadien & Lovell (2008)
Panopea globosa	Dall, 1898	Gulf of California, Mexico	Aragón-Noriega et al. (2007), Rocha-Olivares et al. (2010)

FLMNH, Florida Museum of Natural History.

phylogenetic study of three species of *Panopea* revealed genetic and morphological variation between *Panopea globosa* from the Gulf of California and *Panopea generosa* from the Pacific coast of Baja California (Rocha-Olivares et al. 2010). The authors of these studies concluded that these species do not share a recent ancestor, and proposed trans-Pacific dispersal or vicariance followed by subsequent reproductive isolation between *Panopea japonica* and *P. generosa* lineages as possible speciation mechanisms.

Genes with lower mutational rates such as 18S and 28S are useful for characterizing relationships between distant taxa and old divergence processes in bivalves (Adamkewicz et al. 1997, Winnepenninckx et al. 1998, Taylor et al. 2007), although cytochrome oxidase c subunit I (CO1) is used frequently to distinguish differences between close species. The goals of the current study were to determine the phylogenetic relationships among commercially fished *Panopea* spp. using molecular markers to infer ancient (18S and 28S) and recent (CO1)

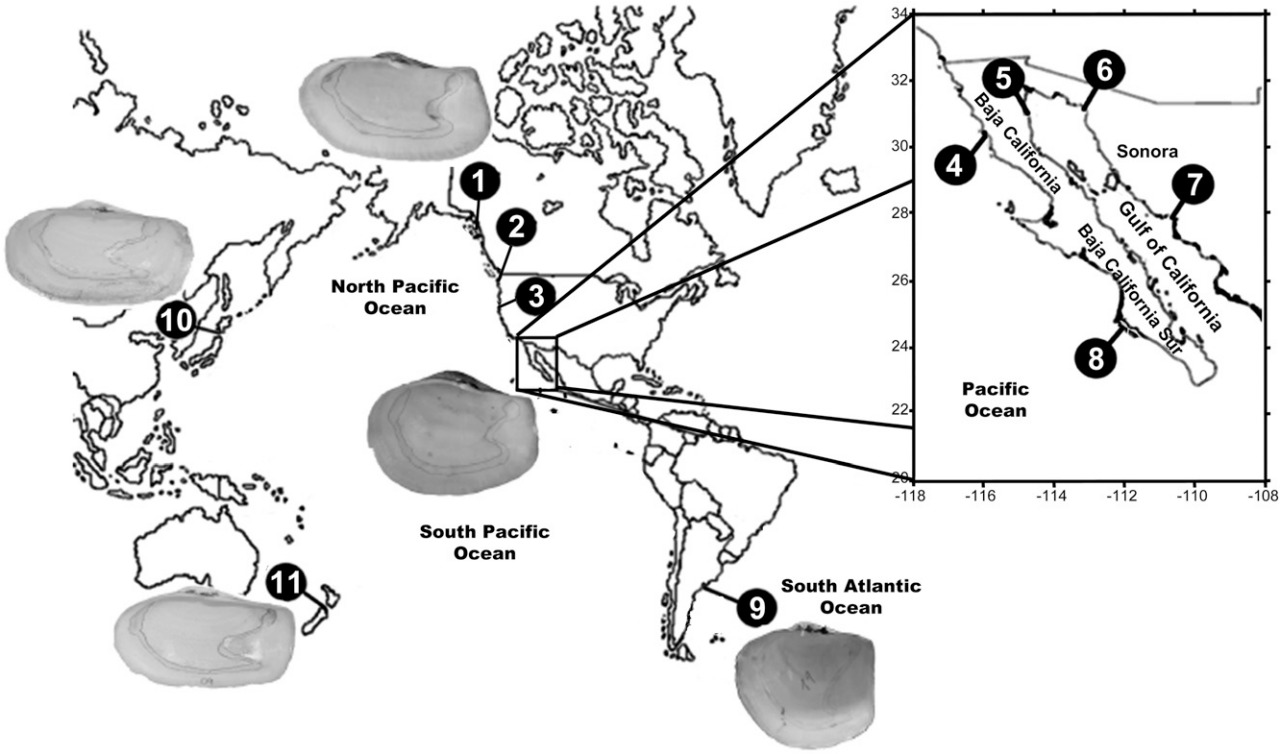


Figure 1. Sampling locales of five geoduck species in the current study.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

divergences, to propose a hypothesis encompassing both their historical distribution and extant biogeography, and to begin to unravel the taxonomic uncertainties in the genus *Panopea*.

MATERIALS AND METHODS

Specimens

A total of 52 specimens from five species in the genus *Panopea* (Fig. 1) were used to obtain individual sequences of the mitochondrial (mtDNA) gene cytochrome oxidase c subunit I (CO1), and the nuclear (nDNA) genes 18S and 28S.

GenBank sequences of *Hiatella arctica* Linnaeus, 1767 (sister genus to *Panopea,* accession no. NC008451, AM774511, AM779685) and two species in the subclass Heterodonta (*Mya arenaria* Lamarck, 1809, accession no. AF120668, AF120560, FM999792; and *Thyasira sarsi* Philippi, 1845, accession no. AM706509, AM774485, AM779659) were selected as out-groups.

DNA Amplification and Sequencing

Genomic DNA samples were obtained from ethanol-preserved siphon tissues using DNeasy Tissue Kits (Qiagen Inc.). From every specimen, a fragment of each gene was amplified with specific primers (CO1, LCO1490-HCO1498 [Folmer et al. 1994]; 28S, 28MF-28MR [Taylor et al. 2007]; and 18S, 18SF-18SR [Hedin & Maddison 2001]), using polymerase chain reactions (PCR) in a total volume of 50 µL with 2 U Platinum Taq polymerase (Invitrogen Inc.) 100 ng template DNA, 1 µM of each primer, 200 µM of each dNTP, 1× PCR buffer, and 2 mM $MgCl_2$. The PCR cycles were carried out in an iCycler PCR System (Bio-Rad Laboratories, CA) under the following conditions: initial denaturation for 5 min at 94°C, followed by 40 cycles of 45 sec at 94°C, 1 min annealing temperature (45°C for CO1; 53°C for 28S and 18S) and 1 min at 72°C, with a final 10-min extension at 72°C.

The length and quality of PCR products were visualized in 1.5% agarose gels stained with ethidium bromide. Purification and sequencing was performed in both directions using the Macrogen sequencing service (Macrogen, Inc. Korea).

Phylogenetic Analyses

The data were quality filtered by excluding individuals with less than three high-quality gene sequences from downstream analyses. The complementary DNA sequence strands were edited manually, assembled, and aligned using the software Sequencher 4.10.1 (Gene Codes, Ann Arbor, MI) using default parameters, and were saved in Nexus format for phylogenetic analyses. The program DnaSP (Librado & Rosas 2009) was used to identify the haplotypes for each gene.

To test for saturation, transitions, and transversions, uncorrected p distances were computed in DAMBE 5.2.18 to verify that the sequences had not experienced enough substitution saturation to obscure phylogenetic relationships (Xia & Lemey 2009). To compare the mutation rates among lineages, Tajima's relative rate test was performed in MEGA 5.03 (Tamura et al. 2011).

The phylogenetic analysis was carried out by using partitioned and complete sequences of each gene (586 bp for CO1, 565 bp for 28S, and 450 bp for 18S), and by using the concatenated set of 1,651 bp. The haplotypes were analyzed with maximum parsimony, Bayesian inference, and maximum likelihood (ML) to estimate tree topology. Maximum parsimony analyses were executed in PAUP 4.10b* (Swofford 2003); node support was assessed via 1,000 bootstrap replicates.

The nucleotide substitution models used in the analyses were chosen for each partition, individual genes, and for the concatenated data set. To determine the best-fit model for Bayesian inference and ML runs, the Akaike information criterion was used as implemented in Modeltest 3.06 (Posada & Crandall 2001, Posada 2009). The ML analysis was performed by a heuristic search with TBR branch swapping and 100 random additions of taxa, performed in PAUP 4.10b*. Node support was obtained by 1,000 bootstrap replicates (Swofford et al. 2001).

Bayesian inference was explored using the program MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003) using four Markov chains and 5,000,000 generations sampled every 100 generations. The ML analyses were carried out using GARLI 0.951 (Zwickl 2006), RAxML GUI v1.1 (Silvestro & Michalk 2011), and Phylogeny.fr (Dereeper et al. 2008) to compare results. Phylogenetic trees were visualized using the program Treeview X (Page 1996).

RESULTS

A total of 120 sequences from five species of *Panopea* (Table 2) were obtained and 35 haplotypes for all analyzed genes were identified. At CO1, 17 haplotypes with 217 informative sites were found. At 28S, 14 haplotypes with 97 informative sites were obtained, whereas at 18S, only four haplotypes with 258 informative sites were found. The concatenated data set of the mtDNA and nDNA genes contained 23 haplotypes with 751 informative sites.

The best evolutionary model for the concatenated, CO1, and 28S genes was the generalized time-reversible model plus gamma. The Kimura (1980) model was superior for 18S. The parameters for the concatenated data were substitution number = 6; base frequencies of A = 0.2114, C = 0.2382, G = 0.2817, and T = 0.2685; and gamma distribution shape parameter = 0.5808.

Within the genus *Panopea,* no saturation signal was observed for individual or concatenated sequences. The saturation by substitution index (0.146) was significantly less than the critical value (0.783) for the concatenated analyses (Xia & Lemey 2009).

The greatest genetic divergence at CO1 was between *Panopea globosa* and *Panopea abbreviata* (18.2%), whereas the lowest divergence was between *Panopea zelandica* and *P. abbreviata* (10%). A divergence of less than 5% was determined between *P. zelandica* and *P. abbreviata* with 28S, whereas the lowest divergence (0.3%) was observed between the northern hemisphere geoducks *Panopea generosa* and *Panopea japonica.* In contrast, 18S revealed smaller differences (1.3%) between *P. zelandica* and its congeners. The clams *P. globosa* and *P. abbreviata* still had the lowest divergence (0.2%) and even shared one haplotype; *P. generosa* and *P. japonica* also shared one haplotype (Table 3).

Phylogenetic Analyses

Maximum parsimony, Bayesian inference, and ML analyses revealed two major clades using both concatenated and individual genes. The concatenated tree (Fig. 2A) showed a polytomy among *Panopea generosa–Panopea japonica–Panopea*

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2.

Haplotypes identified within the five species of the genus *Panopea* from Bahia Magdalena, Puerto Peñasco, Guaymas, San Felipe, Gulf of San Matias, New Zealand, Ensenada, California, Alaska, Washington, and Japan for mitochondrial (CO1) and nuclear genes (28S and 18S).

Species	Locality	Sample	Voucher ID	Haplotype CO1	GenBank accession no.	Haplotype 28S rRNA	GenBank accession no.	Haplotype 18S rRNA	GenBank accession no.	Concatenated haplotype
Panopea globosa	BM	**BM1**	1	HCO1	JQ071876	**H286**	**JQ071883**	H181	JQ071895	HCN10
P. globosa	BM	**BM2**	2	**HCO9**	**JQ071868**	**H287**	**JQ071886**	H181	JQ071895	HCN11
P. globosa	BM	**BM3**	3	HCO1	JQ071876	**H289**	**JQ071882**	H181	JQ071895	HCN13
P. globosa	BM	**BM4**	4	HCO1	JQ071876	**H288**	**JQ071884**	**H181**	**JQ071895**	HCN12
P. globosa	BM	BM5	5	HCO1	JQ071876	H286	JQ071883	H181	JQ071895	HCN10
P. globosa	PP	**PP1**	8	**HCO1**	**JQ071876**	**H282**	**JQ071891**	H181	JQ071895	HCN5
P. globosa	PP	**PP2**	9	**HCO3**	**JQ071878**	**H285**	**JQ071885**	H181	JQ071895	HCN9
P. globosa	PP	**PP3**	10	**HCO5**	**JQ071872**	H284	JQ071889	H181	JQ071895	HCN8
P. globosa	PP	PP4	11	HCO1	JQ071876	H282	JQ071891	H181	JQ071895	HCN5
P. globosa	PP	**PP5**	12	**HCO7**	**JQ071862**	H282	JQ071891	H181	JQ071895	HCN3
P. globosa	GU	**GU1**	13	**HCO6**	**JQ071870**	**H281**	**JQ071892**	H181	JQ071895	HCN2
P. globosa	GU	GU2	14	HCO1	**JQ071876**	H281	**JQ071892**	H181	JQ071895	HCN1
P. globosa	GU	GU3	15	HCO1	JQ071876	H281	JQ071892	H181	JQ071895	HCN1
P. globosa	GU	**GU4**	16	**HCO1**	**JQ071876**	H281	JQ071892	H181	JQ071895	HCN1
P. globosa	GU	GU5	17	HCO8	JQ071865	H281	JQ071892	H181	JQ071895	HCN4
P. globosa	SF	**SF3**	6	**HCO4**	**JQ071871**	**H283**	**JQ071890**	H182	JQ071897	HCN6
P. globosa	SF	**SF5**	7	**HCO2**	**JQ071877**	**H284**	**JQ071889**	**H182***	**JQ071897**	HCN7
Panopea abbreviata	GSM	**Pabb1**	36	**HCO16**	**JQ071864**	**H2813**	**JQ071887**	**H182***	**JQ071898**	HCN23
P. abbreviata	GSM	**Pabb2**	37	**HCO17**	**JQ071866**	H2813	JQ071887	H182	JQ071898	HCN22
P. abbreviata	GSM	Pabb3	38	HCO17	JQ071866	H2813	JQ071887	H182	JQ071898	HCN22
P. abbreviata	GSM	Pabb4	39	HCO16	JQ071864	H2813	JQ071887	H182	JQ071898	HCN23
P. abbreviata	GSM	Pabb5	40	HCO16	JQ071864	H2813	JQ071887	H182	JQ071898	HCN23
Panopea zelandica	NZ	**NZel3**	18	**HCO10**	**JQ071875**	**H2814**	**JQ071888**	**H183**	**JQ071896**	HCN14
P. zelandica	NZ	NZel4	19	HCO10	JQ071875	H2814	JQ071888	H183	JQ071896	HCN14
P. zelandica	NZ	NZel5	20	HCO10	JQ071875	H2814	JQ071888	H183	JQ071896	HCN14
Panopea generosa	ENS	Ens1	21	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN15
P. generosa	ENS	Ens2	22	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN15
P. generosa	ENS	Ens3	23	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN15
P. generosa	ENS	Ens4	24	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN15
P. generosa	CAL	Cal1	25	HCO12	JQ071869	H2810	JQ071879	H184	JQ071893	HCN21
P. generosa	CAL	**Cal2**	26	HCO11	JQ071867	**H2810**	**JQ071879**	H184	JQ071893	HCN15
P. generosa	ALA	Ala77	27	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN15
P. generosa	ALA	Ala80	28	HCO11	JQ071867	H2811	JQ071880	H184	JQ071893	HCN15
P. generosa	ALA	**Ala82**	29	**HCO13**	**JQ071863**	H2811	JQ071880	H184	JQ071893	HCN17
P. generosa	ALA	Ala83	30	HCO11	JQ071867	H2810	JQ071879	H184	JQ071893	HCN17
P. generosa	WASH	**Wash97**	31	**HCO12**	**JQ071869**	**H2810**	**JQ071883**	H184	JQ071893	HCN16
P. generosa	WASH	**Wash101**	32	**HCO11**	**JQ071867**	**H2811**	**JQ071880**	**H184†**	**JQ071893**	HCN18
Panopea japonica	JAP	**Jap1**	33	**HCO14**	**JQ071873**	**H2812**	**JQ071881**	**H184†**	**JQ071894**	HCN19
P. japonica	JAP	Jap2	34	HCO14	JQ071873	H2812	JQ071881	H184	JQ071894	HCN19
P. japonica	JAP	**Jap3**	35	**HCO15**	**JQ071874**	H2812	JQ071881	H184	JQ071894	HCN20

continued on next page

TABLE 2.
continued.

Species	Locality	Sample	Voucher ID	Haplotype CO1	GenBank accession no.	Haplotype 28S rRNA	GenBank accession no.	Haplotype 18S rRNA	GenBank accession no.	Concatenated haplotype
Hiatella arctica	—	—	—	HCO18	NC008451	H2815	AM779685	H185	AM774511	—
Mya arenaria	—	—	—	HCO19	AF120668	H2816	FM999792	H186	AF120560	—
Thyasira sarsi	—	—	—	HCO20	AM706509	H2817	AM779659	H187	AM774485	—

ALA, Alaska; BM, Bahia Magdalena; CAL, California; ENS, Ensenada; GSM, Gulf of San Matias; GU, Guaymas; JAP, Japan; NZ, New Zealand; PP, Puerto Peñasco; SF, San Felipe; WASH, Washington. Samples in bold type were used to characterize the haplotypes (bold). * One shared haplotype between *Panopea globosa* and *Panopea abbreviata*. † One shared haplotype between *Panopea generosa* and *Panopea japonica*.

abbreviata, placing *Panopea globosa* and *Panopea zelandica* in one major clade (C1), and *P. generosa*, *P. japonica*, and *P. abbreviata* in a second clade (C2). Similar topology was present for the CO1 tree (Fig. 2B) although with this gene, *P. zelandica* was placed as the basal species of the genus. On the 28S tree (Fig. 2C), *P. zelandica* was included with *P. globosa* and a polytomy is shown among *P. generosa, P. japonica*, and *P. abbreviata*, whereas the 18S tree (Fig. 2D) showed a basal polytomy among *P. globosa*, *P. zelandica*, and the others. As expected, we found that the relative rates of evolution of the *Panopea* genes were 18S rRNA < 28S rRNA < CO1.

DISCUSSION

Contrary to expectations based on geographic proximity, *Panopea generosa* and *Panopea globosa* belong to distinct lineages. In addition, the geographically distant species *P. generosa* and *Panopea japonica* were included in the same clade, and showed lower divergence at both mitochondrial and nuclear loci, suggesting a close evolutionary relationship.

The results from analyzing concatenated and individual genes provide evidence of two principal lineages and reveal surprising phylogenetic relationships within the *Panopea* genus. Based on the hypothesis of parapatric speciation between *Panopea generosa* and *Panopea globosa*, nuclear genes were used to provide molecular evidence of ancient phylogeny between them, and included other species of the genus for a broader comparison.

Phylogenetic analyses reveal that the clade containing *Panopea abbreviata, Panopea generosa*, and *Panopea japonica* is consistent among the concatenated mtDNA and nDNA sequences. The concatenated tree also suggests that *P. abbreviata* and *Panopea zelandica* may share a common ancestor. The individual genes, however, did not yield sufficient information to resolve the phylogenetic relationships among boreal and austral congeners. The relationships between *Panopea zelandica* and congeners were dependent on the gene analyzed, whereas *P. abbreviata* appears to have a close phylogenetic relationship with temperate species from the northern hemisphere at both 28S and CO1. Differences among tree topologies may be the result of distinct mutation rates, although other variables such as the evolutionary history of each gene and the phylogenetic algorithms used can influence results.

The species *Panopea* was a cosmopolitan group during the Triassic period. For example, species such as *Panopea glycimeris* were widely distributed in the past (Kensley 1974). Extant aggregations of this species now occur from northern Spain to South Africa (Kensley 1976, Rolán 1983, Thomsen et al. 2009, Scotti et al. 2011). Faunal interchange and the speciation process of *Panopea zelandica* and *Panopea abbreviata* may have been favored by geological and climatic events. Before the breakup of the Gondwana landmass ~55 million y ago, New Zealand began separating from Antarctica. During this time, Australian species such as *Panopea worthingtoni*, *Panopea andreae*, and *Panopea philippii* occurred in New Zealand, Antarctica, and South America. The progressive movement of the southern continents during the Early Cenozoic resulted in the breakup of the Weddellian Province into smaller, discrete biogeographic units; the distribution of paleoaustral molluscs changed as a result of

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 3.

Divergence percentages within and between *Panopea* spp. at mitochondrial and nuclear genes using the Kimura two-parameter model.

	Cytochrome oxidase c subunit I				
Species	***Panopea generosa***	***Panopea globosa***	***Panopea abbreviata***	***Panopea zelandica***	***Panopea japonica***
P. generosa	0.16				
P. globosa	17.7	0.4			
P. abbreviata	12.6	18.2	0.1		
P. zelandica	12.6	15.1	10.0	–	
P. japonica	10.9	17.0	11.6	10.0	0.3
28S rRNA					
P. generosa	0.3				
P. globosa	3.1	0.4			
P. abbreviata	2.1	3.8	–		
P. zelandica	3.8	4.0	4.6	–	
P. japonica	0.3	3.1	2.1	3.7	–
18S rRNA					
P. generosa	–				
P. globosa	2.6	–			
P. abbreviata	2.6	0.2	–		
P. zelandica	1.3	1.3	1.3	–	
P. japonica	–	2.6	2.6	1.3	–

–, No observed genetic divergence.

the separation and isolation of New Zealand from Antarctica (Zinsmeister 1982).

Past faunal interchange between South America and New Zealand is exemplified by *Xymene* and *Antimelatoma*. These genera originated in Patagonia and dispersed to New Zealand three different times: during the Oligocene–Early Miocene, Late Miocene–Pliocene, and Pleistocene–Recent, whereas species of the genera *Crosseola*, *Trichosirius*, *Ataxocerithium*, *Penion*, *Xymenella*, *Zeacuminia*, *Austromitra*, and *Eoturris* dispersed from New Zealand to Patagonia during the Early Miocene (Del Río 2004). Before the Tasmanian Seaway and Drake Passage were open and the Isthmus of Panama was closed, ancestors of *Panopea zelandica* and *Panopea abbreviata* may have been broadly distributed along the southern Pacific Ocean.

During the Paleogene (23–65 million y ago), global temperatures may have been 10°C warmer than the current temperature (Lyle et al. 2008), making species flow possible across the Arctic. Modeling studies indicate that ocean circulation during the Cenozoic was similar to the modern geographic distribution of circulation gyres and upwelling systems (Thomas et al. 2006, Lyle et al. 2008, Ogasawara et al. 2008). A close relationship between extant species from the northern hemisphere is consistent with the hypothesis of a correlation between the fauna of northwestern Japan and southern California during the Late Miocene (Otuka 1934), as well as the presence of *Panopea generosa* fossils in Miocene (Nomura & Niino 1932, Nomura 1935), Pliocene (Yokoyama 1923, Yokoyama 1925), and Pleistocene (Yokoyama 1922) sediments of Japan. Based on the geographic isolation hypothesis, Matsubara (2011) proposed that *Panopea japonica* has been a distinct species from *P. generosa* since the Early Miocene, and suggested performing morphology and molecular phylogeny studies to resolve this question. The question of synonymy between *P. generosa* and *P. japonica* is a recurrent topic (Coan et al. 2000, Vadopalas et al. 2010).

At CO1, a genetic divergence was observed between *Panopea generosa* and *Panopea japonica* of approximately 11%. Divergence values between 10% and 22% at CO1 are considered sufficient to identify separate bivalve species (Therriault et al. 2002, Therriault et al. 2004, Xue et al. 2012), whereas values around of 0.6%–2.0% are typically observed at the intraspecific level (Baldwin et al. 1996, Arnaud et al. 2000, Xue et al. 2012). Thus, the results of the current study are in accord with the hypothesis of Matsubara (2011) that *P. generosa* and *P. japonica* are distinct species. However, both nuclear genes revealed low genetic divergence between *P. generosa* and *P. japonica*, in accord with the slight 18S gene divergence between *P. generosa* and *P. japonica* reported by Rocha-Olivares et al. (2010). Taken together, the results of the current study suggest ancient gene flow between these boreal species. After carefully ruling out contamination or error through repetition of the analyses, the shared 18S haplotype between *P. generosa* and *P. japonica* also supports this hypothesis.

The fossil data reveal that despite the close geographic proximity of *Panopea globosa* and *Panopea generosa*, they were distinct species prior to the formation of the Gulf of California. The fossil record also indicates that during the Late Miocene to Pleistocene (~10–0.12 million y ago), *P. generosa* and *P. globosa* coexisted in the Salton Trough, California (N. Scott-Rugh, SDNHM, pers. comm., 2010) and in the upper Gulf of California (Judith Terry-Smith, USNMH, pers. comm., 2011). The genetic results from the current study indicate that *P. generosa* is not the ancestral species of *P. globosa*, and that they are from distinct basal lineages, given the 17% divergence at CO1. Results similar to these were obtained using ITS and 18S rDNA sequences (Rocha–Olivares et al. 2010). Because of the current lack of knowledge of *Panopea* biogeography, the possibility cannot be excluded that extant aggregations of both species occur in sympatry along the Baja Peninsula.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

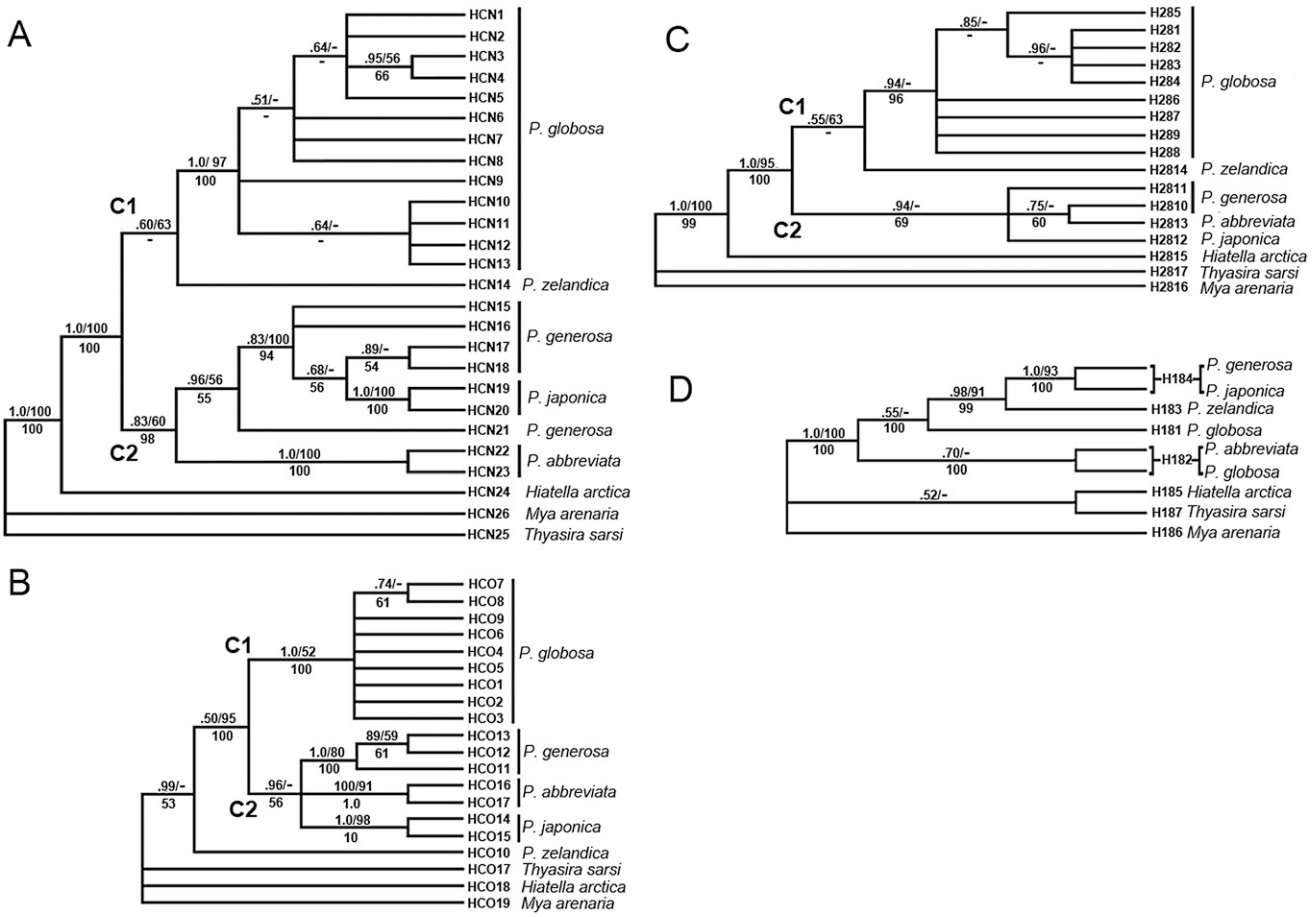


Figure 2. Phylogenetic reconstruction of mitochondrial and nuclear genes between five *Panopea* species. (A) Concatenated sequences. (B) CO1. (C) 28S. (D) 18S. Values over nodes indicate Bayesian interference/maximum likelihood branch support; under nodes, maximum parsimony bootstrap values. Names refer to the haplotype number.

Knowledge of the historical geographic distribution of *Panopea globosa* is unknown. However, *P. globosa* fossils collected from Miocene (SDNHM 97243) Pliocene (SDNHM 12085, SDNHM 12104), and Pleistocene (USNM11SJ1, USNM86SJ10, and SDNHM2555-108) sediments in southern California, the Gulf of California, and along the Pacific coast of southern Baja California indicate that *P. globosa* had a wide geographic distribution before the last glacial period. Valves of *P. globosa* have also been found in Nayarit, Mexico (SBMNH 135157) and Tumbes, Peru (SBMNH 149357); however, there are no known extant aggregations at these locales. Other bivalves, such as *Atrina maura* and *Argopecten ventricosus*, have a distribution range from the Baja Peninsula to Peru (Keen 1971).

Both the genetic affinity between *Panopea globosa* and *Panopea zelandica* at 28S, and the shared 18S haplotype between *P. globosa* and *Panopea abbreviata* suggest the possibility of a wide-range, warm-water *Panopea* clade distinct from a cold-water clade. As Smith (1991) proposed for several bivalve species, it is speculated that the ancestral species of *P. globosa* dispersed from the western Atlantic to the eastern Pacific by seaways across southern Costa Rica and Panama.

Gene flow between eastern Pacific and western Atlantic fauna has been proposed previously (e.g., Rathbun 1918, Marko 2005, Poupin et al. 2005). Before the formation of the Isthmus of Panama, the Atlantic Ocean was a considerably narrower ocean basin than today, and current-mediated larval transport across it may have been feasible during the life span of marine planktonic larvae (Woodring 1982, Schubart et al. 2005). The marine fauna interchange between the Caribbean and the eastern Pacific may have been influenced not only by the closure of the Isthmus of Panama, but also by climate shifts in the Arctic region and the concomitant changes to current systems of the Pacific and Atlantic oceans (Ogasawara et al. 2008).

The only subtropical species known in the genus *Panopea*—*Panopea globosa*—had the greatest number of autapomorphies at CO1 (49), whereas *Panopea generosa* and *Panopea japonica* had only 22 at the same gene. This difference between tropical and temperate species might be related to environmental adaptations and life cycle differences. Studies of reproductive biology indicate that *P. globosa* is well adapted to warm temperatures; their reproductive cycle commences in late summer, when sea surface temperatures reach 28°C, and spawning occurs during winter months, when temperatures are close to 20°C (Aragón-Noriega et al. 2007). Conversely, *P. generosa* spawning peaks in late spring and early summer at temperatures closer to 12°C (Goodwin & Pease 1989, Aragón-Noriega et al. 2007, Arámbula-Pujol et al. 2008). The maximum age recorded

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

for *P. globosa* is 47 y (González-Peláez et al. 2013) whereas *P. generosa* can live as long as 168 y (Bureau et al. 2002). Nucleotide substitution rates can be correlated with species body size, metabolic rate, generation time, and environmental temperature (Gillooly et al. 2005, Bromham 2009). Thomas et al. (2010) observed that invertebrate species with shorter generation times exhibited greater substitution rates. Adaptation to warmer temperatures and the shorter generation time for *P. globosa* may likewise be correlated with a greater number of private mutations than its congeners.

Both morphology and genetics have been used to elucidate the taxonomy and phylogeny of bivalves (Giribet & Wheeler 2002, Giribet & Distel 2003, Kappner & Bieler 2006, Owada 2007). Although the general *Panopea* morphotype is a successful adaptation given that no significant morphological changes are evident during the past 50,000,000 y, species in the genus *Panopea* can be readily differentiated using shell morphological characteristics (Leyva-Valencia 2012, Leyva-Valencia et al. 2012, Leyva-Valencia et al. 2013). The current results indicate that *Panopea* congeners can also be discriminated via high interspecific genetic variation.

Based on the results of this study, it is hypothesized that the early evolution of *Panopea* occurred in two main lineages. One lineage, associated with colder waters, includes *Panopea abbreviata*, *Panopea generosa*, and *Panopea japonica*. The second lineage, associated with warmer waters, includes the subtropical species *Panopea globosa* and the geographically distant species *Panopea zelandica*.

It is inferred that the ancestor of *Panopea globosa* was widely distributed during the Middle Miocene, when the Salton Sea was connected with the Pacific Ocean the proto-Gulf of California opened and the Baja California Peninsula began its separation from mainland Mexico (Helenes & Carreño 1999). This hypothesis will be tested in future studies to help elucidate the evolution of the genus *Panopea*.

ACKNOWLEDGMENTS

The authors thank Sergio González (CIBNOR) and Sergio Pérez (CEDO) for providing technical help with sampling. They are grateful to Enrique Morsan, Brooke McVeigh, Kevin Heasman, Emilio Rolán, Paul Valentich Scott, Francisco Fonseca, Tizoc Moctezuma, Concepción Enciso, Alberto Aragón, Edgar Alcántara, Humberto García, Gianfranco Scotti, Iku Kiryu, Nick King, and Ellie Watts for generously donating tissue samples for this study. They thank paleontologists Tom Demeré and N. Scott-Rugh for providing space in their facilities for their work at the San Diego Natural History Museum. They are indebted to Amanda Lawless, Yolanda Villacampa, Judith Terry Smith, Barbara Studencka, and Claudia del Río for providing valuable information about and images of *Panopea* fossils. They thank Miguel Cordoba, Diana Dorantes, and Gopal Murugan (CIBNOR); Gabriela Navas (Moss Landing Marine Laboratory); Claire Olson, Emma Timmins-Schiffman, Kristina Straus, and Fred Utter (University of Washington); and two anonymous referees for providing detailed editorial comments and constructive criticisms that greatly improved the manuscript. The research was funded by Consejo Nacional de Ciencia y Tecnología (CONACYT, grant 106905). ILV was the recipient of a CONACYT doctoral fellowship (no. 98412).

LITERATURE CITED

Adamkewicz, S. L., M. G. Harasewych, J. Blake, D. Saudek & C. J. Bult. 1997. A molecular phylogeny of the bivalve molluscs. *Mol. Biol. Evol.* 14:619–629.

Aragón-Noriega, E. A., J. Chávez-Villalba, P. E. Gribben, E. Alcántara-Razo, A. Maeda-Martínez, E. M. Arámbula-Pujol, A. García-Juárez & R. Maldonado-Amparo. 2007. Morphometric relationships, gametogenic development and spawning of the geoduck clam *Panopea globosa* (Bivalvia: Hiatellidae) in the central Gulf of California. *J. Shellfish Res.* 26:423–431.

Arámbula-Pujol, E. M., A. R. García-Juarez, E. Alcántara-Razo & E. A. Aragón-Noriega. 2008. Aspectos de biología reproductiva de la almeja de sifón *Panopea globosa* (Dall 1898) en el Golfo de California. *Hidrobiológica* 18:89–98.

Arnaud, S., M. Monteforte, N. Galtier, F. Bonhomme & F. Blanc. 2000. Population structure and genetic variability of pearl oyster *Pinctada mazatlanica* along Pacific coasts from Mexico to Panama. *Conserv. Genet.* 1:299–307.

Baldwin, B. S., M. Black, O. Sanjur, R. Gustafson, R. A. Lutz & R. C. Vrijenhoek. 1996. A diagnostic molecular marker for zebra mussels (*Dreissena polymorpha*) and potentially co-occurring bivalves: mitochondrial CO1. *Mol. Mar. Biol. Biotechnol.* 5:9–14.

Beu, A. G. & P. A. Maxwell. 1990. Cenozoic mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* no. 58. Lower Hutt, New Zealand. 518 pp.

Breen, P. C., C. Gabriel & T. Tyson. 1991. Preliminary estimates of age, mortality, growth and reproduction in the hiatellid clam *Panopea zelandica* in New Zealand. *New Zeal. J. Mar. Fresh.* 25:231–237.

Bromham, L. 2009. Why do species vary in their rate of molecular evolution? *Biol. Lett.* 5:401–404.

Bureau, D., W. Hajas, N. Surry, C. Hand, G. Dovey & A. Campbell. 2002. Age, size structure and growth parameters of geoducks (*Panopea abrupta*, Conrad 1849) from 34 locations in British Columbia sampled between 1993 and 2000. Canadian Technical Report Fisheries and Aquatic Sciences. Nanaimo, British Columbia, Canada. no. 2413. 84 pp.

Cadien, D. & L. Lovell (Eds.) 2008. A taxonomic listing of benthic macro- and megainvertebrates from infaunal and epibenthic monitoring programs in the southern California bight. 214 pp. Available at: http://www.scamit.org

Coan, E. V., P. Valentich-Scott & F. R. Bernard. 2000. Bivalves seashells of western North America. Marine bivalve mollusks from Arctic to Baja California. Santa Barbara, CA: Santa Barbara Museum of Natural History Monographs. Studies in Biodiversity no. 2. 764 pp.

Cox, R., N. D. Newell, B. W. Boyd, C. C. Branson, R. Casey, A. Chavan, A. H. Coogan, C. Dechesaux, C. A. Fleming, F. Haas, I. G. Hertlein, A. Kauffman, M. Keen, A. La Roque, A. I. McAlester, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner & J. Weir. 1969. Part N. Mollusca 6: Bivalvia. In: R. C. Moore, editor. Treatise on invertebrate paleontology, vol. 2. Geological Society of America Inc. and University of Kansas Press. p. N491.

Dall, W. 1898. Contribution to the tertiary fauna of Florida. Transactions of the Wagner Free Institute of Science of Philadelphia. vol. III, part IV. pp. 827–832.

Dall, W. 1918. Pleistocene fossils of Magdalena Bay, Lower California, collected by Charles Russell Orcutt. *Nautilus* 32:23–26.

Del Río, C. 2004. Tertiary marine molluscan assemblages of eastern Patagonia (Argentina): a biostratigraphic analysis. *J. Paleontol.* 78:1097–1122.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Dereeper, A., V. Guignon, G. Blanc, S. Audic, S. Buffet, F. Chevenet, J. F. Dufayard, S. Guindon, V. Lefort, M. Lescot, J. M. Claverie and O. Gascuel. 2008. Phylogeny. fr: robust phylogenetic analysis for the non-specialist. *Nucl. Acids Res*. 36:W465–W469.

Feldman, K., B. Vadopalas, D. Armstrong, C. Friedman, R. Hilborn, K. Naish, J. Orensanz, J. Valero, J. Ruesink, A. Suhrbier, A. Christy, D. Cheney & J. Davis. 2004. Comprehensive literature review and synopsis of issues relating to geoduck (*Panopea abrupta*) ecology and aquaculture production. Olympia, WA: Washington State Department of Natural Resources. 140 pp.

Folmer, O., M. Black, W. Hoeh, R. Lutz & R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol*. 3:294–299.

Gillooly, J. F., A. P. Allen, G. B. West & J. H. Brown. 2005. The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl. Acad. Sci. USA* 102:140–145.

Giribet, G. & D. I. Distel. 2003. Bivalve phylogeny and molecular data. In: C. Lydeard & D. R. Lindberg, editors. Molecular systematics and phylogeography of molluscs. Washington, DC: Smithsonian Books. pp. 45–90.

Giribet, G. & W. Wheeler. 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebr. Biol*. 121:271–324.

González-Peláez, S. S., I. Leyva-Valencia & D. B. Lluch-Cota. 2013. Distribution limits of the geoduck clams *Panopea generosa* and *P. globosa* on the Pacific coast of Mexico. *Malacologia* 56:85–94.

Goodwin, L. & B. Pease. 1989. Species profiles: life histories and environmental requirements of coastal fish and invertebrates (Pacific Northwest): Pacific geoduck clam. U.S. Fish and Wildlife Service biological report no. 82 (11.120). TR EL-82-4. Vicksburg, MS: U.S. Army Corps of Engineers. 14 pp.

Grove, S. 2011. A guide to the seashells and other marine molluscs of Tasmania. Available at: http://www.molluscsoftasmania.net/Species%20locality%20pages/Panopea%20australis.html

Hedin, M. C. & W. P. Maddison. 2001. A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae, Salticidae). *Mol. Phylogenet. Evol*. 18:386–403.

Helenes, J. & A. Carreño. 1999. Neogene sedimentary evolution of Baja California in relation to regional tectonics. *J. South Am. Earth Sci*. 12:589–605.

Hertlein, L. G. & W. K. Emerson. 1956. Marine Pleistocene invertebrates from near Puerto Peñasco, Sonora, Mexico. *Trans. San Diego Soc. Nat. Hist*. 12:154–176.

Kappner, I. & R. Bieler. 2006. Phylogeny of Venus clams (Bivalvia: Veneridae) as inferred from nuclear and mitochondrial gene sequences. *Mol. Phylogenet. Evol*. 40:317–331.

Keen, M. 1971. Sea shells of tropical West America: marine molluscs from Baja California to Peru. Stanford, CA: Stanford University Press. 1064 pp.

Kensley, B. 1974. The status of the Plio-Pleistocene *Panopea* in southern Africa (Mollusca, Bivalvia, Hiatellidae). *Ann. South Afr. Mus*. 65:199–215.

Kensley, B. 1976. *Panopea glycimeris* (Mollusca, Pelecypoda) in the South African faunal province. *Zool. Afr*. 12:236–237.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol*. 16:111–120.

Leyva-Valencia, I. 2012. Diferencias morfométricas en dos especies de la almeja generosa: *Panopea generosa* (Gould 1850) y *P. globosa* (Dall 1898) y filogenia molecular de cinco especies del género *Panopea*. PhD diss., Centro de Investigaciones Biológicas del Noroeste, 104 pp.

Leyva-Valencia, I., S. T. Álvarez-Castañeda, D. B. Lluch-Cota, S. González-Peláez, S. Pérez-Valencia, B. Vadopalas, S. Ramírez-Pérez & P. Cruz-Hernández. 2012. Shell shape differences between two *Panopea* species and phenotypic variation among *P. globosa* at different sites using two geometric morphometrics approaches. *Malacologia* 55:1–13.

Leyva-Valencia, I., B. Vadopalas, P. Cruz-Hernández, D. B. Lluch-Cota & D. I. Rojas-Posadas. 2013. Reclassification of *Panopea generosa* var. *taeniata* Dall 1918 as a fossil morphotype of *P. globosa* Dall 1898. *Malacologia* 56:315–319.

Librado, P. & J. Rosas. 2009. DNASP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25:1451–1452.

Lyle, M., J. Barron, T. J. Bralower, M. Huber, A. Olivares, A. C. Ravelo, D. K. Rea & P. A. Wilson. 2008. Pacific Ocean and Cenozoic evolution of climate. *Rev. Geophys*. 46:1–47.

Marko, P. B. 2005. Fossil calibration of molecular clocks and the divergence times of germinate species pairs separated by the Isthmus of Panama. *Mol. Biol. Evol*. 19:2005–2021.

Matsubara, T. 2011. Miocene shallow marine mollucs from the Hokutan group in the Tajima area, Hyôgo Prefecture, southwest Japan. *Bull. Mizunami Fossil Mus*. 37:51–113.

Morsán, E. & N. Ciocco. 2004. Age and growth model for the southern geoduck, *Panopea abbreviata*, off Puerto Lobos (Patagonia, Argentina). *Fish. Res*. 69: 343–348.

Nomura, S. 1935. A note on some fossil Mollusca from Takikawa beds of the northwestern part of Hokkaido, Japan. *Sci. Rep. Tohoku Imperial Univ. Sendai Japan* 18:31–39.

Nomura, S. & H. Niino. 1932. Fossil Mollusca from Izu and Hakone. *Sci. Rep. Tohoku Imperial Univ. Sendai Japan* 15:1–188.

Ogasawara, K., M. Takano, H. Nagato & N. Takanori. 2008. Cenozoic molluscan faunas and climatic changes in the northern Pacific related to Pacific gateways: review and perspective. *Bull. Jpn. Geol. Surv*. 59:355–364.

Otuka, Y. 1934. Tertiary structures of the northwestern end of Kitakami mountainland, Iwate Prefecture, Japan. *Earthquake Res. Ins. Bull*. 12:566–638.

Owada, M. 2007. Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia: Mytilidae): a third functional clade. *Mar. Biol*. 150:853–860.

Page, R. D. M. 1996. TREEVIEW: an application to display phylogenetic trees on personal computers. *Comput. Appl. Biosci*. 12:357–358.

Posada, D. 2009. Selecting models of evolution. In: P. Lemey, M. Salemi & A. M. Vandamme, editors. The phylogenetic handbook: a practical approach to DNA and protein phylogeny. New York: Cambridge University Press. pp. 345– 353.

Posada, D. & K. A. Crandall. 2001. Selecting the best-fit model of nucleotide substitution. *Syst. Biol*. 50:580–601.

Poupin, J. P. J. F. D. & J. C. Cexus. 2005. A revision of the genus *Pachygrapsus* Randall, 1840 (Crustacea: Decapoda: Brachyura, Grapsidae), with special reference to the Southwest Pacific species. *Zootaxa* 1015:1–66.

Rathbun, M. J. 1918. The grapsoid crabs of America. *Bull. U. S. Nat. Mus*. no. 97. 368 pp.

Robertson, R. 1963. Bathymetric and geographic distribution of *Panopea bitruncata*. *The Nautilus*. 76:75–82.

Rocha-Olivares, A., L. Calderon-Aguilera, E. A. Aragón-Noriega, N. C. Saavedra-Sotelo & V. M. Moreno Rivera. 2010. Genetic and morphological variation of northeast Pacific *Panopea* clams: evolutionary implications. *J. Shellfish Res*. 29:327–335.

Rolán, E. 1983. Algunas observaciones sobre *Panopea glycimeris* (Von Born, 1778 Mollusca; Bivalvia) en la Ria de Vigo. *Thalassas* 1:59–65.

Ronquist, F. & J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.

Schubart, C. D., J. A. Cuesta & D. L. Felder. 2005. Phylogeography of *Pachygrapsus transversus* (Gibbes, 1850): the effect of the American continent and the Atlantic Ocean as gene flow barriers and recognition of *Pachygrapsus socius* Stimpson 1871 as a valid species. *Nauplius* 13:99–113.

Scotti, G., S. Antioco, F. Andaloro & R. Chemello. 2011. Finding of a living population of *Panopea glycimeris* (Von Born, 1778) (Bivalvia;

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Hiatellidae) in eastern Sicily (Mediterranean Sea). *J. Biol. Res. Thessalon*. 15:151–154.

Silvestro, D. & I. Michalak. 2012. raxmlGUI: a graphical front-end for RAxML. *Org. Divers. Evol*. 12:335–337.

Smith, J. T. 1991. Cenozoic marine molluscs and paleogeography of the Gulf of California: Physical oceanography, primary productivity, sedimentology. Chapter 31: Part V:637–666. In: J. P. Dauphin & B. R. T. Simoneit, editors. The Gulf and peninsular province of the Californias. Memoir 47. Tulsa, OK: American Association of Petroleum Geologists. pp. 637–666.

Studencka, B. 1991. A new species of genus *Panopea* (Bivalvia) from King George Island. *Antarctica Polish Polar Res*. 12:363–368.

Suárez-Moo, P. J., L. E. Calderon-Aguilera, H. Reyes-Bonilla, G. Díaz-Erales, V. Castañeda-Fernandez de Lara, E. A. Aragón-Noriega & A. Rocha-Olivares. 2012. Integrating genetic, phenotypic and ecological analyses to assess the variation and clarify the distribution of the Cortes geoduck (*Panopea globosa*). *J. Mar. Biol. Assoc. U. K*. 93:809–816.

Swofford, D. L. 2003. PAUP*: phylogenetic analysis using parsimony (* and other methods), version 4.0b 10. Sunderland, MA: Sinauer Associates.

Swofford, D. L., P. J. Waddell, J. P. Huelsenbeck, P. G. Foster, P. O. Lewis & J. S. Rogers. 2001. Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. *Syst. Biol*. 50:525–539.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei & S. Kumar. 2011. MEGA 5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol*. 28:2731–2739.

Taylor, J. D., S. T. Williams, E. A. Glover & P. Dyal. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. *Zool. Scr*. 36:587–606.

Therriault, T. W., M. F. Docker, M. I. Orlova, D. D. Heath & H. J. MacIsaac. 2004. Molecular resolution of the family Dreissenidae (Mollusca:Bivalvia) with emphasis on Ponto-Caspian species, including first report of *Mytilopsis leucophaeata* in the Black Sea basin. *Mol. Phylogenet. Evol*. 30:479–489.

Therriault, T. W., I. A. Grigorovich, M. E. Cristescu, H. A. Ketelaars, M. Viljanen, D. D. Heat & H. J. MacIsaac. 2002. Taxonomic resolution of the genus *Bythotrephes* Leydig using molecular markers and re-evaluation of its global distribution. *Divers. Distrib*. 8:67–84.

Thomas, E., H. Brinkhuis, M. Huber & U. Röhl. 2006. An ocean view of the early Cenozoic greenhouse world. *Oceanography* 19:94–103.

Thomas, J. A., J. J. Welch, R. Lanfear & L. Bromham. 2010. A generation time effect on the rate of molecular evolution in invertebrates. *Mol. Biol. Evol*. 27:1173–1180.

Thomsen, E., J. Knudsen & E. Koskeridou. 2009. Fossil panopeans (Bivalvia, Hiatellidae) from Rhodes, Greece. *Steenstrupia* (*Cph*.) 30:163–176.

Vadopalas, B., T. Pietsch & C. Friedman. 2010. The proper name for the geoduck: resurrection of *Panopea generosa* Gould, 1850, from the synonymy of *Panopea abrupta* (Conrad, 1849) (Bivalvia: Myoida: Hiatellidae). *Malacologia* 52:169–173.

Winnepenninckx, B., D. Reid & T. Backeljau. 1998. Performance of 18S rRNA in littorinid phylogeny (Gastropoda: Caenogastropoda). *J. Mol. Evol*. 47:586–596.

Woodring, W. P. 1982. Geology and paleontology of Canal Zone and adjoining parts of Panama: descriptions of Tertiary molluscs. *U.S. Geol. Surv. Prof. Pap*. 306-E:541–743.

Xia, X. & P. Lemey. 2009. Assessing substitution saturation with DAMBE. In: P. Lemey, M. Salemi, & A. M. Vandamme, editors. The phylogenetic handbook: a practical approach to DNA and protein phylogeny. New York: Cambridge University Press. pp. 615–630.

Xue, D., H. Wang, T. Zhang, Y. Gao, S. Zhang & F. Xu. 2012. Morphological and genetic identification of the validity of the species *Atrina chinensis* (Bivalvia: Pinnidae). *J. Shellfish Res*. 31:739–747.

Yokoyama, M. 1922. Fossils from the upper Musashino of Kazusa and Shimosa. *J. Coll. Sci. Imperial Univ. Tokyo*. Vol. 44, 200 pp.

Yokoyama, M. 1923. Tertiary Mollusca from Dainichi in Totomi. *J. Coll. Sci. Imperial Univ. Tokyo*. 45:1–8.

Yokoyama, M. 1925. Molluscan remains from the uppermost part of the Jo-Ban Coal-Field. *J. Faculty Sci. Imperial Univ. Tokyo*. 45:1–34.

Yonge, C. 1971. On functional morphology and adaptative radiation in the bivalve superfamily Saxicavacea (*Hiatella* (= *Saxicava*), *Saxicavella, Panomya, Panopea, Cyrtodaria*). *Malacologia* 11:1–44.

Zinsmeister, W. 1982. Late Cretaceous–Early Tertiary molluscan biogeography of the southern circum-Pacific. *J. Paleontol*. 56:84–102.

Zinsmeister, W. 1984. Late Eocene bivalves (Mollusca) from the La Meseta Formation, collected during the 1974–1975 Joint Argentine–American expedition to Seymour Island, Antarctic Peninsula. *J. Paleontol*. 58:1497–1527.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. diss., University of Texas at Austin. 125 pp.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Shellfish-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use