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ORIGINAL ARTICLE

Distribution patterns of the genus *Pacifigorgia* (Octocorallia: Gorgoniidae): track compatibility analysis and parsimony analysis of endemicity

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ABSTRACT

Aim We analysed the distribution patterns of the eastern Pacific octocoral genus *Pacifigorgia* and deduced its ancestral distribution to determine why *Pacifigorgia* is absent from the Gulf of Mexico, the Caribbean of central America, and the Antilles. We also examined the current patterns of endemism for *Pacifigorgia* to look for congruence between hot spots of endemism in the genus and generally recognized areas of endemism for the eastern Pacific.

Location The tropical eastern Pacific and western Atlantic, America.

Methods We used track compatibility analysis (TCA) and parsimony analysis of endemicity (PAE) to derive ancestral distribution patterns and hot spots of endemism, respectively. Distributional data for *Pacifigorgia* were gathered from several museum collections and from fieldwork, particularly in the Pacific of Costa Rica and Panama.

Results A single generalized track joined the three main continental eastern Pacific biogeographical provinces and the western Atlantic. This track can be included within a larger eastern Atlantic–eastern Pacific transoceanic track that may be the oldest transoceanic track occurring in the region. PAE results designate previously recognized eastern Pacific biogeographical provinces as *Pacifigorgia* hot spots of endemism. The number of endemic species, which for other taxonomic groups is similar among the eastern Pacific provinces, is higher in the Panamic province for *Pacifigorgia*.

Main conclusions We propose that the absence of *Pacifigorgia* from the Gulf of Mexico, the Caribbean of central America, and the Antilles is the result of an ancient absence of the genus from these areas rather than the consequence of a major, recent, extinction episode. The Cortez province and the Mexican province appear together as a result of either non-response to vicariance or dispersal across the Sinaloan Gap. We posit that the Central American Gap acts as a barrier that separates the Panamic province from the northern Cortez–Mexican province.

Keywords
Gorgoniidae, historical biogeography, marine biogeography, octocoral biogeography, Octocorallia, ***Pacifigorgia***, parsimony analysis of endemicity, track compatibility analysis, tropical eastern Pacific.

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INTRODUCTION

Gorgonian octocorals (order Alcyonacea) are the most abundant components of shallow eastern Pacific marine communities (Breedy & Guzman, 2003a). They occur mainly in zones of strong current swell and breaking surf, attached to rocky bottoms, shells, and small rock fragments (Breedy & Guzman, 2002). Although abundant, the eastern Pacific octocoral fauna was considered poorly known by Bayer (1981) and is currently under extensive revision. To date, eleven genera in four families have been reported (Breedy & Guzman, 2003a); of these, *Pacifigorgia* Bayer, 1951 is one of the most diverse and

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abundant, with 35 known species (Breedy, 2001; Breedy & Guzman, 2002, 2003a,b, 2004; Williams & Breedy, 2004).

Bayer (1951) proposed the genus *Pacifigorgia* for reticulate gorgonids lacking scaphoid sclerites, and designated *Pacifigorgia stenobrochis* (Valenciennes, 1846) as the type species for the genus. In a 2002 publication, Breedy and Guzman revised the genus, clarifying and updating its taxonomy. These authors recognized 19 valid species and subsequently described nine new species for the Pacific coast of Costa Rica (Breedy & Guzman, 2003a) and four new species for Panama (Breedy & Guzman, 2003b, 2004). In addition, three new species have been described for the Galápagos archipelago (Williams & Breedy, 2004).

The distribution of *Pacifigorgia* is somewhat intriguing: 34 species are restricted to the Pacific coast and oceanic islands of the Americas; only one, *Pacifigorgia elegans* (Milne Edwards & Haime, 1857), occurs in the western Atlantic and southern Caribbean (Breedy & Guzman, 2002). Although a concise taxonomic framework for the genus now exists, no quantitative analysis of distribution patterns or work on biogeography existed prior to this study.

The goal of this study was to reconstruct the ancestral distribution of *Pacifigorgia* and to identify hot spots of endemism for the genus within the eastern Pacific: the results will improve our understanding of the historical factors responsible for the current distribution patterns of the genus. Furthermore, this is the first study dedicated to the historical biogeography of octocorals from the eastern Pacific region.

MATERIALS AND METHODS

Abbreviations

BM: The Natural History Museum, London, UK; CASIZ: California Academy of Science, Invertebrate Zoology, San Francisco, USA; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN: Museum National d'Histoire Naturelle, Paris, France; USNM: National Museum of Natural History (formerly the United States National Museum), Smithsonian Institution, Washington, DC, USA; YPM: Yale Peabody Museum of Natural History, New Haven, USA.

Track compatibility analysis

Species records and distribution ranges were obtained after reviewing the octocoral collections deposited at BM, CASIZ, MCZ, MNHN, USNM and YPM, and reference collections deposited at the Museo de Zoología, Universidad de Costa Rica (Costa Rica) and the Smithsonian Tropical Research Institute (Panama). These collections were chosen because they contain type specimens of most *Pacifigorgia* species and because they have extensive records of the eastern Pacific shallow octocoral fauna. For all the distribution analyses, the four species with doubtful taxonomic status [*Pacifigorgia arenata* (Valenciennes, 1846), *Pacifigorgia cribrum* (Valenciennes, 1846), *Pacifigorgia douglasii* (Hickson, 1928), and *Pacifigorgia tabogae* (Hickson, 1928)] were not included.

We created distribution maps for various *Pacifigorgia* species using ArcView 3.2 (ESRI) with a 5° latitude by 5° longitude grid size (see the Supplementary Material). For each grid cell, we documented the presence/absence of 31 *Pacifigorgia* species (Table 1). Because compatibility determination between individual tracks requires species with at least three distributional points, we used only the 15 species that met this condition for the track compatibility analysis (TCA) (Morrone & Crisci, 1995).

We used the nearest-neighbour joining criterion to determine individual tracks for each of the 15 species. An individual track represents a graphical interpretation of a species' distributional data, and it provides information about spatial discontinuities and putative vicariance (subdivision) events related to these discontinuities. When individual tracks are congruent or can be superimposed on each other they can be combined into generalized tracks, and a generalized track represents the common ancestral distributional pattern for the taxon in question (Grehan, 2001).

Page (1987) clarified the theoretical foundations of TCA and its relationship with other phylogeny-based historical biogeography methodologies, in particular component analysis. According to Page, TCA and component analysis are analytically identical in that they employ the same concepts of relationship (i.e. exclusion, inclusion, replication, and non-combinability), between binary characters and components, respectively, and in the fact that binary-coded characters are equivalent (in information content) to cladistic components.

Track analysis is useful when no cladistic information is available for the group under scrutiny or when more than one hierarchical pattern is suspected for the areas under consideration. In this study, we used the program clique (phylip v. 3.63, Felsenstein, 2004) to derive the generalized tracks from the 15-species matrix. The generalized tracks obtained were mapped using ArcView v. 3.2 (ESRI).

Determining hot spots of endemism

To identify hot spots of endemism for the genus *Pacifigorgia*, we ran a parsimony analysis of endemicity (PAE; Morrone & Crisci, 1995) using winclada v. 1.00.08 (Nixon, 2000). PAE uses a grid cell × species matrix to identify hot spots of endemism for a group. Unlike TCA, PAE does not exclude species known only from single localities, and thus all 31 species were included in this analysis.

The results of PAE can be interpreted statically or dynamically. The static interpretation of the PAE tree can be used to identify hot spots of endemism, which generally can be assessed by comparing them with hot spots defined for other taxa or with previously determined areas of endemism for the region. From a dynamic point of view, the PAE cladogram indicates area relationships (Cardoso da Silva & Oren, 1996). Recently, this latter interpretation of the PAE tree has been

Table 1 Distribution of *Pacifigorgia* species in the main eastern Pacific biogeographical provinces, Isla del Coco (IC), and the western Atlantic (WA). The species used in the track compatibility analysis (TCA) and/or parsimony analysis of endemicity (PAE) are indicated.

		Province			
Species	Analysis	Cortez–Mexican	Panamic	Galapagos	Other
Pacifigorgia adamsii (Verril, 1868c)	TCA, PAE		X		
Pacifigorgia agassizii (Verril, 1864)	TCA, PAE	X			
Pacifigorgia bayeri Breedy, 2001	PAE		X		
Pacifigorgia cairnsi Breedy & Guzman, 2003a	TCA, PAE		X		
Pacifigorgia catedralensis Breedy & Guzman, 2004	PAE		X		
Pacifigorgia curta Breedy & Guzman, 2003a	PAE				X(IC)
Pacifigorgia dampieri Williams & Breedy, 2004	PAE			X	
Pacifigorgia darwinii (Hickson, 1928)	PAE			X	
Pacifigorgia elegans (Milne Edwards & Haime, 1857)	TCA, PAE				X(WA)
Pacifigorgia englemanni (Horn, 1860)	PAE	X			
Pacifigorgia exilis (Verrill, 1870)	PAE	X			
Pacifigorgia eximia (Verrill, 1868c)	TCA, PAE		X		
Pacifigorgia ferruginea Breedy & Guzman, 2004	TCA, PAE		X		
Pacifigorgia firma Breedy & Guzman, 2003a	TCA, PAE		X		
Pacifigorgia flavimaculata Breedy & Guzman, 2003a	PAE		X		
Pacifigorgia gracilis (Kükenthal, 1924)	PAE	X			
Pacifigorgia irene Bayer, 1951	TCA, PAE		X		
Pacifigorgia lacerata Breedy & Guzman, 2003a	PAE		X		
Pacifigorgia media (Verrill, 1864)	TCA, PAE	X	X		
Pacifigorgia pulchra (Verrill, 1870)	TCA, PAE	X			
Pacifigorgia rubicunda Breedy & Guzman, 2003a	TCA, PAE		X		
Pacifigorgia rubinoffi Breedy & Guzman, 2003b	PAE		X		
Pacifigorgia rubripunctata Williams & Breedy, 2004	PAE			X	
Pacifigorgia rutila (Verrill, 1868c)	PAE	X			
Pacifigorgia samarensis Breedy & Guzman, 2003a	TCA, PAE		X		
Pacifigorgia sculpta Breedy & Guzman, 2004	TCA, PAE		X		
Pacifigorgia senta Breedy & Guzman, 2003a	TCA, PAE	X	X		
Pacifigorgia smithsoniana Breedy & Guzman, 2004	PAE		X		
Pacifigorgia stenobrochis (Valenciennes, 1846)	TCA, PAE	X	X		
Pacifigorgia symbiotica Williams & Breedy, 2004	PAE			X	
Pacifigorgia tupperi Breedy & Guzman, 2003a	PAE		X		
Number of endemics		6	16	4	2
Number of shared species		3			

discouraged because it relies on a very restrictive set of *a priori* assumptions about the historical processes shaping biotic distributions (Brooks & van Veller, 2003).

We used PAE in a static way to identify hot spots of endemism for *Pacifigorgia*. In PAE, when two or more grid cells are joined together in the PAE tree, the distributions of the shared species between the cells are superimposed to derive the hot spots of endemism for the taxon under study. A minimum of two shared species is necessary to justify the postulation of a hot spot of endemism (Morrone, 1994); joined grid cells with no shared species (i.e. arbitrary resolutions) are not considered to be hot spots of endemism. We refer to the areas identified by PAE as hot spots of endemism, rather than as the commonly used areas of endemism, because the analysis is restricted to the genus *Pacifigorgia* and problems of non-independence resulting from phylogenetic autocorrelation may arise.

The hot spots identified by this method can be interpreted as being included within previously recognized areas of endemism if extensive correspondence with these areas exists (Cardoso da Silva & Oren, 1996). Areas of endemism represent regions of spatial homology where similar historical factors are proposed to be responsible for the current diversity patterns. Our inclusion of the PAE-identified *Pacifigorgia* hot spots within recognized eastern Pacific areas of endemism allows us to interpret *Pacifigorgia* endemism patterns within a general historical framework for the region.

We used the presence/absence data for the 31 *Pacifigorgia* species (Table 1) for each 5° × 5° grid cell to obtain a matrix, which we analysed using the program NONA (Goloboff, 1999). 1000 independent replicates were performed using the tree bisection reconnection algorithm, and all most parsimonious trees were saved. Arbitrary resolutions were avoided by collapsing zero-length branches using the 'ksave' command. We included a zero vector to root the tree as recommended by Morrone (1994) and Morrone & Escalante (2002).

RESULTS

Track compatibility analysis

The mapped distributional data for the eastern Pacific *Pacifigorgia* species revealed three main groups occurring in the following locales: the Gulf of California and along the Pacific coast of Mexico; the Costa Rica and Panama coastlines and continental islands; and all along the eastern Pacific region coastlines (Fig. 1; right side). *Pacifigorgia elegans*, the only non-eastern Pacific species, occurs in Venezuela, Trinidad and Tobago, and Maranhao, Brazil (Fig. 1; right side).

TCA resulted in a single clique, or generalized track, that included 13 of the 15 species used in the analysis. The generalized track (Fig. 1; right side) extends from the Gulf of California to the western Atlantic region, joining together the three main continental eastern Pacific biogeographical provinces, namely the Cortez, the Mexican, and the Panamic provinces (Walker, 1960; Hastings, 2000). TCA also revealed the existence of a unique ancestral *Pacifigorgia* biota that subsequently divided to result in the current distribution of the group.

Parsimony analysis of endemicity

PAE produced a single most parsimonious tree (L = 29, Ci = 89, Ri = 90) (Fig. 1; left side) after 1000 independent replicates. The cladogram shows three main hot spots of endemism, all of which correspond to previously recognized eastern Pacific provinces (i.e. Cortez–Mexican, Panamic, and Galápagos). The Cortez and Mexican provinces appear together in the tree and constitute an area highly differentiated from that of the Panamic province (species listed in Table 1). Accordingly, the number of species shared between the Panamic province and the Cortez–Mexican provinces is low (3 species). The number of endemics is greater in the Panamic province (16 species) than in both the Cortez and Mexican provinces combined (6 species).

The Galápagos province is easily recognizable by the presence of four endemic species and constitutes an isolated eastern Pacific area of endemism. Other oceanic islands, such as Isla del Coco and Revillagigedo Archipelago, appear dispersed in the cladogram. Revillagigedo shows affinity with the Cortez-Mexican province. Both Isla del Coco and the western Atlantic cluster are defined by one endemic each, namely *Pacifigorgia curta* Breedy & Guzman, 2003a and *P. elegans*, respectively.

DISCUSSION

Track compatibility analysis

TCA of the genus *Pacifigorgia* resulted in a single generalized track joining together the eastern Pacific and western Atlantic

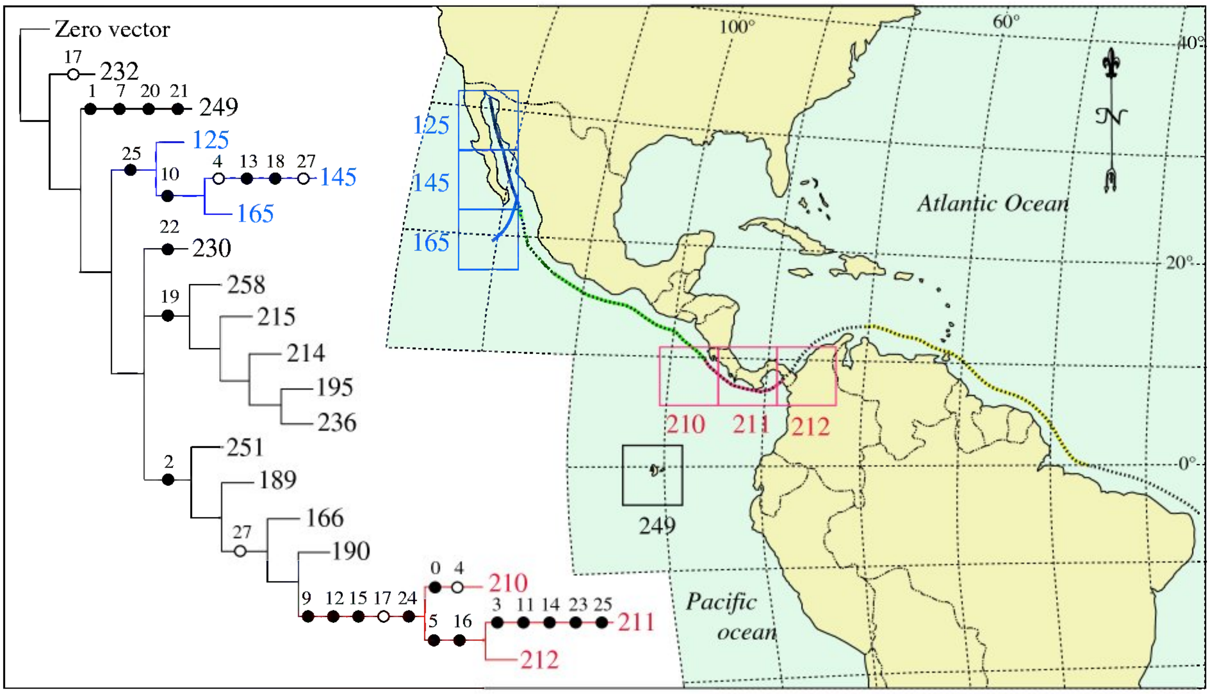

Figure 1 Diversity patterns of the genus *Pacifigorgia*. Right side: *Pacifigorgia* generalized track (dotted line). Coloured lines represent the individual tracks of the *Pacifigorgia* species that inhabit the California Gulf (blue line) and the Panamic province (red line), as well as species that occur along the Pacific coast of the Americas (green line) and the southern Caribbean and western Atlantic (yellow line). Left side: parsimony analysis of endemicity (PAE) tree. Coloured clades and coloured quadrants on the map correspond to established eastern Pacific provinces: the Cortez–Mexican province (blue), the Panamic province (red), and the Galápagos province (black). Black hash marks in the PAE tree represent endemic species for the area, and white hash marks correspond to species shared with other areas. The leaves in the PAE tree and the numbers in the quadrants correspond to grid-cell codes (see Supplementary Material).

regions. Interestingly, this track corresponds to the transisthmian component (Banford *et al.*, 1999) of a larger track that joins together the eastern Atlantic (i.e. Africa) and the eastern Pacific regions.

The eastern Atlantic–eastern Pacific (EA/EP) transoceanic track was deduced by Rosen (1975) by a simple superposition of the distributional data of several taxa (see Rosen, 1975, for a list of the taxa used). In his seminal paper on Caribbean historical biogeography, Rosen identified the EA/EP transoceanic track as the oldest occurring in the region and postulated the existence of a vicariance event that led to the separation of the faunas of the eastern and western Atlantic. This vicariance event dates the EA/EP transoceanic track back to the Cenozoic opening of the Atlantic Ocean (Banford *et al.*, 1999).

The inclusion of *Pacifigorgia* within the ancient faunal assemblage implied by the EA/EP transoceanic track may help to explain the absence of the genus from the Caribbean (i.e. the Gulf of Mexico, the Caribbean of central America, and the Antilles). Two possibilities exist: either the genus became extinct sometime during the biogeographical history, or the genus may have never occurred in the area (i.e. the absence of the genus is ancient rather than recent).

Based on pretectonic models, Bayer (1953) proposed that *P. elegans*, the only non-Pacific species of the genus, represents a relict species. This premise supports the first possibility - that *Pacifigorgia* was distributed both in the eastern Pacific and in the Caribbean and subsequently disappeared from the Gulf of Mexico, central America, and the Antilles.

We argue that the absence of *Pacifigorgia* from the Gulf of Mexico, central America, and the Antilles is ancient. Studies on members of the EA/EP transoceanic track have revealed a close phylogenetic relationship between the eastern Pacific and western Atlantic clades and have dated, using a molecular clock, this eastern Pacific–western Atlantic divergence back to the late Miocene (Banford *et al.*, 1999, 2004).

The Late Miocene–Early Pliocene represents a period of high origination rates for scleractinian corals, both at the genus and at the species level (Budd, 2000). Thus, *P. elegans* may represent a species that originated at this time in the southern Caribbean from an eastern Pacific ancestor and that survived the Plio-Pleistocene extinction episode. Budd & Johnson (1999) suggested that taxa that survived this extinction episode originated during a 2 to 3 million-year interval of early Pliocene climatic amelioration that preceded Northern Hemisphere glaciation.

Miocene–Pliocene origination patterns have been found in the fish genera *Scomberomorus* (Banford *et al.*, 1999), *Ophioblenius* (Muss *et al.*, 2001), and *Strongylura* (Banford *et al.*, 2004). These studies reported an ancient separation of the eastern Pacific and Brazil lineages of these genera that occurred *c.* 7 Ma. Similar molecular work with *Pacifigorgia* is needed to test the hypothesis proposed here; if a *c.* 7 million-year divergence time is discovered for *P. elegans*, our hypothesis that the absence of *Pacifigorgia* from the Caribbean basin is ancient would be strengthened.

Parsimony analysis of endemicity

Widely recognized biogeographical provinces within the eastern Pacific region were identified by PAE as *Pacifigorgia* hot spots of endemism. The Cortez and Mexican provinces showed no evident separation, suggesting a shared biogeographical history owing to species dispersal between the provinces or to the lack of a vicariance response to the Sinaloan Gap (from Topolobampo to Sinaloa, Hastings, 2000) (Brooks, 1990; Brooks *et al.*, 2001).

The precise limits of the Sinaloan Gap and its efficiency as a barrier for marine organisms have been questioned because of the existence of isolated rocky environments such as the Isla San Ignacio de Farallón (Hastings, 2000). Dispersal across this barrier, perhaps in a stepping-stone way, may well be possible for octocorals if these isolated rocky environments provide a suitable habitat for octocoral settlement.

As expected by the presence of the Central American Gap, the Panamic province represents a historical unit separate from the Cortez–Mexican province. The Central American Gap has been postulated to be a highly effective barrier for chaenopsid fishes (Hastings, 2000); the low number of shared species between the Cortez–Mexican province and the panamic Province may reflect a similar vicariant effect for octocorals (Table 1).

With the exception of the Galápagos archipelago, which constitutes an area of endemism within the eastern Pacific, the oceanic islands appear dispersed in the deduced PAE tree. These islands have never been formally designated as biogeographical provinces and have not been included in the Galápagos province (Hastings, 2000). The Revillagigedo faunal affinities with the Cortez–Mexican province are in accordance with patterns observed in scleractinian corals (Glynn & Ault, 2000). The western Atlantic cluster and Isla del Coco are defined by a single endemic species each, namely *P. elegans* in the western Atlantic and *P. curta* in Isla del Coco, and these two species may constitute peripheral isolates of a Panamic widespread ancestor.

As shown by TCA (Fig. 1; right side), the relationship between the eastern Pacific and western Atlantic is old (Rosen, 1975). The western Atlantic contains members of a track with three possible vicariance events, resulting in a complex biota (McLennan & Brooks, 2002): the west Atlantic–east Atlantic vicariance event was caused by the growth of the Atlantic basin; and the Antillean and the Isthmian eastern Pacific–Caribbean vicariance events were caused by the passage of the Greater Antilles through the central American seaway and by the closure of the Isthmus of Panama, respectively. Further research in the region may help to clarify the role played by these events in shaping diversity patterns both in the eastern Pacific and in the Caribbean region.

The high levels of endemism observed for *Pacifigorgia* in the Panamic province differ from the levels observed for chaenopsid fishes (Hastings, 2000) and scleractinian corals (Reyes-Bonilla, 1993; Reyes-Bonilla & López-Pérez, 1998) in these two groups the number of endemic species is similar for the Panamic and the Cortez–Mexican provinces. The historical factors that account for the overwhelming diversity of *Pacifigorgia* within the Panamic province and the relative contribution of the various speciation models (Brooks, 1985) to current marine diversity in this region remain to be elucidated. The role of dispersal in shaping the distribution of *Pacifigorgia* is also unclear. The fauna inhabiting the Galápagos province may provide further insights into this subject, given the relative isolation of this province from other eastern Pacific biogeographical provinces.

Concluding remarks

In summary, we have identified three main *Pacifigorgia* hot spots of endemism within the eastern Pacific. These areas correspond to well-established biogeographical provinces (Cortez–Mexican, Panamic, and Galápagos provinces), a fact that may allow researchers to explore aspects of the speciation processes that account for the diversity of this octocoral genus within a general biogeographical framework for the region. Extensive surveys around the eastern Pacific oceanic islands, and more detailed cladistic biogeographical analyses, are still needed to identify historical relationships between biogeographical provinces within the eastern Pacific and to clarify the historical forces responsible for the current diversity patterns in the region.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Figure S1 5° latitude by 5° longitude grid used for the spatial analysis of *Pacifigorgia* distribution patterns. For each grid cell the presence/absence of 31 *Pacifigorgia* species was determined and subsequently used for track compatibility analysis (TCA) and/or parsimony analysis of endemicity (PAE).

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BIOSKETCH

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