

The Great American Schism: Divergence of Marine Organisms After the Rise of the Central American Isthmus

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Key Words

adaptation, molecular clock, molecular substitution rate, Panama, productivity

Abstract

After a 12-million-year (My) process, the Central American Isthmus was completed 2.8 My ago. Its emergence affected current flow, salinity, temperature, and primary productivity of the Pacific and the Atlantic and launched marine organisms of the two oceans into independent evolutionary trajectories. Those that did not go extinct have diverged. As no vicariant event is better dated than the isthmus, molecular divergence between species pairs on its two coasts is of interest. A total of 38 regions of DNA have been sequenced in 9 clades of echinoids, 38 of crustaceans, 42 of fishes, and 26 of molluscs with amphi-isthmian subclades. Of these, 34 are likely to have been separated at the final stages of Isthmus completion, 73 split earlier and 8 maintained post-closure genetic contact. Reproductive isolation has developed between several isolates, but is complete in only the sea urchin *Diadema*. Adaptive divergence can be seen in life history parameters. Lower primary productivity in the Caribbean has led to the evolution of higher levels of maternal provisioning in marine invertebrates.

INTRODUCTION

When the Central American Isthmus joined North and South America by uninterrupted land, the migration of terrestrial animals led to monumental species range expansions, radiations, and extinctions in both subcontinents (Marshall et al. 1982, Webb & Barnosky 1989). The apt name “Great American Interchange” was coined for this event (Stehli & Webb 1985). What was a great interchange on land was a great schism in the sea. Before the ranges of terrestrial species started to expand, the ranges of marine species were being sundered by an uninterrupted barrier that neither larvae nor adults could cross, starting them on a path of independent evolutionary trajectories. For some species, these trajectories ended in extinction. Others are still in today’s oceans presenting the opportunity to determine what changes can occur in a minimum of 2–3 million years (My) of separate evolution. Such sister species have been named geminate by Jordan (1908). Geminate species represent initially similar genomes placed into separate environments and constitute a natural experiment that can tell us much about evolutionary divergence and its causes.

Since the publication of past reviews of the isthmian schism (T. Collins 1996, Glynn 1982, Jones & Hasson 1985, Lessios 1998), new studies in stratigraphy and paleontology have added to the understanding of events that have led to the assembly of tropical Atlantic and Pacific faunas after isolation (reviews in Allmon 2001, Budd 2000, L. Collins & Coates 1999, Jackson et al. 1996a). This review focuses on the divergence of sister clades with extant members on the two sides of the Isthmus. To understand what led to present day divergence, one needs to know what happened in the past, so I start by summarizing information about the geological event that initiated the entire process and about its environmental consequences before addressing the questions: (a) At what rate did geminate clades diverge? (b) Which of the environmental differences between the oceans have been important for divergence of what traits? And, (c) What can be learned about speciation through comparisons of populations isolated from each other for 3 My?

THE GEOLOGICAL EVENT AND ITS ENVIRONMENTAL CONSEQUENCES

The geological history of the Central American Isthmus, from the time that it started forming in deep water to the time that it emerged to become dry land, is reviewed by Coates & Obando (1996) and by Coates (1997). The completion of the Isthmus most likely occurred in the late Pliocene, 2.8 My ago (Mya) (Coates et al. 2005), but the process lasted for approximately 12 My. Until the middle Miocene, 16–15 Mya, there were abyssal water connections between the two oceans. At 8 Mya, the depth of the Atrato Strait next to Colombia was at least 150 m deep (Duque-Caro 1990), while the Panama Canal basin had shoaled temporarily to about 25 m, only to become 200 m deep at 6 Mya (L. Collins et al. 1996a). By 3 Mya, only narrow channels remained, which were filled with sediment soon thereafter to completely separate the waters of the tropical western Atlantic (WA) and the tropical eastern Pacific (EP).

The shoaling of the Isthmus had dramatic effects on the physical environments of both oceans. Circulation of deep water began to be affected by 5–4 Mya (Keigwin 1982, Haug & Tiedemann 1998). Surface salinities in the WA started increasing about the same time (Keigwin 1982). A warm circumtropical surface current that was flowing westward through the seaway until 3.65 Mya was blocked (Kameo & Sato 2000). The Isthmus deflected the Atlantic North Equatorial Current northward and intensified the flow of the Gulf Stream (Berggren & Hollister 1974, Burton et al. 1997). Caribbean water became warmer and saltier and, when transported northward, resulted in higher precipitation over land at high latitudes and more influx of fresh water into the Arctic, thus initiating the formation of land-based ice sheets (Bartoli et al. 2005, Driscoll & Haug 1998, Haug

& Tiedemann 1998, Lear et al. 2003, but see Raymo 1994 and Lunt et al. 2008). The glaciation cycles, which first appeared in Atlantic subpolar regions at 3.2 Mya and intensified at 2.7 Mya, caused fluctuations in global sea level, thus affecting the evolution of tropical as well as temperate shallow water marine organisms.

One question germane to the interpretation of biotic divergence across the Isthmus is whether the land barrier closed only once. That a possible land bridge existed between North and South America in the Paleogene has been suggested on biogeographic grounds (White 1986, Rage 1988). However, the patterns of distribution of terrestrial groups that prompted the land bridge hypothesis can also be accommodated by the hypothesis that herald taxa crossed between the subcontinents by being ferried on islands during these tectonically active times, or by swimming (Webb 2006). There is no unambiguous geological evidence that North and South America were connected by an uninterrupted land bridge since the time that they were both attached to Gondwana in the middle Mesozoic (Iturralde-Vinent & MacPhee 1999). There is evidence, however, of a breach of the Isthmus after its initial completion 3.1–2.8 Mya. A trend of decreasing salinity in two WA deep-sea cores, dated at 2 Mya, is interpreted by Cronin & Dowsett (1996) as evidence that EP waters may have spilled over the isthmus during a high sea level stand. This breach was short lived. By 1.9 Mya salinity differences between the two oceans were restored.

Physical Environments on the Two Sides of the Isthmus

Today, shallow-water geminate species exist in physical environments that are quite different (reviews in Glynn 1972, 1982; Jackson & D’Croz 1997). From January to April, the low pressure region of the Intertropical Convergence Zone is situated to the South of Central America. The trade winds blowing from the North push surface waters away from the EP coast in places where the mountains are low, such as central Panama, the Gulf of Papagayo, and the Isthmus of Tehuantepec (Amador et al. 2006, Pennington et al. 2006). Cold, nutrient-rich water upwells into the euphotic zone to replace the displaced surface water. Temperature in the Bay of Panama can drop from 27°C to 15°C within 24 hours (Glynn 1972). Primary productivity in the EP increases dramatically during these periods, but also remains higher than that of the WA during the rest of the year (D’Croz & Robertson 1997, Pennington et al. 2006). The EP is also subject to El Niño Southern Oscillation (ENSO) fluctuations that disrupt upwelling (Glynn 1990, Kessler 2006), whereas the WA is only affected by the global climatic effects of this phenomenon (McPhaden et al. 2006). Surface temperatures in the WA are higher than in the EP, leading to higher evaporation. Water vapor produced in the WA crosses over the Isthmus continental divide and flows into the EP, thus maintaining lower salinity (Benway & Mix 2004). The diurnal tidal range on the Pacific side of the Isthmus is as wide as 6 m, whereas on the Caribbean coast it is <0.5 m (Glynn 1972). In addition to being more variable in time, the EP physical environment is also more variable in space. Upwelling and its concomitant fluctuations in temperature, salinity, and primary productivity are limited to certain sections of the coast (D’Croz & O’Dea 2007). In the Caribbean, upwelling only occurs off small parts off the coasts of Colombia and Venezuela.

These environmental differences would be expected to affect the divergence of EP and WA biota, but only if they have been in place for sufficient time to influence their evolution. Microfossil and stable isotope evidence, as well as global climatic modeling, provide estimates of how long ago each of the existing differences came into being. By 4–3 Mya the thermocline in the EP was shallow, permitting upwelling to occur (Fedorov et al. 2006, Rickaby & Halloran 2005). Surface nutrients in the EP have been high for the last 5 My and steadily increasing since then (Cannariato & Ravelo 1997). Pliocene and Pleistocene bivalve shells from the Bay of Panama show evidence of seasonal upwelling (Teranes et al. 1996). In the WA, however, primary productivity has declined

since the Pliocene (Allmon et al. 1996, Jain & Collins 2007). Seasonal changes in zooid size of cupuladriid bryozoans from the Atlantic coasts of Panama and Costa Rica indicate that intra-annual temperatures have fluctuated greatly between roughly 10 and 4 Mya, which O'Dea et al. (2007) attribute to seasonal upwelling. Between 4.25 and 3.45 Mya, this apparent seasonality stopped.

Other differences between the physical environments of the two oceans appear to also have an ancient origin. Salinity was already different at 4.7–4.2 Mya (Keigwin 1982, Haug et al. 2001). Tidal ranges must have been large even in the late Pliocene EP, because it was open to the entire Pacific ocean, whereas in the Caribbean, with its spatially more variable bathymetry and narrow channels between islands (Iturralde-Vinent & MacPhee 1999), they must have been comparable to what they are today. Thus, populations on the two coasts of Central America have been experiencing different regimes of temperature, salinity, productivity, and seasonality for practically the entire time that they have been isolated by the Isthmus.

Biotic Environments on the Two Sides of the Isthmus

Partly owing to the physical differences, partly owing to historical contingency, but mostly for reasons we do not yet understand, the biotic environments on the two sides of the Isthmus are very different. The most prominent difference in shallow water is the absence in the EP of sea grass beds that are so common in the WA. Although *Thalassia* is listed as occurring in the Bay of Panama (Brasier 1975), the extensive communities formed by marine angiosperms (and all the organisms that are associated with them) have yet to be reported from anywhere in the EP (Jackson & D'Croz 1997). These angiosperms are thought to have invaded the Neotropics from the Indo-West Pacific in the Miocene, then to have virtually disappeared from the EP after the closure of the Isthmus (Brasier 1975).

Coral reefs are also very different in the WA and the EP (Cortés 1993, Glynn 1982). In the Caribbean, accreting reefs date back to the early Pleistocene, and a single reef system can cover hundreds of hectares. EP reefs are mostly composed of loose *Pocillopora* framework, do not date further back than the Holocene, and do not extend to more than a few hectares. WA reefs contain three times more species of corals and much more habitat diversity. Bioerosion is lower in the Caribbean than in the EP (Highsmith 1980).

Historical Diversity on the Two Sides of the Isthmus

Taxa with good fossil records indicate that any reconstruction of divergence across the Central American Isthmus should consider the possibility that modern-day patterns have been shaped by extinction. Pulses of extinction and species origination of molluscs and corals in the WA since the Pliocene are well documented, but the record from the EP is poorer. Gastropods and bivalves suffered a pulse of extinction in the Pleistocene (about 2 Mya) that was apparently more severe in the WA than in the EP (Stanley 1986, Todd et al. 2002, Vermeij 1978). However, extinction was balanced by species origination (Allmon et al. 1993; Jackson et al. 1993, 1996b). Scleractinian corals have also been undergoing major faunal turnovers on both sides of the Isthmus since the Pliocene (Budd 2000, Budd et al. 1996). The depauperate modern EP coral fauna may contain some taxa that have survived since the time it was united with the WA, but also bears the effects of major extinctions and possible reintroductions from the central Pacific after it was separated from the Caribbean (Budd 1989, Dana 1975). The diversification rate of benthic foraminifera in the Caribbean increased in the Miocene (L. Collins et al. 1996b), then again in the Pleistocene (L. Collins & Coates 1999); unfortunately there are as yet no equivalent data for this group from the EP.

Although it is impossible to know exactly what happened in the past 3 My to taxa with poor fossil records, biogeographic patterns of extant species suggest that high rates of species turnover may not apply to all groups (Jackson & D’Croz 1997). For example, out of 20 genera of shallow water echinoids in the modern WA and 21 in the EP, 17 are represented in both regions (Chesher 1972), mostly by a single species on each side. The few described fossils in each of the two oceans are similar enough to modern forms to have been included into the extant species (review in Lessios 1998). This pattern would suggest that—unless each lineage extinction on one side was mirrored by the extinction of its sister lineage on the other—nearly every echinoid lineage isolated in each ocean by the Isthmus in the Pliocene has survived to recent times.

Extinctions are relevant to the study of divergence resulting from vicariance because they can cause the false appearance that extant sister species were separated contemporaneously with the barrier formation. The most insidious form of this false pattern occurs when two lineages already differentiated before the closure of the barrier leave behind one representative of each lineage on each side. Without fossil information, one will misconstrue the phylogeny of extant taxa as indicating that the surviving sister species, now one on each side of the barrier, coalesce at the barrier formation, when in fact they have coexisted as separate clades before that time (Knowlton & Weigt 1998, Lessios 1998, Marko 2002). For taxa with poor fossil records, only molecular dating, based on a molecular clock assumption, can guard against this error.

Isolation Between Ocean Biota

Was the completion of the Isthmus the last barrier to isolate populations into their separate realms in the EP and the WA? Large, eurythermal, strong swimmers, such as whales, tuna, and large sharks, still have the potential of crossing between oceans at high latitudes. But what about shallow-water tropical organisms? The rise of the Isthmus would only keep biota from the Atlantic and the Pacific from mingling if all other avenues of exchange were closed. One such potential path is around or across the American continent. The Bering Strait was opening at about the same time that the tropical Isthmus was closing, but as this was also the time of the initiation of Northern Hemisphere glaciations (Nof & Van Gorder 2003), it is unlikely that any tropical organism maintained contact through this connection. In the Southern Hemisphere, the Drake passage also cooled down in the mid-Pliocene 3.5–3.2 Mya (Hodell & Warnke 1991).

A new potential avenue of direct gene flow between the WA and the EP opened with the completion of the Panama Canal in 1914. Nine species of euryhaline fish are known to have crossed through the fresh water of the Canal, but only one is known to have established reproductive populations on the other side (McCosker & Dawson 1975, Rubinoff & Rubinoff 1969). Planktonic organisms and larvae of benthic or pelagic ones may be transiting the Isthmus through ballast water of ships (Chesher 1968). Fouling organisms riding on the hulls of ships may also have been transported. Mitochondrial DNA (mtDNA) haplotypes of *Ophiactis savignyi* in the Caribbean, identical to ones found in the western Pacific, have led Roy & Sponer (2002) to suggest that these sponge-dwelling brittle stars have been recently transported between oceans on ship hulls.

Connections between tropical organisms on the two sides of tropical America through a circum-global route is also a possibility. Global phylogeographies have produced evidence that genes of certain taxa have traveled around the world at some point in the last 3 My (Bowen et al. 2001, 2006; Lessios et al. 2001; Rocha et al. 2005). As the Tethyan Sea, connecting the Indian Ocean to the Atlantic, had become completely closed in the Middle Miocene (Steininger & Rögl 1984), these connections must have been maintained through the Benguela upwelling off Southwest Africa, and through the 5000-km stretch of deep water between the central and the eastern Pacific (the Eastern Pacific Barrier). The Benguela upwelling has been operating at least since the early

Pliocene, intensified at 3.2 Mya, but ameliorated and became intermittent at 2.0–1.4 Mya (Marlow et al. 2000), thus permitting some species to cross. The Eastern Pacific Barrier has been in place for the entire Cenozoic (Grigg & Hey 1992) and accounts for the deepest cladogenic events in many taxa, but is also known to have been breached after the rise of the Isthmus by sea urchins (Lessios et al. 1996, 1998, 2003) and fish (Robertson et al. 2004, Lessios & Robertson 2006). Thus, for globally distributed genera it is not always safe to assume that their species on the two sides of the Isthmus were actually separated by the isthmian schism.

DIVERGENCE OF GEMINATE SPECIES

Molecular Divergence

Molecular divergence has received more attention than any other aspect of differentiation across the Isthmus. The reason is that the relative constancy of rates of molecular evolution through time (the molecular clock hypothesis) permits dating of cladogenic events, information that is otherwise unavailable for organisms with poor fossil records. In order to date such events, a calibration of the rate of substitution in each DNA region is needed. Vicariant events can potentially provide such dates, and no vicariant event is better dated than the isthmian schism. Calibration of rates obtained from the Isthmus present the problem of uncertainty as to the elapsed interval from the point that clades had split to the point that is used to deduce a date—a problem also shared by fossils. One cannot be sure how much earlier than the final isthmian closure a particular pair of geminate clades has split, as one does not know how long after a taxon's appearance a fossil was formed. However, dating by a vicariant event has the advantage that divergence of many taxa from independent phylogenies can be used for the same calibration. Assuming that substitution rates of the same gene in closely related groups are similar, comparisons of divergence between species pairs with members on either side of a barrier can help determine which splitting events occurred simultaneously and are thus likely to be contemporaneous with the emergence of the barrier. Thus, rates obtained from the geminate species of Panama are seen by molecular evolutionists as a means of obtaining a measure of the number of substitutions per unit time. As of January 2008, there have been 251 studies that used a calibration obtained from the isthmian schism to date phylogenetic events that have occurred elsewhere (list available from the author).

Based on the previous section regarding the slow rise of the Isthmus, the early diversion of currents, the possibility that, once completed, the Isthmus may have become breached, and the possibility of circumglobal genetic connections in some marine taxa, one might conclude that dating molecular phylogenies by calibrations obtained from the Isthmus is a hopeless exercise. And yet, a compilation of divergence values in 115 geminate clades with members on the two sides of the Isthmus indicates that—even though there is ample reason for a cautious approach—there is hope that at least a rough measure of rates of molecular divergence can be gleaned.

Measures of transisthmian molecular divergence in coding and noncoding DNA regions of five classes of animals are presented in **Tables 1–4**. The data come from studies, each of which used a model of DNA evolution most appropriate to their entire phylogeny, but I have retrieved the sequences from GenBank to calculate a single measure, Kimura's two-parameter distance, in order to preserve their compatibility. To assess the degree to which selection may affect the comparisons, I have also calculated the divergence of coding genes in silent sites, which is less likely to be adaptive.

Explanations are needed for some of the values that appear in **Tables 2** and **3**. The transisthmian divergence values most often cited in the literature for calibrations of cytochrome oxidase subunit I (COI) are those obtained from alpheid shrimp by Knowlton & Weigt (1998), but some of the sequences used in that paper were subsequently shown by Williams & Knowlton (2001) to be

Table 1 Mean Kimura two-parameter (K_2) percent difference in all sites and in silent sites (K_s) between sister clades of Echinoidea on either side of Central America^a

Genus	Eastern Pacific	Western Atlantic	N_p	N_A	bp	K_2	K_s^b	Reference
Mitochondrial regions								
Cytochrome oxidase subunit I (COI)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1551	4.2	14.7	2
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	13	2	639	4.8	18.2	3, 9
<i>Meoma</i>	<i>ventricosa grandis</i>	<i>ventricosa ventricosa</i>	4	5	640	4.5	16.8	3
<i>Tripneustes</i>	<i>(depressus, gratilla)^d</i>	<i>ventricosus</i>	118	47	639	8.7 ^c	31.7	4
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1551	9.5	37.3	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	24	58	640	9.5	37.7	5
<i>Astropyga</i>	<i>pulvinata</i>	<i>magnifica</i>	4	2	654	9.9	41.5	3
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	2	1551	10.3	40.6	2
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	14	59	631	10.8	43.2	6
<i>Arbacia</i>	<i>stellata (= incisa)</i>	<i>(punctulata, lixula)</i>	19	108	660	13.5	61.8	7
<i>Lytechinus</i>	Pacific clade ^e	<i>(variegatus, williamsi)</i>	13	124	640	13.5	61.4	8
ATP synthetase 8 (ATPase 8)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	44	82	171	2.7	3.9	3
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	10	165	7.8	18.9	5
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	3	3	168	8.1	21.7	9
<i>Tripneustes</i>	<i>depressus</i>	<i>ventricosus</i>	3	4	165	10.1	16.7	9
<i>Lytechinus</i>	<i>panamensis</i>	<i>variegatus</i>	1	1	165	24.3	69.0	9
ATP synthetase 6 (ATPase 6)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	44	82	356	4.4	11.1	3
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	10	349	8.8	31.2	5
<i>Tripneustes</i>	<i>depressus</i>	<i>ventricosus</i>	3	4	350	10.1	29.1	9
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	3	3	349	8.6	26.4	9
<i>Lytechinus</i>	<i>panamensis</i>	<i>variegatus</i>	1	1	388	16.7	80.0	9
Cytochrome <i>b</i> (CytB)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1140	5.0	16.9	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1140	14.0	53.4	2
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	2	1140	14.7	59.7	2
Cytochrome oxidase subunit II (COII)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	687	3.6	11.9	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	687	6.1	22.4	2
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	2	687	10.4	40.8	2
Cytochrome oxidase subunit III (COIII)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	780	4.5	14.7	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	780	10.3	37.5	2
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	2	780	12.4	48.4	2
NADH dehydrogenase subunit 1 (ND1)								
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	978	6.0	19.8	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	978	12.8	47.1	2
<i>Echinometra</i>	<i>vanbrunti</i>	<i>(lucunter, viridis)</i>	1	2	978	13.6	50.2	2

(Continued)

Table 1 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
			NADH dehydrogenase subunit 2 (ND2)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1059	5.9	16.7	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1059	11.8	37.0	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	1059	14.4	51.0	2
			NADH dehydrogenase subunit 3 (ND3)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	351	3.6	8.5	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	351	14.3	42.9	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	351	18.4	68.3	2
			NADH dehydrogenase subunit 4 (ND4)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1392	8.0	23.6	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	1392	16.8	59.8	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1392	17.0	61.9	2
			NADH dehydrogenase subunit 4L (ND4L)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	294	4.7	13.3	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	294	10.9	37.1	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	294	16.8	57.8	2
			NADH dehydrogenase subunit 5 (ND5)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1932	7.8	19.8	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1932	17.0	57.4	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	1932	16.4	54.3	2
			NADH dehydrogenase subunit 6 (ND6)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	504	8.2	26.1	2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	504	15.0	56.4	2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	504	16.4	64.1	2
			Small subunit rDNA (12S)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	954	4.6		2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	957	5.6		2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	954	6.1		2
			Large subunit rDNA (16S)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	1	1	1538	2.7		2
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	1	2	1548	6.5		2
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	1588	7.0		2
<i>Lytechinus</i>	<i>panamensis</i>	<i>variegatus</i>	4	2	611	12.8		9
Nuclear regions								
			Reverse transcriptase of retroviral-like elements (SURL)					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	3	11	250	1.3	1.8	10
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	8	15	250	3.4	5.1	10
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	10	9	253	3.5	7.0	10
<i>Astropyga</i>	<i>pulvinata</i>	<i>magnifica</i>	3	2	253	3.6	4.4	10
<i>Arbacia</i>	<i>stellata</i> (= <i>incisa</i>)	<i>punctulata</i>	2	10	253	4.8	4.6	10, 14
<i>Tripneustes</i>	(<i>depressus</i> , <i>gratilla</i>)	<i>ventricosus</i>	8	5	250	7.6	21.6	10, 14

(Continued)

Table 1 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
			Bindin exons					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	5	19	1260	1.7	3.2	7
<i>Tripneustes</i>	(<i>depressus</i> , <i>gratilla</i>)	<i>ventricosus</i>	10	6	735	2.0	2.6	11
<i>Arbacia</i>	<i>stellata</i> (= <i>incisa</i>)	(<i>punctulata</i> , <i>lixula</i>)	5	10	1298	2.7	9.2	12
<i>Lytechinus</i>	Pacific clade ^c	(<i>variegatus</i> , <i>williamsi</i>)	10	19	819	5.4	12.4	8
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	16	64	938	6.0	11.9	13
			Bindin intron					
<i>Diadema</i>	<i>mexicanum</i>	<i>antillarum-a</i>	3	16	513	4.3		7
<i>Tripneustes</i>	(<i>depressus</i> , <i>gratilla</i>)	<i>ventricosus</i>	10	5	869	4.3		11
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	6	47	516	5.8		13
<i>Arbacia</i>	<i>stellata</i> (= <i>incisa</i>)	(<i>punctulata</i> , <i>lixula</i>)	1	2	400	16.9		12
			Small subunit rDNA (18S)					
<i>Eucidaris</i>	<i>tbouarsi</i>	<i>tribuloides</i>	1	1	575	0.0		9
<i>Astropyga</i>	<i>pulvinata</i>	<i>magnifica</i>	2	1	1768	0.2		9
<i>Echinometra</i>	<i>vanbrunti</i>	(<i>lucunter</i> , <i>viridis</i>)	3	4	1771	0.3		9

^aFor full citation information for the references in this table, see the **Supplementary Literature Cited**. (Follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>.)

Legend: N_P, number of sequences of Pacific clade; N_A, number of sequences of Atlantic clade.

^bDivergence in silent sites estimated according to the method of Pamilo & Bianchi (1993).

^cShading indicates values of divergence assumed to have been initiated at the final closure of the Isthmus.

^dParentheses are used to designate phylogenetic arrangement of clades.

^ePacific clade of *Lytechinus*: [(*pictus*, *anamesus*)(*semituberculatus*, *panamensis*)].

References: 2, Medina & Lessios, unpublished; 3, Lessios et al. 2001; 4, Lessios et al. 2003; 5, Lessios et al. 1999; 6, McCartney et al. 2000; 7, H. Lessios et al., unpublished data; 8, Zigler & Lessios 2004; 9, H. Lessios, unpublished; 10, Gonzalez & Lessios 1999; 11, Zigler & Lessios 2003; 12, Metz et al. 1998; 13, McCartney & Lessios 2004; 14, Springer et al. 1995.

pseudogenes. For this reason, the values in **Table 2** are based on sequences from Williams et al. (2001), which were mostly obtained from complementary DNA. The newer data have revised rate estimates somewhat, but they have not changed the main conclusions of Knowlton & Weigt (1998). The same cannot be said for the conclusions of Bellwood et al. (2004) regarding transisthmian divergence in angelfish (**Table 3**). Their rejection of a calibration based on the isthmus in favor of one obtained from fossils was based on an erroneous topology of *Holacanthus*, which showed the Atlantic *Holacanthus bermudensis* as the geminate of the Pacific *H. passer*. A reanalysis of their sequences shows that the correct sister clade of *H. passer* is composed of both *H. bermudensis* and *H. ciliaris*; the split between the two Atlantic species occurred after the transisthmian divergence. The revised rates for 12S and 16S based on this topology agree well with that obtained from other species (**Table 3**) and with Bellwood et al.'s fossil estimates. Many of the other comparisons in **Tables 1–4** are based on a single sequence from each side of the Isthmus and thus lack internal checks for possible species misidentifications, PCR artifacts, or the existence of pseudogenes. Partial sequences of the same gene from different studies are not always from exactly the same DNA region. The good agreement between divergence estimates obtained from the entire *COI* gene and from a 640-base pair (bp) segment of it in sea urchins (**Table 1**) suggests that this may not be introducing major artifacts in the comparisons.

Arrangement of geminate clades in ascending order of transisthmian divergence in each gene in **Tables 1–4** facilitates comparisons of the degree to which relative differentiation across the Isthmus is the same in different genes. There is good correlation between K₂ and K_s, indicating

Table 2 Mean Kimura two-parameter (K_2) percent difference in all sites and in silent sites (K_s) between sister clades of crustaceans on either side of Central America^a

Genus	Eastern Pacific	Western Atlantic	N_P	N_A	bp	K_2	K_s^b	Reference
Mitochondrial regions								
						Cytochrome oxidase subunit I (COI)		
<i>Sesarma</i>	<i>rhizophorae</i>	<i>S. reticulatum</i> clade ^c	1	3	551	4.1 ^d	13.6	1
<i>Alpheus</i>	<i>antepenultimus A</i>	<i>chacei</i>	3	2	564	5.4	16.9	2
<i>Sesarma</i>	(<i>sulcatum</i> , <i>aequatoriale</i>) ^e	<i>crassipes</i>	2	1	551	6.2	23.3	1
<i>Alpheus</i>	<i>rostratus</i>	<i>paracrinatus</i> spot	2	3	564	6.4	24.1	2
<i>Alpheus</i>	<i>colombiensis</i>	<i>estuairensis</i>	3	3	564	6.8	25.3	2
<i>Alpheus</i>	<i>websteri</i>	<i>websteri</i>	2	2	564	7.3	24.9	2
<i>Alpheus</i>	<i>cylindricus</i>	<i>cylindricus</i>	2	2	637	8.7	31.0	2
<i>Synalpheus</i>	<i>brevicarpus</i>	<i>brevicarpus</i>	2	2	541	8.7	31.1	3
<i>Alpheus</i>	<i>floridanus B'</i>	<i>floridanus B</i>	2	2	564	9.4	36.4	2
<i>Alpheus</i>	<i>canalis</i> -sp. <i>B</i> (blue) = <i>millsae</i>	<i>nuttingi</i>	2	3	564	9.4	37.1	2
<i>Alpheus</i>	<i>paracrinatus</i> no spot	<i>paracrinatus</i> no spot	2	4	564	9.5	37.1	2
<i>Alpheus</i>	<i>panamensis</i>	<i>formosus</i> -sp. <i>A</i>	1	2	564	9.5	38.4	2
<i>Synalpheus</i>	<i>digueti</i>	<i>minus</i>	2	2	541	9.5	33.6	3
<i>Alpheus</i>	<i>bouvieri</i>	<i>bouvieri</i>	2	2	564	11.0	46.6	2
<i>Xiphopenaeus</i>	<i>riveti</i>	sp. 2	4	3	621	11.1	41.5	4
<i>Alpheus</i>	<i>malleator</i>	<i>malleator</i>	2	2	564	11.5	50.1	2
<i>Synalpheus</i>	<i>fritzmuelleri</i>	<i>fritzmuelleri</i>	2	1	541	12.1	53.8	3
<i>Penaeus</i>	<i>vannamei</i>	<i>P. duorarum</i> clade ^f	1	3	558	12.1	51.6	5
<i>Alpheus</i>	<i>umbo</i>	<i>schmitti</i>	1	1	564	13.2	56.2	2
<i>Alpheus</i>	<i>saxidomus</i>	<i>simus</i>	2	2	564	13.9	54.0	2
<i>Alpheus</i>	<i>floridanus A'</i>	<i>floridanus A</i>	2	2	564	15.1	67.0	2
<i>Alpheus</i>	<i>normanni</i>	<i>normanni</i> Brazil	1	2	564	15.5	81.4	2
<i>Emerita</i>	<i>ratbbunae</i>	<i>E. brasiliensis</i> clade ^g	1	5	626	15.8	93.7	6
<i>Alpheus</i>	(<i>naos</i> , <i>aequus</i>)	<i>christofferseni</i>	2	2	649	17.8	83.8	11
<i>Alpheus</i>	<i>crutulifrons</i>	<i>crutulifrons</i>	2	3	564	18.9	97.9	2
<i>Austinixa</i>	<i>felipensis</i>	<i>A. cristata</i> clade ^h	1	6	589	19.5	> 100	7
<i>Synalpheus</i>	<i>bannerorum</i>	<i>dominicensis</i>	1	1	541	22.6	> 100	3
						Small subunit rDNA (12S)		
<i>Callinectes</i>	<i>toxotes</i>	<i>sapidus</i>	1	1	411	2.0		12
<i>Callinectes</i>	<i>arcuatus</i>	<i>ornatus</i>	2	2	411	3.0		12
						Large subunit rDNA (16S)		
<i>Chtbamalus</i>	" <i>mexicanus</i> "	<i>proteus</i>	1	1	489	0.6		8
<i>Petrolisthes</i>	<i>P. armatus</i>	<i>P. armatus</i>	1	1	514	1.6		9
<i>Callinectes</i>	<i>toxotes</i>	<i>sapidus</i>	1	3	574	1.9		12
<i>Sesarma</i>	<i>rhizophorae</i>	<i>reticulatum</i> clade	1	3	502	2.0		1
<i>Callinectes</i>	<i>arcuatus</i>	<i>ornatus</i>	2	4	545	2.1		12
<i>Euraphia</i>	<i>eastropacensis</i>	<i>rhizophorae</i>	1	1	489	2.3		8
<i>Uca</i> (<i>Minuca</i>)	<i>vocator</i>	<i>vocator</i>	1	1	462	2.4		10
<i>Sesarma</i>	(<i>sulcatum</i> , <i>aequatoriale</i>)	<i>crassipes</i>	2	1	507	2.9		1
<i>Petrolisthes</i>	<i>P. galathinus</i>	<i>P. galathinus</i>	3	8	515	3.7		9

(Continued)

Table 2 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
<i>Petrolisthes</i>	<i>tonsorius</i>	<i>tonsorius</i>	1	1	518	4.9		9
<i>Synalpheus</i>	<i>digueti</i>	<i>minus</i>	1	1	497	5.8		3
<i>Petrolisthes</i>	<i>glasselli</i>	<i>rosariensis</i>	1	4	514	6.7		9
<i>Synalpheus</i>	<i>brevicarpus</i>	<i>brevicarpus</i>	1	1	509	6.8		3
<i>Synalpheus</i>	<i>fritzmuelleri</i>	<i>fritzmuelleri</i>	1	1	507	8.2		3
<i>Austinixa</i>	<i>felipensis</i>	<i>A. cristata</i> clade	1	6	555	8.3		7
<i>Petrolisthes</i>	(<i>baigae</i> , <i>hirtispinosus</i>)	<i>marginatus</i>	2	2	515	11.2		9
<i>Synalpheus</i>	<i>bannerorum</i>	<i>dominicensis</i>	1	1	506	15.2		3

Nuclear regions

		Glucose 6 phosphate isomerase (GPI)						
<i>Alpheus</i>	<i>floridanus</i> A'	<i>floridanus</i> A	1	1	466	0.0	0.0	2
<i>Alpheus</i>	<i>floridanus</i> B'	<i>floridanus</i> B	1	1	466	0.0	0.0	2
<i>Alpheus</i>	<i>malleator</i>	<i>malleator</i>	1	1	466	0.2	0.0	2
<i>Alpheus</i>	<i>rostratus</i>	<i>paracrinitus</i> spot	2	1	466	0.4	1.3	2
<i>Alpheus</i>	<i>saxidomus</i>	<i>simus</i>	1	1	466	0.4	1.4	2
<i>Alpheus</i>	<i>panamensis</i>	<i>formosus</i> sp.A	1	2	466	0.4	0.7	2
<i>Alpheus</i>	<i>bouvieri</i>	<i>bouvieri</i>	2	1	466	0.6	0.6	2
<i>Alpheus</i>	<i>antepenultimus</i>	<i>chacei</i>	2	1	466	0.6	0.7	2
<i>Alpheus</i>	<i>cylindricus</i>	<i>cylindricus</i>	1	1	466	0.6	1.3	2
<i>Alpheus</i>	<i>websteri</i>	<i>websteri</i>	1	1	466	0.6	1.3	2
<i>Alpheus</i>	<i>paracrinitus</i> no spot	<i>paracrinitus</i> no spot	2	2	466	0.7	2.2	2
<i>Alpheus</i>	<i>colombiensis</i>	<i>estuarensis</i>	2	2	466	1.0	0.0	2
<i>Alpheus</i>	<i>canalissp.B</i> (blue) = <i>millsae</i>	<i>nuttingi</i>	2	2	466	1.1	1.6	2
<i>Alpheus</i>	<i>normanni</i>	<i>normanni</i> Brazil	1	1	466	1.5	7.8	2
<i>Alpheus</i>	<i>umbo</i>	<i>schmitti</i>	2	2	466	1.9	5.7	2
<i>Alpheus</i>	<i>crutulifrons</i>	<i>crutulifrons</i>	1	1	388	7.7	18.2	2
		Elongation factor 1 α (EF-1 α)						
<i>Alpheus</i>	<i>websteri</i>	<i>websteri</i>	1	1	401	0.0	0.0	2
<i>Alpheus</i>	<i>umbo</i>	<i>schmitti</i>	2	2	401	0.1	0.7	2
<i>Alpheus</i>	<i>floridanus</i> A'	<i>floridanus</i> A	1	1	401	0.3	0.8	2
<i>Alpheus</i>	<i>rostratus</i>	<i>paracrinitus</i> spot	1	1	401	0.3	0.8	2
<i>Alpheus</i>	<i>colombiensis</i>	<i>estuarensis</i>	1	2	401	0.3	0.8	2
<i>Alpheus</i>	<i>panamensis</i>	<i>formosus</i> sp.A	1	1	401	0.3	1.4	2
<i>Alpheus</i>	<i>normanni</i>	<i>normanni</i> Brazil	1	1	401	0.5	2.3	2
<i>Alpheus</i>	<i>paracrinitus</i> no spot	<i>paracrinitus</i> no spot	2	2	401	0.5	1.6	2
<i>Alpheus</i>	<i>malleator</i>	<i>malleator</i>	2	1	401	0.5	2.2	2
<i>Alpheus</i>	<i>antepenultimus</i>	<i>chacei</i>	2	1	401	0.6	2.3	2
<i>Alpheus</i>	<i>bouvieri</i>	<i>bouvieri</i>	1	1	401	0.8	0.8	2
<i>Alpheus</i>	<i>floridanus</i> B'	<i>floridanus</i> B	1	1	401	0.8	3.0	2
<i>Alpheus</i>	<i>cylindricus</i>	<i>cylindricus</i>	2	1	401	0.8	2.2	2

(Continued)

Table 2 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
<i>Alpheus</i>	<i>canalisp.B (blue) = millsae</i>	<i>nuttingi</i>	2	1	401	0.9	2.8	2
<i>Alpheus</i>	<i>saxidomus</i>	<i>simus</i>	1	1	401	1.5	5.8	2
<i>Alpheus</i>	<i>cristulifrons</i>	<i>cristulifrons</i>	1	1	401	2.3	7.1	2

^aFor full citation information for the references in this table, see the **Supplementary Literature Cited**. Legend: N_P, number of sequences of Pacific clade; N_A, number of sequences of Atlantic clade.

^bDivergence in silent sites estimated according to the method of Pamilo & Bianchi (1993).

^c*S. reticulatum* clade: (*reticulatum*, *sp. nr. reticulatum*, *curacaoense*).

^dShading indicates values of divergence assumed to have been initiated at the final closure of the Isthmus.

^eParentheses are used to designate phylogenetic arrangement of clades.

^f*P. duorarum* clade: [*duorarum (paulensis, setiferus)*].

^g*E. brasiliensis* clade: [*brasiliensis (benedicti, talpoida)*].

^h*A. cristata* clade: *cristata* {[*cbacci, bebreae*][*gorei (bardyi, aidae)*]}.**Rose***Add 4th-level brackets*

References: 1, Schubart et al. 1998; 2, Williams et al. 2001; 3, Morrison et al. 2004; 4, Gusmao et al. 2006; 5, Baldwin et al. 1998; 6, Haye et al. 2002; 7, Harrison 2004; 8, Wares 2001; 9, Hiller et al. 2006; 10, Strumbauer et al. 1996; 11, Anker et al. 2007; 12, Robles et al. 2007.

that differences between divergence values of different geminate clades are not due to selective constraints on a gene of a particular species pair. Nuclear genes clearly do not diverge at a fast enough rate to provide information on variation between transisthmian divergences. Relative divergences in different mitochondrial DNA regions would be expected to agree with each other because of lack of recombination, which would cause the coalescence process to affect them in the same manner. They generally do, but some regions stand out as exceptions. These are 16S in crustaceans and ATPase8, 12S and D-loop in fish. What do the rest of the data have to tell us regarding the question of how separation by the isthmus affected different geminate clades?

Early studies of isozyme divergence across the Isthmus took for granted that geminate species were isolated at roughly the same time and sought explanations for the variation in the amount of divergence observed between geminate pairs (e.g., Bermingham & Lessios 1993; Lessios 1979, 1981; Vawter et al. 1980). Examination of **Tables 1–4**, however, shows that if there is any regularity to molecular evolution, then sister species on each side of the Isthmus were most likely isolated from each other during different time intervals, even in cases in which morphological divergence would suggest otherwise (such as the fish *Heteropriacanthus*, **Table 3**). The challenge, both for the sake of understanding the history of WA and EP biota and for calibrating molecular clocks, is to determine which species were separated at each time interval. This is a question with two components: (a) Which species were separated at the same time? And (b) which cluster of divergence values represents separation by the Isthmus completion?

The difficulty with the first question lies in deciding how much of the variation in transisthmian divergence is due to different times since separation, and how much due to other factors, such as different effective population sizes, different mutation rates, or different modes and intensities of selection. Hickerson et al. (2006) devised an approximate Bayesian computation method for taking into account variation owing to stochasticity in the coalescence and mutational processes in answering this question. Applying this method to COI divergence between WA and EP members of sea urchin geminate pairs (**Table 1**), Hickerson et al. concluded that the null hypothesis of simultaneous separation could not be rejected for most transisthmian pairs of species. The exception was the pair that consists of *Diadema antillarum* and *D. mexicanum*. By this analysis, they have become isolated more recently, a conclusion also supported by the worldwide phylogeny of the genus (Lessios et al. 2001), which shows a close relationship between Atlantic and Indian Ocean populations. A statistical analysis of the rest of the data listed in **Tables 1–4** is complicated by small intraspecific sample sizes in most of the transisthmian comparisons. Nevertheless, the

Table 3 Mean Kimura two-parameter (K_2) percent difference in all sites and in silent sites (K_s) between sister clades of fishes on either side of Central America

Genus	Eastern Pacific	Western Atlantic	N_P	N_A	bp	K_2	K_s^b	Reference	
Mitochondrial regions									
			Cytochrome oxidase subunit I (COI)						
<i>Melichthys</i>	<i>niger</i>	<i>niger</i>	4	2	650	0.2	0.4	1	
<i>Diodon</i>	<i>hystrix</i>	<i>hystrix</i>	5	3	650	0.6	1.2	1	
<i>Alutera</i>	<i>scripta</i>	<i>scripta</i>	2	4	650	0.9	2.3	1	
<i>Mulloidichthys</i>	<i>dentatus</i>	<i>martinicus</i>	5	5	650	1.3	3.2	1	
<i>Abudefduf</i>	<i>concolor</i>	<i>taurus</i>	8	6	628	1.4	4.0	2	
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	6	6	650	1.6	3.1	1	
<i>Rypticus</i>	<i>bicolor</i>	<i>saponaceus</i>	8	4	650	3.2 ^c	8.5	1	
<i>Lutjanus</i>	<i>argentiventris</i>	<i>apodus</i>	11	6	650	3.5	10.2	1	
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	3	3	650	4.4	12.7	1	
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	8	10	628	4.5	13.6	1	
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	10	2	650	4.8	14.6	1	
<i>Holacanthus</i>	<i>passer</i>	<i>ciliaris</i>	8	4	650	4.9	14.6	1	
<i>Gerres</i>	<i>cinereus</i>	<i>cinereus</i>	3	4	650	5.1	15.3	1	
<i>Scorpaena</i>	<i>mystes</i>	<i>plumieri</i>	5	3	650	5.5	16.7	1	
<i>Halichoeres</i>	<i>nicholsi</i>	<i>H. bivittatus</i> clade ^d	1	4	650	7.1	26.2	3	
<i>Chromis</i>	<i>atrilobata</i>	<i>multilineata</i>	8	4	650	9.4	30.2	1	
<i>Halichoeres</i>	<i>dispilus</i>	<i>pictus</i>	1	1	650	10.2	41.9	3	
<i>Chaetodon</i>	<i>humeralis</i>	<i>striatus</i>	8	4	650	10.4	35.7	1	
<i>Heteropriacanthus</i>	<i>cruentatus</i>	<i>cruentatus</i>	4	6	650	10.7	39.1	1	
<i>Ophioblennius</i>	<i>steindachneri</i>	<i>atlanticus</i>	8	8	650	12.4	43.1	1	
			ATP synthetase 8 (ATPase 8)						
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	1	1	168	0.0	0.0	4	
<i>Diodon</i>	<i>hystrix</i>	<i>hystrix</i>	3	2	168	0.0	0.0	5	
<i>Mulloidichthys</i>	<i>M. dentatus</i> clade ^e	<i>martinicus</i>	117	45	168	0.1	0.2	6	
<i>Alutera</i>	<i>scripta</i>	<i>scripta</i>	2	2	168	0.3	0.9	5	
<i>Diodon</i>	<i>bolacanthus</i>	<i>bolacanthus</i>	55	8	168	0.3	1.2	5	
<i>Abudefduf</i>	<i>concolor</i>	<i>taurus</i>	1	1	168	0.6	1.8	4	
<i>Melichthys</i>	<i>niger</i>	<i>niger</i>	2	2	168	0.6	1.8	5	
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	2	2	168	1.2	3.5	5	
<i>Holacanthus</i>	<i>passer</i>	<i>ciliaris</i>	2	2	168	1.2	1.8	5	
<i>Gerres</i>	<i>cinereus</i>	<i>cinereus</i>	2	2	168	2.7	13.2	8	
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	5	4	168	2.7	13.2	8	
<i>Lutjanus</i>	<i>argentiventris</i>	<i>apodus</i>	2	4	168	4.0	12.2	5	
<i>Tylosurus acus</i>	<i>(a. melanotus, a. pacificus)</i> ^f	<i>T. a. acus</i> clade ⁱ	6	5	168	4.2	13.0	9	
<i>Chromis</i>	<i>atrilobata</i>	<i>multilineata</i>	2	2	168	4.3	13.1	5	
<i>Scomberomorus</i>	<i>(sierra, concolor)</i>	<i>(regalis, brasiliensis)</i>	3	11	168	4.7	15.9	7	
<i>Rypticus</i>	<i>bicolor</i>	<i>saponaceus</i>	12	11	168	5.4	23.7	8	
<i>Ophioblennius</i>	<i>steindachneri</i>	<i>atlanticus</i>	1	1	168	5.6	22.7	5	
<i>Chaetodipterus</i>	<i>zonatus</i>	<i>faber</i>	2	2	168	6.4	20.9	8	
<i>Stegastes</i>	<i>S. arcifrons</i> clade ^g	<i>S. fuscus</i> clade ^h	17	52	168	11.4	31.2	5	

(Continued)

Table 3 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
<i>Chaetodon</i>	<i>humeralis</i>	<i>striatus</i>	2	2	168	14.0	45.0	5
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	2	168	15.6	31.6	9
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	4	3	168	19.6	19.1	5
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (S. sp.)]	2	10	168	20.0	44.4	9
<i>Heteropriacanthus</i>	<i>cruentatus</i>	<i>cruentatus</i>	32	77	168	25.2	57.9	6
ATP synthetase 6 (ATPase 6)								
<i>Diodon</i>	<i>bystrix</i>	<i>bystrix</i>	3	2	684	0.0	0.0	5
<i>Alutera</i>	<i>scripta</i>	<i>scripta</i>	2	2	684	0.1	1.9	5
<i>Melichthys</i>	<i>niger</i>	<i>niger</i>	2	2	684	0.4	1.0	5
<i>Diodon</i>	<i>bolacanthus</i>	<i>bolacanthus</i>	55	8	684	0.6	1.4	5
<i>Mulloidichthys</i>	<i>M. dentatus</i> clade ^c	<i>martinicus</i>	117	45	684	0.7	2.0	6
<i>Abudefduf</i>	<i>concolor</i>	<i>taurus</i>	1	1	684	1.6	4.8	4
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	2	2	684	1.9	5.5	5
<i>Chaetodipterus</i>	<i>zonatus</i>	<i>faber</i>	2	2	684	3.0	8.3	8
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	3	2	684	3.8	10.8	8
<i>Gerres</i>	<i>cinereus</i>	<i>cinereus</i>	2	2	684	3.9	12.1	8
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	1	1	684	4.3	12.3	4
<i>Rypticus</i>	<i>bicolor</i>	<i>saponaceus</i>	12	11	684	4.6	11.4	8
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	6	5	684	5.7	16.9	9
<i>Holacanthus</i>	<i>passer</i>	<i>ciliaris</i>	2	2	684	5.8	13.6	5
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	4	3	684	6.7	14.3	5
<i>Lutjanus</i>	<i>argentiventris</i>	<i>apodus</i>	2	4	684	6.8	20.4	5
<i>Scomberomorus</i>	(<i>sierra</i> , <i>concolor</i>)	(<i>regalis</i> , <i>brasiliensis</i>)	3	11	684	6.9	21.1	7
<i>Stegastes</i>	<i>S. arcifrons</i> clade ^g	<i>S. fuscus</i> clade ^h	17	52	687	11.9	41.1	6
<i>Ophioblennius</i>	<i>steindachneri</i>	<i>atlanticus</i>	1	1	684	12.7	54.1	5
<i>Strongylura</i>	<i>exilis</i>	(<i>marina</i> S. sp.)	2	10	684	14.6	45.2	9
<i>Chromis</i>	<i>atrilobata</i>	<i>multilineata</i>	2	2	684	15.4	51.7	5
<i>Chaetodon</i>	<i>humeralis</i>	<i>striatus</i>	2	2	684	16.0	55.5	5
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	2	684	16.6	55.4	9
<i>Heteropriacanthus</i>	<i>cruentatus</i>	<i>cruentatus</i>	32	77	684	20.9	65.8	6
Cytochrome <i>b</i> (CytB)								
<i>Abudefduf</i>	<i>concolor</i>	<i>taurus</i>	1	1	1140	1.7	4.8	4
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	8	5	692	2.0	6.2	10
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	8	15	692	3.3	9.6	10
<i>Sphyrna</i>	<i>tiburo</i>	<i>tiburo</i>	1	1	1146	3.5	10.3	11
<i>Rypticus</i>	<i>bicolor</i>	<i>saponaceus</i>	2	2	790	3.6	11.6	12
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	3	3	800	4.4	13.6	9
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	1	1	1140	4.8	15.7	4
<i>Hippocampus</i>	(<i>ingens</i> , <i>fisheri</i>)	(<i>reidi</i> , <i>algiricus</i>)	6	4	718	5.1	15.5	13
<i>Alphistes</i>	(<i>immaculatus</i> , <i>multiguttatus</i>)	<i>afer</i>	2	1	491	7.2	28.1	14
<i>Dermatolepis</i>	<i>dermatolepis</i>	<i>inermis</i>	1	1	437	8.2	24.5	14
<i>Chromis</i>	<i>atrilobata</i>	<i>multilineata</i>	4	2	616	9.9	37.8	15

(Continued)

Table 3 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
<i>Evorthodus</i>	<i>minutus</i>	<i>lyricus</i>	1	1	610	13.5	57.6	28
<i>Ophioblennius</i>	<i>steindachneri</i>	<i>atlanticus</i>	4	5	630	14.2	64.3	16
<i>Strongylura</i>	<i>exilis</i>	(<i>marina</i> , <i>S. sp.</i>)	1	3	800	14.2	55.2	9
<i>Nicholsina</i>	<i>denticulata</i>	<i>usta</i>	1	3	615	19.5	> 100	23
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	800	21.6	76.3	9
			NADH dehydrogenase subunit 2 (ND2)					
<i>Scomberomorus</i>	(<i>sierra</i> , <i>concolor</i>)	(<i>regalis</i> , <i>brasiliensis</i>)	3	4	1047	6.5	20.2	7
			NADH dehydrogenase subunit 5 (ND5)					
<i>Centropomus</i>	<i>robalito</i>	<i>ensiferus</i>	1	1	825	17.0	54.0	17
			NADH dehydrogenase subunit 6 (ND6)					
<i>Centropomus</i>	<i>robalito</i>	<i>ensiferus</i>	1	1	66	12.1	29.4	17
			Control region (D-loop)					
<i>Sphyrna</i>	<i>lewini</i>	<i>lewini</i>	11	9	548	2.2		18
<i>Hippocampus</i>	(<i>ingens</i> , <i>fisheri</i>)	(<i>reidi</i> , <i>algericus</i>)	5	5	379	4.2		13
<i>Merluccius</i>	<i>albidus</i>	<i>productus</i>	1	1	408	5.4		19
<i>Rypticus</i>	<i>bicolor</i>	<i>saponaceus</i>	9	10	536	9.7		5
<i>Abudefduf</i>	<i>concolor</i>	<i>taurus</i>	1	2	648	9.8		5
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	1	2	587	11.3		5
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	2	2	594	11.4		5
<i>Mulloidichthys</i>	<i>M. dentatus</i> clade ^e	<i>martinicus</i>	117	45	582	11.5		6
<i>Centropomus</i>	<i>robalito</i>	<i>ensiferus</i>	1	1	931	17.6		5
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	2	2	596	19.5		5
<i>Holacanthus</i>	<i>passer</i>	<i>ciliaris</i>	1	2	632	22.4		5
<i>Gerres</i>	<i>cinereus</i>	<i>cinereus</i>	2	2	682	22.0		5
			Small subunit rDNA (12S)					
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	1	1	417	0.2		26
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	3	3	431	0.8		9
<i>Epinephelus</i>	<i>clippertonensis</i>	<i>adscencionis</i>	1	1	412	0.9		26
<i>Dermatolepis</i>	<i>dermatolepis</i>	<i>inermis</i>	1	1	433	1.0		14
<i>Cephalopholis</i>	<i>panamensis</i>	<i>cruentatus</i>	1	1	412	1.2		26
<i>Mycteroperca</i>	<i>jordani</i>	(<i>bonaci</i> , <i>venenosa</i>)	1	2	421	1.6		26
<i>Holacanthus</i>	<i>passer</i>	(<i>ciliaris</i> , <i>bermudensis</i>)	1	2	440	1.8		21
<i>Pomacanthus</i>	(<i>paru</i> , <i>arcuatus</i>)	<i>zonipectus</i>	2	1	346	2.1		21
<i>Halichoeres</i>	<i>nicholsi</i>	<i>H. bividatus</i> clade ^d	1	4	733	2.5		3
<i>Alpbastes</i>	(<i>immaculatus</i> , <i>multiguttatus</i>)	<i>afer</i>	2	1	439	3.2		14
<i>Halichoeres</i>	<i>dispilus</i>	<i>pictus</i>	1	1	733	4.1		3
<i>Nicholsina</i>	<i>denticulata</i>	<i>usta</i>	1	3	387	4.7		23
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (<i>S. sp.</i>)]	1	8	433	5.1		9
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	3	433	10.9		9
			Large subunit rDNA (16S)					
<i>Holacanthus</i>	<i>passer</i>	(<i>ciliaris</i> , <i>bermudensis</i>)	1	1	539	0.7		21
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	3	3	566	0.7		9
<i>Halichoeres</i>	<i>nicholsi</i>	<i>H. bividatus</i> clade ^d	1	4	610	1.3		3

(Continued)

Table 3 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference	
<i>Halichoeres</i>	<i>dispilus</i>	<i>pictus</i>	1	1	610	1.5		3	
<i>Centropomus</i>	<i>medius</i>	<i>pectinatus</i>	1	1	647	1.6		20	
<i>Chromis</i>	<i>atrilobata</i>	<i>multilineata</i>	4	2	539	1.7		15	
<i>Dermatolepis</i>	<i>dermatolepis</i>	<i>inermis</i>	1	1	600	1.7		14	
<i>Hippocampus</i>	(<i>ingens, fisberi</i>)	(<i>reidi, algiricus</i>)	6	4	527	1.9		13	
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	1	1	578	2.1		26	
<i>Mycteroperca</i>	<i>jordani</i>	(<i>bonaci, venenosa</i>)	1	28	610	2.2		26, 27	
<i>Alphestes</i>	(<i>immaculatus, multiguttatus</i>)	<i>afer</i>	2	1	603	2.3		14	
<i>Epinephelus</i>	(<i>clippertonensis, labriformis</i>)	<i>adscencionis</i>	2	1	565	2.6		26	
<i>Cephalopholis</i>	<i>panamensis</i>	<i>cruentatus</i>	1	1	590	2.6		26	
<i>Centropomus</i>	<i>robalito</i>	<i>ensiferus</i>	1	1	647	2.7		20	
<i>Pomacanthus</i>	(<i>paru, arcuatus</i>)	<i>zonipectus</i>	2	1	549	2.9		21	
<i>Centropomus</i>	<i>poeyi</i>	<i>undecimalis</i>	1	1	647	5.3		20	
<i>Nicholsina</i>	<i>denticulata</i>	<i>usta</i>	1	3	551	5.4		23–25	
<i>Strongylura</i>	<i>exilis</i>	(<i>marina</i> S. sp.)	1	3	565	8.2		9	
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	565	11.2		9	
Nuclear regions									
			Histone subunit 3 (H3)						
<i>Epinephelus</i>	(<i>clippertonensis, labriformis</i>)	<i>adscencionis</i>	2	1	348	0.3	0.0	26	
<i>Mycteroperca</i>	<i>jordani</i>	(<i>bonaci, venenosa</i>)	1	2	363	0.6	0.0	26	
<i>Parantbias</i>	<i>colonus</i>	<i>furcifer</i>	1	1	348	2.6	0.8	26	
<i>Alphestes</i>	<i>immaculatus</i>	<i>afer</i>	1	1	346	2.8	2.7	26	
			S7 ribosomal protein						
<i>Anisotremus</i>	<i>interruptus</i>	<i>surinamensis</i>	8	3	529	0.4		10	
<i>Hippocampus</i>	(<i>ingens, fisberi</i>)	(<i>reidi, algiricus</i>)	5	4	579	0.9		13	
<i>Anisotremus</i>	<i>taeniatus</i>	<i>virginicus</i>	8	14	529	1.7		10	
			Aldolase						
<i>Scomberomorus</i>	(<i>sierra, concolor</i>)	(<i>regalis, brasiliensis</i>)	3	4	110	0.0	0.0	7	
<i>Hippocampus</i>	(<i>ingens, fisberi</i>)	(<i>reidi, algiricus</i>)	2	2	186	0.5	0.0	13	
			Tmo-4C4 (anonymous locus)						
<i>Dermatolepis</i>	<i>dermatolepis</i>	<i>inermis</i>	1	1	542	0.0		14	
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (S. sp.)]	2	2	484	0.2		22	
<i>Mycteroperca</i>	<i>jordani</i>	(<i>bonaci, venenosa</i>)	1	2	544	0.4		26	
<i>Alphestes</i>	(<i>immaculatus, multiguttatus</i>)	<i>afer</i>	2	1	546	0.8		14	
<i>Epinephelus</i>	(<i>clippertonensis, labriformis</i>)	<i>adscencionis</i>	2	1	547	0.9		26	
<i>Cephalopholis</i>	<i>panamensis</i>	<i>cruentatus</i>	1	1	531	1.2		26	
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	2	484	1.5		22	
			Recombination activating gene-1 (<i>RAG1</i>)						
<i>Abudefduf</i>	<i>trosbelii</i>	<i>saxatilis</i>	1	1	1500	0.3	0.6	4	
<i>Nicholsina</i>	<i>denticulata</i>	<i>usta</i>	1	2	496	1.7	3.3	23	
			Recombination activating gene-2 (<i>RAG2</i>)						
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (S. sp.)]	2	2	1000	1.3	3.1	22	
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	2	1000	1.5	4.0	22	

(Continued)

Table 3 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
			Creatine kinase exon 1					
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	1	1	154	0.0	0.0	9
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (<i>S. sp.</i>)]	1	2	154	0.7	3.3	9
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	154	2.7	3.8	9
			Creatine kinase exon 2					
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	1	1	120	0.0	0.0	9
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	120	0.8	0.0	9
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (<i>S. sp.</i>)]	1	2	120	1.7	5.1	9
			Creatine kinase exon 2b					
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	1	1	205	0.0	0.0	9
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (<i>S. sp.</i>)]	1	2	207	0.5	0.0	9
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	207	2.0	0.0	9
			Creatine kinase intron 1					
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	1	1	427	0.2		9
<i>Strongylura</i>	<i>exilis</i>	[<i>marina</i> (<i>S. sp.</i>)]	1	2	424	0.7		9
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	424	1.2		9
			Creatine kinase intron 2					
<i>Strongylura</i>	<i>scapularis</i>	<i>fluviatilis</i>	1	1	113	0.9		9
<i>Tylosurus acus</i>	(<i>a. melanotus</i> , <i>a. pacificus</i>)	<i>T. a. acus</i> clade ⁱ	1	1	116	0.9		9
<i>Strongylura</i>	<i>exilis</i>	[(<i>marina</i> (<i>S. sp.</i>)]	1	2	113	1.3		9

^aFor full citation information for the references in this table, see the **Supplementary Literature Cited**. Legend: N_P, number of sequences of Pacific clade; N_A, number of sequences of Atlantic clade.

^bDivergence in silent sites estimated according to the method of Pamilo & Bianchi (1993).

^cShading indicates values of divergence assumed to have been initiated at the final closure.

^d*H. bivittatus* clade: [(*bivittatus*, *garnoti*) (*radiatus*, *poeyi*)].

^e*M. dentatus* clade: (*dentatus*, *vanicolensis*, *mimicus*).

^fParentheses are used to designate phylogenetic arrangement of clades.

^g*S. arcifrons* clade: [(*arcifrons*, *redemptus*) *acapulcoensis*].

^h*S. fuscus* clade: {[(*fuscus trinidensis*) *imbricatus*] *planifrons* [*rocasensis*, *sanctipauli*]}.
ⁱ*T. acus* clade: [*a. rafale* (*a. imperialis*, *a. acus*)].

References: 1, Bermingham et al. 1997; 2, Lessios et al. 1995; 3, Barber & Bellwood 2005; 4, Qeunouille et al. 2004; 5, H. Lessios, unpublished data; 6, H. Lessios et al., unpublished data; 7, Banford et al. 1999; 8, Lessios & Robertson 2006; 9, Banford et al. 2004; 10, Bernardi & Lape 2005; 11, Martin et al. 1992; 12, McCartney et al. 2003; 13, Teske et al. 2007; 14, Craig et al. 2004; 15, Dominguez et al. 2005; 16, Muss et al. 2001; 17, Donaldson & Wilson 1999; 18, Duncan et al. 2006; 19, Quinteiro et al. 2000; 20, Tringali et al. 1999; 21, Bellwood et al. 2004; 22, Lovejoy & Collette 2002; 23, Robertson et al. 2006; 24, Westneat & Alfaro 2005; 25, Streelman et al. 2002; 26, Craig & Hastings 2007; 27, Arias-Gonzalez et al., unpublished data; 28, Rocha et al. 2005.

compilation of these values is a useful guide for deciding which geminate clades deserve further attention as good candidates for having roughly simultaneous separations. By necessity, arbitrary decisions need to be made as to which genetic distances are close enough to each other to be considered as a cluster signifying similar times of isolation. My arbitrary decisions, based on the assumption that substitution rates tend to be fairly constant in COI, ATPase6, and Cyt-B within a class of animals, are shown in the tables. In most cases, the difference between the smallest and the largest genetic distance of pairs I have assumed to have been split at the same time is approximately twofold. However, if substitution rates in COI are assumed to vary by a factor of 2, then they must vary by a factor of 8 in 16S in order to include the two pairs of *Synalpheus* that are judged to be geminate by COI (**Table 2**). Rate variation in 16S of crustacean species has been documented

Table 4 Mean Kimura two-parameter (K_2) percent difference in all sites and in silent sites (K_s) between sister clades of molluscs on either side of Central America^a

Genus	Eastern Pacific	Western Atlantic	N_p	N_A	bp	K_2	K_s^b	Reference
Mitochondrial regions								
Cytochrome oxidase subunit I (COI)								
Gastropoda								
<i>Strombus</i>	<i>peruvianus</i>	<i>raninus</i>	1	1	638	7.4 ^c	23.5	1
<i>Tegula</i>	<i>verrucosa</i>	<i>viridula</i>	1	1	639	7.6	24.0	2
<i>Crepidula</i>	<i>incurva</i> "Peru"	<i>convexa</i> "Bocas"	1	1	647	8.6	30.3	3
<i>Conus</i>	<i>gladiator</i>	(<i>mus</i> , <i>tabidus</i>) ^d	1	2	658	9.2	29.6	4
<i>Echinolittorina</i>	[<i>aspera</i> (<i>dubiosa</i> , <i>tenuistriata</i>)]	<i>interrupta</i>	6	2	1219	11.4	42.8	5
<i>Macrocyprea</i>	<i>cervinetta</i>	(<i>zebra</i> , <i>cervus</i>)	1	2	614	11.5	44.5	6
<i>Echinolittorina</i>	(<i>modesta</i> , <i>conspersa</i>)	(<i>ziczac A</i> , <i>ziczac B</i>)	4	4	1219	11.7	47.3	5
<i>Strombus</i>	<i>gracilior</i>	(<i>alatus</i> , <i>pugilis</i>)	1	2	638	12.1	44.3	1
<i>Echinolittorina</i>	<i>penicillata</i>	<i>angustior</i>	2	2	1219	12.3	46.5	5
<i>Echinolittorina</i>	<i>galapagensis</i>	<i>E. tuberculata</i> clade ^d	2	8	1219	14.0	60.1	5
<i>Elysia</i>	<i>diomedea</i>	(<i>crispata</i> , <i>clarki</i>)	1	25	630	14.7	70.8	13
<i>Echinolittorina</i>	(<i>apicina</i> , <i>paytensis</i>)	<i>riisei</i>	4	2	1219	15.2	64.1	5
<i>Echinolittorina</i>	<i>peruviana</i>	<i>lineolata</i>	2	2	1219	15.3	63.8	5
<i>Conus</i>	(<i>bartschii</i> , <i>brunneus</i>)	<i>regius</i>	2	1	658	15.4	62.0	4
<i>Tegula</i>	<i>corteziana</i>	<i>fasciata</i>	1	1	639	15.8	64.2	7
Bivalvia								
<i>Arcopsis</i>	<i>solida</i>	<i>adamsi</i>	2	2	603	12.9	55.5	8
<i>Barbatia</i>	<i>reeveana</i>	<i>candida</i>	3	2	603	14.8	53.6	8
<i>Barbatia</i>	<i>illota</i>	<i>tenera</i>	2	4	603	16.0	72.3	8
<i>Brachidontes</i>	<i>semilaevis</i>	(<i>exustus</i> -Gulf-Atlantic)	9	51	660	21.4	99.7	9
<i>Brachidontes</i>	<i>adamsianus</i>	<i>exustus</i> -W. Caribbean	30	15	660	23.7	> 100	9
<i>Anadara</i>	<i>nux</i>	<i>chenmitzii</i>	1	1	586	24.7	> 100	8
<i>Barbatia</i>	<i>gradata</i>	<i>domingensis</i>	4	2	603	24.9	> 100	8
<i>Arca</i>	<i>mutabilis</i>	<i>imbriata</i>	2	3	573	27.5	> 100	8
Cytochrome <i>b</i> (CytB)								
<i>Plicopurpura</i>	<i>patula</i>	<i>pansa</i>	1	1	239	16.0	60.6	10
Small subunit rDNA (12S)								
Gastropoda								
<i>Echinolittorina</i>	[<i>aspera</i> (<i>dubiosa</i> , <i>tenuistriata</i>)]	<i>interrupta</i>	6	2	356	4.5		5
<i>Echinolittorina</i>	(<i>modesta</i> , <i>conspersa</i>)	(<i>ziczac A</i> , <i>ziczac B</i>)	4	3	356	4.9		5
<i>Echinolittorina</i>	<i>penicillata</i>	<i>angustior</i>	2	2	356	6.8		5
<i>Echinolittorina</i>	(<i>apicina</i> , <i>paytensis</i>)	<i>riisei</i>	4	2	356	7.1		5
<i>Echinolittorina</i>	<i>galapagensis</i>	<i>E. tuberculata</i> clade ^e	2	9	356	8.9		5
<i>Tegula</i>	<i>corteziana</i>	<i>fasciata</i>	1	1	468	11.6		7
<i>Echinolittorina</i>	<i>peruviana</i>	<i>lineolata</i>	2	2	356	12.1		5

(Continued)

Table 4 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
			Large subunit rDNA (16S)					
Gastropoda								
<i>Conus</i>	<i>gladiator</i>	(<i>mus</i> , <i>tabidus</i>)	1	2	582	0.6		11
<i>Conus</i>	<i>purpurascens</i>	<i>ermineus</i>	1	1	582	2.1		12
<i>Crepidula</i>	<i>incurva</i> "Peru"	<i>convexa</i> "Bocas"	1	1	533	3.3		3
<i>Macrocypraea</i>	<i>cervinetta</i>	(<i>zebra</i> , <i>cervus</i>)	1	2	463	4.6		6
<i>Conus</i>	<i>perplexus</i>	<i>puncticulatus</i>	1	1	582	6.4		11
<i>Elysia</i>	<i>diomedea</i>	(<i>crispata</i> , <i>clarki</i>)	2	2	444	11.2		13
			Nuclear regions					
			Histone subunit 3 (H3)					
Gastropoda								
<i>Strombus</i>	<i>peruvianus</i>	<i>raninus</i>	1	1	327	0.6	2.6	1
<i>Strombus</i>	<i>gracilior</i>	(<i>alatus</i> , <i>pugilis</i>)	1	2	327	1.3	3.6	1
<i>Elysia</i>	<i>diomedea</i>	(<i>crispata</i> , <i>clarki</i>)	1	5	321	9.2	46.8	13
Bivalvia								
<i>Anadara</i>	<i>nux</i>	<i>cbemmitzii</i>	1	1	324	0.0	0.0	8
<i>Barbatia</i>	<i>reeveana</i>	<i>candida</i>	1	1	324	0.3	0.9	8
<i>Arca</i>	<i>mutabilis</i>	<i>imbricata</i>	1	1	324	0.3	0.9	8
<i>Acroposis</i>	<i>solida</i>	<i>adamsi</i>	1	1	324	0.6	1.7	8
<i>Barbatia</i>	<i>gradata</i>	<i>domingensis</i>	1	1	324	2.2	8.4	8
			Large subunit rDNA (28S)					
Gastropoda								
<i>Crepidula</i>	<i>incurva</i> "Peru"	<i>convexa</i> "Bocas"	1	1	460	0.5		3
<i>Echinolittorina</i>	<i>penicillata</i>	<i>angustior</i>	1	1	1368	0.7		5
<i>Echinolittorina</i>	[<i>aspera</i> (<i>dubiosa</i> , <i>tenuistriata</i>)]	<i>interrupta</i>	6	1	1368	0.7		5
<i>Echinolittorina</i>	(<i>apicina</i> , <i>paytensis</i>)	<i>riisei</i>	4	1	1368	0.7		5
<i>Echinolittorina</i>	(<i>modesta</i> , <i>conspersa</i>)	(<i>ziczac A</i> , <i>ziczac B</i>)	3	3	1368	0.8		5
<i>Echinolittorina</i>	<i>galapagensis</i>	<i>E. tuberculata</i> clade ^c	1	7	1368	1.4		5
<i>Echinolittorina</i>	<i>peruviana</i>	<i>lineolata</i>	1	1	1368	2.1		5
Bivalvia								
<i>Brachidontes</i>	<i>semilaevis</i>	<i>exustus</i> -Gulf-Atlantic	2	4	734	0.5		9
<i>Brachidontes</i>	<i>adamsianus</i>	<i>exustus</i> -W. Caribbean	4	1	734	0.7		9
			Internal transcribed spacer-1 (ITS-1)					
Bivalvia								
<i>Brachidontes</i>	<i>adamsianus</i>	<i>exustus</i> -W. Caribbean	5	3	606	4.7		9
<i>Brachidontes</i>	<i>semilaevis</i>	<i>exustus</i> -Gulf-Atlantic	2	3	606	5.2		9
			Calmodulin exon					
Gastropoda								
<i>Conus</i>	(<i>bartschii</i> , <i>brunneus</i>)	<i>regius</i>	2	1	52	2.0	6.4	11
<i>Conus</i>	<i>purpurascens</i>	<i>ermineus</i>	1	1	52	2.0	6.2	11
<i>Conus</i>	<i>gladiator</i>	<i>mus</i>	1	1	52	4.0	14.2	11
<i>Conus</i>	<i>perplexus</i>	<i>puncticulatus</i>	1	1	52	4.0	0.0	11

(Continued)

Table 4 (Continued)

Genus	Eastern Pacific	Western Atlantic	N _P	N _A	bp	K ₂	K _s ^b	Reference
			Calmodulin intron					
Gastropoda								
<i>Conus</i>	<i>gladiator</i>	<i>mus</i>	1	1	340	2.8		11
<i>Conus</i>	<i>purpurascens</i>	<i>ermineus</i>	1	1	340	2.8		11
<i>Conus</i>	(<i>bartschii</i> , <i>brunneus</i>)	<i>regius</i>	2	1	340	4.3		11
<i>Conus</i>	<i>perplexus</i>	<i>puncticulatus</i>	1	1	340	6.3		11

^aFor full citation information for the references in this table, see the **Supplementary Literature Cited**. Legend: N_P, number of sequences of Pacific clade; N_A, number of sequences of Atlantic clade.

^bDivergence in silent sites estimated according to the method of Pamilo & Bianchi (1993).

^cShading indicates values of divergence assumed to have been initiated at the final closure.

^dParentheses are used to designate phylogenetic arrangement of clades.

^e*E. tuberculata* clade: {[*tuberculata*, *vermeiji*] [*granosa* (*miliaris*, *helenae*)]}

References: 1, Latiolais et al. 2006; 2, Helberg & Vacquier 1999; 3, Collin 2003; 4, Duda & Rolan 2005; 5, Williams & Reid 2005; 6, Meyer 2003; 7, Hellberg 1998; 8, Marko 2002; 9, Lee & O'Foighil 2005; 10, Collins et al. 1996; 11, Duda & Kohn 2005; 12, Duda & Palumbi 2004; 13, Pierce et al. 2006.

along nonisthmian branches of the phylogenies of *Petrolisthes* (Hiller et al. 2006) and *Cbthamalus* (Wares 2001).

Having chosen species pairs that are likely to have been split simultaneously, one then needs to know which of these simultaneous separations was contemporaneous with the Isthmus completion. In a few cases, such as that of gastropods (T. Collins et al. 1996, Williams & Reid 2004), clams (Marko 2002), sharks (Martin et al. 1992), and angelfish (Bellwood et al. 2004, as corrected here), fossil dating of other nodes of a phylogenetic tree can aid in determining the time of splitting of geminate clades, but for the majority of species we have no external temporal information, and the decision needs to be made only by a comparison of the geminate divergence values. It would seem reasonable to assume that the smallest divergences reflect the final stages of the isthmian schism (Knowlton & Weigt 1998), and this logic would, indeed, be compatible with the data from crustaceans. Among crustaceans, the genera that contain the smallest values of transisthmian differentiation are ones found in shallow waters, such as the intertidal species of *Sesarma*, *Petrolisthes*, and *Alpheus* (Table 2). Such organisms are expected to have maintained genetic connections even when the only salt water connections between the EP and the WA consisted of swamps. Some fishes, however, show transisthmian divergence values that are far too small to consider them as having accumulated in 2–3 My (Table 3). A global phylogeny of the goatfish *Mulloidichthys* has found that the WA species *M. martinicus* maintained genetic contact with the EP species *M. dentatus* until the Pleistocene via the Indo-Pacific (H. Lessios, D.R. Robertson & B. Kessing, unpublished data). All fish geminate pairs with less transisthmian divergence than *Mulloidichthys* are composed of populations that, on the basis of morphology, are assigned to a single pantropical species, indicating that by both molecular and morphological criteria they are also likely to have maintained gene flow on a global scale until recently. One of them, *Diodon holacanthus*, has crossed the Eastern Pacific Barrier massively at about 0.15 Mya and has maintained fairly high rates of migration since then (Lessios & Robertson 2006). Thus, the cutoff point in divergence values that dates the Isthmus completion should be set higher than that seen in *Mulloidichthys*. Exactly where this point should be in fishes is not entirely clear. Bermingham et al. (1997) came to the tentative conclusion that the geminate species included in the shaded area of Table 3 for COI were most likely to have been separated at the closure of the Isthmus. Bernardi & Lape (2005), however, assumed that the *Anisotremus*

interruptus-*A. surinamensis* pair dates the Isthmus, because it shows less divergence than the *A. taeniatus*-*A. virginicus* pair.

Molluscs (**Table 4**) present a different problem: Even the pairs of congeneric species separated by the smallest transisthmian genetic distances may have been formed before the closure of the Isthmus. This is almost certainly the case in bivalves. Calibrating the rate of molecular evolution in arcid bivalves by fossils at three points of the phylogeny, Marko (2002) reached the conclusion that time of splitting in the most recently divergent transisthmian pair was 10 Mya. The only other comparison of bivalves, that of two pairs in the genus *Brachidontes* (Lee & O' Foighil 2005), shows more divergence in COI than arcids and thus is also likely to predate the completion of the Isthmus. Among gastropods, a global phylogeny of *Echinolittorina* identified six transisthmian pairs of species (Williams & Reid 2004). Despite the preference of the genus for upper intertidal habitats, an assumption of a geminate split contemporaneous with the closure of the Isthmus would suggest that the genus is only 9 My old, whereas fossil evidence suggests that it goes back to 40 My. If rates of substitution in *Echinolittorina* are calibrated by fossil evidence, transisthmian divergences represent cladogenesis that occurred between 32 and 14 Mya. Similarly, the cross-validating rate of divergence in *Plicopurpura* with fossil evidence from *Nucella* would suggest that *P. patula* and *P. pansa* (T. Collins et al. 1996) split 11.4–5.6 Mya (Cunningham & Collins 1994). Thus, among the gastropod genera that have been compared to date, the only ones that could contain species likely to have maintained genetic contact until the final completion of the Isthmus are *Strombus*, *Crepidula*, and *Comus*. It has been pointed out that the severe extinctions of molluscs in the Pleistocene may account for the rarity of recent geminate pairs in this phylum (Marko 2002, Williams & Reid 2004). However, given that mollusc extinctions were balanced with species originations in the Pleistocene (Allmon et al. 1993, Jackson et al. 1993), extinctions would not necessarily result in a paucity of geminate clades. If the new species arose in situ, from lineages that were split by the Isthmus, their divergence would still reflect the isthmian schism, regardless of how many speciation and extinction events have occurred on each side.

The conclusion from the compilation of data from 115 pairs of geminate clades is that 34 are likely to have been split at the time of the Isthmus completion, 8 may have maintained connections after that time, but the bulk (approximately 70 allowing for uncertainty with regard to some pairs) were split at some point during the long period of geological upheavals associated with the rising Isthmus. Thus, dates that have been obtained from molecular transisthmian comparisons should be viewed as hypotheses to be further tested with more data and with statistical techniques that allow the calculation of the degree of variation expected in substitution rates. Calibrations of molecular clocks are subject to large errors, and so is their application to entire phylogenies (Pulquério & Nichols 2007), and it is certainly true that the degree of uncertainty that surrounds them has often been understated (Graur & Martin 2004). But a comparison of the state of knowledge regarding transisthmian molecular divergences today with what was available the last time that the subject was reviewed (T. Collins 1996) indicates the abundance of data that has accumulated in a decade. Comparison of many divergences across the Isthmus (combined with global phylogenies of genera that can reveal transoceanic connections postdating the isthmian schism) can help identify true geminate clades to be used in molecular calibrations.

Adaptive Divergence

Studies of DNA divergence may be helpful in estimating the time since the splitting of Atlantic and Pacific species (an essential datum for interpreting other aspects of evolution) but are otherwise not useful in understanding evolutionary forces imposed by the environment. Phenetic studies that quantify overall morphological divergence across the Isthmus (Lessios 1981, Lessios & Weinberg

1994, Marko & Jackson 2001, Weinberg & Starczak 1989) are not particularly informative in that respect either. Studies of life histories of species on the two sides of the Isthmus, however, are illuminating as to how adaptation to different environments can produce important differences between initially similar organisms.

Differences in primary productivity between the EP and WA have been consistently linked to life histories of invertebrate species that live in each ocean. Developmental mode and egg size are important life-history characteristics in marine animals. In waters of low productivity, such as the WA, offspring need to be provisioned to a higher degree than in waters of high productivity, such as the EP. Transisthmian comparisons show that this is the case. Higher productivity in the EP was postulated by Lessios (1990) as the explanation for smaller egg size in six out of seven echinoderm species that live in this ocean, relative to their congeneric counterparts in the WA. Productivity differences have also been suggested by Moran (2004) as the cause of the same trend in egg sizes in six pairs of arcid bivalves. By studying the prodissoconch of fossils in one of these pairs, Moran concluded that the difference between modern species was due to a decrease of egg size in the EP, while size stayed constant in the WA. Using protoconch morphology to determine larval feeding mode, Jackson et al. (1996b) found that the proportion of strombinid gastropods with direct development increased during the Pliocene in the WA but not in the EP, which may also reflect adaptive changes to the developing productivity differences between the two basins. The percent of strombinids with planktotrophic larvae is higher in modern faunas of the EP than in the WA (Fortunato 2004). A comparison in a geminate pair of alpheid shrimp has also shown that the WA member hatches at a more advanced stage than the EP one, presumably as a result of the need for more maternal provisioning in nutrient-poor waters (Wehrmann & Albornoz 2002).

In addition to maternal provisioning, other life-history parameters also show differences between the EP and the WA that are consistent with the hypothesis that they are adaptations to different regimes of productivity. Cupuladriid bryozoans show lower growth rates and lower rates of asexual reproduction in the WA than the EP, which O'Dea et al. (2004) ascribe to differences in productivity. Fossil corbulid bivalves demonstrate a trend of decreasing size in the WA from the late Pliocene to the Holocene, while their size in the EP was increasing (Anderson 2001). Thus, comparisons of species that shared a recent common ancestor and of the proportion of species in each fauna show invertebrates to have adapted (or to have gone selectively extinct) in a minimum of 3 My to the different productivity regimes that were established soon after the isthmian schism. In the single study involving vertebrates, comparisons between congeneric species of damselfish and of wrasses from the two sides of the Isthmus found only small and inconsistent tranisthmian differences in egg size, hatchling size, larval growth rate, larval duration, and settlement size (Wellington & Robertson 2001).

Speciation

As Mayr (1954) realized early on, the organisms separated by the isthmian schism are prime examples of organisms that are in the initial, allopatric stage of speciation. Studying speciation on the two sides of the Isthmus has advantages that are hard to find in other settings, in that there is a readily identified and fairly well-dated barrier that is absolute, and in that the timescale of about 3 My (or even 15 My) is sufficient for divergence to accumulate, but not so ancient as to erase all information about the evolutionary trajectories of the isolates (Lessios 1998). What can the geminate species of Panama tell us about the process of speciation?

Speciation has two components, genetic divergence and the emergence of reproductive isolation. Genomic divergence between the geminates as seen in molecules has already been discussed. What converts geographically isolated populations into new species is differentiation that leads

to the acquisition of reproductive isolation. Studies of reproductive isolation between allopatric species are essentially efforts to predict whether populations have developed inherent properties that would keep them from interbreeding if the barrier were lifted. Long generation times of most marine organisms make assessment of postzygotic reproductive barriers difficult, and the dangers of environmental disruption advise against field experiments that would introduce organisms from one ocean into the other to assess prezygotic ones. Thus, despite the advantages of the isthmian setting, only a handful of studies on reproductive isolation have been conducted to date.

An early study was on behavioral isolation between three species of the goby *Bathygobius* (Rubinoff & Rubinoff 1971). According to isozyme data, *B. soporator* and *B. andrei* are the geminate pair, while the Pacific *B. ramosus* is distantly related to them (Vawter et al. 1980). Rubinoff & Rubinoff (1971) found that, though they do not mate indiscriminately, the two geminates are incompletely isolated from each other. Reproductive barriers of *B. ramosus* are complete toward its sympatric counterpart, *B. andrei*, but incomplete toward the allopatric *B. soporator*, which is consistent with the hypothesis of speciation by reinforcement. Lessios (1984) found that the EP sea urchin *D. mexicanum* and the WA *D. antillarum* spawn in lunar cycles 15 days out of phase with each other. Given that, unlike annual cycles, lunar ones are more likely to be under genetic control (Lessios 2007), these two species—although isolated for less than 3 My—appear to have evolved a complete reproductive barrier that would keep them from fusing if the Isthmus were breached. Lessios & Cunningham (1990) and McCartney & Lessios (2002) compared gametic compatibility between sympatric and allopatric species of the sea urchin *Echinometra*. The isthmian schism separated the EP *E. vanbrunti* from a lineage that would subsequently give rise to two extant WA species *E. lucunter* and *E. viridis* (McCartney et al. 2000). One of the two Atlantic species, *E. lucunter*, is capable of fertilizing both of the other two species, but its eggs will not permit fertilization by either. This is consistent with the pattern found in the evolution of the gamete recognition molecule, bindin. Bindin coats the acrosome process of the sperm and is recognized by egg receptors. McCartney & Lessios (2004) found that the vast majority of amino acid replacements in the genealogy of bindin among Neotropical species of *Echinometra* has occurred along the branch that leads to *E. lucunter*. That one of the species that has evolved under the challenge of a sympatric congener has developed protection against heterospecific fertilizations would appear to be consistent with the hypothesis of reinforcement, but in fact, the eggs of *E. lucunter* are less compatible with sperm of the allopatric *E. vanbrunti* than with the sympatric *E. viridis*. Knowlton et al. (1993) assessed the degree of aggression between EP and WA species of the shrimp *Alpheus* in experiments that placed males and females together. Most of the compared species pairs had speciated before the Isthmus completion, but two of the tested pairs probably split 3 Mya. One of these pairs shows the highest degree of behavioral compatibility among all comparisons, and the other is close to the median of the range. Thus in shrimp, fish, and sea urchins, geminate species that were separated 3 Mya are on their way to being reproductively isolated, but they have not completed the process. Only one, *Diadema*, shows complete reproductive isolation. The conclusion would be that 3 My in allopatric existence is barely enough for the emergence of reproductive isolation. This is roughly the same period of time estimated by Coyne & Orr (1997) to be necessary for development of reproductive isolation among allopatric species of *Drosophila*.

CONCLUSIONS

By sundering gene pools and placing them in different environments the isthmian schism has allowed research addressing questions about which only speculation is possible in connection to other geological events. We are still at the stage of answering the four basic questions posed by Jackson & Budd (1996) in their prologue to the compendium of paleontological isthmian

studies: “What happened?,” “Where did it happen?,” “When did it happen?,” and “Why did it happen?” In the process we have learned a fair amount about the rate at which genes evolve, we have learned that marine invertebrate life histories respond to 3 My of being placed in different primary productivity regimes, and we have learned that barriers of reproductive isolation can evolve (though not necessarily be perfected) in this length of time. The research that has been conducted to date is indicative of what could potentially be learned from further study of contemporary trans-isthmian populations and from combining this information with increasingly more sophisticated reconstructions of paleo-environments.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

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