

GRADUAL MIOCENE TO PLEISTOCENE UPLIFT OF THE CENTRAL AMERICAN ISTHMUS: EVIDENCE FROM TROPICAL AMERICAN TONNOIDEAN GASTROPODS

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ABSTRACT—Tonnoidean gastropods have planktotrophic larval lives of up to a year and are widely dispersed in ocean currents; the larvae maintain genetic exchange between adult populations. They therefore are expected to respond rapidly to new geographic barriers by either extinction or speciation. Fossil tonnoideans on the opposite coast of the Americas from their present-day range demonstrate that larval transport still was possible through Central America at the time of deposition of the fossils. Early Miocene occurrences of *Cypraecassis tenuis* (now eastern Pacific) in the Caribbean probably indicate that constriction of the Central American seaway had commenced by Middle Miocene time. Pliocene larval transport through the seaway is demonstrated by *Bursa rugosa* (now eastern Pacific) in Caribbean Miocene-latest Pliocene/Early Pleistocene rocks; *Crossata ventricosa* (eastern Pacific) in late Pliocene rocks of Atlantic Panama; *Distorsio clathrata* (western Atlantic) in middle Pliocene rocks of Ecuador; *Cymatium wiegmanni* (eastern Pacific) in middle Pliocene rocks of Atlantic Costa Rica; *Sconsia sublaevigata* (western Atlantic) in Pliocene rocks of Darien, Pacific Panama; and *Distorsio constricta* (eastern Pacific) in latest Pliocene-Early Pleistocene rocks of Atlantic Costa Rica. Continued Early or middle Pleistocene connections are demonstrated by *Cymatium cingulatum* (now Atlantic) in the Armuelles Formation of Pacific Panama. Tonnoideans indicate that the Central American seaway began to be constricted after early Miocene time, and some larval transport through the seaway was possible throughout Pliocene time. Intermittent marine connections were maintained at least during late Pliocene to early Pleistocene interglacial periods of high sea-level, and alternated with a land bridge during glacial periods of low sea-level.

INTRODUCTION

THE CLOSURE of the Isthmus of Panama in the mid-Pliocene is one of the most accessible model systems for assessing evolutionary responses to a vicariant event followed by large scale environmental change (deMaintenon, 1998). But when did this “event” occur? Increasingly, evidence now indicates a long, complex uplift history for the development of the Central American dispersal barrier, rather than a single event. As the “molecular clock” partly has been calibrated by the date of closure of the Central American seaway, the date assumes some importance in evolution and biogeography.

The “Great American Interchange” of terrestrial mammals that resulted from the exposure of a land connection between North and South America is one of the best-studied phenomena in biogeography. Of course, the uplift of this impenetrable dispersal barrier caused a concomitant revolution in the marine biota, and ultimately was one of the causes of Pleistocene glaciation because of the resulting reorganisation of world ocean circulation. Although it was perhaps less spectacular than the terrestrial one, the marine faunal revolution certainly is just as interesting a natural experiment for its contribution to the understanding of mechanisms and timing of extinction, dispersal and speciation. But this contribution also operates from the opposite point of view; widely and rapidly dispersed marine taxa such as tonnoidean gastropods provide data for understanding the timing of uplift of the barrier to marine dispersal. Accurate biostratigraphic and other dating of marine fossils on either side of the barrier then can provide dates for the uplift of the barrier.

Tonnoideans are a large superfamily of exclusively marine, benthic, carnivorous gastropods. Families included in the superfamily are Bursidae, Cassidae (with subfamilies Cassinae and Phaliinae), Laubierinidae, Personidae, Pisanianuridae, Ranellidae (with subfamilies Ranellinae and Cymatiinae) and Tonnidae (Warén and Bouchet, 1990; Riedel, 1995, 2000; Beu, 1998a; Beu and Bouchet, in preparation, “Revision of world deep-water Cassidae”). Several species in these families are well known for their enormously and unusually wide present ranges. The slow-moving, benthic adults live in intertidal, continental shelf and/or slope environments, and yet such species as *Charonia lampas*, *Cymatium parthenopeum* and *C. labiosum* are comprised of many disjunct

populations throughout much of the tropical and warm-temperate oceans. (Author’s names and dates for all species are provided in Table 1, and are not used in the text, other than for species that do not occur in the Central American region.) A large number of other species live throughout the Indo-West Pacific province, in its broadest sense (Abbott, 1968; Beu, 1987, 1998b; Marshall, 1992) and some of these intermittently extend their ranges to the eastern Pacific (Emerson, 1991). Early assumptions that the wide distributions of these species resulted from a long-lived larval life (e.g., Powell, 1933) amply have been justified by Scheltema’s research on the dispersal of molluscan veliger larvae (e.g., Scheltema, 1966, 1971, 1972, 1986, 1988; Scheltema and Williams, 1983; Pechenik et al., 1984). Scheltema demonstrated that some of the very widely distributed tonnoideans have larval lives of up to a year, and their larvae are planktotrophic and can postpone metamorphosis to the benthic adult stage until a suitable substrate for settling is reached. They therefore are capable of being dispersed passively in ocean currents throughout much of the world ocean. These animals should be thought of as having two distinct and equally important life history stages; the widely disjunct, benthic, reproducing adult populations are linked by the continuously distributed, continually dispersed planktotrophic larval stage.

The important point here is that the continually dispersed larvae maintain genetic continuity between the widely disjunct adults. Species in this group of gastropods can help the understanding of Panamic biogeography because of their continuous larval dispersal. They would be expected to have been distributed throughout the region as long as a marine connection existed through Panama, and rapidly to reflect disjunction of their ranges, through uplift of the land barrier, by extinction or speciation on one or the other coasts of the Americas. The precision of the date of uplift provided by tonnoidean gastropods depends on the type of evidence they provide. The most useful evidence is that provided by tonnoideans that are limited to only one or the other coast of the Americas at present, but occur as fossils on the *opposite* coast of the Americas. These clearly demonstrate that the Central American dispersal barrier had not been uplifted enough to prevent larval dispersal at the time of deposition of the fossils. A narrowly constrained date of deposition of the enclosing rock then provides a well-constrained date when the barrier is known *not* to have

TABLE 1—Neogene and living Tonnoidean gastropods of the Central American region, with some of their main synonyms, and their time and geographic ranges. Abbreviations: Calif, California; CR, Costa Rica; DR, Dominican Republic; E, Early or eastern; Fla, Florida; Fm, Formation; IWP, Indo-West Pacific province; L, Late; Med, Mediterranean; Mid, Middle; Mio, Miocene; N, north; O, Ocean; Oligo, Oligocene; Pleist, Pleistocene; Plio, Pliocene; Rec, Recent; S, south; W, west.

BURSIDAE

1. *Bursa amphitrites* (Maury, 1917): L Mio-Early Plio, Caribbean.
2. *B. asperrima* Dunker, 1862: Rec, IWP; common at E Pacific offshore islands.
3. *B. chipolana* Schmelz, 1997: late E Mio, Chipola Fm, Fla.
4. *B. corrugata* (Perry, 1811): Rec, E Pacific, E and W Atlantic; Plio, Mexico; Pleist, Med [very similar to *B. victrix* Dall, 1916, Oligo, Georgia].
5. *B. granularis* (Röding, 1798) (= *cubaniana* Orbigny, 1841): Rec, IWP and E and W Atlantic, few records E Pacific; Pleist, Cuba, DR, Barbados, Atlantic Panama.
6. *B. grayana* Dunker, 1862 (= *bufoniopsis* Maury, 1917, = *pacamoni* Matthews and Coelho, 1971): L Mio-Plio, DR, Mexico, Pacific Panama; Rec, W Atlantic.
7. *B. natalensis* Coelho and Matthews, 1970: Rec, W Atlantic [closely similar to *B. latitudo* Garrard, 1961, Rec, IWP].
8. *B. ranelloides* (Reeve, 1844) (= *tenuisculpta* Dautzenberg and Fischer, 1906, = *finlayi* McGinty, 1962, etc.): Mid Mio, Trinidad; Plio, Atlantic CR and Panama; Rec, Japan and Indian O, S Africa, E and W Atlantic.
9. *B. rhodostoma* (G. B. Sowerby II, 1835) (= *thomae* Orbigny, 1841): Rec, IWP and E and W Atlantic; late E Mio-Pleist, W Atlantic.
10. *B. rugosa* (G. B. Sowerby II, 1835) (= *boussingaulti* Rutsch, 1934; = *calcipicta* of Keen, 1958 and 1971 [not of Dall, 1908, = *Crossata californica* Hinds]): Mio-Rec, E Pacific; Mid Mio-Plio/E Pleist, W Atlantic.
11. *B. scrobilator* (Linné, 1758): Pleist-Rec, Med-W Africa; Plio-Pleist, Atlantic Colombia, Panama and CR.
12. *Bufo* (*Aspa*) *marginata* (Gmelin, 1791): Mio-Rec, Europe-W Africa; Late Plio/Early Pleist, Limon, Atlantic CR.
13. *Crossata ventricosa* (Broderip, 1833) (= *californica* Hinds, 1844, = *calcipicta* Dall, 1908, not Keen, 1958 and 1971): Mio?; Plio-Recent, California-Peru; L Plio, Atlantic Panama.
14. *Marsupina bufo* (Bruguère, 1792) (= *crassa* Dillwyn, 1817, = *proavus* Pilsbry, 1922, = *bowdenensis* Woodring, 1928, etc.): Plio, Rio Vaca, Pacific CR; Mio-Rec, W Atlantic.
15. *M. freya* (Olsson, 1932): Mio, E Pacific (CR—Ecuador).
16. *M. nana* (Broderip and Sowerby, 1829) (= *albofasciata* G. B. Sowerby II, 1835): Plio-Rec, E Pacific.
17. *M. strongi* (Jordan, 1936): Pleist (oxygen isotope stage 5e), Baja California.
18. *Marsupina* n. sp.: Mio, Punta Judas, CR (and Ecuador?).

PERSONIDAE

19. *Distorsio clathrata* (Lamarck, 1816) (= *robinsoni* Petuch, 1987): L Mio-Rec, W Atlantic; Mid Plio, Ecuador.
20. *D. constricta* (Broderip, 1833): Mio-Rec, E Pacific; L Plio/E Pleist, Limon, Atlantic CR.
21. *D. decussata* (Valenciennes, 1832) (= *gatunensis* Toulou, 1909): late E Mio, El Porvenir beds, N Venezuela; Mio-Plio, Panama; Plio-Rec, E Pacific.
22. *D. floridana* (Gardner, 1947): Mio, Shoal River Fm, Fla (and Plio, Panama?).
23. *D. jenniernestae* Emerson and Piech, 1992: Plio-Rec, E Pacific.
24. *D. mcgintyi* Emerson and Puffer, 1953: late E Mio-Recent, W Atlantic.
25. *D. minoruohishii* Parth, 1989: Plio-Rec, E Pacific.
26. *D. perdistorta* Fulton, 1938: Rec, IWP and E and W Atlantic.
27. *D. ringens* (Philippi, 1887) (= *thersites* Philippi, 1887): Mio, Peru-Chile.
28. *D. simillima* (G. B. Sowerby II, 1850): Mid Mio-L Plio/E Pleist, W Atlantic.
29. *Distorsio* n. sp.: late E Mio, Cantaure, Venezuela (and Chipola?, Fla).

RANELLIDAE

Ranellinae

30. *Fusitriton oregonensis* (Redfield, 1846): Rec, N Pacific-Pacific Panama; Pleist, Baja California.
31. *Halgryneum louisae* (Lewis, 1974): L Plio/E Pleist, Limon, CR; Rec, IWP and E and W Atlantic.
32. *Ranella gemmifera* (Euthyme, 1889): Rec, W Atlantic, South Africa, St Paul and Amsterdam Islands.
33. *R. olearia* (Linné, 1758): Mio-Rec, Europe-Mediterranean; Rec, E and W Atlantic—South Africa—New Zealand (not Australia).

Cymatiinae

34. *Cabestana felipponei* (Ihering, 1907): Holocene, Uruguay; Rec, S Brazil—central Argentina.
35. *Charonia lampas* (Linné, 1758) (= *rubicunda* Perry, 1811, = *nodiferum* Lamarck, 1822, = *weisbordi* Gibson-Smith, 1976, etc.): Mio-Rec, Europe, E and W Atlantic—South Africa—New Zealand—Australia—New Caledonia—Japan.
36. *C. variegata* (Lamarck, 1816) (= *seguenzae* Aradas and Benoit, 1870): Mio-Rec, E and W Atlantic—Med.
37. *C. tritonis* (Linné, 1758): Mio-Rec, IWP; few records Rec, E Pacific.
38. *Cymatium* (*Cymatium*) *femorale* (Linné, 1758) (= *raderi* D'Attilio and Myers, 1984): L Plio-Rec, W Atlantic.
39. *C. (Cymatium) praefemorale* (Maury, 1917): L Mio-E Plio, DR and Atlantic Panama.
40. *C. (Cymatium) tigrinum* (Broderip, 1833): Rec, E Pacific (Pleist, Galapagos Is?).
41. *C. (Gelagna) succinctum* (Linné, 1771): Rec, IWP, E Pacific and E and W Atlantic.
42. *C. (Gutturium) muricinum* (Röding, 1798): Pleist-Rec, IWP, E Pacific and E and W Atlantic.
43. *C. (Linatella) cingulatum* (Lamarck, 1822) (= *cutaceum* Lamarck, 1816, not Linné, 1767, = *caudatum* Gmelin, 1791 (not *C. (Ranularia) caudatum* Gmelin, 1791), = *poulsenii* Mörch, 1877, etc.): Mio-Rec, IWP and E and W Atlantic; Mio, Pacific CR; E to Mid Pleist, Pacific Panama.
44. *C. (Monoplex) amictum* (Reeve, 1844) (= *amictoideum* Keen, 1971): Plio-Rec, E Pacific.
45. *C. (Monoplex) aquatile* (Reeve, 1844): Mio-Rec, IWP and E and W Atlantic; few records Rec, E Pacific; Plio, Ecuador.
46. *C. (Monoplex) cercadicum* (Maury, 1917): late E Mio, Cantaure, Venezuela; L Mio-E Plio, DR.
47. *C. (Monoplex?) chlorostomoides* (Maury, 1924): late E Mio, Brazil [relationships?].
48. *C. (Monoplex) comptum* (A. Adams, 1855): Rec, IWP and E and W Atlantic.
49. *C. (Monoplex) exaratum* (Reeve, 1844): Pleist-Rec, IWP, South Africa, Red Sea, ?W Atlantic.
50. *C. (Monoplex) gurabonicum* (Maury, 1917): L Mio-E Plio, DR.
51. *C. (Monoplex?) infelix* (Maury, 1924): late E Mio, Brazil [relationships?].
52. *C. (Monoplex) keenae* Beu, 1970: Pleist-Rec, E Pacific.
53. *C. (Monoplex) krebsii* (Mörch, 1877) (= *henicum* Woodring, 1959): Mio-Rec, W Atlantic and Panama; Rec, E Atlantic.
54. *C. (Monoplex) lignarium* (Broderip, 1833) (= *kugleri* Rutsch, 1942): Mio-Plio, W Atlantic; Rec, E Pacific.
55. *C. (Monoplex) macrodon* (Valenciennes, 1832): Rec, E Pacific.
56. *C. (Monoplex) martinianum* (Orbigny, 1841): late E Mio-Rec, W Atlantic; Rec, E Atlantic.
57. *C. (Monoplex) mundum* (Gould, 1849): Pleist-Rec, IWP, E Pacific and W Atlantic.
58. *C. (Monoplex) nicobaricum* (Röding, 1798): Pleist-Rec, IWP and E and W Atlantic.
59. *C. (Monoplex) parthenopeum* (von Salis Marschlins, 1793): Mio-Rec, IWP and E and W Atlantic, Europe-Med.
60. *C. (Monoplex) pharcidum* (Dall, 1889): Rec, E and W Atlantic [closely similar to *C. tenuiliratum* (Lischke, 1873), Plio-Rec, IWP].
61. *C. (Monoplex) ritteri* Schmelz, 1989: late E Mio, Chipola Fm, Fla and Cantaure, Venezuela.
62. *C. (Monoplex) tranquebaricum* (Lamarck, 1816): Mio-Rec, W Atlantic; Rec, E Atlantic.
63. *C. (Monoplex) trigonum* (Gmelin, 1791) (= *ficoides* Reeve, 1844): Rec, E and W Atlantic; Pleist, Med.

TABLE 1—Continued.

64. *C. (Monoplex) vespaceum* (Lamarck, 1822): Mio-Rec, IWP; Rec, W Atlantic.
 65. *C. (Monoplex) vestitum* (Hinds, 1844): Plio-Rec, E Pacific.
 66. *C. (Monoplex) wiegmanni* (Anton, 1838): Plio-Rec, E Pacific; Mid Plio, Rio Banano, Atlantic CR.
 67. *C. (Monoplex?) williamsi* (Maury, 1924): late E Mio, Brazil [relationships?].
 68. *C. (Monoplex)* n. sp. A: Mio-E Plio, Venezuela.
 69. *C. (Monoplex)* n. sp. B: Plio, Atlantic and Pacific Panama.
 70. *C. (Ranularia) cynocephalum* (Lamarck, 1816) (= *caribbaeum* Clench and Turner, 1957): Pleist-Rec, W Indian Ocean, E and W Atlantic.
 71. *C. (Ranularia) gallinago* (Reeve, 1844): W Indian Ocean, Brazil.
 72. *C. (Ranularia) rehderi* A. H. Verrill, 1950: Rec, W Atlantic [closely similar to *C. testudinarium* A. Adams and Reeve, 1850, Rec, IWP].
 73. *C. (Reticutriton) carlotae* (Ferreira and da Cunha, 1957): late E Mio, Brazil (?= *pfeifferianum* Reeve, 1844)
 74. *C. (Reticutriton) elsmerense* (English, 1914): Plio, S California, USA.
 75. *C. (Reticutriton) lineatum* (Broderip, 1833): Plio-Rec, Galapagos Is.
 76. *C. (Reticutriton) pfeifferianum* (Reeve, 1844): Mio-Rec, IWP; Recent, W Atlantic.
 77. *Cymatium (Reticutriton)* n. sp.: late E Mio, Cantaure, Venezuela.
 78. *C. (Septa) occidentale* (Mörch, 1877): L Plio/E Pleist-Rec, IWP and E and W Atlantic.
 79. *C. (Septa)* n. sp.: late E Mio-E Plio, DR.
 80. *C. (Turrutriton) domingense* (Gabb, 1873): Late Mio-Plio, DR, Venezuela and Atlantic Panama.
 81. *C. (Turrutriton) gibbosum* (Broderip, 1833): Plio, Atlantic Colombia; Pleist-Rec, E Pacific.
 82. *C. (Turrutriton) labiosum* (Wood, 1828): Mio-Rec, IWP; L Plio/E Pleist-Rec, W Atlantic; Rec, E Atlantic and E Pacific.
 83. *Sassia (Sassia) cf. appenninica* (Sassi, 1827): late E Mio, Carriacou; Mio-Plio, Europe.
 84. *Sassia (Sassia) lewisi* Harasewych and Petuch, 1980: Rec, E and W Atlantic.
 85. *Sassia (Sassia)* n. sp.: L Mio-E Plio, DR.
 86. *Sassia (Cymatiella)* n. sp.: L Mio-E Plio, DR; Mio, Trinidad.
- CASSIDAE
 Cassinae
87. *Cassis delta* Parker, 1948: late E Mio, Chipola Fm, Fla.
 88. *C. flammea* (Linné, 1758): Late Plio-Rec, W Atlantic [and Plio, Calif?].
 89. *C. floridensis* Tucker and Wilson, 1932 (= *schnireli* Petuch, 1994): Plio-Pleist, Fla.
 90. *C. ketteri* Parodiz and Tripp, 1992: Plio, Florida.
 91. *C. madagascariensis* Lamarck, 1822 (= *spinella* Clench, 1944): L Plio-Rec, W Atlantic.
 92. *C. norae* Prati Musetti, 1995: Rec, Cape Verde Is and Curaçao.
 93. *C. sulcifera* (G. B. Sowerby II, 1850): Mid Mio-Early Plio, W Atlantic.
 94. *C. tuberosa* (Linné, 1758): L Plio-Rec, E and W Atlantic.
 95. *Cassis* n. sp. A: Plio, CR and E and W Panama.
 96. *Cassis* n. sp. B: Plio, Atlantic Panama.
 97. *Cypraecassis (Cypraecassis) tenuis* (Linné, 1758): Rec, E Pacific; Oligo, Panama; ?Mio, CR; late E Mio, Cantaure, Venezuela and Chipola Fm, Fla.
 98. *C. testiculus* (Linné, 1758): late E Mio-Rec, E and W Atlantic.
 99. *C. (Levenia) coarctata* (G. B. Sowerby I, 1825): Pleist-Rec, E Pacific.
 100. *Dalium dalli* Böse, 1906: L Mio-E Plio, Mexico and DR.
 101. *D. ecuadorianum* Olsson, 1942: Mid Plio, Ecuador.
 102. *D. solidum* Dall, 1889: Rec, S Caribbean.
 103. *Galeodea* aff. *echinophora* (Linné, 1758): Mio-E Plio, DR.
 104. "*Oocorys*" (n. gen.) *barbouri* Clench and Aguayo, 1939: Rec, NE Caribbean, deep water.
 105. "*O.*" (n. gen.) *bartschi* Rehder, 1943: Rec, N Caribbean.
 106. *Oocorys clericus* Quinn, 1980: Plio, Atlantic Panama; Rec, Caribbean.
 107. *O. elevata* Dall, 1889: Rec, E Pacific, deep water.
 108. *O. pacifica* (Dall, 1896): Rec, Gulf of Panama, deep water (?= *verrillii* Dall, 1889).
 109. *O. rotunda* Dall, 1908: Rec, Gulf of Panama-W Pacific, deep water.
 110. *O. sulcata* Fischer, 1883 (= *abyssorum* Verrill and Bush in Verrill, 1884, etc.): Rec, IWP and E and W Atlantic, deep water.
 111. *O. verrillii* (Dall, 1889) (= *cancellata* Dautzenberg & Fischer, 1897, etc.): Rec, E and W Atlantic, IWP, deep water.
 112. *Oocorys* n. sp. aff. *elevata* Dall, 1908: late E Mio, Cantaure, Venezuela.
 113. *Sconsia alexarthuri* Parth, 1994: Rec, Caribbean.
 114. *S. grayi* (A. Adams, 1855) (= *striata* Lamarck, 1816, not of J. Sowerby, 1812; = *bocasensis* Olsson, 1922, = *lindae* Petuch, 1987): L Plio-Rec, W Atlantic.
 115. *S. hodgii* (Conrad, 1841) (= *prolongata* Petuch, 1994, = *metae* Petuch, 1994): Plio-Pleist, Florida-South Carolina, USA.
 116. *S. laevigata* (G. B. Sowerby II, 1850): late E Mio-E Plio, Caribbean.
 117. *S. nephele* Bayer, 1971: Rec, S Caribbean [?status: ? = *S. grayi*].
 118. *S. sublaevigata* Guppy, 1866 (= *gabby* Olsson, 1922): Plio, Atlantic Panama and Caribbean; Plio, Darien, Pacific Panama.
- Phaliinae
119. *Casmaria erinacea vibexmexicana* (Stearns, 1894): Rec, E Pacific.
 120. *C. atlantica* Clench, 1944: Rec, W Atlantic (?= *C. perryi* (Iredale, 1912), Rec, IWP).
 121. *Echinophoria coronadoi* (Crosse, 1867): Rec, W Atlantic.
 122. *E. famulans* (Jung, 1971): Mio, Carriacou I, Caribbean.
 123. *E. hadra* (Woodring and Olsson, 1957) (= *dalli* Anderson, 1929, not of Dickerson, 1917, = *andersoni* Abbott, 1968): late E Mio-Plio, W Atlantic.
 124. *E. pilsbryi* (Woodring and Olsson, 1957): Rec, Galapagos Is-Ecuador.
 125. *Semicassis aldrichi* (Dall, 1890): Mio, W Atlantic.
 126. *S. centiquadrata* (Valenciennes, 1832): Mio-Rec, E Pacific.
 127. *S. granulata* (Born, 1778) (= *cicatricosum* Gmelin, 1791, = *gibbum* Gmelin, 1791, = *abbreviata* Lamarck, 1822, = *peristephes* Pilsbry and McGinty, 1939, = *alligator* Petuch, 1991, = *loxahatcheensis* Petuch, 1994, etc.): Plio-Rec, W Atlantic.
 128. *S. murrayi* (Schmelz, 1996): Mid Mio, Shoal River Fm, Fla.
 129. *S. maleaformis* (H. E. Vokes, 1938): Late Mio, Trinidad.
 130. *S. paraensis* (Maury, 1924): late E Mio, Brazil [relationships?].
 131. *S. reclusa* (Guppy, 1873) (= *monilifera* Guppy, 1866, not of G. B. Sowerby II, 1846): Mio-Plio, Caribbean.
 132. *S. semmi* (Rutsch, 1934): E Plio, Punta Gavilan, Venezuela.
 [*Neosconsia ecuadoriana* Olsson, 1964: Plio, Ecuador; remove to Buccinidae].
- TONNIDAE
133. *Eudolium bairdii* (Verrill and Smith in Verrill, 1881): Rec, IWP and E and W Atlantic, Med.
 134. *E. crosseanum* (Monterosato, 1869): Rec, E and W Atlantic, Med [closely similar to *E. pyriforme* (G. B. Sowerby III, 1914), Rec, IWP].
 135. *E. marylandicum* Petuch, 1988: L Mio, Maryland, Virginia, and Florida.

TABLE 1—Continued.

136. <i>E. subfasciatum</i> Sacco, 1891: Mio, Caribbean and Europe.
137. <i>Malea camura</i> Guppy, 1866: Mio-Plio, W Atlantic.
138. <i>M. densecostata</i> (Rutsch, 1934): E Plio, Punta Gavilan, Venezuela.
139. <i>M. elliptica</i> Pilsbry and Johnson, 1917: Mio-Plio, DR and Panama.
140. <i>M. goliath</i> Pilsbry and Johnson, 1917: Mio-Plio, DR and Panama.
141. <i>M. mareana</i> Weisbord, 1962: Plio, Caribbean-Fla.
142. <i>M. norohnensis</i> Kempf and Matthews, 1969: Rec, Fernando de Noronha I., N Brazil.
143. <i>M. ringens</i> (Swainson, 1822) (= <i>latilabris</i> Valenciennes, 1832, etc.): Plio-Rec, E Pacific and E and W Panama; ?Plio, California.
144. <i>M. springi</i> Petuch, 1989: Plio, Florida.
145. <i>Tonna galea</i> (Linné, 1758) (= <i>brasiliiana</i> Mörch, 1877, = " <i>Malea</i> " <i>petiti</i> Petuch, 1989): Mio-Recent, E and W Atlantic and Med; IWP?.
146. <i>T. maculosa</i> (Dillwyn, 1817): Mio-Rec, E and W Atlantic.

been effective. The other type of information provided by tonnoideans (as well as many other molluscs) is the occurrence of a member of a geminate species pair on either side of the Central American isthmus. Geminate species pairs (in the strict sense) are assumed to have arisen by differentiation from an original pan-Central American species, as a result of uplift of the dispersal barrier and subsequent genetic drift in one (or perhaps both) of the daughter populations. Clearly, the evidence of the date of uplift of the dispersal barrier is much less precise than in the first type of evidence, as 1) the fossil occurrence may not record the earliest date of differentiation of the species; and 2) the period between uplift of the barrier and differentiation of the species is of unknown length. While differentiation possibly was instantaneous, at least in geological terms, it also might have taken a geologically appreciable period. These two types of evidence are the subject of the present paper.

The data listed here result from a revision of Neogene fossil tonnoideans of the Central American region—a contribution to both the Dominican Republic and Panama Paleontology Projects (Beu, in preparation). To a lesser extent, some of the data result also from a revision of world deep-water Cassidae related to *Gal- eodea*, *Oocorys*, *Sconsia* and *Echinophoria* (Beu and Bouchet, in preparation). Some of the surprising range extensions in the late Pliocene-early Pleistocene Moin Formation of Atlantic Costa Rica have been pointed out by Robinson (1993). The data set for this paper consists of the records of the 146 species of fossil and living tonnoideans from the Central American region (Table 1). The geographic limits of the data set need to be established; it includes essentially the tropical taxa, i.e., from Florida to Brazil, and from southern California, USA, and the Galapagos Islands to Peru. For example, *Eudolium marylandicum* is included, even though it was based on specimens from Maryland, as it subsequently has been recorded from Miocene limestone in Florida (Petuch, 1994, pl. 35C, D); other tonnoideans from Maryland to South Carolina have not been included.

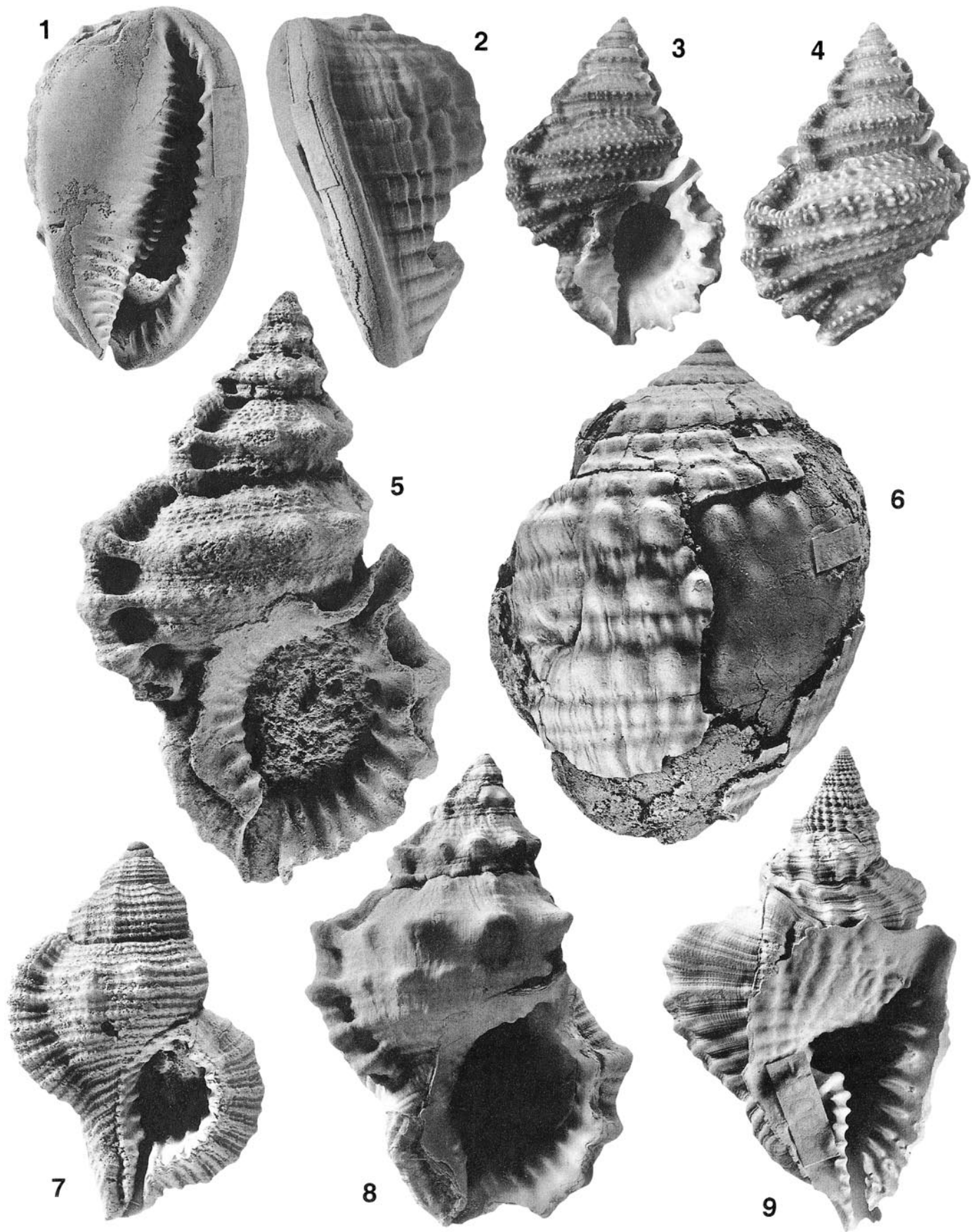
It is clear from Table 1 that, contrary to the expected uniform distribution throughout Central America, some species and even a few genera have never strayed from the region they inhabit at present. All possible combinations of ranges are seen, from occurring uniformly throughout the eastern Pacific, the western Atlantic and West Africa (*Bursa corrugata*, only; i.e., this is the one exception to the tonnoidean rule of differentiation following the uplift of the Central American barrier), to limited to one province or even to one small island (*Malea norohnensis*). Several genus-group taxa are limited geographically (*Crossata* in the eastern Pacific only; *Sconsia* and *Cassis* in the western Atlantic only, at least at present; *Cymatium* (*Ranularia*), *C. (Septa)*, *Sassia*, *Eudolium* and *Tonna* seem never to have inhabited the eastern Pacific). Vermeij (1993, 1997) has pointed out that these geographically restricted genera (such as the muricid genus *Chicoreus* in the western Atlantic) are empirical biogeographical facts that complicate the interpretation of Central American uplift. They

make it difficult to distinguish between the existence and effectiveness of a dispersal barrier and genera that merely are restricted geographically.

In the following text, institutions in which cited material is housed are abbreviated as follows: NMB—Naturhistorisches Museum Basel, Switzerland (locality numbers; includes all material cited here with Tu numbers, originally Tulane University locality numbers; individual NMB registration numbers for type and figured specimens prefixed H); PPP—Panama Paleontology Project locality numbers, cited in Collins and Coates (1999), but catalogued in NMB by their concordant NMB numbers, also cited here; USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, DC (including all USGS numbers cited, = United States Geological Survey Cenozoic fossil locality numbers).

FOSSILS ON THE OPPOSITE COAST OF THE AMERICAS FROM THE PRESENT RANGE OF THE SPECIES

Cypraecassis tenuis (Fig. 1.1, 1.2, 1.6).—Fragments and rare small whole specimens of a coarsely sculptured species of *Cypraecassis* occur in the late Early Miocene Cantaure Formation of Paraguana Peninsula, Venezuela (NMB 17519, one; NMB 17520, one, Fig. 1.6; B. Landau Colln., one small complete specimen; a useful account of fossil localities and their stratigraphy in northern Venezuela was provided by Gibson-Smith and Gibson-Smith, 1979) and in the coeval Chipola Fm of Florida (NMB 17597, = Tu 820, one fragment, Fig. 1.1, 1.2; NMB 17588, = Tu 830, one fragment). They are indistinguishable from the living eastern Pacific species *Cypraecassis tenuis*, and are very distinct from the smaller, much more finely sculptured Atlantic species, *Cypraecassis testiculus*. Other possible fossil records of *C. tenuis* are "*Semicassis* (*Echinophoria*) *apenes*" Woodring (1959, p. 198, pl. 26, figs. 11, 17), based on poorly preserved, elongate specimens from the Oligocene Caimito Formation of Panama, and an internal mould recorded by Woodring and Malavassi (1961) from the Valle Centrale of Costa Rica (Miocene). *Cypraecassis testiculus* is first recorded in the late Early Miocene Baitoa Formation of the Dominican Republic and the coeval Cantaure Formation of northern Venezuela (i.e., it is sympatric with *Cypraecassis tenuis* in the Cantaure Formation) and is common in the Late Miocene–Early Pliocene rocks of the Dominican Republic. These occurrences indicate that these species originally were sympatric, at least during late Early Miocene time, in the Caribbean. *Cypraecassis tenuis* subsequently has become limited to the eastern Pacific. The immediate ancestor of *Cypraecassis testiculus* seems likely to have been the very similar European Miocene–Pliocene species *C. cypraeformis* (Borson) (Miocene) and *C. pseudocrumena* (Sacco) (Pliocene) (see Abbott, 1968, p. 74, 75) which differ from *C. testiculus* only in having a thicker, more laterally extended callus on both sides of the ventral shield. Abbott (1968) suggested that these forms might be conspecific. Ecological competition with *C. testiculus* is an unlikely reason for the extinction



of *C. tenuis* in the Caribbean, as it is much larger than *C. testiculus*, and the two species likely predate different echinoderm species. However, ecological competition with *Cassis* species is a possible explanation of the extinction of *C. tenuis* in the Caribbean, as *Cassis* is almost unknown in the eastern Pacific (only 3 Pliocene fossil specimens are recorded). The extinction of *C. tenuis* in the Caribbean and its retreat to the Eastern Pacific imply either unsuccessful ecological competition with *Cassis* species or, more probably, the appearance of a filter barrier to dispersal in the Central American region by at least Middle Miocene time.

Bursa rugosa (Fig. 1.3–1.5).—The coarsely sculptured, small to moderate-sized species of *Bursa* that occurs abundantly at many Late Miocene to Late Pliocene localities in the Caribbean area is indistinguishable from the common intertidal species living now in Panama Bay, i.e., in the eastern Pacific, but not living on the Atlantic coast of the Americas. This species usually has been known as either *B. albofasciata boussingaulti* Rutsch (Rutsch, 1934, p. 58, pl. 3, figs. 3, 4; specimen from the type locality in Fig. 1.5) or “*B. caelata amphitrites*” when Caribbean and Panamic fossils were identified (e.g., Woodring, 1959, p. 207, pl. 28, figs. 1, 2, 7, 8), and as *B. calcipicta* Dall, 1908 when Panama Bay living specimens were identified (e.g., Keen, 1971, p. 508, fig. 965; but note that Keen’s illustration shows the holotype of *Bursa calcipicta*, not the eastern Pacific intertidal species). *Bursa amphitrites* is a larger, more finely nodulous species limited to the Late Miocene–Early Pliocene rocks of the Dominican Republic and northern Venezuela, and the holotype of *B. calcipicta* is an immature specimen of *Crossata ventricosa*. Three “probable” syntypes of *Ranella rugosa* G. B. Sowerby II, 1835 in the Natural History Museum, London (no. 1989133/1–3) (Fig. 1.3, 1.4) do not closely resemble Sowerby’s (1835, pl. 85, fig. 7) figured specimen in details of coloration and the shape of the anterior canal and fasciole, but in the absence of any other type material are assumed to be syntypes. The collector, Hugh Cuming, wrongly stated their locality as “Manila,” but they are almost certainly from Panama Bay. The earliest name for the Panama Bay living and Caribbean fossil species is *B. rugosa*.

This therefore is a good example of what Woodring (1966; see also Jackson et al., 1996) called a “paciphile” species; most fossil records are from the Atlantic coast, whereas all Recent records are from the Pacific coast of the Americas. A few eastern Pacific specimens are known from the Pliocene of Darien, Pacific Panama, and several from the Miocene and Pliocene of Ecuador. However, the paucity of eastern Pacific records of fossils probably merely means that suitable shallow-water faunas to record the presence of this species are rare along the Pacific coast; Collins and Coates (1999, p. 7) commented on the paucity of Neogene fossil localities along the Pacific coast of Central America. Fossils occur at many Caribbean localities up to Late Pliocene or Early Pleistocene in age (Bowden, Jamaica; Limon, Costa Rica; Valiente Peninsula, Bocas del Toro Basin, Atlantic Panama). Along with several other taxa listed here (*Crossata ventricosa*, *Marsupina*

bufo, *Distorsio constricta*, *Cymatium wiegmanni*, *Sconsia sublaevigata*, *Malea ringens*), this distribution implies genetic continuity with the eastern Pacific population until at least early in Pleistocene time, i.e., larval transport through a Central American seaway still open at that time.

Crossata ventricosa (Fig. 1.8).—In my opinion Parth (1996, p. 133) was correct to suggest that the northern form (previously known as “*Bursa*” or *Crossata californica* Hinds, 1844) and the southern form (*C. ventricosa*) belong in the one intergrading species, *Crossata ventricosa*, limited at present to the eastern Pacific from southern California to Peru and perhaps northern Chile. Small deep-water specimens from the tropical Panama-Costa Rica area (such as the holotype of *Bursa calcipicta*) seem to be immature specimens resulting from metamorphosis of the larval, dispersing population that links the more northern and southern breeding populations. A single fossil specimen (Fig. 1.8) is known from the Atlantic coast of Panama (NMB 17854, = PPP 480, Escudo de Veraguas, near base of Escudo de Veraguas Fm, Bocas del Toro, late Early to Middle Pliocene, c. 3–3.5 Ma; Coates, 1999, fig. 5, p. 21; appendix B, column 11). This adds to the evidence from *Bursa rugosa* that larval transport through a Central American seaway still was possible during Early to mid-Pliocene time.

Marsupina bufo.—The *Marsupina bufo* species “complex,” with finely and evenly granulous sculpture over the entire exterior, has a long and full fossil record in the Caribbean, but is absent from the fossil and Recent record of the eastern Pacific, other than the single specimen recorded here. This group is replaced in the eastern Pacific by two quite different species groups of *Marsupina* (*M. freya*, Miocene, apparently descended from *M. chira* Olsson, 1930 and *M. yasila* Olsson, 1930, species with a much shorter and wider shape than *M. bufo*; and *M. nana* and an unnamed, apparently ancestral Miocene species, which have much weaker exterior sculpture than *M. bufo*). A single specimen of *M. bufo* is known from Pliocene rocks at Rio Vaca, Progreso-Largato trail, Puntarenas Province, Pacific Costa Rica (USGS 24792, in USNM). This therefore provides further evidence that larval transport still was possible through a Central American seaway at the time when the Rio Vaca rocks were deposited.

Distorsio clathrata.—The eastern Pacific occurrences of this strongly atlantiphile species (in the Middle Pliocene Esmeraldas Formation of Ecuador; age from Cotton, 1999, fig. 4) have been commented on by Olsson (1964, p. 175, pl. 30, fig. 1–1b). A total of five specimens is known to me (besides the two reported from the Middle Pliocene at Punta Gorda by Olsson (1964), the following specimens have been seen: NMB 12816, Borbon Formation, Middle Pliocene, E of Punta Same, Esmeraldas, one; NMB 12822, Esmeraldas Formation, Middle Pliocene, Esmeraldas, two). *Distorsio clathrata* lives now only in the western Atlantic, and all fossil records other than the Ecuadorian ones are in the

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FIGURE 1—Some Neogene and Recent tonnoidean gastropods of the Central American region. 1, 2, *Cypraecassis tenuis* (Wood), NMB 17597 (=Tu 820), Chipola Formation (late Early Miocene), Ten Mile Creek, Chipola River, Florida, USA (2 views of incomplete specimen, enlarged $\times 1.5$; H 17984, NMB). 3, 4, *Bursa rugosa* (G. B. Sowerby II), one of three “probable” syntypes; “Manila” (wrong, =Panama Bay), enlarged $\times 1.25$ (Natural History Museum, London, no. 1989133/1). 5, *Bursa rugosa* (Sowerby), from type locality of *Bursa albofasciata boussingaulti* Rutsch, NMB 17531, Early Pliocene, Punta Gavilan, northern Venezuela, coll. W. and J. Gibson-Smith (enlarged $\times 2$; H 17896, NMB). 6, *Cypraecassis tenuis* (Wood), NMB 17520, upper Cantaure Formation shell bed (late Early Miocene), near Casa Cantaure, Paraguana Peninsula, northern Venezuela; coll. W. and J. Gibson-Smith (incomplete specimen, enlarged $\times 1.5$; H 18052, NMB). 7, *Cymatium (Monoplex) lignarium* (Broderip), paratype of *Cymatium kugleri* Rutsch, NMB 13112, Caujarao Formation (Late Miocene), Cementario de Carrizal, northern Venezuela (enlarged $\times 3$; H 17948, NMB). 8, *Crossata ventricosa* (Broderip), NMB 17854, Early-Middle Pliocene, Valiente Peninsula, Bocas del Toro Basin, Atlantic coast of Panama (enlarged $\times 2$; H 17902, NMB). 9, *Distorsio constricta* (Broderip), NMB 19008 (=Tu 1240), Moin Formation (latest Pliocene–Early Pleistocene), Limon, Atlantic coast of Costa Rica (outer lip incomplete; enlarged $\times 2$; H 17920, NMB).

area where the species still lives. The Middle Pliocene occurrences in the eastern Pacific once again demonstrate larval transport through a Central American seaway still open during Middle Pliocene time.

Distorsio constricta (Fig. 1.9).—This is the reverse of the case of *D. clathrata*; living specimens are recorded only from the eastern Pacific (Emerson and Piech, 1992) and almost all of the few fossil records are from within its living range. The one exception is the latest Pliocene-earliest Pleistocene Moin Formation of Limon area, Atlantic coast of Costa Rica, where this species is common (Fig. 1.9). The similar Atlantic species *Distorsio mcgintyi* is the member of this species group present at all other Atlantic fossil localities. However, the distinctive, tall and narrow protoconch of *D. constricta*, present on Limon specimens, demonstrates once again that larvae must have been able to be transported through a Central American seaway still during latest Pliocene or earliest Pleistocene time (c. 1.7–1.5 Ma; Coates, 1999, fig. 6, p. 22). The stratigraphy and ages of Pliocene-Pleistocene rocks of the Limon area have been revised in detail by McNeill et al. (2000). However, a detailed stratigraphic location is not available for the Tulane University collections that are the source of my records. I assume the material is from the lagoonal mudstone of the Moin Formation, of earliest Pleistocene age (e.g., in the Empalme Mollusk section; McNeill et al., 2000, figs. 9E, 15).

Cymatium (Monoplex) *lignarium* (Fig. 1.7).—Again this is limited now to the eastern Pacific. All fossil records are from Late Miocene rocks of the Caribbean area (where it has been identified as the synonym *Cymatium kugleri* Rutsch) and Panama: Springvale Quarry, Trinidad (holotype of *C. kugleri*, and USGS 21809, one); NMB 17530, Caujarao Fm, Cemeterio de Carrizal, Falcon, Venezuela, four, plus the paratypes of *C. kugleri* (Fig. 1.7); and Gatun Formation of the Panama Canal area (USGS 21016, Cativa; USGS 22019, Payardi I.; NMB 17643, Payardi I.; Tu 960, Tu 962, refinery, Colon; Cativa, Colon, in B. Landau Coll.; one specimen in each). This distribution implies a pan-Central American range during Late Miocene time, i.e., larval transport through a seaway still widely open at this time.

Cymatium (Monoplex) *wiegmanni*.—This is an almost identical case to that of *Distorsio constricta*; all Recent and most fossil records are from the eastern Pacific. However, a single fossil specimen is recorded from the Middle Pliocene rocks of the Rio Banano at Bomba, near Limon, near the Atlantic coast of Costa Rica (NMB 17784), in the upper part of the Rio Banano Formation. Larval transport through an open Central American seaway is again implied during Middle Pliocene time (c. 3.0 Ma; Coates, 1999, fig. 6, p. 22; Cotton, 1999, fig. 4).

Sconsia sublaevigata.—The genus *Sconsia* has a long and complex fossil record in the Caribbean Sea, but is almost entirely absent from the fossil and Recent record of the eastern Pacific. The exception is two samples of *S. sublaevigata* from Early Pliocene rocks of Darien, Pacific Panama (NMB 18184, Rio Chucunaque, 4 specimens; NMB 18510, Rio Tuquesa, one specimen). These occurrences therefore provide one of the most convincing pieces of evidence that larval transport was possible through a Central American seaway during Early Pliocene time.

Malea ringens.—The genus *Malea* provides much valuable biogeographic evidence on the closure of the Central American seaway. It had a diverse and quite complex fossil record in the Caribbean area, but most Recent records are from either the eastern Pacific (which is occupied by the very large species *M. ringens*) or the tropical Indo-West Pacific (where the small species *M. pomum* (Linné, 1758) is very widespread). Another living species, *M. norohnensis*, was found quite recently to be common at Fernando de Noronha Island, off northeastern Brazil (Kempf and Matthews, 1969). At least six further species are recognized in the fossil record, all from the Caribbean area, in Miocene to Late

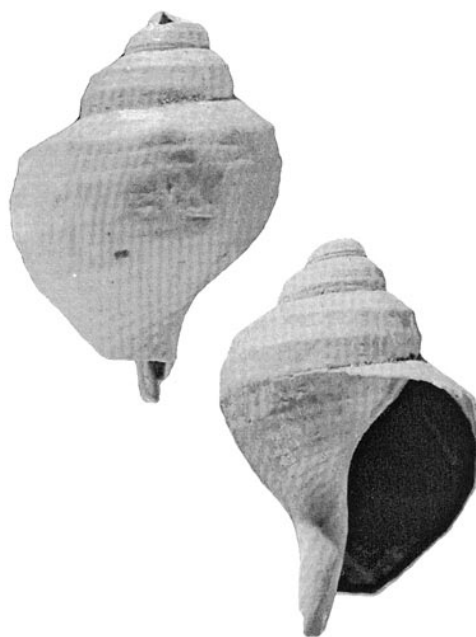


FIGURE 2—*Cymatium* (*Linatella*) *cingulatum* (Lamarck), NMB 17442, Armuelles Fm (Early to Middle Pleistocene), Rio Rabo de Puerco, Burica Peninsula, western Pacific Panama (enlarged $\times 1.5$; H 18261, NMB).

Pliocene rocks as far north as Florida, USA (Petuch, 1989), besides another species in Miocene and Pliocene rocks of Europe, *M. orbiculata* (Brocchi, 1814). Fossil specimens attributed to *M. ringens* have been collected from widespread localities in the eastern Pacific, from the Pliocene Imperial Formation at Coyote Mountain, California, USA (Hanna, 1926; Powell, 1988) and the Pacific coasts of Costa Rica, Panama and Darien, south to at least Peru. Most interesting for the present discussion, however, is the many Late Miocene and Pliocene records of *M. ringens* from the Atlantic coast of Panama, in both the Bocas del Toro Basin and the Colon area (a total of 28 localities in NMB collections). *M. ringens* therefore is particularly useful in demonstrating that a significantly open connection between the two coasts of the Americas allowed larvae of this species to be transported throughout a central Panamic province for all of Late Miocene to Middle Pliocene time.

Cymatium (*Linatella*) *cingulatum* (Fig. 2).—This species provides the most useful evidence for the present discussion. *C. cingulatum* is the species that was identified by Clench and Turner (1957) as *C. poulsonii* (Mörch, 1877), and by Beu (1998b) as *C. cutaceum* (Lamarck, 1816). It is very widespread in the Indo-West Pacific province, from South Africa and the Red Sea eastward to the Hawaiian Islands (Kay, 1979), and from southern Japan (Beu, 1999) southward to northern New Zealand (Beu and Cernohorsky, 1986, as *Linatella caudata* Gmelin). It also is very widespread in the western Atlantic, from Chincoteague Inlet, Virginia (Merrill and Porter, 1966) southward to Rio de Janeiro, Brazil (Rios, 1994), and in the eastern Atlantic has been recorded from the Canary and Cape Verde Islands. However, there are no records whatever from the eastern Pacific (Emerson, 1991).

Despite the lack of Recent eastern Pacific records, *Cymatium cingulatum* is recorded as a fossil from the Miocene of Pacific Costa Rica (NMB 17764, Quepos, Punta Judas, 1 specimen). Most critically, it also is recorded from the Early to Middle Pleistocene (c. 0.5–1.2 Ma; Cotton, 1999, fig. 4) Armuelles Formation of the Burica Peninsula, northwestern Panama (NMB 17442, =

PPP 1761, Rio Rabo de Puerco, five specimens; Fig. 2). The internationally accepted boundary between the Early and Middle Pleistocene is at the Brunhes-Matuyama magnetic reversal (0.78 Ma; Bassinot et al., 1994) so deposition of the Armuelles Formation spanned this boundary. This is the youngest tonnoidean example of larval dispersal through the Central American seaway. It demonstrates that the seaway was open at least from Miocene to early Middle Pleistocene time, the latter presumably during interglacial periods of high sea-level.

GEMINATE SPECIES PAIRS

Considerable weight in interpreting the evolutionary significance and time of closure of the Central American seaway has been given in the past to geminate species pairs, in which one species of each pair is limited to each coast of the Americas (e.g., Jordan, 1908; Woodring, 1966; Vermeij, 1978; T. Collins, 1996, p. 311). The earliest fossil record of one of the species in a pair gives an approximate date for the speciation event, i.e., for the uplift or at least constriction of the Central American dispersal barrier. The present review has shown that, as has already been pointed out by T. Collins (1996), considerable care must be taken in determining the taxonomic status of apparent pairs; apparent geminate pairs have several possible degrees of relationship. Some apparent pairs in fact have an origin quite separate from the uplift of the dispersal barrier. Others range from possible but long-past relationships, to such close similarity that some authors have questioned a distinction at the species level. What appears to be a common relationship among tonnoidean gastropods is a long-lived, ancestral species persisting on one coast of the Americas, and its geologically recent daughter species living on the other coast. Evolution of the daughter species resulted from genetic drift following uplift of the Central American Isthmus and subdivision of an originally pan-Central American population. The best tonnoidean example I am aware of is the *Cymatium* (*Monoplex*) *parthenopeum* complex, in which *C. keenae* and *C. vestitum* seem to have been segregated in the eastern Pacific as the result of two distinct invasions from the Atlantic, whereas the very widespread parent species, *C. parthenopeum*, has a record from at least early Miocene time in Europe and still inhabits the Mediterranean, Atlantic, and Indo-West Pacific. Other possible examples are *Distorsio mcgintyi* and *D. constricta*, *Dalium solidum* and *D. ecuadorianum* and, in a more complex scenario with differentiation of more widespread species, 1) *Cymatium* (*Monoplex*) *corrugatum* (Mediterranean and eastern Atlantic), *C. krebsii* (western Atlantic), and *C. amictum* (eastern Pacific); and 2) *Cymatium* (*Monoplex*) *pileare* (Linné, 1758) (Indo-West Pacific), *C. martinianum* (Atlantic) and *C. macrodon* (eastern Pacific).

A single tonnoidean species, *Bursa corrugata*, remains inseparable on the two coasts at present and does not occur in the Indo-West Pacific. This is the one pan-Central American tonnoidean that apparently has undergone no extinction or genetic change since the dispersal barrier arose. However, this is a very widely distributed species (it lives still in West Africa as well, from Morocco to Angola, and occurred in Europe and the Mediterranean during Miocene to Pleistocene time) so this possibly is a case of a wide geographic range and long time range conferring a robust level of low genetic variability. A few other species are reported rarely from the eastern Pacific (mostly from the offshore islands rather than the mainland; Emerson, 1991) and still live both in the Indo-West Pacific and the western Atlantic (*Bursa granularis*, *Cymatium succinctum*, *C. muricinum*, *C. aquatile*, *C. mundum*, *C. labiosum*). These probably exist only as "pseudo-populations" in the eastern Pacific (non-breeding specimens resulting from occasional larval dispersal across the eastern Pacific filter barrier) and are not regarded as possible Panamic members of geminate species pairs. Possible examples of geminate species

pairs are listed here (the western Atlantic species is listed first in all cases).

Bursa natalensis and *B. latitudo* Garrard, 1961.—This is an example of a distinctive class of taxa that might be considered as geminate species pairs, but in which no member still lives in the eastern Pacific. Instead, the Pacific member species is distributed widely in the Indo-West Pacific—in this case, *B. latitudo*. Other examples (not individually listed again here) are *Cymatium pharacidum* and the Indo-West Pacific species *C. tenuiliratum* (Lischke, 1873), *C. rehderi* and the Indo-West Pacific species *C. testudinarium* (A. Adams and Reeve, 1850), *Eudolium crosseanum* and the Indo-West Pacific species *E. pyriforme* (G. B. Sowerby III, 1914) (Marshall, 1992), and *Malea norohnensis* and the Indo-West Pacific species *M. pomum* (Linné, 1758). If these really are species pairs, they imply not only transport of larvae through the Central American seaway, but also subsequent extinction in the eastern Pacific and the lack of a fossil record of any former occurrence in the eastern Pacific. More probably, they are not species pairs at all, and have never inhabited the eastern Pacific.

Marsupina bufo and *M. nana*.—While these two rather similar species constitute a species pair in a geographic sense, they do not constitute one in a phylogenetic sense. *M. bufo* has a long fossil history, with little or no evolutionary change, from Early Miocene to Pleistocene time in the western Atlantic (see also above). Similarly, *M. nana* seems likely to have descended from a similar but shorter and wider, thick-shelled, unnamed species in Miocene rocks of Punta Judas, Pacific Costa Rica. *M. bufo* and *M. nana* have distinct phylogenetic histories, and consequently have nothing to say about the uplift of a Central American dispersal barrier. Other examples of such apparently geminate species pairs that actually are not related phylogenetically (again, not individually listed again here) are *Cymatium* (*Reticutriton*) *pfeifferianum* and *C. lineatum*, and *C. (Turritriton) labiosum* and *C. gibbosum*.

Distorsio mcgintyi and *D. constricta*.—These species are similar enough in teleoconch characters that Lewis (1972) regarded them as geographic subspecies of one species. It is now clear that their protoconchs differ markedly, that of *C. constricta* being significantly taller and narrower than that of *C. mcgintyi*. Nevertheless, it is quite feasible that they are closely related phylogenetically. *D. mcgintyi* occurs commonly in the Late Miocene–Early Pliocene rocks of the Dominican Republic, as well as in many younger units, and a single specimen is present in collections from the late Early Miocene Cantaure Formation of Paraguana Peninsula, northern Venezuela (NMB 17516). *D. constricta* has few fossil records, but a specimen was recorded from the Pleistocene uplifted terrace ("tablazo") at Mancora, Peru by Bosworth (1922), a few specimens are known from Pliocene rocks of western Panama. It also is the common *Distorsio* species in the Late Pliocene–Early Pleistocene Moin Formation at Limon, on the Atlantic coast of Costa Rica (Fig. 1.9). If this relationship is as close as teleoconch characters suggest, the species dichotomy apparently occurred before late Early Miocene time and, as with the *Cypraecassis* species discussed above, would appear to reflect a very early stage in seaway constriction rather than the final closure. However, the strongly distinct protoconchs (in a genus in which most species have conservative, closely similar protoconchs) probably indicates that, once again, these are not really a geminate species pair in a phylogenetic sense.

Cymatium (*Cymatium*) *femorale* and *C. tigrinum*.—This appears to be one of the few straight-forward tonnoidean examples of a geminate species pair. One species is limited to each coast of Central America. Neither has a fossil record before Late Pliocene–Pleistocene time, and it seems likely that both descended from the Late Miocene–Pliocene Caribbean species *C. praefemorale*. Although *C. praefemorale* previously has been recorded

only from the Late Miocene-Early Pliocene rocks of the Dominican Republic, a single large, incomplete specimen is present in NMB 17962, Cayo Agua, in the Pliocene Cayo Agua Formation of Atlantic Panama.

Cymatium (Monoplex) *krebsii* and *C. amictum*.—These are part of a “complex” of species related to *Cymatium* (*Monoplex*) *corrugatum* (Lamarck, 1822). *C. corrugatum* lives now in the Mediterranean Sea and in the eastern Atlantic from southern Portugal to Angola. It is similar to the American species in most characters, but reaches a markedly larger size. The status of *C. krebsii* as a species distinct from *C. corrugatum* is demonstrated by the occurrence of *C. krebsii* in the eastern Atlantic at the Canary Islands (García-Talavera, 1983, 1987), where it is sympatric with *C. corrugatum*. The American species differ in the markedly weaker spiral sculpture and apertural ridges of *C. amictum* than of *C. krebsii*, and these distinctions hold for fossil specimens of at least Pliocene age. *C. krebsii* has a fossil record from the Late Miocene Gatun Formation of Panama (= *C. pileare henicum* Woodring, 1959) and in the Late Miocene-Early Pliocene rocks of the Dominican Republic, whereas *C. amictum* is first recorded from the mid-Pliocene Esmeraldas Formation of Ecuador. This record makes it impossible to distinguish whether these are sister species that had diverged by Middle Miocene time, or *C. krebsii* was a widespread Central American species that gave rise to *C. amictum* early in Pliocene time as a result of subdivision of the population through uplift of the Central American dispersal barrier.

Cymatium (Monoplex) *cercadicum* and *C. wiegmanni*.—*Cymatium* (*Monoplex*) *cercadicum*, from the Late Miocene-Early Pliocene rocks of the Dominican Republic, differs from the living eastern Pacific species *C. wiegmanni* in its smaller maximum size, its shorter form, its slightly narrower and more prominent spiral cords, its smaller, more constricted aperture, its longer anterior canal, and its more strongly out-turned outer lip. Other characters such as the presence of only a terminal varix in most specimens and unusually prominent transverse ridges on both lips of the aperture are common to both species, and suggest that these are a closely related species pair. In this case, though, as *C. wiegmanni* is not recorded before Pliocene time, it is feasible that *C. cercadicum* simply was the direct ancestor of *C. wiegmanni*.

Cymatium (Monoplex) *parthenopeum*, *C. keenae*, and *C. vestitum*.—The complex of species that closely resemble (and so are assumed phylogenetically to be related to) *C. parthenopeum* in the Central American region seems to provide one of the best examples of speciation as a result of constriction or uplift of the Central American dispersal barrier. *Cymatium parthenopeum* is one of the planktotrophic species for which Scheltema (1966, 1971) demonstrated a very extended larval life. Consequently, it is more widely distributed than almost all other benthic, shallow-water gastropods. Specimens identical to the living Mediterranean type population live throughout the temperate and tropical Atlantic, in South Africa and possibly all along the coast of East Africa, in the Red Sea and around the Arabian Gulf, in southern Japan to Taiwan, in New Zealand, southern Australia and New Caledonia and, uncommonly, in Hawaii (Beu, 1998b). A similar form widespread in the eastern Pacific (Baja California and the Galapagos Islands to Peru) consistently has slightly more numerous spiral cords and significantly more numerous, more closely spaced axial ridges than *C. parthenopeum*, and was named *C. parthenopeum keenae* by Beu (1970). Whether this relationship is expressed at the species or subspecies rank is immaterial to the argument; the point is that they are distinguishable, and evidently represent subdivision of a formerly continuous Central American population. There are no records of *C. keenae* before Late(?) Pliocene-Pleistocene time (Galapagos Islands; Beu, 1970) so this might well have been a Late Pliocene speciation event. This case

is unusual because of the occurrence of another endemic eastern Pacific species, *C. vestitum*, which differs from both *C. parthenopeum* and *C. keenae* only in its smaller maximum size, its overall darker exterior shell colour, and its slightly narrower and more prominent spiral cords. It seems likely that *C. vestitum* resulted from an earlier appearance of a *C. parthenopeum* population in the eastern Pacific, and its subsequent evolution as a result of an earlier constriction event in the Central American seaway. The fossil record of *C. vestitum* (Charco Azul Fm, Pliocene, Quebrada la Penita, Burica Peninsula, Pacific Costa Rica, B. Landau Colln., one; NMB 17441, Armuelles Fm, Early to Middle Pleistocene (Cotton, 1999, fig. 4), Rio Rabo de Puerco, W of Puerto Armuelles, Pacific Panama, one large) at least supports the possibility of Pliocene constriction of the seaway. This species group seems to indicate that *C. parthenopeum* was dispersed to the eastern Pacific on at least two separate occasions, each of which was followed by seaway constriction and subsequent genetic drift in the eastern Pacific population.

Cymatium (Monoplex) *martinianum* and *C. macrodon*.—Beu and Kay (1988) demonstrated that these two forms, each limited to one coast of the Americas, are distinct taxa, with consistently different spire heights and protoconch proportions. Again, whether they are to be treated as species or geographic subspecies is immaterial to the argument; the important point is that they are distinguishable. Both species are similar to the living Indo-West Pacific tropical species *C. pileare* (Linné, 1758). It appears feasible that this is a case of a formerly single, pantropical species that has been subdivided into three as a result of the uplift of the Central American land barrier and the development of the eastern Pacific filter. Again, as *C. martinianum* has a fossil record from the Late Miocene-Early Pliocene rocks of the Dominican Republic, this would appear to be a Middle Miocene event. However, the complete absence of a fossil record for *C. macrodon* means that the possibility cannot be discounted of the earlier (Miocene) evolution of *C. martinianum*, and the later (Pliocene or Pleistocene) differentiation of *C. macrodon* following uplift of the Central American dispersal barrier. In this case, *C. macrodon* is much more nearly similar to *C. martinianum* than either is to *C. pileare*, supporting the second possible explanation rather than the first.

Dalium solidum and *D. ecuadorianum*.—This is parallel to the sixth example above, of *Cymatium cercadicum* and *C. wiegmanni*. The slightly shorter and more weakly sculptured Ecuadorian Pliocene fossil species *Dalium ecuadorianum* might well simply have been the direct ancestor of the western Atlantic living species *D. solidum*. The latter lives in quite deep water, and so has no fossil record to support any particular interpretation of this case.

Casmaria atlantica and *C. erinacea vibexmexicana*.—This example has no fossil record whatever, and therefore is not interpretable for biogeography. Abbott (1968) regarded *C. erinacea vibexmexicana* as more closely related to the living Indo-West Pacific species *C. erinacea* (Linné, 1758) whereas he regarded *C. atlantica* as more closely related to the other widespread living Indo-West Pacific species, *C. ponderosa* (Gmelin, 1791). If this is correct (which is far from certain, as cassid taxonomy at the species level remains poorly understood), these are not sister species, but might have resulted from the subdivision of separate species that both formerly inhabited the Central American region. An alternative scenario suggested by Gibson-Smith and Gibson-Smith (1981) is that *C. atlantica* merely is a homeomorph of Indo-West Pacific *Casmaria* species, and arose independently from a Caribbean *Semicassis* ancestor. If the narrow shell form and the denticles around the outer edge of the anterior end of the outer lip are accepted as generic characters of *Casmaria*, this alternative scenario is unlikely to be correct, but homeomorphy always must be considered as an alternative to widely disjunct

relationships in biogeography. A still further explanation suggested by Parth (2000) is that *C. atlantica* is a synonym of the widespread Indo-West Pacific species *C. perryi* (Iredale, 1912); it then would have nothing to say about Panamic uplift. More probably, *C. perryi* would then be one of the many tonnoideans that entered the Atlantic from the Indo-West Pacific via South Africa after the closure of the Central American seaway (as suggested for other mollusks by Vermeij and Rosenberg, 1993). Other western Atlantic tonnoideans that are common in the Indo-West Pacific and have no western Atlantic fossil record before the Pleistocene include *Bursa granularis*, *Ranella gemmifera*, the genus *Cabestana*, *Cymatium (Gelagna) succinctum*, *C. (Gutturnium) muricinum*, *C. (Monoplex) comptum*, *C. (Monoplex) mundum*, *C. (Monoplex) nicobaricum*, *C. (Monoplex) vespaceum*, *C. (Ranularia) cynocephalum*, *C. (Ranularia) gallinago*, and possibly *Bursa natalensis* and *Eudolium bairdii*. These 12–13 examples all seem likely to have entered the Atlantic only during Pleistocene time, and suggest that this is quite a large biogeographic element in the Atlantic tonnoidean fauna.

Semicassis granulata and *S. centiquadrata*.—This might well be another case of a straight-forward geminate species pair, although Abbott (1968) regarded these taxa as geographic subspecies of one species. Both species have a fossil record commencing in the Miocene or Pliocene (*S. centiquadrata*: NMB 17753, 17754, Punta Judas, Costa Rica, Miocene, seven specimens; Esmeraldas, Ecuador, Middle Pliocene (Pilsbry and Olsson, 1941; age from Cotton, 1999, fig. 4); *S. granulata*: widespread in the Plio-Pleistocene of Florida (e.g., Petuch, 1994, pl. 38 A, B, E); Plio-Pleistocene of Atlantic Costa Rica, Panama and northern Venezuela). If these are (as seems likely) sister species, differentiation of these two species apparently resulted from Late Miocene or earliest Pliocene uplift of the Central American dispersal barrier.

TIMING OF UPLIFT OF THE CENTRAL AMERICAN DISPERSAL BARRIER

The concept of a seaway through Central America, formerly uniting the tropical oceans, dates back at least to Spencer (1897), who envisaged a connection through the Isthmus of Tehuantepec, Mexico. More recent efforts have concentrated on the concept of straits through northern Colombia (the Atrato corridor), through the present area around the Panama Canal, and through the low-lying parts of Costa Rica (Coates et al., 1992; Jackson et al., 1993; Coates and Obando, 1996). Most earlier statements about such a concept (e.g., Keigwin, 1978) seemed to imply a single, climactic event in which the seaway suddenly was cut off and “the Great American Interchange” of mammals began. More gradual disconnection of the oceans and linking of the continents is indicated, however, by new evidence. Firstly, it is now clear that North American mammals such as gomphotheres (Proboscidea), camels and tapirs arrived in Peru, Colombia and Brazil by at least Late Miocene time (Campbell and Frailey, 1996). Secondly, L. Collins (1996) stated that during Miocene time, the Central American seaway area was a complex archipelago. She demonstrated that an “effective biogeographic barrier between Pacific and Caribbean surface waters” had formed by 8 Ma (L. Collins, 1996, p. 78), but that by about 6 Ma a strait at least 200 m deep had opened again through Central America. The evidence from both onshore and offshore stratigraphy and faunal change, summarised by Coates and Obando (1996), also demonstrates that uplift was a long, gradual process. They concluded that “The formation of the Isthmus of Panama has been a complex and extended process stretching over the last 15 m.y., . . . finally raised to a complete marine barrier about 3.1–2.8 Ma” (Coates and Obando, 1996, p. 21). These authors also suggested that “temporary breaching of

this barrier may also have occurred in the late Pliocene as a result of eustatic sea-level changes” (Coates and Obando, 1996, p. 21).

The scenario that results from the dates derived from tonnoidean gastropod biogeography strongly supports the concept of long, gradual, complex uplift of the Central American dispersal barrier over the last 15 m.y. During this time some taxa became restricted to parts of their former range, other taxa became extinct or evolved into sister or daughter species, and several others were transported briefly outside their normal ranges during periods of high sea-level. A long-drawn-out final closure seems necessary to explain the pattern of tonnoidean dispersal. A shallow marine connection probably reappeared during interglacial periods of high sea-level, and alternated with a land connection that probably reappeared during glacial periods of low sea-level for at least much of Late Pliocene to Early and perhaps even Middle Pleistocene time.

CONCLUSIONS

1) Tonnoidean gastropods indicate that speciation events and reorganization of distributions occurred in Central America during Middle and Late Miocene time (e.g., *Cypraecassis tenuis* and *C. testiculus*; *Semicassis centiquadrata* and *C. granulata*). These indicate that constriction of the Central American seaway was beginning as early as early Middle Miocene time, although larvae still were dispersed through the seaway.

2) The record of tonnoideans in the Central American region indicates that a seaway (or seaways) still operated, at least intermittently during interglacial periods of high sea-level, to connect the Atlantic and Pacific oceans and transport tonnoidean larvae out of their normal province late in Pliocene time. Taxa recorded above from the opposite coast of the Americas to the one they are restricted to at present are *Bursa rugosa* (common in the Caribbean in Miocene–Pliocene and perhaps Early Pleistocene rocks; living only in the eastern Pacific), *Crossata ventricosa* (a specimen in the Pliocene of Valiente Peninsula, Atlantic Panama, all other records in the eastern Pacific), *Distorsio clathrata* (five specimens from the Middle Pliocene of Esmeraldas, Ecuador, all other records Caribbean), *D. constricta* (common in the Late Pliocene–Early Pleistocene Moin Formation, Atlantic Costa Rica, all other records from the eastern Pacific), *Sconsia sublaevigata* (two lots from the Pliocene of Darien, Pacific Panama, all other records of the genus from the Caribbean), and *Cymatium wiegmanni* (one specimen from the mid-Pliocene of Rio Banano, Atlantic Costa Rica, all other records from the eastern Pacific). Most significantly, the occurrence of *Cymatium cingulatum* in the Early to Middle Pleistocene Armuelles Formation of the Burica Peninsula, western Pacific Panama, indicates that at least some marine connections still occurred between the Atlantic and Pacific oceans during Early–Middle Pleistocene interglacial periods, and perhaps later.

3) The scenario indicated for the uplift of the central American dispersal barrier is one of gradual constriction and fragmentation of marine connections after Early Miocene time. Marine basins frequently formed and disappeared again through the combination of active tectonics and the rapidly oscillating sea-levels of Late Miocene–Pleistocene time. At least intermittent marine connections probably continued during Late Pliocene–Early and perhaps Middle Pleistocene interglacial periods. For much of Late Pliocene–Early Pleistocene time, the isthmus would have alternated between a dry land bridge during glacial periods of low sea-level and a (number of?) shallow, constricted waterway(s) during interglacial periods of high sea-level.

ACKNOWLEDGMENTS

Supported by the New Zealand Government’s Marsden Fund, administered by the Royal Society of New Zealand. Too many

people helped me with this project over too many years to list them all. I am grateful to P. Jung (NMB) for the opportunity and for financial assistance from the Kugler Fund to work on the Naturhistorisches Museum Basel collections, and for much support over more than 20 years. R. Panchaud, F. Weidenmayer, A. Heitz and J. Meier of the same institution curated specimens, sent manuscript corrections, lent much material over many years, and supported this project substantially. D. Miller (NMB) supplied age data for collections and discussed many stimulating ideas. E. Vokes (formerly of Tulane University) loaned huge collections over many years. W. and J. Gibson-Smith (England, and at NMB) helped greatly by donating their magnificent Venezuelan collections to NMB, and by discussing ideas and ages, and B. Landau (Albufeira, Portugal) lent valuable material from his excellent collection. The "ranellid fraternity" (particularly G. Kronenberg, Eindhoven, and B. J. Piech, Hokessin, DE) have provided much discussion and help with specimens. B. Marshall (National Museum of New Zealand) and the referees, G. Vermeij (University of California, Davis) and P. Jung, suggested helpful improvements to the manuscript. A. Dreadon (Institute of Geological and Nuclear Sciences library) helped with rare publications. Photographs are by S. Dahint (NMB), except Figure 1.3 and 1.4, which are by W. St George (Institute of Geological and Nuclear Sciences), and Figure 2, which is by D. Miller. IGNS contribution no. 1903.

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ACCEPTED 15 NOVEMBER 2000