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MESOZOIC BRACHIOPODS OF MEXICO—A REVIEW AND SOME COMMENTS ON THEIR PALEOBIOGEOGRAPHIC AFFINITIES AND PALEOECOLOGY

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ABSTRACT

Recent work on the taxonomy and paleobiogeographic affinities of Mesozoic brachiopods from Mexico is reviewed. Brachiopods are lesser components of Mesozoic marine fossil assemblages from Mexico but they are abundant at certain horizons. Triassic brachiopod faunas are very poorly known and few have been described. A greater number of papers have described brachiopods from the Jurassic and Cretaceous. During the Jurassic-Cretaceous opening of the Central Atlantic Ocean the number of brachiopod genera in common with faunas from western Europe increased.

Key words: Brachiopods, Mesozoic, paleobiogeography, paleoecology, Mexico.

RESUMEN

En este estudio se presenta una revisión sobre la taxonomía y las afinidades paleobiogeográficas de los braquiópodos mesozoicos de México. Los braquiópodos son componentes menores de las asociaciones marinas fósiles del Mesozoico de México, pero son abundantes en ciertos niveles estratigráficos. Las faunas de braquiópodos triásicos son aún poco conocidas y sólo unos cuantos de ellos han sido descritos. Por el contrario, se ha publicado muchos más trabajos acerca de los braquiópodos jurásicos y cretácicos. Durante el Jurásico–Cretácico y al tiempo de la apertura del océano Atlántico central hubo un incremento en México del número de géneros de braquiópodos del occidente de Europa.

Palabras clave: Braquiópodos, Mesozoico, paleobiogeografía, paleoecología, México.

INTRODUCTION

In contrast to the abundant and diverse articulate brachiopod faunas of the Paleozoic, Mesozoic brachiopods have been largely neglected in paleobiogeographic and paleoecological studies in the Americas. This neglect is not surprising, given the scarcity of these fossils in the field and in museum collections. However, there were times during the Mesozoic when conditions were right and brachiopods well represented in normal marine, generally shallow-water environments in the Americas.

In terms of interpreting the record of fossil brachiopods in Mesozoic rocks of North America, the surface has only been scratched. In South America, Miguel Manceñido has been working primarily on Jurassic brachiopods of Argentina for a number of years and has erected zonal schemes incorporating brachiopods (*e.g.*, Manceñido, 1991).

Brachiopods are generally interpreted as "minimalists" by biologists and paleobiologists in terms of their nutrient requirements—and this is seen as an important factor as to why the phylum has survived through the entire Phanerozoic. They are known from a range of marine habitats in the Mesozoic (Figure 1).

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The time of major crisis and extinction for the group was the end-Paleozoic. Many groups of marine organisms did not survive (*e.g.*, trilobites). Clearly the Brachiopoda did not come through this unscathed, but did survive—and the die was cast for the character of the Mesozoic articulate brachiopod fauna (dominated by rhynchonellids, terebratulids, and to a lesser extent spiriferids). The end-Paleozoic extinction was important for shaping the nature of Mesozoic-Cenozoic brachiopod faunas. Spire-bearers such as the spiriferids and athyrids survived into the Triassic from the Permian, and were very successful at times in the Triassic. However, by the end of the Early Jurassic the articulates with a complex calcified spiral brachidium (spiralium) were extinct.

In the lowermost Triassic of Nevada, U.S.A., the occurrence of stromatolites and other fossils including the inarticulate brachiopod *Lingula* have been interpreted as "disaster forms" (Schubert and Bottjer, 1992), *i.e.*, they were "pioneer colonizers" that temporarily replaced extinct or displaced organisms until they were ousted or restricted by re-radiating forms.

MESOZOIC BRACHIOPODS FROM MEXICO—RECENT STUDIES

TRIASSIC

Two species of brachiopod were described from the lower Norian (Upper Triassic) of the Antimonio Formation by Sandy (*in* Stanley, *et al.*, 1994). These were identified as the

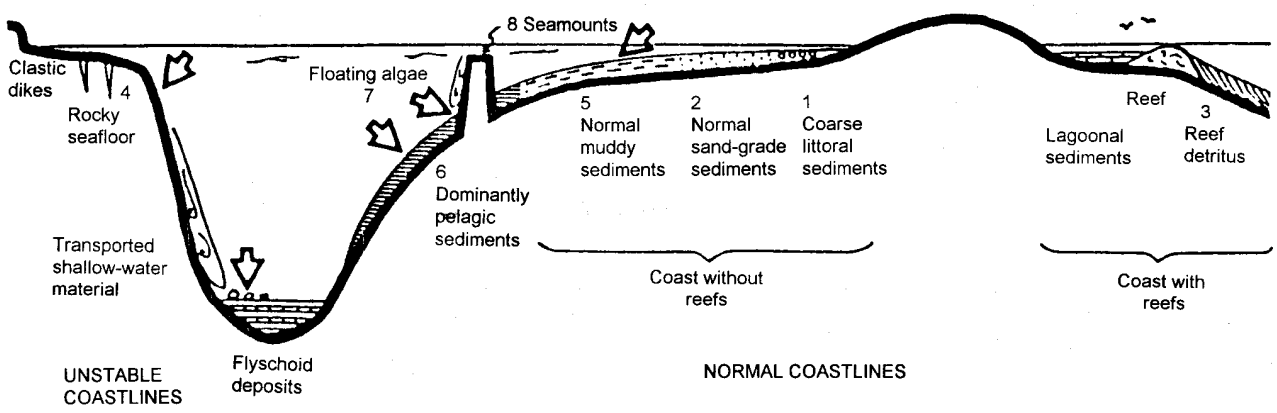

Figure 1. The different habitats of Mesozoic brachiopods modified from Ager (1993) to include schematically cold seep chemosynthetic communities (arrows) in the Mesozoic. Modern cold seep communities have been identified in a range of marine environments and tectonic settings (*e.g.*, subduction zones in active continental margins, brine seeps in passive margins, petroleum seeps in active and passive margins and submarine fans (references in Callender *et al.*, 1992) from depths between 75 to 3,850 m in several oceans (references in Beauchamp *et al.*, 1989; Von Bitter *et al.*, 1992). High-temperature hydrothermal vents, not under consideration, occur on oceanic rises. From Sandy (1993) (modified from Ager, 1993).

widespread spiriferid *Spondylospira* (cosmopolitan in the "East Pacific", see Figure 2) and a new terebratulid genus *Pseudorhaetina* which is so far only known from Sonora. The general lack of information on Triassic brachiopods from Mexico is reflected by their absence from the review papers of Dagys (1993) and Manceñido and Dagys (1992).

The Triassic was a critical time in the history of the Brachiopoda. The Rhynchonellida and Terebratulida both survived through from the end-Paleozoic extinctions, continued into the Mesozoic, and through to the present day. A number of superfamilies, families, and subfamilies of the Order Terebratulida originated in the Triassic (*e.g.*, Muir-Wood *et al.*, 1965); a Triassic origin appears likely for the Terebratuloidea, the archetypal "modern" short-looped terebratulid brachiopod.

The Triassic marks the start of a post-Paleozoic radiation among the Terebratulida based on generic lists made available by Rex Doescher (personal communication, 1987); much of this information was listed in Doescher (1981). The Terebratulida appear to have taken advantage of niches that became available after the end-Permian extinctions. Examination of the ranges of Middle-Late Triassic brachiopod genera plotted by Dagys (1974) indicates a series of step-like radiations and extinctions associated with successive stages: Anisian, Ladinian, Carnian, Norian, and Rhaetian. However, this may be an artifact of extension of ranges through entire stages. Currently there is not enough information available from the North American Triassic to comment on this observation. The brachiopods do have some potential for paleogeographic reconstruction.

By the Late Triassic the spire-bearing Spiriferida were diverse at the genus-level and well represented in marine sequences (*e.g.*, Dagys, 1974; Pearson, 1977), although they did not survive beyond the Early Jurassic. The rhynchonellids underwent a renewed radiation in the Triassic. However, neither the Spiriferida nor the Rhynchonellida repeated their Paleozoic generic diversities. Currently evidence points to very low diversity brachiopod faunas in the earliest Triassic (*e.g.*, Xu and Grant, 1994). However, the unusual terebratulids described by Hoover (1979) from the Lower Triassic of the Western Interior of the United States of America suggest that radiation was already underway. By the Middle Triassic brachiopod generic diversity was much higher, and continued to increase into the Late Triassic (Dagys, 1974).

Vörös (1993) has described aspects of brachiopod radiation in the Early Jurassic, following Late Triassic extinctions.

JURASSIC

Published occurrences and descriptions of Jurassic brachiopods are rare: Alencáster and Buitrón (1965) recorded the rhynchonellid genus *Rhynchonella*; Alencáster (1977) recorded a terebratulid from the Upper Jurassic of Chiapas; later Bouillier and Michaud (1987) described terebratulids from the Upper Jurassic of Chiapas, referred to the genus *Xestosina* Cooper, 1983—Alencáster's (1977) material is also considered to belong here; and Ochoterena (1960) described the terebratulid *Parathyridina* from the Upper Jurassic, later referred by Cooper (1983) to the genus *Mexicaria*. Early Jurassic brachiopods have recently been collected from Sierra de Santa Rosa, NW Sonora (C.M. González-León, personal communication); this material has not yet been described.

CRETACEOUS

A few Early Cretaceous brachiopod species from Mexico were discussed by Owen (1981) and redescribed by Sandy (1990a; Table 1). These dealt essentially with material originally collected and described by Ralph Imlay earlier in the century (Imlay, 1937, 1940). The material was collected from

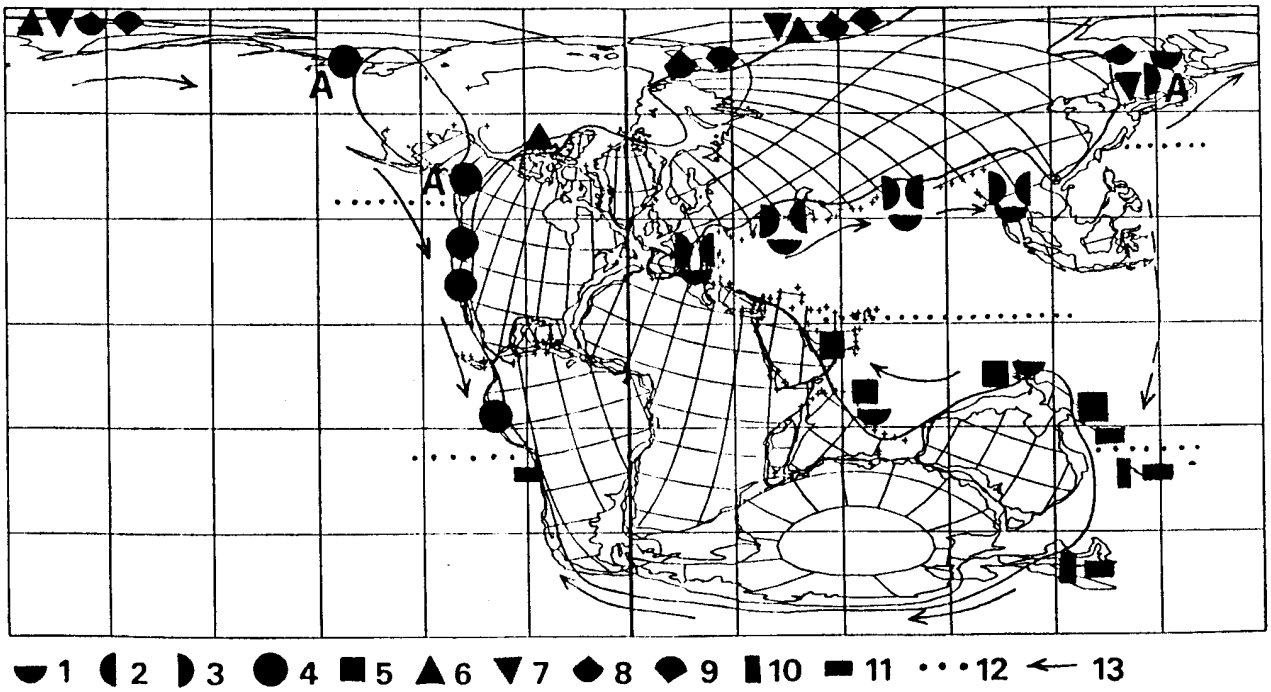

Figure 2. Distribution of selected Late Triassic brachiopod genera (from Dagys, 1993). *1*, Koninckinacea; *2*, Thecospiracea; *3*, Retziacea; *4*, *Spondylospira; 5*, *Misolia; 6*, *Canadospira; 7*, *Viligella; 8*, *Aulacothyroides; 9*, *Pseudohalorella; 10*, *Rastelligera;* 11, *Clavigera; 12*, supposed boundary between realms; *13*, supposed directions of brachiopod migration; *A*, data from suspect terranes.

Coahuila, Durango, and Tamaulipas. The biogeographic significance of these species was linked to cosmopolitan Early Cretaceous genera (rhynchonellid *Ptilorhynchia*) and low-latitude Tethyan forms migrating via the opening Central Atlantic Ocean (terebratulid *Sellithyris*) (Figure 3). Another terebratulid indicating Tethyan links with European faunas, *Moutonithyris*, was recorded by Chiodi and collaborators (1988) (see Figure 4). Brachiopod species from the Lower Cretaceous of Sonora (González-León and Jacques-Ayala, 1988) have close affinities with those described from Arizona by Cooper (1955). A recent report of the brachiopod genus *Peregrinella* from the Lower Cretaceous of Mexico is discussed below.

"BRACHIOPOD SPIKES"

It was recently suggested that the relatively high diversity of Upper Triassic (Norian) Luning Formation brachiopods represents a "brachiopod spike" (Hogler, 1994), where inferred primary productivity crashes allow "minimalists" (*i.e.*, brachiopods) to thrive. However, the brachiopods appear to be very much facies controlled in their distribution in the Luning Formation, related to bathymetric conditions (Hogler, 1991; Sandy, 1995a). To date no inarticulate brachiopods have been recorded. Other invertebrates in the brachiopod-bearing part of the Luning Formation indicate shallow marine waters with corals, sponges, bivalves, along with brachiopods. The "brachiopod spike"/reduction in primary productivity was possibly linked to the formation of the Manicouagan crater in Quebec (Hogler, 1994). The Luning Formation contains the highest diversity brachiopod fauna to be described from the Mesozoic of North America (Sandy and Stanley, 1993; Hogler, 1994) but in reality only nine species are represented. How many species make a spike? Is this more a consequence of facies and environments than drops in primary productivity?

BRACHIOPODS AND CHEMOSYNTHETIC COMMUNITIES

An interesting addition to paleoecological interpretations over the last few years is the recognition of probable fossil cold-seep chemosynthetic communities in rocks ranging from the Paleozoic through to the Recent (*e.g.*, Campbell and Bottjer, 1995). These are in addition to fossil hydrothermal vent communities identified during the 1980s.

The collisional tectonic regime along the western margin of North America through much of the Mesozoic provides the potential for discovery of more chemosynthetic fossil communities.

A number of "unusual" occurrences of brachiopods may be candidates for chemosynthetic occurrences. This may be the case for monospecific accumulations of brachiopods in laterally impersistent carbonate lenses (that are not surprisingly most conspicuous in clastic-dominated sequences), for example, the middle Cretaceous of the Canadian Arctic Islands (Beauchamp *et al.*, 1989; Beauchamp and Savard, 1992) and the Jurassic-Cretaceous of the Great Valley Group, California (Campbell *et al.*, 1993).

Table 1. Original and revised designations for Early Cretaceous brachiopods described by Imlay (1937, 1940) from Mexico. From Sandy (1990a).

Original designation	Revised designation
"Rhynchonella" miquihuanensis Imlay, 1937*	*Ptilorhynchia (Proteorhynchia) miquihuanensis* (Imlay)#
?*Cyclothyris subtrigonalis* Imlay, 1937*	*Ptilorhynchia (Proteorhynchia)* ?*miquihuanensis* (Imlay)
?*Antiptychina mullerriedi* Imlay, 1937*	*Colinella mullerriedi* (Imlay)# (after Owen, 1981)
?*Antiptychina lata* Imlay, 1937*	*Colinella lata* (= ?*mullerriedi*) (Imlay)
"Terebratula" sillimani Imlay, 1937*	*Cyrtothyris sillimani* (Imlay) (after Owen, 1981)
"Terebratula" tamaulipana Imlay, 1937	*Cyrtothyris sillimani* (Imlay)
?*Antiptychina formosa* Imlay, 1940*	*Colinella formosa* (Imlay)
"Rhynchonella" durangensis Imlay, 1940	*Ptilorhynchia (Proteorhynchia) durangensis* (Imlay)$
"Terebratula" coahuilensis Imlay, 1940*	*Sellithyris coahuilensis* (Imlay)$
"Terebratula" kanei Imlay, 1940	?*Sellithyris coahuilensis* (Imlay)/?*Loriolithyris* sp.

* = serial sections given by Imlay; # = serial sections given by Owen (1981); $ = serial sections given in Sandy (1990a).

Some brachiopods with disjunct distributions may be associated with chemosynthetic communities. Other criteria need to be considered in identifying seep-suspect sites (Campbell *et al.*, 1993). The disjunct development of such environments may help to explain the unusual paleobiogeographic patterns and paleoecologic interpretations for some of these fossils that have perplexed paleontologists over the years. A number of brachiopod genera are possible candidates (Sandy, 1995b) such as the large-sized rhynchonellid *Halorella* reported from the Upper Triassic of Europe, the U.S.A., and elsewhere; *Anarhynchia* from the Lower Jurassic of California; and from the Cretaceous, the small-sized terebratulid *Modestella* from Canada (Beauchamp *et al.*, 1989; Sandy, 1990b), and the large-sized rhynchonellid *Peregrinella* from California (Campbell *et al.*, 1993).

The rhynchonellid *Peregrinella* has recently been recorded from Lower Cretaceous sedimentary rocks of the Guerrero terrane, Mexico associated with an island arc (Ortiz-Hernández and Martínez-Reyes, 1993; Ortiz-Hernández, personal communication). In European and American material this brachiopod may reach 10 cm in length and width. The brachiopod, considered to be reworked, is found in carbonate sediment (La Perlita limestone) unconformably overlying pelagic sediments. A detailed taxonomic account of this material is awaited. The author of the present paper had previously anticipated that the discovery of *Peregrinella* in Mexico would sup-

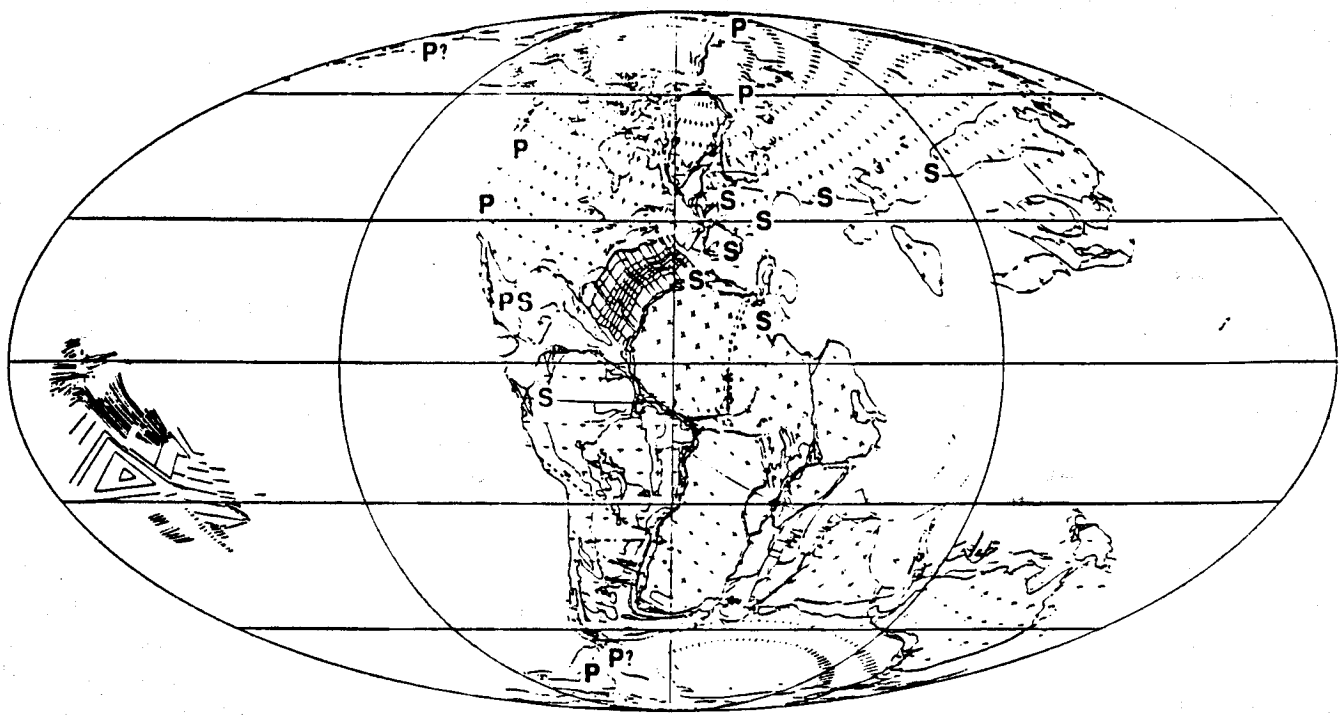

Figure 3. Paleobiogeographic distribution of *Sellithyris* (S) and *Ptilorhynchia* (P). This is a "time-composite" representation for both genera and is not intended to indicate contemporaneous occurrences (although some are). Compiled from various sources. Base map for Valanginian 130.2 Ma, from Scotese and collaborators (1989). From Sandy (1990a).

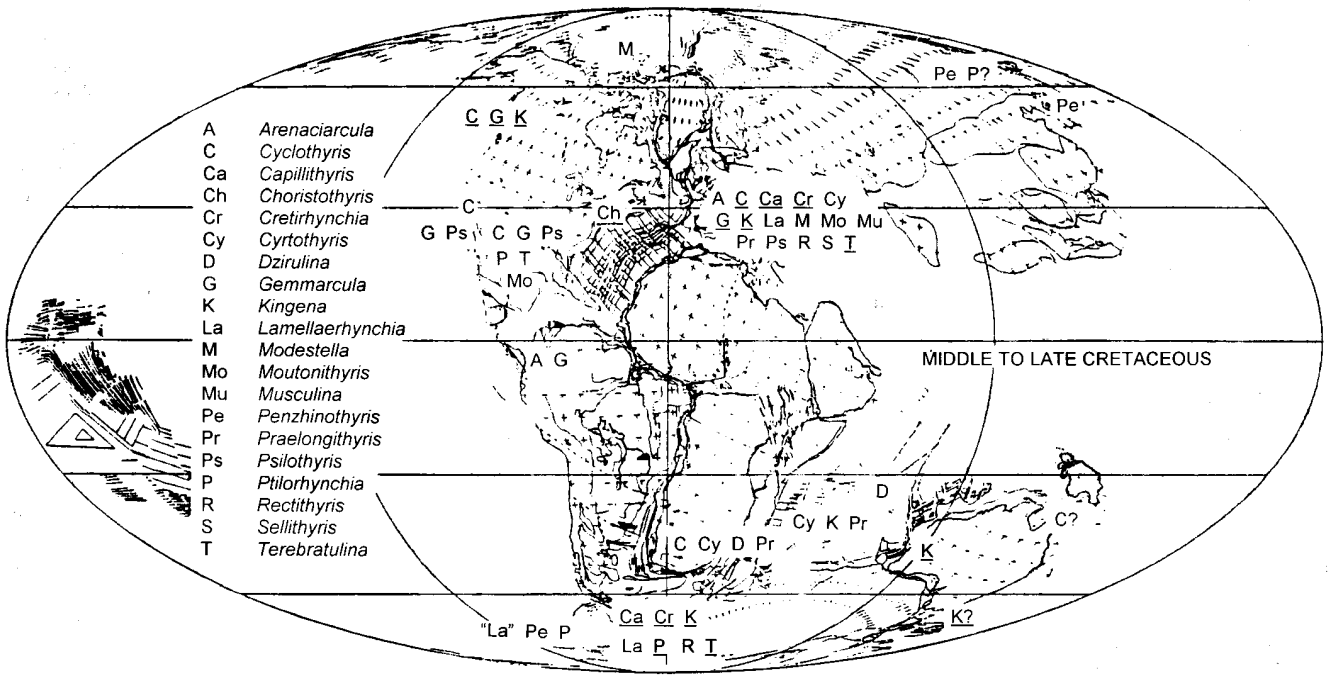

Figure 4. Distribution of widespread brachiopods in the mid- (Aptian-Cenomanian) to Late (Turonian-Maastrichtian) Cretaceous. Genera plotted are those from northwestern Europe that are known elsewhere. Key to genera on left of map. ?: uncertain assignation. Late Cretaceous occurrences are underlined. Compiled from numerous sources. Base map for Aptian 118.7 Ma, from Scotese and collaborators (1989). From Sandy (1991b).

port transatlantic dispersal for this genus (Sandy, 1991a). However, its record from a Pacific-located suspect terrane in the Cretaceous does not necessarily confirm this. A species of *Peregrinella* was recently described from the Cretaceous of Alaska (Sandy and Blodgett, 1996).

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