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BRACHIOPODS ANCIENT AND MODERN
A Tribute to G. Arthur Cooper

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LIFE BEYOND THE PERMIAN—MESOZOIC-CENOZOIC BRACHIOPOD PALEOBIOGEOGRAPHY, PALEOECOLOGY, AND EVOLUTION

MICHAEL R. SANDY
Department of Geology, University of Dayton, 300 College Park, Dayton, OH 45469-2364 USA

The main focus here is the paleobiogeography and paleoecology of Mesozoic-Cenozoic Brachiopoda, mostly the forms referred to as articulated brachiopods. These are the forms I have worked on primarily for the past two decades. To put these creatures in context some attention should be paid to their evolutionary developments during this time (Fig. 1). The articulated brachiopods that continued into the Mesozoic from the Paleozoic are the rhynchoelullides (internally with two processes or prongs, crura, to support the lophophore, Fig. 2.1; examples of external morphology shown in Figs. 3.1–3.5, 4.1); the terebratulides with a brachidium in the form of a loop to support the lophophore (“short-looped” in the Terebratulida, Figs. 2.2, 2.3, 3.6–3.8, 4.2–4.5; “long-looped” in the Terebratellida, Figs. 2.4, 2.5, 3.9–3.13); and two forms with a spiral lophophore support, the athyridides and spiriferides (these latter two both become extinct during the Mesozoic; Figs. 2.6, 2.7, 3.14–3.16). The thecideides are micromorphic, cryptic, articulated brachiopods (Fig. 3.17) that have much-debated origins (Baker, 1990; Jaecks, 2000).

As for the inarticulated brachiopods, they show continuity from the Paleozoic into the Mesozoic, and on through the Cenozoic (Fig. 1). Today these forms are generally considered to have better dispersal ability in the larval stage, and living discinisids have been recovered from water depths up to 5,500 m (Emig, 1997a). Therefore, the inarticulated forms seem well-adapted to survive extinction threats whereas the articulated forms, with more of a propensity to endemism, could be considered somewhat more extinction-prone. However, terebratulides and rhynchoelullides are still an ongoing component of modern marine faunas.

There is a long history of study of Mesozoic and Cenozoic brachiopods from the nineteenth century to the present day. The fact that much of this research has occurred outside of the United States is reflected in the very brief mention of Mesozoic and Cenozoic brachiopods in the 1981 “Lophophorates” Short Course by the Paleontological Society (Dutro and Boardman, 1981), which is the forerunner of this volume.

One goal of this contribution is to illustrate that the Brachiopoda were (and still are) “alive and well” beyond the Permian. In this personal account, I have written separate sections on evolution, paleobiogeography, and paleoecology. However, there is overlap among these topics so they are somewhat artificial. I preface this with some considerations of the main players in the story.

WHO’S WHO—MORPHOLOGICAL CONSIDERATIONS

One significant aspect of Mesozoic-Cenozoic brachiopod faunas is their reduced diversity at the ordinal, genus, and species level compared to their Paleozoic diversity (Fig. 1). Through much of the Mesozoic-Cenozoic the rhynchoelullides (Order Rhynchoellida) and terebratulides (Order Terebratulida) have been the major articulated brachiopod orders. Although these two orders show a wide range of morphological variability there can also be a large degree of morphological similarity between different evolutionary stocks within, and also between these and other brachiopod orders (Figs. 3.7, 3.11, 3.12, 3.13, 3.16). This is the phenomenon of homeomorphy that adds a degree of challenge in
FIGURE 1—Classification for Phylum Brachiopoda proposed by Williams et al. (1996), showing three subphyla and eight classes in the two left-hand columns. The rest of the figure shows the geologic ranges of the main brachiopod orders. Abbreviations for geologic periods shown below geologic eras. Abbreviations for classes: Li = Lingulata; Pa = Paterinata; Cr = Cranata; Ch = Chileata; Ob = Obolellata; Ku = Kutorginata; St = Strophomenata; Rh = Rhynchonellata. Base of Cambrian taken at 545 Ma. Modified from Williams et al., 2000.
identifying brachiopods. Homeomorphy is neither restricted to Mesozoic-Cenozoic representatives, nor to the brachiopods (nature abounds with examples; the similar gross morphology of the Mesozoic marine reptile *Ichthyosaurus* and the present-day marine mammal, the dolphin, provides a good example, where there has been convergence of form around a specific lifestyle). A “classic” example of brachiopod homeomorphy is seen between a Triassic athyridid and two unrelated Jurassic terebratulides (Figs. 3.12, 3.13, 3.16) where a strongly carinate ornament develops.

One might consider the “typical” rhynchonellide morphology to include an external ornament with costation of the shells (Figs. 3.1, 3.5, 4.1). However, strong costation may also develop in both short-looped (Fig. 3.7) and long-looped (Fig. 3.11) terebratulides. Because both of these orders have a curved, aristrophic hingeline it is perhaps easy to see how they can be and have sometimes been confused for one another. If the pedicle foramen is visible it is located in the delthyrium in the rhynchonellides, whereas it is found apically in terebratulides, migrating beyond the triangular outline of the delthyrium. Spiriferides typically have a ribbed or costate ornament (Fig. 3.14). However, smooth forms are also rather common (Fig. 3.15) and this is the common condition for athyridides. Sometimes confusion with smooth-shelled terebratulides is possible from external examination, although the straight hingeline of the spiriferides should allow differentiation. Distinguishing short-looped from long-looped terebratulides by external morphology is often possible because the short-looped forms typically have rounded beak ridges (Fig. 3.6) and the long-looped forms have sharp beak ridges (Figs. 3.9, 3.10) and the trace of a median septum is often visible in the brachial (dorsal) valve (Fig. 3.9). There is a tendency for long-looped terebratulides to have a sulcate shell form (Fig. 3.10), or a truncated, square, or indented anterior shell margin (Fig. 3.9). Some stocks of
rhynchonellides have a strong tendency towards shell asymmetry (Fig. 3.5). These are some general observations based on external morphology...but in the world of brachiopods “Sod’s Law” prevails (to every rule there is an exception)!

External homeomorphy between different evolutionary stocks means that a knowledge of shell structure and internal structures (the nature of the brachidial support and the presence or absence of a median septum and other “plate-like” structures) is desirable when investigating brachiopods in order to determine their identity and evolutionary affinities. In the study of Mesozoic articulated brachiopods, the technique of making serial sections combined with taking acetate peels is commonly used for investigating internal structures (e.g., technique

FIGURE 3—Examples of typical and atypical brachiopod morphologies. 1–5, Rhynchonellides. 6–8, Short-looped terebratulides. 9–13, Long-looped terebratulides. 14–15, Spiriferides. 16, Athyriddae. 17, Thecideide. 18, Aberrant brachiopod; spiriferide? 19–20, Inarticulated brachiopods. 1–16 show three views: dorsal, lateral, and anterior. Magnification x1. 1, Rimirhynchia rimosae, Pliensbachian, Lower Jurassic, Germany. Small, costate, typical rhynchonellide. 2, Rhynchonellina ex gr. bittneri, Sinemurian, Lower Jurassic, Italy. Smooth and sulcate rhynchonellide, an uncommon morphology. 3, Austrihyntychia coronigera, Rhaetian, Upper Triassic, Austria/Tirol. A small, costate rhynchonellide with unique lateral extensions. 4, Acanthothiris spinosa, Bathonian, Middle Jurassic, Switzerland. The bases of broken delicate spines can be seen on the valves. The spines are thought to have helped to stabilize the brachiopod in a high-energy environment with shifting sediments on the sea floor. The spines are a very rare ornament in rhynchonellides but the shape and costation is typical of rhynchonellides. 5, Lacunosella cracoviensis, Kimmeridgian, Upper Jurassic, Switzerland. An asymmetrically developed rhynchonellide. 6–8, Short-looped terebratulides. 6, Selithyris sella, Barremian, Lower Cretaceous, Switzerland. A “typical” short-looped terebratulide with a well-developed folding of the anterior commissure. 7, Glossodesia semistriata, Hauterivian, Lower Cretaceous, Switzerland. A costate short-looped terebratulide; although an unusual ornament, it is not rare. 8, Coenothyris vulgaris, Anisian, Middle Triassic, Austria. 9–13, Long-looped terebratulides. 9, Omithella moeschi, Kimmeridgian, Upper Jurassic, Switzerland. A typical zelleriid terebratulide with sharp beak ridges, a median septum showing, and an indented anterior margin. 10, Aulacothyris alveata, Bathonian, Middle Jurassic, Switzerland. A sulcate zelleriid terebratulide, a fairly common shell form. 11, Helvetella arziersiens, Valanginian, Lower Cretaceous, Switzerland. A costate terebratellide, atypical but not a rare condition. 12, Cheirothyris fleuriausa, Kimmeridgian, Upper Jurassic, Germany. A carinate brachiopod, homeomorphic with 15. Carinates may represent an adaptation to high-energy environments. 13, Trigonellina subtrigonella, Oxfordian, Upper Jurassic, Switzerland. 14–15, Spiriferides. 14, Spiriferina volcotti, Sinemurian, Lower Jurassic, Switzerland. A typical spiriferide with costation and a fold of the commissure. 15, Liospiriferina alpina, Lower Lias, Lower Jurassic, Italy. An atypical spiriferide in its lack of costate ornament. 16, Athyriddae. 16, Tetractinella trigonella, Anisian, Middle Triassic, Switzerland. An atypical athyriddide. Athyriddides typically have a smooth shell and folded commissure. 17, Thecideide. 17, Thecida antiqua, ventral valve, dorsal valve interior. Kimmeridgian, Upper Jurassic, Germany. 18, Cadomella quenstedti, Pliensbachian, Lower Jurassic, Germany. This rare form has been considered a holdover from the Paleozoic strophomenides; however, Brunton and MacKinnon (1972) suggested it was a spiriferide. 19–20, Inarticulated brachiopods. 19, Disciniscus papyracea, dorsal valve, Posidonienschiefer, Lower Jurassic, Switzerland. A typical disciniscid. 20, Lingula tenuissima, ventral valve, Ladinian, Middle Triassic, Switzerland. A typical lingulide. All figures and identifications from Sulzer, 1999.
FIGURE 4—Morphology of some eye-catching Mesozoic brachiopods. 1, The rhynchonellid Peregrinella from the Lower Cretaceous, Switzerland; dorsal, lateral, and anterior views. 2–5, Pygopid brachiopods. 2, Pygope janitor, Tithonian, Upper Jurassic, France; dorsal view. 3, Pygites diphyoides, Valanginian, Lower Cretaceous, Switzerland; dorsal, lateral, ventral, and anterior views. 4, Pygope catulloi, Tithonian, Upper Jurassic, France; dorsal view. 5, Pygope diphyo, Tithonian, Upper Jurassic; dorsal view. All figures and identifications from Sulser, 1999. Magnification x1.
described in Sandy, 1989). The valves of Mesozoic creatures are usually conjoined and serial sectioning is often used; it is more common for Cenozoic brachiopod investigations to involve the removal of matrix infilling the valves because unconsolidated infilling sediments are more frequently (although not always) found in these younger sediments.

**EVOLUTION**

The end-Paleozoic mass extinction is the major trauma for the articulated brachiopods in the whole of the Phanerozoic (Fig. 1); although this needs some qualification, for it is the orthides, productides, and orthotetides that become extinct very close to the Permno-Triassic boundary (Williams et al., 1996). The dicyonellides were lost at about the middle of the Permian. For the inarticulated brachiopods (Lingulida and Craniida), the end-Permian extinction appears to be a non-event, at least at the family level. Ager et al. (1972) provided an overview of the evolution of the Mesozoic Rhyconellida.

**Triassic.**—During the Mesozoic, brachiopod faunas start to resemble much more closely the present-day extant brachiopod fauna. This started in the Triassic with rhyconellides and terebratulides becoming a significant component of articulated brachiopod faunas. Brachiopods bearing a spiral brachidium were still represented in the Triassic by the spiriferides and the athyridides and were indeed abundant at times; the atypides, the “other” spire-bearers, suffered extinction at the Devonian Frasnian-Famennian boundary.

Information on the nature of Early Triassic brachiopod faunas is sketchy (e.g., Hoover, 1979; Dagys, 1993). What is known is that faunas are typically of low diversity in the post-extinction recovery, including shelf-dwelling lingulides and articulateles. These appear to be examples of disaster forms, recolonizing shelf niches (Rodland and Botter, 2001; cf. Schubert and Botter, 1992, who used this term for Early Triassic stromatolite occurrences). The rhyconellides, spiriferides, terebratulides, and athyridides rebounded to moderate diversity both in terms of numbers of species and morphological variability by the Middle Triassic; this trend continued into the Late Triassic (Dagys, 1974; Sandy, 1998). Although this abundance has been primarily recorded in Europe and Asia (e.g., references in Ager and Sun, 1988; Dagys, 1993), inroads are being made into understanding faunas in North America (e.g., Hoover, 1979, 1991; Lees, 1934; Logan, 1964, 1967; Sandy and Stanley, 1993). The thecideides are first known in the Triassic-Jurassic interval and have been variously considered derived from strophomenides, spire-bearers, and terebratulides (Baker, 1990; Jaceks, 2000). Derivation from the spiriferides appears the most convincing at present; they are considered a separate order in the revised Treatise (Williams et al., 2000).

**Jurassic.**—The end of the Triassic saw the end of the athyridides apart from diminutive aberrant forms, and considerable restriction of the Triassic spiriferide radiation. The spiriferides continued into the Jurassic to become extinct by the end of the Early Jurassic (Fig. 1). It has been suggested elsewhere that spiriferides favored deeper-water shelf environments in the Early Mesozoic (Tehoumatchenco, 1972; Sandy, 1994). Early Jurassic anoxia in shelf seas evidenced by widespread black shale deposition is considered the most likely reason for the expiration of the spiriferides (e.g., Thomas, 1978; Ager, 1986; Vörös, 1993a).

During the Jurassic, terebratulides and rhyconellides diversified in shallow-shelf sea environments. The phylum shows peaks in diversity in the Early and Middle Jurassic (Vörös, 1993a, 1995). At the end of the Jurassic, terebratulides and rhyconellides are associated with Tithonian reefal environments of southern Europe, as they had been towards the end of the Triassic. Now the specialized spire-bearers with conical pedicle valves (e.g., Zugmayerella) are absent and large terebratulide forms with elongated pedicle umbos (Weberithyris) may have occupied niches that the spire-bearers had inhabited during Late Triassic reef development. This is based on a comparison of brachiopod taxa associated with Late Triassic and Late Jurassic environments in southern Europe (e.g., Golebiowski, 1991; Sandy, 1988). These reef-associated forms do not appear to fare well at the end of the Tithonian, probably as a consequence of end-Jurassic marine regression (Sandy, 1988).
Cretaceous.—The Cretaceous and succeeding Cenozoic are times of moderately diverse terebratulide and rhyynchonellide faunas. In the middle Cretaceous, Middlemiss (1984) identified an "evolutionary burst" in northwest Europe among the terebratulides—an increase in species diversity. Shallow shelf seas and sandy substrates abounded. Owen (in Macleod et al., 1997) has pointed out that the brachiopod extinction reported from Denmark at the end of the Cretaceous is not significant when brachiopods are considered in a broader geographic and ecological framework. Anything resembling a significant extinction event among brachiopods at the Cretaceous-Tertiary boundary therefore appears to be apparent rather than real (in reality there is scant detailed information available on brachiopods for the K-T extinction event). This is reiterated by the inarticulated forms, based on their Mesozoic and Cenozoic representatives.

Cenozoic.—No major new groups of brachiopods appear during the Cenozoic (Fig. 1). However, it is clear that Cenozoic brachiopods have undergone phases of adaptation and diversification, at least as far as the terebratellides are concerned (Richardson, 1997a). Their biogeography is a reflection of adaptation around a fragmenting Gondwanaland (Richardson, 1997a; Fig. 9—see discussion in paleobiogeography section).

The brachiopods have continued to be a viable but clearly minor component of most marine faunas. However, their abundance at certain locales particularly in the southern oceans today indicates a degree of continued success in exploiting marine environments. The cryptic, cemented habitat of the thecideides and other attached forms also indicates adaptation to environments in which brachiopods can successfully make a living, and have been doing so for much of the Phanerozoic. Cementing to a substrate was common among articulated brachiopods in the Late Paleozoic but is now confined to the cranides and thecideides (Rowell and Grant, 1987). The survival of the Brachiopoda throughout the Phanerozoic would appear to be aided by their "minimalist" lifestyle in terms of their nutrient requirements (e.g., discussion in Peck, 2001a [this volume, Physiology chapter]).

PALEOBIOGEOGRAPHY

Paleobiogeography has been a direct consequence of paleontology since paleontologists first started describing and recognizing fossils from more than one locality. Derek Ager made a number of advances by studying the distributions of Jurassic brachiopods, and specific brachiopod morphologies (e.g., 1965, 1967). Owen (1973), Middlemiss (1973), Michalik (1992), Smirnova (1997), Sandy (1997), and Gaspard (1999) have provided summaries of distributions for Cretaceous representatives. Dagys (1974) provided an overview of Triassic brachiopod distributions, and subsequently published a paper on their Triassic paleobiogeography (Dagys, 1993). These papers have dealt with the distributions of brachiopods in relation to climatic, bathymetric, and sedimentologic controls and have generally identified Tethyan and Boreal faunal elements.

Ager and Sun (1988) summarized distributions of Mesozoic brachiopods in the Tethyan region but also considered other regions. Theirs represents the most complete effort to summarize aspects of Mesozoic brachiopod biogeography. In more recent years efforts have been made to describe faunas from the suspect terranes of the North American Cordillera (summarized in Sandy, in press). In these North American faunas the identification of forms as Tethyan, Eastern Pacific, or Boreal can help to ascertain the latitudinal origin of crustal slices in much the same way as has been applied to other fossil groups (e.g., ammonites, Taylor et al., 1984; bivalves, Aberhan, 1999). Late Triassic brachiopod faunas from the western Cordillera provide the best evidence for origination and movement of some lithotectonic terranes from lower latitudes, e.g., Chulitna and Alexander terranes (Sandy, in press).

Living articulated brachiopods have been observed to have non-planktotrophic larvae, in contrast to inarticulated brachiopods (Richardson, 1997a; Peck, 2001b [this volume, Ecology chapter]). This has important implications, with the former far more likely to develop endemic elements. Richardson (1997a) considered that extant terebratellides presented the clearest, most overt
SANDY—LIFE BEYOND THE PERMIAN

paleobiogeographic story in the Cenozoic due to their restricted distributions. The more cosmopolitan forms such as the rhynchonellid and terebratulid (and inarticulated forms, Emig, 1997a) are perhaps more difficult to interpret due to their longer history and potential for dispersal. Peck (2001b [this volume, Ecology chapter]) commented on the work of Cohen et al. (1993) that indicated very little genetic divergence between populations of the Recent terebratulid *Terebratulina retusa* from Scotland, Norway, and the Mediterranean, thereby suggesting significant larval dispersal for this articulated brachiopod species.

The Cenozoic dispersal and diversification of the Southern Hemisphere terebratellids has left a strong biogeographic signal related to today’s tectonic map (e.g., Fig. 9); the fact that other more cosmopolitan brachiopod groups have an evolutionary history grounded in the Paleozoic and/or Mesozoic would provide the time necessary for ancient diversification and distributional events to have a bearing on their modern distributions. We are therefore dependent on analyses of older fossil distributions for insights into Paleozoic and Mesozoic paleobiogeographic histories. Richardson (1997a) considered that the non-terebretellide articulate had not undergone significant radiation or dispersal since the Jurassic. However, it is clear that non-terebretellide forms are also of use in paleobiogeographic studies.

There are some articulated brachiopods that appear cosmopolitan or broadly distributed in the Triassic such as *Oxycolpella, Coenothyris* (Fig. 3.8), and *Rhaetina* (e.g., Kristan-Tollmann, 1987; Hagdorn and Sandy, 1998; Sandy and Stanley, 1993). If these distributions are real (often such reported distributions lack modern taxonomic investigations), one is tempted to invoke a generalist lifestyle in the sense of Richardson (i.e., adapted to a wide range of substrate sizes, 1997b), or, more

![Map of brachiopod distribution](image)

**FIGURE 5**—Distribution of selected brachiopod taxa during the Late Triassic. The five brachiopod realms of Dagys (1993) are indicated in capitals; geographic regions and oceans in italics. 1 = Koninckinacea; 2 = Thecospiracea; 3 = Retziacea; 4 = *Spondylospira*; 5 = *Misolia*; 6 = *Canadospira*; 7 = *Viligella*; 8 = *Aulacothyridae*; 9 = *Pseudohalorella*; 10 = *Rastelligera*; 11 = *Clavigera*; 12 = supposed boundary between realms; 13 = supposed directions of brachiopod migration; A = data from suspect terranes. Modified from Dagys, 1993.
speculatively, a planktotrophic larval stage to aid their dispersal (but cf. Cohen et al., 1993). *Coenothyris* and *Rhaetina* are likely to have been generalists, *Oxycolpella* perhaps adapted to a relatively deeper-water environment (cf. Golebiowski, 1991, Fig. 14 herein). Krobicki (1993) considered that the widespread distribution of the “key-hole” terebratulide *Pygope* (Figs. 4.2, 4.4, 4.5) in Jurassic-Cretaceous carbonate facies in southern Poland indicated it was an r-selected, eurybathic organism.

**Triassic.**—In terms of Triassic paleobiogeography it is perhaps the Middle and Late Triassic that allow us to piece together reasonable interpretations of brachiopod biogeography because faunas are common and diverse by this time. Ager and Sun (1988) provide distribution maps for the Triassic, and Dagys (1993; Fig. 5) also undertook an analysis of Triassic brachiopods. There are clearly Tethyan and Boreal components in the Triassic (e.g., Ager and Sun, 1988; Dagys, 1993); by the Ladinian (Middle Triassic) a distinctive fauna in New Zealand is considered part of a Maorian Realm (see Ager and Sun, 1988). The spiriferide *Spondylospira* is typically found distributed in Late Triassic rocks along the margins of the eastern Pacific, indicating an eastern Panthalassic distribution (Fig. 5).

By building up an understanding of distributions and paleoecological associations, brachiopods can be used in paleogeographic reconstruction. Palfy and Torok (1992) considered that two terebratulides previously identified as *Coenothyris vulgaris* (Fig. 3.8) from the Mecsek Mountains (Y of Fig. 6) and the Balaton Highland (X of Fig. 6) of Hungary were in fact two separate forms. One form possessed the internal dental lamellae of the Germanic “true” *vulgaris* (the Mecsek form); the other lacked the dental lamellae and was an Alpine homeomorph (the Balaton Highland form). This observation led Palfy and Torok to suggest that the two regions had been tectonically reversed since Triassic time, the two blocks having changed relative positions from south to north, and vice versa (Fig. 6). Ager (e.g., in Ager and Sun, 1988) has argued that Late Triassic and Early Jurassic brachiopod faunas from Turkey with central European affinities should place Turkey on the northern shores of Tethys in the Mesozoic, as opposed to its southern shore placement in plate tectonic reconstructions.

**Jurassic.**—Ager undertook some of the pioneer studies in Jurassic brachiopod paleobiogeography

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**FIGURE 6**—Brachiopods and tectonic reconstruction, Triassic of Hungary. 1, Representative serial sections of the so-called *Coenothyris*. 2, Outline map of Hungary showing location of the so-called *Coenothyris* from the Balaton Highland = X, and *Coenothyris* from the Mecsek Mountains = Y. 3, Representative serial sections of *Coenothyris*. The so-called *Coenothyris* has Alpine (Tethyan) affinities and therefore indicates that the block from which it is found was tectonically displaced and X and Y have changed relative positions since the Triassic. Bp = Budapest. Adapted from Palfy and Torok, 1992.
SANDY—LIFE BEYOND THE PERMIAN

(e.g., 1967). Since then detailed paleobiogeographic and paleoecologic studies have continued in Europe by, for example, Tchoumatchenko (e.g., 1972) and Vörös (e.g., 1986), among others. These studies are often combined with biostratigraphic studies thereby refining stratigraphic ranges of fossil taxa.

The theme of Boreal and Tethyan associations continues from the Triassic (e.g., Ager and Sun, 1988). Ager (1967) considered sulcate rhynchonellides and sulcate terebratulides to be indicative of poorly-oxygenated, deeper-water environments of the Alpine Jurassic (Tethyan) region. However, Vörös (1986) has shown that such a morphological/ecological association does not exist.

In a study of Late Jurassic terebratulides with perforated shells (the pygopids; Figs. 4.2–4.5) Kázmér (1998) was able to show that the development of the perforation early in ontogeny was an adaptation by forms inhabiting deeper-water environments (Pygope catulloi and Pygope diphya) whereas later development during ontogeny of a larger, more centrally located perforation was characteristic of forms occupying uplifted tectonic blocks (Fig. 7). Previously, the janitor-diphyoides group was considered characteristic of the northern margins of Tethys while the catulloi-diphya group was thought to occupy deeper environments of the Mediterranean microcontinent (Kázmér, 1993). Michalik (1996) disputed that these distributions were mutually exclusive. The more recent study by Kázmér (1998) does lend support to the bathymetric distribution of these associations.

This unusual group of brachiopods spans the Jurassic-Cretaceous boundary and the perforation has been interpreted as a way for the animal to direct exhalent currents away from the sea floor (Vogel, 1966), thus eliminating recycling of nutrient-poor waters.

Vörös (1993b) used the distributions of brachiopods in the Jurassic to reconstruct the

![Diagram]

FIGURE 7—Distribution of Late Jurassic pygopid brachiopods across the Gorba High, Hungary. The *Pygope janitor* (Fig. 4.2)-*Pygites diphyoides* (Fig. 4.3) group occurs on the Gorba High, while the *Pygope catulloi* (Fig. 4.4)-*Pygope diphya* (Fig. 4.5) group is distributed in the surrounding basin. From Kázmér, 1998.
paleogeographic relationships of microplates in the western Tethys.

Manceñido (e.g., 1991) has done much to further understanding of distributions of Jurassic brachiopods in South America by his detailed work on faunas from Argentina that indicate links with European faunas during the opening of the Atlantic Ocean.

Walsh (1996) plotted the distributions of Jurassic rhyonchellide genera with respect to paleolatitude and noted that their mid-latitude, extra-tropical peaks in generic diversity appear to mirror those of Recent articulated brachiopod distributions (Fig. 8).

**Cretaceous.**—The Cretaceous also contains taxa (again based on studies of articulated brachiopods) that have been identified as Tethyan and Boreal. Middlemiss (1973) identified a Jura fauna in the Cretaceous in an intermediate position between the Tethyan and Boreal; it was referred to as a western, northern margin of Tethys fauna in Middlemiss and Smirnova (1988), and as Subtethyan by Michalik (1992) and Gaspard (1999). Masse (1992) considered this Jura fauna to be a facies-controlled fauna in a region of predominantly calcareous shale deposition (marl). In a review of Neocomian (Berriasian-Barremian) brachiopod paleobiogeography, Smirnova (1997) identified the following brachiopod regions for forms from the former Soviet Union: Mediterranean, European, Pacific, and Arctic.

The occurrence of pygopid brachiopods in the Early Cretaceous of Greenland has attracted a lot of attention (e.g., Muir-Wood, 1953; Ager, 1967, 1986;

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**FIGURE 8**—(A) Recent latitudinal distribution of articulated brachiopod genera (data from Rudwick, 1970); (B) Recent latitudinal distribution of articulated genera in the Atlantic and Pacific Oceans, incorporating post-1970 data. From Walsh, 1996.
Owen, 1976; Sandy, 1991a; Masse, 1992). The modus operandi had been that pygopods represent "deep water" forms in the Tethys. It is generally considered that the perforation is an adaption to living in oxygen-poor and nutrient-poor bottom waters having evolved from the sulcate-shelled Nucleata stock in the Jurassic. The Greenlandic pygopods were seen as indicating warm waters drifting up the opening North Atlantic Ocean (Ager, 1967). However, as the pygopods are considered deeper-water in Tethys they would also likely be cool-water forms too (Sandy, 1991a). They are found in a fine-grained limestone with other "Tethyan" elements, Lacunosella and Nucleata? in Greenland (Owen, 1976). Their occurrence in cool, shallower-water environments at higher latitudes would therefore not necessarily be an indication of "warm" Tethyan waters, but of cool waters at lesser depths with increasing latitude (Masse, 1992).

Sandy (1991b) illustrated in a rudimentary statistical way the decrease in similarity at the generic level for articulated brachiopods through the Cretaceous Period as the Atlantic Ocean increased in width.

Cenozoic.—Richardson (1997a) has provided a recent summary of the biogeography of Recent articulated brachiopods, which is a reflection of their ancestry in the Cenozoic.

Richardson (1997a) states that it is currently difficult to assess the role of physical factors in living brachiopod distributions because of the lack of data on water depth, temperature, latitude, or energy of environment (see also Peck, 2001b [this volume, Ecology chapter]). Distribution appears most closely related to morphology in terms of adaptation to a particular type or range of substrates (Richardson, 1997a). Generalists can attach to a variety of substrate sizes that typically characterize shoreline environments, whereas specialists are more restricted to a particular sediment type. The abundance and broad distribution of the ubiquitous Triassic brachiopod Coenothyris in Europe can probably be related to a generalist strategy.

Austral and Boreal families were first identified by Beecher (1892) among extant brachiopods. This type of biogeographic pattern is evident at times in the fossil record, with Tethyan and Boreal components often recognized, with a distinct southern high-latitude fauna at times (Austral). The actual controls on the distributions are debated and the role of physical factors in Recent brachiopod distribution poorly understood.

<table>
<thead>
<tr>
<th>Taxonomic category</th>
<th>Southern area</th>
<th>Northern Pacific</th>
<th>Northern area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhynchonelloidea</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Terebratuloida</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Cancellothyrida</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Thecideoida</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Terebratelloidea</td>
<td>Y</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terebratellidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most members of Laqueidae</td>
<td></td>
<td></td>
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<tr>
<td>Laqueids</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Economiosa gerda (laqueid exception)</td>
<td></td>
<td></td>
<td>Y</td>
</tr>
</tbody>
</table>
FIGURE 9—Distribution of Recent species of the terebratulide subfamily Terebratellinae. Numbers plotted for species distributions have been supplemented with genus/species abbreviations to aid interpretation. Genus/species abbreviations placed close to numeric distributions, but are for representational purposes only. 1, Magellania joubini (Mj); 2, Magellania fragilis (Mf); 3, Fosteria spinosa (Fs); 4, Terebratella dorsata (Td); 5, Magellania venosa (Mv); 6, Aneboconcha obscura (Ao); 7, Calloria inconspicua (Ci); 8, Magasella sanguinea (Ms); 9, Neothyris lenticularis (Nl); 10, Symtomaria curiosa (Sc); 11, Dyscrtosia secreta (Ds); 12, Calloria variegata (Cv); 13, Magasella haurakiensis (Mh); 14, Neothyris compressa (Nc); 15, Neothyris dawsoni (Nd); 16, Gyrothyris mawsoni (Gm); 17, Magellania flavescens (Mf); 18, Jaffaia jaffaensis (Jj); 19, Aerothyris macquariensis (Am); 20, Aerothyris kerguelensis. Modified from Richardson, 1997a (see Richardson, 1997a for this map without the genus/species abbreviations).
(see paragraph above). Living articulated brachiopods show three major distributional patterns (Richardson, 1997a): the southern area, the northern Pacific, and the northern area (Atlantic, Mediterranean, North Sea, and circumpolar northern seas). The faunal associations are shown in Table 1; the Terebratellidae are restricted to the southern area and the Laqueidae are mainly northern Pacific forms. The presence of taxa in polar faunal realms, and lower latitude, temperate, or tropical realms, is a characteristic that can be traced back through the Phanerozoic (e.g.,

FIGURE 10—Geographic distribution of Recent inarticulated brachiopod genera. From Emig, 1997b.
Fig. 5, showing Late Triassic faunal realms based on articulated brachiopod taxa.

The subfamily Terebratellinae of the family Terebratellidae gives the best biogeographic resolution according to Richardson (1997a; Fig. 9). The Terebratellinae includes generalists that can inhabit both hard and soft substrates and are sedentary (attached) or free-living. In Calloria inconspicua attached in rocky intertidal pools and shallow waters the specimens are smaller, less convex, and appear stunted compared with representatives from benthic populations (Richardson, 1997a). The Anakineticinae and Bouchardiinae, the other subfamilies of the southern Terebratellidae, are specific to bryozoan sands and are smooth, free-living brachiopods. During the Cenozoic, generalist forms inhabited shoreline environments from the Eocene in Australia and New Zealand; they do not appear to have suffered from end-Miocene regression. Specialists were less fortunate, particularly in New Zealand (Richardson, 1997a).

Emig (1997b) provided a recent summary of the biogeography of inarticulated brachiopods (Fig. 10). Living inarticulated brachiopod genera are generally cosmopolitan, reflecting their ancestry back to the Paleozoic (Emig, 1997b) and their larval ecology. Today the Lingulidae are most common in tropical and subtropical waters and it is probably reasonable to assume this for the Mesozoic and Cenozoic too. The Discinidae are mainly found in intertropical areas. The Cranidae are more widely distributed and the discinide Pelagodiscus mirrors this distribution also (Emig, 1997b). Of the living representatives whose reproductive strategies are known, the lingulides and the discinides have planktotrophic larvae whilst the cranide Neocrania anomala has lecithotrophic larvae.

The response of terebratulides to paleobiogeographic and environmental change is illustrated by the interesting study of MacKinnon (1987). The development of the circum-Antarctic current in the Late Oligocene led to a decline in seawater temperature and changes in sedimentation, as well as more intense circulation patterns (Fig. 11). Several pioneer terebratulide genera have been identified in the Early Miocene of New Zealand with similar gross morphology suggestive of a free-living lifestyle in mobile substrates. During the Late Miocene-Pliocene there was a reduction in seawater temperature and a change in tectonic regime from transient to convergent along the Alpine Fault in New Zealand. This resulted in habitat reduction by loss of suitable

![Paleogeographic reconstructions of the Australasian region for the Early and Late Oligocene showing the change in bottom-water circulation pattern (arrowed) as a result of the continued northward drift of Australia and the initiation of the circum-Antarctic Current. The broken lines approximate the 3,000 m isobath around the landmasses. After MacKinnon, 1987.](image-url)
shallow marine shelf environments. Consequently, brachiopods are much less common on the New Zealand mainland during this time interval.

Manceñido and Griffin (1988) noted that the distribution of *Bouchardia* (a terebratulide) is offset northward in the southernmost part of the Southern Hemisphere from the Paleogene to Neogene to Recent (Fig. 12). This offset is also interpreted as related to the development of the circum-Antarctic current, driving the brachiopods northward from Antarctica, Tierra del Fuego, and adjacent areas to higher latitudes in Argentina, Brazil, and Uruguay.

**ASPECTS OF PALEOECOLOGY**

Recent reviews on the ecology of extant brachiopods were given by Richardson (1997b; see also Peck, 2001b [this volume], articulated brachiopods) and Emig (1997a, inarticulated brachiopods) in the recent revision of Part H of the *Treatise on Invertebrate Paleontology*. As more is learnt of the ecology of brachiopods we have the potential to learn more about Mesozoic-Cenozoic brachiopods as many of the living forms have ancestry through this time interval.

Derek Ager made significant contributions in the study of the paleoecology of Mesozoic brachiopods; in his paper on the adaptation of Mesozoic brachiopods to environment (1965) he related morphology to environment. The likely association of some brachiopods with chemosynthetic communities is an addition to his analysis (arrows on Fig. 13).

**FIGURE 12**—Distribution of the long-looped terebratulide *Bouchardia* during the Paleogene, Neogene, and Recent. For Paleogene and Neogene maps oceanic circulation patterns compiled and tentative, each black dot represents up to three fossil localities, larger black circle at least 4 localities; for Recent map, most frequently reported localities indicated by denser hatching, dotted line represents the 15°C (winter) isotherm. Adapted from Manceñido and Griffin, 1988.
Some of the above comments in the paleobiogeography section also pertain to paleoecology (e.g., discussion of pygopod brachiopods, larval ecology); I will not repeat them here. I will however comment briefly on some recent work that sheds light on brachiopod paleoecology.

**Brachiopod biofacies and niche replacement.**—
Golebiowski (1991) analysed the distributions of latest Triassic (Rhaetian) brachiopods from the Kossen Beds in Austria in relation to environment/substrate and identified eight brachiopod biofacies (Fig. 14). In the transgressive, shallowest-water environment of the Kossen Basin the terebratulide *Rhaetina* (a generalist) predominated followed by more taxonomically diverse faunas in the succeeding facies. Ultimately, the relatively deeper parts of the Kossen Basin were inhabited by a mixed brachiopod fauna that was dominated by the spire-bearing athyridid *Oxycopella* (Fig. 14). The lack of rhynchonellids and the relative abundance of spiriferids in the Luning Formation (Early Norian) of Nevada led Sandy and Stanley (1993) to suggest that small spiriferids (now referred to *Spiriferina*) may have been occupying the niche typically inhabited by rhynchonellids. Sandy (1994) suggested that athyridids associated with deeper-water environments in the Late Triassic were replaced by spiriferids in the Early Jurassic and, subsequent to the demise of the spiriferids, by long-looped terebratulids. In the Jurassic, rhynchonellids diversified in shallow-water marine environments.

**Color banding.**—Color banding is quite

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**FIGURE 13**—The different habitats of Mesozoic-Cenozoic brachiopods, including cold seep chemosynthetic communities (arrows). Modified from Ager 1965, 1993; Sandy 1997.

**FIGURE 14**—Brachiopod biofacies from the Kossen Formation, Late Triassic (Rhaetian), Austria. The brachiopod biofacies reflect different paleoecology and paleobathymetry. The stratigraphically youngest unit is on the left of the diagram. The pie chart for Starhembergkalk represents a locality in Lower Austria, not part of the succession on which the other six successive plots are based. The six plots are based on sections near Steinplatte, Salzkammergut, Austria. The bold numbers 1–6 represent successive brachiopod biofacies: 1, *Rhaetina*; 2, *Zugmayerella*; 3, *Zugmayerella*; 4, *Fissirhynchia*; 5, *Fissirhynchia*; 6, *Oxycopella*. Brachiopod species 1–8 for the pie charts are: 1, *Rhaetina gregaria*; 2, *Rhaetina pyriformis*; 3, *Zeillenia norica*; 4, *Austriirhynchia comigera*; 5, *Fissirhynchia fissicostata*; 6, *Sinucosta emmmchi*; 7, *Zugmayerella koessenensis* and *Zugmayerella uncinata*; 8, *Oxycopella oxycolpos*. Species 1 and 2 are short-looped terebratulides; species 3 is a long-looped terebratulide; species 4 and 5 are rhynchonellids; species 6–8 are spire-bearers (6 and 7 are spiriferides, 8 is an athyrid). From Golebiowski, 1991.
SANDY—LIFE BEYOND THE PERMIAN

Detritus-Schlammkalk Bereich

Korallenkalk Bereich

Dachsteinkalk Lurnachellen-Bereich

Oxycolpella-Biofazies

Fissirhynchia-Biofazies

Starhembergkalk

Zugmayerella-Biofazies

Rhaetina-Biofazies

Eiberg Member

Hochalm Member
commonly reported from Paleozoic brachiopods but reports tend to deal with only one or a few individual specimens (Blodgett et al., 1988). One aspect of Mesozoic-Cenozoic brachiopods that contrasts with the Paleozoic is the frequency with which color banding may be preserved at certain times. This could be a reflection of the propensity for this phenomenon to be reported from terebratuloides but it is certainly not restricted to these brachiopods in Recent representatives (Daphne Lee, pers. comm., 1995). The Triassic terebratulide genus *Coenothyris* appears to be unique among Mesozoic brachiopods in the frequency with which it is preserved with color banding (Hagdorn and Sandy, 1998; Fig. 15). The brachiopods were commonly attached to other specimens of *Coenothyris* and were low-tiered epibenthic organisms, covering the sea floor in places; the color banding functioned as camouflage in the photic zone.

**Brachiopods and chemosynthetic environments.**—Perhaps the largest of Mesozoic brachiopods is the rhynonellide *Peregrinella* (e.g., Fig. 4.1), which can attain a length and width of 10 cm—a monster for the Mesozoic! Another aspect of this beautiful brachiopod is that it has a very puzzling paleobiogeography that is intimately linked to its paleoecology. There certainly is no doubt that this brachiopod had a Tethyan distribution in the Cretaceous (e.g., Ager, 1967, 1986), the genus being known from southern Europe, California, and Tibet (e.g., Ager and Sun, 1988). However, this distribution is very disjunct and *Peregrinella* is not found in normal platform carbonates with other Tethyan brachiopods. Ager (1965) considered that the brachiopod inhabited rocky shorelines and was washed down-slope, basinward, to be preserved in deeper-water settings. In the Vocontian Trough in southeastern France, the occurrence of a thin limestone containing *Peregrinella* and accompanying bivalves and gastropods (Thieuloy, 1972) within deeper-water interbedded limestone-shales was considered the result of temporary uplifting of the basin floor. These explanations were not entirely satisfactory in that this appeared to be the only brachiopod occurring in such a way in the Mesozoic.

Subsequently Campbell et al. (1993) made the important observation that the long-known records of *Peregrinella* from the Cretaceous of California were associated with serpentinites and that the smooth, sulcate Late Jurassic rhynonellide *Coopererrynchia* (Sandy and Campbell, 1994) occurred in a possible chemosynthetic carbonate lens. Both occurrences are in the Great Valley Group, California. Campbell et al. (1993) considered them associates of chemosynthetic environments. The *Peregrinella*-bearing carbonate from France had earlier been suggested to be of hydrothermal origin (Lemoine et al., 1982).

![Germanic Muschelkalk](image)

**Coenothyris vulgaris** (V. Schlotheim, 1820)

**Color bands**

- **Radial bands**
  - A: many delicate striae or narrow bands
  - B: fewer but wider bands
  - C: short bands along anterior margin

- **Concentric bands**
  - radial + concentric bands
  - concentric bands along anterior margin
  - pigmented blotches + short radial bands

**Irregular pigmentation**

**FIGURE 15**—Examples of different types of color banding in the terebratulide *Coenothyris vulgaris* from the Germanic Muschelkalk (Middle Triassic); radial bands contain 3 subtypes of banding: A, B, and C. From Hagdorn and Sandy, 1998.
SANDY—LIFE BEYOND THE PERMIAN

Sandy and Blodgett (1996) described a species of *Peregrinella* from Alaska that was associated with the Boreal bivalve *Buchia*. This indicates that this species probably lived in cool waters at high paleolatitudes (however, as this material was not collected *in situ* its palaeoecologic relationships are conjectural), and suggests that an exclusively Tethyan distribution for the genus is not in fact the case. The seemingly peculiar palaeoecologic association of *Peregrinella* with chemo-synthetic environments (Campbell and Bottjer, 1995a) appears to be the control on its distribution, not paleolatitudinal constraints. It represents a brachiopod with an alternative lifestyle.

While much remains to be done to substantiate possible occurrences of brachiopods as associates of chemo-synthetic communities, there are a number of potential candidates (e.g., Campbell and Bottjer, 1995b; Sandy, 1995). Currently, the best chance to identify brachiopods associated with possible fossil chemo-synthetic environments seems to be when monospecific brachiopod occurrences are found in isolated limestone lenses or pods in clastic-dominated deep-water successions, in association with other taxa, such as molluscs, that are known to be associates of chemo-synthetic environments. The attraction of brachiopods associated with chemo-synthetic environments as a palaeoecologic model in the fossil record is that it provides a very convincing model to explain the highly disjunct distributions of brachiopods such as *Peregrinella, Carapezzia, Cooperrhynchia*, and *Anarhynchia*.

It appears very likely that organisms associated with deep-water chemo-synthetic environments have the potential to survive the rigors of extinction events (McArthur and Tunncliffe, 1998) that affect photosynthetic-based shallow-water or terrestrial ecosystems, and thereby to record evolution beating to a different drum.

ACKNOWLEDGMENTS

I have been fortunate enough to have been encouraged by many paleontologists of whom Frank Middlemiss, Ellis Owen, Attila Vörös, Robert Blodgett, George Stanley, Norm Silberling, Jim Haggart, and Mike Orchard come immediately to mind. Thank you.

This paper is dedicated to the memory of the many brachiopod workers on whose work we strive to build. In particular I am grateful to the late G. Arthur Cooper for his generosity and encouragement when I had the opportunities to meet him at the Smithsonian; also the late Dick Grant, the late Derek Ager, and the late Algirdas Dagys. Thanks to Sandy Carlson and Howard Feldman for reviewing the manuscript. Thanks to my family, Chuck Ritter and family, and Paul Mormon, University of Dayton, for their support and encouragement.

REFERENCES


SANDY—LIFE BEYOND THE PERMIAN


