ECOLOGY OF ARTICULATED BRACHIOPODS

JOYCE R. RICHARDSON
[Museum of Victoria, Australia]

Living articulated brachiopods are notably uniform in appearance and function. The soft parts are enclosed within two valves, one of which is almost invariably beaked. They are suspension feeders with separate sexes; they produce larvae; and they lead a solitary, nonsocial existence. Substrate relationships are governed by the pedicle system, which, with the beak, is present in all living adults except for the members of one order, the Spiriferida. The presence or absence of the pedicle system is correlated with differences in the morphological diversity of living and fossil faunas. Recent articulated brachiopods have little diversity, while the greater diversity of shape in fossil assemblages is derived from forms in which the pedicle is presumed to have been absent and in which substrate relationships are governed by the shell in place of the pedicle system.

All articulated brachiopods are marine, most occupying the waters of the continental shelves and bathyal slopes. Some extend into or are exclusive to abyssal depths; few species are found intertidally; and none is known to be restricted to this zone.

The geographical distribution of living species is correlated at the family level (see section on the biogeography of articulated brachiopods, p. 464), a difference first noted by BEECHER (1892), who differentiated austral and boreal faunas on the mode of the development of their loops. BEECHER's austral fauna consists of those members of the family Terebratellidae that are found in the higher latitudes of the southern hemisphere. From the Oligocene onward they have formed the greatest proportion of fossil brachiopods found in South America, Antarctica, Australia, and New Zealand. They are no less common in modern seas as has been described for Antarctica and the South Pacific (FOSTER, 1974, 1989), South America (MCCAMMON, 1970, 1973; COOPER, 1973, 1982), the subantarctic waters of the Indian and Atlantic oceans (COOPER, 1981, 1982), New Zealand, and Australia (RICHARDSON, 1981c, 1987). These terebratellids from southern waters are a prime source of most new information on ecology since they are abundant, diverse, and accessible.

SUBSTRATE RELATIONSHIPS

The concept of articulated brachiopods as a sedentary group has undergone a radical change in the past two decades, which is one consequence of the opportunities scuba has given for the direct study of those species that occupy benthic sediments. The common notion of articulated brachiopods as a group with a uniform life-style has been replaced by one of variable substrate relationships that includes both sedentary and active species. Although the pedicle has been generally considered to be an organ for attachment, its function is more closely comparable with an appendage than with a stalk; i.e., it adjusts the position of the organism relative to its external environment. Adjustments in position for life on different types of surfaces require different actions, and the structure of the pedicle is modified for a range of different life-styles. In this respect, it is analogous with the single foot of a mollusc but is morphologically less variable.

All observations of living articulated brachiopods show that movements are directed toward the maintenance of a stable position at the water-substrate interface, an essential requirement for suspension feeders. The pedicle system is adapted in a variety of ways to fulfill this need, and adaptations differ with the energy of the environment, as the pedicles of *Parakinetica stewarti* and *Abyssothyris wyvillei* illustrate. The pedicle of *P. stewarti* is free, and its ratcheting action prevents burial by shifting bryozoan sands in a tidal environment (Fig. 388). The pedicle of *A. wyvillei* tethers the organism to foraminiferal sands, an environment in which

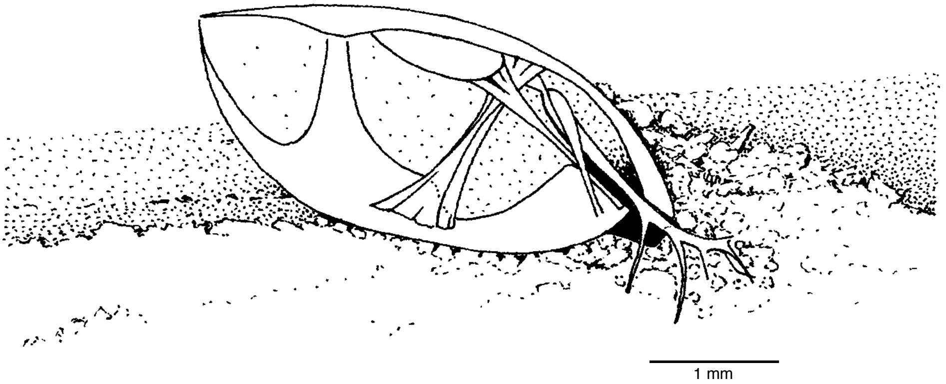

FIG. 388. *Parakinetica stewarti;* western Bass Strait, Australia, fine bryozoan sand, 82 m; the larval substrate is outgrown early in development, and the ratchetlike action of a free pedicle with long, blind processes moves the organism upward and forward to maintain a position at the water-sediment interface. Differential thickening and muscle extent limit the space available within the mantle cavity, which houses an annular loop (new).

movement of the organism may be unnecessary because water and sediment at abyssal depths move very little (Fig. 389). Studies show that the muscles of abyssal species do little more than hold the valves in position, probably constantly open at the sediment-water interface.

The concept of the pedicle as a stalk and anchor developed as a result of the difficulties in observing living articulated brachiopods except for those found on rocks and reefs in shallow water. These are now known to be specialized for that type of habitat. In environments of this type articulated brachiopods follow a sedentary existence, with the pedicle functioning as an organ for attachment to the substrate. As a consequence, the presence of a pedicle was regarded as a sign of attachment, and foramen size was thought to be correlated with strength of attachment. Dredged collections tended to confirm these assumptions because the individuals of some species that were retrieved had pieces of the substrate adhering to the tip of the pedicle.

The principal benefit derived from the study of species from shelf sediments has been to clarify the role that the substrate bonded to the pedicle plays in the life of different brachiopods, that is, the substrate on which the larvae settled. For example, differences in life-style can be observed among individuals of a number of shoreline species that have been defined as generalists. Some are fixed to rock faces; others lie freely on the sea floor with those components characteristic of the sediment cover adhering to the tip of the pedicle. This pattern of distribution shows, in the first place, that larval settlement is random with respect to grain size of the substrate and, second, that substrate is used for anchorage in one environment but not in others.

These differences in the substrate relationships of individuals within a species are a consequence of the relationship between the pedicle system, shell, and bonded substrate. The pedicle muscles lie between the proximal tip of the pedicle and the inner surfaces of the valves. The distal tip of the pedicle is bonded with substrate, and, since that junction is immovable, the two function as one unit. Such stimuli as sediment on the valve surfaces cause contractions of the pedicle muscles. The response differs, however, according to the mass of substrate bonded with the pedicle tip. Contractions of the muscles cause rotation either of the shell in those individuals bonded to large masses or of the pedicle in those bonded to small masses (Fig. 390).

This mechanism of movement means that the behavior of individuals of generalist species is flexible and highly idiosyncratic. Those larvae that settle on a stable rock surface will, as adults, follow a sedentary life-style. Other larvae may settle on substrates made of particles that either have less mass than the adult will have or those that are apt to disintegrate, for example, the empty shell of a brachiopod or mollusc. In such instances, a free life-style will follow a sedentary phase. In other words, the life-style of generalist species is governed by the life history of the substrate.

Given these attributes, it may be seen that, while generalist species (which invariably retain the larvae's substrate) have been described as permanently attached, only those individuals bonded with large masses are also sedentary. Furthermore, the retention of substrates that differ in mass means that for free individuals the bonded and underlying substrates differ, whereas they are the same for sedentary individuals. Sedentary and free individuals also differ in visible movement. Contractions of the dorsal adjustor muscles of sedentary individuals twist the shell; the ventral adjustors pull the shell closer to the substrate. The same contractions by free individuals twist and withdraw the pedicle. These movements of the pedicle cause reactive movements of the shell, and together they maintain the position of a buoyant body at the surface of an inert medium. Although the movements of these individuals may seem undirected, they are effective because they prevent the accumulation of loose sediment on the top and sides of the shell.

Movements of either or both shell and pedicle prevent burial by dislodging sediment from the surfaces of the valve, and, as a result, maintain the position at the water-sediment interface. The movements generated by contractions of the pedicle muscles are, of course, augmented by the adductors and diductors, which open and close the shell; and they not only prevent the build up of sediment but inhibit overgrowth by colonial sponges and ascidians.

The differentiation of species as generalists is based on their ecology, generalists having the capacity to occupy the widest range of substrates on which they may live as sedentary or free forms and at any orientation. Other species are consistent in orientation (with either dorsal or ventral valve uppermost) and in life habit (either sedentary or free) and are morphologically adapted to either hard or soft substrates. As a general rule, species adapted to hard surfaces are sedentary, and those adapted to soft surfaces are free-living forms that may be either active or inactive. The pedicle system of inactive or free-lying forms is reduced or atrophied as in *Neothyris lenticularis* (Fig. 391.2). Active species possess either a free or bonded

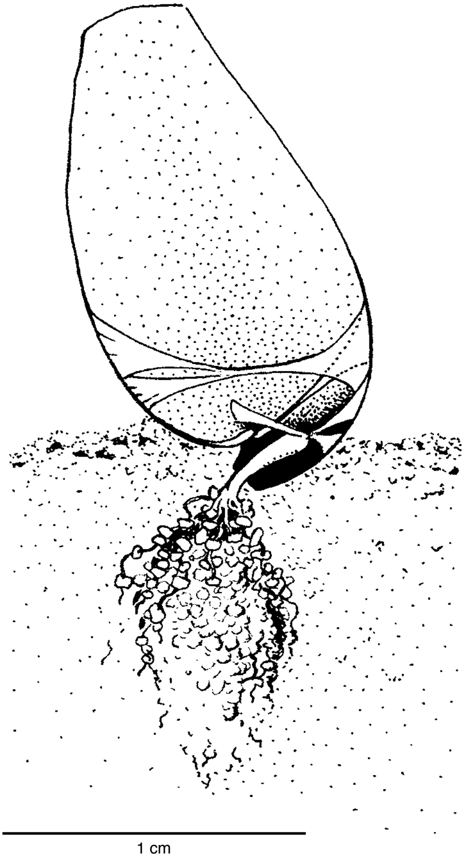

FIG. 389. *Abyssothyris wyvillei;* Tasman Sea, foraminiferal sand, 1,463 m; the pedicle is used for tethering and is variable in length and in the number of distal processes that extend from the shaft. In the individual illustrated, each process is bonded with a foraminiferum (new).

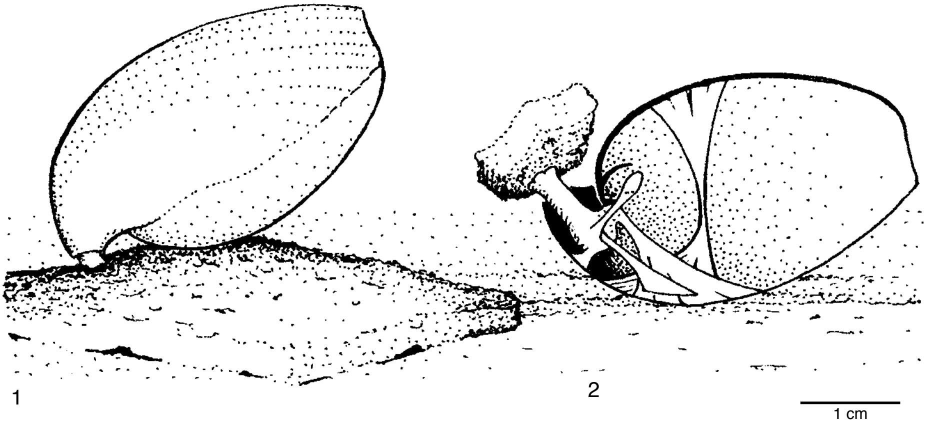

FIG. 390. *Magasella sanguinea;* the larval substrate is retained throughout the life of the individual; contraction of the dorsal adjustor muscles causes rotation of either *1,* the shell or *2,* the pedicle according to the mass of substrate bonded to the pedicle. Free individuals may lie on either the dorsal or ventral valve (new).

pedicle, with ratcheting movements being characteristic of the former (*Anakinetica, Parakinetica, Bouchardia*) and twisting movements of the latter (*Neothyris compressa*).

GENERALIST SPECIES

Generalist species may be found on an apparently unlimited range of substrates and in low- to high-energy regimes (Fig. 392). Highest population densities occur around shorelines where rocky surfaces are adjacent to gravel, sand, or mud. Both sedentary and free populations have been observed for the antipodean members of the Terebratellinae, *Magellania flavescens, Calloria inconspicua,* and *Magasella sanguinea,* and RICHARDSON (1994) inferred that they are also characteristic of *Laqueus californianus,* species of *Terebratalia* from the northwestern and northeastern Pacific, and species of *Magellania* from the Ross Sea shelf of Antarctica.

The pedicle of a terebratelloidean generalist is squat and cylindrical with its distal tip bonded closely with a substrate (Fig. 390). Pedicle muscles are stout and are clearly defined. Free individuals have no preferred orientation and may lie on either the dorsal or ventral valve. All are biconvex without differential thickening and with a short rostrate beak, submesothyrid to mesothyrid foramina, and moderate size ranging approximately from 28 to 40 mm. They vary in shape according to life-style and the energy of the environment occupied (ALDRIDGE, 1981; STEWART, 1981) with the morphological variants of *Terebratalia transversa* differentiated as spirifer, atrypa, and terebratula types (SCHUMANN, 1991). The most extensively documented taxa are the New Zealand terebratellid *Magasella sanguinea* (RICHARDSON & MINEUR, 1981; FOSTER, 1989) and the northwestern American laqueid *Terebratalia transversa* (HERTLEIN & GRANT, 1944; MATTOX, 1955; BERNARD, 1972), which show considerable conformity in distribution with substrate and in morphological character.

While members of superfamilies other than the Terebratelloidea are similar in their adaptations for hard and soft surfaces (see below), generalists of these superfamilies are either less common or are not accessible for study. The only member of the Terebratuloidea described with free and sedentary populations is *Terebratulina septentrionalis* (CURRY, 1981). No recent member of the Rhynchonelloidea is known with generalist characters, but older taxa, for example, the Lower Devonian *Pachyplax gyralea,* resemble modern terebratelloids in those morphological features linked with substrate relationships (ALVAREZ & BRUNTON, 1990).

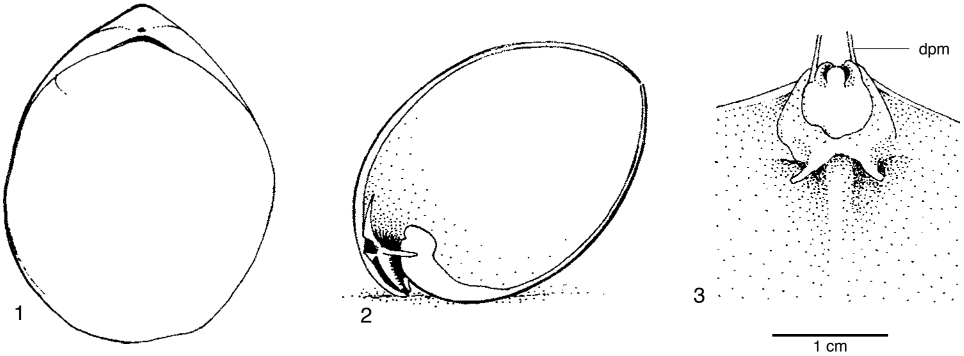

FIG. 391. *1–3, Neothyris lenticularis;* Port Pegasus, Stewart Island, New Zealand, mud, 18 m; a free-lying and immobile species in which the pedicle system is atrophied and any action of the dorsal adjustor muscles is prevented by thickening of the cardinal process; *dpm,* dorsal pedicle muscle (new).

Because the pedicle system and associated characters of generalist species give individuals the physical means of occupying a wide range of substrates, they also have the capacity to live in areas in which substrates are less variable than those around shorelines. For example, the bryozoan sands of the Australian shelf contain populations of anakineticinids, a group highly adapted to this medium. The generalist species *Magellania flavescens* occurs most commonly in the inlets around the Australian coast. Individuals may also be collected from the middle shelf but only as sedentary forms bonded with local reefs and outcrops on the shelf. The absence of any free-lying individuals on the sediments illustrates that in areas of high energy the limited movements possible with the pedicle system make maintenance of a surface position difficult. The sedentary individuals collected are invariably stunted.

ADAPTATIONS FOR SOFT SURFACES

The diversity of life-styles possible with two variables, substrate and the pedicle system, can be illustrated clearly in those species that are specialized to varying degrees for soft surfaces. Species may be tethered or free and, if free, active or inactive. The larvae's substrate is retained in tethered forms and in some free and active species such as *Neothyris compressa* (Fig. 393; RICHARDSON, 1981d). It is outgrown in other free and active forms (*Anakinetica* and *Bouchardia*) and in free but inactive species (*Eohemithiris*). That the larvae's substrate is not lost but actively outgrown can be seen during growth of the pedicle as described for *Anakinetica cumingi* (RICHARDSON, 1987).

Apparently progressive stages in the occupation of soft sediments are evident in terebratelline species. One group (*Magellania venosa, Terebratella dorsata,* and species of *Aerothyris*) dredged from varied shelf sediments is similar to generalists in morphological character and in the retention of substrate. They appear to differ only in the presence of differential thickening in some individuals and populations. Differential thickening is not a variable character in *Gryphus vitreus* (BRUNTON, 1988) or in species of *Neothyris*, *Gyrothyris* (FOSTER, 1974), and *Pictothyris* (ENDO, 1987); and its distribution in these genera gives an orientation with the dorsal valve lying next to the substrate. Species of *Neothyris* are all free, but they differ in extent of activity; and these differences are evident in the outgrowth or retention of the larvae's substrate (Fig. 391–392). In this genus retention indicates some activity, and outgrowth indicates inactivity. *Neothyris lenticularis* is widely distributed geographically; it occupies varied sediments, the pedicle system is reduced in size, and retention of the larvae's substrate is variable. The larvae's

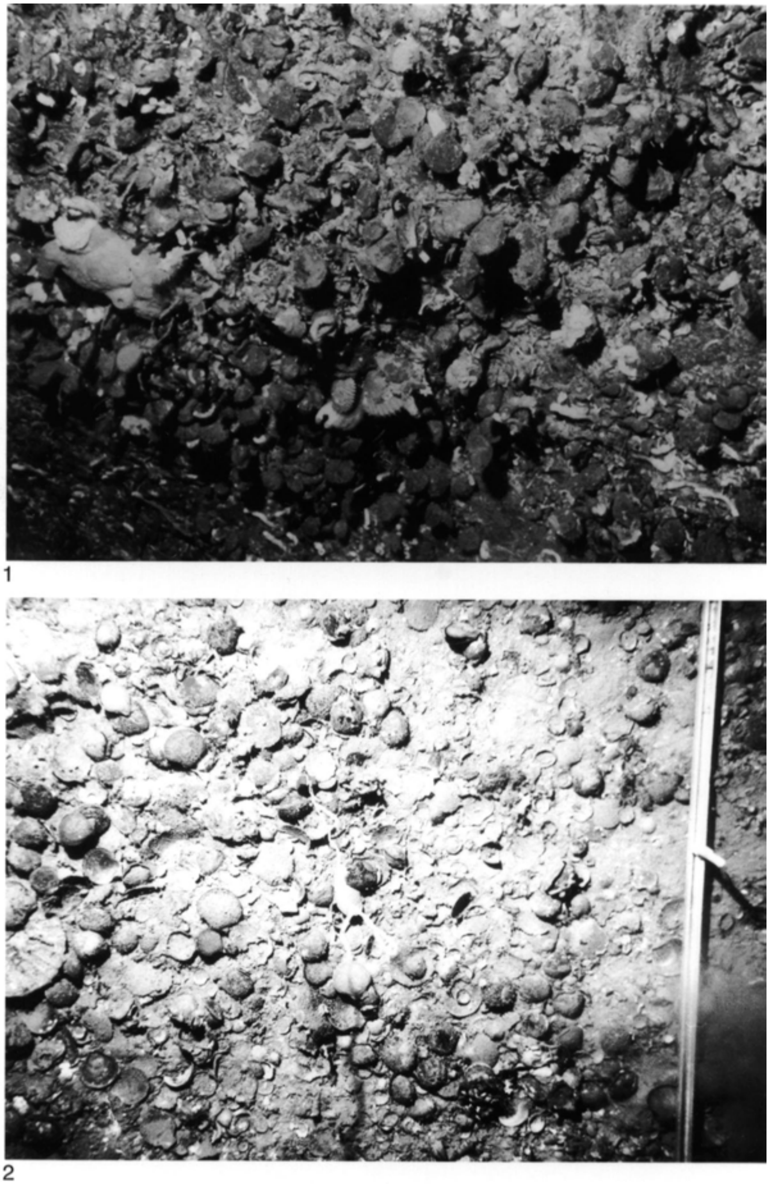

FIG. 392. *Magasella sanguinea;* a species with the physical capacity to live on a wide range of substrates and with no apparent physiological barrier to the occupation of environments ranging from mud to rock walls; *1,* rock face, Cunaris Sound, New Zealand, 25 m; sedentary individuals covered with coralline algae, ×.16; *2,* Paterson Inlet, Stewart Island, New Zealand; free individuals on coarse sand and shell, 38 m, ×.18; *3,* Crail Bay, Marlborough Sounds, New Zealand; sedentary individuals fixed to a horse mussel, free individuals on mud, ×.22; *4, Xenophora neozelanica* as substrate, ×2.78 (new).

substrate is invariably outgrown in populations from muddy inlets, whereas it tends to be retained in those found on shell gravel, although weak activity is indicated by reduction of the areas of attachment (by differential thickening) of the pedicle muscles. *Neothyris compressa* has been collected only from sediments of shell grit and gravel in areas

3

4

FIG. 392 (continued). *For explanation, see facing page.*

with strong tidal currents. The larvae's substrate is invariably retained, and movements of the pedicle stabilize the position of individuals, preventing dispersal and disorientation in strong current regimes. The life-style of *Gryphus vitreus* is similar (EMIG, 1987).

Similarly, a group of anakineticines varies in degree of specificity for occupation of

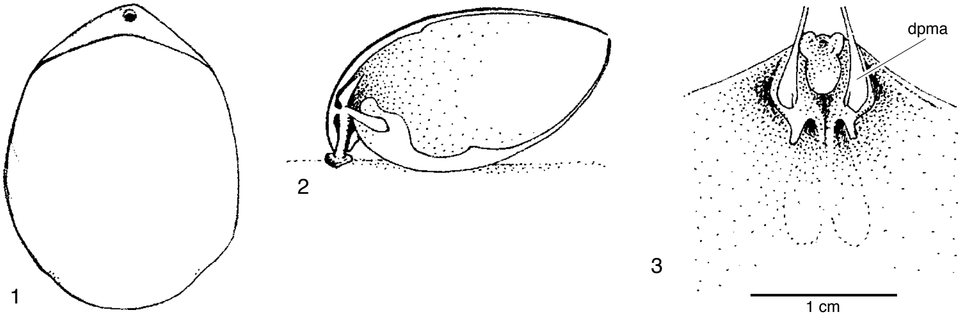

FIG. 393. *1–3, Neothyris compressa;* Stephens Island, New Zealand, shell grit and gravel, 19 m; a free-living, active species that retains the larval substrate and is oriented with the dorsal valve and beak next to the underlying substrate; *dpma,* dorsal pedicle muscle anterior attachments (new).

Australian bryozoan sands (RICHARDSON, 1987). Some, *Magadinella mineuri* for example, retain the substrate, and movements of the pedicle give the capacity to maintain or regain positions at the sediment-water interface. In other anakineticines (*Anakinetica* and *Parakinetica*) the larvae's substrate is outgrown early in ontogeny, and the ratcheting action of a free and active pedicle gives individuals the capacity to surface. The pedicle differs in the length and spacing of its processes for life in coarse (*Anakinetica*) or fine sands (*Parakinetica*). This type of pedicle also occurs in *Bouchardia rosea,* a Brazilian species also from bryozoan sands (TOMMASI, 1970a; MANCENIDO & GRIFFIN, 1988).

Similar adaptations of the pedicle for life in such abyssal sediments as foraminiferal oozes may be seen in genera from all superfamilies: *Cryptopora* (Rhynchonelloidea), *Chlidinophora* (Cancellothyroidea), *Abyssothyris* (Terebratuloidea), and *Phaneropora* (Terebratelloidea). In general, the pedicle is frayed in appearance with rootlets from its end penetrating shells or fragments. Considerable intraspecific variation is evident in pedicle length, however, and also in number of rootlets in these species (Fig. 394). Individuals of *Abyssothyris wyvillei* have been collected with a short pedicle bonded to a manganese nodule, while others are extensively frayed with each rootlet terminating in the shells of foraminifera. Movement of individuals would be unlikely in view of the state and size of muscles, and it appears that in life the pedicle sat vertically in the sediment with the shell lying open at the sediment-water interface.

Gwynia capsula is the only interstitial species known (SWEDMARK, 1971), a permanent member of the fauna of shell and sand debris. The shell is tiny with a diameter of 1 mm, and the pedicle adheres to the sand grains on which the larvae settle.

ADAPTATIONS FOR HARD SUBSTRATES

Notosaria nigricans is adapted for sedentary life. The attachment area of the pedicle is large and irregular (Fig. 395.2), and it may differ in size among individuals. Unlike the pedicles of most other species, it cannot be withdrawn or covered by the shell; and the exposed parts are heavily chitinized. The position of the dorsal pedicle muscles relative to the pedicle shows that tilting but not rotation of the shell is possible (RICHARDSON, 1981b). The beak of *N. nigricans* is apicate and the foramen hypothyrid.

A trend toward the loss of movement is also evident in sedentary and pediculate species from hard surfaces, which are most commonly represented by members of the Platididae, Megathyrididae, and Kraussinidae. In these species the pedicle and pedicle muscles are not clearly differentiated, and together they function as one contractile unit. Therefore movements generated by the pedicle system are restricted to raising and lowering the shell, and the capacity to twist the shell

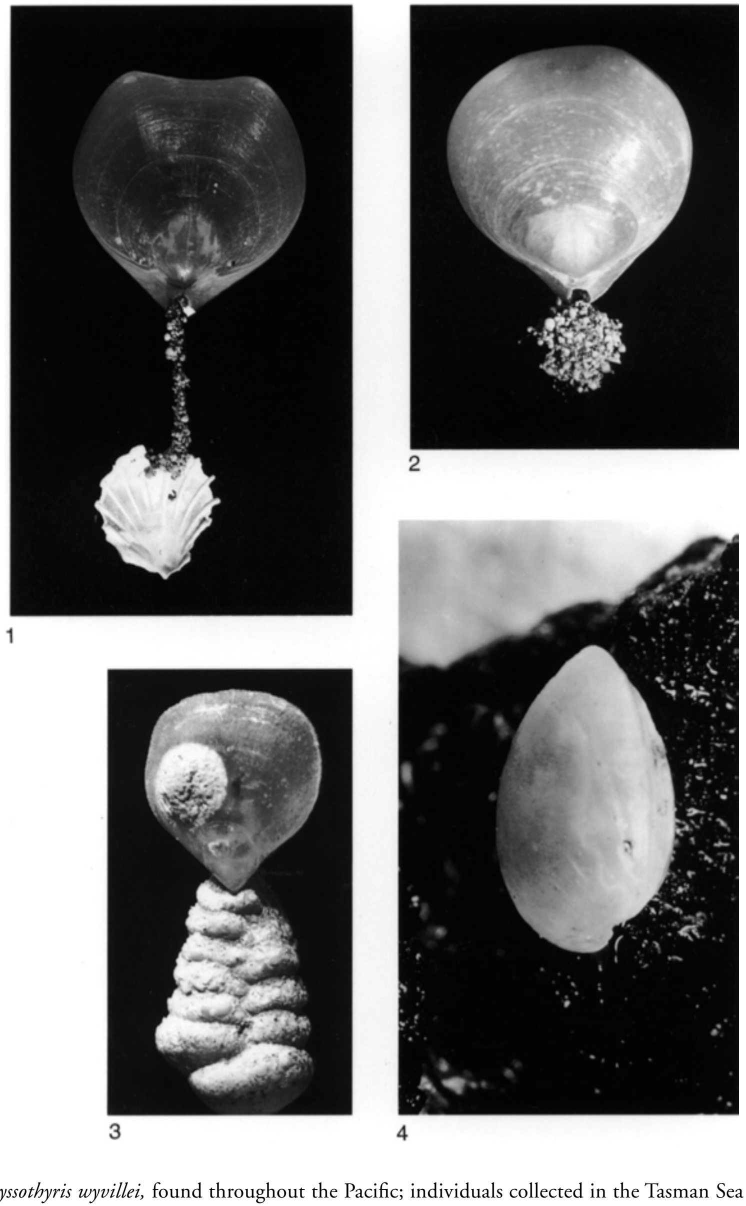

FIG. 394. *Abyssothyris wyvillei,* found throughout the Pacific; individuals collected in the Tasman Sea and bonded with *1–3,* shell fragments and foraminifera at 1,463 m, ×4.42; *4,* a manganese nodule from 4,548 to 4,714 m, ×4.42 (new).

has been lost. A nonrostrate beak and amphithyrid foramen are associated with pedicle systems of this type.

Thecideidines are the only living articulated brachiopods known in which the pedicle is lost following larval settlement and in which the shell of the adult is fixed directly to the substrate. As a consequence, shell movements other than opening and closing are not possible (Fig. 395.4).

ORIENTATION

The positions of individuals relative to the substrate differ with morphological character. The substrate relationships of generalists are variable; that is, they have the capacity to

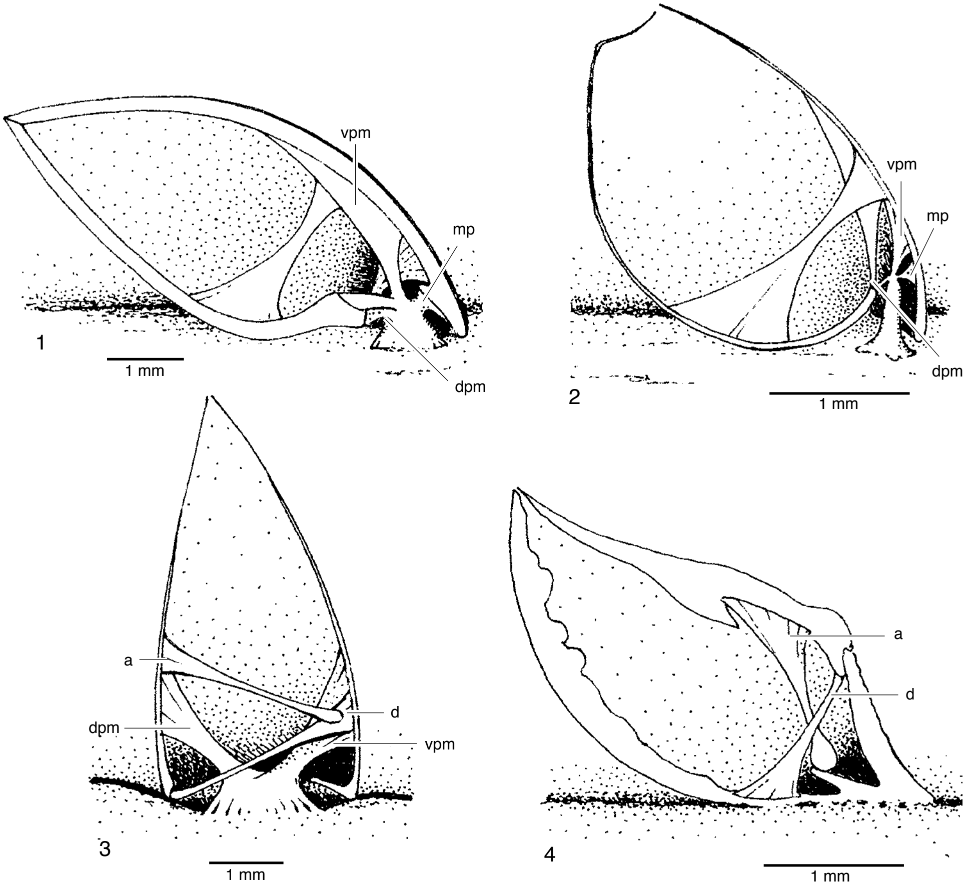

FIG. 395. Species adapted for a sedentary life on hard substrates. The pedicle system is absent in the adult of *Thecidellina maxilla,* and the ventral valve is cemented to the substrate. The other three species possess a nonrostrate beak and vary in the degree of differentiation of the pedicle and its muscles. The absence of a sharp distinction between muscles and pedicle is associated with movement restricted to tilting and raising the shell and the absence of twisting movements of the shell; *1, Megerlina lamarckiana;* intertidal, Port Jackson, Australia; *2, Notosaria nigricans;* Paterson Inlet, Stewart Island, New Zealand, 10 m; *3, Argyrotheca johnsoni;* Discovery Bay, Jamaica, 29 m; *4, Thecidellina maxilla;* off Murray Island, Torres Strait, Australia, 15 m; *a,* adductor muscle; *d,* diductor muscle; *dpm,* dorsal pedicle muscle; *mp,* median pedicle muscle; *vpm,* ventral pedicle muscle (new).

live fixed to a rock face or to lie freely on the sea floor, resting on either valve (Fig. 390, 393). It is a characteristic of nongeneralist species that substrate relationships are constant; and, with the exception of some species of *Argyrotheca,* the dorsal valve lies next to the substrate whether species are sedentary or free and whether individuals hang grapelike (Fig. 396–397) from the substrate (*Liothyrella neozelanica*) or hug the substrate (*Magasella sanguinea*). Although *L. neozelanica* and *M. sanguinea* are respectively uniplicate and sulcate, this difference in orientation means that the curvature of the anterior commissure appears to be the same in a frontal, *in situ* view of individuals of each species. Some species of *Argyrotheca* (Fig. 395.3) are fixed with the anterior-posterior axis at right angles to the substrate (COOPER, 1977; ASGAARD & STENTOFT, 1984).

The orientation of free-lying and free-living species is effected by thickening, which is distributed so that the individual lies in a stable position with the ventral valve uppermost, with the beak lying next to the substrate, and with the anterior end elevated above the surface.

Laboratory studies by LaBarbera (1977) suggested that some orientations of the shell assist pumping by the lophophore. Eshleman and Wilkens (1979b) also noted that among *in situ* sedentary populations of *Terebratalia transversa,* 70 percent of individuals were consistently oriented relative to the current, with the anteroposterior axis of the shell lying nearly at right angles to the ambient current. Other *in situ* studies (Richardson, 1981d; Emig, 1987) have shown that active orientation with the current occurs in exclusively free-lying or free-living species that are, therefore, differentially thickened. In these examples, the anteroposterior axis commonly lays parallel to the current (Fig. 398). Active orientation has not been observed in free populations of generalist species or of exclusively sedentary forms. The orientation of individuals in crowded and clustered populations appears to be quite random, and individuals in the populations observed showed no reorientation in response to currents (Fig. 399). It is possible therefore that stability may be of greater importance in determining orientation than the direction of water flow.

DISTRIBUTION

The role played by abiotic factors in the distribution of articulated brachiopods is difficult to assess given that current strength, salinity, light, and temperature are rarely if ever recorded. Some data of this nature are available for *Terebratulina septentrionalis* and *T. retusa* but from only one part of the range of each species, and both are widely distributed geographically. Therefore information is not available on the range of salinity and temperature that can be tolerated. Experimental laboratory work is of questionable value since articulated brachiopods have the capacity to survive for periods in excess of one year in seawater and in the absence of a food supply. No records exist of breeding in captivity, but artificial insemination has made studies of larval development possible (Long, 1964; Webb, Logan, & Noble, 1976; Stricker & Reed, 1985a). The role of environmental parameters, however, can be assessed from other sources: from the geographic and bathymetric ranges of species, from the occurrence of species in areas in which physical factors differ (tidal and sheltered environments) and in which they may fluctuate (fiords), and from the character of those areas in which densities are greatest.

The extent of the geographic and bathymetric ranges of many species is notable; for example, *Macandrevia americana* occurs in the eastern Pacific between San Diego, California, and the Antarctic at depths of 112 to 4,066 m; *Platidia anomioides* is found in the Mediterranean Sea and the Atlantic, southern Indian, and South Pacific oceans from 18 to 2,190 m (Foster, 1989). Such tolerance of differences in latitude and depth suggests that consequential factors such as temperature and food supply are unlikely to limit distribution. Furthermore, of those species cited as temperature limited, factors other than temperature may account for distribution. For example, collections of *Frenulina sanguinolenta* are only from shallow waters (30 to 92 m) of the Pacific Ocean (35°S to 20°N), and the species is cited as temperature limited. Since the patchy color pattern of the species indicates adaptation for coral-reef environments, however, substrate may be the limiting factor. *F. sanguinolenta* is the only articulated brachiopod collected so far from Australia's Great Barrier Reef.

In general most species show a considerable bathymetric range (Zezina, 1985; Logan, 1993), but inhabitants of the intertidal zone are rare, and the members of those species collected littorally are far more abundant in subtidal waters. In shallow, subtidal waters, articulated brachiopods occur only in such cryptic habitats as under surfaces and in crevices. Individuals have been found on upper surfaces at depths greater than 40 m in the Mediterranean Sea (Logan, 1979), below 25 m in Canada's Bay of Fundy (Noble, Logan, & Webb, 1976), and below 73 m in

FIG. 396. *Liothyrella neozelanica;* Long Sound, Preservation Inlet, New Zealand, 20 m; population on granite wall, ×.2 (new).

the Caribbean Sea (COOPER, 1977). These differing values suggest that light intensity may differ in each of the areas. The intensity of light is low in the saline waters of New Zealand fiords, and articulated brachiopods are found from depths of 6 m, i.e., immediately below the thermocline separating a thin layer of cold, brackish water from warmer, underlying saline water. These records and larval preferences for areas of settlement in poor light all indicate that light intensity plays a role in distribution.

Fiords are areas of particular value in the study of those physical factors that influence distribution because of the environmental restraints in fiords, that is, an association in shallow water of rock substrates and unidirectional currents of low velocity. The subtidal walls below the thermocline provide continuous, vertical change in light intensity on the same kind of granite substrate with little variation in salinity, in the observed strength and direction of water movement, in temperature, or in the amount of suspended material in the water. Articulated brachiopods have been recorded from two fiords in British Columbia (MCDANIEL, 1973; TUNNICLIFFE, 1981), Norway's Trondhjem Fjord (NORMAN, 1893), all of New Zealand's fiords (RICHARDSON, 1981c), and Chilean fiords. The New Zealand fiords contain species of all brachiopod genera described from New Zealand waters, species of *Neocrania, Notosaria, Liothyrella, Terebratulina, Platidia, Pumilus, Amphithyris, Calloria, Magasella,* and *Neothyris;* and most occur in great abundance. With the exception of *Neothyris lenticularis,* all species from the fiords are either generalists or are species adapted to hard substrates. *N. lenticularis,* the only free-living form, is found on a shallow, sandy spit (20 m) in the Long Sound fiord.

Unlike fiords studied in other parts of the world, in New Zealand fiords the halocline was present in all seasons during a five-year-long survey. In those fiords studied in the northern hemisphere (PEDERSEN, 1978), the halocline breaks down during the summer and so facilitates the renewal of saline waters by winds and tides. Periodic breakdown of the halocline means loss of protection from light and water movement for varying periods of two to three months and may be one of the factors responsible for differences evident between fiord-basin faunas of New Zealand and British Columbia. Typical algae-dominated, shallow-water assemblages occur above 30 m in Saanich Inlet, British Columbia; in New Zealand they are found only above the halocline breakdown of 4 to 5 m. In addition, the articulated brachiopod fauna of Saanich Inlet is less varied and abundant than that of New Zealand's fiords, which resulted from the difference in the stocks available in southern and northern waters for recolonization at the end of the last ice age.

The difficulty in defining the impact of different physical factors is well illustrated by the distribution of articulated brachiopods in New Zealand and South Africa. They dominate the rich, rock-wall life of fiords; and their abundance suggests that the degree of shelter found in these enclaves provides optimum conditions. Although all 14 New Zealand fiords appear to provide similar conditions, occurrences of species vary. All species occur within the Long Sound fiord; the others differ such that one species may dominate and others may be rare or absent. Furthermore, some of the rock-wall species occur on the sea floor of Foveaux Strait, an area with strong tidal flow separating the South Island of New Zealand from Stewart Island. The inlets of Stewart Island also contain rich populations of *Calloria, Magasella, Neothyris, Notosaria,* and *Liothyrella* that occur in various current regimes and with free-lying and free-living forms on a variety of sediments.

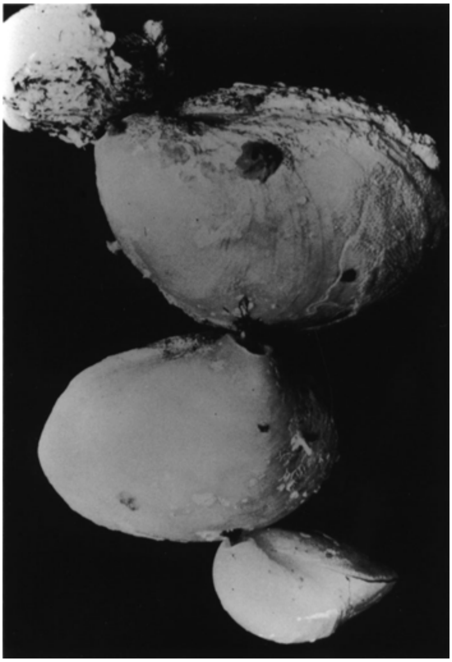

FIG. 397. *Liothyrella neozelanica;* Long Sound, Preservation Inlet, New Zealand, 20 m; three individuals of different age illustrating the orientation characteristic of the species, i.e., suspended from the substrate, ×1.28 (new).

In South Africa distribution appears to be influenced by two major oceanographic systems (ZEZINA, 1987; HILLER, 1991). The warm Mozambique and Agulhas currents flow southwestward along the east coast, and the west coast is washed by the north-flowing waters of the cold Bengula system. Some species occur around the entire coastline; others are restricted to one or another of the coasts. Given the depth ranges of the species, it seems likely that the differences in geographical distribution are not associated with water temperature but with larval dispersal from different areas.

In the Mediterranean Sea, studies using submersibles showed an association between the densities of benthic populations and current velocity (EMIG, 1987, 1989c). Populations of *Gryphus vitreus* were recorded on detritral sand of the bathyal slope at depths of 103 m to 260 m with highest densities (700 to 800 m^2) occurring in an area in which the current velocity was 1.5 to 3

FIG. 398. *Neothyris lenticularis;* Paterson Inlet, Stewart Island, New Zealand, shell gravel, 42 m; free individuals oriented with the anterior-posterior axis parallel to ambient current (4.5 km/hr at time of sampling), ×.26; *arrow* indicates direction of bottom current (new).

km/hr. A similar correlation of population density with current strength has been noted for the free-lying form *Neothyris lenticularis* in an inlet within which both substrate and energy regimes differ (RICHARDSON, 1981d).

Similarities have been noted in faunas from the Caribbean Sea and adjacent waters (COOPER, 1977; ASGAARD & STENTOFT, 1984; LOGAN, 1990), the Mediterranean Sea (LOGAN, 1979; BRUNTON, 1988; ASGAARD & BROMLEY, 1991), mid-Pacific atolls (GRANT, 1987), and the Red Sea (JACKSON, GOREAU, & HARTMAN, 1971). Brachiopods from rocky substrates and coral reefs in these areas are commonly members of the Thecideoidea, Kraussinidae, Platidiidae, and Megathyrididae. These suites of brachiopods appear to be characteristic of shallower waters in low latitude regions. Many of the individual species they contain, however, are not restricted in distribution; for example, *Cryptopora gnomon* occurs from 76°N (Franz Joseph Land) to 51°S (Falkland Islands) at depths ranging from 300 to 4,060 m; *Platidia anomioides* occurs at from 18 to 2,190 m in the Mediterranean Sea, West Indies, Atlantic, southern Indian, and South Pacific oceans. Furthermore, they are all small forms adapted for a sedentary existence, and the presence of reefs in the areas in which they are most commonly found may be a factor in their distribution.

Cold-water coral banks also provide a substrate for brachiopods (TEICHERT, 1958; LOGAN, 1979). The branching calcareous skeletons of species of *Lophelia, Madrepora, Stylaster,* and *Allopora,* together with the smaller scleractinians with which they are associated, provide a rigid, sediment-bonding framework that furnishes an environment for an abundant benthic fauna. The minimum depth of these banks has been recorded as 56 m, but they are more common at 182 to 274 m, and living *Lophelia* have been recorded from 914 m. Coral banks have been described from Norwegian and western European waters and from the Mediterranean Sea, and coral-brachiopod associations

FIG. 399. Varied orientation of sedentary individuals in *1,* populations of *Calloria inconspicua* and *Notosaria nigricans,* Port Pegasus, Stewart Island, New Zealand, 15 m, ×1.2; *2,* cluster of living individuals from the floor of Paterson Inlet, Stewart Island, New Zealand at 27 m; cluster made up of one individual of *Neothyris lenticularis,* six of *Terebratella sanguinea,* and three of *Calloria inconspicua,* ×.66 (new).

are known from deep water south of both New Zealand and Australia.

The substrate occupied may provide one of the best guides from which to evaluate factors that govern distribution. For example, the Australian species *Aulites brazieri* occupies a wide range in latitude (23° to 39°S), longitude (113° to 154°E), and depth (40 to 250 m) but is found only in bryozoan sands and fixed to the undersides of the free-living bryozoan species *Selenaria maculata* and *Lunulites capulus* (RICHARDSON, 1987). In contrast, such generalist species as *Magasella sanguinea* and *Terebratalia transversa* may be bonded to substrates of any size and composition, and the free-living populations of these species can live on sediments of any type and therefore in a wide range of energy regimes. *Magasella sanguinea* is the dominant brachiopod on the walls of the New Zealand fiord, George Sound, and on the muddy sediments of Paterson Inlet. These distributions together with the comparative anatomy of the pedicle system (Richardson, 1981b) indicate, first, that no apparent physiological barrier exists to the occupation of a wide range of regimes (Richardson, 1981a) and, second, that the range of habitats occupied is correlated with pedicle type and associated characters (Richardson & Mineur, 1981). Some types of pedicle systems give species the capacity to colonize and survive as adults in or on a wide range of substrates, while others restrict them to specific types or ranges of substrate.

Substrate is also considered to be a factor in the predominance of small taxa in abyssal environments (Foster, 1989). A survey of South Pacific localities showed that populations collected from areas with numerous, hard surfaces contained large individuals, whereas populations in areas with few, hard objects contained individuals of small size. This conclusion was drawn from work on living populations and accords with that drawn from studies of Cretaceous brachiopods from the Danish chalk (Surlyk, 1972), in which the lack of surface area of hard substrates limited populations. Variations in substrate type appear to determine the assemblages found in different zones of the Mediterranean Sea (Logan, 1979) and the Caribbean Sea (Asgaard & Stentoft, 1984). The presence of suitable substrate is considered to be the most important factor controlling the distribution of *Terebratulina septentrionalis* (Noble, Logan, & Webb, 1976) and, along with pedicle type, the distribution of *Terebratulina retusa* (Curry, 1982) since the pedicle of the latter species is considered to give the capacity to colonize a wide range of substrates.

Known factors that limit the distribution of articulated brachiopods are therefore the capacity to disperse and the nature of the pedicle system, i.e., whether it is adapted to substrates of a particular type. The patterns of settlement and survival in New Zealand's Paterson Inlet illustrate the latter point. Paterson Inlet contains four species, all of which settle at random on surfaces of any size and composition (Richardson, 1981d). Only the generalists *Magasella sanguinea* and *Calloria inconspicua* survive as adults on the larvae's substrates of any grain size. One species (*Notosaria nigricans*) is restricted to coarse-grained or stable substrates; the other (*Neothyris lenticularis*) is confined to fine-grained substrates. This pattern also suggests that any preferences for substrate that have been recorded for species are unlikely to be larval preferences but reflect the requirements of the morphology that is expressed as development proceeds. Within the range of substrates for which species are adapted, greatest densities occur in areas in which light intensity is low.

Such other physical factors as depth, temperature, and energy of the water have not yet been shown to limit distribution, as is evident from what is known of the distributions of some species. For example, *Liothyrella neozelanica* has been collected from rock surfaces in New Zealand in two of ten fiords, in one of the two straits that separate the three islands, in one of the three inlets studied around Stewart Island, and from the Chatham Rise. If it were possible to establish why the species is not present in Paterson Inlet, which is dominated by articulated brachiopods, or in Foveaux Strait, then it might be possible to gain further insight into the role of physical factors in distribution.

In contrast with the predominately shallow-water studies outlined above, examination of brachiopod distribution in deeper waters (Zezina, 1985) has led to the conclusion that the diversity of articulated brachiopods is higher in the bathyal than in sublittoral and abyssal zones and that this can be attributed to a guaranteed food supply and biotopic variability in this region.

DEMOGRAPHY

Articulated brachiopods are seasonal breeders with determinate growth and variable recruitment. They produce lecithotropic eggs and brood larvae through all developmental stages prior to settlement. The strong correlation between densities of recruits and residents in populations (Doherty, 1979; Noble & Logan, 1981) is an indication of the limited capacity for dispersal of articulated brachiopod larvae.

Some insight into the physical and biological factors that control population structure has been derived from size-frequency distributions when these distributions have been related to recruitment, longevity, and mortality. Most population studies recorded before 1979 were those of species from the littoral zone (Percival, 1944; Rudwick, 1962b; Paine, 1969; Rickwood, 1977; Thayer, 1977; Lee, 1978), a zone rarely colonized by living species or represented in fossil collections. Size-frequency distributions constructed from dredged collections of four species from the San Juan Islands, Washington (Thayer, 1975), indicated episodic recruitment at irregular intervals.

Studies of subtidal populations in different geographic areas of both Canada and New Zealand are of particular interest. All areas studied had optimal conditions for brachiopods as was shown by high population densities. All were studied by scuba, and samples were taken from more than one locality in each area. Populations of *Terebratulina septentrionalis* had high juvenile peaks in populations from both the Bay of Fundy (Fig. 400; Noble & Logan, 1981) and the Gulf of Maine (Fig. 401; Witman & Cooper, 1983). The Gulf of Maine populations were collected from the same depth (33 m) and from adjacent but different habitats: upper rock surfaces and rock wall. Although both populations were dominated by juveniles, adult modes occurred at different shell lengths in each—at 14 to 15 mm in the population from rock surfaces and at 19 to 20 mm in that from the rock wall. It was presumed (Witman & Cooper, 1983) that the shorter life span of rock-surface brachiopods could be attributed to predation by cod, which ingested the substrates to which the brachiopods were attached, especially tubicolous polychaetes and red algae that are absent from the rock-wall habitat.

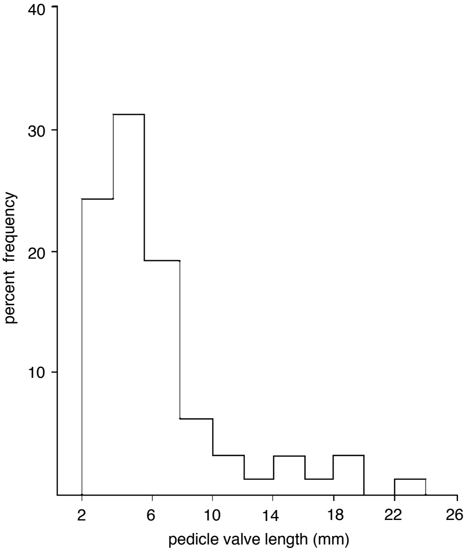

Fig. 400. Size-frequency histogram of living population of *Terebratulina septentrionalis* from the cave at Simpson's Island; $n = 103$ (Noble & Logan, 1981).

The subtidal populations of *Calloria inconspicua* studied in northern New Zealand at monthly intervals for one year (Fig. 402; Doherty, 1979) were either bimodal or left-skewed (dominated by adults), a pattern attributed to the high rate of attrition of postlarval stages and to seasonal recruitment. The structure of hard-bottom, subtidal populations of *C. inconspicua* was recorded from southern New Zealand in one summer and compared with intertidal and soft-bottom, benthic populations in the same area (Fig. 403; Stewart, 1981). Size-frequency histograms were distinctive for the three habitats. Intertidal populations were

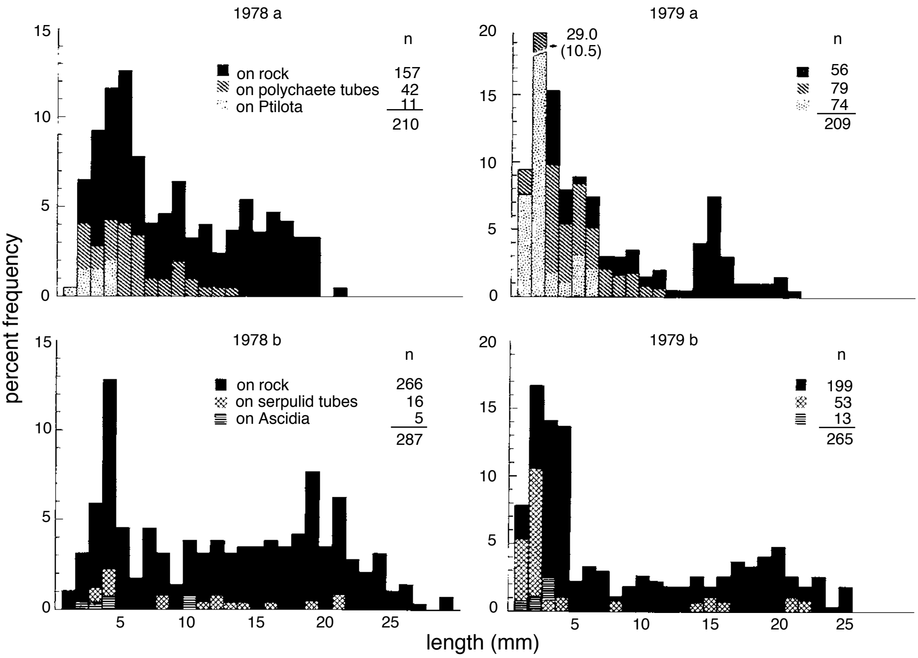

FIG. 401. Substratum specific size-frequency distributions of *Terebratulina septentrionalis* collected by airlift sampling in *1,* upper rock surface and *2,* rock wall habitats during 1978 and 1979: in upper surface habitats, diagonally hatched bars represent brachiopods attached to sandy polychaete tubes; *dotted bars* refer to individuals attached to *Ptilota serrata;* in rock wall habitats brachiopods attached to calcareous serpulid tubes (*crosshatched bars*) and to *Ascidia callosa* (*horizontally hatched bars*); *black bars* represent brachiopods attached directly to rock; note the restricted size range (1 to 13 mm) of brachiopods on polychaete tubes and *Ptilota* in upper rock surface habitats (Witman & Cooper, 1983).

right-skewed; subtidal ones were also right-skewed but with an adult mode varying in prominence with depth. Benthic populations were bimodal, and the same pattern was evident in benthic populations of *Magasella sanguinea* and *Neothyris lenticularis* from the same area (Paterson Inlet). *N. lenticularis* is an exclusively free-living and benthic form; *M. sanguinea* and *C. inconspicua* are opportunistic species with the capacity to settle and survive on substrates of any size. While the larvae of *N. lenticularis* also settle on any available substrate, adults can function only if bonded to small fragments that they frequently outgrow. Shell shape, thickening, and pedicle-system structure of this species preclude a mechanically stable position on coarse substrates.

CURRY (1982; Fig. 404; Table 34) examined the structure of populations of *Terebratulina retusa* from a depth of 200 m from Scotland's Firth of Lorne, but he did not state whether mature individuals were fixed and sedentary or were free (with only a small mass of substrate bonded to the pedicle). He attributed the bimodality shown in histograms to biannual spawning periods assumed to be late spring and autumn. A subsequent study of *Terebratulina retusa* (COLLINS, 1991) from the same area included brephic specimens that permitted an extension of the growth-rate curve from a logarithmic to a sigmoidal shape and implied that conditions for rapid, early growth may be more favorable in shallow than in deep water. The New Zealand species *Notosaria nigricans* and *Calloria inconspicua,* however, had slower rates of growth in intertidal than in subtidal habitats; and the subtidal and benthic species *Magasella sanguinea* and *Neo-*

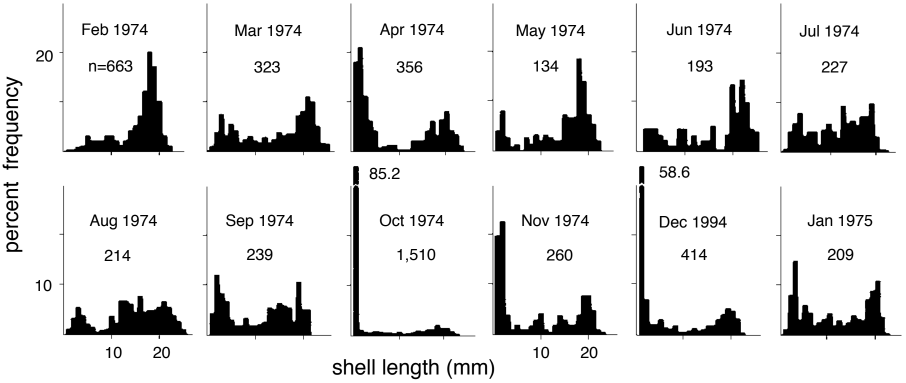

FIG. 402. *Calloria inconspicua;* size-frequency distributions from monthly sampling of the canyon population; area of samples: February, 0.25 m^2; November, 150 cm^2; all others, 625 cm^2 (Doherty, 1979).

thyris lenticularis grew rapidly initially (STEWART, 1981).

Spawning periods have been determined in most instances from the preponderance of postlarval stages in size-frequency distributions, and observations of the spontaneous release of larvae from the female have been rare. The linkage of spawning time with any physical factor is difficult given the times of the year recorded from different geographical regions and the differences of seasons from the two hemispheres. Spawning of subtidal populations of *Calloria inconspicua* from northern New Zealand was observed in September (DOHERTY, 1979), in May in intertidal populations from the mid-eastern coast (PERCIVAL, 1944), and in July in subtidal populations from the middle to southern west coast. Spawning of *Magasella sanguinea, Neothyris lenticularis, N. compressa,* and *Notosaria nigricans* during mid-July was also observed; but only some stages in the development in the latter have been documented (HOVERD, 1985). In the northern hemisphere, *Terebratulina septentrionalis* is presumed to spawn between May and August (MORSE, 1873; NOBLE, LOGAN, & WEBB, 1976; WEBB, LOGAN, & NOBLE, 1976); and an estimate of dates of settlement of *Terebratulina retusa* indicated spawning periods in spring and autumn (CURRY, 1982; COLLINS, 1991). Mediterranean species of *Argyrotheca* are thought to spawn late in the year with the possibility of a further spawning period in early summer (ASGAARD & BROMLEY, 1991). A further factor to take into account in any attempt to reconcile the differences in spawning periods is that ripe gonads occur in most specimens of *Terebratulina septentrionalis* in every month of the year with larvae present within the females from December to April (WEBB, LOGAN, & NOBLE, 1976). Ripe gonads were also present in February in those New Zealand species that were observed to spawn during July (TORTELL, 1981).

In general, size-frequency distributions show that intertidal populations are not as heavily skewed toward large individuals as are subtidal populations, which may indicate a shorter life expectancy or slower rates of growth. The main cause of death of *Calloria inconspicua* from subtidal populations on rock walls was thought to be old age (DOHERTY, 1979), and survivorship curves of both this species and *Magasella sanguinea* from soft surfaces show relatively constant mortality rates in the adult size ranges.

The high mortality of juveniles shown in size-frequency distributions has been attributed to overcrowding, grazing, and overgrowth. Size-frequency distributions of individuals bonded to rock and associated with conspecifics have shown that the latter group have a shorter life expectancy as adults. The need to be wary in drawing conclusions from

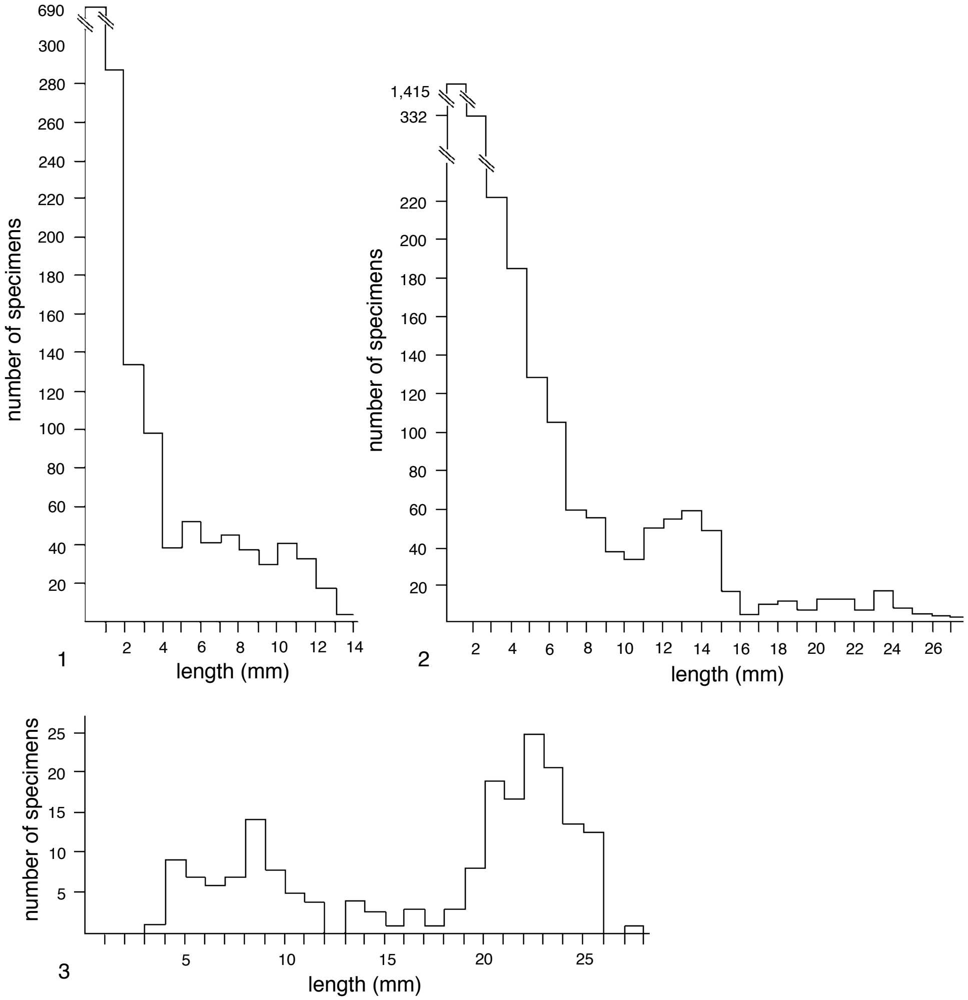

FIG. 403. Length-frequency histograms of populations of *Calloria inconspicua;* all stations in Paterson Inlet, Stewart Island, New Zealand; *1,* live population, station K1019, intertidal, *n* = 1,553; *2,* live population, station K993, rock slope, subtidal at 7 m; *n* = 2,894; *3,* live population, station K989, floor of muddy sand, benthic at 22 m; *n* = 194 (Stewart, 1981).

size-frequency distributions only, however, has been graphically illustrated by the effect on the population structure of two adjoining populations of *Terebratulina septentrionalis* as a result of fish predation of the underlying animal substrate of one of those populations (WITMAN & COOPER, 1983).

PREDATION AND PARASITISM

Significant levels of predation, parasitic infection, or disease have not been reported for articulated brachiopods. Predators are probably limited by the fact that most living articulated brachiopods contain an internal skeleton or spicules, that biomass is slight, and that the shell invariably encloses all soft parts with the occasional exception of the distal portion of the pedicle. This section of the pedicle is covered with a thick coat of chitin in those species in which it is exposed, for example in *Notosaria nigricans,* in living anakineticinids, and in such terebratellids as *Liothyrella notorcadensis* and *Magellania flavescens* in which the pedicle varies in length.

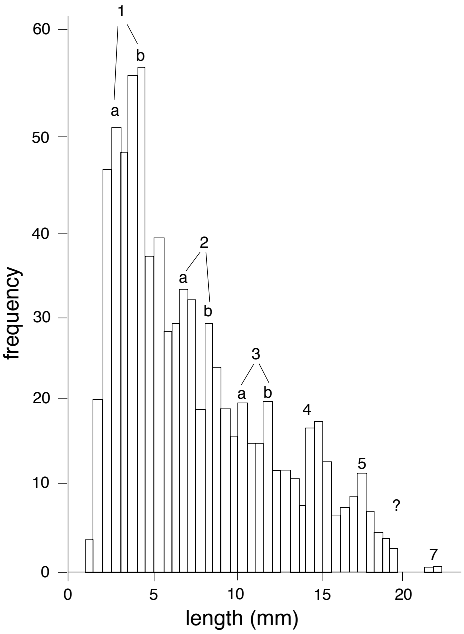

FIG. 404. Length-frequency histogram of *Terebratulina retusa,* from the Firth of Lorne, 22 March 1977 sample (ZB3727–ZB3736; see Table 34 for analysis); *1a,b, 2a,b,* etc., settlement cohorts; *n* = 811 (Curry, 1982).

The principal impact of other organisms appears to be drilling by carnivorous gastropods and grazing pressure on juvenile populations either directly by echinoderms and chitons or indirectly as a consequence of those sites chosen by larva for attachment. In some areas colonized by *Calloria inconspicua,* overgrowth by an encrusting sponge had smothered young but not adult individuals, which were protected by the capacity of sedentary individuals to twist the shell from side to side and moderately high elevation of the feeding aperture above the substrate (DOHERTY, 1979).

Studies of *Terebratulina septentrionalis* from upper rock surfaces and lower rock walls of the Gulf of Maine, Canada, demonstrated that juveniles were taken by cod from only the upper rock surfaces (WITMAN & COOPER, 1983). Selective indices showed that the cod feed preferentially on tube-dwelling polychaetes, which, along with red algae, are the principal substratum of brachiopods on upper rock surfaces and which are absent from the lower rock walls.

TABLE 34. Analysis of the 22 March 1977 length-frequency histogram (see Fig. 404). All measurements are in mm (adapted from Curry, 1982).

Annual increment	Peak	Biannual increment	Date of settlement	Year/ Class
	2.75	1.5	Autumn1976	1a
4	4.25		Spring 1976	1b
4	6.75	1.5	Autumn 1975	2a
3.5	8.25		Spring 1975	2b
3.5	10.25	1.5	Autumn 1974	3a
	11.75		Spring 1974	3b
3	14.75		1973	4
2.5	17.25		1972	5
2.5	19.75		1971	6
1.75	21.50		1970	7

Fishermen from Paterson Inlet, New Zealand, have noted the presence of small terebratellids in the guts of bottom-feeding fish. It is probable, however, that since the species are dominant members of the benthos in this inlet, they would have been engulfed with other material.

Brachiopods in both the Gulf of Maine and Paterson Inlet have been extensively studied using scuba. Occasional instances of asteroids feeding on adult brachiopods have been observed in the Gulf of Maine and once in Paterson Inlet (Fig. 405). Predation by asteroids on subtidal populations of *Terebratalia transversa* in Puget Sound has also been recorded (MAUZEY, BIRKELAND, & DAYTON, 1968).

Drill holes in the shells of terebratuloid species have been recorded from Canadian inlets (NOBLE & LOGAN, 1981; WITMAN & COOPER, 1983), the Caribbean Sea (LOGAN, 1990), the Mediterranean Sea (LABARBERA, 1977), the Sea of Alboran (TADDEI RUGGIERO, 1991), and New Zealand (STEWART, 1981). In most instances drill holes occur in the posterior half of the shell. The size and shape of these holes are like those made by carnivorous gastropods; they are circular and tapered with an outer diameter ranging from 0.45 to 1.05 mm (WITMAN & COOPER, 1983). An example of microborings in the shell of *Magasella sanguinea* is presumed to have been caused by boring fungi and is of interest because the borings do not penetrate

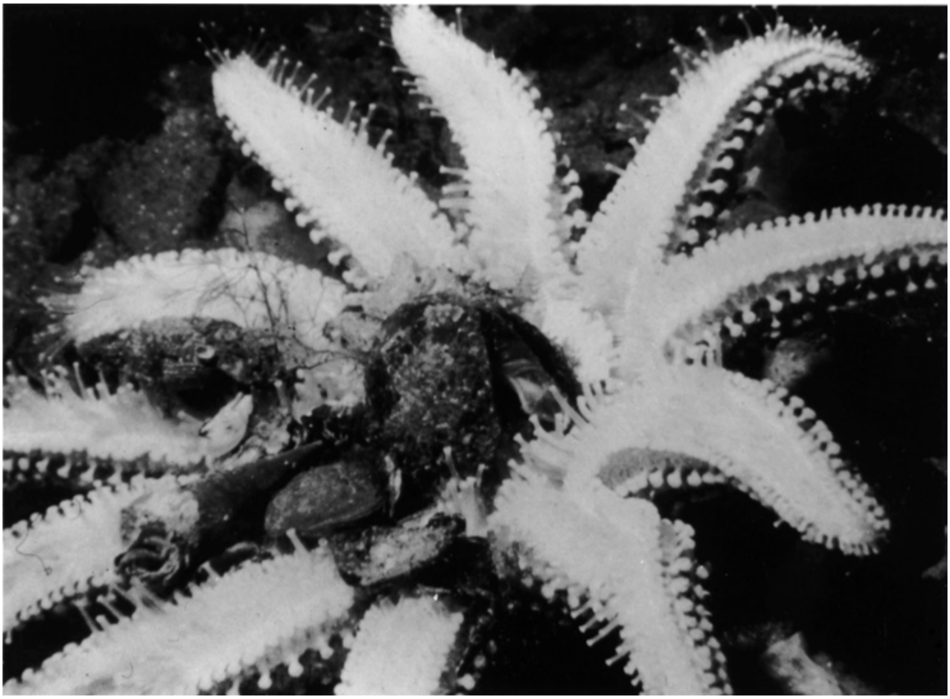

FIG. 405. *Magasella sanguinea* with predator *Coscinasterias calamaria,* ×.63 (new).

areas of the shell that overlie the caecae (CURRY, 1983).

An association of the amphipod *Aristias neglectus* with two brachiopod species, *Macandrevia cranium* and *Terebratulina retusa,* has been recorded from Swedish and Norwegian waters (VADER, 1970). An amphipod was found in the mantle cavity of one individual; other amphipods were obtained from the rinsing of samples, so the nature of the association is unknown. Another amphipod was associated with an unnamed brachiopod species from the Indian Ocean (WALKER, 1909).

BIOGEOGRAPHY OF ARTICULATED BRACHIOPODS

JOYCE R. RICHARDSON
[Museum of Victoria, Australia]

Fundamental differences in larval type indicate that patterns and paths of distribution differ for inarticulated and articulated brachiopods. The planktotrophic larvae of the inarticulated brachiopods are globally distributed and result in the absence of endemic genera. In contrast, the larvae of articulated brachiopods are nonplanktotrophic and short-lived, and faunas of articulated brachiopods have major differences both between widely separated areas (austral and boreal zones) and narrowly separated areas (Japan and China). Some of these differences in geographical distribution can be accounted for with the knowledge of living species, both from their capacity to disperse and colonize and from factors that may limit distribution.

FACTORS GOVERNING DISTRIBUTION

Distribution is concerned with both the means and pathways of distribution and so requires knowledge of the capacity for dispersal of both the larva and the adult and of their capacity for colonization.

Field studies of articulated brachiopod species indicate that the larvae are brooded, either within pouches or in the lophophore. Pouches have been described for *Lacazella mediterranea* (LACAZE-DUTHIERS, 1861), *Gwynia capsula* (SWEDMARK, 1971), and *Argyrotheca cordata* and *A. cuneata* (ATKINS, 1960a). Brooding within the lophophore has been described for *Pumilus antiquatus* (RICKWOOD, 1968), *Hemithiris psittacea* (LONG, 1964), *Notosaria nigricans* (HOVERD, 1985), *Calloria inconspicua* (DOHERTY, 1979), *Terebratulina septentrionalis* (WEBB, LOGAN, & NOBLE, 1976), and *T. unguicula* (LONG, 1964). The free-swimming phase of the larvae is brief, and laboratory studies indicate that settlement occurs between one hour and one to two days. Patterns of settlement are consistent with limited dispersal (NOBLE, LOGAN, & WEBB, 1976; WEBB, LOGAN, & NOBLE, 1976; DOHERTY, 1979; CURRY, 1982), and the density of recruits is positively correlated with the density of residents. The diversity of sites of settlement is shown in the nature of substrates bonded with the pedicle in those individuals that retain the larval substrate in adult life. Strong preferences have been recorded for settlement on conspecifics, however.

The extent of dispersal is also correlated with adult life-style (see section on ecology of articulated brachiopods, p. 441–462). With the exception of exclusively sedentary forms, all other species possess some capacity to move in relation to their external surroundings. Movements appear to be limited to those that maintain an individual's position at the sediment-water interface, i.e., those that shed sediment from the surfaces of the valves and so prevent burial. Therefore the direction of movement in soft sediments tends to be vertical rather than horizontal except for species of *Parakinetica,* which display some capacity for horizontal progression. The influence of currents and the mobility of sediments must also be taken into account for free-lying and free-living species and for interstitial species that would behave as grains of sand and so move with the sediment. Articulated brachiopods have also been found fixed to the valves of vagile sea scallops in Canada (LOGAN, NOBLE, & WEBB, 1975) and New Zealand (ALLAN, 1937). In New Zealand they also commonly occur on such gastropods as *Astraea* and *Xenophora* (Fig. 392.4).

As reviewed in the section on the ecology of articulated brachiopods (p. 441–462), it is difficult to assess the role of physical factors in distribution because of the lack of data. At present there is no direct evidence to show that depth, temperature, latitude, or energy of the water limit distribution. The distribution of living species is most closely related to morphology, that is, whether it is adapted to a specific range or type of substrate. Species differ, therefore, in their capacity to colonize different substrates. Having no specific requirements, generalists can colonize substrates of any size and composition and, consequently, are less affected by those environmental events that result in changes of the substrate. Generalists occur in greatest abundance in shoreline areas where settlement surfaces range in size from rock faces to the components of sea floor sediments. In these areas since life-style is governed by the mass of substrate used for settlement (see section on ecology of articulated brachiopods, p. 441), substrate relationships are varied, i.e., the life-style of an individual may be sedentary or free or a combination of both. The capacity for colonization is related to degree of specialization since specialists can colonize only those substrates for which they are morphologically adapted. For example, *Neothyris lenticularis* has the capacity to live on sediments ranging from muddy sand to gravel, whereas *Parakinetica mineuri* is specific to fine, bryozoan sands. The pedicle systems of such exclusively sedentary forms as *Platidia, Megerlina,* and *Kraussina* can function only if bonded to substrates in which the substrate is of greater mass than the individual. Hence generalist species possess a greater capacity for colonization and can spread around shorelines and onto shelf sediments. They are restricted in their dispersal only by the length of time spent in the larval stage.

DISTRIBUTION OF FAMILIES

Differences in taxonomic philosophies (FOSTER, 1989) and difficulties in sampling present considerable problems in biogeographic analyses. The common range of depth of articulated brachiopods is down to 600 m, and littoral species are rare. Difficulties in tracing relationships are well illustrated by the families of micromorphs: Platidiidae, Kraussinidae, and Megathyrididae. These so-called neotenous forms are grouped together on the basis of size in combination with lack of development of the cardinalia and loop that is characteristic of other members of the Terebratelloidea. Relationships between the genera within each family, however, are unknown. Similarly the neotenous origin and masking effects of convergent evolution combine to obscure lines of descent within the Thecideoidea (BAKER, 1990).

Despite such problems, however, the predominance of families in some areas is quite clear. Austral and boreal families were first differentiated by the mode of development of the loop (BEECHER, 1892). At present, three broad, regional patterns can be recognized.

1. The southern area includes Australia, New Zealand, South America, the southern Indian Ocean, and circumpolar southern seas and is occupied by representatives of all superfamilies and families belonging to the Rhynchonelloidea, Terebratuloidea, Cancellothyroidea, Thecideoidea, and Terebratelloidea.
2. The northern Pacific region has representatives of all families except the Terebratellidae and most members of the Laqueidae.
3. The northern area (Atlantic, Mediterranean Sea, North Sea, and circumpolar northern seas) has representatives of all families except the terebratellids and the laqueids, with the exception of one species in the Gulf of Mexico (*Ecnomiosa gerda*).

Therefore, the family Terebratellidae is exclusive to the southern sector; the Laqueidae is a predominately northern Pacific group, while families of the Rhynchonelloidea, Terebratuloidea, and Cancellothyroidea and the families Macandreviidae, Dallinidae, Kraussinidae, and Platidiidae are worldwide in distribution.

Except for the high latitudes of the southern hemisphere, articulated brachiopods are not a common constituent of grab or dredge hauls, and their abundance in southern waters is due to the presence of members of two terebratellid subfamilies, the Anakineticinae and the Terebratellinae.

Those families that are restricted in distribution with either geography, time, depth, or substrate provide some insight into paths of dispersal. Few data can be obtained from the families that appear to be unlimited in distribution and in which genera contain species from widely separated geographical areas. Accordingly the following account excludes those families contained in the Rhynchonelloidea, Terebratuloidea, and Cancellothyroidea.

TEREBRATELLIDAE

The family Terebratellidae, in particular the subfamily Terebratellinae, gives the best basis for analysis because more information is available about its members than for any other group of living articulated brachiopods. It is also the group in which taxonomy causes few problems, first because the Terebratellinae contains polytypic species accessible to study in one geographical area and second because the variability of populations has been studied in many parts of the range of each species (McCammon & Buchsbaum, 1968; McCammon, 1970; Foster, 1974, 1989; Aldridge, 1981, 1991; Cooper, 1981, 1982; Stewart, 1975, 1981). This means that distribution can be analyzed from populations and species rather than from genera, which in most other articulated families include species from widely separated geographical areas (Fig. 406).

The subfamily Terebratellinae contains 20 genera, five from the Tertiary and recent, seven from the Tertiary alone, and eight restricted to the recent. They are confined to the southern hemisphere between the Antarctic shoreline and a latitude of approximately 35°S and exist in very large numbers in areas shallower than 1,000 m; for example, species of *Magellania* are the most prominent on the entire Antarctic shelf (Foster, 1974), and species of *Neothyris, Magasella,* and *Calloria* are dominant forms in a number of fiords and inlets in southern New Zealand (Richardson, 1981c). Most of the Antarctic species are found at all depths (100 to 1,000 m) of the Ross Sea shelf (Foster, 1974) and of the New Zealand shelves and neighboring rises (Chatham Rise and Campbell Plateau) that rarely exceed depths of 400 m. The South American species *Magellania venosa* is most common at shelf depths of approximately 300 m but has been recorded from 5 to 1,900 m (Foster, 1989) and is the only terebratelline species known from a slope.

All living terebratelline species (19 species belonging to 13 genera) have been collected from a variety of shelf sediments including gravels, coarse and fine sands, and muds. Individuals of the same species may also be found on subtidal rocks, while rare occurrences in the littoral zone are known for only two species, *Magellania flavescens* and *Calloria inconspicua.* Although *Magellania flavescens* is found in shallow water throughout southern Australia, intertidal populations have been found at only one site.

The kind of substrate occupied, morphological character, and life-style of terebratellines are strongly correlated. Species with populations living on both hard and soft surfaces are generalists and follow a sedentary or free existence (see section on the ecology of articulated brachiopods: substrate relationships, p. 441). Species exclusive to unconsolidated sediments are free living or free lying, and no terebratelline species has been described that is exclusively sedentary, i.e., restricted, like micromorphs and the rhynchonellid *Notosaria nigricans,* to coarse-grained or stable substrates. Australian and New Zealand terebratellines can be studied directly, but South American, subantarctic, and Antarctic species are known only from dredged collections. Most of these species appear to be generalists judging from morphology, from the nature and size of material adhering to the pedicle, and from the nature of the sediment. *Terebratella dorsata* and species of *Aerothyris* are generalists with the exception of one feature, differential thickening. Free-living and free-lying taxa are invariably thickened. Species observed to have the capacity to follow both sedentary and free modes of life are invariably not thickened. The variability of this character in *T. dorsata* and in *Aerothyris* indicates a trend, if not already established, toward a free lifestyle. An opposite trend toward a sedentary

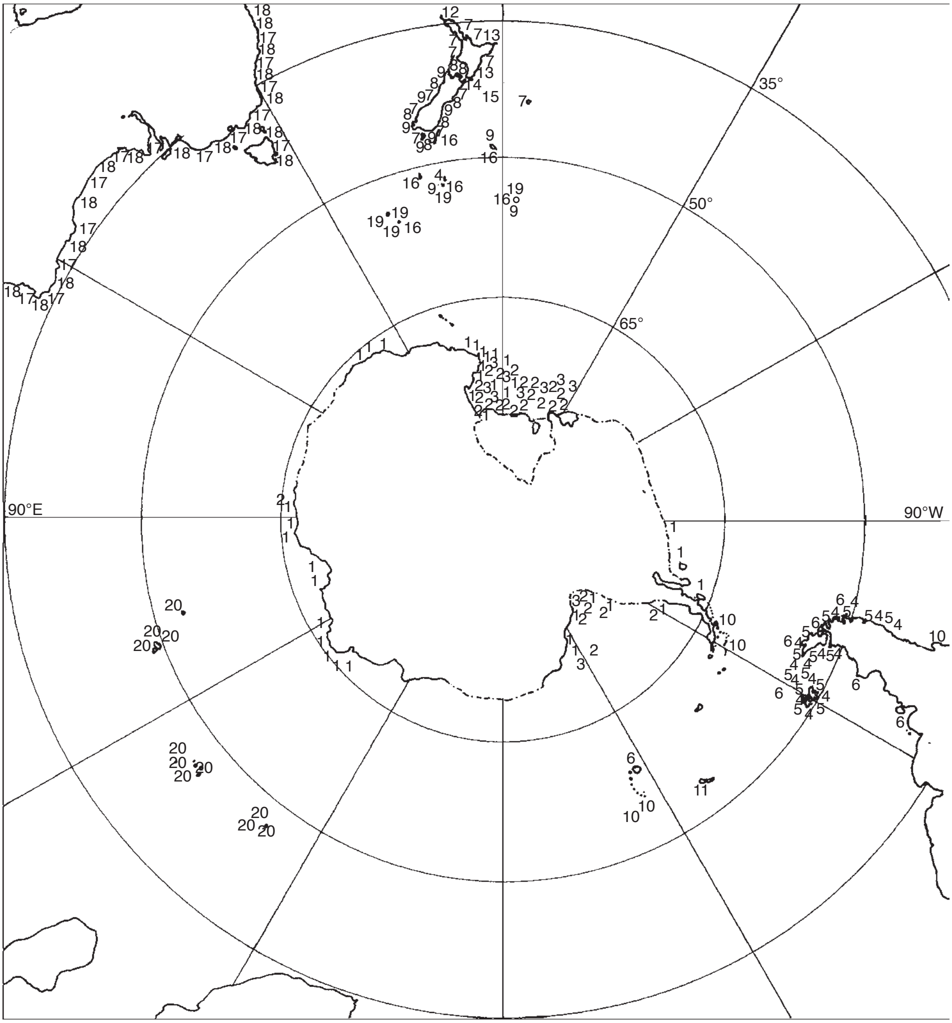

FIG. 406. Distribution of the species of the subfamily Terebratellinae from the records of COOPER (1973, 1981, 1982), COOPER and DOHERTY (1993), FOSTER (1974, 1989), MCCAMMON (1973), and RICHARDSON (1981c); *1, Magellania joubini; 2, Magellania fragilis; 3, Fosteria spinosa; 4, Terebratella dorsata; 5, Magellania venosa; 6, Aneboconcha obscura; 7, Calloria inconspicua; 8, Magasella sanguinea; 9, Neothyris lenticularis; 10, Syntomaria curiosa; 11, Dyscritosia secreta; 12, Calloria variegata; 13, Magasella haurakiensis; 14, Neothyris compressa; 15, Neothyris dawsoni; 16, Gyrothyris mawsoni; 17, Magellania flavescens; 18, Jaffaia jaffaensis; 19, Aerothyris macquariensis; 20, Aerothyris kerguelensis* (new).

life on hard surfaces may be inferred from the distribution of species of *Calloria. C. inconspicua* is found on surfaces of all types but more commonly on rocky substrates. The populations from rocky intertidal and shallow subtidal habitats differ from benthic populations in the mean size and shape of individuals. Sedentary individuals are smaller and less convex and appear to be stunted (STEWART, 1981). A new variegated species has been collected only from rocky substrates (COOPER & DOHERTY, 1993) and closely resembles *C. inconspicua* from the same type of habitat except in the color patterns of the shell.

Members of the other southern terebratellid subfamilies, Anakineticinae and Bouchardiinae, are all specific to bryozoan sands and are smooth, free-living forms with little variability in the shape and size of species (Richardson, 1987). In comparison, terebratelline species show little specialization in life-style and substrate occupied. They vary in shape, size, and ornamentation, and relationships within the subfamily provide some insight into its origins. The difficulties all workers (Allan, 1949; Foster, 1974; Cooper, 1981; Richardson, 1994) have experienced in separating the nonspecialist members of the subfamily is an indicator of the close relationship between species now attributed to *Aerothyris, Aneboconcha, Calloria, Dyscritosia, Fosteria, Magasella, Magellania, Syntomaria,* and *Terebratella.* These similarities are the result of relatedness, not of convergence, because they occur in sets of characters that appear to be unrelated to the environment, including the shape of the cardinal process, presence of a hinge plate, and position of the beak ridge. The most specialized terebratellines are the species included in *Neothyris* and *Gyrothyris.* They occupy soft sediments but not, as in the Anakineticinae, of a particular size range or composition and are considered to have evolved from *Magasella*-like ancestors (Thomson, 1927), i.e., from more generalist stocks. Similar relationships occur within Australian terebratellines: such free-living forms as *Victorithyris* appear to have been derived from *Magellania*-type stock (Richardson, 1980).

Members of the Terebratellidae have occupied shorelines and shelves throughout the Tertiary. Forms not confined to a specific substrate (*Calloria, Magasella, Magellania,* and *Terebratella*) are found from Eocene and later strata of Australia and New Zealand and from Oligocene and Miocene strata in Antarctica. The occurrence of shelf forms can be correlated with the Tertiary history of different areas. The New Zealand record shows that the sediment changes that accompanied Miocene regressions led to the extinction of all substrate-specific terebratelline (*Waiparia, Stethothyris,* and *Pachymagas*) and anakineticine (*Rhizothyris* and *Magadina*) genera. Species of *Neothyris* are found in a variety of originally soft sediments only from the Pliocene and Pleistocene periods (Allan, 1960; Neall, 1972). Australian Tertiary deposits consist almost exclusively of originally soft sediments, and there is an almost continuous record of anakineticines from the Eocene. Unlike in New Zealand, the deposits of shelly limestones that are similar to those occupied by modern, rocky-shoreline assemblages are not found in Australia. Species with nonspecialist characters occur in Australian Eocene deposits, while those terebratellines specialized to varying degrees for limestones (*Austrothyris, Cudmorella, Stethothyris,* and *Victorithyris*) are found in Oligocene and Miocene rocks and were lost during Miocene regressions. The only living terebratellines found in Australian waters are *Magellania flavescens* and *Jaffaia jaffaensis.*

Distributions of fossil taxa indicate that, in Australia and New Zealand at least, nonspecialist forms have occupied shoreline habitats since the Eocene and were apparently unaffected by the lowering of sea level at the end of the Miocene. At this time all terebratellines and anakineticines that were specialized for life on the shelf, occurring in greensands, calcarenites, and calcilutites, were lost in New Zealand. In Australia, only terebratellines in calcilutites became extinct. The persistence of the anakineticines in calcarenites throughout the Cenozoic may be attributed to the areal extent of the calcarenites and to their position on the shelf. Calcarenites now cover the middle and outer shelves, whereas extinct terebratellines have been collected from deposits that formed the floor of former inlets, the Murray and Gippsland basins.

LAQUEIDAE

The family Laqueidae contains 13 living genera, most of which are found around the North Pacific rim. *Coptothyris, Jolonica,* and *Pictothyris* occur in Japan only. *Terebratalia* and *Laqueus* occur between California and Japan, and *Tythothyris* and *Simplicithyris* are found in the northwestern Pacific. *Frenulina* occurs in the central Pacific (southern China Sea, Philippines, Indonesia, and Hawaii), in Australia, and in the western Indian Ocean. One species of *Ecnomiosa* is recorded from the Gulf of Mexico and another from South Crozet Island in the southern Indian Ocean, while *Compsoria* occurs in the eastern Indian Ocean and off Mozambique.

Two groups of genera, therefore, differ in area of distribution: those from the North Pacific are considered as one section of the family (HATAI, 1940), while *Ecnomiosa, Frenulina,* and *Compsoria* are found in the central and southern Pacific and the eastern and southern Indian Ocean. With respect to fossil occurrences, most members of the northern group are represented in Tertiary and Quaternary deposits of the areas they now occupy. *Frenulina* is found in the Australian Miocene to Pliocene, and *Ecnomiosa* is related to Australian stock from the Cretaceous (*Kingena*) and Miocene (*Paraldingia*). *Aldingia willemoesi* was recorded from Australian seas (THOMSON, 1927) but is unknown in any Australian collections. The existence of natural seaways across parts of Columbia, Panama, and Costa Rica afforded free communication between the Pacific and the Caribbean Sea or western Atlantic up to the end of the Miocene or Pliocene and may account for the presence of *Ecnomiosa gerda* in the Gulf of Mexico.

Laqueidae is unknown from northern or southern circumpolar seas, from the Atlantic, or from abyssal sediments.

Shell color patterns and associations with coral reefs indicate that *Frenulina* is probably exclusive to shallow, coralline substrates. *Pictothyris picta* and all Japanese species of *Laqueus* except *L. blanfordi* and *L. quadratus* are differentially thickened forms and have been retrieved from sands at depths of approximately 100 m off the coast of Japan (ENDO, 1987). Both sedentary and free populations of *Laqueus californianus* (BERNARD, 1972; ASGAARD & BROMLEY, 1991) and of species of *Terebratalia* (DU BOIS, 1916; RICHARDSON, STEWART, & XIXING, 1989; SCHUMANN, 1991) have been described.

DALLINIDAE

The Dallinidae is a family of which little is known of habitat, life-style, or morphological variability. Species have been collected from bottom sediments; but the species of only one genus, *Nipponithyris,* are differentially thickened, an indicator of a free mode of life. The genera included in the family differ in cardinalia and in the presence or absence of dental plates, leading to the conclusion that the family is made up of distinct stocks.

One genus, *Dallina,* contains species from the Pacific, Antarctic, and the North to South Atlantic oceans. Fossil representatives from the Eocene and later times are as widely distributed as those from the recent and have been collected in Italy, Japan, Norway, New Hebrides, and Fiji. *Fallax* contains two species that are difficult to separate (FOSTER, 1974), one from the northeastern Atlantic (from 686 to 1,408 m) and the other from the southwestern Pacific (2,285 to 2,342 m); and the genus has been recorded from the Pliocene of Sicily. Both *Campages* and *Nipponithyris* are found in the Miocene of Japan. In modern seas *Nipponithyris* occurs in New Caledonia and Japan, and *Campages* is found in Japan, Australia, and the Philippines. *Glaciarcula* with two species occurs in the northern circumpolar region and in the Pleistocene of Scandinavia.

MACANDREVIIDAE

The family Macandreviidae, with a single exception, contains abyssal species that occur in greatest numbers in the northwestern Atlantic region. *Diestothyris* contains 1 and *Macandrevia* contains 11 recent species. *D. frontalis* has been collected in the North Pacific from depths of 0 to 435 m and has also been described from the Miocene of Alaska and Japan. Other species of the genus are known from the Miocene of Canada and the Pliocene and Pleistocene of the Kamchatka Peninsula and Japan.

In modern seas *Macandrevia* is recorded almost exclusively from abyssal waters (COOPER, 1975). One species (*M. cranium*) is found from 9 to 2,492 m. *M. americana* occurs from 112 to 4,066 m, and *M. tenera* is found from 207 to 2,652 m. Other species occur at depths that exceed 2,000 m.

Species have been described from Atlantic, Mediterranean, Antarctic, and eastern Pacific waters. The wide geographical distribution of species is noteworthy; for example, *M. americana* has been recorded from San Diego, California, south to Antarctica and the southernmost South Atlantic. Fossil members of the genus have been collected from Quaternary deposits of Norway, Sweden, and Italy. The shell is unthickened in all forms except for one unnamed species collected from a rock near hydrothermal vents of the western Pacific at 2,700 m.

MEGATHYRIDIDAE

Members of the three genera attributed to the Megathyrididae are found principally in European and West Indian waters. They are small, sedentary forms commonly bonded so closely with the substrate that the beak and parts of the dorsal valve are misshapen and worn. They have been collected from cryptic habitats in shallow water but are not restricted in depth.

Gwynia is known from the Pleistocene of Norway and the one living species is found along the coasts of the United Kingdom, France, and the Netherlands from 15 to 46 m (Brunton & Curry, 1979). It has also been recorded from north of the Azores at 4,060 m (Fischer & Oehlert, 1892). Species of *Megathiris* have been described from the Mediterranean Sea, eastern Atlantic, and South Africa; and fossil species are known from the European Late Cretaceous to Pliocene.

Argyrotheca contains 22 named and 6 unnamed living species from the West Indies (Cooper, 1977; Asgaard & Stentoft, 1984), Mediterranean Sea (Logan, 1979; Brunton, 1988), Red Sea (Jackson, Goreau, & Hartman, 1971), southeastern North Atlantic (Logan, 1983), Mozambique Channel (Zezina, 1987), South Africa, Australia, and eastern and western Pacific (Grant, 1987). Argyrothecans are common from Tertiary deposits in Europe, United States, West Indies, Peru, Mexico, and Europe; and *Argyrotheca* is 1 of only 3 articulated brachiopod genera that crossed the Cretaceous-Tertiary boundary (Cooper, 1988). Most species occupy cryptic habitats in shallow-water, but many have a considerable depth range. For example, *A. barrettiana* has been collected from 1,473 m (Cooper, 1977).

KRAUSSINIDAE

Kraussina contains five species from South Africa with a depth range of 18 to 366 m (Hiller, 1991); one of these species is also found in the southeastern North Atlantic (Logan, 1983). Most species of *Megerlina* have been collected from low tide to 274 m in South Africa, southern Indian Ocean, and Australia. Fossils of either genus are unknown.

Megerlia has been described from the European Miocene and, in recent seas, from South Africa, southeastern North Atlantic, Mediterranean Sea, West Indies, southern Indian Ocean, Red Sea, and Australia. *Pumilus* is found in shallow water in New Zealand.

PLATIDIIDAE

Like the families Megathyrididae and Kraussinidae, platidiids are small, sedentary forms requiring a hard, stable surface for permanent attachment. *Platidia* is considered to contain three species (Foster, 1989), one from the Gulf of Mexico (*P. clepsydra*) and one from the Mediterranean Sea, the southeastern North Atlantic, the West Indies, and Argentina (*P. davidsoni*). *P. anomioides,* the third, is the only species in Tertiary rocks and is almost worldwide in distribution throughout the Cenozoic.

Amphithyris contains three species, two from New Zealand and one from the Ross Sea (Antarctica). Three species have also been assigned to *Annuloplatidia* from different regions of the Pacific Ocean. One, *A. indopacifica,* has a depth range of 370 to 5,800 m (Zezina, 1985).

THECIDELLINIDAE AND THECIDEIDAE

Thecideidine brachiopods are uniform in life-style, habitat occupied, and morphology and are restricted in depth and to latitudes lower than 35 degrees.

Thecidellina is the only living member of the Thecidellinidae, and *Lacazella* and *Pajaudina* are the only living Thecideidae. They are also the only living taxa in which the pedicle is absent in adults that are sessile forms cemented to substrates. Living specimens have been collected from cryptic, reef habitats and from depths of 5 to 176 m. The latitudinal range of the group is from 20°S in Australia to 35°N in the Mediterranean Sea.

Thecidellina has been described from the western and central Pacific Ocean, the Caribbean Sea, and the Indian Ocean, with fossils collected from the Eocene and Miocene of the Gulf and Atlantic coasts of the United States, the Eocene of the west coast of the United States, the Eocene of France, and the Miocene of the Pacific Ocean (Cooper, 1977). *Pajaudina* is found in the southeastern North Atlantic, and species of *Lacazella* occur in the Mediterranean Sea, southeastern North Atlantic, Indian Ocean, and Caribbean Sea. Fossil *Lacazella* occur in Eocene to Miocene deposits of Cuba and in Eocene deposits of the Gulf and Atlantic coasts of the United States.

FAMILY ORIGINS AND PATHS OF DISPERSAL

Examination of the distribution of different families shows clear linkages between the age of a family and some aspects of composition and distribution. Older families are cosmopolitan. As a rule members do not occur in abundance, but they do occupy slopes and the abyss. The youngest families are restricted in distribution. They may occur in abundance at the shoreline and on shelves but are not found on slopes or in the abyss. Families of the Rhynchonelloidea, Cancellothyroidea, and Terebratuloidea were all more common in past eras. Numbers of genera in the Rhynchonelloidea, for example, declined from 113 in the Jurassic to 17 in the recent. The Terebratuloidea declined in numbers from 136 to 19 in the same periods (Cooper, 1988). Age, together with sparse occurrence and cosmopolitan distribution, means that the present composition of these superfamilies is unrepresentative of the past diversity and distribution: they are relict groups that have shown no evidence of diversification at least since the Jurassic. Therefore relationships between species and genera would be difficult if not impossible to determine. As a consequence, the present composition and distribution of nonterebratelloid families can provide little information on the origins and paths of dispersal of articulated brachiopods.

Terebratelloid families are also cosmopolitan except for the southern Terebratellidae and northern members of the family Laqueidae. The Terebratellidae and Laqueidae are presumed to be the youngest articulated brachiopod families, and in modern seas they appear to be as common as or more common than in the Tertiary. Also, unlike other families, polytypic genera may be found in the same geographical area. Therefore, they provide the most reliable sources from which to speculate on origins of modern articulated brachiopod assemblages and paths of dispersal.

Terebratellids and laqueids are consistent in patterns of distribution with the nature of species, i.e., generalist species are most abundant in areas in which substrates available for settlement vary in mass, and these patterns of living faunas conform with those from Tertiary deposits. Species not specific to a particular substrate are widely distributed both geographically and with respect to substrate and are variable in such characters linked with the environment as differential thickening, beak shape, size, and shape. Species specialized for shelf sediments may be more limited in distribution and are less variable morphologically, both distribution and variability being related to degree of specialization. Japanese and New Zealand seas contain members of most living families, but the major components of articulated brachiopod faunas of the Cenozoic are members respectively of the Terebrataliidae (Laqueidae) and the Terebratellinae (Terebratellidae if Tertiary forms are included). In both areas, generalist species of *Terebratalia* and *Magasella* are widespread on shorelines and shelves, and species of *Coptothyris* (Nomura & Hatai, 1936), *Dallinella* (Thomson, 1927), and *Neothyris* (Richardson, 1994) adapted to shelf sediments are endemic and are considered to have been derived from the generalist stocks found in these areas.

The differences in the patterns of distribution of the Laqueidae (in Japan) and Terebratellidae (in New Zealand) from those of other articulated brachiopod families may be attributed to differences in the opportunities for colonization. One reason for the absence of any evidence of diversification in older families since the end of the Jurassic (Cooper, 1988) could be the absence of those substrates that existing faunas have the capacity to colonize. For example, members of the Bouchardiinae and Anakineticinae are found on bryozoan sands off Brazil and Australia, the only areas in which these sands are common and which members of the subfamilies are specialized to occupy. Their specificity for this kind of sediment and a short larval life mean that transoceanic dispersal was not possible.

The contrast between Japanese and Chinese articulated brachiopod faunas provides good evidence that transoceanic migration is an unlikely means of dispersal and that species differ in capacities for colonization. The Cenozoic Japanese fauna is abundant (50 species in 18 genera) and consists of a major component of endemic terebratelloid genera and a lesser component of genera belonging to older cosmopolitan families (Hatai, 1940). In contrast only four living species (*Terebratalia coreanica, Campages mariae, Terebratulina hataiana,* and *Frenulina sanguinolenta*) occur in Chinese waters; none is endemic, and no articulated brachiopods are known from the Chinese Tertiary (Richardson, Stewart, & Xixing, 1989). *Terebratalia coreanica* is a generalist species common around the shorelines and shelves of Japan and Korea. *Campages mariae* has been collected from shelf sediments around Japan and is not known to be specific to any particular grain size or composition. *Terebratulina hataiana* has been collected from sandy sediments of the South China Sea and has also been described from seas around the Philippine Islands. *Frenulina sanguinolenta* is widely distributed in low to mid-latitudes of the Indo-Pacific and has been collected from coral reefs around islands in the South China Sea. Thus Japan and China, although near neighbors, provide the strongest contrast between a rich, indigenous fauna and a sparse, immigrant fauna.

Differences in the faunal composition of other neighboring areas also contribute to an understanding of factors governing geographic distribution. The living faunas off Australia and New Zealand are dominated by terebratellids but by members of different subfamilies, the Anakineticinae in Australia and the Terebratellinae in New Zealand. This is one consequence of differences in the stability of the two areas during the Tertiary, which has resulted in different shelf sediments in modern seas. Anakineticines are adapted for life in either greensands or bryozoan sands, and the stability of the Australian continent has meant that a shelf cover of the sands has been maintained from at least the Eocene. Anakineticines were also common in the greensand sandstones and bryozoan sandstone of the New Zealand Oligocene and Miocene but became extinct before the end of the Miocene. These two kinds of sand now support different terebratellid faunas—anakineticines in Australia's bryozoan sands and terebratellines in the New Zealand terrigenous sediments. Hence the Australian fauna has been unchanged throughout the Cenozoic, whereas the present New Zealand shelf fauna is of relatively recent, Pliocene origin.

The endemic nature of the terebratellid faunas around Australia, New Zealand, and other southern land masses led earlier workers (Blochmann, 1908; Thomson, 1918; Allan, 1963) to the conclusion that their probable source of origin was Gondwana and that pre-Tertiary land bridges would have provided routes for the dispersal of ancestral forms. Plate tectonics, of course, has provided the means of distribution without the need to postulate land bridges. It seems unlikely that the patterns of distribution of terebratellid brachiopods in earlier periods would differ appreciably from those evident throughout the Cenozoic. Therefore in the absence of evidence to the contrary, it is safe to surmise that the shorelines and shelf of Gondwana were occupied by generalist species and by species specialized to varying degrees for life on the shelf. With the break up of the continent their survival would have been inversely correlated with the extent of loss or change of substrate. Differences in the requirements of generalists and specialists mean that generalists are more likely to survive periods of environmental change as illustrated by the extinction of all taxa specialized for shelf sediments during periods of instability in the New Zealand Miocene.

The break up of Gondwana and the differential survival of species account for the present distribution in which generalists and near-generalists occur around southern, Gondwana-derived land masses except for South Africa. The only specialists that occur in Tertiary deposits of both Australia and New Zealand are three conspecifics, one cancellothyrid and two terebratellid species, all of which were adapted for life in carbonate sands. The presence of these conspecifics indicates that they evolved before the break up of Gondwana and that parts of the Gondwana shelf contributed to the shelves of Australia and New Zealand. Any transoceanic dispersal between Australia and New Zealand is precluded by length of larval life and by the absence of carbonate sands bridging the Australian and New Zealand shelves. All other specialists found in southern latitudes are endemics; i.e., they evolved in the area they now occupy and are more likely to have been derived from nonspecialist or generalist stock of that area, not from species with similar adaptations from a different geographical area. For example, studies of growth stages show that species of *Neothyris* and *Victorithyris* are more closely related respectively to species of *Magasella* and to *Magellania* than to any other species. The absence of any member of the Terebratellidae from the Cenozoic of South Africa suggests that those sections of the Gondwana shoreline and shelf that contained members of the family did not contribute to the southern part of Africa.

The similarities in the distribution of the Terebratellidae and northern Laqueidae suggest that processes of diversification were similar and that they occurred in different areas. Laqueid generalists are found around the shorelines of the northern Pacific, and diversification of this stock has resulted in species specialized for different shelf sediments, for example those in Japan and California. Generalist species of the Terebratellinae occur around Gondwana-derived land masses, and genera specialized for life in shelf sediments are endemic to Australia, New Zealand, and South America. Although other families are not restricted in distribution, fossil occurrences together with preponderances of living faunas indicate the centers from which each group may have originated and dispersed. For example, the family Kraussinidae is a predominately South African family (HILLER, 1991). The family Megathyridiidae is found principally in European and West Indian waters, and living species shared between these two areas (LOGAN, 1993) and in the fossil record (ELLIOTT, 1951; COOPER, 1977) have led workers to conclude that at some time in the past the coasts were close together. Given the age of articulated brachiopod families and the difficulties of transoceanic travel, vicariance seems to be the principal means of distribution; i.e., the diversification of most families occurred during periods when shorelines were close together. In addition it seems that, with the obvious exception of substrate-specific taxa, the extent of geographic and bathymetric distribution may be correlated with age of families rather than a consequence of inherent limiting factors. The present restriction of the Terebratellinae to high latitudes and to waters exceeding depths of 1,000 m may be an indicator not of a preference for cold water but a consequence of relatively recent origin and slow rates of dispersal.