

ECOLOGY OF INARTICULATED BRACHIOPODS

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INTRODUCTION

Living inarticulated brachiopods are a highly diversified group. All are marine, with most species extending from the littoral waters to the bathyal zone. Only one species reaches abyssal depths, and none is restricted to the intertidal zone. Among the living brachiopods, the lingulides, which have been most extensively studied, are the only well-known group.

Both living lingulide genera, *Lingula* and *Glottidia*, are the sole extant representatives of a Paleozoic inarticulated group that have evolved an infaunal habit. They have a range of morphological, physiological, and behavioral features that have adapted them for an endobiont mode of life that has remained remarkably constant at least since the early Paleozoic. The lingulide group shares many features that are characteristic of this mode of life including a shell shape that is oblong oval or rectangular in outline with straight, lateral, subparallel to parallel margins and an anterior margin that is straight to slightly concave for burrowing; a complex muscle system that operates the inarticulated valves; a mantle margin and its setae that serve several basic purposes; and a pedicle that anchors the animal at the bottom of the burrow and shifts the position of the shell. Such characteristics can be considered as plesiomorphic among the Brachiopoda.

The ecological requirements of inarticulated brachiopods indicate the need for a life-history approach that emphasizes aspects of populations rather than individuals because many such factors as reproduction, survivorship, dispersion, and evolution depend on populations. Accordingly there is no single factor that determines the occupancy of a niche by a population and that is always directly related to the biocoenosis in which the population is living. Those requirements

need to be analyzed carefully at the population level before using them to interpret species and genera.

Assemblages with lingulides are routinely interpreted as indicating intertidal, brackish, and warm conditions, but the evidence for such assumptions is mainly anecdotal. In fact, formation of lingulide fossil beds generally occurred during drastic to catastrophic ecological changes.

BEHAVIOR

INFAUNAL PATTERN: LINGULIDAE

Burrows

Lingulides live in a vertical burrow in a soft substrate. Their burrow has two parts (Fig. 407): the upper part, oval in section, about two-thirds of the total length of the burrow, in which the shell moves along a single plane, and the cylindrical lower part in which only the pedicle moves (EMIG, 1981b, 1982). In a homogenous fine sand the length of the whole burrow is about ten times the length of the shell (Fig. 407), but it can be reduced when the coarse fraction increases at depth in the sediment or when a hard layer occurs (EMIG, 1982). In tropical areas, a layer formed by pieces of coral and pebbles or by shell fragments often limits the thickness of the sandy sheet to about 15 to 20 cm. The pedicle is anchored within this coarse layer, and the detrital mass of the bulb is less than that of individuals living in thick, sandy sediment. The extension of the pedicle can reach a length 20 times that of the shell to compensate for sedimentation (EMIG, 1983a). Fossil burrows with lingulide shells *in situ* show the same structure (Fig. 407). Thus when determining the relationship of the burrow to the length of the shell, the compaction of the sand layer can be estimated at about one-third (EMIG & others, 1978; EMIG, 1982).

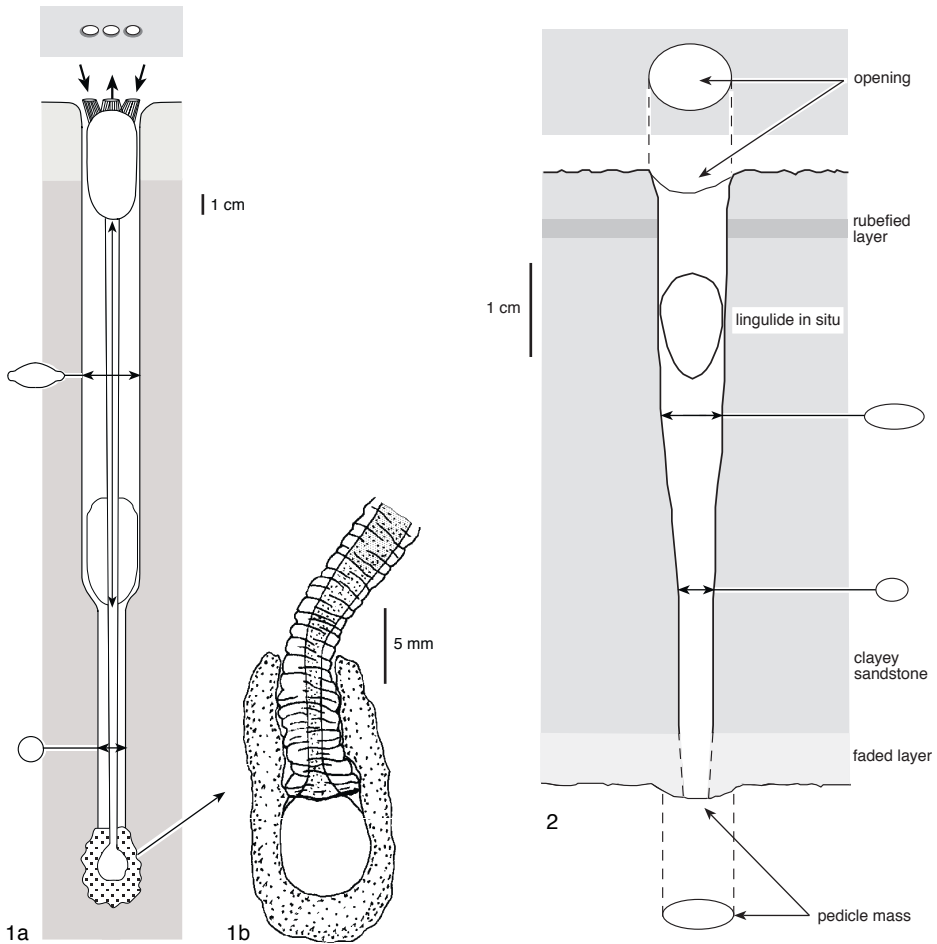


FIG. 407. *1a*, Longitudinal section of a burrow of a living lingulide with the shell in normal position and retracted (and *1b*, detailed pedicle mass); and *2*, of a fossil lingulide (Triassic of Vosges Mountains; Emig & others, 1978).

The walls of the burrow are lined with mucus secreted by the edges of the mantle and the pedicle (EMIG, 1982). The mucous layer binds the walls and lubricates the movements of the animal in its burrow. Only the distal bulb of the pedicle, surrounded by a mass of sand and various detrital particles agglutinated by the bulb's sticky mucous secretion, is firmly anchored into the substratum at the bottom of the burrow (Fig. 407). The size of this mass depends upon characteristics of the sediment. Functioning like the ampulla in the Phoronida, the distal bulb of the lingulides is able, by turgescence un-

der coelomic pressure, to reinforce the anchoring in the substratum and is enhanced by crenulation of the pedicle bulb.

The lingulides often live in sediment that is in a reducing environment below the upper 2 to 5 centimeters, but the peripheral substrate, which is up to 1 to 2 mm thick along the burrow walls, is oxygenated by continuously renewed water in the burrow (Fig. 407).

Continuous filtering indicates that the normal position of the lingulide shell is at the top of the burrow (EMIG, 1982). To maintain this position (Fig. 408), a weak

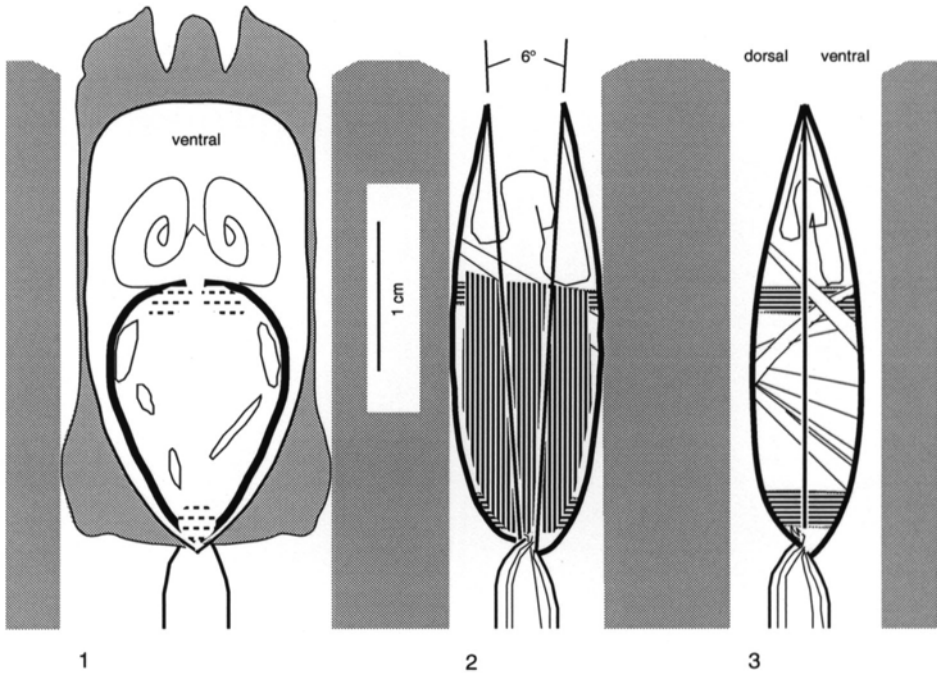


FIG. 408. Longitudinal section of a lingulide in its burrow; 1, ventral side showing the mantle setae length; 2, normal position (lateral view) by contraction of the lateral muscles; 3, quick valve closure by contraction of the anterior and posterior adductor muscles, first step of the escape reflex (new).

contraction of the lateral body muscle layer produces a hydrostatic pressure on the body's coelomic cavity; the body volume is shifted posteriorly and laterally; the valves gape about 6° to rest against the lateral burrow walls, which act as supports; and the lophophore extends to become functional within an enlarged pallial cavity. The normal life position is static and can be maintained without much effort. The pedicle plays no role in the maintenance of this position. Occasional scissorlike movements of the valves assist in maintenance of the burrow (Fig. 409).

Coarser or muddier substrates are less well suited for providing stable burrow walls. Consequently, the animal is unable to live or to survive in sediment that is too coarse or too muddy, contrary to general assumptions about habitats of lingulides. Thus living lingulides have rarely been found in muddy sediments with a fine fraction ($< 63 \mu\text{m}$) higher than 35 to 40 percent because in such

fluid sediments the walls, even when bonded by mucous secretion, inadequately support the shell in its normal filtering position (EMIG, 1983a).

At the surface of the sediment, three characteristic pseudosiphons indicate the presence of a lingulide in normal, life position (Fig. 407–408, 410; Table 35). They are shaped by the highly specialized anterior setae of the mantle. At the level of the shortest setae, the anterior mantle margin of each valve develops an epidermal crest. These come into contact with each other and induce tilting and interlacing of the setae borne by the crests. Simultaneously the longest setae, which can be as long as a third of the shell length, remain vertical (Fig. 408). The central aperture is exhalant, while the two lateral apertures are inhalant. The exhalant and inhalant water streams are completely separated by the mantle crests and internally by tentacle tips without any mixing of the flows. The diameter of setae varies

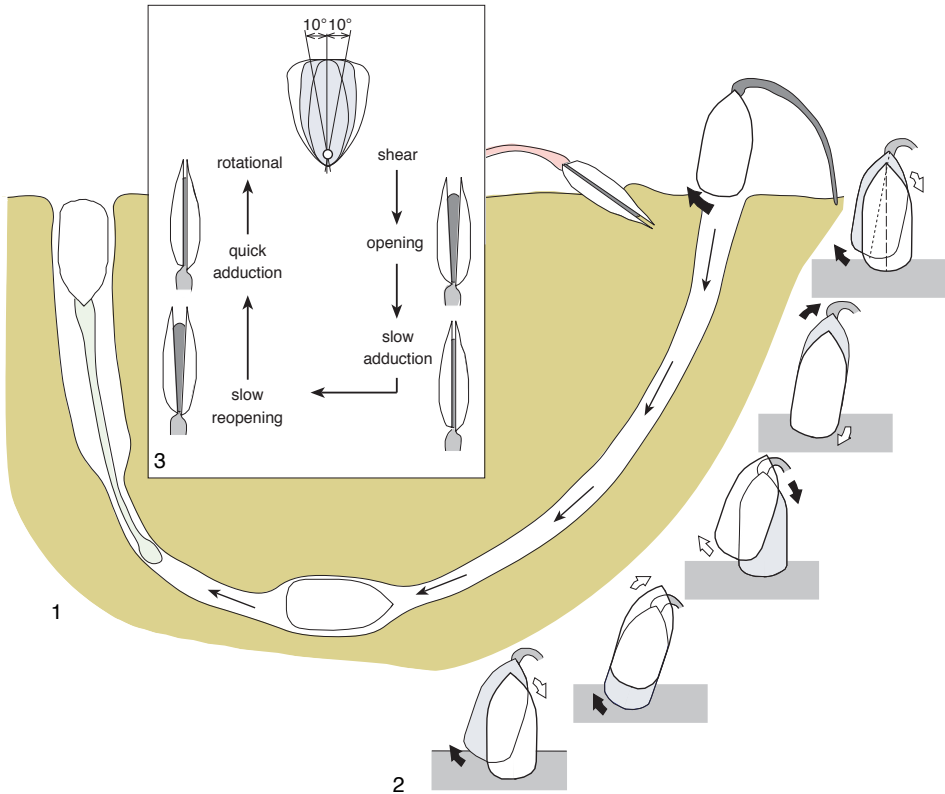


FIG. 409. 1, U-shaped reburrowing by *Glottidia* (Emig & others, 1978); 2, sequence of the scissors burrowing movements of *G. pyramidata* (Thayer & Steele-Petrovic, 1975); 3, patterns in the burrowing sequence of *Lingula anatina* (Savazzi, 1991).

from 15 to 60 μm , and they occur at intervals of 15 to 30 μm so that they exclude large particles from the pallial cavity. Contrary to general assumptions (PAINE, 1970; THAYER & STEELE-PETROVIC, 1975), the absence of lingu-
 lides from mud is not related to clogging of the lophophoral cavity by fine particles. In a turbid water mass, fine particles may be retained in large masses by the mucus on the setae of the pseudosiphons and do not enter the pallial cavity but are flushed out periodically by scissorlike movements of the shell (EMIG, 1983a).

No orientation related to current direction has been observed (WORCESTER, 1969; EMIG, 1981b) because the strong, jetlike, exhalant current precludes possible recycling by the inhalant currents. A turn of the shell plane of about 25 to 30° from the near-bottom cur-

rent direction appears to be sufficient to avoid recycling (Fig. 410).

Shell Movements and Burrowing

Shell movements and burrowing behavior are similar in both extant lingu-
lingula and *Glottidia* (YATSU, 1902b; THAYER & STEELE-PETROVIC, 1975; EMIG, 1981b, 1982, 1983b; TRUEMAN & WONG, 1987; SAVAZZI, 1991), and have probably been practiced by oblong or rectangular lingu-
 loides since early Paleozoic times (EMIG, 1984b; SAVAZZI, 1991).

Opening and slow closing movements (Fig. 408–409) of the valves are governed by fluctuations in pressure within the meta-
 coelomic body cavity and are generated by contraction of the lateral muscle layers of the body, which are composed of circulo-

TABLE 35. Summary of the two adult lophophore types in living inarticulated brachiopods in relation to the number of inhalant (*in*) and exhalant (*ex*) compartments and apertures in the shell and shell orientation in or on substratum (new).

Taxa	Genera	Species	Shell orientation	Schizolophe <i>of Pelagodiscus atlanticus</i>	Spirolophe
Lingulides	2	12	shell vertical	-	2 in + 1 ex ¹
Craniids	4	19	dorsal valve above, ventral valve below	-	2 in + 1 ex ¹
Discinids	1	1	dorsal valve above, ventral valve below	1 in + 2 ex	
	3	11	dorsal valve above, ventral valve below	-	1 in + 2 ex

¹in these groups, there are two small additional exhalant apertures behind the shell.

longitudinal fibers. This body cavity functions as a single, fluid-filled chamber, although partially divided by a gastroparietal band and, with the coelomic canal of the pedicle, acts as a fluid reservoir in the hydraulic system. This system that opens the valves performs the same function as the elastic hinge ligament of the molluscs and the diductor muscles of articulated brachiopods. Quick closure is obtained by the contraction of the anterior and posterior adductor muscles. Scissorlike movements of the valves occur by contraction of the well-developed, oblique muscles. This complex body musculature sustains the unique, infaunal mode of life of these brachiopods.

When a lingulide is on a sandy substrate, fluctuations in pressure within the coelomic body and pedicle cavities open and close the valve. When the lingulide starts to burrow (Fig. 409), the pedicle stiffens with its distal bulb pressing downward to prop up the valves, thereby bringing the anterior margins of the valves into contact with the sediment. Penetration takes place by means of a combination of scissorlike movements of the valves and ejection of water from them that loosen the sand prior to a downward movement of the shell and an upward transportation of mucous-bound sand by the lateral setae of the mantle.

The typical burrowing sequence consists of the following phases (Fig. 409). First, scissorlike movements occur by oscillatory rotation of the valves about an axis passing dorsoventrally through the posterior shell; the movements coincide with small, pressure

pulses and, although the shell is moderately gaping, the setae, which prevent sediment particles from entering the mantle cavity, aid in the burrowing process. A complete rotation takes five to eight seconds. Second, there is a slow opening of the valve of one to five seconds in duration, followed by a short pause (up to three seconds). Third, a slow closure and then reopening of the valves are followed by a quick contraction of the adductor muscles that forces water jets into the surrounding sediment. Fourth, there is a pause of variable length.

Progression into the sand coincides with large pressure pulses and is facilitated by the secretion of a large amount of mucus. Contrary to popular belief, the lingulide pedicle is not used for burrowing; it is unable to dig into the sediment. Instead it acts as a support or prop while repeated scissorlike movements, shell closure with water injection, and shell openings accompanied by pressure pulses result in successively deeper penetration. Burrowing follows a semicircular course, the radius of which probably depends on shell size. The animal burrows obliquely downward to a depth that has not yet been established in natural conditions, then curves upward and burrows vertically until it reaches the surface of the sediment. Pedicle anchoring following burial is achieved by mucoadhesion of sand and various particles. Some fossil U-shaped burrows could be related to reburrowing features (EMIG & others, 1978). While reentering the sediment the animal is extremely susceptible to predation.

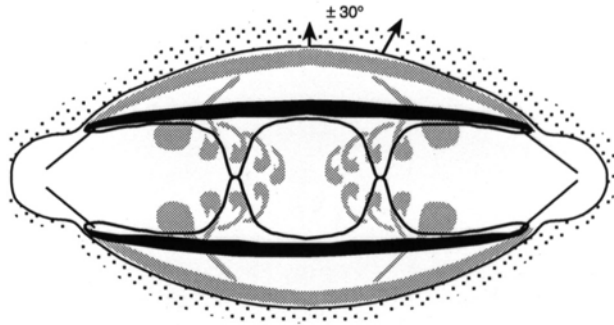


FIG. 410. Composite of two transverse sections of a lingulide in its burrow, one section at the level of the anterior mantle margin showing the epidermal crests and inhalant and exhalant opening (shown in *heavy lines*), the other at the level of the lophophore (*shaded in gray*) (adapted from Emig, 1982).

Burrowing is faster in small individuals than in larger ones, and failure to reburrow increases in *Lingula* with shell lengths exceeding 1.7 to 2 cm (MORSE, 1902; AWATI & KSHIRSAGAR, 1957; WORCESTER, 1969; EMIG, 1981b, 1982, 1983a; HAMMOND, 1983; SAVAZZI, 1991). Reburrowing could be interpreted as a size-related process, but such a performance seems to vary between geographic populations, as contradicting accounts have shown (EMIG, 1983a; SAVAZZI, 1991). In experimental conditions the burrowing speed is always five to ten times faster than in natural conditions (Table 36). Upward burrowing is essential for the survival of the lingulides and can be accelerated to compensate for sedimentation above their burrows, perhaps a response to the increase of the sediment pressure (Table 36). A rapid influx of coarse sediment, which is not typical of the environments of lingulides, however, may occur during high-energy events (HAMMOND, 1983). The nature of the sediment has a direct influence on burrowing capability, which is about twice as fast in a sandy substrate as in coarser sediment (particles > 2 mm). In experimental conditions *Lingula anatina* was able to burrow upward in coarse sediment but was unable to construct a stable burrow and finally emerged onto the sediment surface, often after autotomy of its pedicle. The results are indecisive under natural conditions (EMIG, 1983a), but the temperature seems to have no influence on the burrowing speed. *Glottidia* is unable

to dig in such coarse sediments (THAYER & STEELE-PETROVIC, 1975; CULTER, 1979).

During rapid experimental sedimentation, autotomy of the pedicle occurs when accumulation exceeds the pedicle extension. A new pedicle is regenerated in four to eight weeks in *Lingula*, but individuals without a pedicle maintain their filtering position with difficulty and generally emerge onto the sediment surface. Any damage to the pedicle always impairs burrowing as it precludes the use of the coelom as a hydraulic system. *L. reevii* is able to move pebbles of several centimeters in diameter that happen to lie on top of its burrow (EMIG, 1981b).

Retraction into the Burrow

Rapid retraction into the burrow is an escape reflex (FRANÇOIS, 1891; MORSE, 1902) that is well known in almost all animals that live in burrows or tubes. This protective reaction in response to unfavorable circumstances in the external environment is accompanied by the rapid closure of the shell. This response by the lingulides is elicited by tactile stimulations of the anterior marginal setae (MORSE, 1902; TRUEMAN & WONG, 1987), by an organism moving over the sediment surface, or by a shadow falling on the brachiopod (EMIG, 1981b). Such stimuli result in a quick closure of the shell with expulsion of water combined with contraction of the pedicle muscle, and the animal withdraws quite quickly into the burrow. If the disturbance continues the animal generally

TABLE 36. Experimental and *in situ* (measurements in italics) burrowing conditions (data from *a*, Emig, 1981b; *b*, Emig, 1983a; *c*, Hammond, 1983; *d*, Paine, 1963; Thayer & Steele-Petrovic, 1975; *e*, Worcester, 1969). Mean burrowing speed is given in parentheses (new).

	<i>L. anatina</i> (b)	<i>L. reevei</i> (a, e)	<i>G. pyramidata</i> (d)
Burrowing speed in normal conditions (cm/h)			
experimental	0.5–1.7 (0.9)	0.2–2.5 (0.75)	0.67–2.7
<i>in situ</i>	<i>0.08–0.21</i>	<i>0.21–0.75</i>	<i>< 0.67–2.7</i>
Mean upward speed (cm/h) during experimental sedimentation			
Thickness of sediment	b c	e	d
10 cm	(0.11) (0.45)	-	(1.3)
15 cm	-	(0.14), (1.07)	-
20 cm	(0.13) (0.58)	-	(0.33)
30 cm	(0.18) -	(0.38)	(0.40)

retracts 1 to 3 cm from the surface into the lower section of the upper part of the burrow. During retraction the upper part (0.5 to 1 cm) of the burrow collapses and is obturated by sand grains, although in compact sand the burrow remains open (EMIG, 1981b, 1982).

At the end of a disturbance, the lingulide is elevated by scissorlike and small opening movements of the shell combined with the action of the setae and copious mucous secretion, all of which restore the upper part of the burrow. During retraction and reextension, the coelomic pedicle canal functions as a hydrostatic skeleton combined with the contractions of the pedicle muscle and coelomic pressures in the body.

In intertidal environments, the lingulide retracts into the burrow during low tide. It follows the water level down and then moves upward again with the advancing tide (CHUANG, 1956, 1961; EMIG & others, 1978).

EPIFAUNAL PATTERN: DISCINIDAE AND CRANIIDAE

The other extant inarticulated brachiopods are epifaunal, attached either by a fixation organ (discinids) or by cementation to some hard substrate (craniids). The ventral valve is always oriented toward the substratum, a feature that the discinids and craniids share with the articulated thecideidines, which is related to the orientation of the

larva during settlement. All discinids are attached by a highly muscular pedicle to hard substrates except for *Pelagodiscus*, which is closely fixed to the hard substrate by means of its two main vertical body muscles. The pedicle is very short, and the shell is held near the substratum. Among living inarticulated brachiopods only the pedicle of the discinids has a dual function. It acts as an anchor, and it supports the weight of the shell and holds it in relative position to the substrate (Fig. 411.2).

The craniids, which are cemented by the entire surface of the ventral valve to a hard substrate, lack a pedicle; the larvae settle with the posterior end expanded along the substrate and secreting the ventral valve, which is cemented to the substrate. This ventral valve is variably calcified in *Neocrania* species and has a calcified, alveolate structure in *Neoancistrocrania norfolki*.

As in lingulides, the strong adductor muscles of discinids and craniids close the shell, which is opened mainly or exclusively by hydrostatic mechanisms with longitudinal and outer body muscles working against the pressure of the coelomic fluid. The setae of the mantle edges of the discinids are as highly specialized as those of lingulides. They have tactile sensitivity, resulting in a protective closure of the shell, which is accompanied by the contraction of the pedicle drawing the shell near the substratum. The craniids have no setae.



FIG. 411. 1, Live *Discradisca strigata* in pumping position, the anterior setae interlocked to form a functional siphon; arrows indicate in- and outcurrent directions (adapted from LaBarbera, 1985); 2, faunal distribution on a rocky substrate. All *D. strigata* are numbered; number 6 bears a *D. strigata* (number 7) and number 22 bears a barnacle; A, anemone; C, solitary coral; G, gastropod (LaBarbera, 1985).

The shells of discinids and craniids gape quite widely at the anterior edge and more narrowly at the posterior margin. A copious, median, inhalant flow enters the shell ante-

riorly and exits through two, posterolateral, exhalant gapes (Table 35; PAINE, 1962b; LABARBERA, 1985; EMIG, 1992). Another disposition for craniids is that two inhalant cur-

rents flow in at the anterolateral margins, while one main exhalant current flows out at the anteromedian edge; additional exhalant currents occur at the posterolateral margins (CHUANG, 1974).

In discinids the densely packed setae of the anterior mantle margin function as an incurrent siphon (Fig. 411.1). These anterior setae can be nearly three times as long as the diameter of the shell, while the length of the setae diminishes rapidly toward the posterior end (MORSE, 1902). Discinids orient the lophophore relative to the current (LABARBERA, 1985); but *Pelagodiscus*, because of the nature of its attachment, probably undergoes a small degree of reorientation against the current. In the cemented craniids the orientation may depend on the larval settlement under the influence of the prevailing bottom current, with adjustments at that stage so that the anterior region faces the local flow direction.

Discradisca strigata has a characteristic behavior pattern (LABARBERA, 1985). At irregular intervals or when disturbed, the valves nearly close, and the dorsal valve rotates clockwise and counterclockwise through an arc of 60 to 120°. This movement rubs the lateral setae of the dorsal valve over and past the ventral setae. The setal siphon is disturbed by this movement but remains potent. When the dorsal valve returns to its normal alignment with the ventral valve, their margins clamp together tightly and both valves rotate as a unit through an arc of 60 to 150°. On returning to a resting position, the margins of the valves remain clamped tightly to the substrate, but within several minutes at most the shell returns to a position slightly elevated above the substrate and the valves slowly reopen. The subcentral foramen of discinids affords greater protection for the pedicle than the posterior opening of articulated brachiopods and ensures that the entire shell margin, including regions adjacent to the pedicle, sweeps through a sizeable arc when the animal rotates, thus inhibiting growth of epifauna at a greater distance from the shell.

LIFE SPAN

The longevity of lingulides based on the length of the shell is a matter of conjecture. The life spans of *Lingula anatina* and *L. reevii* have been recently estimated theoretically from five to eight years, while *Glottidia pyramidata* is said to live from 14 months to less than two years (Fig. 412; MORSE, 1902; PAINE, 1963; CULTER, 1979). Shell growth in *Lingula anatina* and *L. reevii* decreases linearly with increasing size (WORCESTER, 1969; MAHAJAN & JOSHI, 1983). *L. anatina* attains a length of 25.6, 36.8, and 47.6 mm at the age of one, two, and three years respectively (Fig. 412); consequently the theoretical life span appears to be six to seven years. Two previous shell growth curves have been established for *Lingula reevii* in Hawaii (WORCESTER, 1969) and for *Lingula anatina* in Australia (Fig. 412; KENCHINGTON & HAMMOND, 1978). Growth in a population in a restricted area, however, is directly related to such local environmental factors as water characteristics, disturbances, nature of the substrate, and nutrients. These time-dependent variations can affect the metabolism of the animal and consequently retard or favor growth, although the shell grows continuously throughout its life. Consequently, individuals of equal shell length may differ in age, sexual maturity, and longevity (CHUANG, 1961; PAINE, 1963; WORCESTER, 1969; C. EMIG, personal unpublished data, 1983).

There are few data on the life spans of other inarticulated brachiopods. Populations of *Discradisca strigata* (LABARBERA, 1985) take more than 10 years to become stabilized. The three to six growth rings in the shell of *Pelagodiscus atlanticus* may be interpreted as evidence of a life span of three to six years. However, shells from the continental slope have a greater length and a narrower relative width and a smoother, less crenulated periostracum than those from the abyssal plain (ZEZINA, 1981). These differences seem to be the results of such environmental factors as temperature variations (2.65 to 3.07°C on the slope, 2.2 to 2.35°C in the

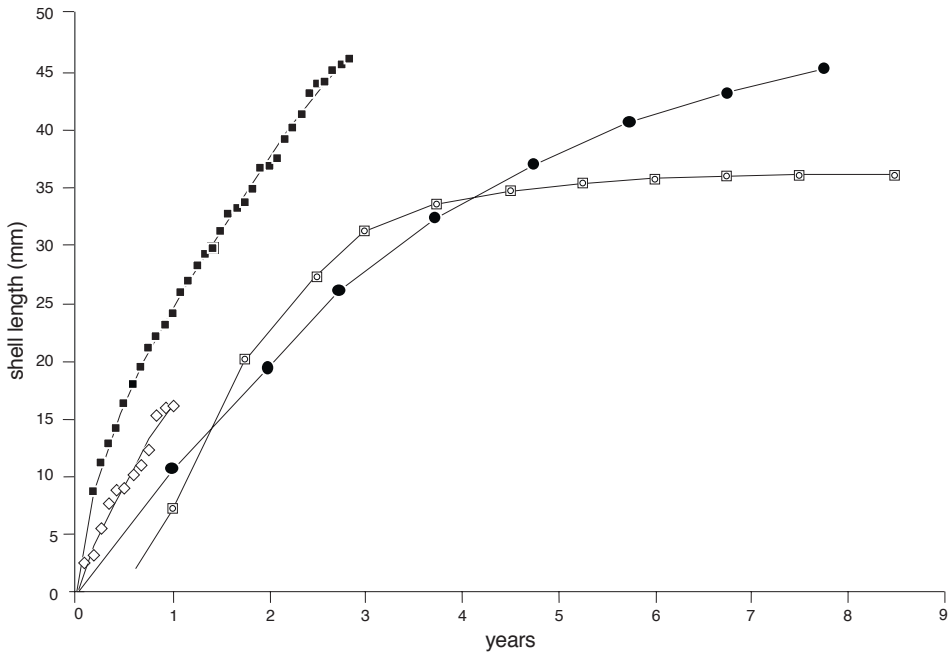


FIG. 412. Growth curves of various lingulide species; ■, *Lingula anatina* (data from Mahajan & Joshi, 1983); ●, *Lingula anatina* (data from Kenchington & Hammond, 1978); □, *Lingula reevii* (data from Worcester, 1969); ◇, *Glottidia pyramidata* (data from Culter, 1979) (new).

plain) and food supply. Presumably these factors control the growth rate more effectively on the slope than on the abyssal plain (ZEZINA, 1981). *Neocrania anomala* lived for 14 months in aquaria at normal laboratory light and without changing the water (JUBIN, 1886).

ECOLOGY

ABIOTIC FACTORS

Substrates

Soft substrates: Lingulidae.—Lingulides live in compact and stable sediments under the influence of moderate, near-bottom currents (PAINE, 1970; EMIG, 1984a). The two preferred substrates are either well-sorted, fine- to very fine-grained sand and clayey sand (in which the 90 to 250 μm fraction comprises more than 50 to 60 percent) and coarse sand grains in a fine-grained or very fine-grained sandy matrix. The sediment can be further stabilized by marine phanerogams

or mangrove tree roots. The grain-size fraction that is transported by saltation (about 90 to 220 μm) and generally associated with the traction-load fraction (> 600 μm) determines lingulide distribution. Where the traction fraction (about 220 to 600 μm) or the suspension fractions (< 90 μm) increase in the sediment relative to the saltation fraction, lingulide density decreases rapidly. The distribution of lingulides in deeper waters sometimes depends on the presence of Quaternary littoral sands, as in New Caledonia. From the few available data, the organic content of substrates containing *Lingula* is rather low (one to four percent) (EMIG & LEOUEFF, 1978; BARON, CLAVIER, & THOMASSIN, 1993). Nevertheless, other ecological features affect the distribution and may be even more important.

Hard substrates: Discinidae and Craniidae.—Discinids attached to various rocky surfaces and to mollusc fragments occur singly or in clusters of many individuals, for ex-

ample, *Discinisca lamellosa*, *D. laevis*, and *Discradisca strigata*. The last species forms clusters of more than 12 individuals separated by less than 2 mm, while solitary individuals are uncommon (LABARBERA, 1985).

Pelagodiscus atlanticus is found attached to rocks ranging in size from pebbles to boulders (FOSTER, 1974) and is sometimes found on bivalve shells (*Vesicomya*, *Bathyarca*), brachiopod shells (COOPER, 1975), scaphopod shells, whale bones, and manganese nodules (ZEZINA, 1981). *P. atlanticus* occurs in deep-sea areas where fine-grained substrates accumulate slowly; both factors appear to limit the distribution of this species (ZEZINA, 1961).

Neocrania species show a wide depth tolerance and a preference for flat, hard surfaces on which they generally grow in clusters. In shallow water *Neocrania* occurs attached to the undersides or sheltered sides of rocky surfaces, including areas of bare rock, substrates coated with coralline algae, and submarine caves. In deeper water, individuals occur on rocks, ranging from pebble to boulder size, shells, hard skeletons of other invertebrates, various hard fragments, and, more rarely, on other brachiopod shells (ROWELL, 1960; BERNARD, 1972; FOSTER, 1974; BRUNTON & CURRY, 1979; LOGAN, 1979; LEE, 1987). *Neocrania* larvae settle on hard substrates where the sedimentation rate is very low and often colonize substrates that are swept by strong currents reaching 3 to 5 km/h (ROWELL, 1960; FOSTER, 1974; LEE, 1987), but they do not occur in more strongly current-swept environments more frequently than other brachiopods. The external shape and height of the craniid shell vary greatly in response to the contours of the substrate to which they are attached (FOSTER, 1974; LOGAN, 1979; LEE, 1987).

Craniscus has been recorded from Japan on various kinds of substrates from sandy mud to rocky bottoms.

Salinity

At present, all inarticulated brachiopods live in seawater of normal salinity; and, be-

cause all are typically quite intolerant of lower salinity, none is adapted to brackish-water or freshwater conditions. Accordingly lingulides actually live in biotopes in normal-marine salinities but are capable of osmotic response to stresses of strong salinity variations, particularly at low tide in the intertidal zone when freshwater input occurs (HAMMEN & LUM, 1977). The salinity range of the populations of a species depends on the geography of its habitat. Yet populations can survive a greater range of salinity than that occurring in its normal environmental conditions. The presence in a deltaic environment does not, therefore, imply that the lingulides constantly live under reduced or highly fluctuating salinities (EMIG, 1981a, 1986). Mean salinities during annual variations as low as 20‰ are exceptionally reported in lingulide environments. Actually lingulides are not tolerant of extremely low salinity except for brief periods, generally less than 24 hours. The lowest limit is about 16 to 18‰, which is not exceptional in comparison to bivalve molluscs (HAMMEN & LUM, 1977).

Temperature

Previously regarded as the limiting factor of the latitudinal extension of the lingulides, the range of temperature tolerance is highly variable among populations; and a population of a given area is generally unable to survive temperature variations, especially low temperatures, larger than those occurring in natural conditions. The salinity or temperature range under which an indigenous population normally lives can be lethal for another population adapted to a different range of conditions. *Lingula anatina* is a good example as is illustrated by comparing the reaction of three populations that are widely dispersed (Table 37; EMIG, 1986, 1988). Neither of the populations from northern Japan and New Caledonia could survive at salinities higher than 40 to 50‰. In northern Japan (EMIG, 1983a) and China (LEROY, 1936) the temperatures remain below 5°C for three months and below 11°C for more

TABLE 37. Annual variations of temperature, salinity, and the bathymetric range of *Lingula anatina* in three locations (Emig, 1988).

	Temperature (°C)	Salinity (g/l)	Depth (m)
Persian Gulf	15–40	55–60	6–16
New Caledonia*	18–30	15–25	intertidal (to 67)
Northern Japan	1–22	28–30	5–18

*lethal conditions at <15 °C and salinity of >40 g/l.

than six months, while populations from New Caledonia that experience experimental temperatures below 15 to 17°C undergo a lethal, irreversible retraction of the mantle.

The onset of breeding and the length of the spawning season of lingulides depend mainly on water temperature and latitudinal and seasonal effects. They vary from a 1.5-month period in midsummer in temperate waters (northern Japan, Virginia) and a five- to nine-month period between late spring and late autumn in warm temperate waters to year-round breeding in tropical waters (southern Florida, Singapore, Burma, and India) if temperatures do not drop below 26 to 27°C.

There are no data on temperature requirements of the discinids except that *Pelagodiscus* is more abundant in the deep sea at temperatures below 3.5°C.

Neocrania species tolerate a wide annual range of temperature related to their geographic and bathymetric distribution, from -2° to 1.5°C for *N. lecointei* (FOSTER, 1974), 14 to 21°C for *N. huttoni* (LEE, 1987), and about 26 to 28°C for species living in equatorial waters. *N. anomala*, which is distributed between 30° to 60°N in the Atlantic Ocean and Mediterranean Sea, has a wide temperature tolerance. The almost complete absence of calcite in the pedicle valve of several species of *Neocrania* does not represent an adaptation to very cold water (FOSTER, 1974). The temperature range of the biotopes of *Craniscus* is from 2 to 18°C.

Oxygen

Lingulides are able to survive temporarily in poorly oxygenated waters because of the

presence of hemerythrin within the coelomocytes (YATSU, 1902b; HAMMEN, HANLON, & LUM, 1962; WORCESTER, 1969). Hemerythrin, however, seems to be used as a store under anoxic conditions or during cessation of respiration, such as may occur intertidally when the burrow is exposed and is part of the oxygen-transporting function in lingulides. Data on the rates of oxygen consumption are available only for lingulides but are difficult to compare because they are based on either total-animal wet weight (HAMMEN, HANLON, & LUM, 1962) or on dry mass of tissue (SHUMWAY, 1982). *Lingula reevii* and *Glottidia pyramidata* have higher rates of oxygen consumption than the articulated *Terebratulina septentrionalis* by a factor of two to nine, and the activity of metabolically important enzymes, such as succinate dehydrogenase, is up to 20 times higher (HAMMEN & LUM, 1977; HAMMOND, 1983). On the other hand, the oxygen consumption rate of *Lingula anatina* is about 2.5 times lower than in three articulated species (SHUMWAY, 1982).

The redox layer, which often occurs some 2 to 5 cm below the sediment-water interface, does not signify a low oxygen concentration in the surrounding water mass, even in the burrow. Such anaerobic conditions as red tides can be responsible for a mass mortality. Although *Glottidia pyramidata* was one of the five species of 22 species surviving such events that temporarily lowered the mean density of the population from 42 to 13 individuals per square meter, two years later this density had risen to 1,332 individuals per square meter (SIMON & DAUER, 1977). Individuals of *Glottidia* are probably able to resist short-term anoxic events because they bear mantle papillae over the secondary mantle canals in the pallial cavity. The papillae allow an increase of the respiratory and nutritional exchanges. On the other hand, the volume of the lophophoral cavity in *Glottidia* is less than that of *Lingula*. In the same way *Lingula anatina* is more resistant to stress from loss of oxygen than bivalves collected from the same locality (ROBERTSON, 1989).

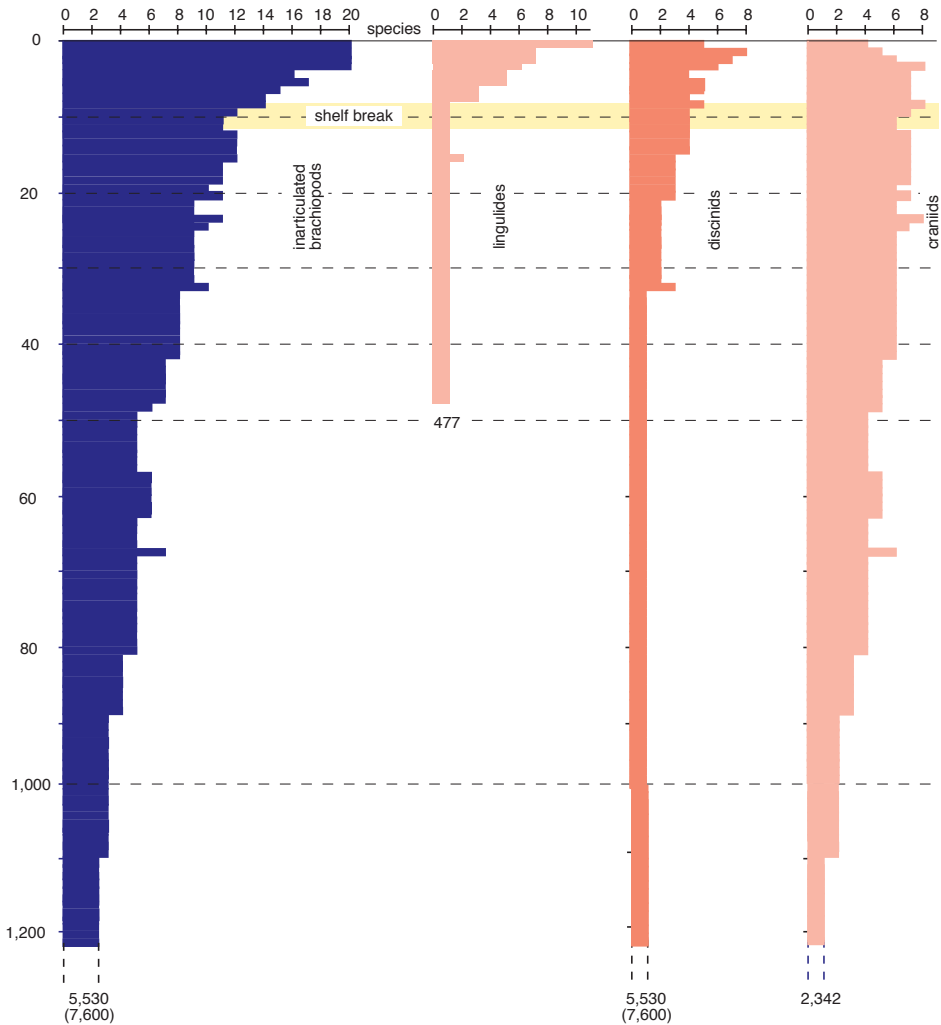


FIG. 413. Bathymetric distribution of the living inarticulated species; numbers at bottom indicate deepest recorded living specimens; those in parentheses indicated deepest recorded empty shells (new).

Depth and density

Many living inarticulated species extend through a remarkable depth range from littoral waters into the bathyal zone (ranging from the shelf break, generally about 100 m, to 3,000 m) down to about 500 m on the slope (Fig. 413). Only *Pelagodiscus atlanticus* occurs at abyssal depths, i.e., in the zone ranging from 3,000 to 6,000 m. Inarticulated brachiopods seem not to have migrated into deeper water in the course of time and cannot be used as indicators of

depth. More than 40 percent of inarticulated brachiopods, mainly lingulide and discinid species, occur between 0 and 60 m depth; and more than 40 percent of the craniids occur between 20 to 420 m.

The optimum environment for living *Lingula* and *Glottidia* species is not intertidal, although 11 of the 12 species of lingulides have been recorded in the intertidal zone (PAINE, 1970; EMIG, 1984a) and in the infralittoral zone from 1 to 2 m to about 20 m. The maximum recorded density of *Lingula reevii* is 500 individuals per square

meter (WORCESTER, 1969); that of *L. anatina* is 864 individuals per square meter (KENCHINGTON & HAMMOND, 1978). *Glottidia pyramidata* reaches concentrations of more than 8,000 individuals per square meter in Florida (CULTER, 1979), and *G. albida* shows a density peak of more than 500 individuals per square meter in depths of 22 to 47 m off the coast of California (JONES & BARNARD, 1963).

Pelagodiscus atlanticus, one of the deepest-water brachiopods, has been recorded throughout the bathyal and abyssal zones with one-third of the occurrences being at depths of more than 4,000 m (ZEZINA, 1961) and only a few of the records of its occurrence being from less than 1,000 m (ZEZINA, 1975). Its density may reach up to 480 individuals per square meter at the foot of seamounts and up to 76 individuals per square meter at 1,500 to 2,000 m in Antarctic waters (ZEZINA, 1961). On the marginal ridge of the Kurile-Kamchatka trench, however, a eutrophic area with a rich food supply and rather active currents, the density of 12 individuals per square meter is comparable to that in the tropical oligotrophic parts of the ocean (ZEZINA, 1981). The other species of discinids are mainly restricted to the continental shelves. Four of the 12 species of discinids have been recorded in the intertidal zone, although all of them are more abundant below the low-tide level or subtidally (Fig. 413).

The craniids extend from shallow waters to the bathyal zone and appear as a deeper-water group among the inarticulated brachiopods. Densities of *N. anomala* up to 500 individuals per square meter have been recorded on small, flat, hard surfaces at various depths between 10 and 200 m. *N. lecointei* has been found alive only on the seaward edge of the continental shelf in the Ross Sea, which belongs presently to the bathyal zone, between approximately 450 and 650 m, where it is the dominant brachiopod with up to 46 individuals per square meter (FOSTER, 1974).

Other Factors

As suspension feeders, brachiopods require good circulation of the water. Seawater constituents also play a role in the ecological requirements. Some are used for formation of the shell and their rate of assimilation may have a direct influence on growth of the shell. Calcium ions, which are taken up from the seawater primarily by the lophophore, move through the coelomic system into the mantle and are eventually deposited in the inner layer of the shell. Yet the major source of inorganic phosphate for shell formation in *Glottidia pyramidata* is likely to be food and not seawater (PAN & WATABE, 1988a).

On the Florida coast, *Glottidia pyramidata*, together with the lancelet *Branchiostoma caribbaeum*, are sensitive to deterioration of water quality and, thus, are used as indicator organisms of unspoiled areas and uncontaminated waters in determining suitability for fishing.

Taphonomy

Recent ecological statements on taphonomic conditions of living lingulides (EMIG, 1986, 1990) have been corroborated by re-interpretations of fossil beds (Fig. 414). The natural death of the lingulides leads to the extrusion of the animal from its burrow (WORCESTER, 1969; EMIG, 1986). The valves become separated, and the organic matrix degrades rapidly due to hydrolysis, microorganisms, and mechanical abrasion. The thin, fragile, chitinophosphatic valves are reduced to unrecognizable fragments, the deterioration occurring from the margins to the central portion of the valve; and in general after two or three weeks the valves have completely disappeared from the sediment (EMIG, 1983a, 1990). This explains why only a catastrophic event, occurring over some days, is the most significant source of mortality with respect to preservation of the shell and ultimate fossilization because there is little potential for fossilization in normal environments (EMIG, 1986). Consequently,

fossil lingulides are not indicators of their biotopes but of drastic environmental changes that led to their burial.

Fossilization can occur either *in situ* in life position, for example, in conditions of rapid temperature decrease, salinity increase, desiccation, emersion of the substratum or drop of sea level, or very fine sedimentation; or it can occur as flat-lying disarticulated valves, for example, after prolonged reduction of salinity, coarse-grained sedimentation, and storms (EMIG, 1986). Data obtained for living species obviously apply to the interpretation of fossils (EMIG, 1986). Nevertheless survivorship under abnormal conditions can vary according to the geographical population and depends also on the synergy of the applicable environmental factors on a given population.

When salinity increases to 40 to 50‰, the death of populations occurs in burrows in a few days. Osmotic pressure empties the animal of its coelomic fluid, and the pedicle becomes detached from the shell. When the salinity decreases below 16 to 18‰, death occurs in one day to several weeks and quickens with lowering salinity, although the salinity of interstitial water remains high for several days. Individuals leave their burrows as their bodies swell under osmotic pressure, and pedicles become limp or detached. The putrefaction of the soft body causes separation of the valves, which are then spread over the sediment surface. Shells rarely float, but it has been reported (EMIG, 1981b). At a salinity of 18‰, the initial body weight increases by 3.3 percent in three hours; at 5‰, it increases by 3.8 percent in one hour. Weight then remains constant for about two hours followed by another weight increase that is lethal (HAMMEN & LUM, 1977). Reduced salinities in rapid transition are tolerated, for example, during tidal cycles in estuarine or deltaic environments where the salinity can drop to less than 10‰. Several observations have reported high mortality after heavy rains of two to three days' duration causing nearby rivers to flood (PAINE,

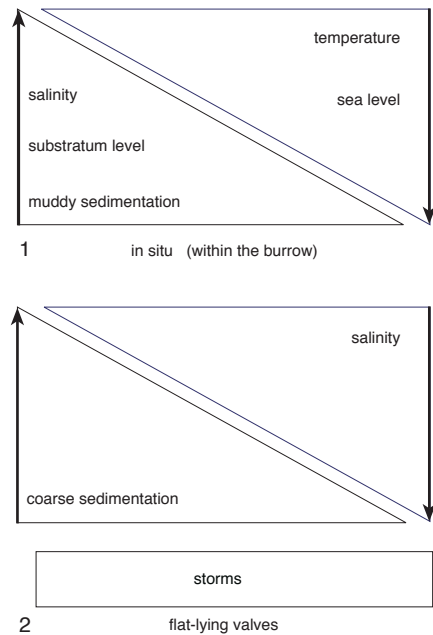


FIG. 414. Diagram summarizing the effects of abiotic factors that may induce lingulide fossilization (new).

1963; SOOTA & REDDY, 1976; EMIG, 1986, and personal observations, 1983). Nevertheless from experimental results the duration of survivorship to low salinity is variable among species. At a salinity of 15‰, *Lingula anatina* in Queensland (Australia) resists longer than *Lingula reevii* in Hawaii, while *Glottidia pyramidata* in Florida has a greater survivorship than populations of *Lingula*.

During an exceptional storm often associated with heavy rains, the sediment is churned up, and the lingulides are washed onto the shoreline and may form shell masses up to 75 cm high (RAMAMOORTHY, VENKATARAMANUJAM, & SRIKRISHNADHAS, 1973; HAMMOND, 1983; EMIG, 1986).

When the sea level drops through tectonism, regression, or high sedimentation, the animal retreats with the water level until it reaches the bottom of its burrow where death occurs in about three days.

Experiments on *Lingula anatina* in New Caledonia with decreasing temperatures

show that below 15 to 17°C (the lowest temperature in natural conditions is 18 to 19°C) individuals go down to and remain at the bottom of their burrows. At 6 to 10°C an irreversible retraction of the mantle occurs over several millimeters from the shell margins leading to death within one to three weeks because the lingulides are unable to form their pseudosiphons, and, consequently, the pallial water streams are highly perturbed (C. EMIG, personal unpublished data, 1983). Mantle regression has been observed in both inarticulated and articulated brachiopods, but a factor specifically responsible for this regression is identified for the first time herein.

When the temperature drops below 10°C in Florida, *Glottidia pyramidata* does not respond to any stimuli, although slow warming after three days at low temperature produced signs of activity at 12°C (PAINE, 1963).

Muddy sediment with more than 35 to 40 percent of very fine fraction (< 50 µm) deposited over original sandy bottoms leads to the death of lingulides within their burrows in several weeks. A lingulide can maintain only sporadically its normal position before collapsing into the sandy layer, and this generally leads to death by debilitation. This observation is of paleoecological importance. When lingulide valves occur at the bottom of a shale overlying a sandstone, the sandstone unit is the normal substrate of the lingulides that are sometimes fossilized within their burrows. The shale cannot be interpreted as the normal substrate for lingulides but as a deposit of muddy sedimentation that was responsible for the death of the lingulide population. Conversely, coarse sedimentation (> 0.5 mm) leads to the emerging of the lingulides at the sediment surface and finally lying on the surface.

The shallow-water species *Discinisca tenuis* occurs intertidally at a few localities. It is known in the Walvis Bay area (Namibia) where large deposits formed by huge numbers of shells are washed up onto the beach. Its occurrence along the Namibian coast is linked to the existence of the Benguela up-

welling system. Such deposits totally dominate the littoral sediment (HILLER, 1993). A correspondence is suggested with the Estonian Lower Ordovician obolid conglomerates, which are likely to have formed under similar conditions of upwelling.

BIOTIC FACTORS

Nutritional sources

Sources of nutrition are known for only a few lingulide species. The type and abundance of ingested particles as well as the importance of direct absorption of nutrients depend on such factors as season, depth, and geographic area. Analyses of gut contents of *Lingula reevii* from Hawaii (EMIG, 1981b) show the presence of two types of food: a vegetal fraction, mainly phytoplanktonic and consisting of diatoms, peridinians, and filamentous algae, and an animal fraction, mainly from the superficial meiobenthos and macrobenthos, i.e., foraminifers, rotifers, polychaetes, oligochaetes, and copepods. Both fractions are mixed with a constant amount of sedimentary particles of 2 to 3 µm and various organic detritus (e.g., spicules and spines). *Glottidia pyramidata* ingests particles smaller than 125 µm in diameter, including sand grains and various vegetal and animal matter, *Coscinidiscus*, gastropod veligers, nauplii, and even *Glottidia* eggs (PAINE, 1963). Food particles from the sediment-water interface may be readily resuspended by tidal or bottom currents or waves, by arm shaking of ophiurians, or by holothurians.

Direct absorption of dissolved nutrients is known to occur in the lophophorates. The lophophore in lingulides (STORCH & WELSCH, 1976) appears to be able to absorb directly dissolved organic matter from seawater. There is also evidence that digestion occurs in the lophophore, attested to by the presence within the tentacles of alkaline phosphatase and three esterases (STORCH & WELSCH, 1976). Like the phoronids, lingulides are able to live in aquaria for some weeks without having the water changed. *Glottidia pyramidata* can be maintained at

least three months under starvation conditions without apparent loss of vitality (PAINE, 1963).

The body weight of *Lingula anatina* varies from 0.13 g for a shell length of 1.35 cm to 5.19 g for a shell length of 4.25 cm. (The mean value is 2.24 g for a length of 3.19 cm; n=346; KAWAGUTI, 1943.) The body weight, like the shell height, increases more rapidly than the shell length. The weight:length ratio of *Glottidia pyramidata* changes at a length of approximately 8 mm corresponding to the development of gonads (PAINE, 1963). In *Lingula* this development occurs at a shell length of 1.5 to 2 cm.

Predation

Lingulides are eaten by such crustaceans as hermit, stone, and portunid crabs, crangonids, stomatopods, shrimps, and amphipods (PAINE, 1963; WORCESTER, 1969; CULTER, 1979; EMIG & VARGAS, 1990). The asteroid *Luidia clathrata* is an important predator of *Glottidia pyramidata*. Forty-three percent of the *Luidia* collected contained *Glottidia* shells with little selectivity for size for shells less than 1 cm long, suggesting that larger individuals may withdraw too deeply into the sediment to be preyed upon. Other echinoderms are also reported as predators, such as the ophiuroid *Amphipholis germinata* and the echinoid *Encope stokessi* (EMIG & VARGAS, 1990). Gastropods (mainly naticids and muricids) are only occasional predators of lingulides, but bored valves can represent up to 14 percent of the valves recovered from the sediment (PAINE, 1963). Dead shells of craniids are sometimes drilled by gastropods (LEE, 1987).

Lingula parva has been recorded during the dry period (March to September 1953) along the Sierra Leone and Nigerian coasts in the stomachs of several demersal fishes (LONGHURST, 1958; ONYIA, 1973). Several tens of *Glottidia pyramidata* shells have been recorded in stomachs of sturgeons and various rays along the Florida coast. The mud flats inhabited by *Glottidia audebarti* are visited seasonally by migratory birds, and at least 13 species were observed foraging at low

tide (VARGAS, 1988); stomach contents of the willet *Catoptrophorus semipalmatus* but more frequently the short-billed dowitcher *Limnodromus griseus* revealed that *G. audebarti* is an important food item. *Catoptrophorus semipalmatus* and the fish *Symphurus plagiusa* are known predators of *Glottidia pyramidata*, which is their main source of food (PAINE, 1963). People also eat *Lingula anatina* and *L. rostrum* on almost all the western Pacific islands from Japan to New Caledonia.

Parasites

Unencysted metacercariae of trematodes of the subfamily Gymnophallinae (usually one to three in an individual) have been seasonally recorded around the nephrostomes and in the gonads of *Glottidia pyramidata*, mainly at the end of summer and in autumn. The infestations can reach 68 percent of the population. These parasites can reduce or destroy the gonads and have a secondary influence on the digestive glands and mantle canals (PAINE, 1962a, 1963). Adult parasites are likely to occur in avian predators of *G. pyramidata*. The occurrence of two species of poecilostomatoid copepods, *Parostrincola lingulae* and *Panjakus platygyrae*, associated with *Lingula anatina* has been reported from Hong Kong (HULMES & BOXSHALL, 1988). Zooxanthellae are abundant within the digestive gland of *Lingula* (KIRTISINGHE, 1949), and monocystid protozoa have been reported in *Neocrania*.

FAUNAL RELATIONSHIPS

Communities

Soft-substrate communities.—By their general characteristics, lingulides are nearly stable in their evolutionary state. They present all the features of a dominant group within a community (EMIG, 1989a): low growth rate, uniformity of shape, larger size than the other members of the community, long life span, low recruitment potential, generally just higher than the population replacement (K-demography), and long geological range. Such characteristics allow high

biomass to develop related to the available energy and result in an excellent ability to integrate and conserve energy. Such a dominant group generally shows plesiomorphic characters compared to other taxa.

Few lingulide communities have been studied. Data on the macrobenthic fauna are given in Tables 38 and 39. *Lingula anatina* has been investigated in the Mutsu Bay (northern Japan) in fine sands and muddy sands from 4 to 18 m depth (TSUCHIYA & EMIG, 1983); on the west coast of Korea in a tidal flat of silty sands from -2.5 to 2.3 m (AN & KOH, 1992) where the number of species collected monthly varies from 28 to 41; in Taiwan in a tidal flat of fine, sandy mud (DÖRJES, 1978); in Phuket Island (Thailand) in front of a mangrove in an intertidal, large, bay-shaped, fine-sand flat dominated by molluscs, mainly the gastropod *Cerithidea cingulata*, where the other most abundant animals are the fiddler crab *Uca lactea* and the sipunculid *Phascolosoma arcuatum* (FRITH, TANTANASIRIWONG, & BHATIA, 1976). In New Caledonia in association with the seaweed *Halodule* on coarse sands the macrofauna is dominated respectively by *Lingula anatina*, molluscs (mainly the bivalve *Gafrarium tumidum* and a gastropod *Cerithium* sp.), and polychaetes (mainly *Caulleriella* sp.) (BARON, CLAVIER, & THOMASSIN, 1993). *Glottidia audebarti* recorded in Costa Rica (VARGAS, 1988; EMIG & VARGAS, 1990) in mud flats exposed only at a tide level below 0.1 m has an associated macrofauna composed mainly of deposit feeders; the meiofauna comprises 88 percent nematodes, 6 percent foraminifers, and 3 percent ostracodes. *Glottidia pyramidata* occurs in Sapelo Island (Georgia, USA) in the *Moira-atrops* community located between 10 and 13 m depth in coarse, relict sand dominated by polychaetes followed in importance by crustaceans, but the fauna shows a generally low density (DÖRJES, 1977). In Winyah Bay (South Carolina, USA) it occurs in medium- to fine-grained sands from 6 to 11 m

(DOLAH & others, 1984). Near Charleston Harbor (Florida, USA) it is present in coarse to fine sands from 8 to 17 m (DOLAH, CALDER, & KNOTT, 1983) with the highest density being at 17 m. In Tampa Bay (Florida, USA) the reestablishment of a benthic community following natural defaunation by red tide has been studied in an intertidal sand flat (SIMON & DAUER, 1977).

The associated fauna of other locations is briefly listed here. On the western Korean coast *Lingula anatina* occurs in sand to sandy mud flats with many other such endobiotic species as polychaetes, crabs, and molluscs, which are dominant quantitatively (FREY & others, 1987). In a New Hebridian mangrove community *L. anatina* occurs seaward of the *Rhizophora* zone dominated by gastropods and crabs (MARSHALL & MEDWAY, 1976). On the western African coast *L. parva* occurs in the *Venus* community, particularly at the *Venus-Amphioplus* transition (LONGHURST, 1958). In the Ebrié Lagoon (Ivory Coast) *L. parva* occurs in a shallow, sandy substrate in the *Corbula trigona* community in which the main species are 12 polychaetes, 9 gastropods, 14 bivalves (dominant), and 10 crustaceans (ZABI, 1984). In Ambon, *L. rostrum* occurs midlittorally seaward of a mangrove stand and on a sandy beach located between the ocypodid zone and the clypeasterid zone (EMIG & CALS, 1979). In a benthic survey on the eastern coast of India (BHAVANARAYANA, 1975) a *Lingula-Solen* zone was reported, almost exclusively populated by both taxa in considerable numbers. Off the Californian coast, *Glottidia albida* occurs at high density in the *Amphioplus* community inhabiting a compact, fine, sandy substrate although it has also been recorded in several other communities, including the *Listrolobus*, *Amphioda*, *Nothria*, and *Tellina* communities (JONES & BARNARD, 1963). In Mission Bay (San Diego, California), *G. albida* occurs with a macrofauna dominated by 65 percent polychaetes, 15 percent

TABLE 38. Richness and percentage of the species of the main taxonomic groups present in various communities in which lingulides occur. The results presented have been calculated from the data given by the cited authors (new).

Location	Polychaetes		Mollusks		Crustaceans		Echinoderms		Others		Lingulide species		Total n
	n	%	n	%	n	%	n	%	n	%	n		
Japan ¹⁰	15-29	39-59	5-12	12-27	3-9	8-21	1-6	3-15	0-4	0-7		<i>L. anatina</i>	30-46
Korea ¹	8-17	39-47	3-14	18-34	4-7	16-29	0-3	0-8	0-1	0-3		<i>L. anatina</i>	17-43
Taiwan ⁵	8	31	7	27	6	23	1	4	3	12		<i>L. anatina</i>	26
Thailand ⁷	9	30	8	27	7	23	-	-	5	20		<i>L. anatina</i>	30
New Caledonia ²	38	45	25	29	12	14	3	4	7	8		<i>L. anatina</i>	85
Western Africa ⁸	38	19	54	28	57	29	27	14	19	10		<i>L. parva</i>	195
Costa Rica ^{6,11}	30-38	38-41	15-18	19	21-25	27	-	-	12-13	13-16		<i>G. audebari</i>	79-93
Georgia ⁴	15-31	38-56	3-18	11-38	5-9	11-19	1-2	4	3-5	6-7		<i>G. pyramidata</i>	27-55
S. Carolina ⁴	-	40-45	-	20-21	-	21-23	2	2	-	12-14		<i>G. pyramidata</i>	37-193
S. Carolina ³	31-88	43-60	9-31	12-29	12-42	22-32	1-7	2-5	-	-		<i>G. pyramidata</i>	54-155
Florida ⁹	32	39	22	27	19	23	-	-	10	12		<i>G. pyramidata</i>	83

¹AN & KOH, 1992; ²BARON, CLAVIER, & THOMASSIN, 1993; ³DOLAH, CALDER, & KNOTT, 1983; ⁴DORRIS, 1977; ⁵DORRIS, 1978; ⁶EMIG & VARGAS, 1990; ⁷FRITH, TANTANASIRWONG, & BHARTIA, 1976; ⁸LONGHURST, 1958; ⁹SIMON & DAUER, 1977; ¹⁰TSUCHIYA & EMIG, 1983; ¹¹VARGAS, 1988.

TABLE 39. Densities per square meter and percentage of the individuals of the main taxonomic groups present in various communities in which lingulides occur. The results presented have been calculated from the data given by the cited authors (new).

Location	Polychaetes		Mollusks		Crustaceans		Echinoderms		Others		Lingulides		Total n
	n	%	n	%	n	%	n	%	n	%	n		
Japan ⁹	195-910	45-77	35-150	3-12	5-230	4-27	5-185	1-26	0-80	0-10		55-150	455-1,195
Korea ¹	8-39	1-49	12-7,000	14-99	2-20	1-6	0-14	0-12	0-9	0-6		1-66	79-7,100
Taiwan ⁵	580	46	340	27	285	23	20	2	15	1		15	1,255
Thailand ⁷	14	9	103	62	27	16	-	-	21	13		1	166
New Caledonia ²	98	22	130	29	29	7	39	9	152	33		151	448
Costa Rica ^{6,10}	-	33-55	-	5-12	-	29-47	-	-	-	4-15		17	3,700-41,000
S. Carolina ⁴	-	15-32	-	24-45	-	5-19	-	1-3	-	22-35		100	438-6,240
S. Carolina ³	308-2,378	27-64	70-424	3-30	98-1,522	5-32	4-48	1-3	158-207	67-53		2-48	1,070-5,132
Florida ^{8,11}	231-868	7-37	4-50	1-4	64-7,877	3-89	-	-	80-261	2-13		50-1,178	646-8,850
Florida ^{8,12}	(336)	(5)	(2,478)	(38)	(2,181)	(34)	-	-	(1,501)	(23)		1,332	(6,496)

¹AN & KOH, 1992; ²BARON, CLAVIER, & THOMASSIN, 1993; ³DOLAH, CALDER, & KNOTT, 1983; ⁴DORRIS, 1977; ⁵DORRIS, 1978; ⁶EMIG & VARGAS, 1990; ⁷FRITH, TANTANASIRWONG, & BHARTIA, 1976; ⁸SIMON & DAUER, 1977; ⁹TSUCHIYA & EMIG, 1983; ¹⁰VARGAS, 1988; ¹¹total data from one area of Florida; ¹²mean data from a different area of Florida.

molluscs, and 11 percent crustaceans, with mean density from 621 to 1,874 individuals per square meter (DEXTER, 1983). On the coasts of Florida, *Glottidia pyramidata* is often associated with the lancelet *Branchiostoma caribbaeum*, polychaetes, cumaceans, and amphipods; and its biomass, which has a mean value of 35 percent, can reach up to 75 percent of the total biomass of the benthic invertebrates. *G. pyramidata* occurs also in the biocoenosis of well-sorted, fine sands with the phoronid *Phoronis psammophila* (PAINE, 1963; EMIG, 1983b).

The associated fauna within a given community seems to play a minor role in lingulide distribution (EMIG, 1984a). Nevertheless, when the density of *Lingula* increases there is a small decrease in the total number of species with an increase of the total number of individuals; when the density of *Glottidia* increases the total number of species and individuals tends to increase. Comparisons of the distribution of the major groups (Table 38–39) with the increase of density of lingulides show in western Korea that polychaetes (number of species and individuals) and crustaceans (number of species) tend to decrease, while echinoderms, mainly suspension feeders, tend to increase or to appear; in the Mutsu Bay, polychaetes, the dominant group, molluscs, and crustaceans tend to decrease; with the muddy fraction increasing with the depth there is a general decrease in the fauna. Near Charleston Harbor the number of individuals of molluscs and the number of individuals and species of polychaetes tend to increase, while on the southwestern coast of Florida opposite variations of the densities have been observed over a year between polychaetes, crustaceans, and *Glottidia*.

Polychaetes are generally the dominant group in numbers of individuals and species followed by molluscs or crustaceans (see Table 38–39). The presence of molluscs is not fundamentally related to the distribution of lingulides (BABIN & others, 1992). Another important feature is the large number of species and individuals of the associated fauna (Table 38–39), which should be taken

into account when analyzing taphonomic factors to explain the poor, associated fauna found in paleocommunities or when speculating about diversity of the fossils. In fossil assemblages lingulides are often the only fossils found, indicating either that other kinds of organisms were not preserved or that the biocoenosis was oligotypical (EMIG, 1989a). The occurrence of such a monospecific assemblage of fossils requires an extensive analysis of the environmental constraints and of the characters of the occurring species to identify any patterns of the original community. The oligotypical biocoenosis presents one or several of the following characteristics: low-energy input resulting from the effects of climatic factors, extreme harshness due to edaphic factors reducing the physiology of the individuals, or high daily or seasonal variations of the edaphic and climatic factors. Thus the biocoenosis is characterized by high dominance in faunal and environmental features and develops conservatism with highly reduced capacity for organisms to evolve.

Hard-substrate communities.—In the deep parts of the slope in the Antarctic regions (FOSTER, 1974), *Pelagodiscus atlanticus* is associated with a very meager fauna. In the lagoonal complex of Cananéia, Brazil (TOMMASI, 1970b), *Discinisca* sp. has been recorded at 6 and 8 m depth on a rocky-sand bottom with the following macrofauna: polychaetes respectively 600 and 60 individuals per square meter (10 and 18 percent of the fauna), molluscs 1,170 and 30 (19 and 9 percent), decapods 380 and 150 (6 and 46 percent), amphipods 2,900 and 0 (47 percent), others 1,080 and 70 (18 and 21 percent), and *Discinisca* 10 and 20 (0.2 and 6 percent). In the Bahía Concepción, Chile, *Discinisca lamellosa* occurs in the intertidal zone with a meager fauna of one cnidarian, one nemertine, two molluscs, two polychaetes, and one to three crustaceans (URIBE & LARRAIN, 1992). In Baja, California, *Discinisca strigata* lives under cobbles and small boulders, patchily distributed on an extensive sandy beach and extending down to the low-water mark (PAINE, 1962b) where it is

associated with sponges, gastropods, and bivalves. The fractional area covered by epifauna averaged 49 percent, and free space ranged from 32 to 74 percent on a rock area from 21 to 116 cm²: *D. strigata* covered 2 to 26 percent of the surface, bryozoans 5 to 38 percent, serpulids 2.5 to 29 percent, spirorbids 0.01 to 7.3 percent, and sponges 0.5 to 8.2 percent.

Neocrania anomala is recorded in shallow waters under rocky surfaces together with a sciaphilic fauna. It also occurs deeper in the sublittoral zone with a fauna dominated by sponges, cnidarians, spirorbid worms, and bryozoans, and on the continental slope below 100 m on smooth, fine-grained, hard substrate to large rocks, particularly within the community dominated by the brachiopod *Gryphus vitreus*. *N. anomala* is also recorded in Scottish lochs with hydroids, sponges, chitons, foraminifers, and molluscs (CURRY, 1982) and in the Strait of Messina between 80 and 200 m under conditions where there are bottom currents where the macrofauna is dominated by anthozoans (eight species), bryozoans (31 species), annelids (14 species), molluscs (20 species), crustaceans (5 species), and echinoderms (2 species) (DI GERONIMO & FREDJ, 1987). *Neocrania huttoni* forms part of a distinctive rocky substrate community with calcareous algae, sponges, serpulids, ascidians, bivalves, barnacles, and bryozoans including a variety of filter feeders (LEE, 1987). *N. lecointei* is associated with a varied fauna that includes corals, polychaetes, ophiuroids, bryozoans, and ascidians (FOSTER, 1974). *N. pourtalesi* occurs not uncommonly throughout some communities of cryptic habitats of coral reefs, where brachiopods and sponges are the dominant taxa (JACKSON, GOREAU, & HARTMAN, 1971). *Craniscus* occurs in Japan with an associated fauna that comprises mainly molluscs and two articulated brachiopod species, *Dallina* and *Terebratulina* (HATAI, 1940).

Population structure

Because the distribution of lingulides is controlled by environmental factors, annual

fluctuations in density are highly variable even within a restricted geographic area. Episodic failure of recruitment observed in lingulide populations can be related to such causes as protracted breeding season, bad environmental conditions for settlement, food supply, and interactions with the surrounding fauna including predation.

Some authors (PAINE, 1970; KENCHINGTON & HAMMOND, 1978) have raised the question of unidentified factors affecting the absence of lingulides in apparently suitable sediments. Actually the distribution of lingulides is restricted within the limits of the biocoenosis in which a lingulide species is living, even if preferred substrates occur beyond the limits of the community (EMIG, 1984a, and personal unpublished data, 1983).

Shell epibionts

Epibionts preferentially settle on the hard substrate provided by the brachiopod shell. According to the infaunal habit of lingulides, almost all epibionts are restricted to the anterior margins of the valves because only these margins are accessible and are not disturbed during withdrawal into the burrow. Cyanobacteria, however, frequently extend to the umbonal region along the margins.

In one locality the following macroorganisms were recorded from 5,000 *Lingula* shells (WORCESTER, 1969): 10 occurrences of algae, 14 anemone *Aptasia*, many bryozoans, 2 polychaetes, 6 barnacles, 1 amphipod and, on 16 percent of the shells, the limpet *Cruciblum spinosum*. From a large list of epibionts (represented by two algal divisions and six animal phyla) on the shells of *Lingula anatina* and *L. reevii* (HAMMOND, 1984), the most commonly recorded taxa are cyanobacteria (frequency up to 30 percent), polychaetes (frequency up to 45 percent), barnacles (frequency up to 20 percent), limpets (frequency up to 16 percent), bryozoans (frequency up to 11 percent), and traces of the attachment of the egg cases of gastropods or the byssal threads of mussels (frequency up to 29 percent). In only ten percent of the infested *Lingula* were both valves affected.

Algae, specifically *Enteromorpha* sp., established itself only on those valves that had regeneration scars (PAINE, 1963). The hydroid Campanulatiidae *Clytia* can occur on up to 20 percent of lingulide individuals with a shell length exceeding 1.4 mm.

An unidentified leptocean bivalve (perhaps *Euciroa*) is found byssally attached to the shell of *Lingula anatina* (SAVAZZI, 1991) in densities of up to nine individuals per shell. The posterior region of the bivalve shell is oriented upward, located at the anterior margin near the exhalant currents of the brachiopod. The bivalve progressively migrates upward as is shown by a trail of byssal filaments left along their paths to compensate for growth of the *Lingula* shell. The bivalve feeds on feces of *L. anatina*. Lingulides were found to carry gastropods near the anterior margin. Egg capsules of gastropods occurred seasonally on the anterior margins of the valves of lingulides; up to 45 *Nassarius* and up to 5 *Olivella* egg capsules were found on a single individual of *Glottidia pyramidata*.

Epibionts like the worm *Polydora* or the mollusc *Brachiodontes* may benefit from lingulide inhalant currents, but their presence can have detrimental effects by causing distortion of the shell of the host (PAINE, 1963; HAMMOND, 1984). The number of worms on a valve varies from one to six, with a typical number of three or four while the number of small *Brachiodontes* may be as many as five.

Among the craniids, *Neocrania* shells frequently bear encrusting organisms including bryozoans, serpulids, barnacles, calcareous algae, and sponges. Most valves carry more than one epibiont, and the percentage of the cover can reach 95 percent.

In some specimens of *Discradisca laevis*, great numbers of full-grown Pedicellinae adhered to the long, barbed setae (DAVIDSON, 1880). One-third of the *Discradisca* shells (17 percent of the total valve area) bore epizoans, primarily bryozoans and spirorbids, and occasional other *Discradisca*, serpulids, and small sponges.

Competitive interactions

Mechanisms of competitive interaction are likely to be characteristic of the discinids and may have been important in ensuring the success of the living genera since their earliest known occurrence in the Triassic (ROWELL, 1961). The only work that has addressed the competitive abilities of inarticulated brachiopods deals with *Discradisca strigata*, which invariably wins competitive interactions for space with other sessile epifauna (LABARBERA, 1985). One such competitive interaction is metamorphosis on the surface of bryozoan colonies facilitated by a reversal of the flow patterns and the possession of a functional anterior siphon that allows juveniles to draw water from above the bryozoan's lophophores, so that mature individuals eventually usurp the space occupied by the colony. Another interaction is maintenance of a pool of particle-depleted water around most of the shell of larger juveniles and adults, which probably inhibits encroachment by bryozoans and sponges. In addition, abrasion of underlying calcareous epifauna by the harder phosphatic shell occurs, which erodes these faunal elements to the level of the substrate. Numerous eroded epizoans occur under the ventral valves of *Discradisca* although no abrasion of the valves themselves was seen. The edge of these valves probably abrades neighboring organisms during rotation of the shell even of juveniles, and it is probably made more effective by the simultaneous sweep of lateral setae that mechanically damage the tissues of surrounding sponges and bryozoans.

Three of these mechanisms are not available to articulated brachiopods, and the fourth is apparently not exploited, which may explain differences in competitive abilities between inarticulated and articulated brachiopods. Numerous examples of apparent spatial competition between *D. strigata* and other epifauna, particularly sponges and bryozoans, have been recorded (LABARBERA, 1985); but this species was spatially dominant on only 3 of the 11 rocks investigated,

even though it dominates in competitive interactions; and no individual appeared to be in any danger of overgrowth. In discinids the foramen, which is more centrally located than in articulated brachiopods, affords greater protection for the pedicle and ensures

that the entire shell margin, including regions adjacent to the pedicle, sweeps through a sizeable arc when the animal rotates. This inhibits growth of epifauna at a greater distance from the shell than is possible for articulated species.

BIOGEOGRAPHY OF INARTICULATED BRACHIOPODS

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INTRODUCTION

The distribution of the inarticulated brachiopods is largely controlled by environmental factors (see chapter on ecology of inarticulated brachiopods, p. 473–495). Most of the inarticulated genera have broad geographic distributions on which the dispersal potential of the larvae has had only a small influence; lingulides and discinids have planktotrophic larvae, while craniids have short-lived, lecithotrophic larvae. The differences between species in their ecological requirements are more related to their ability to settle, which is induced by biotic or abiotic factors of the biocoenosis to which the species belongs. All adult inarticulated brachiopods are exclusively sedentary.

PATTERNS IN DISTRIBUTION

Because the biogeographic analyses of the inarticulated taxa, especially discinids and craniids, cannot presently be based on infra-generic and subtle ecological distinctions or broad geographic records, this account will be limited to the distribution of the genera. Many published records are deficient in precise information on the biogeography and ecology of species. Sampling inarticulated brachiopods at depths beyond the range of scuba may also present a misleading picture of brachiopod distribution and abundance. The use of submersibles provides reliable information only on large species that can be observed directly or by video. Another factor that introduces bias is the propensity of craniids and discinids to settle on more or less extensive, hard substrates that are difficult to investigate with traditional oceanographic sampling gear. Furthermore, the attention paid to brachiopods in benthic studies and during oceanographic cruises is frequently perfunctory so that large gaps

persist in our knowledge of the distribution and ecology of inarticulated species.

Populations of inarticulated species undergo seasonal to continuous recruitment depending on their latitudinal distribution. The early, shelled larvae of the lingulides are common members of the tropical plankton. A *Lingula* female can spawn 28,000 oocytes over a six-month period, and a *Glottidia* female may produce 130,000 ova over a four-month period. The duration of the planktonic stage of lingulide larvae varies from 3 to 6 weeks (CHUANG, 1959a; PAINE, 1963).

Discinid larvae, at least *Discinisca* itself, are also planktotrophic and acquire valves only in late stages (CHUANG, 1977). Discinid larvae have been reported from marine plankton from the water surface to depths of 3,000 m, sometimes at great distances from the shore (HELMCKE, 1940; ODHNER, 1960; CHUANG, 1977). Larvae of *Discinisca* have been recorded from littoral waters down to 350 m, while discinid larvae recorded from deep waters belong probably to *Pelagodiscus atlanticus*. For example, *Pelagodiscus* larvae have been collected with a calculated density of 2 to 3.5 larvae per 1,000 m³ (MILEIKOVSKY, 1970) between depths of 500 and 2,000 m in the northwestern Pacific Ocean. Postlarval specimens dredged from great depths (2,700 to 3,200 m) indicate that *Pelagodiscus* larvae become sedentary at different valve sizes.

The lecithotrophic larva of *Neocrania anomala*, the only craniid species in which development has been studied (NIELSEN, 1991), has a short swimming stage of about four to six days before settlement. Hydrodynamic conditions that occur in the biotope of *N. anomala* (EMIG, 1989b) can disperse larvae over several hundred kilometers during this short stage. Hence, the gregarious pattern of *Neocrania* species must be related to an environmental factor that attracts and

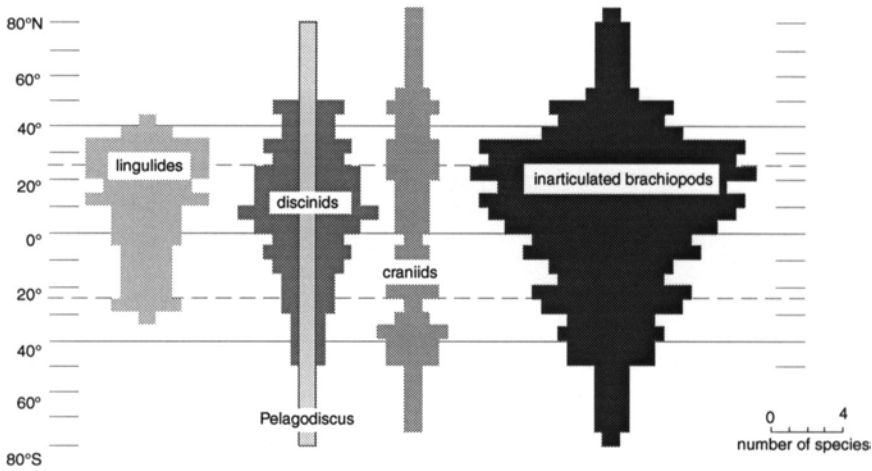


FIG. 415. Latitudinal distribution of inarticulated brachiopods (new).

induces larval settlement close to the adult forms, not to the short swimming stage of the larvae.

The upper and lower limits of tolerance to such factors as temperature, salinity, and depth have been used generally to explain the range of geographic distribution of the species. As stated in the section on the ecology of inarticulated brachiopods (Table 37, p. 484), however, such tolerances can vary subtly even among populations and have to be analyzed carefully before being used to explain the biogeographic distribution of higher taxa.

DISTRIBUTION OF FAMILIES AND GENERA

The three extant inarticulated families have a worldwide distribution. The Lingulidae are dominant in tropical and subtropical areas; the Discinidae occur mainly in intertropical areas; the Craniidae are widely distributed from northern to southern high latitudes, into which the discinid *Pelagodiscus* also extends (Fig. 415). The latitudinal dis-

tribution of inarticulated taxa can be globally related to their bathymetric extension (see Fig. 413) although more constraints are involved than the temperature, pressure, and dynamics of seawater.

Most inarticulated genera are cosmopolitan (Fig. 416) and were common in past eras. Indeed among living brachiopod families only the Lingulidae, Discinidae, and Craniidae can be traced back to the early Paleozoic. The radiations of the inarticulated species and genera represented in recent marine faunas (Table 40) are related to geological events. Most genera began their development in the Cenozoic with the global biotope changes marking the end of the Cretaceous crisis, at the end of the Paleogene threshold, and during the Neogene as a result of changes in the circulation of the ocean waters that allowed the development of deep-sea species.

LINGULIDAE

Living Lingulidae belong to two genera: *Lingula* (seven species), which is worldwide in distribution, except along the coasts of

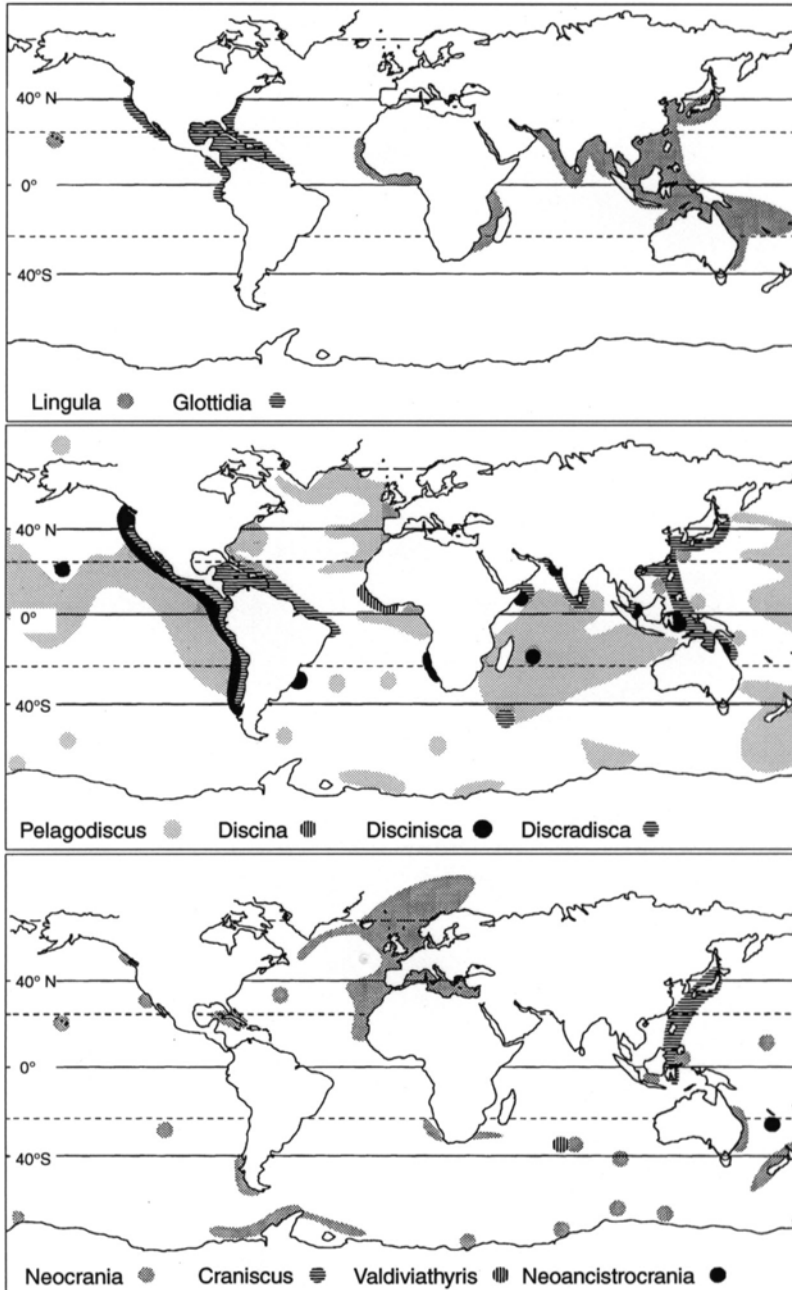


FIG. 416. Geographic distribution of inarticulated brachiopod genera (new).

TABLE 40. First geological record of the inarticulated genera represented in present marine faunas (new).

	Lingulidae	Discinidae	Craniidae
Triassic		<i>Discinisca</i>	
Upper Jurassic			<i>Craniscus</i>
Paleocene	<i>Lingula?</i> <i>Glottidia?</i>	<i>Discradisca</i>	
Eocene			<i>Neocrania</i>
Miocene		<i>Pelagodiscus</i>	
Holocene		<i>Discina</i>	<i>Valdiviathyris?</i> <i>Neoancistrocrania</i>

America, where *Glottidia* (five species) occurs exclusively (Fig. 416). Large variations in edaphic factors during the late Mesozoic (EMIG, 1984b; BIERNAT & EMIG, 1993) are probably responsible for the radiation of both genera. *Glottidia* may have originated on the western coast of North and Central America and *Lingula* possibly in the islands of the western Pacific. Their latitudinal distribution occurs within the 40° belt from temperate to equatorial areas (Fig. 417), and their bathymetric distribution is restricted to the continental shelf except for *Glottidia albidia*, which extends onto the upper part of the bathyal slope. Such a geographic distribution appears to be a consequence of the opening of the Atlantic Ocean and of the Paleocene-Eocene extension of the tropical-subtropical belt to about 45° latitude, with optimal conditions for the development of new temperate marine biotopes with good prospects for speciation. Yet the distribution of the lingulides appears rather similar at least since the early Paleozoic when taking into account the paleolatitudinal positions in correlation with temperatures of water masses.

DISCINIDAE

Pelagodiscus atlanticus occurs worldwide in deep water in the bathyal and abyssal zones and is undoubtedly the most widespread brachiopod species geographically and bathymetrically (Fig. 416–417). *Discinisca* (four species) and *Discradisca* (six species) have a warm-temperate to tropical, cosmo-

politan distribution and extend mainly over the continental shelf. *Discina striata* has a restricted distribution in the intertropical zone of the western coast of Africa.

CRANIIDAE

Neocrania (13 species) has a worldwide distribution (Fig. 416). Its latitudinal range is as wide as that of *Pelagodiscus*, but its bathymetric distribution is from shallow waters of the continental shelf to about 1,000 m depth on the bathyal slope (Fig. 417). Only one species, *Neocrania lecointei*, is recorded in the deeper parts of the bathyal zone (to 2,342 m). The two other genera have restricted distributions. *Craniscus japonicus* occurs in the western Pacific from 23 to 885 m, while *Valdiviathyris quenstedti* is known from a single location at 672 m. *Neoancistrocrania norfolki* has been collected in two locations of the South Pacific Ocean at 233 and 250 m depth.

All three inarticulated brachiopod families are of ancient stocks and are fairly cosmopolitan in distribution, extending from the shoreline to the bathyal depths. Most species have a distribution restricted to the 45° latitudinal belt and occur on the continental shelf from intertidal to a depth of about 100 m. Species extending to latitudes higher than 45° occur also in the bathyal zone (between about 100 and 3,000 m). Their bathymetric extent, however, is limited mainly to the upper bathyal part (to 1,000 m). Only *Pelagodiscus atlanticus*, one of the most recent species, is widespread in the abyssal zone (3,000 to 6,000 m). Species of the two monospecific genera *Discina striata* and *Valdiviathyris quenstedti* and also *Neoancistrocrania norfolki*, which is said to be recent as well, have a restricted geographic and bathymetric distribution (Fig. 416–417).

In contrast to the lingulides, speculating on the origins and paths of dispersal of the discinids and craniids is difficult. The present distribution of inarticulated taxa cannot be explained as the consequence of their age or their dispersal rate as suggested for the taxa of articulated brachiopods. The

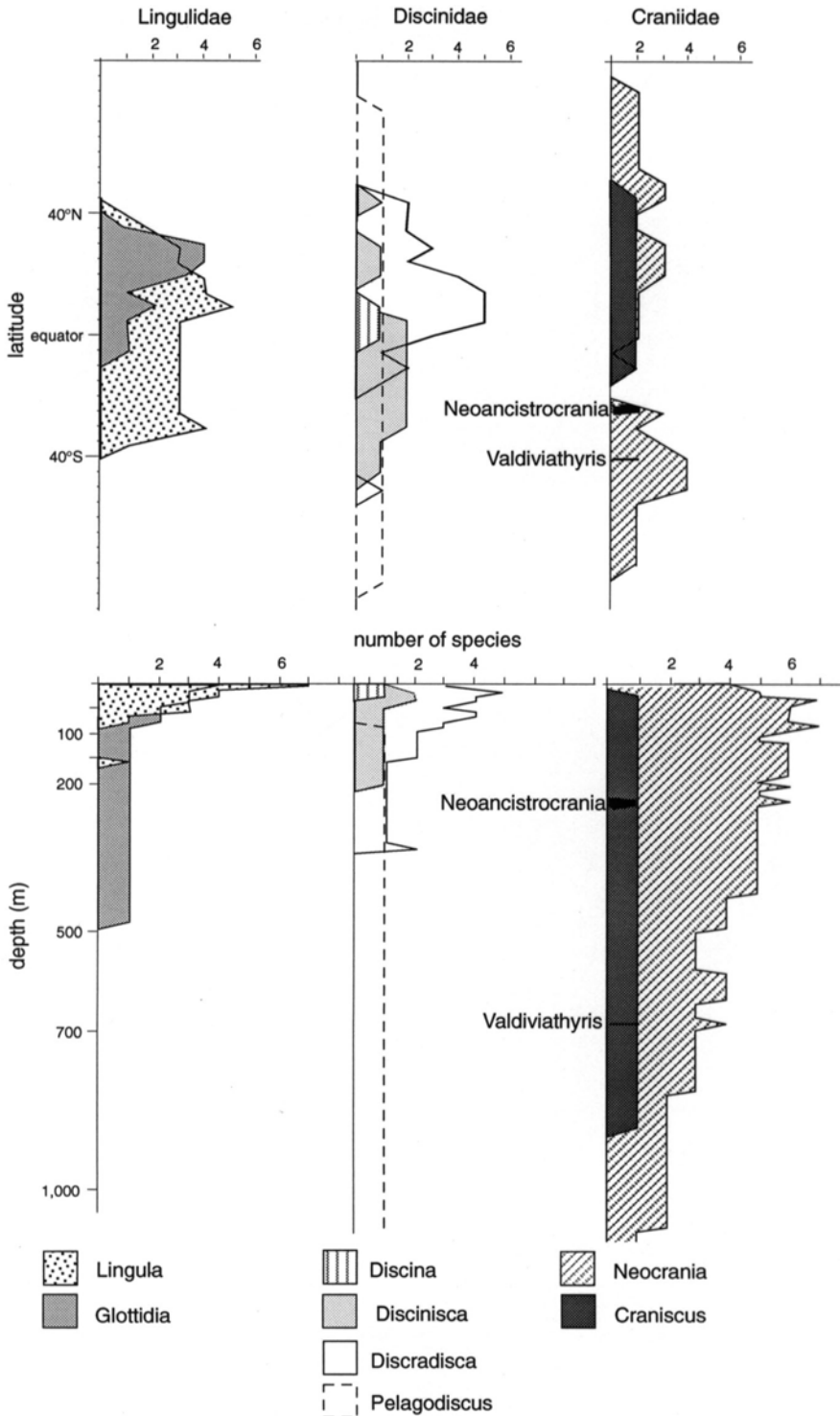


FIG. 417. Latitudinal and bathymetric extension of inarticulated brachiopod genera (new).

diversification of the genera and the long geological history of species are relevant to our understanding of the extent of the geographic and bathymetric distribution of inarticulated brachiopods. As ZEZINA (1970) previously stated the reasons for the biogeography of supraspecific brachiopod taxa are elusive.