176. Emig C. C., 1997. Ecology of the inarticulated brachiopods. *In*: R. L. Kaesler, ed. Treatise on Invertebrate Paleontology. Part H. Brachiopoda revised. Geological Society of America and University of Kansas. Boulder, Colorado, and Lawrence, Kansas, vol. 1, pp.473-495.

177. Emig C. C., 1997. Biogeography of the inarticulated brachiopods. *In*: R. L. Kaesler, ed. Treatise on Invertebrate Paleontology. Part H. Brachiopoda revised. Geological Society of America and University of Kansas. Boulder, Colorado, and Lawrence, Kansas, vol. 1, pp. 497-502.

References pp. 503-526.

TREATISE ON INVERTEBRATE PALEONTOLOGY

Part H

BRACHIOPODA

Revised

Volume 1: Introduction

ALWYN WILLIAMS, C. H. C. BRUNTON, and S. J. CARLSON with
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ECOLOGY OF INARTICULATED BRACHIOPODS

CHRISTIAN C. EMIG
[Centre d'Océanologie de Marseille]

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).

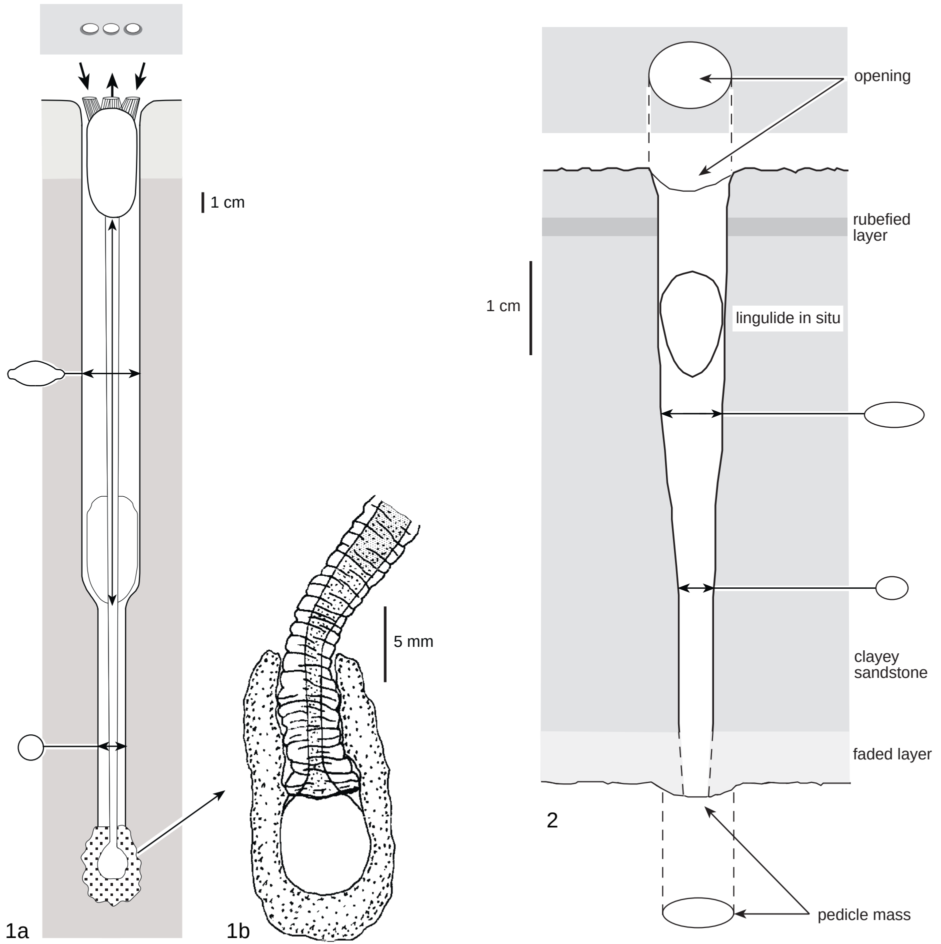

FIG. 407.*1a,* Longitudinal section of a burrow of a living lingulide with the shell in normal position and retracted (and *1b,* detailed pedicle mass); and *2,* of a fossil lingulide (Triassic of Vosges Mountains; Emig & others, 1978).

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 under 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

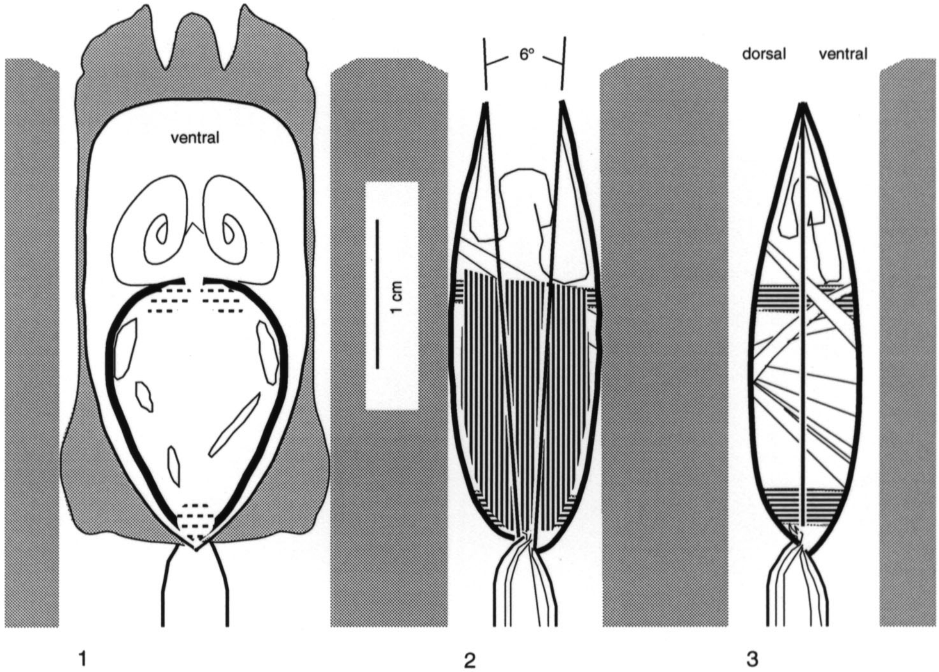

FIG. 408. Longitudinal section of a lingulide in its burrow; *1,* ventral side showing the mantle setae length; *2,* normal position (lateral view) by contraction of the lateral muscles; *3,* quick valve closure by contraction of the anterior and posterior adductor muscles, first step of the escape reflex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

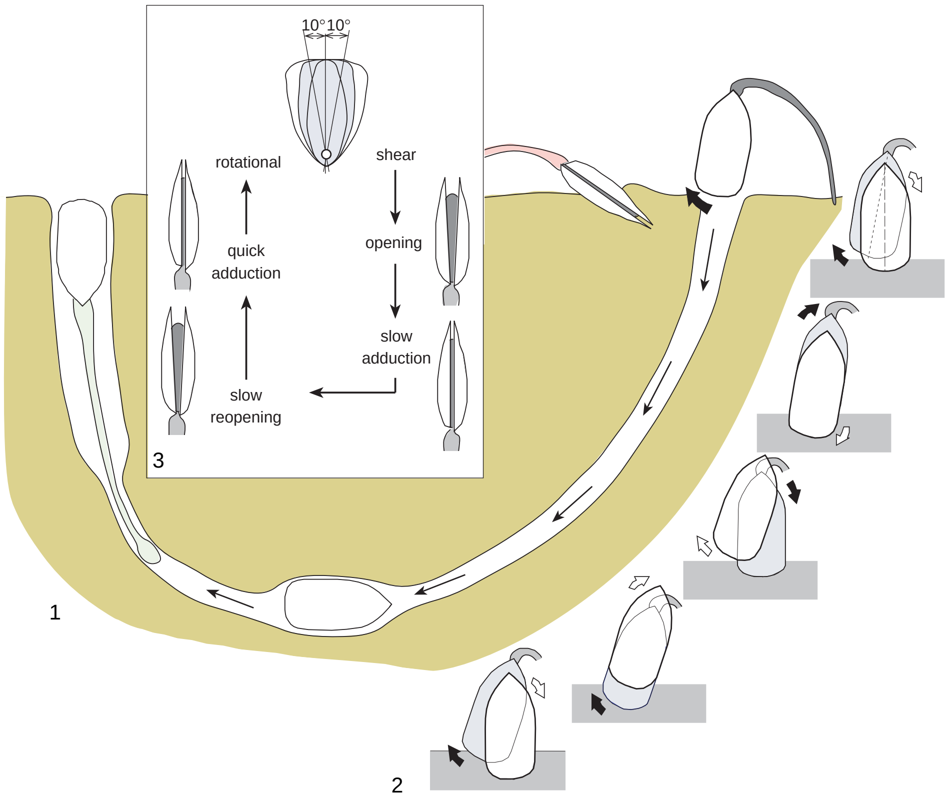

FIG. 409. *1,* U-shaped reburrowing by *Glottidia* (Emig & others, 1978); *2,* sequence of the scissors burrowing movements of *G. pyramidata* (Thayer & Steele-Petrovic, 1975); *3,* patterns in the burrowing sequence of *Lingula anatina* (Savazzi, 1991).

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

Shell Movements and Burrowing

Shell movements and burrowing behavior are similar in both extant lingulide genera, *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 linguloides 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 metacoelomic 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 of *Pelagodiscus atlanticus*	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

[1]in 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 mucoid adhesion 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.

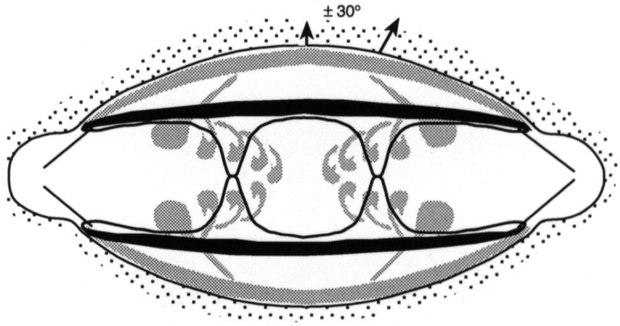

FIG. 410. Composite of two transverse sections of a lingulide in its burrow, one section at the level of the anterior mantle margin showing the epidermal crests and inhalant and exhalant opening (shown in *heavy lines*), the other at the level of the lophophore (*shaded in gray*) (adapted from Emig,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

	L. anatina (b)		*L. reevei* (a, e)	*G. pyramidata* (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
in situ	*0.08–0.21*		*0.21–0.75*	*< 0.67–2.7*
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.

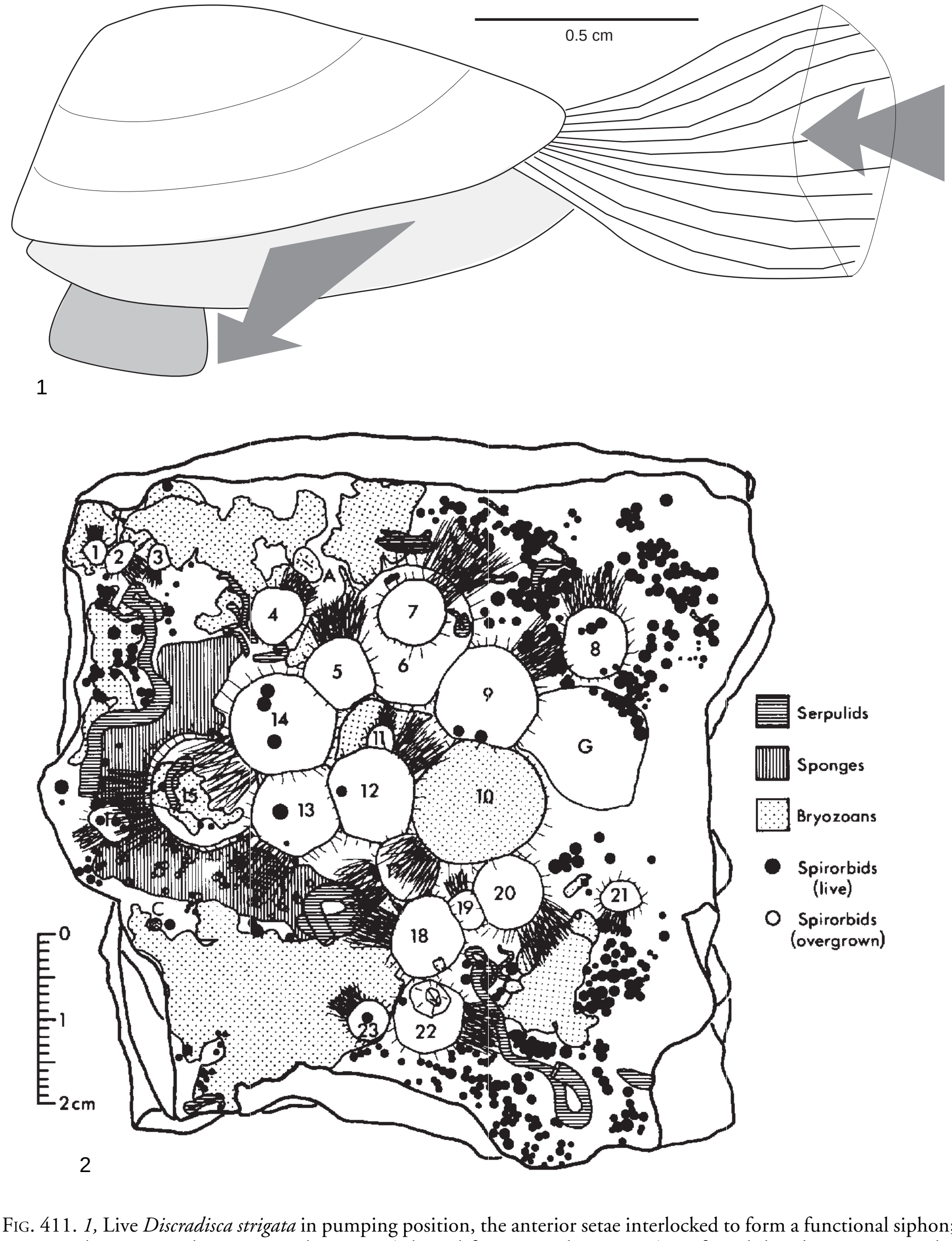

FIG. 411. *1,* Live *Discradisca strigata* in pumping position, the anterior setae interlocked to form a functional siphon; *arrows* indicate in- and outcurrent directions (adapted from LaBarbera, 1985); *2,* faunal distribution on a rocky substrate. All *D. strigata* are numbered; number 6 bears a *D. 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 anteriorly and exits through two, posterolateral, exhalant gapes (Table 35; PAINE, 1962b; LABARBERA, 1985; EMIG, 1992). Another disposition for craniids is that two inhalant currents 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

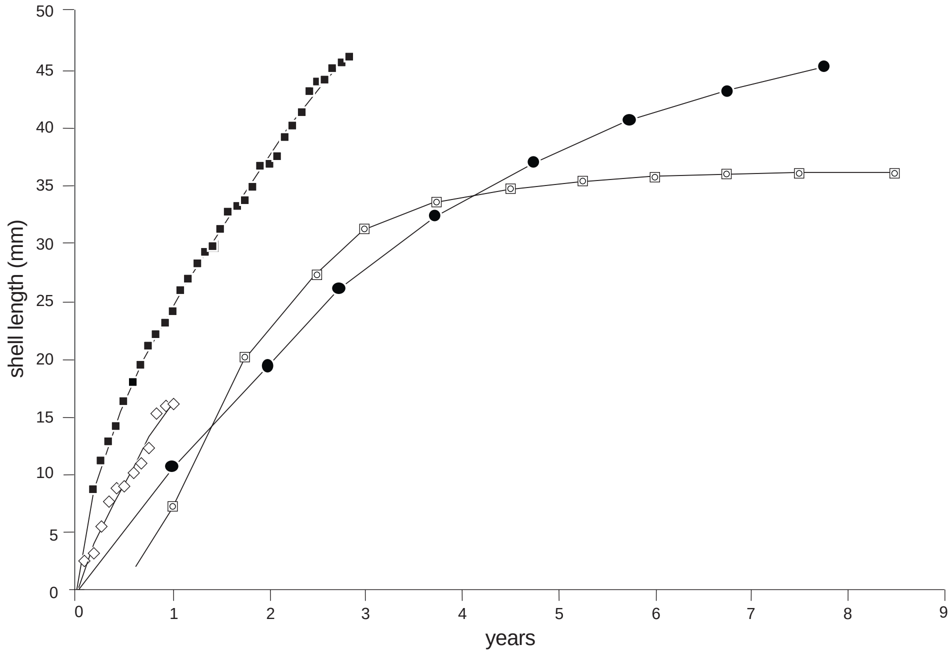

FIG. 412. Growth curves of various lingulide species; ■, *Lingula anatina* (data from Mahajan & Joshi, 1983); ●, *Lingula anatina* (data from Kenchington & Hammond, 1978; ⧈, *Lingula reevii* (data from Worcester, 1969); ◇, *Glottidia pyramidata* (data from Culter, 1979) (new).

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 (JOUBIN, 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 & LELOEUFF, 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 example, *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, because 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).

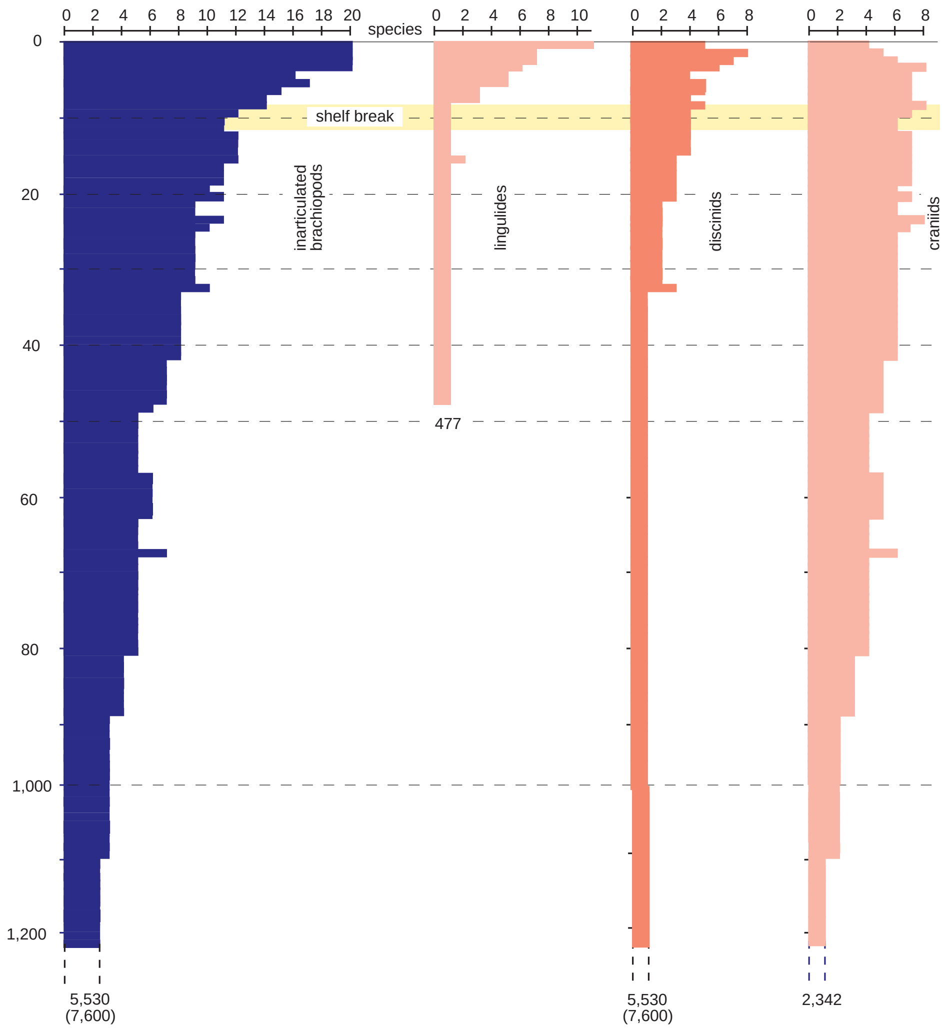

FIG. 413. Bathymetric distribution of the living inarticulated species; numbers at bottom indicate deepest recorded living specimens; those in parentheses indicated deepest recorded empty shells (new).

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 reinterpretations 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, 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.*

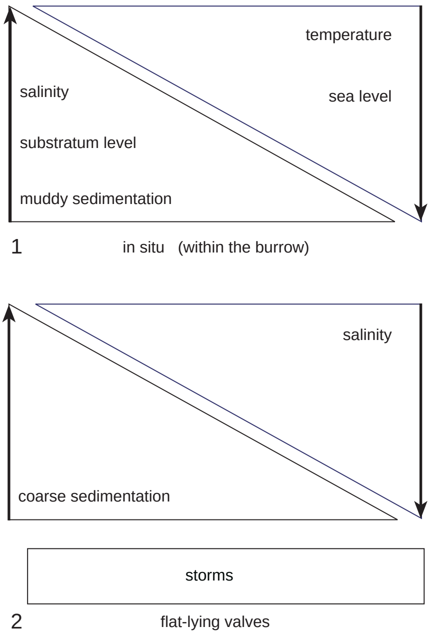

FIG. 414. Diagram summarizing the effects of abiotic factors that may induce lingulide fossilization (new).

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 (RAMAMOORTHI, 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 upwelling 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 endobiont 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
Japan[10]	15–29	39–59	5–12	12–27	3–9	8–21	1–6	3–15	0–4	0–7	*L. anatina*	30–46
Korea[1]	8–17	39–47	3–14	18–34	4–7	16–29	0–3	0–8	0–1	0–3	*L. anatina*	17–43
Taiwan[5]	8	31	7	27	6	23	1	4	3	12	*L. anatina*	26
Thailand[7]	9	30	8	27	7	23	-	-	5	20	*L. anatina*	30
New Caledonia[2]	38	45	25	29	12	14	3	4	7	8	*L. anatina*	85
Western Africa[8]	38	19	54	28	57	29	27	14	19	10	*L. parva*	195
Costa Rica[6,11]	30–38	38–41	15–18	19	21–25	27	-	-	12–13	13–16	*G. audebarti*	79–93
Georgia[4]	15–31	38–56	3–18	11–38	5–9	11–19	1–2	4	3–5	6–7	*G. pyramidata*	27–55
S. Carolina[4]	-	40–45	-	20–21	-	21–23	-	2	-	12–14	*G. pyramidata*	37–193
S. Carolina[3]	31–88	43–60	9–31	12–29	12–42	22–32	1–7	2–5	-	-	*G. pyramidata*	54–155
Florida[9]	32	39	22	27	19	23	-	-	10	12	*G. pyramidata*	83

[1]An & Koh, 1992; [2]Baron, Clavier, & Thomassin, 1993; [3]Dolah, Calder, & Knott, 1983; [4]Dörjes, 1977; [5]Dörjes, 1978; [6]Emig & Vargas, 1990; [7]Frith, Tantanasiriwong, & Bhatia, 1976; [8]Longhurst, 1958; [9]Simon & Dauer, 1977; [10]Tsuchiya & Emig, 1983; [11]Vargas, 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)

[1]An & Koh, 1992; [2]Baron, Clavier, & Thomassin, 1993; [3]Dolah, Calder, & Knott, 1983; [4]Dörjes, 1977; [5]Dörjes, 1978; [6]Emig & Vargas, 1990; [7]Frith, Tantanasiriwong, & Bhatia, 1976; [8]Simon & Dauer, 1977; [9]Tsuchiya & Emig, 1983; [10]Vargas, 1988; [11]total data from one area of Florida; [12]mean 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 Bahia Conceptión, 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, *Discradisca 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 cm^2: *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

CHRISTIAN C. EMIG
[Centre d'Océanologie de Marseille]

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 infrageneric 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 m^3 (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

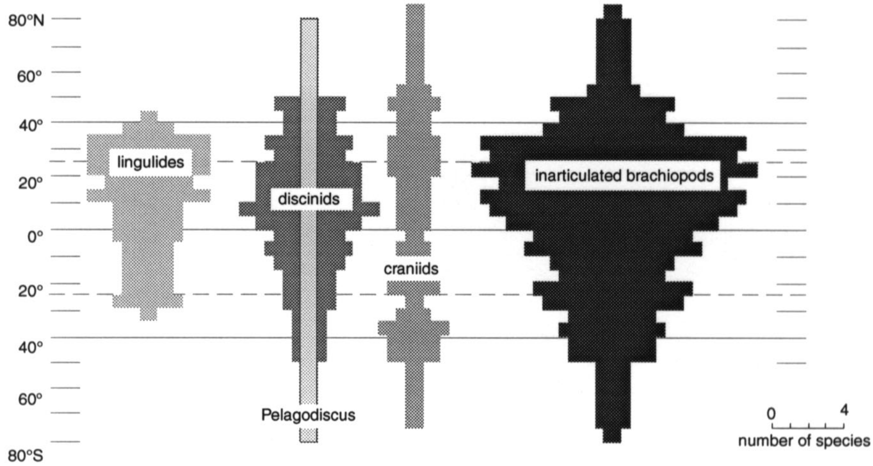

FIG. 415. Latitudinal distribution of inarticulated brachiopods (new).

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 distribution 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

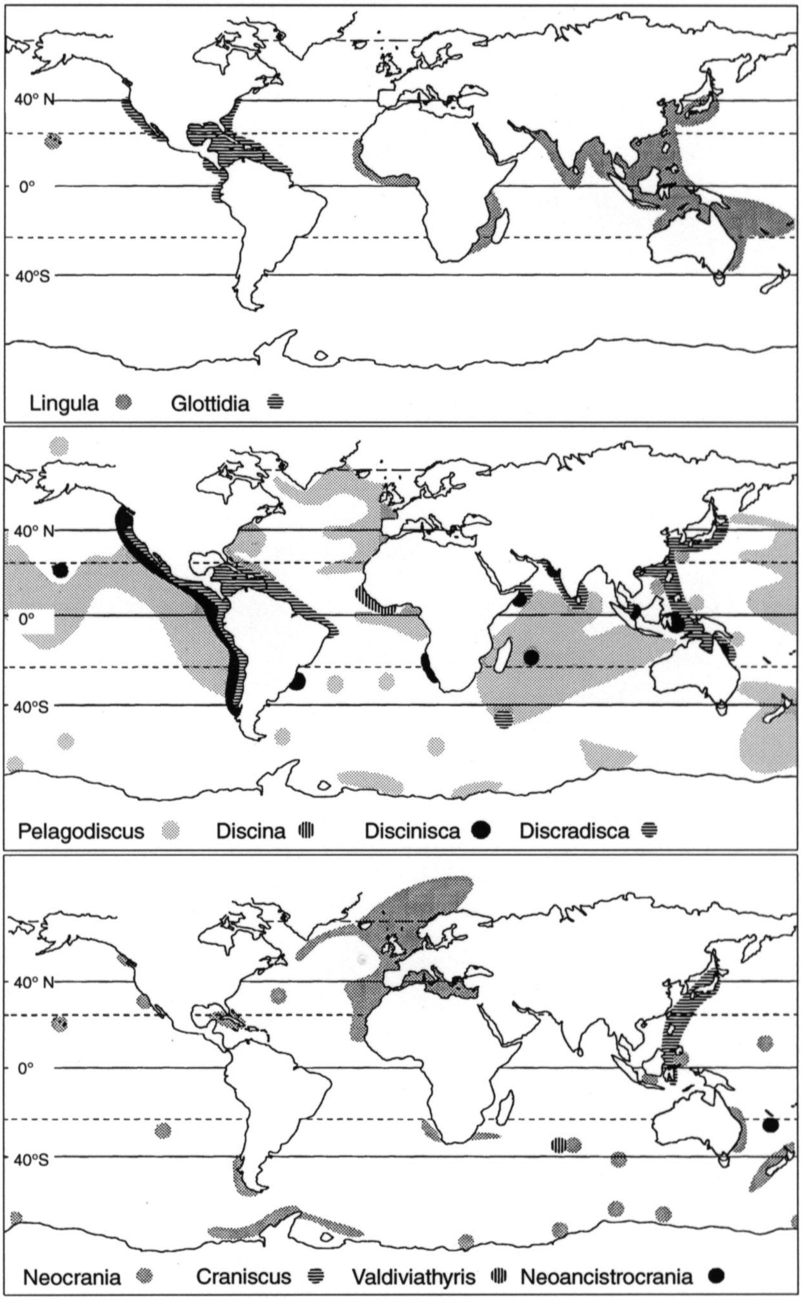

FIG. 416. Geographic distribution of inarticulated brachiopod genera (new).

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

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

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 albida,* 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, cosmopolitan 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

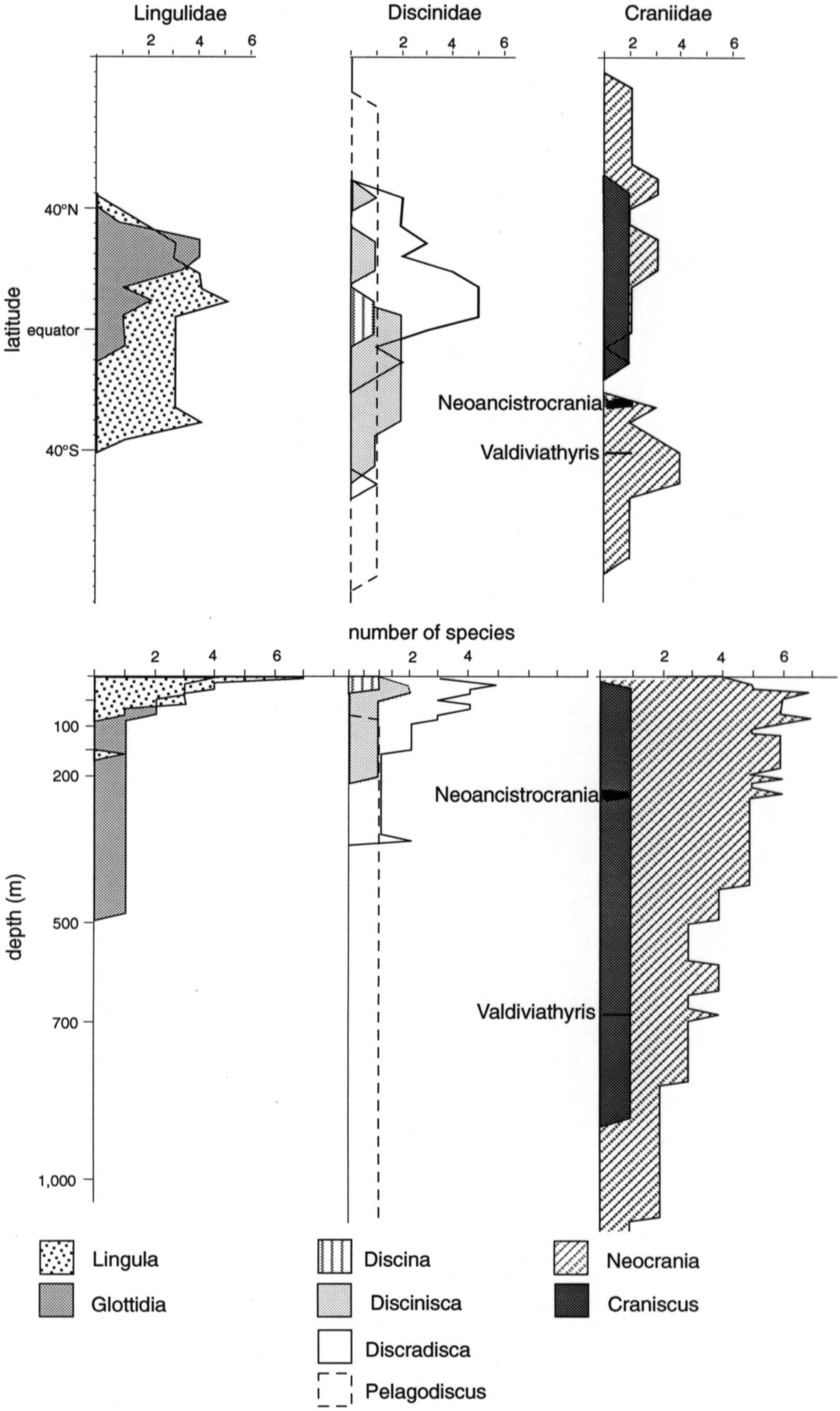

FIG. 417. Latitudinal and bathymetric extension of inarticulated brachiopod genera (new).

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.

REFERENCES

Ackerly, Spafford. 1991. Hydrodynamics of rapid shell closure in articulate brachiopods. Journal of Experimental Biology 156:287–314.

———. 1992. Rapid shell closure in the brachiopods *Terebratulina retusa* and *Terebratalia transversa.* Journal of the Marine Biological Association of the United Kingdom 72:579–598.

Adoutte, André, & H. Philippe. 1993. The major lines of metazoan evolution: summary of traditional evidence and lessons from ribosomal RNA sequence analysis. *In* Y. Pichon, ed., Comparative Molecular Neurobiology. Birkhauser. Basel. p. 1–30.

Afzelius, B. A. 1979. Sperm structure in relation to phylogeny in the lower Metazoa. *In* D. W. Fawcett & J. M. Bedford, eds., The Spermatozoon. Maturation, Motility, Surface Properties and Comparative Aspects. Urban and Schwarzenberg. Baltimore. p. 243–251.

Afzelius, B. A., & M. Ferraguti. 1978. Fine structure of brachiopod spermatozoa. Journal of Ultrastructural Research 63:308–315.

Afzelius, B. A., & H. Mohri. 1966. Mitochondria respiring without exogenous substrate. A study of aged sea urchin spermatozoa. Experimental Cell Research 42:11–17.

Aldridge, A. E. 1981. Intraspecific variation of shape and size in subtidal populations of two recent New Zealand articulate brachiopods. New Zealand Journal of Zoology 8:169–174.

———. 1991. Shape variation of *Neothyris* (Brachiopoda, Terebratellinae). *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 115–122.

Alexander, R. R. 1986. Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geologic time. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 159–166, pl. 1.

Allan, R. S. 1937. On a neglected factor in brachiopod migration. Records of the Canterbury Museum 4:157–165.

———. 1949. Notes on a comparison of the Tertiary and recent Brachiopoda of New Zealand and South America. Transactions of the Royal Society of New Zealand 77:288–289.

———. 1960. The succession of Tertiary brachiopod faunas in New Zealand. Records of the Canterbury Museum 7:233–268.

———. 1963. On the evidence of Austral Tertiary and recent brachiopods on Antarctic biogeography. *In* Proceedings of the 10th Science Congress of the Pacific Science Congress, University of Hawaii, Honolulu. Bishop Museum Press. Honolulu. p. 451–454.

Al-Rikabi, Ikbal. 1992. A molecular approach to palaeontology: Biochemical method applications of brachiopod proteins. Master of Science thesis. University of Glasgow. 116 p.

Alvarez, Fernando. 1990. Devonian athyrid brachiopods from the Cantabrian Zone (N.W. Spain). Biostratigraphie du Paléozoïque 11:311 p., 30 pl.

Alvarez, Fernando, Covadonga Brime, & G. B. Curry. 1987. Growth and function of the micro-frills present on the Devonian brachiopod *Athyris campomanesi* (Verneuil & Archiac). Transactions of the Royal Society of Edinburgh 78:65–72.

Alvarez, Fernando, & C. H. C. Brunton. 1990. The shell-structure, growth and functional morphology of some Lower Devonian athyrids from northwest Spain. Lethaia 23(2):117–131, 12 fig.

Amsden, T. W. 1953. Some notes on the Pentameracea, including a description of one new genus and one new subfamily. Washington Academy of Sciences, Journal 43(5):137–147, 7 fig.

An, S., & C. H. Koh. 1992. Environments and distribution of benthic animals on the Mangyung-Dongjin tidal flat, west coast of Korea. Journal of the Oceanological Society of Korea 27(1):78–90.

In Korean.

Arber, M. A. 1942. The pseudodeltidium of the strophomenid brachiopods. Geological Magazine 79:170–187.

Armstrong, J. 1969. The cross-bladed fabrics of the shells of *Terrakea solida* (Etheridge and Dun) and *Streptorhynchus pelicanensis* Fletcher. Palaeontology 12:310–320.

Asgaard, Ulla, & R. G. Bromley. 1991. Colonization by micromorph brachiopods in the shallow subtidal of the eastern Mediterranean Sea. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 261–264.

Asgaard, Ulla, & N. Stentoft. 1984. Recent micromorph brachiopods from Barbados; palaeoecological and evolutionary implications. Géobios, Mémoire spécial 8:29–37, pl. 1–2.

Ashworth, J. H. 1915. On larvae of *Lingula* and *Pelagodiscus* (Discinisca). Transactions of the Royal Society of Edinburgh 51:45–69, pl. 4–5.

Atkins, Dorothy. 1956. Ciliary feeding mechanisms of brachiopods. Nature 177:706.

———. 1958. A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. Proceedings of the Zoological Society of London 131:559–581.

———. 1959. The growth stages of the lophophore of the brachiopods *Platidia davidsoni* (Eudes Deslongchamps) and *P. anomioides* (Phillipi), with notes on the feeding mechanism. Journal of the Marine Biological Association of the United Kingdom 38:103–132.

———. 1960a. A new brachiopod from the Western Approaches, and the growth stages of the lophophore. Journal of the Marine Biological Association of the United Kingdom 39:71–89, fig. 1–14, pl. 1.

———. 1960b. The ciliary feeding mechanism of the

Megathyridae (Brachiopoda), and the growth stages of the lophophore. Journal of the Marine Biological Association of the United Kingdom 39:459–479.

———. 1961a. A note on the growth stages and structure of the adult lophophore of the brachiopod *Terebratella (Waltonia) inconspicua* (G. B. Sowerby). Proceedings of the Zoological Society of London 136:255–271.

———. 1961b. The growth stage of the adult structure of the lophophore of the brachiopod *Megerlia truncata* (L.) and *M. echinata* (Fischer & Oelhert). Journal of the Marine Biological Association of the United Kingdom 41:95–111.

———. 1963. Notes on the lophophore and gut of the brachiopod *Tegulorhynchia nigricans* (G. B. Sowerby). Proceedings of the Zoological Society of London 140:15–24.

Atkins, Dorothy, & M. J. S. Rudwick. 1962. The lophophore and ciliary feeding mechanism of the brachiopod *Crania anomala* (Müller). Journal of the Marine Biological Association of the United Kingdom 42:469–480.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman & Hall. New York & London. 511 p.

Awati, P. R., & G. R. Kshirsagar. 1957. *Lingula* from western coast of India. Zoological Memoirs of the University of Bombay 4:1–87.

Ayala, F. J., J. W. Valentine, T. E. DeLaca, & G. S. Zumwalt. 1975. Genetic variability of the Antarctic brachiopod *Liothyrella notorcadensis* and its bearing on mass extinction hypotheses. Journal of Paleontology 49:1–9.

Babin, C., J. H. Delance, C. C. Emig, & P. R. Racheboeuf. 1992. Brachiopodes et Mollusques Bivalves: concurrence ou indifférence? Géobios, Mémoire spécial 14:35–44.

Backeljau, T., B. Winnepenninckx, & L. De Bruyn. 1993. Cladistic analysis of metazoan relationships: a reappraisal. Cladistics 9:167–181.

Bada, J. L., M. Y. Shou, E. H. Man, & R. A. Schroeder. 1978. Decomposition of hydroxy amino acids in foraminifera tests; kinetics, mechanism and geochronological implications. Earth and Planetary Science Letters 41:67–76.

Baker, P. G. 1970a. Significance of the punctation mosaic of the Jurassic thecidellinid brachiopod *Moorellina.* Geological Magazine 107:105–113.

———. 1970b. The growth and shell microstructure of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. Palaeontology 13:76–99.

———. 1990. The classification, origin and phylogeny of thecideidine brachiopods. Palaeontology 33(1):175–191, 3 fig.

———. 1991. Morphology and shell microstructure of Cretaceous thecideidine brachiopods and their bearing on thecideidine phylogeny. Palaeontology 34:815–836.

Baker, P. G., & D. G. Elston. 1984. A new polyseptate thecideacean brachiopod from the middle Jurassic of the Cotswolds, England. Palaeontology 27:777–791.

Baker, P. G., & K. Laurie. 1978. Revision of the Aptian thecideidine brachiopods of the Faringdon sponge gravels. Palaeontology 21:555–570.

Balakirev, E. S., & G. P. Manchenko. 1985. High levels of allozymic variation in brachiopod *Coptothyris grayii* and Ascidia *Halocynthia aurantium.* Genetika 21:239–244.

Balinski, Andrzej. 1975. Secondary changes in microornamentation of some Devonian ambocoeliid brachiopods. Palaeontology 18:179–189.

Bancroft, B. B. 1945. The brachiopod zonal indices of the stages Costonian-Onnian in Britain. Journal of Paleontology 19:181–252, pl. 22–38.

Baron, J., J. Clavier, & B. A. Thomassin. 1993. Structure and temporal fluctuations of two intertidal seagrass-bed communities in New Caledonia (SW Pacific Ocean). Marine Biology 117:139–144.

Bassett, M. G., L. E. Holmer, L. E. Popov, & John Laurie. 1993. Phylogenetic analysis and classification of the Brachiopoda—reply and comments. Lethaia 26:385–386.

Bayne, B. L., & R. C. Newell. 1983. Physiological energetics of marine molluscs. *In* A. S. M. Saleuddin & K. M. Wilbur, eds., The Mollusca, Vol. 4. Academic Press. New York. p. 407–515.

Bayne, B. L., J. Widdows, & R. J. Thompson. 1976. Physiological integrations. *In* B. L. Bayne, ed., Marine Mussels: Their Ecology and Physiology. Cambridge University Press. Cambridge. p. 261–291.

Beecher, C. E. 1891. Development of the Brachiopoda. Part I. Introduction. American Journal of Science (series 3) 41:343–357.

———. 1892. Development of the Brachiopoda. Part II. Classification of the stages of growth and decline. American Journal of Science (series 3) 44:133–155.

———. 1897. Morphology of the brachia. Bulletin of the United States Geological Survey 87:105–112.

Beecher, C. E., & J. M. Clarke. 1889. The development of some Silurian Brachiopoda. New York State Museum Memoir 1(1):1–95, pl. 1–8.

Bemmelen, J. F. van. 1883. Untersuchungen über den anatomichen und histologichen Bau der Brachiopoda Testicardina. Jena. Zeitschrift für Naturwissenschaften 16:88–161.

Benigni, Chiara, & Carla Ferliga. 1988. Carniana *Thecospiridae* (Brachiopoda) from San Cassiano Formation (Cortina d'Ampezzo, Italy). Rivista Italiana di Palaeontologia 94:515–560.

Benson, D. A., M. Boguski, D. L. Lipman, & J. Ostell. 1994. GenBank. Nucleic Acids Research 22:3441–3444.

Benton, M. J., ed. 1993. The Fossil Record 2. Chapman & Hall. London. 845 p.

Bernard, F. R. 1972. The living Brachiopoda of British Columbia. Syesis 5:73–82.

Beyer, H. G. 1886. A study of the structure of *Lingula (Glottidia) pyramidata* Stim. (Dall). Studies from the Biology Laboratory, Johns Hopkins University 3:227–265.

Bhavanarayana, P. V. 1975. Some observations on the benthic faunal distribution in the Kakinada Bay. *In* R. Natarajan, ed., Recent Researches in Estuarine

Biology. Hindustan Publishing Co. Dehli. p. 146–150.

Biernat, Gertrude, & C. C. Emig. 1993. Anatomical distinctions of Mesozoic lingulide brachiopods. Acta Palaeontologica Polonica 38(1/2):1–20, 8 fig.

Biernat, Gertrude, & Alwyn Williams. 1970. Ultrastructure of the protegulum of some acrotretide brachiopods. Palaeontology 13:491–502.

———. 1971. Shell structure of the siphonotretacean Brachiopoda. Palaeontology 14:423–430.

Bitter, P. H. von, & R. Ludvigsen. 1979. Formation and function of protegular pitting in some North American acrotretid brachiopods. Palaeontology 22:705–720.

Blochmann, F. 1892. Untersuchungen über den Bau der Brachiopoden. I. Die Anatomie von *Crania anomala* (Müller). Jena. Gustav Fischer. p. 1–65.

———. 1898. Die larve von *Discinisca* (Die Muellersche Brachiopodenlarve). Zoologische Jahrbücher Abteilungen Anatomie und Ontogenie der Tiere 11:417–426.

———. 1900. Untersuchungen über den Bau der Brachiopoden. I, Die Anatomie von *Crania anomala* O.F.M. (1892). II. Die Anatomie von *Discinisca lamellosa* (Broderip) und *Lingula anatina* (Bruguière). Gustav Fischer. Jena. p. 1–124.

———. 1906. Neue Brachiopoden der Valdivia-und Gaussexpeditionen. Zoologischer Anzeiger 30:690–702.

———. 1908. Zur Systematik und geographischen Verbreirung der Brachiopoden. Zeitschrift für wissenschaftliche Zoologie 90:596–644, pl. 36–40.

Boore, J. L., & W. M. Brown. 1994. Complete DNA sequence of the mitochondrial genome of the black chiton, *Katharina tunicata.* Genetics 138:423–443.

Borman, A. H., E. W. de Jong, R. Thierry, P. Westbroek, & L. Bosch. 1987. Coccolith-associated polysaccharides from cells of *Emiliania huxleyi* (Haptophycae). Journal of Phycology 23:118–123.

Bosi Vanni, M. R., & A. M. Simmonetta. 1967. Contributo alla conoscenza dell'anatomia ed isologia di *Muehlfedtia disculus* (Pallas) 1766 (Brachiopoda, Testicardines). Gli apparati lofoforale, digerente, nefridial e reproduttore. Societa Toscana di Scienze Naturali, Memorie (series B) 74B:21–34.

Boucot, A. J. 1959. Brachiopods of the lower Devonian rocks at Highland Mills, New York. Journal of Paleontology 33(5):727–769, 5 fig., pl. 90–103.

Bozzo, M. G., R. Bargalló, M. Durfort, R. Fontarnau, & J. López-Camps. 1983. Ultrastructura de la coberta des oòcits de *Terebratula vitrea* (Brachiopoda: Testicardina). Butllettí de la Institució Catalana d'Història Natural 49 (Secció de Zoologia, 5):13–18, fig. 1–11.

Brafield, A. E., & D. J. Solomon. 1972. Oxycalorific coefficients for animals respiring nitrogenous substrates. Comparative Biochemistry and Physiology 43A:837–841.

Branch, G. M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. Oceanography and Marine Biology: An Annual Review 19:235–380.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803.

Britten, R. J., & E. H. Davidson. 1971. Repetitive and non-repetitive DNA sequences and a speculation on the origins of evolutionary novelty. Journal of Molecular Evolution 46:111–133.

Britten, R. J., & D. E. Kohne. 1968. Repeated sequences in DNA. Science 161:529–540.

Bromley, R. G., & Finn Surlyk. 1973. Borings produced by brachiopod pedicles, fossil and recent. Lethaia 6:349–365.

Brooks, W. K. 1879. The development of *Lingula* and the systematic position of the Brachiopoda. Johns Hopkins University, Chesapeake Zoology Laboratory, Scientific Results of the Session of 1878:34–112.

Brown, I. A. 1953. *Martinopsis* Waagen from the Salt Range, India. Journal and Proceedings of the Royal Society of New South Wales 86:100–107, 3 fig., pl. 9.

Brunton, C. H. C. 1966. Silicified productoids from the Visean of County Fermanagh. British Museum (Natural History) Bulletin (Geology) 12(5):175–243, pl. 1–19.

———. 1969. Electron microscopic studies of growth margins of articulate brachiopods. Zeitschrift für Sellforsch 100:189–200.

———. 1971. An endopunctate rhynchonellid brachiopod from the Viséan of Belgium and Britain. Palaeontology 14:95–106.

———. 1972. The shell structure of chonetacean brachiopods and their ancestors. Bulletin of the British Museum of Natural History (Geology) 21:1–26.

———. 1988. Some brachiopods from the eastern Mediterranean Sea. Israel Journal of Zoology 35:151–169.

Brunton, C. H. C., & G. B. Curry. 1979. British brachiopods. Synopses of the British fauna (new series) 17:64 p., 30 fig.

Brunton, C. H. C., & Norton Hiller. 1990. Late Cainozoic brachiopods from the coast of Namaqualand, South Africa. Palaeontology 33(2):313–342, 11 fig.

Brunton, C. H. C., & D. J. C. Mundy. 1988. Strophalosiacean and aulostegacean productoids (Brachiopoda) from the Craven Reef Belt (late Viséan) of North Yorkshire. Proceedings of the Yorkshire Geological Society 47:55–88.

Brusca, R. C., & G. J. Brusca. 1990. Invertebrates. Sinauer Associates, Inc. Sunderland, Massachusetts. 922 p.

Buchan, P., L. S. Peck, & N. Tublitz. 1988. A light, portable apparatus for the assessment of invertebrate heart beat rate. Journal of Experimental Biology 136:495–498.

Bullivant, J. S. 1968. The method of feeding of lophophorates (Bryozoa, Phoronida, Brachiopods). New Zealand Journal of Marine and Freshwater Research 2:135–146.

Bulman, O. M. B. 1939. Muscle systems of some inarticulate brachiopods. Geological Magazine 76:434–444.

Campbell, K. S. W., & B. D. E. Chatterton. 1979. *Coelospira:* do its double spires imply a double

lophophore? Alcheringa 3:209–223, fig. 1–7.
Carlson, S. J. 1989. The articulate brachiopod hinge mechanism: morphological and functional variation. Paleobiology 15(4):364–386, 13 fig.
———. 1993a. Investigating brachiopod phylogeny and classification—response to Popov *et al.* 1993. Lethaia 26:383–384.
———. 1993b. Phylogeny and evolution of "pentameride" brachiopods. Palaeontology 36(4):807–837, 10 fig.
Carpenter, W. B. 1851. On the intimate structure of shells of Brachiopoda. *In* T. Davidson, British Fossil Brachiopoda. Monograph of the Palaeontographical Society 1:22–40.
Carter, J. L., J. G. Johnson, R. Gourvennec, & H.-F. Hou. 1994. A revised classification of the spiriferid brachiopods. Annals of the Carnegie Museum 63:327–374.
Caryl, Anthony. 1992. DNA fingerprinting of brachiopod DNA. Unpublished Honours Bachelor of Science thesis. University of Glasgow. 37 p.
Chuang, S. H. 1956. The ciliary feeding mechanisms of *Lingula unguis* (L.) (Brachiopoda). Proceedings of the Zoological Society of London 127(2):167–189.
———. 1959a. The breeding season of the brachiopod *Lingula unguis* (L.). Biological Bulletin, Marine Biology Laboratory, Woods Hole, Massachusetts 117(2):202–207.
———. 1959b. The structure and function of the alimentary canal in *Lingula unguis* (L.) Brachiopoda. Proceedings of the Zoological Society of London 132:283–311.
———. 1960. An anatomical, histological and histochemical study of the gut of the brachiopod *Crania anomala.* Quarterly Journal of Microscopical Science 101:9–18.
———. 1961. Growth of the postlarval shell in *Lingula unguis* (L.) (Brachiopoda). Proceedings of the Zoological Society of London 137(2):299–310.
———. 1968. The larvae of a discinid (Inarticulata, Brachiopoda). Biological Bulletin 135:263–272.
———. 1971. New interpretation of the morphology of *Schizambon australis* Ulrich and Cooper (Ordovician siphonotretid inarticulate brachiopod). Journal of Paleontology 45:824–832.
———. 1973. The inarticulate brachiopod larvae of the International Indian Ocean Expedition. Journal of the Marine Biological Association of India 15:538–544.
———. 1974. Observations on the ciliary feeding mechanisms of the brachiopod *Crania anomala.* Journal of the Zoological Society of London 173:441–449.
———. 1977. Larval development in *Discinisca* (inarticulate brachiopod). American Zoologist 17:39–53.
———. 1983a. Brachiopoda. *In* K. G. Adiyodi & R. G. Adiyodi, eds., Reproductive Biology of Invertebrates. Oogenesis, Oviposition and Oosorption, Vol. I. John Wiley and Sons Ltd. p. 571–584.
———. 1983b. Brachiopoda. *In* K. G. Adiyodi & R. G. Adiyodi, eds., Reproductive Biology of Invertebrates. Spermatogenesis and Sperm Function, Vol. II. John Wiley and Sons Ltd. p. 517–530.
———. 1990. Brachiopoda. *In* K. G. Adiyodi & R. G. Adiyodi, eds., Reproductive Biology of Invertebrates. Fertilisation, Development and Parental Care, Vol. VI. John Wiley and Sons Ltd. p. 211–254.
———. 1991. Common and evolutionary features of recent brachiopods and their bearing on the relationship between, and the monophyletic origin of, the inarticulates and the articulates. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 11–14.
Clegg, H. 1993. Biomolecules in recent and fossil articulate brachiopods. Ph.D. thesis. University of Newcastle Upon Tyne. 246 p.
Cloud, P. E. Jr. 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. Geological Society of America Special Paper 38:1–182, pl. 1–26.
———. 1948. Notes on recent brachiopods. American Journal of Science 246:241–250.
Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. Quarterly Review of Biology 41:131–190.
Cohen, B. L. 1992. Utility of molecular phylogenetic methods: a critique of immuno-taxonomy. Lethaia 24:441–442.
———. 1994. Immuno-taxonomy and the reconstruction of brachiopod phylogeny. Palaeontology 37:907–911.
Cohen, B. L., Peter Balfe, Moyra Cohen, & G. B. Curry. 1991. Molecular evolution and morphological speciation in North Atlantic brachiopods (*Terebratulina* spp.). Canadian Journal of Zoology 69:2903–2911.
———. 1993. Molecular and morphometric variation in European populations of the articulate brachiopod *Terebratulina retusa.* Marine Biology 115:105–111.
Cohen, B. L., Peter Balfe, & G. B. Curry. 1986. Genetics of the brachiopod *Terebratulina. In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 55–63.
Cohen, B. L., A. B. Gawthrop, & T. Cavalier-Smith. In preparation. Phylogeny of lophophorates, especially brachiopods, based on nuclear-encoded SSU rRNA gene sequences.
Collins, M. J. 1991. Growth rate and substrate-related mortality of a benthic brachiopod population. Lethaia 24:1–11.
Collins, M. J., G. B. Curry, G. Muyzer, R. Quinn, S. Xu, P. Westbroek, & S. Ewing. 1991. Immunological investigations of relationships within the terebratulid brachiopods. Palaeontology 34:785–796.
Collins, M. J., G. B. Curry, R. Quinn, G. Muyzer, T. Zomerdijk, & P. Westbroek. 1988. Sero-taxonomy of skeletal macromolecules in living terebratulid brachiopods. Historical Biology 1:207–224.
Collins, M. J., G. Muyzer, G. B. Curry, P. Sandberg, & P. Westbroek. 1991. Macromolecules in brachiopod

shells: characterisation and diagenesis. Lethaia 24:387–397.

Collins, M. J., G. Muyzer, P. Westbroek, G. B. Curry, P. A. Sandberg, S. J. Xu, R. Quinn, & D. I. MacKinnon. 1991. Preservation of fossil biopolymeric structures: conclusive immunological evidence. Geochimica et Cosmochimica Acta 55:2253–2257.

Conklin, E. G. 1902. The embryology of a brachiopod, *Terebratulina septentrionalis* Couthouy. Proceedings of the American Philosophical Society 41:41–76.

Conover, R. J., & E. D. S. Corner. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. Journal of the Marine Biological Association of the United Kingdom 48:49–75.

Conway Morris, Simon. 1994. Why molecular biology needs palaeontology. *In* M. Akam, P. Holland, P. Ingham, & G. Wray, eds., The Evolution of Developmental Mechanisms. Development, 1994 Supplement. Company of Biologists. Cambridge. p. 1–13.

———. 1995. Nailing the lophophorates. Nature 375:365–366.

Conway, Morris, Simon, B. L. Cohen, A. B. Gawthrop, T. Cavalier-Smith, & B. Winnepenninckx. 1996. Lophophorate phylogeny. Science 272:282.

Conway Morris, Simon, & J. S. Peel. 1995. Articulated halkieriids from the Lower Cambrian of north Greenland and their role in early protostome evolution. Philosophical Transactions of the Royal Society (series B) 347:305–358.

Cooper, G. A. 1942. New genera of North American brachiopods. Washington Academy of Sciences Journal 32(8):228–235.

———. 1952. Unusual specimens of the brachiopod family Isogrammidae. Journal of Paleontology 26:113–119, pl. 21–23.

———. 1954. Unusual Devonian brachiopods. Journal of Paleontology 28:325–332, 5 fig., pl. 36–37.

———. 1955. New genera of middle Paleozoic brachiopods. Journal of Paleontology 29:45–63, pl. 11–14.

———. 1956. New Pennsylvanian brachiopods. Journal of Paleontology 30:521–530, pl. 61.

———. 1957. Loop development of the Pennsylvanian terebratuloid *Cryptacanthia.* Smithsonian Miscellaneous Collection 134(3):1–18, pl. 1–2.

———. 1973. Vema's Brachiopoda (recent). Smithsonian Contributions to Paleobiology 17:1–51.

———. 1975. Brachiopods from west African waters with examples of collateral evolution. Journal of Paleontology 49:911–927, fig. 1–7, pl. 1–4.

———. 1977. Brachiopods from the Caribbean Sea and adjacent waters. Studies in Tropical Oceanography Miami 14. Rosenstiel School of Marine and Atmospheric Science. University of Miami Press. 212 p., 6 fig., 35 pl.

———. 1981. Brachiopods from the southern Indian Ocean. Smithsonian Contributions to Paleobiology 43:1–93, fig. 1–30, pl. 1–14.

———. 1982. New Brachiopoda from the southern hemisphere and *Cryptopora* from Oregon (recent). Smithsonian Contributions to Paleobiology 41:1–43, fig. 1–4, pl. 1–7.

———. 1983. The Terebratulacea (Brachiopoda), Triassic to recent: A study of the brachidia (loops). Smithsonian Contributions to Paleobiology 50:1–445, 17 fig., 77 pl., 86 tables.

———. 1988. Some Tertiary brachiopods of the east coast of the United States. Smithsonian Contributions to Paleobiology 64:1–45.

Cooper, G. A., & P. J. Doherty. 1993. *Calloria variegata,* a new recent species of brachiopod (Articulata: Terebratulida) from northern New Zealand. Journal of the Royal Society of New Zealand 23:271–281.

Cooper, G. A., & R. E. Grant. 1974. Permian brachiopods of West Texas, II. Smithsonian Contributions to Paleobiology 15:233–793.

———. 1975. Permian brachiopods of West Texas, III. Smithsonian Contributions to Paleobiology 19:795–1298, pl. 192–502.

———. 1976. Permian brachiopods of West Texas, IV. Smithsonian Contributions to Paleobiology 21:1923–2285, pl. 503–662.

Cooper, G. A., & F. G. Stehli. 1955. New genera of Permian brachiopods from West Texas. Journal of Paleontology 29:469–474, pl. 52–54.

Copper, Paul. 1965. A new Middle Devonian atrypid brachiopod from the Eifel, Germany. Senckenbergiana Lethaea 46(4/6):309–325, 13 fig., pl. 27.

———. 1986. Evolution of the earliest smooth spire-bearing Atrypoids (Brachiopoda: Lissatrypidae, Ordovician–Silurian). Palaeontology 29(4):827–866, pl. 73–75.

Cornish-Bowden, A. 1983. Relating proteins by amino acid composition. Methods in Enzymology 91:60–75.

Cowen, R. 1966. The distribution of punctae on the brachiopod shell. Geological Magazine 103:269–275.

———. 1968. A new type of delthyrial cover in the Devonian brachiopod *Mucrospirifer.* Palaeontology 11:317–327, pl. 63–64.

Cowen, R., & M. J. S. Rudwick. 1970. Deltidial spines in the Triassic brachiopod *Bittnerula.* Palaeontologische Zhurnal 44:82–85, pl. 9.

Crenshaw, M. A. 1972. The soluble matrix from *Mercenaria mercenaria* shell. Biomineralization 6:6–11.

Culter, J. M. 1979. A population study of the inarticulate brachiopod *Glottidia pyramidata* (Stimpson). Unpublished master of science thesis. University of South Florida. Tampa. 53 p.

———. 1980. The occurrence of hermaphrodites of the inarticulate brachiopod *Glottidia pyramidata.* Florida Scientist 43(1):20.

Culter, J. M., & J. L. Simon. 1987. Sex ratios and the occurrence of hermaphrodites in the inarticulate brachiopod, *Glottidia pyramidata* (Stimpson) in Tampa Bay, Florida. Bulletin of Marine Science of the Gulf and Caribbean 40:193–197.

Curry, G. B. 1981. Variable pedicle morphology in a population of the recent brachiopod *Terebratulina septentrionalis.* Lethaia 14:9–20.

———. 1982. Ecology and population structure of the

recent brachiopod *Terebratulina retusa* from Scotland. Palaeontology 25(2):227–246.
———. 1983. Microborings in recent brachiopods and the functions of caeca. Lethaia 16:119–127.
Curry, G. B., & A. D. Ansell. 1986. Tissue mass in living brachiopods. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 231–241.
Curry, G. B., A. D. Ansell, Mark James, & L. S. Peck. 1989. Physiological constraints on living and fossil brachiopods. Transactions of the Royal Society of Edinburgh, Earth Sciences 80:255–262.
Curry, G. B., Maggie Cusack, Kazuyoshi Endo, Derek Walton, & R. Quinn. 1991. Intracrystalline molecules from brachiopod shells. *In* S. Suga & H. Nakahara, eds., Mechanisms and Phylogeny of Mineralization in Biological Systems. Springer-Verlag. Tokyo. p. 35–40.
Curry, G. B., Maggie Cusack, Derek Walton, Kazuyoshi Endo, H. Clegg, G. Abbott, & H. Armstrong. 1991. Biogeochemistry of brachiopod intracrystalline molecules. Philosophical Transactions of the Royal Society of London 333B:359–366.
Curry, G. B., R. Quinn, M. J. Collins, Kazuyoshi Endo, S. Ewing, G. Muyzer, & P. Westbroek. 1991. Immunological responses from brachiopod skeletal macromolecules; a new technique for assessing taxonomic relationships using shells. Lethaia 24:399–407.
———. 1993. Molecules and morphology—the practical approach. Lethaia 26:5–6.
Cusack, Maggie, G. B. Curry, H. Clegg, & G. Abbott. 1992. An intracrystalline chromoprotein from red brachiopod shells: implications for the process of biomineralisation. Comparative Biochemistry and Physiology 102B:93–95.
Cusack, Maggie, & Alwyn Williams. 1996. Chemico-structural degradation of Carboniferous lingulid shells. Philosophical Transactions of the Royal Society of London B351:33–49.
Dagys, A. S. 1968. Jurskiye i rannemelovye brakhiopody Severa Sibiri [Jurassic and Early Cretaceous brachiopods from northern Siberia]. Akademia Nauk SSSR Sibiroskoe Otdelenie Institut Geologii I Geofiziki (IGIG) Trudy [Institute of Geology and Geophysics, Academy of Sciences of the USSR, Siberian Branch, Transactions] 41:167 p., 81 fig., 26 pl.
———. 1972. Postembrional'noye razvitiye brakhidiya pozdnepaleozoyskikh i rannemezozoyskikh Terebratulida [Postembryonic development of the brachidium of late Paleozoic and early Mesozoic terebratulids]. *In* A. S. Dagys & A. B. Ivanovskii, eds., Morphologicheskiye i filogeneticheskiye voprosy paleontologii [Morphological and Phylogenetic Questions of Paleontology]. Akademia Nauk SSSR Sibiroskoe Otdelenie Institut Geologii I Geofiziki (IGIG) Trudy [Institute of Geology and Geophysics, Academy of Sciences of the USSR, Siberian Branch, Transactions] 112:22–58, fig. 1–28.
———. 1974. Triasovye brakhiopody (morfologiya, sistema, filogeniya, stratigraficheskoye znacheniye i biogeografiya) [Triassic Brachiopoda (morphology, systematics, phylogeny, stratigraphic distribution, and biogeography)]. Akademia Nauk SSSR Sibiroskoe Otdelenie Institut Geologii I Geofiziki (IGIG) Trudy [Institute of Geology and Geophysics, Academy of Sciences of the USSR, Siberian Branch, Transactions] 214:386 p., 171 fig., 49 pl.
Darwin, Charles. 1859a. On the Origin of Species. 1st edition. John Murray. London. 490 p.
———. 1859b. On the origin of the species by means of natural selection or the preservation of favoured races in the struggle for life. The Folio Society edition (1990). 298 p.
Davidson, Thomas. 1850. Sur quelques Brachiopodes nouveaux ou peu connus. Bulletin de la Société Géologique de France (série 2) 8:62–74, 1 pl.
———. 1853. A Monograph of the British fossil Brachiopoda (Volume 1: General introduction). Palaeontographical Society (London) Monograph 7:1–136, pl. 1–9.
———. 1880. Report on the Brachiopoda dredged by the HMS *Challenger* during the years 1873–1876. Report of the Scientific Results of the Voyage of HMS Challenger 1(1):1–67, pl. 1–4.
Davis, C. C. 1949. Observations of plankton taken in marine waters of Florida in 1947 and 1948. Quarterly Journal of the Florida Academy of Science 11:67–103.
Degens, E. T., D. W. Spencer, & R. H. Parker. 1967. Paleobiochemistry of molluscan shell proteins. Comparative Biochemistry and Physiology 20:553–579.
Devereaux, P., P. Haeberli, & O. Smithies. 1984. A comprehensive set of sequence analysis programs for the VAX. Nucleic Acids Research 12:387–395.
Dexter, D. M. 1983. Soft bottom infaunal communities in Mission Bay. California Fish Game 69(1):5–17.
Di Geronimo, I., & G. Fredj. 1987. Les fonds à *Errina aspera* et *Pachylasma giganteum.* Documents et Travaux de l'Institut de Géologie "Albert de Lapparent" (Paris) 11:243–247.
Doherty, P. J. 1976. Aspects of the feeding ecology of the subtidal brachiopod, *Terebratella inconspicua* (Sowerby, 1846). Master of Science Thesis. Department of Zoology, University of Auckland. 183 p.
———. 1979. A demographic study of a subtidal population of the New Zealand articulate brachiopod *Terebratella inconspicua.* Marine Biology 52:331–342.
———. 1981. The contribution of dissolved amino acids to the nutrition of brachiopods. New Zealand Journal of Zoology 8:183–188.
Dolah, R. F. van., D. R. Calder, & D. M. Knott. 1983. Assessment of the benthic macrofauna in an ocean disposal area near Charleston, South Carolina. Technical Report, South Carolina Marine Resource Center 56:1–97.
Dolah, R. F. van., D. M. Knott, E. L. Wenner, T. D. Mathews, & M. P. Katuna. 1984. Benthic studies and sedimentological studies of the Georgetown

ocean dredged material disposal site. Technical Report, South Carolina Marine Resource Center 59:1–97.

Donoghue, M. J., & P. D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Systematic Botany 9:192–202.

Dörjes, J. 1977. Marine macrobenthic communities of the Sapelo island, Georgia region. *In* B. C. Coull, ed., Ecology of Marine Benthos. University of South Carolina Press, Columbia, Belle W. Baruch Library in Marine Science 6:399–421.

———. 1978. Sedimentology and faunistics of tidal flats in Taiwan. II. Faunistic and ichnocoenotic studies. Senckenbergiana Maritima 10(1/3):85–115.

Doumen, C., & W. R. Ellington. 1987. Isolation and characterization of a taurine-specific opine dehydrogenase from the pedicles of the brachiopod, *Glottidia pyramidata.* Journal of Experimental Zoology 243:25–31.

Du Bois, H. M. 1916. Variation induced in brachiopods by environmental conditions. Publications of the Puget Sound Marine Station 1:177–183.

Dunning, H. N. 1963. Geochemistry of organic pigments: carotenoids. *In* I. A. Berger, ed., Organic Geochemistry. Macmillan. New York. p. 367–430.

Dweltz, N. E. 1961. The structure of β-chitin. Biochimica et Biophysica Acta 51:283–294.

Eernisse, D. J., J. S. Albert, & F. E. Anderson. 1992. Annelida and arthropoda are not sister taxa: a phylogenetic analysis of spiralian metazoan morphology. Systematic Biology 41:305–330.

Eernisse, D. J., & A. G. Kluge. 1993. Taxonomic congruence versus total evidence and amniote phylogeny inferred from fossils, molecules and morphology. Molecular Biology and Evolution 10:1170–1195.

Eglinton, G., & G. A. Logan. 1991. Molecular preservation. Philosophical Transactions of the Royal Society of London 333B:315–328.

Egorov, A. N., & L. Ye. Popov. 1990. Novyi rod Lingulid iz niznepermskikh otlozhenii Sibroskoi Platformy [A new lingulid genus from the Early Permian deposits of the Siberian Platform]. Paleontologicheskii Zhurnal 1990(4):111–115, fig. 1–3.

Eichler, P. 1911. Die Brachiopoden der deutschen Südpolar-Expedition 1901 bis 1903. Deutsche Südpolar-Expedition 1901–1903 (series 12) Zoologie 4:381–401.

Ekman, T. 1896. Beitrage zur Kenntnis des Steiles der Brachiopoden. Zeitschrift für Wissenschaftliche Zoologie 62:169–249.

Elliott, G. F. 1951. On the geographical distribution of terebratelloid brachiopods. Annals and Magazine of Natural History (series 12) 5:305–333.

———. 1953. Brachial development and evolution in terebratelloid brachiopods. Cambridge Philosophical Society Biological Reviews 28:261–279, 9 fig.

Emig, C. C. 1976. Le lophophore-structure significative des Lophophorates (Brachiopoda, Bryozoa, Phoronida). Zoologica Scripta 5:133–137.

———. 1981a. Implications de données récentes sur les lingules actuelles dans les interprétations paléoécologiques. Lethaia 14(2):151–156.

———. 1981b. Observations sur l'écologie de *Lingula reevii* Davidson (Brachiopoda: Inarticulata). Journal of Experimental Marine Biology and Ecology 52(1):47–61.

———. 1982. Terrier et position des lingules (brachiopodes, inarticulés). Bulletin de la Société Zoologique de France 107(2):185–194.

———. 1983a. Comportement expérimental de *Lingula anatina* (brachiopode, inarticulé) dans divers substrats meubles (Baie de Mutsu, Japon). Marine Biology 75(2/3):207–213.

———. 1983b. Taxonomie du genre *Glottidia* (brachiopodes inarticulés). Bulletin du Museum National d'Histoire Naturelle de Paris (série 4) 5(section 4; no. 2):469–489.

———. 1984a. Importance du sédiment dans la distribution des lingules (brachiopodes, inarticulés). Lethaia 17:115–123.

———. 1984b. Pourquoi les lingules (brachiopodes, inarticulés) ont survécu à la transition Secondaire-Tertiaire. Bulletin de la Commission des Travaux historiques et scientifiques, Section Sciences 6:87–94.

———. 1986. Conditions de fossilisation du genre *Lingula* (Brachiopoda) et implications paléoécologiques. Palaeogeography, Palaeoclimatology, Palaeoecology 53:245–253.

———. 1987. Offshore brachiopods investigated by submersible. Journal of Experimental Marine Biology and Ecology 108:261–273.

———. 1988. Les brachiopodes actuels sont-ils des indicateurs (paléo) bathymétriques? Géologie Méditerranéenne 15(1):65–71.

———. 1989a. Les lingules fossiles, représentants d'écosystèmes oligotypiques? Atti 3° Simposio di Ecologia e Paleoecologia delle Comunita bentoniche, Catania 1985:117–121.

———. 1989b. Distribution bathymétrique et spatiale des populations de *Gryphus vitreus* (brachiopode) sur la marge continentale (Nord-Ouest Méditerranée). Oceanologica Acta 12(2):205–209.

———. 1989c. Distributional patterns along the Mediterranean continental margin (upper bathyal) using *Gryphus vitreus* (Brachiopoda) densities. Palaeogeography, Palaeoclimatology, Palaeoecology 71:253–256.

———. 1990. Examples of post-mortality alteration in recent brachipod shells and (paleo) ecological consequences. Marine Biology 104:233–238.

———. 1992. Functional disposition of the lophophore in living Brachiopoda. Lethaia 25:291–302.

Emig, C. C., & P. Cals. 1979. Lingules d'Amboine, *Lingula reevii* Davidson et *Lingula rostrum* (Shaw), données écologiques et taxonomiques concernant les problèmes de spéciation et de répartition. Cahiers de l'Indo-pacifique 2:153–164.

Emig, C. C., J. C. Gall, D. Pajaud, & J. C. Plaziat. 1978. Réflexions critiques sur l'écologie et la systématique des Lingules actuelles et fossiles. Géobios 11(5):573–609.

Emig, C. C., & P. LeLoeuff. 1978. Description de *Lingula parva* Smith (Brachiopoda, Inarticulata), récoltée en Côte d'Ivoire avec quelques remarques sur l'écologie de l'espèce. Téthys 8(3):271–274.
Emig, C. C., & J. A. Vargas. 1990. Notes on *Glottidia audebarti* (Broderip) (Brachiopoda, Lingulidae) from the Gulf of Nicoya, Costa Rica. Revista de Biologia Tropical 38(2A):251–258.
Endo, Kazuyoshi. 1987. Life habit and relative growth of some laqueid brachiopods from Japan. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 147:180–194.
———. 1992. Molecular systematics of recent and Pleistocene brachiopods. Ph.D. thesis. University of Glasgow. 208 p.
Endo, Kazuyoshi, & G. B. Curry. 1991. Molecular and morphological taxonomy of a recent brachiopod genus *Terebratulina. In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 101–108.
Endo, Kazuyoshi, G. B. Curry, R. Quinn, M. J. Collins, G. Muyzer, & P. Westbroek. 1994. Re-interpretation of terebratulide phylogeny based on immunological data. Palaeontology 37:349–373, fig. 1–10.
Erdmann, V. A., J. Wolters, E. Huysmans, & R. De Wachter. 1985. Collection of published 5S, 5.8S and 4.5S ribosomal RNA sequences. Nucleic Acids Research 13:r105–r153.
Eshleman, W. P., & J. L. Wilkens. 1979a. Actinomysin ATPase activities in the brachiopod *Terebratalia transversa.* Canadian Journal of Zoology 57:1944–1949, fig. 1–3.
———. 1979b. Brachiopod orientation to current direction and substrate position (*Terebratalia transversa*). Canadian Journal of Zoology 57:2079–2082, fig. 1.
Eshleman, W. P., J. L. Wilkens, & M. J. Cavey. 1982. Electrophoretic and electron microscopic examination of the adductor and diductor muscles of an articulate brachiopod, *Terebratalia transversa.* Canadian Journal of Zoology 60:550–559, fig. 1–5.
Farris, J. S. 1972. Outgroups and parsimony. Systematic Zoology 31:328–334.
Felsenstein, Joseph. 1993. PHYLIP (Phylogeny Inference Package). Computer program distributed by the author. Department of Genetics, University of Washington. Seattle, Washington.
Field, Katherine, G. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace, & R. A. Raff. 1988. Molecular phylogeny of the animal kingdom. Science 239:748–753.
Fischer, P., & D.-P. Oehlert. 1892. Brachiopodes de l'Atlantique Nord. Resultats des Campagnes Scientifiques du Prince de Monaco 3:1–30.
Flower, N. E., & C. R. Green. 1982. A new type of gap junction in the phylum Brachiopoda. Cell and Tissue Research 227:231–234.
Folmer, O., M. Black, W. Hoeh, R. Lutz, & R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3:294–299.
Foster, M. W. 1974. Recent Antarctic and subantarctic brachiopods. Antarctic Research Series 21:1–189.
———. 1989. Brachiopods from the extreme South Pacific and adjacent waters. Journal of Paleontology 63:268–301.
Fouke, B.W. 1986. The functional significance of spicule-reinforced connective tissues in *Terebratulina unguicula* (Carpenter). *In* P. R. Racheb*œ*uf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 271–279, fig. 1–4.
François, P. 1891. Choses de Nouméa. II. Observations biologiques sur la lingule. Archives de Zoologie expérimentale et générale (2)9:229–245.
Franzen, Åke. 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zoologiska Bidrag fran Uppsala 31:355–482.
———. 1969. On the larval development and metamorphosis in *Terebratulina,* Brachiopoda. Zoologiska Bidrag fran Uppsala 38:155–174.
———. 1982. Ultrastructure of spermatids and spermatozoa in three polychaetes with modified biology of reproduction: *Autolytus* sp., *Chitinopoma serrula* and *Capitella capitata.* International Journal of Invertebrate Reproduction 5:185–200.
———. 1987. Spermatogenesis. *In* A. C. Giese, J. S. Pearse, & V. B. Pearse, eds., Reproduction of Marine Invertebrates. Volume 9. General aspects: seeking unity in diversity. Blackwell Scientific Publications. California. p. 1–47.
Freeman, Gary. 1994. The endocrine pathway responsible for oocyte maturation in the inarticulate brachiopod *Glottidia.* Biological Bulletin 186:263–270.
Frey, R. W., J. S. Hong, J. D. Howard, B. K. Park, & S. J. Han. 1987. Zonation of benthos on a macrotidal flat, Inchon, Korea. Senckenbergiana Maritima 19(5/6):295–329.
Frith, D. W., R. Tantanasiriwong, & O. Bhatia. 1976. Zonation of macrofauna on a mangrove shore, Phuket island. Phuket Marine Biological Center Research Bulletin 10:1–37.
Gaspard, Danièle. 1978. Biominéralisation chez les brachiopodes articulés—microstructure et formation de la coquille. Annales de Paléontologie 64:1–25.
———. 1982. Microstructure de térébratules biplisées (Brachiopodes) du Cénomanien de la Sarthe (France). Affinités d'une des formes avec le genre *Sellithyris* Midd. Annales de Paléontologie (Vertébrés-Invertébrés) 68(1):1–14, 3 pl.
———. 1986. Aspects figurés de la biominéralisation unités de base de la sécrétion carbonatée chez les Terebratulida actuels. *In* P. R. Racheb*œ*uf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 77–83.
———. 1989. Quelques aspects de la biodégradation

des coquilles de brachiopodes; conséquences sur leur fossilisation. Bulletin de la Société Géologique de France 6:1207–1216.

———. 1990. Diagenetic modifications of shell microstructure in the Terebratulida (Brachiopoda, Articulata) II. *In* J. G. Carter, ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Volume 1. Van Nostrand Reinhold. New York. p. 53–56.

———. 1991. Growth stages in articulate brachiopod shells and their relation to biomineralization. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 167–174.

Gee, Henry. 1995. Lophophorates prove likewise variable. Nature 374:493.

George, T. N. 1932a. *Ambocoelia* Hall and certain similar British Spiriferidae. Geological Society of London, Quarterly Journal 87:30–61, pl. 3–5.

———. 1932b. The British Carboniferous reticulate Spiriferidae. Geological Society of London, Quarterly Journal 88:516–575, pl. 31–35.

Ghiselin, M. T. 1988. The origin of molluscs in the light of molecular evidence. *In* P. H. Harvey & L. Partridge, eds., Oxford Surveys in Evolutionary Biology. Oxford University Press. Oxford. p. 66–95.

Giese, A. C., J. S. Pearse, & V. B. Pearse. 1987. Reproduction of Marine Invertebrates. Volume 9. General aspects: seeking unity in diversity. Blackwell Scientific Publications. California. 712 p.

Gilmour, T. H. J. 1978. Ciliation and function of the food-collecting and waste-rejecting organs of the lophophorates. Canadian Journal of Zoology 56:2142–2155.

———. 1981. Food-collecting and waste-rejecting mechanisms in *Glottidia pyramidata* and the persistence of lingulacean brachiopods in the fossil record. Canadian Journal of Zoology 59:1539–1547.

Golding, G. B., & R. S. Gupta. 1994. Protein-based phylogenies support a chimeric origin for the eukaryotic genome. Molecular Biology and Evolution 12:1–6.

Gorjansky, V. Iu. [see also Gorjansky, W. Ju.], & L. E. Popov. 1985. Morphologiia, systematicheskoe polozhenie I proiskhozhdenie bezzamkovykh brakhiopod s karbonatnoi rakovinoi [Morphology, systematic position and origin of inarticulate brachiopods with a carbonate shell]. Paleontologicheskii Zhurnal 1985(3):3–14, 5 fig., pl. 1.

Gorjansky, W. Ju. [see also Gorjansky, V. Iu.], & L. Ye. Popov. 1986. On the origin and systematic position of the calcareous-shelled inarticulate brachiopods. Lethaia 19:233–240, fig. 1–3.

Gourvennec, Rémy. 1987. Morphologie des épines chez les brachiopodes Delthyrididae. Lethaia 20:21–31.

———. 1989. Radial microornament in spiriferid brachiopods and paleogeographical implications. Lethaia 22:405–411.

Gourvennec, Rémy, & Michel Mélou. 1990. Découverte d'un cas d'ornamentation épineuse chez les Orthida (Brachiopoda). Compte-Rendus de l'Académie des Sciences de Paris 311(II):1273–1277.

Grant, R. E. 1963. Unusual attachment of a Permian linoproductid brachiopod. Journal of Paleontology 37:134–140, 1 fig., pl. 19.

———. 1968. Structural adaptation in two Permian brachiopod genera, Salt Range, West Pakistan. Journal of Paleontology 42:1–32.

———. 1972. The lophophore and feeding mechanism of the Productidina (Brachiopoda). Journal of Paleontology 46:213–248, pl. 1–9.

———. 1980. Koskinoid perforations in brachiopod shells: function and mode of formation. Lethaia 13:313–319.

———. 1987. Brachiopods of Enewetak Atoll. *In* D. M. Devaney & others, eds., The Natural History of Enewetak Atoll, vol. 2. Office of Scientific and Technical Information, U. S. Department of Energy. Oak Ridge, Tennessee. p. 77–84.

Gratiolet, M. P. 1860. Études anatomiques sur la *Lingule anatine* (*L. anatina* Lam.). Journal de Conchyliologie 4:49–172.

Gustus, R. M., & R. A. Cloney. 1972. Ultrastructural similarities between setae of brachiopods and polychaetes. Acta Zoologica 53:229–233.

Halanych, K. M. 1991. 5S ribosomal RNA sequences inappropriate for phylogenetic reconstruction. Molecular Biology and Evolution 8:249–253.

Halanych, K. M., J. D. Bacheller, A. M. A. Aguinaldo, S. M. Liva, D. M. Hillis, & J. A. Lake. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. Science 267:1641–1643.

Hall, J., & J. M. Clarke. 1892–1894. An introduction to the study of the genera of Palaeozoic Brachiopoda. New York Geological Survey 8. Pt. 1(1892):i–xvi, 1–367, pl. 1–20; Pt. 2: i–xvi, 1–394, pl. 21–84.

———. 1894–1895. An introduction to the study of the Brachiopoda intended as a Handbook for the use of Students. New York State Geologist Annual Report for 1891 (1894):134–300, pl. 1–22; continuation (pt. 2) New York State Geologist Annual Report for 1893 (1894) [1895]:751–943, pl. 23–54.

Hammen, C. S. 1968. Aminotransferase activities and amino acid excretion of bivalve molluscs and brachiopods. Comparative Biochemistry and Physiology 26:697–705.

———. 1969. Lactate and succinate oxidoreductases in marine invertebrates. Marine Biology 4:233–238.

———. 1971. Metabolism of brachiopods and bivalve molluscs. *In* R. Alvardo, E. Gadea, & A. de Haro, eds., Actas del I Symposio International de Zoofilogenia, Salamanca, 1969, Acta Salmanticensia, Ciencias 36:471–478.

———. 1977. Brachiopod metabolism and enzymes. American Zoologist 17:141–147.

Hammen, C. S., & R. C. Bullock. 1991. Opine oxidoreductases in brachiopods, bryozoans, phoronids and molluscs. Biochemical Systematics and Ecology 19:263–269.

Hammen, C. S., D. P. Hanlon, & S. C. Lum. 1962. Oxidative metabolism of *Lingula.* Comparative Biochemistry and Physiology 5:185–192.

Hammen, C. S., & S. C. Lum. 1966. Fumarate reductase and succinate dehydrogenase activities in bivalve mollusks and brachiopods. Comparative Biochemistry and Physiology 19:775–781.

———. 1977. Salinity tolerance and pedicle regeneration of *Lingula.* Journal of Paleontology 51:548–551.

Hammen, C. S., & P. J. Osborne. 1959. Carbon dioxide fixation in marine invertebrates: a survey of major phyla. Science 130:1409–1410.

Hammond, L. S. 1980. The larvae of a discinid (Brachiopoda, Inarticulata) from inshore waters near Townsville, Australia, with revised identifications of previous records. Journal of Natural History 14:647–661.

———. 1982. Breeding season, larval development and dispersal of *Lingula anatina* (Brachiopoda, inarticulata) from Townsville, Australia. Journal of Zoology, London 198:183–196.

———. 1983. Experimental studies of salinity tolerance, burrowing behavior and pedicle regeneration in *Lingula anatina* (Brachiopoda, Inarticulata). Journal of Paleontology 57:1311–1316.

———. 1984. Epibiota from the valves of recent *Lingula* (Brachiopoda). Journal of Paleontology 58:1528–1531.

Hammond, L. S., & I. R. Poiner. 1984. Genetic structure of three populations of the "living fossil" brachiopod *Lingula* from Queensland, Australia. Lethaia 17:139–143.

Hancock, A. 1859. On the organisation of the Brachiopoda. Philosophical Transactions of the Royal Society 148:791–869.

Hare, P. E. 1962. The amino acid composition of the organic matrix of some recent and fossil shells of some west coast species of *Mytilus.* Ph.D. thesis. California Institute of Technology.

Hare, P. E., & R. M. Mitterer. 1969. Laboratory simulation of amino acid diagenesis in fossils. Carnegie Institute of Washington Yearbook 67:205–208.

Haro, A. de. 1963. Estructura y anatomia comparadas des las gonadas y pedunculo des los Braquiópodos testicardinos. Publicaciones del Instituto de Biología Applicada, Barcelona 35:97–117.

Harvey, E. N. 1928. The oxygen consumption of luminous bacteria. Journal of General Physiology 11:469–475.

Hatai, K. M. 1940. The Cenozoic Brachiopoda of Japan. Science Reports of the Tohoku Imperial University, Sendai, Japan (second series, Geology) 20:1–413, pl. 1–12.

Haugen, J.-E., H.-P. Sejrup, & N. B. Vogt. 1989. Chemotaxonomy of Quaternary benthic foraminifera using amino acids. Journal of Foraminiferal Research 19:38–51.

Havlīčék, Vladimir. 1961. Rhynchonelloidea des Boehmischen aelteren palaeozoikums (Brachiopoda). Ustredni Ustav Geologicky Rozpravy 27:211 p., 27 pl.

———. 1982. Lingulacea, Paterinacea and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. Sbornik Geologickych ved (Paleontologie) 25:9–82, 16 fig., pl. 1–16.

Hay-Schmidt, A. 1992. Ultrastructure and immunocytochemistry of the nervous system of the larvae of *Lingula anatina* and *Glottidia* sp. (Brachiopoda). Zoomorphology 112:189–205.

Heinrikson, R. L., & S. C. Meredith. 1984. Amino acid analysis by reverse-phase high-performance liquid chromatography: precolumn derivatization with phenylisothiocyanate. Analytical Biochemistry 136:65–74.

Heller, M. 1931. Exkretorische Tätigkeitder Brachiopoden. Zeitschrift für Morphologie und Oekologie der Tiere 24:238–258.

Helmcke, J. G. 1940. Die Brachiopoden der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899. G. Fischer Verlag, 1932–1940. Jena. Wissenschaftliche Ergebnissen der deutschen Tiefsee-Expedition 24(3):217–316.

Hemmingsen, A. M. 1960. Energy metabolism as related to body size and respiratory surfaces and its evolution. Report to the Steno Memorial Hospital 9:7–110.

Hennig, Willi. 1966. Phylogenetic Systematics. University of Illinois Press. Urbana. 263 p.

Hertlein, L. G., & U. S. Grant IV. 1944. The Cenozoic Brachiopoda of western North America. Publications of the University of California at Los Angeles in Mathematical and Physical Sciences 3:236 p., pl. 1–21.

Hiller, Norton. 1988. The development of growth lines on articulate brachiopods. Lethaia 21:177–188.

———. 1991. The southern African recent brachiopod fauna. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 439–445.

———. 1993. A modern analogue of the Lower Ordovician *Obolus* conglomerate of Estonia. Geological Magazine 130(2):265–267.

Hillis, D. M., & M. T. Dixon. 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. Quarterly Review of Biology 66:411–453.

Hillis, D. M., J. P. Huelsenbeck, & C. W. Cunningham. 1994. Application and accuracy of molecular phylogenies. Science 264:671–677.

Hillis, D. M., & D. Moritz. 1990. Molecular Systematics. Sinauer Associates, Inc. Sunderland, Massachusetts. 588 p.

Hirai, E., & T. Fukushi. 1960. The development of two species of lamp shells, *Terebratalia coreanica* and *Coptothyris grayi.* Bulletin of the Ashamushi Marine Biological Station 10:77–80.

Hochachka, P. W., & G. H. Somero. 1973. Strategies of Biochemical Adaptation. W. B. Saunders Company. Philadelphia. 358 p.

———. 1984. Biochemical Adaptation. Princeton University Press. Princeton. 480 p.

Holland, P. W. H. 1992. Homeobox genes in vertebrate evolution. BioEssays 14:267–273.

Holland, P. W. H., & B. L. M. Hogan. 1986. Phylogenetic distribution of Antennapedia-like homeoboxes. Nature 321:251–253.

Holland, P. W. H., N. A. Williams, & J. Lanfear. 1991. Cloning of segment polarity gene homologues from the unsegmented brachiopod *Terebratulina retusa* (Linnaeus). Federation of European Biochemical Societies Letters 291:211–213.

Holmer, L. E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. Fossils and Strata 26:1–172, 118 fig.

Holmer, L. E., & L. Ye. Popov. 1990. The Acrotretacean brachiopod *Ceratreta tanneri* (Metzger) from the Upper Cambrian of Baltoscandia. Geologiska Foreningens i Stockholm Forhandlingar 112(3):249–263.

d'Hondt, Jean-Loup. 1986. Étude de l'intestin et de la glande digestive de *Terebratulina retusa* (L.) (Brachiopode). IV. Comparaison avec les activités enzymatiques d'autres brachiopodes du même biotope. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 301–305.

d'Hondt, Jean-Loup, & E. Boucaud-Camou. 1982. Étude l'intestin et de la glande digestive de la *Terebratulina retusa* (L.) (Brachiopode). Ultrastructure et recherche d'activités amylasiques et protéasiques. Bulletin de la Société Zoologique de France 107(2):207–216.

Hori, H., B. L. Lim, T. Ohama, T. Kumazaki, & S. Osawa. 1985. Evolution of organisms deduced from 5S rRNA sequences, p. 369–384. *In* T. Ohta & A. Aoki, eds., Population Genetics and Molecular Evolution. Springer. Berlin. 503 p.

Hori, H., & S. Osawa. 1986. Evolutionary change in 5S rRNA secondary structure and a phylogenetic tree of 352 5S rRNA species. BioSystems 19:163–172.

Hoverd, W. A. 1985. Histological and ultrastructural observations of the lophophore and larvae of the brachiopod, *Notosaria nigricans* (Sowerby, 1846). Journal of Natural History 19:831–850.

———. 1986. The adult lophophore of *Notosaria nigricans* (Brachiopoda). *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 307–312.

Huelsenbeck, J. P. 1995. Performance of phylogenetic methods in simulation. Systematic Biology 44:17–48.

Hughes, W. W., G. D. Rosenberg, & R. D. Tkachuck. 1988. Growth increments in the shell of the living brachiopod *Terebratalia transversa.* Marine Biology 98:511–518.

Hulmes, A. G., & G. A. Boxshall. 1988. Peocilostome copepods associated with bivalve molluscs and a brachiopod at Hong-Kong. Journal of Natural History 22(2):537–544.

Huson, D. H., & R. Wetzel. 1994. SplitsTree 1.0: Computer program distributed by the authors. Mathematics Department, University of Bielefeld, Germany. Bielefeld.

Huxley, J. S. 1932. Problems of Relative Growth. The Dial Press. New York. 244 p.

Hyman, L. H. 1959a. The Invertebrates: Smaller Coelomate Groups. Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, Sipunculida, the Coelomate Bilateria, Vol. 5. McGraw-Hill. New York, London, Toronto. viii + 783 p., fig. 1–240.

———. 1959b. The Lophophorate Coelomates—Phylum Brachiopoda. *In* L. H. Hyman, The Invertebrates: Smaller Coelomate Groups. McGraw-Hill. New York, London, Toronto. p. 228–609.

Iijima, M., T. Hiroko, M. Yutaka, & K. Yoshinori. 1991. Difference of the organic component between the mineralized and the non-mineralized layers of *Lingula* shell. Comparative Biochemistry and Physiology 98A:379–382.

Iijima, M., H. Kamemizu, N. Wakamatsu, T. Goto, & Y. Moriwaki. 1991. Thermal decomposition of *Lingula* shell apatite. Calcified Tissue International 49:128–133.

Iijima, M., & Y. Moriwaki. 1990. Orientation of apatite and organic matrix in *Lingula unguis* shell. Calcified Tissue International 47:237–242.

Iijima, M., Y. Moriwaki, Y. Doi, & Y. Kuboki. 1988. The orientation of apatite crystals in *Lingula unguis* shell. Japanese Journal of Oral Biology 30:20–30.

Iijima, M., Y. Moriwaki, & Y. Kuboki. 1991. Orientation of apatite and the organic matrix in *Lingula* shells, p. 433–437. *In* S. Suga & H. Nakahara, eds., Mechanisms and Phylogeny of Mineralization of Biological Systems. Springer-Verlag. Tokyo.

Ikeda, T. 1974. Nutritional ecology of marine zooplankton. Memoires of the Faculty of Fisheries, Hokkaido University 21:19–112.

Irwin, D. H. 1991. Metazoan phylogeny and the Cambrian radiation. Trends in Ecology and Evolution 6:131–134.

Ishikawa, Hajime. 1977. Comparative studies on the thermal stability of animal ribosomal RNAs: V. Tentaculata (Phoronids, moss-animals and lampshells). Comparative Biochemistry and Physiology 57B:9–14.

Ivanov, C. P., & R. Z. Stoyanova. 1972. Aliphatic hydrocarbons in fossils of Mesozoic belemnites. Comptes-Rendus de l'Académie Bulgare des Sciences 25(5):637–639.

Ivanov, C. P., R. Z. Stoyanova, & C. P. Daskalov. 1975. Content and composition of higher fatty acids in fossils of Mesozoic belemnites. Comptes-Rendus de l'Académie Bulgare des Sciences 28(7):935–938.

Iwata, K. 1981. Ultrastructure and mineralization of the shell of *Lingula unguis* Linné (Inarticulate Brachiopod). Journal of the Faculty of Science of Hokkaido University (series IV) 20(1):35–65.

———. 1982. Ultrastructure and calcification of the shells in inarticulate brachiopods Part 2. Ultrastructure of the shells of *Glottidia* and *Discinisca.* Journal of the Geological Society of Japan 88:957–966, 5 pl.

Jaanusson, Valdar. 1971. Evolution of the brachiopod hinge. *In* J. T. Dutro, Jr., ed., Paleozoic Perspectives:

A Paleontological Tribute to G. Arthur Cooper. Smithsonian Contributions to Paleobiology 3:33–46, 6 fig., pl. 1–2.

Jackson, J. B., T. F. Goreau, & W. D. Hartman. 1971. Recent brachiopod-coralline sponge communities and their paleoecological significance. Science 173:623–625.

Jacobs, H. T., P. Balfe, B. L. Cohen, A. Farquharson, & L. Comito. 1988. Phylogenetic implications of genome rearrangement and sequence evolution in echinoderm mitochondrial DNA. *In* C. R. C. Paul & A. B. Smith, eds., Echinoderm Phylogeny and Evolutionary Biology. Clarendon Press. Oxford. p. 121–137.

Jaeger, J. A., D. H. Turner, & M. Zuker. 1989a. Improved predictions of secondary structure for RNA. Proceedings of the National Academy of Sciences, USA 86:7706–7710.

———. 1989b. Predicting optimal and suboptimal secondary structure for RNA. Methods in Enzymology 183:281–306.

James, M. A., A. D. Ansell, & G. B. Curry. 1991a. Reproductive cycle of the brachiopod *Terebratulina retusa* on the west coast of Scotland. Marine Biology 109:441–451.

———. 1991b. Functional morphology of the gonads of the articulate brachiopod *Terebratulina retusa.* Marine Biology 111:401–410.

———. 1991c. Oogenesis in the articulate brachiopod *Terebratulina retusa.* Marine Biology 111:411–423.

James, M. A., A. D. Ansell, M. J. Collins, G. B. Curry, L. S. Peck, & M. C. Rhodes. 1992. Biology of living brachiopods. Advances in Marine Biology 28:175–387.

Jin, Yu-gan, & Hua-yu Wang. 1992. Revision of the Lower Cambrian brachiopod *Heliomedusa* Sun & Hou, 1987. Lethaia 25(1):35–49, fig. 1–14.

Johnson, J. G., & P. Westbroek. 1971. Cardinalia terminology in rhynchonellid brachiopods. Geological Society of America Bulletin 82:1699–1702.

Jones, G. J., & J. L. Barnard. 1963. The distribution and abundance of the inarticulate brachiopod *Glottidia albida* (Hinds) on the mainland of southern California. Pacific Naturalist 4(2):27–52.

Jope, H. M. 1965. Composition of brachiopod shell. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 156–164.

———. 1967a. The protein of brachiopod shell. I. Amino acid composition and implied protein taxonomy. Comparative Biochemistry and Physiology 20:593–600.

———. 1967b. The protein of brachiopod shell. II. Shell protein from fossil articulates: amino acid composition. Comparative Biochemistry and Physiology 20:601–605.

———. 1969a. The protein of brachiopod shell. III. Comparison with structural protein of soft tissue. Comparative Biochemistry and Physiology 30:209–224.

———. 1969b. The protein of the brachiopod shell. IV. Shell protein from fossil inarticulates: amino acid composition and disc electrophoresis of fossil articulate shell protein. Comparative Biochemistry and Physiology 30:225–232.

———. 1971. Constituents of brachiopod shells. *In* M. Florkin & E. H. Stotz, eds., Comprehensive Biochemistry. Elsevier. Amsterdam. p. 749–784.

———. 1973. The protein of brachiopod shell. V. N-terminal end groups. Comparative Biochemistry and Physiology 45B:17–24.

———. 1977. Brachiopod shell proteins: their function and taxonomic significance. American Zoologist 17:133–140.

———. 1979. The protein of brachiopod shell. VI. C-terminal end groups and sodium dodecylsulphate-polyacrylamide gel electrophoresis: molecular constitution and structure of the protein. Comparative Biochemistry and Physiology 63B:163–173.

———. 1980. Phylogenetic information from fossil brachiopods. *In* P. E. Hare, T. C. Hoering, & K. J. King, eds., Biogeochemistry of Amino Acids. John Wiley & Sons. New York. p. 83–94.

———. 1986. Evolution of the Brachiopoda: the molecular approach. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 103–111.

Jørgensen, C. B. 1981. A hydromechanical principle for particle retention in *Mytilus edulis* and other ciliary suspension feeders. Marine Biology 61:277–282.

Jørgensen, C. B., T. Kiørboe, F. Mohlenberg, & H. U. Riisgard. 1984. Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. Marine Ecology Progress Series 15:283–292.

Joshi, J. G., & B. Sullivan. 1973. Isolation and preliminary characterisation of haemerythrin for *Lingula unguis.* Comparative Biochemistry and Physiology 44B:857–867.

Joubin, L. 1886. Recherches sur l'anatomie des brachiopodes inarticulés. Archives de Zoologie Expérimentale et Générale (série 2) 4:161–303.

Jux, U., & F. Strauch. 1966. Die mitteldevonische Brachiopoden-Gattung *Uncites* de France 1825. Palaeontographica 56:176–222.

Källersjö, M., J. S. Farris, A. G. Kluge, & C. Bult. 1992. Skewness and permutation. Cladistics 8:275–287.

Karlin, S., & A. M. Campbell. 1994. Which bacterium is the ancestor of the animal mitochondrial genome? Proceedings of the National Academy of Sciences, USA 91:12842–12846.

Kawaguti, S. 1941. Hemerythrin found in the blood of *Lingula.* Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University, Formosa (Zoology, Number 12) 23:95–98.

———. 1943. A biometrical study on *Lingula unguis* (Linné). Venus 12(3/4):171–182.

In Japanese.

Kelly, P. G., P. T. P. Oliver, & F. G. E. Pautard. 1965. The shell of *Lingula unguis. In* Proceedings of the

Second European Symposium on Calcified Tissue. Liège, Belgium. p. 337–345.

Kemezys, K. J. 1965. Significance of punctae and pustules in brachiopods. Geological Magazine 102:315–324.

———. 1968. Arrangements of costellae, setae and vascula in enteletacean brachiopods. Journal of Paleontology 42:88–93, 1 fig.

Kenchington, R. A., & L. S. Hammond. 1978. Population structure, growth and distribution of *Lingula anatina* (Brachiopoda) in Queensland, Australia. Journal of Zoology 184:63–81.

Kimble, J. 1994. An ancient molecular mechanism for establishing embryonic polarity? Science 266:577–578.

King, K., Jr., & P. E. Hare. 1972. Amino acid composition of the test as a taxonomic character for living and fossil planktonic foraminifera. Micropaleontology 18:285–293.

Kirtisinghe, P. 1949. Unicellular algae in association with invertebrates. Nature 164:970.

Kleiber, M. 1947. Body size and metabolic rate. Physiological Reviews 27:511–541.

———. 1965. Metabolic body size. *In* K. L. Blaxter, ed., Energy Metabolism. Proceedings of the 3rd Symposium, Troon, Scotland. Academic Press. London. p. 427–435.

Klippenstein, G. L. 1980. Structural aspects of haemerythrin and myohaemerythrin. American Zoologist 20:39–51.

Kniprath, E. 1975. Das Wachstum des Mantels von *Lymnaea stagnalis* (Gastropoda). Cytobiologie 10:260–267.

Knowlton, N. 1993. Sibling species in the sea. Annual Review of Ecology and Systematics 24:189–216.

Kolesnikov, C. M., & E. L. Prosorovskaya. 1986. Biochemical investigation of Jurassic and recent brachiopod shells. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 113–119.

Komiya, H., N. Shimizu, M. Kawakami, & S. Takemura. 1980. Nucleotide sequence of 5S ribosomal RNA from *Lingula anatina.* Journal of Biochemistry 88:1449–1456.

Kovalevskiy, A. O. 1874. Nablyudeniya Nad Razvitiem Brachiopoda [On the development of the Brachiopoda]. Izvestiya Obschestvo Liubiteley Estestvoznaniya, Anthropologii i Etnografii [Proceedings of the Imperial Society for Natural Science, Anthropology, and Ethnology, Moscow] 14:1–40, pl. 1–5.

In Russian.

———. 1883. Observations sur le développement des brachiopodes, Analyse par Oehlert et Deniker. Archives de Zoologie Expérimentale et Générale (series 2) 1:57–76.

Kozlowski, Roman. 1929. Les brachiopodes gothlandiens de la Podolie polonaise. Palaeontologia Polonica 1:1–254, pl. 1–12.

Krans, Th. F. 1965. Études morphologiques de quelques spirifères Dévoniens de la Chaine Cantabrique (Espagne). Leidse Geologische Mededelingen 33:73–148, 71 fig., pl. 1–16.

Kuga, Hiroto, & Akira Matsuno. 1988. Ultrastructural investigations on the anterior adductor muscle of a brachiopod, *Lingula unguis.* Cell Structure and Function 13:271–279.

Kume, M. 1956. The spawning of *Lingula.* Natural Science Report of Ochanomizu University, Tokyo 6:215–223.

Kume, M., & K. Dan. 1968. Invertebrate Embryology. Nolit Publishing House. Belgrade. 605 p.

LaBarbera, Michael. 1977. Brachiopod orientation to water movement. I. Theory, laboratory behavior and field observation. Paleobiology 3:270–287.

———. 1978. Brachiopod orientation to water movement: functional morphology. Lethaia 11:67–79.

———. 1981. Water flow patterns in and around three species of articulate brachiopods. Journal of Experimental Marine Biology and Ecology 55:185–206.

———. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. American Zoologist 24:71–84.

———. 1985. Mechanisms of spatial competition of *Discinisca strigata* (Inarticulata: Brachiopoda) in the intertidal of Panama. Biological Bulletin 168(1):91–105.

———. 1986a. The evolution and ecology of body size. *In* D. M. Raup & D. Jablonski, eds., Patterns and Processes of Life, Dahlem Conferenzen. Springer-Verlag. Berlin, Heidelberg. p. 69–98.

———. 1986b. Brachiopod lophophores: functional diversity and scaling. *In* P. R. Racheboeuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 313–321.

———. 1989. Analyzing body size as a factor in ecology and evolution. Annual Review of Ecology and Systematics 20:97–117.

———. 1990. Principles of design of fluid transport systems in zoology. Science 249:992–1000.

Lacaze-Duthiers, F. J. H. de. 1861. Histoire naturelle des Brachiopodes vivantes de la Méditerranée. Iie Monographie. Histoire naturelle de la Thécide (Thecidium mediterraneum). Annales des sciences naturelles Zoologie (série 4) 15:259–330.

Lankester, E. R. 1873. Summary of zoological observations made at Naples in the winter of 1871–1872. Annals and Magazine of Natural History (series 4) 11:81.

Laurie, John. 1987. The musculature and vascular systems of two species of Cambrian Paterinide (Brachiopoda). Bureau of Mineral Resources Journal of Australian Geology and Geophysics 10:261–265.

Law, R. H., & C. W. Thayer. 1991. Articulate fecundity in the Phanerozoic: Steady state or what? *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 183–190.

Lee, D. E. 1978. Aspects of the ecology and paleoecology of the brachiopod *Notosaria nigricans* (Sowerby). Journal of the Royal Society of New Zealand 8:395–417.

———. 1987. Cenozoic and recent inarticulate brachiopods of New Zealand: *Discina, Pelagodiscus* and *Neocrania.* Journal of the Royal Society of New Zealand 17(1):49–72.

LeGeros, R. Z., C.-M. Pan, S. Suga, & Norimitsu Watabe. 1985. Crystallo-chemical properties of apatite in atremate brachiopod shells. Calcified Tissue International 37:98–100.

Leroy, P. 1936. "*Lingula anatina*" Lamarck (1809) dans les mers froides de Chine. Bulletin de la Société des Sciences de Nancy 5:121–124.

Livingstone, A. 1983. Invertebrate and vertebrate pathways of anaerobic metabolism: evolutionary considerations. Journal of the Geological Society of London 140:27–37.

Livingstone, D. R., A. De Zwann, M. Leopold, & E. Marteljn. 1983. Studies on the phylogenetic distribution of pyruvate oxidoreductases. Biochemical Systematics and Ecology 11:415–425.

Lockhart, P. J., M. A. Steel, M. D. Hendy, & D. Penney. 1994. Recovering evolutionary trees under a more realistic model of sequence evolution. Molecular Biology and Evolution 11:605–612.

Logan, Alan. 1979. The recent Brachiopoda of the Mediterranean Sea. Bulletin de l'Institut Océanographique de Monaco 72(1434):1–112, 10 pl.

———. 1983. Brachiopoda collected by CANCAP 1-111 expeditions to the south-east North Atlantic. 1976–1978. Zoologische Mededelingen 57:165–189, 1 pl.

———. 1988. A new thecideid genus and species (Brachiopoda, recent) from the southeast North Atlantic. Journal of Paleontology 62:546–551.

———. 1990. Recent Brachiopoda from the Snellius and Luymes expeditions to the Surinam-Guyana Shelf, Bonaire-Curacao, and Saba Bank, Caribbean Sea, 1966 and 1969–1972. Zoologische Mededelingen 63:123–136.

———. 1993. Recent brachiopods from the Canarian-Cape Verdean region: diversity, biogeographic affinities, bathymetric range and life habits. Courier Forschungs-Institut Senckenberg, Frankfurt-am-Main 159:229–233.

Logan, Alan, J. P. A. Noble, & G. R. Webb. 1975. An unusual attachment of a recent brachiopod, Bay of Fundy, Canada. Journal of Paleontology 49:557–558.

Long, J. A. 1964. The embryology of three species representing three superfamilies of articulate Brachiopoda. Unpublished Ph.D. thesis. University of Washington. Seattle. 184 p.

Long, J. A., & S. A. Stricker. 1991. Brachiopoda. *In* A. Geise, J. S. Pearse, & V. B. Pearse, eds., Reproduction of Marine Invertebrates, Vol. 6. Blackwell Scientific. California. p. 47–84.

Longhurst, A. R. 1958. An ecological survey of the west African marine benthos. Colonial Office Fishery Publications 11:1–102.

Ludvigsen, R. 1974. A new Devonian acrotretid (Brachiopoda, Inarticulata) with unique protegular ultrastructure. Neues Jahrbuch für Geologie und Palaeontologie, Monatshefte 3:133–148.

Lum, S. C., & C. S. Hammen. 1964. Ammonia excretion in *Lingula.* Comparative Biochemistry and Physiology 12:185–190.

Lutz, R. A., & D. C. Rhoads. 1977. Anaerobiosis and a theory of growth line formation. Science 198:1222–1227.

Mackay, Sarah, & R. A. Hewitt. 1978. Ultrastructural studies on the brachiopod pedicle. Lethaia 11: 331–339.

Mackay, Sarah, D. I. MacKinnon, & Alwyn Williams. 1994. Ultrastructure of the loop of terebratulide brachiopods. Lethaia 26:367–378.

MacKinnon, D. I. 1971. Perforate canopies to canals in the shells of fossil Brachiopoda. Lethaia 4:321–325.

———. 1974. The shell structure of spiriferide Brachiopoda. British Museum (Natural History) Bulletin (Geology) 25(3):189–261, 27 fig., pl. 1–32.

———. 1977. The formation of muscle scars in articulate brachiopods. Philosophical Transactions of the Royal Society of London (series B, Biological Sciences) 280(970):1–27, 86 fig., pl. 1–11.

———. 1991. A fresh look at growth of spiral brachidia. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 147–153, 6 fig.

MacKinnon, D. I., & Alwyn Williams. 1974. Shell structure of terebratulid brachiopods. Palaeontology 17(1):179–202, 3 fig., pl. 21–27.

Macomber, R. W., & Lenore Macomber. 1983. Ribbing patterns in the brachiopod *Diceromyonia.* Lethaia 16:25–37.

Maddison, W. P., M. J. Donoghue, & D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33:83–103.

Mahajan, S. N., & M. C. Joshi. 1983. Age and shell growth in *Lingula anatina* (Lam.). Indian Journal of Marine Sciences 12:120–121.

Maidak, B. L., N. Larsen, M. J. McCaughey, R. Overbeek, G. L. Olsen, K. Fogel, J. Blandy, & C. R. Woese. 1994. The ribosomal database project. Nucleic Acids Research 22:3485–3487.

Malakhov, V. V. 1976. Certain stages of embryogenesis in *Cnismatocentrum sakhaliensis parvum* (Brachiopoda, Testicardines) and the problem of evolution of the way of origin of coelomic mesoderm. Zoologicheski Zhurnal 55:66–75.

Manankov, I. N. 1979. Pseudopunctae in strophomenids. Paleontological Journal 3:332–338.

Translation of O psevdoporakh strofomenid. Paleontologicheskii Zhurnal 3(13):72–78.

Mancenido, M. O., & Miguel Griffin. 1988. Distribution and palaeoenvironmental significance of the genus *Bouchardia* (Brachiopoda, Terebratellidina): its bearing on the Cenozoic evolution of the South Atlantic. Revista Brasileira de Geociencias 18(2):201–211, pl. 1.

Mano, R. 1960. On the metamorphosis of the brachiopod *Frenulina sanguinolenta* (Gmelin). Bulletin of

the Marine Biological Station of Asamushi 10:171–175.
Marshall, A. G., & L. Medway. 1976. A mangrove community in the New Hebrides, southwest Pacific. Biological Journal of the Linnean Society 8:319–336.
Martinez-Chacon, M. L., & J. L. Garcia-Alcalde. 1978. La genesis del koskinoide en braquiopodos articulados. Revista de la Facultad de Ciencias, Universidad de Oviedo 17–19:261–279.
Mattox, M. T. 1955. Observations on the brachiopod communities near Santa Catalina. *In* Essays in the Natural Sciences in Honor of Captain Allan Hancock. University of Southern California Press. Los Angeles. p. 73–86.
Mauzey, K. P., C. Birkeland, & P. K. Dayton. 1968. Feeding behaviour of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49:603–619.
Mayzaud, P. 1973. Respiration and nitrogen excretion of zooplankton II. Studies of the metabolic characteristics of starved animals. Marine Biology 21:19–28.
McCammon, H. M. 1965. Filtering currents in brachiopods measured with a thermistor flowmeter. Ocean Science Engineering 2:772–779.
———. 1969. The food of articulate brachiopods. Journal of Paleontology 43:976–985.
———. 1970. Variation in recent brachiopod populations. Bulletin of the Geological Institutions of the University of Uppsala (new series) 2:41–48.
———. 1971. Behaviour in the brachiopod *Terebratulina septentrionalis* (Couthouy). Journal of Experimental Marine Biology and Ecology 6:35–45.
———. 1973. The ecology of *Magellania venosa,* an articulate brachiopod. Journal of Paleontology 47:266–278.
———. 1981. Physiology of the brachiopod digestive system. *In* T. W. Broadhead, ed., Lophophorates, Notes for a Short Course. University of Tennessee Department of Geological Sciences, Studies in Geology 5:170–204.
McCammon, H., & R. Buchsbaum. 1968. Size and shape variation of three recent brachiopods from the Strait of Magellan. Antarctic Research Series 2:215–225.
McCammon, H. M., & W. A. Reynolds. 1976. Experimental evidence for direct nutrient assimilation by the lophophore of articulate brachiopods. Marine Biology 34:41–51.
McConnell, D. 1963. Inorganic constituents in the shell of the living brachiopod *Lingula.* Geological Society of America Bulletin 74:363–364.
McCrady, J. 1860. On the *Lingula pyramidata* described by Mr. W. Stimpson. American Journal of Science Arts (series 2) 30:157–158.
McDaniel, N. G. 1973. A survey of the benthic macroinvertebrate fauna and solid pollutants in Howe Sound. Fisheries Board of Canada, Technical Report 385:1–64.
Mickwitz, August. 1896. Über die Brachiopodengathung *Obolus* Eichwald. Académie Impériale des Sciences de St. Petersbourg, Mémoires (série 8) 4(2):215 p., 7 fig., 3 pl.
Mileikovsky, S. A. 1970. Distribution of pelagic larvae of bottom invertebrates in Kurile-Kamtchatka area. *In* V. G. Bogorov, ed., Fauna of the Kurile-Kamtchatka Trench and Its Environment. Nauka. Moscow. p. 124–143.

In Russian, translated in English.

Mineur, R. J., & J. R. Richardson. 1984. Free and mobile brachiopods from New Zealand Oligocene deposits and Australian waters. Alcheringa 8(3–4):327–334, fig. 1–5.
Mohlenberg, F., & H. U. Riisgard. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 14:239–246.
Moore, R. C., ed. 1965. Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & The University of Kansas Press. New York & Lawrence. xxxii + 927 p., 746 fig.
Morse, E. S. 1873. Embryology of *Terebratulina.* Memoirs of the Boston Society of Natural History 2:249–264, pl. 8–9.
———. 1902. Observations on living Brachiopoda. Memoirs of the Boston Society of Natural History 5(8):313–386.
Morton, J. E. 1960. The functions of the gut in ciliary feeders. Biological Reviews 35:92–140.
Muir-Wood, H. M. 1934. On the internal structure of some Mesozoic Brachiopoda. Royal Society of London Philosophical Transactions (series B) 223:511–567, pl. 62–63.
———. 1962. On the morphology and classification of the brachiopod suborder Chonetoidea. British Museum (Natural History), monograph. viii + 132 p., 24 fig., 16 pl.
———. 1965. Mesozoic and Cenozoic Terebratulidina. *In* R. C. Moore, ed., Treatise of Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. Boulder & Lawrence. p. 762–816, fig. 622–695.
Muir-Wood, H. M., & G. A. Cooper. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). Geological Society of America Memoir 81:477 p., 135 pl.
Muir-Wood, H. M., G. F. Elliott, & Kotora Hatai. 1965. Mesozoic and Cenozoic Terebratellidina. *In* R. C. Moore, ed., Treatise of Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. Boulder & Lawrence. p. 816–857, fig. 696–741.
Müller, F. 1860. Beschreibung einer Brachiopoden Larva. Archives für Anatomie und Physiologie:72–79.
Neall, V. E. 1972. Systematics of the endemic New Zealand brachiopod *Neothyris.* Journal of the Royal Society of New Zealand 2:229–247.
Negri, A., G. Tedeschi, F. Bonomi, J-H. Zhang, & D. M. Kirtz. 1994. Amino-acid sequences of the alpha- and beta-subunits of hemerythrin from *Lingula reevii.* Biochimica et Biophysica Acta 1208:277–285.
Nekvasilova, O., & D. Pajaud. 1969. Le mode de fixation chez *Bifolium lacazelliforme* Elliot (Thecideidae Gray, Brachiopodes) au substrat. Casopis pro

Mineralogii a geologii 14:323–330.
Nielsen, Claus. 1987. The structure and function of metazoan ciliary bands and their phylogenetic significance. Acta Zoologica 68(4):205–262.
———. 1991. The development of the brachiopod *Crania (Neocrania) anomala* (O. F. Müller) and its phylogenetic significance. Acta Zoologica 72:7–28.
———. 1994. Larval and adult characters in animal phylogeny. American Zoologist 34:492–501.
———. 1995. Animal Evolution: Interrelationships of the Living Phyla. Oxford University Press. Oxford. 467 p.
Nixon, K. C., & J. M. Carpenter. 1993. On outgroups. Cladistics 9:413–426.
Noble, J. P. A., & A. Logan. 1981. Size-frequency distributions and taphonomy of brachiopods: a recent model. Palaeogeography, Palaeoclimatology, Palaeoecology 36:87–105.
Noble, J. P. A., A. Logan, & G. R. Webb. 1976. The recent *Terebratulina* community in the rocky subtidal zone of the Bay of Fundy, Canada. Lethaia 9:1–17.
Nomura, S., & K. M. Hatai. 1936. A note on *Coptothyris grayi* (Davidson). Saito Ho-on Kai Museum Research Bulletin 10:209–217.
Norford, B. S., & H. M. Steele. 1969. The Ordovician trimerellid brachiopod *Eodinobolus* from southeast Ontario. Palaeontology 12(1):161–171, pl. 32–33.
Norman, A. M. 1893. A month on the Trondhjem. Annals and Magazine of Natural History (series 6) 12:340–367.
Odhner, N. H. 1960. Brachiopoda. Report of the Swedish Deep-Sea Expedition 2(4):23.
Ohuye, T. 1937. On the coelomic corpuscles in the body fluid of some invertebrates VIII. Supplementary note on the formed elements in the coelomic fluid of some Brachiopoda. Scientific Reports of Tohoku University (series 4, Biology) 11:231–238.
Olsen, G. J., H. Matsuda, R. Hagstrom, & R. Overbeek. 1994. fastDNAml: a tool for construction of phylogenetic trees of DNA sequences using maximum likelihood. Computer Applications in the Biological Sciences 10:41–48.
Onyia, A. D. 1973. Contribution to the food and feeding habit of the threadfin *Galeoides decadactylus.* Marine Biology 22(4):371–378.
Öpik, A. A. 1930. Brachiopoda protremata der estlandischen Ordovizischen kukruse-stufe. Tartu Ulikooli Geoloogia-Instituudi Toimestuesed Acta et Commentationes Universitatis Tartuensis 17:1–261, pl. 1–22.
———. 1933. Über die Plectamboniten. Tartu Ulikooli Geoloogia-Instituudi Toimestuesed Acta et Commentationes Universitatis Tartuensis 28:1–79, 6 fig., pl. 1–12.
———. 1934. Über die Klitamboniten. Tartu Ulikooli Geoloogia-Instituudi Toimestuesed Acta et Commentationes Universitatis Tartuensis 39:1–239, 55 fig., pl. 1–48.
Oró, J. & H. B. Skewes. 1965. Free amino acids on human fingertips: the question of contamination in microanalysis. Nature 207:1042–1045.
Owen, G., & Alwyn Williams. 1969. The caecum of articulate Brachiopoda. Proceedings of the Royal Society of London (series B) 172:187–201.
Paine, R. T. 1962a. Ecological notes on a gymnophalline *Metacercaria* from the brachiopod *Glottidia pyramidata.* Journal of Parasitology 48(3):509.
———. 1962b. Filter-feeding pattern and local distribution of the brachiopod *Discinisca strigata.* Biological Bulletin 123:597–604.
———. 1963. Ecology of the brachiopod *Glottidia pyramidata.* Ecological Monographs 33:187–213.
———. 1969. Growth and size distribution of the brachiopod *Terebratalia transversa* Sowerby. Pacific Science 23:337–343.
———. 1970. The sediment occupied by recent lingulid brachiopods and some paleoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 7:21–31.
Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? Nature 292:150–152.
———. 1983. Relative cost of producing skeletal organic matrix versus calcification: evidence from marine gastropods. Marine Biology 75:287–292.
Pan, C.-M., & Norimitsu Watabe. 1988a. Uptake and transport of shell minerals in *Glottidia pyramidata* Stimpson (Brachiopoda: Inarticulata). Journal of Experimental Marine Biology and Ecology 118:257–268, fig. 1–14.
———. 1988b. Shell growth of *Glottidia pyramidata* Stimpson (Brachiopoda: Inarticulata). Journal of Experimental Marine Biology and Ecology 119:43–53, fig. 1–21.
———. 1989. Periostracum formation and shell regeneration in the lingulid *Glottidia pyramidata* (Brachiopoda: Inarticulata). Transactions of the American Microscopical Society 108(3):283–289.
Pandian, T. J., & F. J. Vernberg. 1987. Animal Energetics, Volume 2, Bivalvia through Reptilia. Academic Press. San Diego. 631 p.
Patel, N. H. 1994. Developmental evolution: insights from studies of insect segmentation. Science 266:581–590.
Patterson, Colin. 1985. Introduction. *In* C. Patterson, ed., Molecules and Morphology in Evolution. Third International Congress of Systematic & Evolutionary Biology, University of Sussex, July 1985. Cambridge University Press. p. 1–22.
———. 1989. Phylogenetic relations of major groups: conclusions and prospects. *In* B. Fernholm, K. Bremer, & H. Jörnvall, eds., The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis. Proceedings from Nobel Symposium 70, 1988. Elsevier. Amsterdam. p. 471–488.
Peck, L. S. 1989. Temperature and basal metabolism in two Antarctic marine herbivores. Journal of Experimental Marine Biology and Ecology 127:1–12.
———. 1992. Body volumes and internal space constraints in articulate brachiopods. Lethaia 25:383–390.
———. 1993. The tissues of articulate brachiopods and their value to predators. Philosophical Transac-

tions of the Royal Society of London (series B) 339:17–32.

Peck, L. S., A. Clarke, & L. J. Holmes. 1987a. Size, shape and the distribution of organic matter in the recent Antarctic brachiopod *Liothyrella uva.* Lethaia 20:33–40.

———. 1987b. Summer metabolism and seasonal changes in biochemical composition of the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). Journal of Experimental Marine Biology and Ecology 114:85–97.

Peck, L. S., G. B. Curry, A. D. Ansell, & Mark James. 1989. Temperature and starvation effects on the metabolism of the brachiopod *Terebratulina retusa* (L.). Historical Biology 2:101–110.

Peck, L. S., & L. J. Holmes. 1989a. Scaling patterns in the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). Journal of Experimental Marine Biology and Ecology 133:141–150, fig. 1–3.

———. 1989b. Seasonal and ontogenetic changes in tissue size in the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). Journal of Experimental Marine Biology and Ecology 134:25–36, fig. 1–2.

Peck, L. S., D. J. Morris, & Andrew Clarke. 1986a. Oxygen consumption and the role of caeca in the recent Antarctic brachiopod *Liothyrella uva notorcadensis* (Jackson, 1912). *In* P. R. Rachebœuf & C. C. Emig, eds., Les Brachiopodes Fossiles et Actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. Biostratigraphie du Paléozoïque 4. p. 349–355.

———. 1986b. The caeca of punctate brachiopods: a respiring tissue not a respiratory organ. Lethaia 19:232, fig. 1.

Peck, L. S., D. J. Morris, A. Clarke, & L. J. Holmes. 1986. Oxygen consumption and nitrogen excretion in the Antarctic brachiopod *Liothyrella uva* (Jackson, 1912) under simulated winter conditions. Journal of Experimental Marine Biology and Ecology 104:203–213.

Peck, L. S., & K. Robinson. 1994. Pelagic larval development in the brooding Antarctic brachiopod *Liothyrella uva.* Marine Biology 120:279–286.

Pedersen, Fl. Bo. 1978. A brief review of present theories of fjord dynamics. *In* C. J. Nihoul, ed., Hydrodynamics of Estuaries and Fjords. Elsevier Scientific Publishing Company. Amsterdam. p. 407–422.

Percival, E. 1944. A contribution to the life-history of the brachiopod *Terebratella inconspicua* Sowerby. Transactions of the Royal Society of New Zealand 74:1–23, pl. 1–7.

———. 1960. A contribution to the life history of the brachiopod *Tegulorhynchia nigricans.* Quarterly Journal of Microscopical Science 101:439–457.

Philippe, Hervé, A. Chenuil, & A. Adoutte. 1994. Can the Cambrian explosion be inferred through molecular phylogeny? *In* M. Akam, P. Holland, P. Ingham, & G. Wray, eds., The Evolution of Developmental Mechanisms. Development, 1994 Supplement. Company of Biologists. Cambridge. p. 15–25.

Plenk, H. 1913. Die Entwicklung von *Cistella (Argiope) neopolitana*. Arbeiten aus dem Zoologischen Institute der Universitaet Wien und der Zoologischen Station in Triest, Wien 20:93–108.

Popov, L. Ye. 1992. The Cambrian radiation of brachiopods. Topics in Geobiology 10:399–423, 6 fig.

Popov, L. Ye., M. G. Bassett, L. E. Holmer, & J. Laurie. 1993. Phylogenetic analysis of higher taxa of Brachiopoda. Lethaia 26:1–5.

Popov, L. Ye., & Yu. A. Tikhonov. 1990. Rannekembriiskie brakhiopody iz iuzhnoi Kirgizii [Early Cambrian brachiopods from south Kirgizii]. Paleontologicheskii Zhurnal 1990(3):33–44, 2 fig., pl. 3–4.

Popov, L. Ye., & G. T. Ushatinskaya. 1987. Novyye dannyye o mikrostrukture rakoviny bezzamkovykh brakhiopod otryada Paterinida [New data on the microstructure of the shell in inarticulate brachiopods of the Order Paterinida]. Doklady Akademii Nauk Soyuza Sovetskikh Sotsialisticheskikh Republik [Academy of Sciences of the USSR, Reports] 293(5):1228–1230.

Popov, L. Ye., O. N. Zezina, & J. Nolvak. 1982. Mikrostruktura apikal'noy chasti rakoviny bezzamkovykh brakhiopod i eye paleoecologicheskoye znacheniye [Microstructure of the apical part of the shell in inarticulate brachiopods and its paleoecological significance]. Byuletin' Moskovskogo obshchestva ispytatelej prirody, otdel biologicheskij [Moscow Society of Natural History, Branch of Biology, Bulletin] 87:94–104.

Poulsen, V. 1971. Notes on an Ordovician acrotretacean brachiopod from the Oslo region. Bulletin of the Geological Society of Denmark 20:265–278.

Powls, R., & G. Britton. 1976. A carotenoprotein violaxanthin, isolated from scenedesmus obliquus D3. Biochimica et Biophysica Acta 453:270–276.

Prenant, M. 1928. Notes histologiques sur *Terebratulina caput-serpentis* L. Bulletin de la Société Zoologique de France 59:113–125.

Pross, A. 1980. Untersuchungen zur Gliederung von *Lingula anatina* (Brachiopoda). Archimerie bei Brachiopoden. Zoologische Jahrbücher, abteilung für Anatomie und Ontogenie der Tiere 103:250–263.

Punin, M. Y., & M. V. Filatov. 1980. The epithelium organisation in the digestive gland of the articulate brachiopod *Hemithyris psittacea.* Citologija 22(3):277–286.

In Russian.

Racheboeuf, P. R. 1973. Données nouvelles sur le développement des épines chez certains Brachiopods Chonetacea du Massif Armoricain. Compte-Rendus de l'Académie des Sciences de Paris 277(D):1741–1744.

Racheboeuf, P. R., & Paul Copper. 1990. The mesolophe, a new lophophore type for chonetacean brachiopods. Lethaia 23(4):341–346, 5 fig.

Raff, R. A., C. R. Marshall, & J. M. Turbeville. 1994. Using DNA sequences to unravel the Cambrian

radiation of the animal phyla. Annual Review of Ecology and Systematics 25:351–375.
Ramamoorthi, K., K. Venkataramanujam, & B. Srikrishnadhas. 1973. Mass mortality of *Lingula anatina* (Lam.) (Brachiopoda) in Porto-Novo waters, S. India. Current Science 42(8):285–286.
Rand, D. M. 1993. Endotherms, ectotherms and mitochondrial genome-size variation. Journal of Molecular Evolution 37:281–295.
Reed, C. G. 1987. Phylum Brachiopoda Coast. *In* M. Strathmann, ed., Reproduction and Development of Marine Invertebrates of the Northern Pacific. University of Washington Press. Seattle. p. 486–493.
Reed, C. G., & R. A. Cloney. 1977. Brachiopod tentacles: ultrastructure and functional significance of the connective tissue and myoepithelial cells in Terebratalia. Cell and Tissue Research 185:17–42.
Regnault, M. 1987. Nitrogen excretion in marine and fresh-water Crustacea. Biological Reviews 62:1–24.
Reynolds, W. A., & H. M. McCammon. 1977. Aspects of the functional morphology of the lophophore in articulate brachiopods. American Zoologist 17:121–132.
Rhodes, M. C. 1990. Extinction patterns and comparative physiology of brachiopods and bivalves. PhD. thesis, Department of Geology, University of Pennsylvania. Philadelphia. 152 p.
Rhodes, M. C., & C. W. Thayer. 1991. Effects of turbidity on suspension feeding: Are brachiopods better than bivalves? *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 191–196.
Rhodes, M. C., & R. J. Thompson. 1992. Clearance rate of the articulate brachiopod *Neothyris lenticularis* (Deshayes, 1839). Journal of Experimental Marine Biology and Ecology 163:77–89.
———. 1993. Comparative physiology of suspension feeding in living brachiopods and bivalves: evolutionary implications. Paleobiology 19:322–334.
Richards, J. R. 1952. The ciliary feeding mechanism of *Neothyris lenticularis* (Deshayes). Journal of Morphology 90:65–91, fig. 1–6.
Richardson, J. R. 1973. Studies on Australian Cainozoic Brachiopods 3. The subfamily Bouchardiinae (Terebratellidae). Royal Society of Victoria Proceedings 86(1):127–132, pl. 7.
———. 1975. Loop development and the classification of terebratellacean brachiopods. Palaeontology 18(2):285–314, 4 fig., pl. 44.
———. 1979. Pedicle structure of articulate brachiopods. Journal of the Royal Society of New Zealand 9:415–436.
———. 1980. Studies on Australian Cainozoic brachiopods 5. The genera *Victorithyris* Allan and *Diedrothyris* nov. Memoirs of the National Museum of Victoria 41:43–52.
———. 1981a. Brachiopods in mud: resolution of a dilemma. Science 211:1161–1163.
———. 1981b. Brachiopods and pedicles. Paleobiology 7:87–95.
———. 1981c. Recent brachiopods from New Zealand. New Zealand Journal of Zoology 8:133–248.
———. 1981d. Distribution and orientation of six articulate species from New Zealand. New Zealand Journal of Zoology 8:189–196.
———. 1986. Brachiopods. Scientific American 254:100–106.
———. 1987. Brachiopods from carbonate sands of the Australian shelf. Proceedings of the Royal Society of Victoria 99:37–50.
———. 1991. Australasian Tertiary Brachiopoda. The subfamily Anakineticinae nov. Proceedings of the Royal Society of Victoria 103(1):29–45, fig. 1–5.
———. 1994. Origins and dispersal of a brachiopod family—the systematics, biogeography and evolution of the Family Terebratellidae. Proceedings of the Royal Society of Victoria 106:17–29.
Richardson, J. R., & R. J. Mineur. 1981. Differentiation of species of *Terebratella* (Brachiopoda: Terebratellinae). New Zealand Journal of Zoology 8:163–168.
Richardson, J. R., I. R. Stewart, & Liu Xixing. 1989. Brachiopods from Chinese Seas. Chinese Journal of Oceanology and Limnology 7:211–219, pl. 1–4.
Richardson, J. R., & J. E. Watson. 1975. Form and function in a recent free living brachiopod *Magadina cumingi.* Paleobiology 1:379–387.
Ricker, W. E. 1971. Methods for assessment of fish production in fresh waters. I. B. P. Handbook No. 3. Blackwell Scientific Publications. Oxford & Edinburgh, United Kingdom. 326 p.
Rickwood, A. E. 1968. A contribution to the life history and biology of the brachiopod *Pumilus antiquatus* Atkins. Transactions of the Royal Society of New Zealand (Zoology) 10:163–182, 10 fig.
———. 1977. Age, growth and shape of the intertidal brachiopod *Waltonia inconspicua* Sowerby, from New Zealand. American Zoologist 17:63–73, fig. 1–9.
Roberts, John. 1968. Mantle canal patterns in *Schizophoria* (Brachiopoda) from the Lower Carboniferous of New South Wales. Palaeontology 11(3):389–405, pl. 74–75.
Robertson, J. D. 1989. Physiological constraints upon marine organisms. Transactions of the Royal Society of Edinburgh, Earth Sciences 80:225–234.
Rokop, F. J. 1977. Seasonal reproduction of the brachiopod *Frieleia halli* and the scaphopod *Cadulus californicus* at bathyal depths in the deep sea. Marine Biology 43:237–246.
Rong, J.-Y., & L. R. M. Cocks. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and "strophodontoid" brachiopods. Palaeontology 37:651–694.
Rosenburg, G. D., & W. W. Hughes. 1991. A metabolic model for the determination of shell composition in the bivalve mollusc, *Mytilus edulis.* Lethaia 24:83–96.
Rosenberg, G. D., W. W. Hughes, & R. D. Tkachuck. 1988. Intermediatory metabolism and shell growth in the brachiopod *Terebratalia transversa.* Lethaia 21:219–230.
Rouse, G. W., & B. G. M. Jamieson. 1987. An ultra-

structural study of the spermatozoa of polychaetes *Eurythoe complanata* (Amphinomidae), *Clymnella* sp. and *Micromaldane* sp. (Maldanidae), with definition of sperm types in relation to reproductive biology. Journal of Submicroscopic Cytology 19:573–584.

Rowell, A. J. 1960. Some early stages in the development of the brachiopod *Crania anomala* (O. F. Müller). Annals and Magazine of Natural History (series 13) 3:35–52.

———. 1961. Inhalant and exhalant feeding current systems in recent brachiopods. Geological Magazine 98(3):261–263.

———. 1977. Valve orientation and functional morphology of the foramen of some siphonotretacean and acrotretacean brachiopods. Lethaia 10:43–50.

———. 1982. The monophyletic origin of the Brachiopoda. Lethaia 15:299–307.

Rowell, A. J., & N. E. Caruso. 1985. The evolutionary significance of *Nisusia sulcata,* an early articulate brachiopod. Journal of Paleontology 59:1227–1242, fig. 1–9.

Rowley, A. F., & P. J. Hayward. 1985. Blood cells and coelomocytes of the inarticulate brachiopod *Lingula anatina.* Journal of Zoology, London (series A) 205:9–18.

Rubenstein, D. I., & M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. American Naturalist 111:981–994.

Rudall, K. M. 1955. The distribution of collagen and chitin. Symposium of the Society for Experimental Biology 9:49–71.

———. 1969. Chitin and its association with other molecules. Journal of Polymer Science (Part C) 28:83–102.

Rudwick, M. J. S. 1959. The growth and form of brachiopod shells. Geological Magazine 94:1–24.

———. 1960. The feeding mechanisms of spire-bearing fossil Brachiopoda. Geological Magazine 97:369–383, 8 fig.

———. 1961. 'Quick' and 'catch' adductor muscles in brachiopods. Nature 191:1021.

———. 1962a. Filter feeding mechanisms in some brachiopods from New Zealand. Journal of the Linnean Society, Zoology 44:592–615.

———. 1962b. Notes on the ecology of brachiopods in New Zealand. Transactions of the Royal Society of New Zealand, Zoology 1:327–335.

———. 1965a. Ecology and paleoecology. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 199–214.

———. 1965b. Sensory spines in the Jurassic brachiopod *Acanthothiris.* Palaeontology 8:604–617, pl. 84–87.

———. 1970. Living and Fossil Brachiopods. Hutchinson and Co. Ltd. London. 199 p., 99 fig.

Runnegar, B., A. Scheltema, L. Jackson, M. Jebb, J. McC. Turbeville, & C. R. Marshall. In preparation. A molecular test of the hypothesis that Aplacophora are progenetic aculifera.

Russell, G. R., & J. H. Subak-Sharpe. 1977. Similarity of the general designs of protochordates and invertebrates. Nature 266:533–535.

Sandy, M. R. 1994. Triassic–Jurassic articulate brachiopods from the Pucará group, central Peru, and description of the brachidial net in the spiriferid *Spondylospira.* Palaeontographica A233:99–126.

Sandy, M. R., & M. R. Langenkamp. 1992. The brachidial net—a unique internal support structure in the Brachiopoda? Geological Society of America, Abstracts with Programs (Boulder) 24(7):A226.

Sass, D. B., E. A. Monroe, & D. T. Gerace. 1965. Shell structure of recent articulate Brachiopoda. Science 149:181–182.

Satake, K., M. Yugi, M. Kamo, H. Kihara, & A. Tsugita. 1990. Hemerythrin from *Lingula unguis* consists of two different subunits, alpha and beta. Protein Sequences and Data Analysis 3:1–5.

Savazzi, E. 1991. Burrowing in the inarticulate brachiopod *Lingula anatina.* Palaeogeography, Palaeoclimatology, Palaeoecology 85:101–106.

Sawada, N. 1973. Electron microscope studies on gametogenesis in *Lingula unguis.* Zoological Magazine 82:178–188.

Schaeffer, C. 1926. Untersuchungen zur vergleichenden Anatomie und Histologie der Brachiopodengattung *Lingula.* Acta Zoologica, Stockholm 7:329–402.

Schägger, H., & G. Von Jagow. 1987. Tricine-sodium dodecyl sulfate-polyacrylamide gel electrophoresis for the separation of proteins in the range from 1 to 100 kDa. Analytical Biochemistry 166:368–379.

Scheid, M. J., & J. Awapara. 1972. Stereospecificity of some invertebrate lactic dehydrogenases. Comparative Biochemistry and Physiology 43B:619–626.

Scheul, H. 1978. Secretory functions of egg cortical granules in fertilisation and development. A critical review. Gamete Research 1:299–382.

Schmidt, Herta. 1937. Zur Morphogenie der Rhynchonelliden. Senckenbergiana 19:22–60, fig. 1–56.

Schmidt-Nielsen, K. 1979. Animal Physiology: Adaptation and environment, second edition. Cambridge University Press. Cambridge. 560 p.

———. 1984. Scaling: Why is animal size so important? Cambridge University Press. Cambridge. 241 p.

Schram, F. R. 1983. Method and madness in phylogeny. *In* F. R. Schram, ed., Crustacean Issues I: Crustacean Phylogeny. Balkema. Amsterdam. p. 331–350.

———. 1991. Cladistic analysis of metazoan phyla and the placement of fossil problematica. *In* A. M. Simonetta & Simon Conway Morris, eds., The Early Evolution of the Metazoa and the Significance of Problematic Taxa. Cambridge University Press. Cambridge. p. 35–46.

Schuchert, Charles, & G. A. Cooper. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. Peabody Museum of Natural History Memoir 49(1):1–270, pl. 1–29.

Schulgin, M. A. 1885. Argiope kowalewskii (ein Beitrag zur Kenntniss der Brachiopoden). Zeitschrift für wissenschaftliche Zoologie 41:116–141.

Schumann, Dietrich. 1969. "Byssus" - artige

Stielmuskel - Konvergenzen bei artikulaten Brachiopoden. Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen 133:199–210.

———. 1970. Inäquivalver Schalenbau bei *Crania anomala.* Lethaia 3:413–421.

———. 1973. Mesodermale Endoskelette terebratulider Brachiopoden. I. Palaeontologische Zeitschrift 47(1–2):77–103, 10 fig., pl. 12–15.

———. 1991. Hydrodynamic influences in brachiopod shell morphology of *Terebratalia transversa* (Sowerby) from the San Juan Islands, USA. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 265–272.

Scott, M. P. 1994. Intimations of a creature. Cell 79:1121–1124.

Senn, E. 1934. Die Geschlechtsuerhaeltnisse der Brachiopoden im besonderen die Spermato—und Oogenese der *Lingula.* Acta Zoologica 15:1–154.

Sewell, R. B. S. 1912. Note on the development of the larva of *Lingula.* Records of the Indian Museum 7:88–90.

Shiells, K. A. G. 1968. *Kochiproductus coronus* sp. nov. from the Scottish Viséan and a possible mechanical advantage of its flange structure. Transactions of the Royal Society of Edinburgh 67:477–510, 20 fig., 1 pl.

Shimizu, N., & K-I. Miura. 1972. Studies on nucleic acids of living fossils. I. Isolation and characterization of DNA and some RNA components from the brachiopod *Lingula.* Animal ribosomes: Experimental studies of the last five years. MSS Information Corporation. New York. p. 19–25.

Shipley, A. E. 1883. On the structure and development of *Argiope.* Zoologie Stazione Neapoli, Mitteilungen 4:494–520.

Shipley, A. E., & E. W. MacBride. 1920. Zoology. 4th edition. Cambridge University Press. Cambridge. 752 p.

Short, G., & S. L. Tamm. 1991. On the nature of paddle cilia and discocilia. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Massachusetts 180:466–474.

Shumway, S. E. 1982. Oxygen consumption in brachiopods and the possible role of punctae. Journal of Experimental Marine Biology and Ecology 58:207–220.

Simon, J. L., & D. M. Dauer. 1977. Reestablishment of a benthic community following natural defaunation. *In* B. C. Coull, ed., Ecology of Marine Benthos. University of South Carolina Press, Columbia, Belle W. Baruch Library in Marine Science 6:139–154.

Singer, T. P. 1965. Comparative biochemistry of succinate dehydrogenase: forms and functions. *In* T. E. King, H. S. Mason, & M. Morrison, eds., Oxidases and Related Redox Systems. Wiley. New York. p. 448–481.

Smirnova, T. N., & E. Popiel-Barczyk. 1991. Characteristics of the shell ultrastructure in Terebratellacea. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 159–165.

Smith, A. B. 1994. Rooting molecular trees: problems and strategies. Biological Journal of the Linnean Society 51:279–292.

Smith, M. J., A. Arndt, S. Gorski, & E. Fajber. 1993. The phylogeny of echinoderm classes based on mitochondrial gene arrangements. Journal of Molecular Evolution 36:545–554.

Soota, T. D., & K. N. Reddy. 1976. On the distribution and habitat of the brachiopod *Lingula* in India. Newsletter of the Zoological Survey of India 2(6):235–237.

Steele, K. P., K. E. Holsinger, R. K. Jansen, & D. W. Taylor. 1991. Assessing the reliability of 5S rRNA sequence data for phylogenetic analysis in green plants. Molecular Biology and Evolution 8:240–248.

Steele-Petrovic, H. M. 1976. Brachiopod food and feeding processes. Palaeontology 19:417–436.

Stehli, F. G. 1956. Evolution of the loop and lophophore in terebratuloid brachiopods. Evolution 10:187–200, 9 fig.

———. 1965. Paleozoic Terebratulida. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 730–762, fig. 594–621.

Steinich, G. 1965. Die articulaten Brachiopoden der ruegener Schreibkreide (Unter-Maastricht). Geologische und Palaeontologische Abhandlungen (Abt. A) 2:220 p., 21 pl.

Stewart, I. R. 1975. Morphological variation within the recent brachiopod genus *Magellania.* Unpublished thesis submitted for Geology Fellowship Diploma. Royal Melbourne Institute of Technology. 13 p.

———. 1981. Population structure of articulate brachiopod species from soft and hard substrates. New Zealand Journal of Zoology 8:197–208.

St. Joseph, J. K. S. 1938. The Pentameracea of the Oslo region. Norsk Geologisk Tidsskrift 17:255–336, pl. 1–8.

Storch, Volker, & Ulrich Welsch. 1972. Über Bau und Entstehung der Mantelrandstacheln von *Lingula unguis* L. (Brachiopoda). Zeitschrift für Wissenschaftliche Zoologie (Leipzig) 183:181–189.

———. 1974. Epitheliomuscular cells in *Lingula unguis* (Brachiopoda) and *Branchiostoma lanceolatum* (Acrania). Cell and Tissue Research 154:543–545.

———. 1975. Elektronenmikroskopische und enzymhistochemische Untersuchungen über die Mitteldarmdrüse von *Lingula unguis* L. (Brachiopoda). Zoologische Jahrbücher, abteilung für Anatomie und Ontogenie der Tiere 94:441–452.

———. 1976. Elektronenmikroskopische und enzymhistochemische Untersuchungen über Lophophor und Tentakeln von *Lingula unguis* L. (Brachiopoda). Zoologische Jahrbücher, abteilung für Anatomie und Ontogenie der Tiere 96:225–237.

Stoyanova, R. Z. 1984. Alkane and fatty acid content and composition in Palaeozoic Brachiopoda fossils. Comptes-rendus de l'Académie Bulgare des Sciences 37(6):771–774.

Strathmann, R. R. 1973. Function of lateral cilia in suspension feeding of lophophorates (Brachiopoda, Phoronida, Ectoprocta). Marine Biology 23:129–136.

Strathmann, R. R., & D. J. Eernisse. 1994. What molecular phylogenies tell us about the evolution of larval forms. American Zoologist 34:502–512.

Stricker, S. A., & C. G. Reed. 1985a. The ontogeny of shell secretion in *Terebratalia transversa* (Brachiopoda, Articulata). I. Development of the mantle. Journal of Morphology 183:233–250.

———. 1985b. The ontogeny of shell secretion in *Terebratalia transversa* (Brachiopoda, Articulata). II. Formation of the protegulum and juvenile shell. Journal of Morphology 183:251–271, fig. 1–45.

———. 1985c. Development of the pedicle in the articulate brachiopod *Terebratalia transversa* (Brachiopoda, Terebratulida). Zoomorphology 105:253–264.

Suchanek, T. H., & J. Levinton. 1974. Articulate brachiopod food. Journal of Paleontology 48:1–5.

Summers, R. G. 1970. The fine structure of the spermatozoon of *Pennaria tiarella* (Coelenterata). Journal of Morphology 131:117–130.

Sundarsan, D. 1968. Brachiopod larvae from the west coast of India. Proceedings of the Indian Academy of Science (section B) 68:59–68.

———. 1970. On a lingulid larva from Coondapur (Mysore State), India. Journal of the Marine Biological Association of India 12:97–99.

Surlyk, Finn. 1972. Morphological adaptations and population structures of the Danish chalk brachiopods (Maastrichtian, Upper Cretaceous). Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 19(2):2–57, 24 fig., pl. 1–5.

Swedmark, B. 1967. *Gwynia capsula* (Jeffreys), an articulate brachiopod with brood protection. Nature 213:1151–1152.

———. 1971. A review of Gastropoda, Brachiopoda, and Echinodermata. Smithsonian Contributions to Zoology 76:41–45.

Swofford, D. L. 1993. PAUP: phylogenetic analysis using parsimony. Computer program distributed by the author. Smithsonian Institution. Washington, D.C.

Taddei Ruggiero, E. 1991. A study of damage evidence in brachiopod shells. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 203–210.

Tanaka, S., K. Anno, & N. Seno. 1982. A novel sulfated glycosaminoglycan, lingulin sulfate, composed of galactose and N-acetylgalactosamine from *Lingula unguis.* Biochimica et Biophysica Acta 704:549–551.

Teichert, Curt. 1958. Cold and deep-water coral banks. Bulletin of the American Association of Petroleum Geologists 42:1064–1082.

Templeton, Alan. 1989. The meaning of species and speciation: a genetic perspective. *In* D. Otte & J. A. Endler, eds., Speciation and Its Consequences. Sinauer Associates, Inc. Sunderland, Massachusetts. p. 3–27.

Thayer, C. W. 1975. Size-frequency and population structure of brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 17:139–148.

———. 1977. Recruitment, growth, and mortality of a living articulate brachiopod, with implications for the interpretation of survivorship curves. Paleobiology 3:98–109.

———. 1986a. Are brachiopods better than bivalves? Mechanisms of turbidity tolerance in articulates and their interaction with feeding in articulates. Paleobiology 12:161–174.

———. 1986b. Respiration and the function of brachiopod punctae. Lethaia 19:23–31.

Thayer, C. W., & R. A. Allmon. 1990. Evolutionary refugia? Oligotrophic marine caves of Micronesia. Abstract. Fourth International Congress of Systematic and Evolutionary Biology. p. A323.

Thayer, C. W., & H. M. Steele-Petrovic. 1975. Burrowing of the lingulid brachiopod *Glottidia pyramidata:* its ecologic and palaeoecologic significance. Lethaia 8:209–221.

Thomas, G. A. 1958. The Permian Orthotetacea of Western Australia. Bureau of Mineral Resources, Geology and Geophysics, Bulletin 39:1–159.

Thompson, R. R., & W. B. Creath. 1966. Low molecular weight hydrocarbons in recent and fossil shells. Geochimica et Cosmochimica Acta 30:1137–1152.

Thompson, R. J., E. Ward, & M. C. Rhodes. 1992. *In vivo* observations of feeding in an articulate brachiopod. Abstract. Annual Marine Benthic Ecology Meeting, Newport, RI, March 1992.

Thomson, J. A. 1918. Brachiopoda. Australasian Antarctic Expedition, 1911–1914, Scientific Reports (series C) 4:1–76, pl. 15–18.

———. 1927. Brachiopod morphology and genera (recent and Tertiary). New Zealand Board of Science and Art, Manual 7:338 p., 103 fig., 2 pl.

Tkachuck, R. D., G. D. Rosenberg, & W. W. Hughes. 1989. Utilization of free amino acids by mantle tissue in the brachiopod *Terebratalia transversa* and the bivalve mollusc, *Chlamys hastata.* Comparative Biochemistry and Physiology 92B:747–750.

Tommasi, L. R. 1970a. Sôbre o braquiopode *Bouchardia rosea* (Mawe, 1823). Boletim do Instituto Oceanografico, Sao Paulo 19:33–42.

———. 1970b. Observaçoes sôbre a fauna bêntico do complexo estuarino-lagunar de Cananéia. Boletim do Instituto Oceanografico, Sao Paulo 19(1):43–56.

Tortell, P. 1981. Notes on the reproductive biology of brachiopods from southern New Zealand. New Zealand Journal of Zoology 8:175–182.

Towe, K. M. 1980. Preserved organic ultrastructure: an unreliable indicator for paleozoic amino acid biogeochemistry. *In* P. E. Hare, T. C. Hoering, & K. J. King, eds., Biogeochemistry of Amino Acids. John Wiley & Sons. New York. p. 65–74.

Towe, K. M., & C. W. Harper, Jr. 1966. Pholidostrophiid brachiopods: origin of the nacreous lustre. Science 154:153–155.

Trueman, E. R., & T. M. Wong. 1987. The role of the

coelom as a hydrostatic skeleton in lingulid brachiopods. Journal of Zoology 213(2):221–232, 3 fig.
Tsuchiya, M., & C. C. Emig. 1983. Macrobenthic assemblages in a habitat of the recent lingulid brachiopod *Lingula anatina* Lamarck at Asamushi, Northern Japan. Bulletin of the Marine Biological Station of Asamushi, Tohoku University 17(3):141–157.
Tunnicliffe, Verena. 1981. High species diversity and abundance of the epibenthic community in an oxygen-deficient basin. Nature 294:354–356.
Tuross, Noreen, & L. W. Fisher. 1989. The proteins in the shell of *Lingula. In* R. E. Crick, ed., Origin, Evolution, and Modern Aspects of Biomineralization in Plants and Animals. Plenum Press. New York. p. 325–328.
Tuross, Noreen, & P. E. Hare. 1990. A 40 kDa protein in modern and fossil *Lingula. In* The Sixth International Symposium on Biomineralization, Conference Abstracts. Kyoritsu Shuppan Co. Ltd. Tokyo, Japan. p. 76.
Ulrich, E. O., & G. A. Cooper. 1938. Ozarkian and Canadian Brachiopoda. Geological Society of America Special Paper 13:viii + 323 p., 14 fig., 58 pl.
Uribe, M. E., & A. P. Larrain. 1992. Estudios biológicos en el enteropneusto *Ptychodera flava* Eschscholtz, 1825, de Bahia Conceptión, Chile. I: Aspectos morphológicos y ecológicos. Gayana, Zoologia 56(3–4):141–180.
Ushatinskaya, G. T. 1988. Obolellidy (Brakhiopody) s zamkovym sochleneniem stvorok iz nizhnego kembriia Zabaikal'ia [Obolellids (Brachiopoda) with a hinge from the Lower Cambrian of the Transbaikal area]. Paleontologicheskii Zhurnal 1988(1):34–39, 1 fig., pl. 3–4.
Vader, W. 1970. The amphipod, *Aristias neglectus* Hansen, found in association with brachiopods. Sarsia 43:13–14.
Valentine, J. W., & F. J. Ayala. 1975. Genetic variation in *Freileia halli,* a deep sea brachiopod. Deep-Sea Research 22:37–44.
Vallentyne, J. R. 1964. Biogeochemistry of organic matter II: Thermal reaction kinetics and transformation products of amino compounds. Geochimica et Cosmochimica Acta 32:1353–1356.
Vandercammen, A., & M. Lambiotte. 1962. Observations sur les sarcoglyphes dans *Atrypa reticularis* (C. Linné, 1767). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Bruxelles 38:1–15, pl. 1.
Van Kleef, F. S. M., W. W. de Jong, & H. J. Hoenders. 1975. Stepwise degradation of the eye lens protein α-crystallin in aging. Nature 258:264–266.
Vargas, J. A. 1988. Community structure of macrobenthos and the results of macropredator exclusion on a tropical intertidal mud flat. Revista de Biología Tropical 36(2A):287–308.
Walker, A. O. 1909. Amphipoda Gammaridea from the Indian Ocean, British East Africa, and the Red Sea. Transactions of the Linnean Society of London (series 2, Zoology) 12:323–344, pl. 42–43.
Walton, Derek. 1992. Biogeochemistry of brachiopod intracrystalline proteins and amino acids. Ph.D. thesis. University of Glasgow. 237 p.
Walton, Derek, & G. B. Curry. 1991. Amino acids from fossils, facies and fingers. Palaeontology 34:851–858.
Walton, Derek, Maggie Cusack, & G. B. Curry. 1993. Implications of the amino acid composition of recent New Zealand brachiopods. Palaeontology 36:883–896.
Wang, Yu, Paul Copper, & Jia-Yu Rong. 1983. Distribution and morphology of the Devonian brachiopod *Punctatrypa.* Journal of Paleontology 57:1067–1089, 11 fig.
Watabe, Norimitsu, & C.-M. Pan. 1984. Phosphatic shell formation in atremate brachiopods. American Zoologist 24:977–985.
Webb, G. R., A. Logan, & J. P. A. Noble. 1976. Occurrence and significance of brooded larva in a recent brachiopod, Bay of Fundy, Canada. Journal of Paleontology 50:869–871.
Weiner, S. 1983. Mollusk shell formation: isolation of two organic matrix proteins associated with calcite deposition in the bivalve *Mytilus californianus.* Biochemistry 22:4139–4145.
Westbroek, Peter. 1967. Morphological observations with systematic implications on some Palaeozoic Rhynchonellida from Europe, with special emphasis on the Uncinulidae. Thesis. Leidse Geologische Mededelingen 41:1–82, 14 pl.
Westbroek, Peter, J. Yanagida, & Y. Isa. 1980. Functional morphology of brachiopod and coral skeletal structures supporting ciliated epithelia. Paleobiology 6:313–330.
Widdows, J. 1985. Physiological procedures. *In* B. L. Bayne, ed., The Effects of Stress and Pollution on Marine Animals. Praeger Scientific. New York. p. 161–178.
Wilkens, J. L. 1978a. Adductor muscles of brachiopods: activation and contraction. Canadian Journal of Zoology 56:315–323.
———. 1978b. Diductor muscles of brachiopods: activation and very slow contraction. Canadian Journal of Zoology 56:324–332.
———. 1987. Tonic free maintenance after the decay of active state in brachiopod smooth adductor muscle. Journal of Comparative Physiology (series B) 157:651–658.
Williams, Alwyn. 1953. North American strophedontids: their morphology and systematics. Geological Society of America Memoir 56:67 p., 13 pl.
———. 1956. The calcareous shell of the Brachiopoda and its importance to their classification. Biological Reviews 31:243–287, fig. 1–7.
———. 1957. Evolutionary rates of brachiopods. Geological Magazine 94:201–211.
———. 1962. The Barr and lower Ardmillian series (Caradoc) of the Girvan district, southwest Ayrshire, with descriptions of the Brachiopoda. Geological Society of London Memoir 3:267 p., 25 pl.
———. 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. Bulletin of the British Museum (Natural History) Geology, Lon-

don 8:327–471, 13 fig., 16 pl.
———. 1965. Stratigraphic Distribution. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 237–250, fig. 148–154.
———. 1966. Growth and structure of the shell of living articulate brachiopods. Nature 211:1146–1148.
———. 1968a. Evolution of the shell structure of articulate brachiopods. Special Papers in Palaeontology 2:1–55, 27 fig., 24 pl.
———. 1968b. Significance of the structure of the brachiopod periostracum. Nature 218:551–554.
———. 1968c. Shell structure of the billingsellacean brachiopods. Palaeontology 11:486–490.
———. 1968d. A history of skeletal secretion among articulate brachiopods. Lethaia 1:268–287.
———. 1970a. Origin of laminar-shelled articulate brachiopods. Lethaia 3:329–342.
———. 1970b. Spiral growth of the laminar shell of the Brachiopod *Crania.* Calcified Tissue Research 6:11–19.
———. 1971a. Comments on the growth of the shell of articulate brachiopods. *In* J. Thomas Dutro, Jr., ed., Paleozoic Perspectives: A Paleontological Tribute to G. Arthur Cooper. Smithsonian Contributions to Paleobiology 3:47–67.
———. 1971b. Scanning electron microscopy of the calcareous skeleton of fossil and living Brachiopoda. *In* V. H. Heywood, ed., Scanning Electron Microscopy. Systematic and Evolutionary Applications. Academic Press. London & New York. p. 37–66.
———. 1973. The secretion and structural evolution of the shell of thecideidine brachiopods. Philosophical Transactions of the Royal Society of London (series B) 264:439–478.
———. 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. Bulletin of the British Museum (Natural History) Geology, Supplement 11:1–163, 11 fig., 28 pl.
———. 1977. Differentiation and growth of the brachiopod mantle. American Zoologist 17:107–120.
———. 1984. Lophophorates. *In* J. Bereiter-Hahn, A. G. Matoltsy, & K. S. Richards, eds., Biology of the Integument, Volume 1, Invertebrates. Springer-Verlag. Berlin, Germany. p. 728–745.
———. 1990. Biomineralization in the lophophorates. *In* J. G. Carter, ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Volume I & II. Van Nostrand Reinhold. New York. p. 67–82.
Williams, Alwyn, & C. H. C. Brunton. 1993. Role of shell structure in the classification of the orthotetidine brachiopods. Palaeontology 36:931–966.
Williams, Alwyn, S. J. Carlson, C. H. C. Brunton, L. E. Holmer, & L. E. Popov. 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London B351:1171–1193.
Williams, Alwyn, & G. B. Curry. 1991. The microarchitecture of some acrotretide brachiopods. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods Through Time, Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 1990. Balkema. Rotterdam. p. 133–140, fig. 1–4.
Williams, Alwyn, Maggie Cusack, & Sarah Mackay. 1994. Collagenous chitinophosphatic shell of the brachiopod *Lingula.* Philosophical Transactions of the Royal Society of London (series B) 346:223–266.
Williams, Alwyn, & R. A. Hewitt. 1977. The delthyrial covers of some living brachiopods. Proceedings of the Royal Society of London (series B) 197:105–129, pl. 1–7.
Williams, Alwyn, & L. E. Holmer. 1992. Ornamentation and shell structure of acrotretoid brachiopods. Palaeontology 35:657–692.
Williams, Alwyn, & Sarah Mackay. 1978. Secretion and ultrastructure of the periostracum of some terebratulide brachiopods. Proceedings of the Royal Society of London (series B) 202:191–209.
———. 1979. Differentiation of the brachiopod periostracum. Palaeontology 22:721–736.
Williams, Alwyn, Sarah Mackay, & Maggie Cusack. 1992. Structure of the organo-phosphatic shell of the brachiopod *Discinisca.* Philosophical Transactions of the Royal Society of London (series B) 337:83–104.
Williams, Alwyn, & A. J. Rowell. 1965a. Brachiopod anatomy. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 6–57, fig. 1–58.
———. 1965b. Morphology. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 57–138, fig. 59–138.
Williams, Alwyn, A. J. Rowell, D. V. Ager, G. F. Elliott, R. E. Grant, H. M. Muir-Wood, & F. G. Stehli. 1965. Morphological terms applied to Brachiopods. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 139–155.
Williams, Alwyn, & A. D. Wright. 1961. The origin of the loop in articulate brachiopods. Palaeontology 4:149–176, fig. 1–13.
———. 1963. The classification of the "*Orthis testudinaria* Dalman" group of brachiopods. Journal of Paleontology 37:1–32, fig. 1–10, pl. 1–2.
———. 1965. Orthida. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 299–359, fig. 188–228.
———. 1970. Shell structure of the Craniacea and other calcareous inarticulate brachiopods. Special Papers in Palaeontology 7:1–51, 15 pl.
Willmer, P. G., & P. W. H. Holland. 1991. Modern approaches to metazoan relationships. Journal of Zoology 224:689–694.
Wilson, G. D. F. 1987. Speciation in the deep sea. Annual Review of Ecology and Systematics 18:185–207.

Wilson, H., & R. K. Cannon. 1937. The glutamic acid-pyrrolidone carboxylic acid system. Journal of Biological Chemistry 119:309–331.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Trudy Belorusskogo gosudarstvennogo universiteta Minske. 253 p.

Translated from Russian by Fisheries Research Board of Canada, Translation Series 194, 1960.

Winnepenninckx, B., T. Backeljau, & R. De Wachter. 1995. Phylogeny of protostome worms derived from 18S rRNA sequences. Molecular Biology and Evolution 12:641–649.

Wisely, B. 1969. Preferential settlement in concavities (rugophilic behaviour) by larvae of the brachiopod *Waltonia inconspicua* (Sowerby, 1846). New Zealand Journal of Marine and Freshwater Research 3:237–280.

Witman, J. D., & R. A. Cooper. 1983. Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* (Couthouy) from two subtidal habits. Journal of Experimental Marine Biology and Ecology 73:57–79.

Worcester, W. 1969. On *Lingula reevii.* Unpublished Master of Science thesis. University of Hawaii. 49 p.

Wourms, J. S. 1987. Oogenesis, p. 49–187. *In* A. C. Giese, J. S. Pearse, & V. B. Pearse, eds., Reproduction of Marine Invertebrates. Volume 9. General aspects: seeking unity in diversity. Blackwell Scientific Publications. California. 712 p.

Wright, A. D. 1966. The shell punctation of *Dicoelosia biloba* (Linnaeus). Geologiska Foreningens I Stockholm Forhandlingar 87:548–556.

———. 1981. The external surface of *Dictyonella* and of other pitted brachiopods. Palaeontology 24:443–481, pl. 62–71.

Yamada, M. 1956. Notes on discinid larvae (Brachiopoda) from Osyro, West coast of Hokkaido. Annotated Zoology of Japan 29:165–167.

Yano, Hiroyuki, K. Satake, Y. Ueno, K. Kondo, & A. Tsugita. 1991. Amino acid sequence of the haemerythrin α subunit from *Lingula unguis*. Journal of Biochemistry 110:376–380.

Yano, Hiroyuki, K. Satake, Y. Ueno, & A. Tsugita. 1991. The amino acid sequence of the β chain of hemerythrin from *Lingula unguis.* Protein Sequences and Data Analysis 4:87–91.

Yatsu, Naukidé. 1902a. On the development of *Lingula anatina.* Journal of the College of Science, Imperial University, Tokyo, Japan 17(4):1–112, pl. 1–8.

———. 1902b. On the habits of the Japanese *Lingula.* Annotationes Zoologicae Japonenses 4(2):61–67.

Young, J. 1884. Notes on the shell structure of *Eichwaldia capewelli.* Geological Magazine 1(series 3):214–218.

Zabi, S. G. 1984. Rôle de la biomasse dans la détermination de l'"importance value" pour la mise en évidence des unités de peuplements benthiques en Lagune Ebrié (Côte d'Ivoire). Documents Scientifiques du Centre de Recherches Océanographiques, Abidjan 15(1/2):55–87.

Zezina, O. N. 1961. Distribution of the deepwater brachiopod *Pelagodiscus atlanticus* (King). Okeanology 5(2):354–358.

In Russian.

———. 1970. Brachiopod distribution in the recent ocean with reference to problems of zoogeographic zoning. Paleontologicheski Zhurnal 2:3–17.

In Russian.

———. 1975. Deep-sea brachiopods from the southeast Pacific and Scotia Sea. Trudy Instituta Okeanologii 103:247–258.

In Russian.

———. 1981. Recent deep-sea Brachiopoda from the western Pacific. Galathea Report 15:7–20.

———. 1985. Sovremennye brakhiopody i problemy batial noi zony okeana [Living brachiopods and problems of the north bathyal oceans]. Nauka. Moscow. 247 p.

———. 1987. Brachiopods collected by BENTHEDI-Cruise in the Mozambique Channel. Bulletin du Muséum Nationale d'Histoire naturelle de Paris (série 4) 9:551–563.

Zhang, J-H., & D. M. Kurtz. 1991. Two distinct subunits of hemerythrin from the brachiopod *Lingula reevii:* an apparent requirement for cooperativity in oxygen binding. Biochemistry 30:9121–9125.

Zittel, K. A. von. 1880. Handbuch der Palaeontologie, Vol. 1, No. 4. R. Oldenbourg. München & Leipzig. p. 641–722.

Zuckerkandl, Emil, & L. Pauling. 1965. Molecules as documents of evolutionary history. Journal of Theoretical Biology 8:357–366.

Zuker, Michael. 1989. On finding all suboptimal foldings of an RNA molecule. Science 244:48–52.

Zwaan, A. de, M. Leopold, E. Marteyn, & D. R. Livingstone. 1982. Phylogenetic distribution of pyruvate oxidoreductases, arginine kinase and aminotransferases. *In* A. D. F. Addink & N. Spronk, eds., Exogenous and Endogenous Influences on Metabolic and Neural Control, Volume 2. Pergamon Press. Oxford. p. 136–137.