

# Functional disposition of the lophophore in living Brachiopoda

CHRISTIAN C. EMIG

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The shape and disposition of adult brachiopod lophophores relate to in- and excurrent apertures, to the internal water irrigation system, to shell orientation at substratum and to near-bottom currents. The arrangement of the mantle canals and gonads of different lophophores are induced by water circulation. The trocholophe (2% of living species) is considered as a plesiomorphic character which represents the basic plan of the lophophore, shared by all Lophophorata. Three different types of schizolophe (10%) are represented in terebratuloids, thecidioids and discinids. The spirolophe (19%), characteristic of rhynchonellides and most inarticulate brachiopods, except the schizolophe *Pelagodiscus*, has evolved divergently into specific arrangements of the mantle canals and gonads. The zygo-plectolophe (67%) is characteristic of most Terebratulida. The ptycholophe (2%) probably evolved independently in *Megathiris* and the thecidioids. The mesolophe, known in the fossil chonetaceans, is considered to be a primitive zygo-plectolophe. The median brachiopod sulcus increases the efficiency of the excurrent system and is considered as an evolved character but a homoplasy within the brachiopods. The characteristics of Recent lophophore types have to be taken into account when reconstructing the lophophore in fossil forms. □ *Brachiopoda, Lophophorata, lophophore, water system, orientation, evolution.*

*Christian C. Emig, Departamento de Biología Animal I (Zoología), Universidad Complutense, 28040 Madrid, Spain. Present address: Centre d'Océanologie de Marseille, Station Marine d'Endoume, Chemin de la Batterie-des-Lions, 13007 Marseille, France; received 28th June, 1991, revised typescript accepted 3rd February, 1992.*

The lophophore, a tentaculated extension of the mesosoma (and its cavity, the mesocoelom) that embraces the mouth but not anus (Hyman 1959; Emig 1976), is a synapomorphic character only shared by the Lophophorata (Phoronida, Brachiopoda and Bryozoa), taken as one of the characters establishing them as a monophyletic group (Rowell 1982; Emig 1985). The lophophore has more importance than just being considered as a feeding mechanism absorbing alimentary particles and dissolved nutrients. Its primary function is a water current system that also acts as a respiratory organ. Furthermore, in Bryozoa and Phoronida it has a protective function enhanced by the presence of a double longitudinal row of sensory cells in each tentacle. It controls brooding patterns in some phoronid species (Emig 1976, 1985). In Brachiopoda it serves to expel waste products and, in some species, as a brood pouch. The tentacles of the lophophore, generally named filaments or cirri in the brachiopods, are homologous within the Lophophorata (Emig, unpublished), thus the term *tentacle* also has to be used in Brachiopoda. Each tentacle bears numerous cilia.

The lophophore of the Brachiopoda, not capable of much extensible movement, is composed of a pair of long lophophoral arms (or brachia), disposed symmetrically about the mouth, attached to the anterior body wall, sometimes to the dorsal mantle surface, and variously looped or coiled. In the articulate brachiopods, it is commonly supplemented to some extent by calcareous supports (spicules or a brachidium). The brachia bear long, slender flexible tentacles, and are arranged in alternating series: inner (ablalial) tentacles and outer (adlabial) tentacles, the latter facing the brachial food groove, are always oriented upflow (see Fig. 2C). This alternating disposition is true only for post-trocholophe stages; even in the adult, the region of the lophophore immediately adjacent to the mouth retains a 'single-row' organization.

The lophophore creates a continuous, laminar water flow, induced by rows of lateral cilia on the tentacles. Their movement draws water through the narrow slits between tentacles. There is no internal mixing and no recirculation of filtered exhalant current (LaBarbera 1981). These currents in and out of the pallial cavity (or mantle

cavity) are used for all metabolic exchanges with the environment (food and oxygen intake, and waste ejection). Consequently, in a living brachiopod, the direction of the current through the lophophore can be deduced directly from lophophore disposition. A palaeofunctional reconstruction must be compatible with such an orientation. Finally, the current system through the pallial cavity governs the arrangement of the mantle canals and gonads in the lophophore types in adult brachiopods.

**Material and methods**

Used as models were *Notosaria* from New Zealand; *Laqueus*, *Hemithiris* and *Terebratulina* from San Juan Archipelago (Washington, USA); *Lingula* and *Glottidia* from various tropical locations; *Gryphus*, *Megerlia*, *Terebratulina*, *Platidia*, *Megathiris*, *Argyrotheca* and *Crania* from the French Mediterranean coasts (Provence and Corsica); *Pelagodiscus* from the deep Northern Atlantic; *Discinisca* and *Discina* in the collection of the Museo Nacional de Ciencias Naturales (Madrid). Specimens from the French Mediterranean coasts were observed in life position, while *Lingula* individuals were studied *in situ* by scuba diving and *Gryphus* using a submersible (three dives).

**Disposition of the lophophore**

The disposition of the adult lophophore is intimately related to its ontogeny. The first stages of the development of the lophophore (terms from Beccher 1987) are shared by all brachiopods during larval ontogeny (Fig. 1). The first stage, *taxolophous stage*, consists of a simple crescentic

structure, a stage bypassed in some articulate species. Then, new tentacles are added in pairs at the distal ends of the lophophoral arms to reach the *trocholophous stage* (or trocholophe), a nearly circular form around the mouth. Although the number and length of the tentacles increase progressively, the width of the slits between them remains almost constant. The last larval *schizolophous stage* (or schizolophe) is formed by the introversion of the anterior edge or its division into two lobes. In some living genera, trocholophes and schizolophes are retained as adult type. Diverging from the schizolophous larval stage, only three types in lophophore complexity have been developed among adult brachiopods (Fig. 1; Table 1): *spirolophe*; *ptycholophe*; *zygolophe*, leading to *plectolophe*. The *mesolophe* recently described in fossil chonetaceans by Rachebocuf and Copper (1990) will be discussed within this context. In all stages and types, the mouth is always located in the brachial food groove in a ventral position, in front of the visceral cavity (Figs. 2-4).

A review of lophophore types in the living brachiopod genera (Table 1) is based on a large number of references. Most of the original descriptions were consulted and the main surprise came from the absence of the description of the lophophore, at least not the type, in almost all papers even when living or fixed specimens were available. Consequently the lophophore type were often deduced from the brachidial form, probably sometimes wrongly. Absence of the study of anatomical characters, such as lophophore, nephridia, digestive tract, mantle canals, muscle arrangement, pedicle type, in the description of species is a major deficiency that should be remedied in future investigation. Furthermore, such a mistake can lead to the assignment of new species to the wrong order. *Cryptopora cu-*

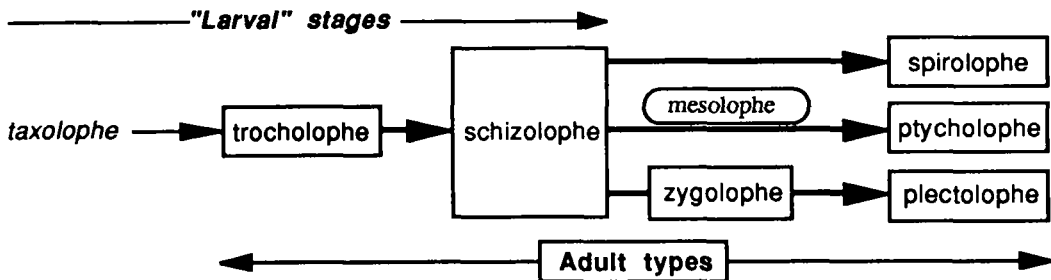


Fig. 1. The different types of the lophophore and their developmental succession in Brachiopoda.

Table 1. List of the various types of lophophore in the living adult brachiopods.

	Family	Lophophore	Genus	Species		
INARTICULATA						
Craniida	Craniidae	Spirolophe	3	18		
Discinida	Discinidae	Spirolophe	3	11		
		Schizolophe	<i>Pelagodiscus</i>	1		
Lingulida	Lingulidae	Spirolophe	2	12		
ARTICULATA						
Rhynchonellida	Basilolidae	Spirolophe	7	12		
	Cryptoporidae	Spirolophe	1	7		
	Frieleiidae	Spirolophe	3	6		
	Hemithyrididae	Spirolophe	3	4		
	Hispanirhynchiidae	Spirolophe	4	4		
Terebratulida						
Terebratelloidea	Aulacothyropsidae	Plectolophe	1	2		
	Dallinidae	Plectolophe	6	23		
	Kraussinidae	Schizolophe	<i>Pumilus</i>	1		
	Kraussinidae	Zygolophe	<i>Kraussina</i>	5		
	Kraussinidae	Plectolophe	3	12		
	Laqueidae	Plectolophe	7	25		
	Macandreviidae	Plectolophe	1	9		
	Megathyrididae	Trocholophe	<i>Gwynia</i>	1		
	Megathyrididae	Schizolophe	<i>Argyrotheca</i>	22		
	Megathyrididae	Ptycholophe	<i>Megathyris</i>	3		
	Megathyrididae	?	<i>Phaeargyrotheca</i>	1		
	Phaneropodidae	Spirolophe	<i>Leptothyrella</i>	1		
	Phaneropodidae	Zygolophe	<i>Phaneropora</i>	2		
	Platidiidae	Schizolophe	<i>Amphithyris</i>	4		
	Platidiidae	Zygolophe	<i>Annuloplatidia</i>	3		
	Platidiidae	Plectolophe	1	5		
	Terebrataliidae	Zygolophe	<i>Bouchardia</i>	1		
	Terebrataliidae	Zygolophe	<i>Anakinetica</i>	1		
	Terebrataliidae	Plectolophe	4	7		
	Terebrataliidae	Plectolophe	14	33		
	Thaumatosiidae	Schizolophe	<i>Thaumatosia</i>	1		
	Tythothyrididae	Schizolophe	<i>Simplicithyris</i>	2		
	Tythothyrididae	Plectolophe	2	2		
	Terebratuloidea	Cancellothyrididae	Zygolophe	<i>Bathynanus</i>	4	
		Cancellothyrididae	Zygolophe	<i>Eucalathis</i>	16	
		Cancellothyrididae	Plectolophe	7	33	
		Cnismatocentridae	Plectolophe	1	1	
		Dyscolidae	Schizolophe	<i>Dyscolia</i>	4	
		Dyscolidae	Trocholophe	<i>Goniobrochus</i>	1	
		Dyscolidae	Plectolophe	2	4	
		Terebratulidae	Plectolophe	15	66	
		Spiriferida	Thecidellinidae	Schizolophe	1	6
			Thecideidae	Ptycholophe	2	4
			112	380		

*riosa* Cooper, 1973 shows a zygolophe or plectolophe according to Cooper's figure (no information appears in text), nevertheless it is described as a rhynchonellid, known to develop a spirolophe. In other words, living brachiopods are much more than just a shell, as are fossil forms, and their taxonomy must take into account soft body characteristics.

### *Trocholophe* – *schizolophe*

In the inarticulate *Pelagodiscus* and some small articulate species, the trocholophe or schizolophe is characteristic of the adult lophophore (Table 1; Figs. 2A, 3A). Both stages, as the taxolophe, show the same water flow system: the current enters downwardly within the lophophoral con-

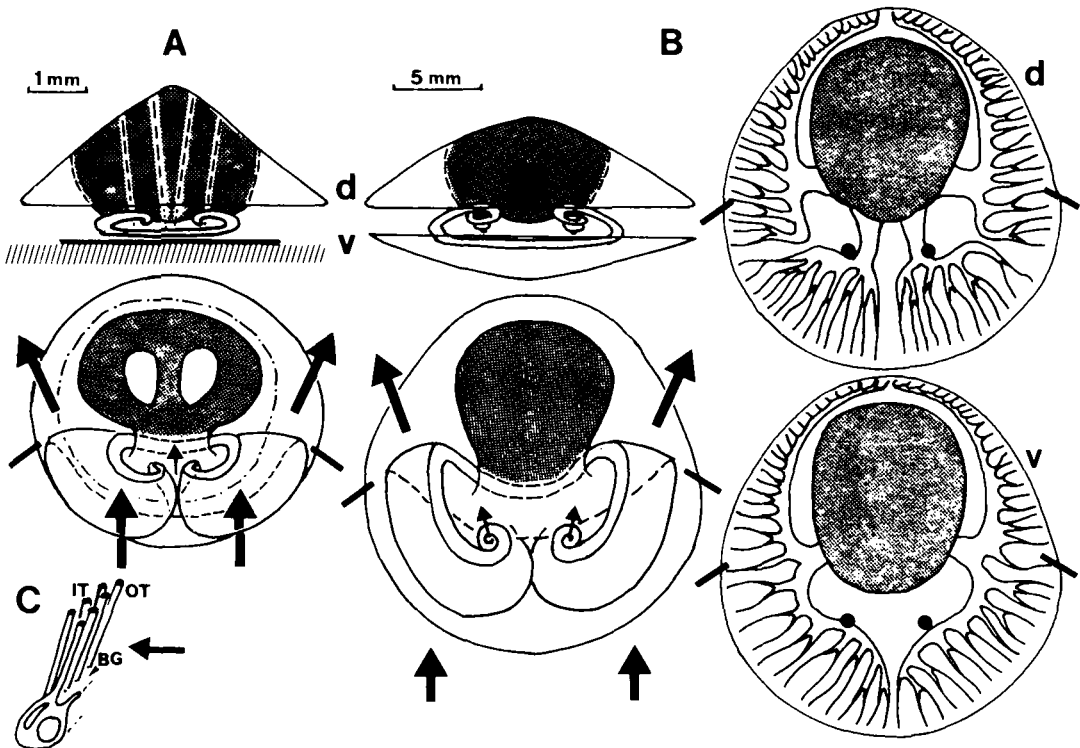


Fig. 2. Lophophores and mantle canals in the Discinidae. [ ] A. *Pelagodiscus atlanticus* (schizolophe): anterior view; view from dorsal side with current system. [ ] B. *Discinisca* (spirolophe): anterior view; view from dorsal side with current system (muscles not drawn); dorsal and ventral arrangement of the mantle canals (black dots indicated the position of the apices of the lophophore). [ ] C. Diagrammatic section of a brachiopod lophophore arm (brachidium) with incurrent direction (BG, brachial food groove; IT, inner tentacle; OT, outer tentacle). (d) Dorsal valve; (v) ventral valve; (vc) visceral cavity.

cavity and escapes outwards, between the tentacles (Fig. 2).

In the articulate species, like *Pumilus antiquatus* (Fig. 3A), the lophophore is attached to the body wall and dorsal mantle surface. The tentacles of the trocholophe project anter-ventrally to form a bell-shaped ring. Only the posterior tentacles (behind the mouth) touch the ventral mantle surface while the other tentacles are apertural and project freely when the valves gape widely (see Rudwick 1962). The schizolophe is horse-shoe shaped, with a similar disposition of the tentacles, except that the median tentacles flex across the median plane to form a tunnel, in which occurs a backward flowing excurrent (Rudwick 1962) according to near-bottom current disposition (Fig. 3A).

In *Pelagodiscus* (Fig. 2A), the lophophore is freely extended into the pallial cavity; the valves gape slightly and the dorsal and ventral tentacles

touch the mantle surface, while the median and lateral ones project freely. Such a disposition seems to be more efficient because the pallial cavity is delimited as a large inhalant compartment formed by the lophophoral basket and two postero-lateral exhalant gapes. The inhalant/exhalant ratio has been estimated as higher than 2.5, thus, the exhalant current velocity is always higher than the inhalant. However, in *Pumilus*, according to the figures of Rudwick (1962), this ratio averages 0.5–0.3.

#### *Ptycholophe*

The ptycholophe involves an expansion of a bilobed schizolophe into a multilobed lophophore by further lateral indentations of the brachia. Only the living megathyridid *Megathiris* (Fig. 3B) and the thecidids *Lacazella* and *Pajaudina* share a four-lobed ptycholophe, with secondary inden-

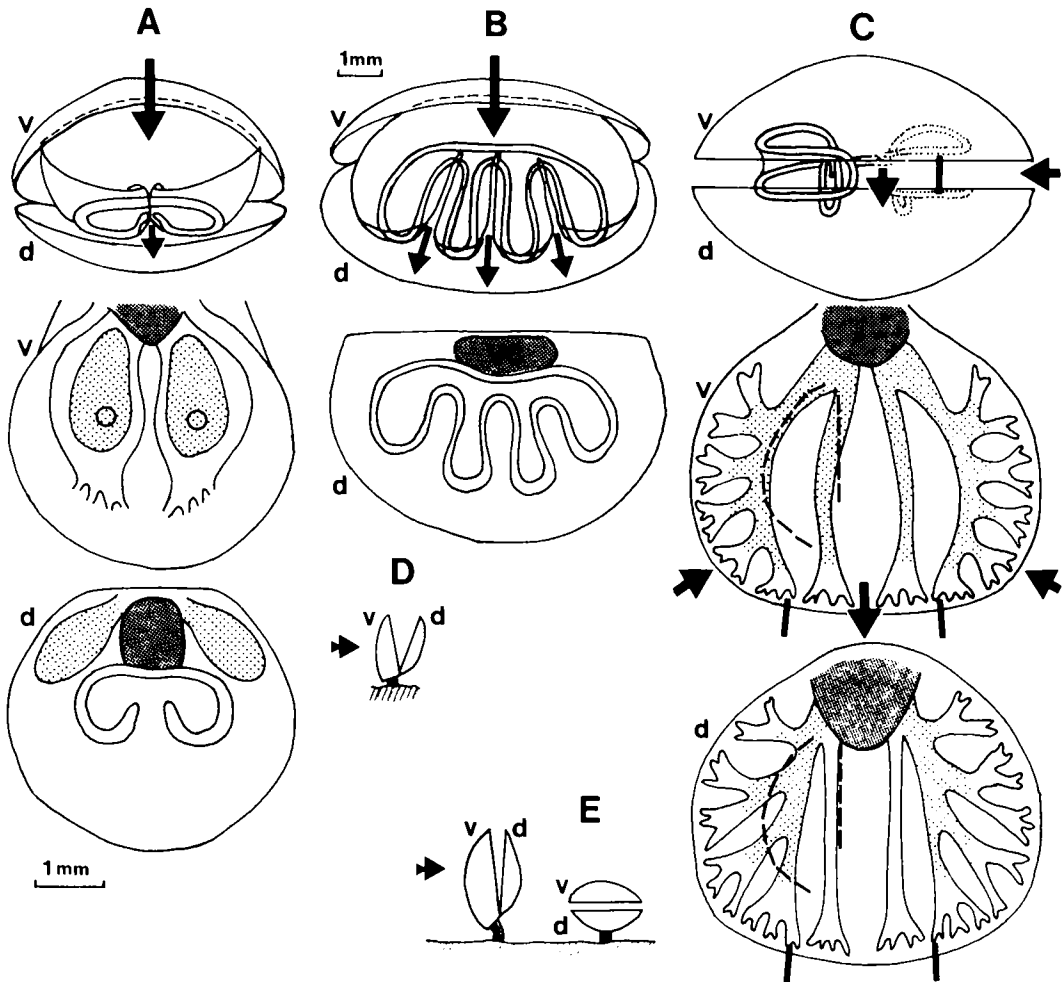


Fig. 3. Lophophores and mantle canals in Terebratulida. □ A. Schizolophous *Pumilus antiquatus*: anterior view with main water current direction; ventral and dorsal valve with gonad (stippled) and canal arrangement (modified from Rickwood 1968; the circles indicate the centre of each lobe of the lophophore). □ B. *Megathiris* (ptycholophe): anterior view with main water current direction; dorsal valve with the lophophore disposition. □ C. Plectolophous terebratulides (diagram from various genera, see text): anterior view with inhalant and exhalant gaps shown on the right side (species with a rectimarginate shell); dorsal and ventral arrangement of the mantle canals (dotted line indicates the position of the left lophophoral arms) and gonads (stippled). □ D, E. Main orientation of the schizolophous and ptycholophous (D) and zygo-plectolophous (E) terebratulides against the bottom current (see text). (d) Dorsal valve; (v) ventral valve; (vc) visceral cavity.

tations in *Pajaudina* (see Logan 1988). Fossil thecidoids have developed a more complex ptycholophe (up to 20 lobes), and probably many strophomenides also bore a ptycholophe (Rudwick 1970; Grant 1972).

The lophophore is supported by a median and two lateral septa. Each of the two antero-lateral indentations acts as an additional exhalant tunnel to the median tunnel, the current system is other-

wise similar to the schizolophe of the articulate (Atkins 1960).

### *Spirolophe*

The lophophore coils freely as a pair of spirals within the mantle cavity. The apices converge towards one another and are generally oriented dorsally, but point medially in the lingulids and

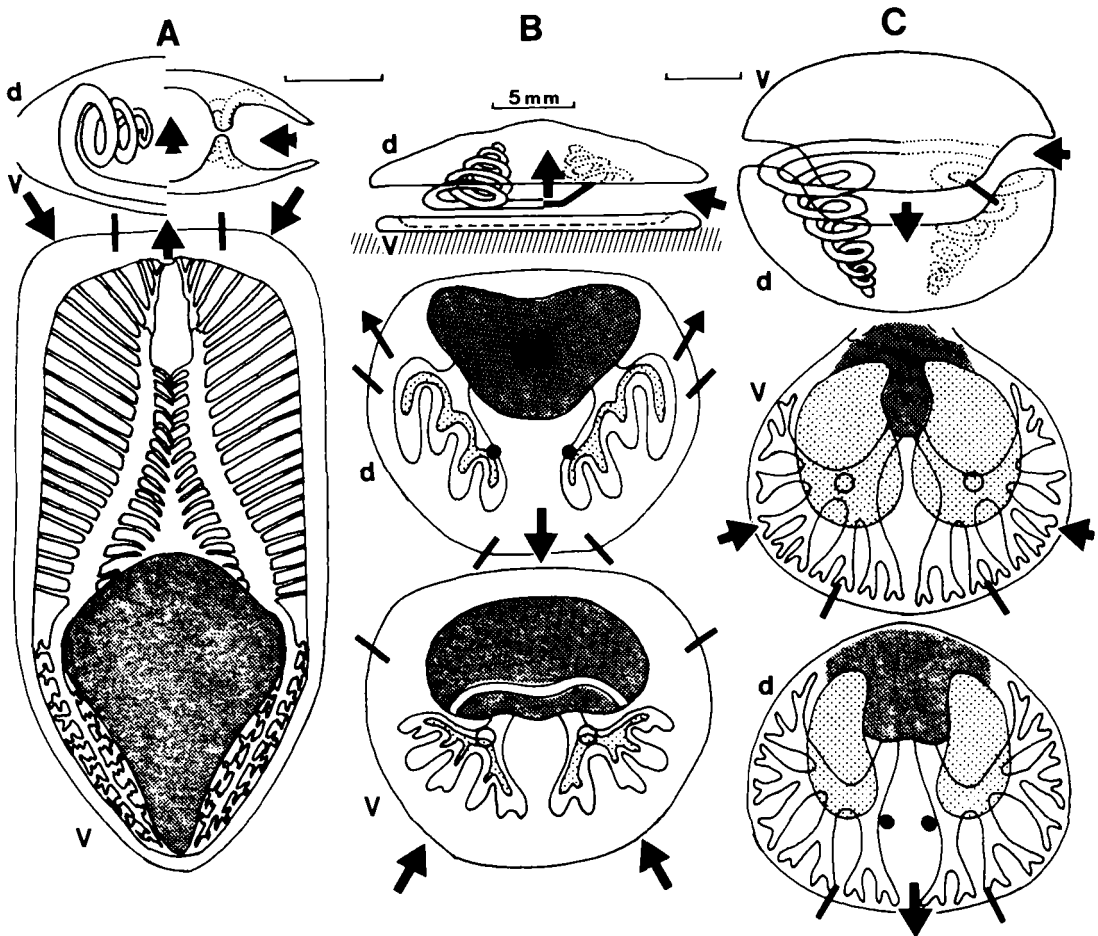


Fig. 4. Lophophores and mantle canals in spirolophous brachiopods. □ A. *Lingula*: anterior view with lophophore coiling (left) and inhalant exhalant apertures (right), divided by mantle edges (modified from Emig 1982a); ventral mantle canals (dorsal are similar). □ B. *Crania*: anterior view with lophophore coiling (left) and inhalant exhalant apertures (right); dorsal and ventral arrangement of the mantle canals and gonads. □ C. Rhynchonellida: anterior view (e.g. *Hemithiris*, species with a plicate shell) with lophophore coiling (left) and inhalant exhalant apertures (right); dorsal and ventral arrangement of the mantle canals and gonads. Gonads are stippled. Small circles indicate the centre of each first whorl of the spiroloph and filled circles the position of the coil apices. (d) Dorsal valve; (v) ventral valve; (vc) visceral cavity.

ventrally in the discinids *Discina* and *Discinisca*, although coiling is similar (Figs. 2B, 4). The spiroloph is characteristic of all living inarticulates (except the schizolophous *Pelagodiscus*) and rhynchonellides. Among the terebratulides, only *Leptothyrella* bears a spiroloph, according to the description of Muir-Wood (1965), and is possibly a juvenile form (or a feature reflecting an atrypaeon or athyrid origin for the terebratuloids). The lophophore acts as a 'soft' hydrostatic skeleton, and is supported basally by crura in

rhynchonellides. There is fossil evidence for spirolophous lophophores in a large proportion of fossil inarticulates, rhynchonellides, certainly in the spiriferides and atrypides, and possibly in the pentamerides as well (Rudwick 1970; Copper 1986).

The tentacles of the proximal (first) whorl touch the mantle surface, the median ones touch each other across the median plane, to separate the two inhalant chambers from the exhalant one and, at the shell edge, the lateral inhalant aper-

tures from the median exhalant. The tentacles of the following spires flex up to the preceding whorl to become a filtering cone which also creates the main exhalant current. Two small postero-lateral apertures exist in craniids and in the growth stages of rhynchonellides (Atkins & Rudwick 1962; Rudwick 1962; Chuang 1974), but not in the discinids, even those with a similar tentacle arrangement (Figs. 2B, 4). According to LaBarbera (pers. comm.), *Crania californica* and *C. pourtelesi* also have a median incurrent flow.

The discinid spirolophore is functionally similar to the schizolophore of *Pelagodiscus* (Fig. 2). The tentacles of the proximal whorl are oriented as in *Pelagodiscus* and those of the small ventrally oriented spires flex dorsally (ventrally in the other spirolophore brachiopods). The efficiency of the lophophore system is not altered and about 20% of the exhalant current passes through those internal spires according to Paine (1962). The discinids show a large, median, inhalant compartment which exteriorly is delimited by the long anterior setae as an incurrent siphon, and two postero-lateral exhalant apertures (Paine 1962; LaBarbera 1985) (Fig. 2B). Thus, the reconstruction proposed by Rowell (1961) for *Disciniscia* can not longer be accepted.

In all spirolophore species, the inhalant/exhalant ratio is always estimated at higher than 2.5.

The shell of almost rhynchonellides has a median deflection in the commissural plane at the level of the median exhalant aperture with a ventral sulcus in most genera (Fig. 4C) but a dorsal one in *Neorhynchia*. The sulcus shifts the exhalant aperture ventrally or dorsally, which consequently is separated from the plane of the lateral inhalant apertures.

However, apertures are never separated by means of erected or fused portions of the mantle edges, except in the lingulids in which the apertures are erected into pseudosiphons by both mantle edges and setae disposition (Emig 1982b) (Fig. 4A).

### *Zygalophore-plectolophore*

The zygalophorous lophophore is arranged as a pair of long lateral arms, more-or-less parallel with the plane of shell symmetry, which project freely into mantle cavity. The arms are connected by a membrane forming a brachial gutter between the dorsal and ventral rows of tentacles. This type is the precursor to the ultimate plectolophous type in which a large plane spiral median coil between the lateral lobes is added (Fig. 3C). Both types are supported by a variety of brachidia. The plectolophore is characteristic of most terebratulides (Table 1), although the zygalophore also occurs in some species belonging to families with plectolophous genera.

The postero-lateral inhalant apertures are defined by the tentacles of the lateral arms, which touch the mantle edges and posteriorly the mantle surface or body wall, except anteriorly where the tentacles separate these apertures from the median exhalant gape (see Rudwick 1962). Water passes mainly through the tentacles of the lateral arms and partly through those of the median coil where the tentacles touch each other across the median plane. This median coil shows about 60% of the volumetric flow rate per unit area of lophophore exhibited by the lateral lophophoral arms and water is then totally expelled through the median excurrent gape (see LaBarbera 1981). At the level of the shell edge, the inhalant/exhalant ratio is estimated at about 3-4. The actual values given for two plectolophous articulate (*Terebratalia transversa* and *Laqueus californianus*) in LaBarbera (1991) are 3.3 and 2.4 respectively. In many terebratulide genera, the excurrent aperture is deflected by a median sulcus, either plicate or sulcate (i.e. dorsal or ventral oriented).

### *Mesolophore*

The mesolophore, unknown in living brachiopods, has been described by Racheboeuf and Copper (1990) for the fossil chonetacean brachiopods. It is composed of two postero-lateral arms, which are fixed or resting on dorsal ridges, situated in the posterior gutters of the dorsal valve. They are supported by the median septum or by accessory septa. The water current enters the lateral shell commissure and escapes anteriorly, with the exhalant current induced by the tentacles of the median loop. The mesolophore is said, by these authors, to have most probably a trocholophore type of lophophore as its origin. Nevertheless, it appears more likely to have evolved from a schizolophore into a peculiar ptycholophore or into a primitive plectolophore; Grant (1972, 1976) suggested also that the chonetacean brachial ridges indicate a kind of ptycholophore. When compared to schizolophous and ptycholophous water circulation in living forms, the mesolophore must have

functioned with the incurrent entering the lophophore anteriorly and excurrents escaping laterally. When compared to that of the plectolophe, the water system appears functionally more consistent with the authors' description which, furthermore, states that the postero-lateral arms could carry a 'double' row of tentacles. The problem of shell orientation remains to be discussed below.

## Shell orientation

Among living brachiopods, there are two shell orientations toward the substrate. In the inarticulates and articulate thecidids, the ventral valve is cemented or oriented towards the substratum (Figs. 2, 4B) except for the lingulids which are embedded vertically in the substrate. In the other articulates, the uppermost ventral valve arches over the dorsal valve which is toward the substratum (Figs. 3D, 3E). Nevertheless, during the study of articulate populations, some individuals have been observed with the dorsal valve uppermost (McCammon 1973; Richardson 1981a).

The orientation or reorientation of the shells against the currents is controlled by the pedicle and muscle systems but is poorly known (see LaBarbera 1978; Richardson 1981b, 1986). Among the inarticulates, lingulids do not orientate with the current because they live in a burrow (Emig 1982a) while craniids are cemented to the substrate. *Discinisca* orientates the lophophore relative to the current (LaBarbera 1985); the lophophore operates as in Bryozoa and Phoronida, that is as a basket facing the current which flows outwards through the tentacles (Fig. 2B). The efficiency of the current may be regulated by the variable gaping of the shell. *Pelagodiscus* is fixed to the substrate by means of its two main body muscles (Fig. 2A) suggesting a small degree of reorientation, although its orientation against the incurrent should be similar to that of other discinids. In craniids which have a cemented shell, the orientation may depend on larval settlement and metamorphosis under the influence of the prevailing bottom current. According to LaBarbera's observations (pers. comm.), the anterior region is facing the local flow direction and the excurrent region is essentially perpendicular to the bottom current: this orientation is functionally identical to that seen in articulates, but anatomically perpendicular to the articulate orientation.

In the articulates with plectolophes and spirolophes, from data published by McCammon (1965, 1973), LaBarbera (1977, 1978, 1981), Richardson (1981a, 1986), and Emig (1987), on the exhalant current speed (0.2–1.2 cm/s) and shell reorientation, no prevailing position occurs when the bottom current is lower than the exhalant current (although the anterior shell edge commonly faces the current). But, when this bottom current becomes stronger than the exhalant one (Fig. 3E), the brachiopod orients the ventral valve either vertically against the bottom current (left–right axis perpendicular or oblique to the current) or closely horizontal (left–right axis parallel to the current). The former position seems to be prevalent in strong bottom currents (4–9 km/h). Some species are known to reorient only to some degree to the ambient currents, for example *Terebratalia transversa* which keeps the second orientation as preferential, as does the rhynchonellid *Hemithiris psittacea* (see LaBarbera 1977, 1981).

In the articulate ptycholophous *Megathiris* and schizolophous *Argyrotheca*, the shell is almost at right angles to the substratum and the valves gape to an angle of 40–45° (Schulgin 1885; Atkins 1960). This suggests that the ventral valve should be nearly vertical (uppermost) and perpendicularly oriented against the current and the dorsal valve oblique (Fig. 3D) with the main excurrent escaping through the median tunnel in schizolophes or three tunnels in ptycholophes (Figs. 3A, 3B). In the ptycholophous thecidids, the ventral valve is cemented to the substrate and the dorsal valve becomes perpendicular during feeding (Lacaze-Duthiers 1861) and is orientated into the prevailing bottom current (Nekvasilová & Pajaud 1969). Such a functional orientation in schizolophous, ptycholophous, and trocholophous articulates is consistent with the above two main positions in plectolophous and spirolophous species which have all trocholophous and schizolophous growth stages. It is also consistent with the orientation in discinids (see above) as well as with the lophophore disposition in Bryozoa and Phoronida (Gilmour 1978; Emig 1982b).

In the mesolophous chonetaceans, the ventral valve of the shell probably rested on the soft bottom with the prevailing water flow coming from behind and the shell could not open more than one-third the shell length (Racheboeuf 1981, 1990). With the dorsal valve uppermost, the



mesolophe functioned as a plectolophe, the water circulation being compatible with the description given by Rachebocuf and Copper (1990). Although a downstream orientation is assumed, a lateral adjustment to the current could also be expected. However, even with the absence of information about a functional pedicle, one could also propose an alternative with the ventral valve facing upstream in an oblique to nearly vertical attitude, and the shell anchored into the sediment by its hinge spines and the pedicle attached to a small hard substrate. Such a position appears functionally more consistent with the inferred mesolophe and the general chonetacean shell shape and would also explain the varied development of hinge spines.

In articulate brachiopods, the significance of the fold and complementary sulcus of the shell needs to be analysed. The sulcus spatially separates the exhalant aperture, which does not lie in the same commissural plane as the inhalant apertures, and its axis is orthogonal to those of the inhalant apertures (Fig. 4C). It is acting as a deflection mechanism for the excurrent, while in rectimarginate species deflection is obtained by an increased current near the dorsal valve (lower current in plicate species) (LaBarbera 1981). On the other hand, according to the figures of this author, the incurrent in plicate *Terebratalia* appears more efficient through the hydrodynamic effect of the sulcus. When a shell faces into the current, the incurrents enter antero-laterally (laterally in the rectimarginate *Laqueus*); when parallel, the downward incurrent passes over the sulcus to enter the shell (over the ventral shell in a rectimarginate species). Consequently, the plicate type appears more functional than the sulcate type which, in turn, is more functional than the rectimarginate type in relation to the shell orientation against the current, which facilitates the flow of the excurrent and precludes recycling. Such a view is strengthened by the reversal of the commissural line in suspended species (like *Liothyrella neozelanica* and *Megerlina pisum*). In contrast, *Terebratalia transversa* and *Anakinetica* (= *Magadina cumingi* with a sulcate shell shows a shell orientation similar to plicate species (McCammon 1973; LaBarbera 1977; Richardson 1986).

The average volumetric flow rate per unit area of the lophophore is also higher in the plicate *Terebratalia* (2.74) than in the rectimarginate *Laqueus* (1.87) and *Terebratulina* (1.55). Finally,

the sulcus can be considered as a feature increasing current efficiency and, therefore, as a phylogenetic novelty, even a homoplasy within the articulate brachiopods.

## Mantle canal and gonad arrangement

The arrangement of the mantle canals, which are long tubular extensions of the metacoelom, can be related to water circulation within the pallial cavity because their principal function is respiratory (they also accommodate parts of the gonads, except in some inarticulates). Unfortunately, there is poor information about the canal arrangement in species bearing a trocholophe, schizolophe and ptycholophe, data being limited to *Pumilus* (Rickwood 1968; see Fig. 3A); *Dyscolia* (Fischer & Oehlert 1891); and *Lacazella* (Lacaze-Duthiers 1861; Muir-Wood 1965: figs. 681, 682). On the studied specimens, the canals were not visible except in an individual *Megathiris*, where the gonads at beginning of maturation in the ventral valve were located like those in *Pumilus*. From the little information available, one may deduce that the gonads seem to have a location similar to those in spirolophous articulates (Figs. 3A, 4C).

Four arrangements occur in spirolophous species and characterize the discinids (Fig. 2B), lingulids (Fig. 4A), craniids (Fig. 4B), and rhynchonellids (Fig. 4C). The presence of postero-lateral canals in discinids and lingulids can be related to posterior excurrents, which are known in lingulids to renew the water within their burrows. In the lingulids, gonads do not develop in the mantle while no information is available for discinids. In craniids, the postero-lateral canals are absent (suggesting that the posterior excurrents are weak), the general arrangement of the canals being similar to that of the rhynchonellides but different in extension (Figs. 4B, 4C); the lophophore in both is also functionally similar. However, although the gonads are similarly located in the postero-lateral parts of the mantle of the dorsal valves of both groups, the gonadal extensions into the ventral mantle are medio-posterior in the rhynchonellides and medio-anterior in the craniids (Figs. 4B, 4C).

Four main canals occur in the zygo-plectolophous brachiopods (Fig. 3C), the lateral ones being arborescent and located at the level of the

incurrent within the pallial cavity. The gonads are mainly developed in these canals. In some species, the median canals are absent in the dorsal valve (e.g. *Kraussina*, *Neothyris*) or the gonads have a larger development over the lateral canals (e.g. *Terebratulina*) or the general arrangement is more specific (e.g. *Fallax*). The general zygo-plectolophous mantle arrangement may be derived from the rhynchonellide type by individualization of the median canals (Figs. 3C, 4C).

In the articulate brachiopods, the gonads are always better developed in the ventral valve than in the dorsal one (Figs. 3A, 3C, 4C), perhaps because the currents are more efficient or better oxygenated along the ventral mantle surface. This assumption certainly holds for rhynchonellides, as the incurrents pass over the ventral mantle before being filtered.

## Discussion

The changes in lophophore coiling during ontogeny maintain a rather constant relationship between the lophophore area and total body cavity, although the number of possible arrangements of the lophophore is limited (Table 2; Rudwick 1962; LaBarbera 1986). Consequently,

only the lophophore type is relevant in a phylogenetic analysis, not, for example, the number of coils in a spirolophe, or even the evolution from zygo-lophe to plectolophe, which needs further evaluation.

Because the lophophore of the brachiopods passes during its ontogeny through the succession of taxo- to trocho- to schizolophous stages, a trocholophe or schizolophe retained in adult lophophore must be considered as plesiomorphic. The ptycholophe, spirolophe and zygo-plectolophe, which occur respectively in 2%, 19% and 67% of living species and represent 3%, 24% and 64% of genera (Tables 1, 2), are known to derive ontogenetically from the schizolophous stage, and all three types are to be considered as apomorphies.

All trocholophous and schizolophous genera (respectively 3% and 6% of living genera, and 2% and 10% of species; Tables 1, 2) have, within their family, relatives bearing one of these three apomorphies. Among the Lophophorata, the trocholophe is the basic plan of the lophophore, which has evolved into a schizolophe in almost all the Brachiopoda, most of the Phoronida (Emig 1985) and in the bryozoan Phylactolaemata. More complex lophophores occur only in brachiopods and phoronids. Although lophophores differ (e.g. a brachial groove in bra-

Table 2. Summary of the various adult lophophore type in articulate (A) and inarticulate (I) living brachiopods in relation to the number of the inhalant (in) and exhalant (ex) compartments and apertures in the shell and to the shell orientation (V/D, ventral valve uppermost; D/V, dorsal valve uppermost; V = D, ventral and dorsal valve vertically embedded into the substrate; see text). Articulate brachiopods: A<sup>R</sup>, rhynchonellides; A<sup>T</sup>, terebratulides; A<sup>Th</sup>, thecidioids. Inarticulate brachiopods: I<sup>C</sup>, craniids; I<sup>D</sup>, discinids; I<sup>L</sup>, lingulids. The mesolophe of the fossil chonetaceans is herein considered as a primitive zygo-plectolophe type. The numbers between brackets are the numbers of the genera (underlined) and the species recorded in each type (from Table 1).

	Trocholophe	Schizolophe	Ptycholophe	Spirolophe	Zygo-plectolophe	
V/D	1 in [3-6]	1 in (1 ex) [5-30]	1 in (3 ex) [1-3]		2 in + 1 ex [7-32] Zygo [64-222] Plecto	A <sup>T</sup>
				2 in + 1 ex [18-33]		A <sup>R</sup>
D = V				2 in + 1 ex (2 ex) [2-12]		I <sup>L</sup>
D/V		1 in (1 ex) [1-6]	1 in (3 ex) [2-4]			A <sup>Th</sup>
				2 in + 1 ex (2 ex) [3-18]		I <sup>C</sup>
		1 in + 2 ex [1-1]		1 in + 2 ex [3-11]		I <sup>D</sup>
<u>110 Genera</u>	<u>3 (3%)</u>	<u>7 (6%)</u>	<u>3 (3%)</u>	<u>26 (24%)</u>	<u>71 (64%)</u>	
378 Species	6 (2%)	37 (10%)	7 (2%)	74 (19%)	254 (67%)	

chiopods, epistome in phoronids and some bryozoans and two alternating types of tentacles in brachiopods compared with a single type in the two other groups), their layout is essentially the same in all lophophorates, which bear a single tentacle row, contrary to Rowell (1982). Trochophores and schizolophes, ontogenetically and functionally similar within the Lophophorata, are phylogenetic characters, consistent with a monophyletic origin of this phylum: a common trochophorous ancestor is shared by the Lophophorata (Emig 1984). However, as has been assumed for the Phoronida (Emig 1985), the brachiopod schizolophe may have evolved at least two divergent trends, the inarticulates with a freely suspended schizolophe (Fig. 2A) and the articulates with a schizolophe attached to the dorsal mantle surface (Fig. 3A). So, the schizolophe could be a different precursor for each apomorphic lophophore type, i.e. the schizolophe of *Pelagodiscus*, the spirolophe of discinids (Figs. 2A, 2B), the schizolophe of *Pumilus*, the plectolophe of *Kraussina* or/and the ptycholophe (cf. Williams & Wright 1961).

The spirolophous groups (Table 2) can be divided into four categories, three within the inarticulates (the lingulids, discinids and the craniids) and the fourth represented by the articulate rhynchonellids. The two last groups show similarities while the lingulids and discinids have distinctive characteristics of lophophore and mantle canal dispositions. The spirolophe has arisen independently at least twice during brachiopod history. In discinids, water enters the lophophoral spires through their apical sides while, in other spirolophous groups, water enters through the base of the cone. LaBarbera (1981) stated that the growth of the lophophore in rhynchonellids like *Hemithiris* increases the amount of energy available and therefore provides an increase in body size. The inarticulate spirolophe, however, implies a limit to achievable body size, due to the disparity in scaling between food acquisition ability and metabolic demands.

The zygo-plectolophe occurs only among articulate terebratulids (Tables 1, 2). The mesolophe may be a primitive variant of a zygo-plectolophous structure. The development of the plectolophe increases disparity between ability to acquire food and energy demand, which precludes any significant increase in body size (LaBarbera 1986). The ptycholophe occurs only in the articulate terebratulid *Megathiris* and thecidoids *Lacazella* and

*Pajaudina*. Such a structure arose probably independently in each group. Because it is structurally and functionally similar to the schizolophe, the ptycholophe can be considered as less complex than the spirolophe and zygo-plectolophe.

LaBarbera (1986) stated the lophophore types are not functionally equivalent due to topological and hydrodynamic constraints, and, that pumping abilities do not appear equivalent in the lophophore areas. Another noteworthy point is the efficiency in creating water currents flowing over the tentacles which vary widely in cilia arrangement and in anatomical detail although the general internal structure remains the same.

A dorsal or ventral sulcus is considered to have an important role in the efficiency of the current system and, consequently, appears to be an evolved character, while a rectimarginate commissure plane is primitive. However, a median fold and complementary sulcus (and variants) have arisen by flexuring of a rectimarginate anterior commissure, not only independently in almost every brachiopod stock of extinct as well as living species but also during shell development (A. Boucot and A. Williams, pers. comm.). For the brachiopods as a whole, the fold/sulcus development is a homoplasy.

To reconstruct spirolophous lophophores of fossil spire-bearers, as in atrypids and spiriferids, one needs to take into account several general characteristics of the brachiopod lophophore: (1) inhalant current passes directly through the tentacles in one-way to enter the exhalant system, water is never refiltered twice during its passage through the mantle cavity; (2) ratio inhalant/exhalant  $>2-2.5$ , obtained by either a large median inhalant aperture and two small exhalant ones or two lateral inhalant and a small median exhalant; (3) a single row of alternating tentacles; (4) brachial food groove upstream; (5) sulcus, when present, indicates the excurrent gape. Consequently, a deuterolophous lophophore cannot be considered as functional according to the reconstruction proposed by Williams (1960), Williams and Wright (1961), and Alvarez (1990).

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