Methods and conclusions in functional analysis: a reply

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This paper is a reply to criticism presented by C. R. C. Paul and R. Cowen in immediately preceding articles in Lethaia. Contrary to the assertion by Paul, the present author did not reject the paradigmatic method but (1) criticized it for its limitations and seemingly erroneous results, (2) applied it to the richthofeniacean and lyttoniacean brachiopods by use of the pump as paradigm, and (3) extended it to include anatomic, metabolic, and phylogenetic considerations that go beyond the structural and mechanistic constraints of the original formulation. The rhythmic flow mechanism was rejected primarily on the basis of evidence for a ptycholophous lophophore in the Productidina, and the relative inefficiency of 'valve flapping' in contrast to ciliary action in pumping nutrient-bearing fluid into the shell. A Chinese blast furnace was claimed by Cowen to employ a single oscillating panel as a pump, but instead this panel must act as a valve that admits air in surges while the draft in the furnace maintains unidirectional flow through the system. This is analogous to ciliary feeding in brachiopods, where unidirectional flow is maintained by ciliary pumping, and the valve opens to admit water. A richthofeniid with a Composita entrapped beneath the apertural meshwork is introduced as additional evidence against the likelihood of 'valve flapping'.

richthofeniacean and lyttoniacean brachiopods fed in the ciliary manner, which is normal for brachiopods, rather than by a 'rhythmic' or 'tidal' flow induced by flapping of the dorsal valve. To counter my contention that no such thing as a single-bladed oscillating pump exists (or is possible) he introduces a 14th Century Chinese blast furnace that supposedly pumps air into a box adjacent to the chimney by opening and closing a large door. I agree that the door to the Chinese furnace is analogous to the dorsal valve of the Richthofeniacea, but not that it functions as a pump. The door to the furnace is a valve that admits air to the system in surges. The pumping action is produced by the fire itself, which creates a continuous unidirectional draft analogous to unidirectional ciliary pumping in the brachiopod. Closing the door causes the chamber to become partly evacuated, and opening it admits air at high velocity to brighten the coals and achieve the desired temperature in the furnace.

Cowen seems to want the same kind of 'pump' to function one way in the Chinese furnace and the opposite way in the richthofeniacean brachiopods. According to Cowen's illustration, closing the door forces air into the furnace, but closing the dorsal valve of a brachiopod vigorously is supposed to flush water out of the shell. This contradiction is resolved upon recognition that neither the furnace door nor the brachiopod valve functions as a pump, but only as a valve that admits or excludes the ambient fluid. The pumping action is accomplished by the fire in the furnace and the cilia on the brachiopod lophophore. The distinction between valve and pump is crucial. Cowen appears to demand the solution to both sides of the question of symbiotic zooxanthellae, as well. He suggests that Richthofeniacea and Lyttoniacea entertained such photosynthetic symbionts despite the constant changing of the angle of incident light that would result from feeding by flapping the valves. These two feeding mechanisms seem to be mutually exclusive, and neither extraordinary mechanism is called for in terms of the evidence and analysis that I presented earlier (Grant 1972).

The crux of the matter lies in the evidence set forth in my paper. I offered ample evidence that the Productidina had a ptycholophous form of lophophore (Fig. 2) (derived from, and frequently remaining at the stage of a schizolophe); that the Richthofeniacea are Productidina (not just 'derived from more normal
Fig. 2. Cross-sectional diagram of the specimen shown in Fig. 1, showing the position of the Composita shell within Hercosestria cribrosa. The Composita could have entered through the network only as a settling larva. That this took place early during the life of the richthofeniacean is suggested by the abnormal curvature of the dorsal valve of H. cribrosa, apparently shaped to accommodate the growing Composita. Hercosestria is reconstructed with the normal kind of productidine lophophore (Grant 1972); the reader may judge the likelihood of working this apparatus up and down while also bumping the Composita against the walls and reticulum of the host during the vigorous ‘flapping’ necessary to produce the eddies that Cowen says would flush water in and out of the shell. The shear effect in the water that would be produced beneath the reticulum during rapid motion of the dorsal valve was pointed out earlier (Grant 1972:238).

Strophomenida as contended by Cowen), and that there is no evidence for any other kind of lophophore in the Productidina. The form of the lyttoniacean ‘dorsal valve’ is easily derived from the complexly lobate kind of ptycholophe of Falafer, and confirms the long standing theory based on shell structure that it is not a normal dorsal valve, but is an exposed brachidium. The small size of Falafer is irrelevant because the brachidium is already complex despite its small size, and has a shape that fits easily into the great variety of the Productidina.

The unifying feature of the Productidina, the ptycholophe, explains so much of their shell morphology, the freedom that they had to try a great variety of shapes, the feeding mechanisms of hitherto puzzling forms, and the origins of the hitherto enigmatic Lyttoniacea, that it is no longer necessary or constructive to view these shells as ‘bizarre’ as Cowen does.

The most ironic feature of Cowen’s critique lies in his repetition of the usual plea for ‘more evidence’, coupled with the surmise that perhaps Cooper and Grant have that evidence in their Texas material. Indeed we have some new evidence not yet discovered when my paper was written (see Figs. 1, 2, and their explanations).

REFERENCES