WHY THE RHYNCHONELLID BRACHIOPODS SURVIVED AND THE SPIRIFERIDS DID NOT: A SUGGESTION

by DEREK V. AGER

ABSTRACT. It is suggested that the rhynchonellid brachiopods survived to the present day whilst all other forms with spirolophous lophophores became extinct because the latter were restrained by calcareous spiralia whereas the former were able to extend their lophophores outside their shells.

ALAN HOVERD has shown recently (1985) that the living rhynchonellid brachiopod *Notosaria nigricans* (Sowerby) can uncoil and extend its lophophore or feeding organ beyond its shell. This had only previously been recorded, in *Hemithiris psittacea* (Gmelin), by Morse (1869) and by implication in other rhynchonellid species by Davidson (1887), who noted that the lophophore might extend more than four times the length of the shell. However, this observation appears to have been subsequently overlooked by other brachiopod workers. Such a capability is obviously advantageous for a suspension feeder, since it greatly extends the area for trapping food particles in the water. Hoverd has shown that it is also advantageous in that the lophophore acts as a brood chamber for the larvae and then liberates them into the water when extended. It is possible that brachiopods adopted a different feeding strategy in the juvenile stage, before the development of calcareous brachidia, but we cannot know about this in the extinct spiriferids.

Rhynchonellid brachiopods have a longer history than any other articulate group, since they range from the Ordovician to Recent, whereas their present-day contemporaries, the terebratuloids, only range back to the Devonian. The rhynchonellids are particularly interesting in that they are the only living group with a spirally coiled fleshy lophophore. However, a similar spiral lophophore was clearly present in the past in the hugely diverse group of brachiopods included within the Order Spiriferida. All these other forms, i.e. the Suborders Atrypidina, Retziidina, Athyridina, and Spiriferidina (including the punctate forms), had calcareous supports in the form of spiralia for their lophophores (text-fig. 1). With such rigid supports it would clearly have been impossible for them to extend their lophophores beyond the shell. Only in the rhynchonellids is the lophophore support limited to simple rods or crura. Generally speaking the crura can only have supported the proximal ends of the lophophore and would still have permitted the main spiral part to extend like a spring. Certain groups of rhynchonellids, for example the stenocismatids, which abound in Permian rocks, have more complex structures, but this group soon became extinct as did those such as *Rhynchonellina*, of the Early Mesozoic, with very long crura.

Among the spire-bearers with calcareous spiralia the most interesting in this connection are the atrypids, which are very common in Silurian and Devonian rocks, but suddenly became extinct, all over the world, at the top of the Frasnian stage (Copper 1966). The distinguishing feature of these atrypids was that their spiralia were directed in a dorsal direction, as are the lophophores in modern rhynchonellids, and not laterally as in all other spire-bearers. I have earlier suggested (Ager 1968) that there was a 'take-over' by the rhynchonellids from the atrypids at the end of Frasnian times. I later demonstrated in the Silurian and Devonian rocks of Morocco (Ager *et al.* 1976) how the rhynchonellids of the Famennian Stage, at the end of Devonian times, may have taken over an exactly similar ecological niche to that previously occupied by atrypids, in this case a colonial development on a substrate of algal turf on a local rise within a shallow muddy sea. It

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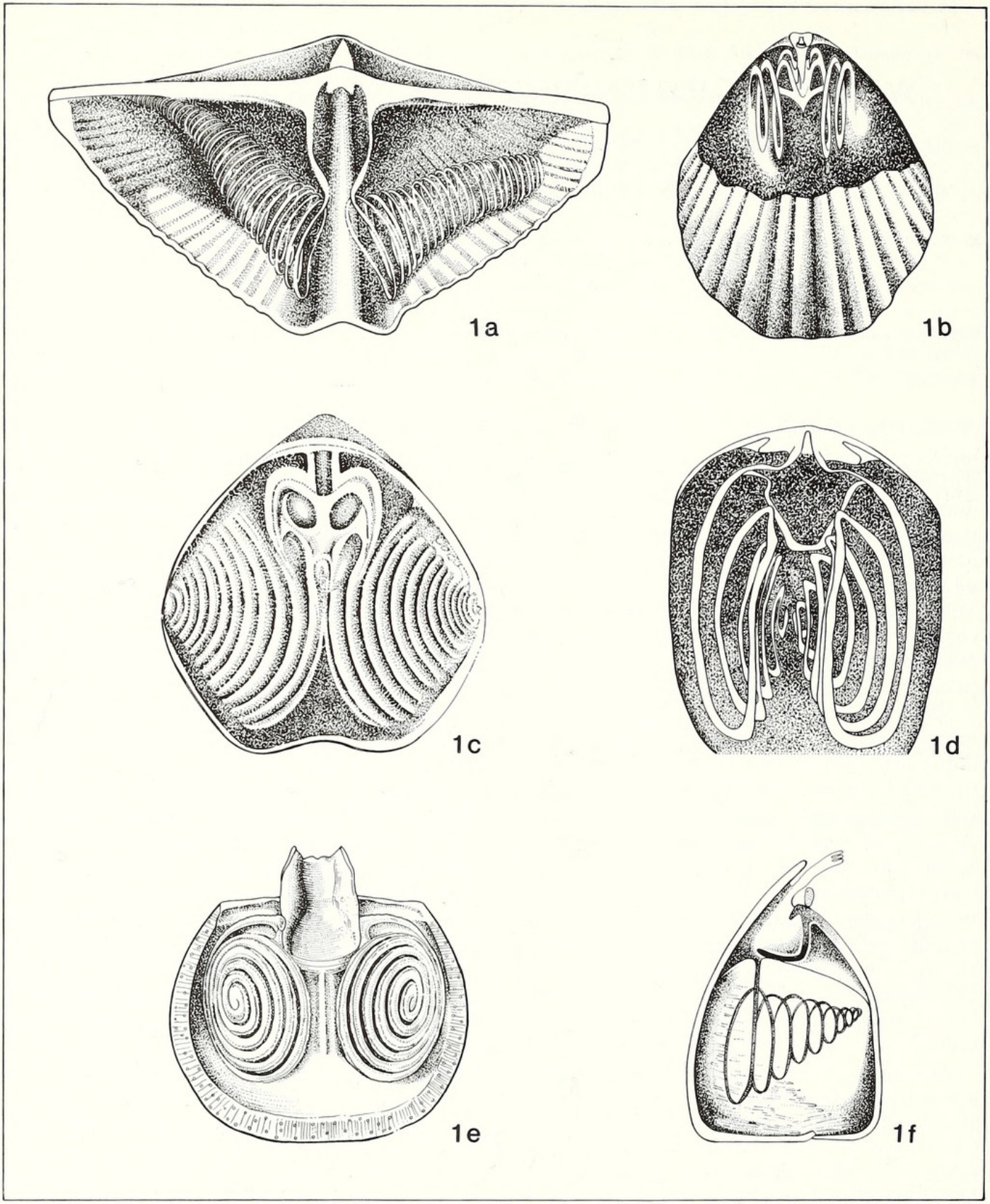


TEXT-FIG. 1. Form of the spiralia in (*a*) the Sub-Order Spiriferidina, (*b*) the Sub-Order Retziidina, (*c*) the Sub-Order Athyridina, (*d*) the Sub-Order Atrypidina, (*e*) the Family Thecospiridae, and (*f*) the *known* form of the lophophore in the Order Rhynchonellida.

is noteworthy that after playing a comparatively minor role in earlier shelf faunas (as far back as the Ordovician), the rhynchonellids suddenly proliferated in the Famennian following the extinction of the atrypids, as illustrated in many papers by Sartenaer (e.g. 1968, 1969) on Famennian rhynchonellids around the world. The only significant difference between the atrypids and the rhynchonellids is the presence in the former of calcareous lophophore supports or spiralia.

The rhynchonellids would have had an obvious advantage over the atrypids if they could then, as now, protrude their lophophores beyond their valves for feeding purposes and as part of the reproductive process. Hoverd also pointed out (1985) that modern rhynchonellids have the further unusual ability of regenerating their lophophores if the ends are snapped off (by the sudden closing of the shell in an emergency when the lophophore is extended).

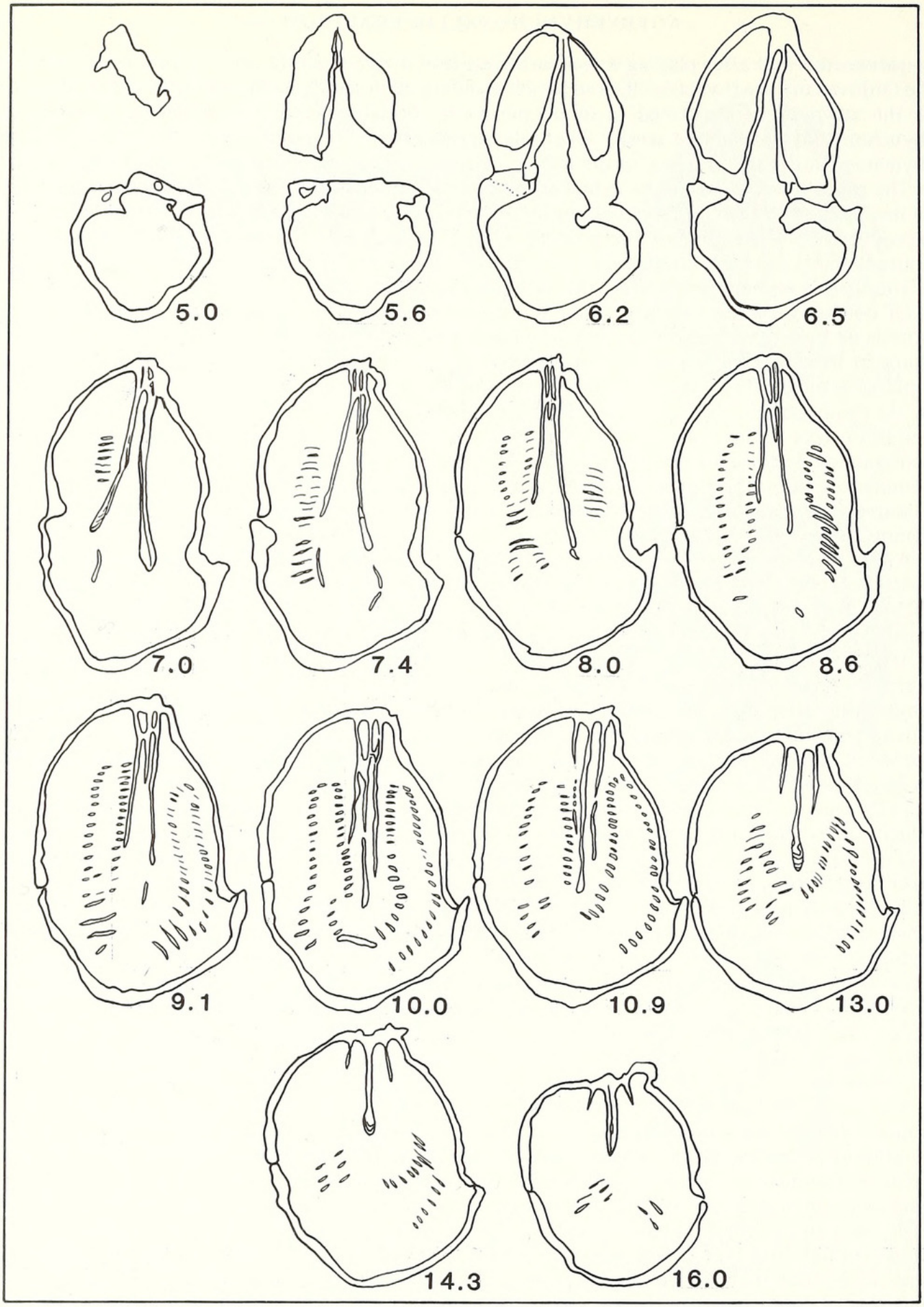
Of course, we know nothing about the lophophores of other important groups such as the orthids and pentamerids, which are long extinct and which have no indication of the lophophore shape in their brachidia. However, it may be significant that just as the atrypids may have been replaced ecologically by the 'ordinary' rhynchonellids, so the pentamerids may have been replaced by the stenocismatid rhynchonellids. Both have a spondylium-type structure in one or both valves and both seem to have prospered in the vicinity of reefs. The stenocismatids began just when the pentamerids declined to extinction in the Mid to Late Devonian and they had a final burst of abundance before their own extinction in the Late Permian. They are particularly common, for example in the vicinity of the Magnesian Limestone reefs of Durham (N. Hollingworth, pers. comm. 1985).

After the extinction of the atrypids, the other forms with laterally directed calcareous spiralia continued to flourish through the Carboniferous, Permian, and even Triassic Periods. Athyrids such as *Tetractinella* were locally abundant, for example in the Italian Middle Triassic, and many other forms lasted as late as the Rhaetian (Pearson 1977). There must have been some advantage in laterally directed lophophores, presumably in the separation of inhalant and exhalant feeding currents. Ager and Wallace (1966) suggested that they permitted a more efficient lateral flow of water rather than that conventionally assumed. However, the laterally directed spiral lophophores still had the limitation of a rigid framework supporting the fleshy lophophores and this presumably could not compete with the more flexible lophophores of the increasingly abundant rhynchonellids. In other words most of the spire-bearers opted for strength rather than flexibility.

In Palaeozoic times there was also the hugely successful order of brachiopods the Strophomenida, which ranged from the early Ordovician to the early Jurassic and which included the chonetids and productids that dominated the brachiopod world of the late Palaeozoic. There is clear evidence (from impressions or ridges inside the valves of genera such as *Leptaenisca* and *Davidsonia*) of spiral lophophores directed dorsally but without calcareous supports. Only in one small group the Thecospiriidae are calcareous spiralia preserved, directed ventrolaterally (text-fig. 1*e*). It may be significant that this family is restricted to rocks of Triassic age, the last of all the Strophomenida apart from the very problematical and isolated superfamily, the Cadomellacea of the Toarcian.

With the coming of Jurassic times the rigid spire-bearers were clearly in a decline and after the widespread extinctions at the end of the Triassic, only one genus—*Spiriferina*—survived, in progressively decreasing diversity, in the Early Jurassic. By the end of the Pliensbachian they had all but disappeared and they only lingered on, very locally, into the earliest Toarcian.

The progressive extinction of the last of the spire-bearers was detailed by Thomas (1978). It is noteworthy that the spire-bearers suffered a major eclipse in the widespread sulphurous black mud conditions at the end of the Triassic in the areas where they were still endemic. Then their final extinction came in the similar conditions of the Toarcian when they were even more localized. Of particular interest is one of the last species: *S. adscendens* (Eudes-Deslongchamps) of the late Pliensbachian, in which Thomas found ventrally directed spiralia (text-fig. 2). No other species is known to have this type of internal structure after the extinction of atrypids in the Late Devonian. One can surmise that this was evolutionary convergence with the contemporaneous rhynchonellids and was perhaps an advantage in the special environment of turbid black sulphurous bottom waters. Miguel Mancenido in fact suggested (in Thomas, p. 291) that this species may have opened



TEXT-FIG. 2. Ventrally directed spiralia in the probably unique species *Spiriferina adscendens* (Eudes-Deslongchamps). By kind permission of Dr Alun Thomas.

its valves as wide as possible withdrawing the spiralia and presenting the unprotected lophophore into the surrounding waters for feeding. However, it is not clear how this could be done and it would appear that this rare species also could not escape the calcareous straight-jacket of its own spiralia so that it, and the whole group of spiralia-bearing brachiopods, soon after became extinct.

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