S P E C I A L

Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications

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Calcareous tube-worms generally identified as *Spirorbis* range from Ordovician to Recent, often profusely encrusting shells and other substrates. Whereas Recent *Spirorbis* is a polychaete annelid, details of tube structure in pre-Cretaceous '*Spirorbis*' suggest affinities with the Microconchida, an extinct order of possible lophophorates. Although characteristically Palaeozoic, microconchid tube-worms survived the Permian mass extinction before being replaced in late Mesozoic ecosystems by true *Spirorbis*. Recent *Spirorbis* is stenohaline but spirorbiform microconchids also colonized freshwater, brackish and hypersaline environments during the Devonian–Triassic. Anomalies in the palaeoenvironmental distributions of fossil '*Spirorbis*' are explained with the recognition of this striking convergence between microconchids and true *Spirorbis*.

Convergent evolution generally results from unrelated species adopting similar lifestyles. Frequently cited examples include birds and bats, and ichthyosaurs and dolphins. Recognizing convergence depends on being able to show that the taxa concerned belong to different biological groups or clades. This is straightforward for the vertebrates cited above because their complex morphologies furnish ample characters amenable to cladistic analysis that reveals their true biological affinities. However, it can be more problematical in fossil invertebrates with simple skeletons. This study concerns some calcareous worm tubes where the failure to recognize convergence has led to false conclusions about their geological longevity and utility as palaeoenvironmental indicators.

Small, planispirally coiled calcareous tube-worms encrust hard and firm substrates of Late Ordovician to Holocene age (Fig. 1). They are routinely identified as *Spirorbis* because of their close resemblance to this polychaete annelid, which is widespread in today's oceans. Supposed species of *Spirorbis* feature in numerous palaeoecological studies of Palaeozoic hard substrates (e.g. Sparks *et al.* 1980; Sando 1984; Nield 1986; Fagerstrom 1996). Taken at face value the genus *Spirorbis* has a remarkable geological longevity of at least 450 Ma (Howell 1962).

Evidence that some Palaeozoic species of '*Spirorbis*' are unrelated to true *Spirorbis* began to emerge during the 1970s. Tube microstructure, internal septa and bulb-like tube origins initially pointed to British Carboniferous specimens being sessile, vermetid-like gastropods (Burchette & Riding 1977; Weedon 1990). Subsequently, affinities with the problematical tentaculitids (Weedon 1990, 1991) and with lophophorates (Weedon 1994) were suggested. The microstructure of minute lath-like crystallites arranged in chevron-shaped growth increments found in Recent *Spirorbis* was shown to contrast markedly with the often punctate, lamellar microstructure of Palaeozoic 'spirorbiform' fossils (Weedon 1994). Unfortunately, these findings have not been adequately assimilated and it is still commonplace to find Palaeozoic spirorbiforms incorrectly identified as *Spirorbis*.

To clarify the true affinities of fossil spirorbiform worms, we have undertaken micro- and macrostructural studies of Silurian–Recent material, coupled with a literature survey. Our results show that two independent clades of 'worms' evolved spirorbiform tubes, employing near-identical ecological strategies for colonizing hard and firm substrates. Those in the Ordovician–Jurassic are interpreted as lophophorates whereas Cretaceous–Recent spirorbiforms are polychaete annelids. Spirorbiform fossils thus provide an outstanding and hitherto unheralded example of convergent evolution. The paradox provided by finds of Devonian–Triassic '*Spirorbis*' in non-marine deposits, whereas modern *Spirorbis* is marine and stenohaline, is explained with the knowledge that these fossils are not spirorbid polychaetes.

Material and methods. Study material comes from the fossil worm collections of the Natural History Museum, London (NHM); a full listing of specimens studied is available online at http://www.geolsoc.org.uk/SUP18238. A hard copy can be obtained from the Society Library. Well-preserved spirorbiform fossils were chosen across their entire stratigraphical range, except for the Ordovician, which is poorly represented in the NHM collections. Surface features were examined mainly using a LEO 1455-VP SEM, a low-vacuum instrument capable of imaging uncoated specimens up to 10 cm or more in diameter. Representative specimens were embedded in epoxy resin and sectioned in a plane parallel to the coiling. After polishing, sections were etched lightly in 1% acetic acid and examined using an SEM. Conventional thin sections were also prepared further to elucidate tube microstructure.

Results. Spirorbiform tubes studied ranged from <1 mm to slightly >3 mm in diameter. Both dextral (clockwise) and sinistral (anticlockwise) tubes occurred, coiling direction being consistent within a species. Tightness of coiling varied between species, from evolute with successive whorls overlapping minimally, to involute with strongly overlapping whorls. In some instances, the outer parts of the tube grow erect to elevate the aperture above the substrate. Whereas some tubes are externally smooth (Fig. 1b), others were ornamented by transverse growth bands (Fig. 1j and k) and/or longitudinal ridges (Fig. 1f). None of these variations in morphology show any clear correlation with geological age.

Early growth stages provide important evidence for distinguishing convergent tube morphologies. True *Spirorbis* from the Recent was found to have tubes open at the origin (Fig. 1g), corroborating information from the literature (Nott 1973). However, this was closed in all pre-Cretaceous spirorbiforms where the origin of the tube could be observed (Fig. 1g), in one species comprising a bulb about 150 μm in diameter (Fig. 1k). Similar structures have previously been noted and/or illustrated in the literature (Beckmann 1954; Burchette & Riding 1977; Senkowiczowa 1985).
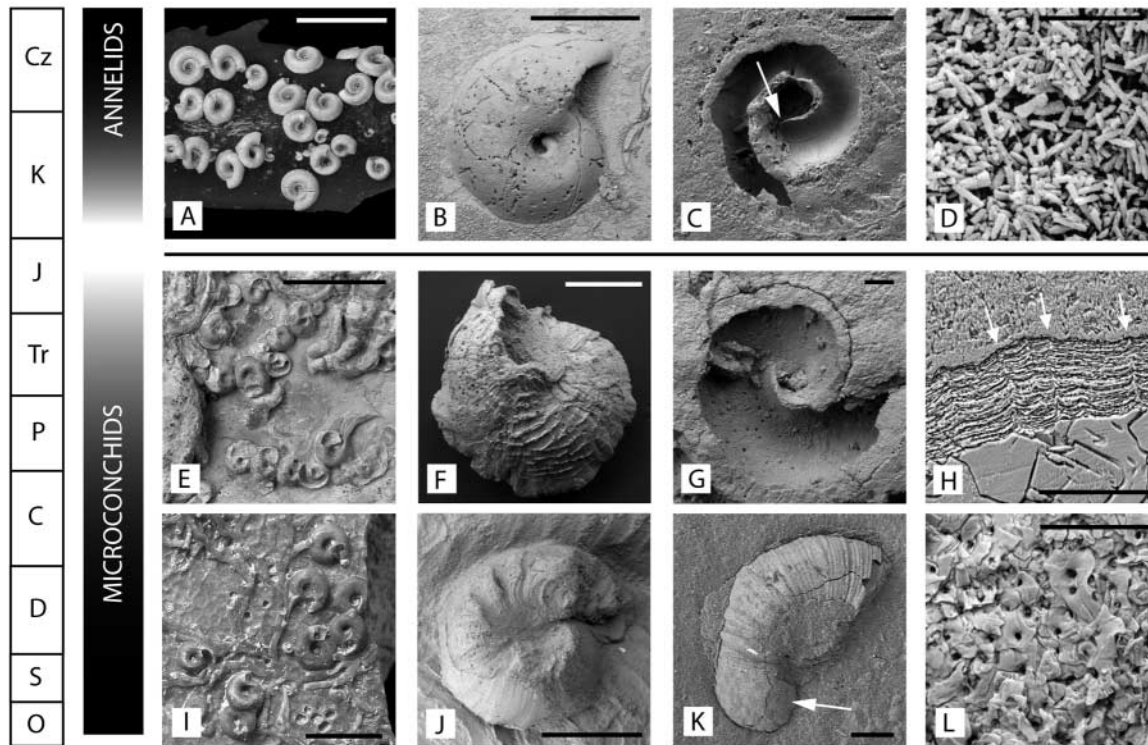
Fig. 1. Morphology of convergent Cretaceous–Recent annelid (**a**–**d**) and Ordovician–Jurassic microconchid (**e**–**l**) worm tubes usually identified as *Spirorbis*. (**a**) Recent *Spirorbis* attached to an algal frond. (**b**) Pliocene *Spirorbis* (Waccamaw Fm., North Carolina, USA) with microbored, tightly coiled tube. (**c**) Underside of Recent *Spirorbis* showing open tube origin (arrowed). (**d**) Microstructure of disordered rods in Recent *Spirorbis*. (**e**) Aggregation of *Microconchus valvata* (Münster) from the Triassic (Muschelkalk, Bindloch, Germany). (**f**) Ridged and porous tube of *Microconchus midfordensis* (Richardson) from the Jurassic (Bajocian, Stroud, Gloucestershire, UK). (**g**) Underside of another example of *Microconchus midfordensis* (Richardson) showing closed tube origin and porous tube wall. (**h**) Polished and etched section of *Microconchus tenuis* (Sowerby) tube from the Silurian (Much Wenlock Limestone Fm., Shropshire, UK), with arrows pointing to positions where pseudopunctae intersect tube outer surface. (**i**) Aggregation of *Microconchus omphalodes* (Goldfuss) from the Devonian (Hamilton Fm., Arkona, Ontario, Canada) intergrown with *Hederella*, a colonial problematicum. (**j**) Individual of *Microconchus* from the same locality showing growth bands. (**k**) Young specimen of *Microconchus pusillus* (Martin) from the British Carboniferous with bulb-like tube origin arrowed. (**l**) Lamellar microstructure and pores visible in exfoliated tube interior of another individual belonging to the same species (Westphalian, Coal Measures, Halifax, Yorkshire, UK). Scale bar represents: 5 mm in (**a**); 0.5 mm in (**b**); 100 μm in (**c**); 5 μm in (**d**); 5 mm in (**e**); 0.5 mm in (**f**); 100 μm in (**g**); 50 μm in (**h**); 5 mm in (**i**); 1 mm in (**j**); 100 μm in (**k**); 50 μm in (**l**).

Longitudinal sections through Cretaceous–Recent spirorbiforms confirmed the chevron-shaped growth increments reported previously (Weedon 1994). However, these were absent in all pre-Cretaceous species. Tube microstructure in Cretaceous–Recent species was extremely fine-grained, consistent with that previously reported in true *Spirorbis* and other serpulimorph annelids (Weedon 1994; Fig. 1d). None of the pre-Cretaceous spirorbiforms had this microstructure. Instead, most were found to have laminated microstructures, with the laminae formed from platy crystallites (Fig. 1h), or alternatively needle-like crystallites arranged transversely or fibres aligned parallel to tube growth direction. Regular cone-shaped inflections in the laminae are present in many species (Fig. 1h). Illustrations of pre-Cretaceous spirorbiforms with similar lamellar tube microstructures can also be found in the literature (Brönnimann & Zaninetti 1972; Burchette & Riding 1977; Warth 1982). Curved internal septa were present in sections of a Devonian species, and have prevously been depicted in a Carboniferous species (Burchette & Riding 1977, fig. 4A), but were not seen in the current study and have not been previously reported in Recent *Spirorbis*.

Although lacking in Cretaceous–Recent species, pores were found to be present in some spirorbiform specimens of Carboniferous, Triassic and Jurassic age. In a Carboniferous species they are very small, about 1.5–2 μm in diameter (Fig. 1l), whereas pores in two Jurassic species are an order of magnitude larger, measuring 15–20 μm in diameter (Fig. 1f and g).

Discussion. *Evolutionary convergence.* The deceptively simple external tube morphology of fossil spirorbiform worms belies significant variations in their internal structure. These differences indicate that spirorbiforms are taxonomically heterogeneous. Cretaceous–Recent examples are polychaete annelids but pre-Cretaceous species share skeletal characteristics with brachiopods and bryozoans. The bulb-like tube origin is reminiscent of the protoecium of stenolaemate bryozoans (Nielsen 1970), which is the first skeletal secretion formed by the newly settled and metamorphosed larva. Laminar skeletal microstructures are widespread among both bryozoans and brachiopods (Williams 1990). Conical inflections in the laminae of pre-Cretaceous spirorbiforms (Fig. 1h) resemble brachiopod pseudopunctae and bryozoan styles, and the pores in some tubes find parallels in brachiopod punctae and cyclostome bryozoan pseudopores.

Pending detailed study, pre-Cretaceous spirorbiforms are here all assigned to *Microconchus* Murchison, 1839, the nominate genus of the Order Microconchida Weedon 1991 (Class Tentaculitoidea Ljyashenko 1957), a presumed lophophorate. *Micro-*

conchus is neither bivalved like a brachiopod nor colonial like a bryozoan but may have been phoronid-like. Phoronids are a small phylum of soft-bodied lophophorates (Emig 1982) that live in chitinous tubes. Their elongate, vermiform bodies could be readily accommodated within a spirorbiform tube.

Contrasting biomineralization and soft tissue organization. In *Spirorbis* the body of the animal is not physically attached to the tube and the skeleton is very different from that of molluscs, brachiopods and bryozoans where epithelial tissues line the skeleton and anchor the body. Serpulimorph tubes grow by periodic application to the tube aperture of a mucus paste containing calcite or aragonite crystallites (Hedley 1958; Neff 1971). Chevron-shaped growth bands mark former positions of this aperture, and the very fine-grained microstructure of the tubes reflects the minute size of the crystallites in the paste (Fig. 1d). Unlike molluscs and brachiopods, there is no organic layer (periostracum) on the outside of the tube to form a template for biomineralization.

Soft tissue organization and mode of tube secretion is inferred to have been very different in *Microconchus*. Tube laminae were evidently secreted by epithelial tissues lining the tube interior. Highest calcification rates around the aperture led to tube extension, and continued calcification on the internal surface caused tube thickening, a pattern much like shell growth in brachiopods and molluscs. In some microconchids secretory epithelium formed septa to seal off older parts of the tube. A fixed epithelium allowed the positional maintenance of pseudopunctae (Fig. 1h) and pores (Fig. 1l), which would have been difficult had the tube been secreted from a paste as in spirorbids. If analogies with biomineralization in brachiopods and bivalves are correct, the calcite tubes of *Microconchus* would have possessed an outer organic layer. The very different modes of biomineralization employed by microconchids and spirorbids means that their calcareous tubes are not homologous structures even though they may be superficially almost identical in appearance.

Parallel palaeoecologies. Apart from the wider salinity tolerance of some species of microconchids (see below), most aspects of their palaeoecology are inferred to have been closely similar to the ecology of modern spirorbid polychaetes. Species belonging to both taxonomic groups recruit in large numbers onto hard and firm substrates (Fig. 1a, e and i), typically forming dense aggregations comprising mixtures of juveniles and adults (e.g. Abe 1943). In Recent *Spirorbis*, aggregation is often due to gregarious behaviour (Knight-Jones 1951), larvae preferentially settling close to adults of the same species. Nield (1986) demonstrated similar clustering of '*Spirorbis*' encrusting Silurian stromatoporoids. A preference for cryptic undersides may be shown by Recent spirorbids (Abe 1943), and this was also true for some Jurassic spirorbiform microconchids (Taylor 1979; Palmer & Fürsich 1981). Among the biotic substrates colonized by *Microconchus* are brachiopods (Fagerstrom 1996), bryozoans (Taylor 1984), bivalve molluscs (Trueman 1942; Van der Heide 1956), trilobites (Snajdr 1983), and marine (Jux 1964) and terrestrial plants (Kelber 1986; Falcon-Lang 2005). Recent spirorbids also encrust a variety of substrates. Although adept at biofouling, both groups are vulnerable to overgrowth by other organisms living on the same substrates (Lamont & O'Connor 1978; Taylor 1984). A strategy they both employ to prevent or delay overgrowth is elevation of the tube aperture (e.g. Brönnimann & Zaninetti 1972, for microconchids; Rzhavsky 1994, for spirorbids). Recent spirorbids are active suspension feeders using the brachial crown cilia to create water currents entraining plankton. Spirorbiform microconchids were also undoubtedly suspension feeders, probably employing cilia on a tentaculate lophophore to propel food particles towards the mouth.

Salinity tolerance. Modern spirorbid annelids are typically fully marine, stenohaline animals; although some species are capable of living in slightly reduced salinities (e.g. Caspers 1957; Ushakova 2003), none occur in freshwater environments. Beginning in the Devonian (Sandberg 1963; Ilyes 1995), spirorbiform microconchids began to inhabit brackish and freshwater environments in addition to marine settings. Carboniferous examples of non-marine '*Spirorbis*' are especially numerous (e.g. Trueman 1942; Van der Heide 1956; Bell 1960; Vasey 1985; Petzold 1986; Falcon-Lang 2005). For example, in Westphalian lacustrine and alluvial sediments of the Warwickshire Group of northern England, '*Spirorbis*' occurs together with non-marine bivalves, ostracodes, conchostracans and fish fragments, sometimes in sufficient abundance to form 'Spirorbis limestones' (Aitkenhead *et al*. 2002). '*Spirorbis*' is abundant in the lower Carboniferous Ballagan Formation of Scotland in deposits recently interpreted as brackish and hypersaline on the basis of sedimentology, stable isotopes and fossil content (Williams *et al*. 2005). The Upper Pennsylvanian Coenemaugh Group of eastern Ohio, USA, contains '*Spirorbis*' in facies interpreted as marginal lacustrine or palustrine (Lewis & Dunagan 2000). Spirorbiform microconchids evidently continued to live in freshwater or brackish-water environments into the Triassic (Gall & Grauvogel 1967; Ball 1980; Warth 1982; Ash 2005).

With the knowledge that the Carboniferous fossils actually belong to a different taxonomic group, uniformitarian reasoning that Carboniferous '*Spirorbis*' was strictly marine like its modern relatives (e.g. Cassle *et al*. 2003) no longer applies. Taken as a group, microconchids were evidently able to tolerate a wider range of salinities than do modern spirorbid annelids. Creationist literature (e.g. Coffin 1975) has argued for the rapid formation of coal in the sea during the Biblical Flood on the basis of finding marine '*Spirorbis*' attached to trees and other terrestrial plants in Carboniferous Coal Measures. This argument becomes untenable with the knowledge that the tube-worms concerned were not stenohaline spirorbid polychaetes.

Evolutionary history of spirorbiform worms. Fossils traditionally identified as '*Spirorbis*' in the geological literature belong to at least two different clades of animals with separate evolutionary histories. Spirorbiform microconchids first appeared in the Late Ordovician and persisted until at least the mid-Jurassic, surviving the end-Permian mass extinction. The extant spirorbiform annelids, including true *Spirorbis* and related genera, may not have appeared until the Cretaceous; Jurassic records (e.g. Parsch 1956; Housa 1974; Ziegler & Michalik 1998) require critical re-evaluation as some may be Serpulidae. However, by Late Cretaceous times, spirorbid annelids had become common (Jäger 1983). They employed closely similar morphological strategies to occupy essentially the same broad ecological niche that had been filled by spirorbiform microconchids from the Ordovician to the Jurassic, except that none are known to have adapted to life in non-marine environments. There is as yet no clear evidence for an overlap in the geological ranges of the two spirorbiform groups, and hence of competitive replacement of spirorbiform microconchids by spirorbid annelids. Rather, it is more probable that extinction of the incumbent microconchids cleared ecospace for spirorbid annelids, which evolved from another group of serpulimorph annelids (Kupriyanova 2003).

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