Phenotypic Reversion to Ancestral Form and Habit in a Marine Snail

In separating the polyphyletic Vermetidae (s.l.) into its separate lineages, Morton[1] noted the extreme anatomical similarity between *Vermicularia* and the coiled turritellids: "It is in fact little more than a turritellid which has taken on a sessile posture embedded in a hard substratum and proceeded to uncoil its shell whorls" (page 80 of ref. 1). *Vermicularia* is a ciliary suspension feeder, a common condition among sessile gastropods[2]. Only a few free living forms feed in this manner and one of these is *Turritella*. *T. communis* burrows into mud and may remain indefinitely in its favoured position. (Apex down and inclined at a high angle to the horizontal. The habits of *Turritella* are described in refs. 3 and 4.) The juvenile, regularly coiled *Vermicularia* lives in the same manner; its later attachment and uncoiling is a response to the availability of firm objects providing a substrate for rapid upgrowth.

In June 1967 I found what I first thought to be *Turritella* living in great numbers in Walsingham Pond, Bermuda—a landlocked water body of normal marine salinity maintained by transport through underground caves. Yet the lack of opercular bristles and the presence of a very few uncoiled shells (Fig. 1) identified these animals as *Vermicularia spirata* Philippi; *Turritella* is unknown in Bermuda. The floor of Walsingham Pond is covered by fine mud composed of decaying organic matter, faecal pellets and shell fragments. Less than 1 per cent of the largest empty shells show any sign of uncoiling. Most of these animals live and die with the external morphology and habits of their ancestor, *Turritella*. Provided with the typical Walsingham Pond environment in a laboratory tank, they burrow into the substrate as does *Turritella*. Placed in the sandy branching coral environment of most Bermudian *Vermicularia*, they cement and uncoil. Most uncoiled Walsingham Pond specimens unwind gradually and lack an attachment scar; the few scarred shells are joined to other *Vermicularia*.

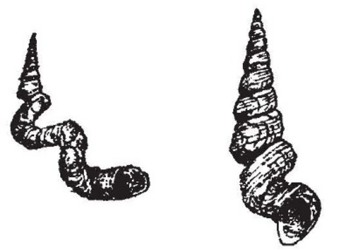

Fig. 1. Left, specimen of *V. spirata* from reef off north shore of Bermuda. Note three scars on uncoiled portion marking points of attachment to *Oculina*. Right, uncoiled *V. spirata* from Walsingham Pond. No attachment scars. (Actual size.)

Almost all Bermudian *Vermicularia* in open marine habitats attach to the branching coral *Oculina*. Massive brain corals, large mollusc shells, sponges and calcareous algae are host to a few *Vermicularia* in habitats lacking *Oculina*. If the primary advantage of uncoiling is rapid upgrowth (both to avoid sedimentary clogging of the ciliary feeding mechanism and to provide earlier access to suspended matter raining down from above), then the strong preference for Bermuda's only common branching coral is easily explained. Table 1 shows the correlation between length at uncoiling and attachment host. *Vermicularia spirata* uncoils at a smaller size when *Oculina*, its preferred host, is available. A further correlation may occur between length at uncoiling and bottom turbulence. The largest *Oculina*-based *Vermicularia* come from the calm inland waters of Harrington Sound; others are from reef tracts off the north shore of Bermuda. Harrington Sound specimens not attached to *Oculina* are significantly larger than those cemented to the branching coral ($t = 3 \cdot 70$ at 32 d.f.). Bottom turbulence may induce early attachment. Walsingham Pond specimens not only lack potential attachment sites, but also inhabit the calmest marine locality of Bermuda.

Table 1. RELATION OF HABITAT TO LENGTH AT UNCOILING IN *V. spirata*

Locality	Substrate	Mean length at uncoiling (mm)	Standard deviation (mm)	No. of specimens
Attached to *Oculina*				
Castle Harbour	*Oculina*	5·00	1·49	21
Three Hills Shoals	*Oculina*	6·40	1·62	22
North of Whalebone Bay	*Oculina*	7·72	1·77	35
Harrington Sound	*Oculina*	8·87	2·14	27
Not attached to *Oculina*				
Various north reef localities	Brain corals	8·72	1·68	6
North of Tobacco Bay	Sponge	9·01	1·37	22
North of Whalebone Bay	Alga (*Udotea*)	12·53		1
Harrington Sound	Clam (*Arca*)	12·11	1·82	7
No available attachment site				
Walsingham Pond	Mud	18·16	4·63	31
V. fargoi, Tampa Bay, Florida*	Mud	22·23	4·18	14

* Including Olsson's type and paratypes.

The discovery of such marked plasticity in length at uncoiling must call into question some *Vermicularia* species distinguished on mean values of this character. Olsson[5], for example, established *Vermicularia fargoi* for specimens from Tampa Bay, Florida, with a large coiled juvenile shell; no other character separates it from typical *V. spirata*. With the Walsingham Pond specimens it shares the large coiled portion, the gradual unwinding without attachment scar and, indeed, the muddy habitat. (Olsson's Tampa Bay *Vermicularia* were described as crawling about on the mud flats[5].) Their coiled portions are somewhat larger than those of Walsingham Pond (Table 1), but this result may be spurious because only uncoiled shells were used to compute the Walsingham mean and many Walsingham specimens showing no sign of uncoiling exceed the largest uncoiled individual. Olsson's *V. fargoi* is therefore rejected as a synonym of *V. spirata*.

The onset of uncoiling in *V. spirata* is so variable that in certain special conditions this defining character of the genus may not appear at all—thus causing a phenotypic reversion to the form of a fully coiled ancestral *Turritella*. This seems to occur when *V. spirata* is transported from its usual sandy reef environment to the muddy habitats preferred by *Turritella*. *Vermicularia* and *Turritella* were once placed in separate families, later in well distinguished genera. Given the plasticity of the defining generic character, I wonder if the world *Vermicularia* fauna can be traced to a single *Turritella* offshoot. It is tempting to think that several lineages of *Turritella* might have independently produced uncoiled derivatives.

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