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ON THE MORPHOECOLOGY OF SPIRORBID TUBES (POLYCHAETA: SPIRORBIDAE)

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ABSTRACT

Morphoecological variations of spirorbid tubes are discussed, and the maximum size of tubes, uncoiling of the whorls, thickness of the tube wall, development of longitudinal ridges, upward turning of the last whorl and some other features are related to environmental conditions.

Keywords: Spirorbidae, morphoecology of the tubes.

INTRODUCTION

The present paper deals with how the morphological variability of spirorbid tubes may relate to the conditions of life. Undoubtedly, certain characters may be variable or stable in different species, yet similar changes may be related to various ecological factors, whilst the same ecological factor may promote different adaptations. Nevertheless, it seems possible to outline the main tendencies in the variability and morphoecology of tubes for the family as a whole. It is hoped that these notes will be useful, because they may allow judgements to be made, from the appearance of fossil and recent specimens, about the conditions in which they lived.

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MATERIAL

At first data were obtained whilst studying the ecology of two Januinae species

(Rzhavsky & Britayev 1984) from the Sea of Japan. Later, looking over collections of spirorbids from the seas of ex-USSR (Rzhavsky 1988a, b, 1989, 1991a, b, 1992a, b) and some other waters (unpublished data), I especially paid attention to the tube morphology and tried to connect it with the ecological data. All these extensive materials were the basis of the present investigation, together with some data from the literature.

RESULTS AND DISCUSSION

Considering size of tube, three size groups can be distinguished. Large thick-walled tubes (diameters of whorls when adult 2.5-7.0 mm) are least variable. These tubes are hard enough to resist destruction by dissecting needles. Among Russian species, some of *Paradexiospira* and *Protoleodora* are most notable. From other waters, there are examples among species of *Bushiella* and *Pileolaria.* In these I did not find any connection between thickness of walls and conditions of life, including exposure to waves. In dense settlements, or on rough substrata, tubes can be deformed, not planospiral; outer whorls can cover the inner; the last whorl may bend upward from the substratum (Fig. 1 D), but the spiral never looks like an untwisting spring. Longitudinal ridges, if present, may be developed to different degrees and may vary in number, but this variability is slight and is probably not connected with conditions of life.

Typically, these species inhabit hard substrata, but only where there are flat areas large enough for attachment of planospiral tubes (rocks, stones, shells, large serpulid tubes, decapods and so on). They are absent from thin, narrow or flexible substrata (algae, marine angiosperms, branching hydrozoans and bryozoans, small pieces of gravel and shells). I found only small juvenile specimens of *Paradexiospira (Spirorbides) vitrea* (Fabricius) on holdfasts of *Laminaria* or on hydrozoans of the genus *Abietinaria.* Perhaps oscillations of flexible substrata cause strains at places of attachment, and a narrow surface does not provide enough area of contact. Worms with large heavy tubes moreover, could not retain attachment to undulating, wave-washed algae, because of their inertia.

Mid-sized tubes with not very thick walls (maximum diameter of whorls when adult about 2-3.5 mm) are most variable. Some species of *Circeis, Bushiella* and *Neodexiospira,* for example, can colonize various substrata and display considerable variations in uncoiling of whorls, thickness of tube walls and appearance of longitudinal ridges.

Species with small tubes, even as adult worms (maximum diameter of whorl 2.5 mm), have an intermediate degree of variability, with general trends like those shown by mid-sized tubes. Small size is itself adaptive, because such species can attach to substrata offering limited surface areas, without deformation of their tubes or untwisting of the whorls. These include *Spirorbis corallinae* De Silva &

Knight-Jones (settles on *Corallina officinalis*); *Bushiella (Jugaria) acuticostalis* Rzhavsky (on branching hydrozoans and bryozoans); some Januinae (on filamentous algae).

The following features may now be considered independently of the size of the tube. Some involve intraspecific variability, but others are typical of species.

1. *Untwisting of the whorls like a spring* (Fig. 1 C). This is often seen in dense settlements, where there is competition for space and feeding. I observed it in *Neodexiospira brasiliensis* (Grube), *Circeis armoricana* Saint-Joseph and *Bushiella (Jugaria) quadrangularis* (Stimpson). It is known for *Neodexiospira foraminosa* Moore & Bush - (see Knight-Jones et al. 1975) and probably seen in many other species with middle or small-sized tubes.

On the other hand, untwisting of the whorls very often takes place in specimens which attach to gravel fragments or thin branches of hydrozoans, bryozoans or algae. The small surfaces of such substrata do not allow planospiral tubes to be formed by worms beyond a certain size. I have observed this not only in *C. armoricana* and *B. (J.) quadrangularis,* but also in *Bushiella (Jugaria) kofiadii* (Rzhavsky). In the last species there are two reasons why this form develops. *B. (J.) kofiadii* very often settles on tubes of *Nothria conchylega* (Polychaeta: Onuphidae), which are formed by small pieces of gravel or shells. Each specimen of *B. (J.) kofiadii* attaches itself to one of these fragments, agreeing with what is written above. *N. conchylega,* however, inhabits soft silty bottom, so another reason why *B. (J.) kofiadii* must untwist its whorls is to avoid being buried by sediment.

Tubes of the antarctic spirorbid *Helicosiphon biscoeensis* Gravier seem to be extreme examples of adaptation to life in fairly deep still water, where silt accumulates (Knight-Jones et al. 1973). They are almost straight, up to 21 mm long and probably lie embedded in sediment more or less vertically. The minute spiral, from which occasional individuals can be seen to have originated, is usually broken away from these large unattached specimens. It was thought that this species may also form coiled tubes attached to littoral rocks, but those tubes proved to belong to a related spirorbid (Knight-Jones 1978). It is now regarded as a separate species, *Helicosiphon platyspira* Knight-Jones.

At the same time arctoboreal *Circeis spirillum* L. and *"Helicosiphon" armiger* (Vine) from the South hemisphere found commonly on hydrozoans and bryozoans, usually have untwisting whorls. Even on bryozoans where the surface of area is enough for the forming of planospiral tubes, untwisting of the whorls is seen in these species, though it may not be clearly expressed and some initial whorls may be planospiral. Probably this untwisting results from competition in feeding with the substratum-host.

2. *The thickness of tube walls.* Specimens of some eurytopic species (such as *C. armoricana* and *B. (J.) quadrangularis)* from algae, sea weeds and other flexible substrata have the walls of their tubes less thick than in specimens from hard substra-

ta (stones, shells etc.). Probably, light thin-walled tubes (having less inertia) are more suitable for being retained on undulating substrata (see above) and are less likely to harm the algae, even if they become abundant. It seems likely that these tubes belong to local populations, producing larvae adapted to seek out and colonize locally abundant algae, as described by Al-Ogily (1985) for *Spirorbis inornatus* L'Hardy & Quievreux. Production of thin-walled tubes would be a further adaptation, beneficial to the spirorbid-algal relationship.

At the same time, unusual thickening of tube walls was noted in *N. brasiliensis* inhabiting rocks and stones from the intertidal zone, exposed to wave action (Rzhavsky & Britayev 1984, as *Janua nipponica*).

3. *Longitudinal ridges.* The number, form and degree of development of longitudinal ridges are often species-specific, although not entirely reliable for taxonomic identification. Different species, or different specimens of one species living in the same conditions may or may not have longitudinal ridges. But for *C. armoricana* and *B. (J.) quadrangularis* mentioned above, and according to Knight-Jones et al. (1979) for *Bushiella (Bushiella) abnormis* (Bush), it was noted that more distinct longitudinal ridges were present on tubes from flexible substrata (algae and marine angiosperms) (Fig. 1 F, K). Perhaps, they serve to strengthen the tube and prevent it being broken by oscillations of these substrata.

On the other hand, it was noted that ridges disappear from *N. brasiliensis* tubes attached to rocks and stones in the surf intertidal zone, probably because of general thickening of the tube walls (see above) (Fig. 1 G, J).

4. *Upward turning of the last whorl* (Fig. 1 A). This is often connected with general deformation of the tubes in dense settlements and, at the same time, with competition for food. It includes turning away from the substratum in overhanging situations and was observed for many specimens of *Bushiella, Circeis, Protoleodora,* and *Neodexiospira.*

Upward turning of the last whorl prevents the tube mouth from being buried in sediment in *B. (J.) kofiadii,* or covered by coralline algae in *Spirorbis rupestris* Gee & Knight-Jones (see Gee & Knight-Jones 1962, Knight-Jones & Knight-Jones 1977).

5. *Turret-shaped tube.* This was noted for the thick-walled species *P. (S.) vitrea* (Fig. 1 B), which often lives in conditions of high sedimentation. The mouth is raised and may thus avoid being smothered, yet the mechanical strength associated with tight coiling is retained.

6. *Peripheral flange* (Fig. 1 I). This feature is very characteristic of *Spirorbis spirorbis* L. The flange is formed around each whorl at the place of attachment of the tubes to the substrata, which are usually very smooth algae. Similar flanges are formed by *S. inornatus.* The advantage seems to be connected with increasing the area and

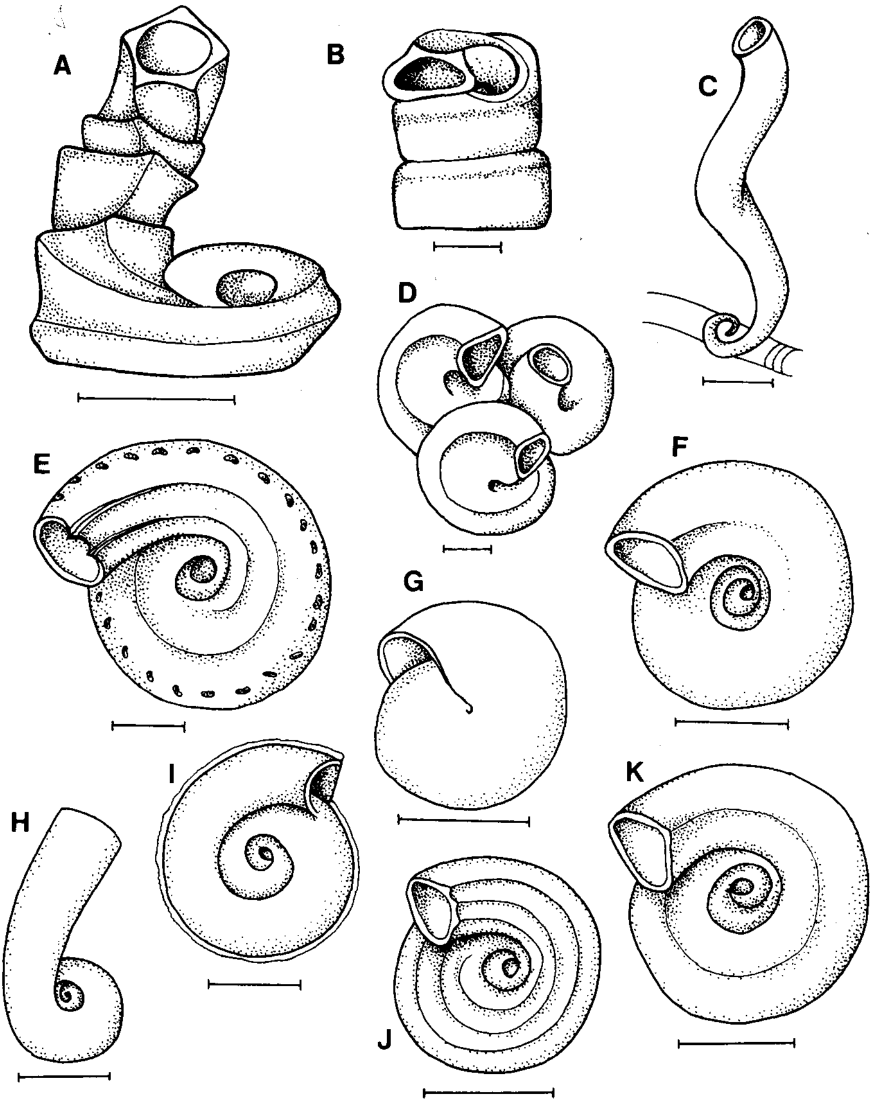

Fig. 1. Some forms of spirorbid tubes. A – *Bushiella (Jugaria) kofiadii,* tube with last whorl turning upward; B – *Paradexiospira (Spirorbides) vitrea,* turret-shaped tube; C – *Circeis spirillum,* uncoiling tube; D – *Protoleodora gracilis,* conglomerate of deformed tubes; E – *Paradexiospira (Spirorbides) cancellata,* tube with alveoli; F – *Circeis armoricana,* tube with rudimentary longitudinal ridge (from hard substrata); G – *Neodexiospira brasiliensis,* thick-walled tube without longitudinal ridges (from surf intertidal zone); H – *Bushiella (Bushiella) evoluta,* tube with evolute last whorl; I – *Spirorbis spirorbis,* tube with peripheral flange; J – *Neodexiospira brasiliensis,* tube with longitudinal ridges; K – *Circeis armoricana,* tube with well-developed longitudinal ridge (from sea weeds). All scale bars = 1 mm.

so the strength of attachment, and a special lobe of the collar is concerned with shaping the flange (Knight-Jones & Knight-Jones 1977).

There are several other characters, which appear regularly in various species. Construction of alveolate tube walls, for example, is characteristic of *Paradexiospira (Spirorbides) cancellata* (Fabricius) (Fig. 1 E) and some species of Januinae. Uncoiling of the last whorl inspired the species name *Bushiella (Bushiella) evoluta* (Bush) (Fig. 1 H) and similar uncoiling is seen in *S. rupestris* (see Knight-Jones & Knight-Jones 1977). But I could not find a suitable interpretation of these features.

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