

## DISTRIBUTION AND INTERRELATIONSHIPS OF NORTHERN SPIRORBID GENERA

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### A B S T R A C T

In the search for a natural system, taxonomy should be tested against geographical distribution. Few representatives of southern subfamilies (Romanchellinae, Paralaeospirinae) have crossed the equator, so most northern spirorbids which incubate within their tubes are Circeinae or Spirorbinae. *Spirorbis* species are mostly boreal and endemic to either the Atlantic or Pacific, but *Spirorbis* (*Spirorbella*) *marioni* and *Spirorbis bidentatus* are circumtropical and circumglobal. *Circeis* and *Paradexiospira* are circumboreal and boreal-arctic, but extend south to Brittany, Maine, California and Japan. Januinae and Pileolariinae are mostly tropical, but *Jugaria*, *Bushiella* and *Protoleodora*, all closely related and derived from *Pileolaria*, are exclusively northern. Probably *Jugaria* originated in the Atlantic and went through the Arctic to the Pacific. There it gave rise to *Bushiella* and *Protoleodora*, with notable speciation around the Sea of Okhotsk.

In the southern hemisphere (Knight-Jones and Knight-Jones, 1984) most spirorbid genera incubate within their tubes, but without attaching the eggs to the tube wall. In the north those southern subfamilies are poorly represented. Using names, definitions and groupings of genera and species which were given previously (Knight-Jones and Fordy, 1979), but modified later (Knight-Jones, 1984), the only Romanchellinae which cross the equator are a few species of *Protolaeospira*. Of that less well-defined group, the Paralaeospirinae, *Eulaeospira orientalis* and *Anomalorbis manuatus* are unusual in being tropical (Vine and Bailey-Brock, 1984); but only *Paralaeospira malardi* has reached Europe, probably by transport on ship's hulls, since it is not found in the warm-water belt which separates it from others of its genus.

In the tropics most spirorbids are Januinae or Pileolariinae (Knight-Jones and Knight-Jones, 1984) which have opercular brood chambers. Some species of several genera are circumglobal, though absent from Patagonia and Cape Town, so they can probably survive ship-borne transit round Africa or through Suez. Januinae are particularly confined to warm latitudes (Knight-Jones et al., 1975), though *Janua pagenstecheri* approaches 68°N sublittorally, at the Lofoten islands (Bergan, 1953). Of the large genus *Neodexiospira* (at least 12 species) only *N. pseudocorrugata* and *N. brasiliensis* reach 51°N in southern Britain (Knight-Jones and Knight-Jones, 1977). In collections from the northwest Pacific (see below), where temperatures are more extreme seasonally, these two species were not found further north than 45°, though they occurred in southern parts of Sakhalin and the Kurile chain, on algae and an angiosperm seed pod. Of the smaller genera, *Leodora knightjonesi* is monotypic and confined to coral areas (Vine et al., 1972), but two species of *Pillaiospira* are recorded from Hokkaido (Uchida, 1978).

The Pileolariinae have over 40 species, twice as many as in any other spirorbid subfamily, including the almost circumtropical *Vinearia koehleri*. These genera are distinguished mainly by the form of the brood chamber (Knight-Jones and Thorp, 1984). In *Nidificaria* the chamber is a simple cup, open distally, and there are a few records of this mainly southern genus up to 45°N, but only in deep water (Bailey-Brock and Knight-Jones, 1977). In *Pileolaria* (about 18 species) and *Simplaria* (about 3) differential growth results in the cup becoming inverted, to give the brood distal protection. The true *Pileolaria moerchi* (Knight-Jones et al., 1979)

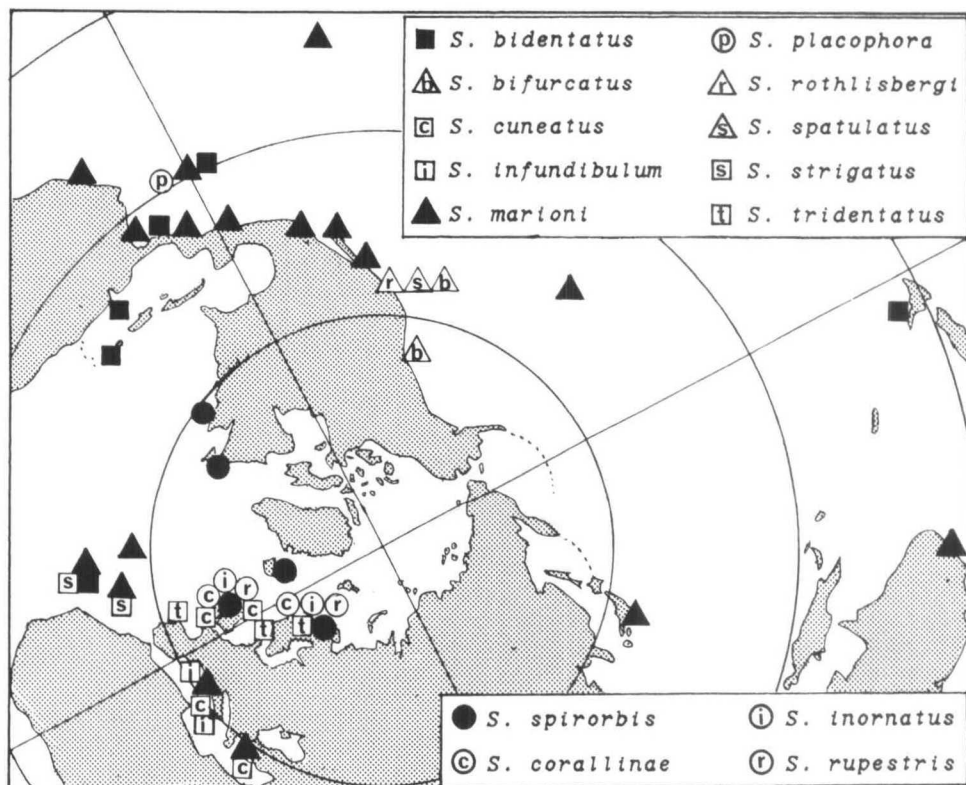


Figure 1. World distribution of *Spirorbis* species.

and an unnamed *Pileolaria* species (Tzetlin, 1985) reach the fringes of the Arctic (on the Atlantic side) but are little known. The truly boreal-arctic or boreal genera *Jugaria*, *Bushiella* and *Protoleodora* have brood chambers like those of *Pileolaria*, but usually capped by distal opercular plates retained from earlier non-brooding stages in the life cycle. It now seems that these three genera include at least six, six and three species respectively. Their distinguishing characters have been considered briefly by Knight-Jones (1984) and Rzhavsky (1988a; 1988b). Their known distributions will be outlined here, following consideration of the *Spirorbinae* and *Circeinae*.

#### SOURCES AND IDENTIFICATION OF MATERIAL

Some old records of species are untrustworthy, so this account relies on our own identifications, except where stated otherwise. Many of our sources were acknowledged previously in guides to spirorbids of northeast Atlantic and northeast Pacific coasts (Knight-Jones and Knight-Jones, 1977; Knight-Jones, 1978; Knight-Jones et al., 1979). Other species which are featured here (Figs. 1–3) but are not represented on those coasts were described from the Galapagos by Bailey and Harris (1968), eastern Canada and USA by Bush (1904), Mediterranean by Bianchi (1981), Arctic by Bergan (1953) and Rzhavsky (1988b), and eastern USSR by Knight-Jones (1984) and Rzhavsky (1988a). In addition, Dr. Helmut Zibrowius told us that *Spirorbis marioni* occurs in ports of the Azores, and forwarded large collections from (a) the Kurile Islands and Sakhalin, which had been sent to him

by Professor Uschakov, (b) the northwest Atlantic, made in 1951 by the PRESIDENT THEODORE TISSIER, research vessel of the French Fisheries Office, and (c) Ile Bonaventure, Quebec, made in 1969 by M. Ledoyer. Other collections were sent from eastern Canada by Dr. Judith Fournier, New Hampshire by Dr. Peter Kinner, the Netherlands Antilles by Dr. H. ten Hove, Turkey by Dr. Zeki Ergen, Shetlands by Drs. Bob Earl and Eyvor Sandison, Norway by Mr. H. Evans, Iceland by Dr. J. Moyse, Japan by Drs. J. A. Bruce and Marian Pettibone, and Vancouver by Eyvor Sandison.

#### LIMITED DISTRIBUTIONS OF NORTHERN *SPIRORBIS* SPECIES

Figure 1 is a polar projection showing a circle at 40°N, an incomplete equator and fragments of an outer circle at 40°S. These southern extensions allow us to outline the known world distributions of *Spirorbis* species, including *Spirorbis marioni*. Peripheral locations of *S. marioni* include Easter Island and Sydney, and it has probably been spread by shipping (Zibrowius and Bianchi, 1981).

*Spirorbis marioni* is dextrospirally, so it is represented on Figure 1 by solid triangles (cf. the Greek capital D). The only other *Spirorbis* which are dextrospirally are three species endemic to the U.S. west coast, shown as open triangles. This possible genetic link suggests that *S. marioni* may have originated on the American west coast, an idea supported by its concentrated distribution between Mexico and Peru and by its history of first sightings: Panama (Caullery and Mesnil, 1897), Mexico (Bush, 1904), southern California (Berkeley and Berkeley, 1941), Galapagos (Bailey and Harris, 1968), Hawaii (Vine et al., 1972), Easter Is. (Kohn and Lloyd, 1973), Canary Is. (pers. obs. 1974), Madeira (H. ten Hove collection in 1976), Azores and Mediterranean in 1977 (Zibrowius and Bianchi, 1981), Japan (Uchida, 1978, as *Spirorbella tricornigera*), Peru (pers. obs. 1981), Sydney and Jervis Bay (pers. obs. 1983). Populations appeared explosively in the Marseille region, where the species could not be found 10 years earlier (E. W. Knight-Jones, pers. obs.).

*Spirorbis marioni* is the type of *Spirorbella* Chamberlin, but that proposed genus differs from *Spirorbis* only in direction of coiling, so we have not yet adopted the name. Although the aggregation of triangles around California in Figure 1 suggests that *Spirorbella* may indeed be a useful taxon, the species concerned include *Spirorbis spatulatus* and *S. bifurcatus*, of which the former is often laeospiral and the latter usually so. These species agree with conclusions based on other genera, that laeospiralling is primitive in spirorbids, and that the more progressive dextrospirally species are also more labile, so likely to undergo back-mutation (Bailey, 1969; Knight-Jones, 1972).

The aggregation of species off Britain and Brittany results more from a diversity of macroalgae there than a concentration of investigators. *Spirorbis spirorbis* and its three close relatives with smooth tubes, indicated by solid and open circles in Figure 1, are epiphytic, with larvae seeking different algae. Careful search in Iceland by John Moyse indicated that *Spirorbis spirorbis* was the only representative there of this quartet. None of the four has been found south of the Bay of Biscay. Rioja (1923) recorded *S. spirorbis* from northwest Spain, but his figure shows that that material was really *Spirorbis tridentatus*, which is abundant at San Sebastian. *S. spirorbis* extends down the U.S. east coast, however, at least as far as Rhode Island. It probably occurs in Greenland (Wesenberg-Lund, 1950) and the White Sea (Fzetlin, 1985), but we have not seen material from those areas. It seems to be absent from the Pacific, despite a few records which were based on misidentifications (Knight-Jones et al., 1979).

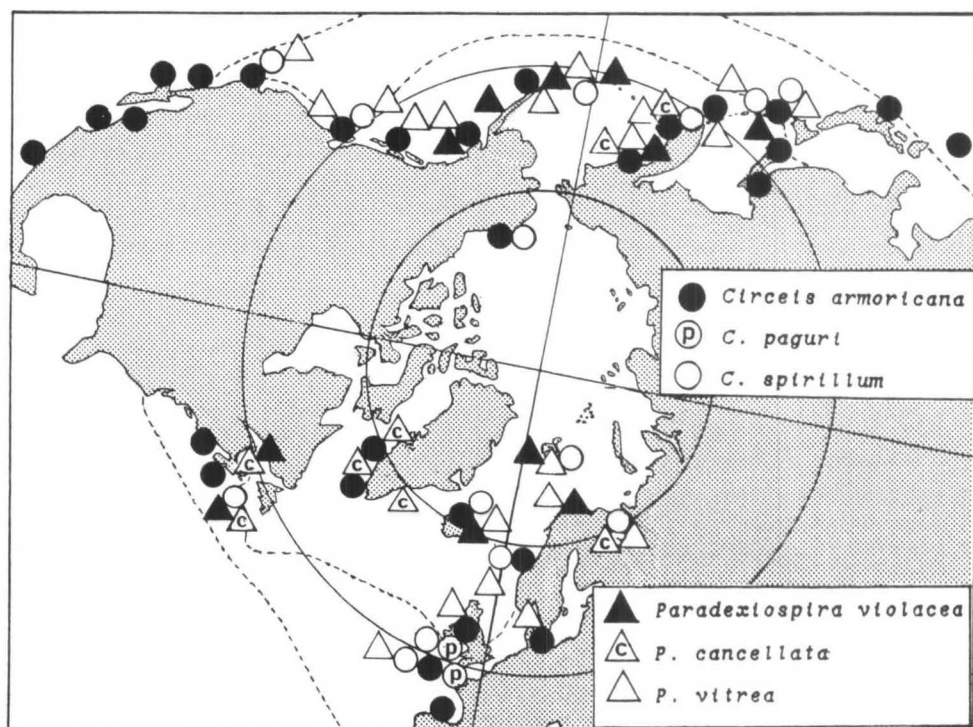


Figure 2. World distribution of Circeinae.

*Spirorbis placophora* from the Galapagos (open circle in Fig. 1) has a smooth tube and flat opercular plate like *S. spirorbis*, but it is really very different, having cross-striated collar chaetae. Other *Spirorbis* species (squares in Fig. 1) have massive or deeply cupped opercula and most have ridged tubes. Only the tropical form *Spirorbis bidentatus* is particularly widespread. It is recorded mostly in very shallow water, but Vine (1977) found it at 50 m depth off New Zealand.

#### THE CIRCUMBOREAL SUBFAMILY CIRCEINAE

Spawned eggs of the genus *Spirorbis* form a string, which is attached to the inside of the tube by a terminal filament. Otherwise this egg string is free and can be removed complete, without damage, if the tube is broken carefully. Circeinae, on the other hand, stick their eggs to the inside of the tube individually, so breaking the tube inevitably separates the egg layer into corresponding pieces (Knight-Jones et al., 1972). This subfamily contains two genera, each with about three species, for we regard *Paradexiospira nakamurai* (Uchida, 1971) as no different from *Paradexiospira vitrea*.

The distributions of these six species can be seen in Figure 2. They mostly stop short of the tropics, so the scale of this projection can be larger than Figure 1, showing just the Arctic Circle and 50°N latitude and (represented by interrupted lines) the mean February and August positions of 15° sea surface isotherms. Reliable records from the literature (Rzhavsky, 1989; Wesenberg-Lund, 1950; Fauvel, 1914; Tzetlin, 1985; Bergan, 1953; Bock, 1953; Rioja, 1925, 1942), for Kamchatka, Greenland, Spitzbergen, White Sea, Oslofjord, Kiel, Spain and southern Mexico respectively, are included here. In *Paradexiospira* the tubes alone are

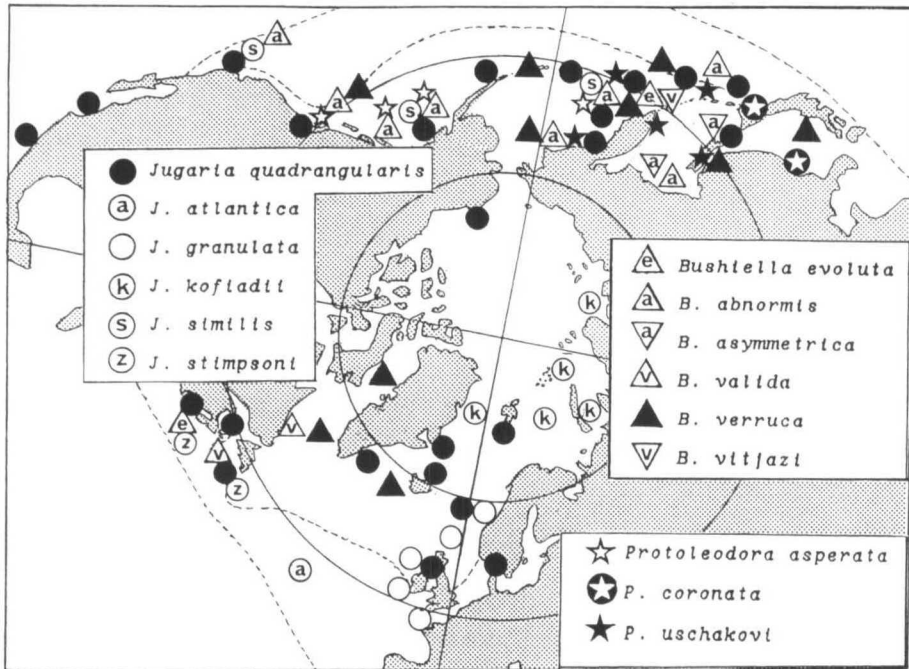


Figure 3. World distribution of *Jugaria*, *Bushiella* and *Protoleodora*.

fairly distinctive. *Circeis armoricana* was confused with *Circeis spirillum*, but we chanced upon the differences when studying choice of substrata by the larvae (Knight-Jones et al., 1975). Substrata are useful though not infallible guides to *Circeis* species. Throughout the Kuriles, America and Europe *Circeis spirillum* is found usually on hydroids and bryozoans, and *Circeis armoricana* on kelp, molluscan shells or decapod crustaceans.

*Circeis paguri* has been found only with large specimens of *Eupagurus bernhardus* (Al-Ogily and Knight-Jones, 1981) and may be confined to northwest Europe. The other five species are circumboreal and Arctic, with *Paradexiospira cancellata* and *Paradexiospira violacea* extending the least into adjacent oceans and *Circeis armoricana* the furthest, reaching subtropical waters near Acapulco and Okinawa. Mean sea surface temperatures in summer are about 28°C at both those places. The southward extensions of *Circeis spirillum* and *Paradexiospira vitrea* are intermediate, similar to each other, and close to the August positions of the 15° isotherms.

#### JUGARIA AND ITS CLOSE RELATIVES

Recent records in Figure 3 include *Bushiella asymmetrica* Rzhavsky (1988a), *Bushiella vitjazi* Rzhavsky (1988a) and *Jugaria kofiadit* Rzhavsky (1988b). We have not seen that material, nor the *Bushiella verruca* from Greenland recorded by Wesenberg-Lund (1950), nor the *Jugaria quadrangularis* from Sweden (Borg, 1917), Spitzbergen (Fauvel, 1914) or Mexico (Rioja, 1942). The last three authors used the name "*Spiroborbis granulatus*," then regarded as a senior synonym of *quadrangularis*. After that confusion was resolved (Knight-Jones and Knight-Jones, 1977) we were given abundant *Jugaria quadrangularis* from Loch Fyne, Scotland, by Dr. M. C. Goff. Those were on *Laminaria*, unusually for *J. qua-*

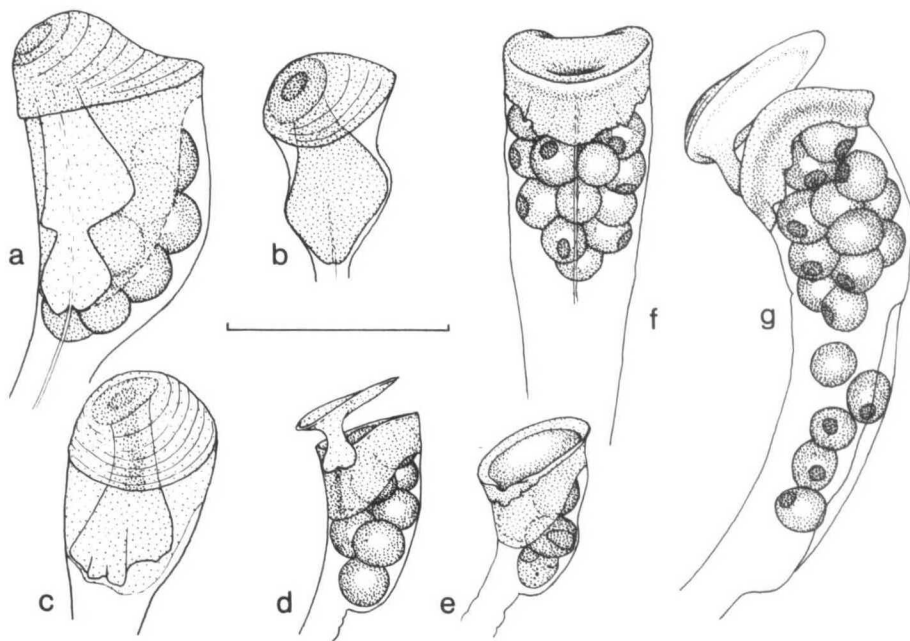


Figure 4. Opercular variation in *Jugaria* species: a, b, and c *J. quadrangularis*, a from Point Barrow, Alaska, b from Bonaventure Island, Quebec, c from Greenland, but similar types may be seen throughout range; d and e *J. granulatus* from Abereiddy, South Wales, d with juvenile operculum more separated than usual from brood chamber, e having shed it altogether; f and g *J. stimpsoni* from Newfoundland Banks. All equally magnified, scale line 1 mm.

*drangularis*, which we have seen mostly on shells or bryozoans. Many had the talon shaped like an angular hourglass, as also seen in *J. quadrangularis* from Point Barrow, Alaska (Fig. 4a).

*Jugaria quadrangularis* has a circumboreal and Arctic distribution, but the other five *Jugaria* species are more localized (Fig. 3). The exclusively Arctic species *Jugaria kofiadii* seems most like *J. quadrangularis*, for both have domed brood chambers, presumably to accommodate large broods. The distensible pouches characteristic of *Protoleodora* brood chambers obviously have a similar function (Knight-Jones, 1984).

*Bushiella* and *Protoleodora* replaced *Sinistrella* Chamberlin, which was pre-occupied. They are alike, and different from *Jugaria* and other Pileolariinae, in having simple collar chaetae. Both genera are centered in the northwest Pacific, having five and three species respectively in or around the Sea of Okhotsk. *Protoleodora asperata* is well known on the Canadian west coast as *Spirorbis medius*. No *Protoleodora* is known from the Arctic;\* in spite of their big brood chambers. *Bushiella verruca* gets through to Greenland, but apparently no further into the Atlantic, perhaps because it has become too cold-adapted. No *Bushiella* reaches Europe and only *B. valida* and *B. evoluta* represent the genus on the American east coast.

#### DISCUSSION

*Bushiella* and *Protoleodora* were probably derived from *Jugaria*, rather than the other way round, for the latter has finned collar chaetae, like those of other

\* Since this was written A. V. Rzhavsky (pers. comm.) has recorded *Protoleodora uschakovi* and *P. asperata* from Wrangel Island, N.W. of the Bering Strait.

Pileolariinae, most spirorbids and some serpulids (and generalized characters are usually regarded as primitive). Amongst *Jugaria* species those in the Atlantic are most like *Pileolaria*, for in *Jugaria granulata* and *J. atlantica* the largest abdominal tori lie posteriorly, as in *Pileolaria militaris* and *P. berkeleyana* (Bailey, 1969), whilst *Jugaria stimpsoni* has them about halfway down the abdomen. (*J. stimpsoni* is rather like *J. granulata*, but larger—see Fig. 4.) In Arctic and Pacific *Jugaria* the largest abdominal tori lie anteriorly, as they do in all *Bushiella* and *Protoleodora* species. These tenuous links suggest that *Jugaria* may have originated in the Atlantic, reached the Pacific via the Arctic, and given rise there to the other two genera, of which a few *Bushiella* species wandered back again. The extraordinary extension of *Jugaria quadrangularis* down the Mexican west coast suggests a long sojourn in the Pacific, but must result from the topography and water temperatures there being particularly favorable. That material was dredged, from unrecorded depths.

The fossil record of coiled tubeworms, probably spirorbids, is long (Knight-Jones, 1981) but unhelpful, because only tubes and sometimes opercula have been found, and these are mostly insufficient to identify genera. Only *Neomicrorbis* Rovert, from the Cretaceous of Britain and Germany, had tube sculpturing so characteristic that it can be recognized unequivocally in *Neomicrorbis azoricus* Zibrowius (1972). The latter was found living in deep water near the Azores and, more recently (Zibrowius, in litt.), in the Indian Ocean. It is a typically asymmetrical spirorbid, but has up to seven thoracic setigers. Tubes identified as *Janua*, from Holocene sediments in the Gulf of Mexico (Kennet and Penrose, 1978), seem indeed to be Januinae from their form, location and recent origin, but could be *Neodexiospira*. Januinae may well have evolved since the Panama Isthmus was formed in the Pliocene (Bailey, 1970) and Palaeocene records of Januinae by Lommerzheim (1981) from the Emperor seamounts must be regarded as tentative, because his taxa were necessarily identified from superficial characters. He attributed many of his dextral tubes to the Circeinae, although those seamounts were further south in the Palaeocene, perhaps in the latitude of Hawaii (Malz, 1981), where no Circeinae are now recorded. Paradoxically, Lommerzheim's fossil *Circeis* are rather convincing, whilst some of his *Janua* material might alternatively be placed in the Circeinae: viz. *Janua? bilineata* (Schmidt) has a two-ridged tube shaped like that of *Paradexiospira violacea*, and the tube (but not the talon) of *Janua quasiaecuta* Lommerzheim recalls *Paradexiospira cancellata*. Perhaps Circeinae, having brooding habits that seem plesiomorphic, are an ancient group which were previously more widespread than they are today.

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