

## **Evolution of spirorbin brooding: a phylogenetic analysis and a test of an oxygen limitation hypothesis**

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**ABSTRACT:** Spirorbinae is a group of small calcareous tubeworms (family Serpulidae) living in flat coiled tubes and incubating their embryos either in tubes or in opercular chambers. The controversy whether tube or opercular incubation is ancestral is unresolved and the costs and benefits of the two incubation types are not understood. The oxygen limitation hypothesis (Harris, 1972) suggests that as opercular incubators predominantly live in tropical waters and opercular incubation evolved as an adaptation to lower oxygen content experienced by embryos of tube incubators. The hypothesis implies that tube incubation is ancestral and opercular incubation evolved as spirorbins penetrated into lower latitudes. The aim of this study was to examine the evolution of brooding in spirorbins. The phylogenetic analysis of morphological characters was used to determine whether the opercular incubation is derived and whether types of opercular incubation evolved independently. We also tested for a relationship between the type of brooding and the geographical distribution in relation to the dissolved oxygen content. The results confirmed that opercular brooding is derived and that two types of opercular brooding originated independently. Tube brooders inhabit waters with higher oxygen content than opercular brooders do. We re-formulated the oxygen limitation hypothesis suggesting that the constraints imposed on tube incubation in warmer waters are related to the increased energetic costs of parental brood ventilation.

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**KEY WORDS:** Serpulidae, Polychaeta, tube brooding, opercular brooding, oxygen consumption.

## **Эволюция инкубации у спирорбин: филогенетический анализ и проверка гипотезы «кислородного ограничения»**

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**РЕЗЮМЕ:** Спирорбины — группа мелких полихет семейства Serpulidae, живущих в плоско закрученных известковых трубках и инкубирующих эмбрионы либо внутри трубок, либо в оперкулярных камерах. Не до конца понятны преимущества и недостатки трубчатой или оперкулярной инкубация, не ясно, какая из них первична. Гипотеза «кислородного ограничения» Харриса (Harris, 1972) предполагает, что поскольку виды, инкубирующие эмбрионы в оперкулярных камерах обитают в основном в тропиках, оперкулярная инкубация возникла как адаптация к пониженной концентрации кислорода, испытываемой эмбрионами, инкубируемыми в трубках. Эта гипотеза неявно предполагает, что инкубация в трубке первична, а оперкулярная инкубация вторично возникла по мере проникновения спирорбин в умеренные широты. Целью данной работы было изучить эволюцию инкубации у спирорбин. Филогенетический анализ морфологических признаков был использован, чтобы определить, является ли оперкулярная инкубация вторичной и эволюционировали ли типы оперкулярной инкубации независимо друг от друга. Мы также протестировали связь между типом инкубации и распределением спирорбин и содержания растворенного в воде кислорода. Результаты исследования подтвердили гипотезу, что оперкулярная инкубация вторична и что два типа такой инкубации возникли независимо друг от друга. Виды, инкубирующие в трубках, обитают в водах с более высоким содержанием кислорода, чем инкубирующие эмбрионы в оперкуломе. Мы переформулировали гипотезу «кислородного ограничения» и предлагаем, что ограничения, налагаемые на трубчатую инкубацию в тропиках связана с повышенными энергетическими затратами на вентиляцию вывода.

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**КЛЮЧЕВЫЕ СЛОВА:** Serpulidae, Polychaeta, трубчатая инкубация, оперкулярная инкубация, потребление кислорода.

## Introduction

Many marine invertebrates brood embryos on the body or inside specialised brooding structures and brooding is commonly associated with small body size (e.g., Chia, 1974; Menge, 1975; Knight-Jones, Bowden, 1979). Several hypotheses have been proposed to explain such a relationship. The most intuitive hypothesis of Chia (1974) states that brooding should be advantageous in small organisms with low energy reserves for gamete production because planktonic mortality is high. Low fecundity (of small species) means there is a high probability that no embryos exposed to the hazards of planktonic life will survive.

According to the recruitment hypothesis (Strathmann, Strathmann, 1982), predictable

recruitment typical for brooding species is more important for small-bodied than for large-bodied species. If recruitment is unpredictable, and larval or juvenile survival is more variable than survival of adults, selection may favour greater adult longevity with ensuring higher fecundity. Thus, varying survival may link absence of brooding to higher longevity and therefore, larger body size. The dispersal hypothesis (Strathmann, Strathmann, 1982) states that the advantages of brooding for smaller species exceed potential advantages provided by greater dispersal. Given that small spirorbins can disperse considerable distances using rafting, drifting and floating, any disadvantages of limited larval dispersal in brooders may be compensated. Long-term dispersal may be disadvantageous and Bhaud & Duchene (1996) even suggested

that brooding evolved as an adaptation for reduced dispersal to ensure fertilisation in a dispersive environment. However, their hypothesis does not suggest that brooding is more beneficial for small species. The allometry hypothesis (Strathmann, Strathmann, 1982) states that with increased body size, the capacity for egg production increases faster than space for brooding. While Hess (1993) found no evidence that scaling limits brood size in spirorbins, her test may not be decisive because she compared four spirorbins with *Pseudochitinopoma occidentalis* (Bush, 1905), the small-bodied serpulid that may provide early embryos with short-term parental care (Kupriyanova *et al.*, 2012). Because the validity of the allometry hypothesis depends on the type and geometry of the brood space, it may be only applicable to certain types of internal brooding. While this hypothesis explains why brooding is not a beneficial strategy for larger organisms, it does not necessarily imply that brooding should be a preferred mode for small species. The model of Havenhand (1993), which stresses the selective pressures toward reduction of development time to metamorphosis, indirectly emphasises the importance of brooding in small organisms, because brooders are normally lecithotrophic and tend to have shorter development time than planktotrophs.

All the hypotheses above are not mutually exclusive and some of them emphasise the association of large body size with absence of brooding more than the association of small size with brooding. In serpulimorph polychaetes (Serpulidae, Annelida) brooding is typical for all spirorbins and small (usually < 10 mm in length) serpulids, whereas larger serpulids with a body size of > 20 mm tend to be broadcasters (Kupriyanova *et al.*, 2001). Spirorbins show two major types of incubation: in the operculum and in the tube. Tube incubation is morphologically simple but is not uniform and its methods vary markedly according to the types of embryo anchorage inside the tube.

The evolution of brooding in spirorbins attracted attention of a number of researchers. It has been argued based on morphological complexity of structures involved in opercular brood-

ing, that this method is an evolutionary novelty in the Spirorbinae. Gee (1964) proposed a hypothetical evolutionary scheme according to which tube incubation precedes all other types of brood protection in spirorbins. The idea of ancestral tube incubation was widely accepted (Thorp, 1975; Knight-Jones, Thorp, 1984; Nishi, 1993). The incubating cups of the Pileolariini are considered to be derived, as they are structurally more complex and exhibit a wider range of forms. The interrelationships of romanchellin, pileolarin and januin brood chambers and possible sequences of their evolution have been considered in Thorp (1975) and Knight-Jones & Thorp (1984). Nishi (1993) proposed only a slight modification of Thorp (1975), suggesting that the tube brooding is ancestral type for the tubular thoracic-stalk brooding of Romanchiellinae. An alternative hypothesis by Thorp & Segrove (1975) suggested that the opercular incubation is ancestral and the tube incubation is derived.

The origin of the opercular brooding method appears to have been an important transition in evolution of spirorbins because it resulted in significant diversification of the group and wide geographical distribution of opercular brooders. However, the costs and benefits of tube vs. opercular incubation are not clearly understood. Opercular brooding appears to have some obvious disadvantages. The larvae could be susceptible to predation because opercula in serpulimorph polychaetes can be easily bitten off (Kupriyanova *et al.*, 2001), whereas tube incubation offers better protection for embryos. Opercular incubation may result in decreased fecundity because brooding space of the opercular brooding chamber is less than that of the tube. The brooding space limitation can result in reduced number of young per brood, although no studies analyzed the relative fecundity of opercular and tube brooders.

The only hypothesis explaining a selective advantage of opercular incubation (Harris, 1972) links oxygen demands of spirorbid embryos and type of incubation based on geographic distribution of selected spirorbins species. The observation that opercular incubators predominantly

live in warm waters led Harris (1972) to suggest that oxygen may be limiting factor for tube incubators. Tube-incubating species should dominate in highly oxygenated waters of high latitudes, whereas opercular incubators should mainly inhabit predominantly warm (and thus, less oxygenated) waters of lower latitudes. Therefore, opercular incubation evolved as an adaptation to reduce oxygen limitation experienced by embryos of tube incubators in warm waters. Although the hypothesis does not address the direction of evolution of brooding, it implies that tube incubation is an ancestral method that had originally emerged in high altitudes and opercular incubation evolved as spirorbins penetrated into lower latitudes. The hypothesis predicts a relationship between the type of brooding in a spirorbin taxon and the geographical distribution of the taxon in relation to the dissolved oxygen in the water.

The aim of this paper is to study of evolution of tube and opercular brooding in spirorbins. The phylogenetic analysis of spirorbid morphological characters was used to determine whether the opercular incubation is derived relative to the tube incubation and whether methods of opercular incubation originated independently. We also tested the prediction of Harris (1972) about a relationship between type of spirorbin incubation and the average concentration of dissolved oxygen on the scale of world-wide distribution.

## Material and methods

The material used in the cladistic analysis of morphological characters and in the analysis of geographical distribution was obtained from the literature (see Kupriyanova *et al.*, 2001) and unpublished data of Rzhavsky who had examined spirorbins deposited in museums worldwide (Rzhavsky, 1991a, b, 1992a, b, c, 1993, 1994, 1997, 1998; Rzhavsky *et al.*, 2018).

The data on average dissolved oxygen concentration corresponding to published and unpublished spirorbin distribution records (coordinates) were obtained from the public database of the National Oceanographic Data Center

(NODC), USA at [www.nodc.noaa.gov](http://www.nodc.noaa.gov). Yearly-averaged data with 1-degree resolution in latitude and longitude and 33 depth points from 0 to 5500 m were used. The species used in the analysis were recorded in the depth range 0-650 m, and most of them were recorded from the depths below 200 m (Table 1). The coordinates and depths of the original spirorbid distribution were rounded to the nearest points of the 3D data grid. Data for some intertidal or shallow subtidal species did not include depth, therefore, because they all fell within the first 0-33-m grid, the depth of such records was assumed to be zero. Some of the obtained nearest points happened to be onshore or below the bottom due to round off errors and/or approximate reporting of the data coordinates in species distributions. Such data points were further rounded towards the nearest grid node within the water. Finally, NODC data were used for the nearest node as the measure of the oxygen contents at the spirorbin location. The distribution of 3 spirorbin genera (10 species, Table 2) was analysed.

A phylogenetic analysis of spirorbin genera was performed using two serpulid species as an outgroup. The list of morphological characters used in the analysis is summarised in Table 3. The 27 spirorbin genera used in the analysis are listed in Table 4. Only the genera were used in the analysis because spirorbins show remarkable uniformity of their brooding within each genus. All characters were unordered and had equal weight. Character 1 (type of incubation) was included in the data matrix. Cladograms were generated with PAUP 4.10 (Swofford, 1999). The size of the data matrix (27 taxa by 35 characters) did not allow the use of exhaustive search; therefore, heuristic search was performed. The search 2000 replications using random addition with tree-bisection-reconnection branch-swapping, with 10 trees being held at each step. Accelerated transformation (ACCTRAN) was used for character-state optimisation.

The hypothesis that spirorbin fecundity is related to the body size was tested using regression analysis. One-way ANOVA was used to

Table 1. Spirorbin records, average dissolved oxygen concentration data, and incubation type.  
Таблица 1. Находки спирорбин, соответствующие им средние значения содержания растворенного в воде кислорода и тип инкубации.

Species	Latitude	Longitude	Depth, m	Incubation	Oxygen, mg.L <sup>-1</sup>
1	2	3	4	5	6
<i>Bushiella (J.) acuticostalis</i>	45°49'N	55°34'W	70	operculum	6.9073
	45°25'N	56°13'W	70	operculum	6.9441
	44°26'N	50°50'W	72	operculum	6.993
	69°19'N	33°52'W	170	operculum	7.0138
	45°00'N	49°40'W	73	operculum	7.1935
	54°52'N	167°26'E	10	operculum	7.4618
	46°26'N	143°35'E	25	operculum	8.0292
<i>Bushiella (J.) granulata</i>	54°06'N	4°48'W	16	operculum	5.75
	50°21'N	4°10'W	5	operculum	6.1259
	54°23'N	10°11'E	0	operculum	6.273
	53°2'N	4°38'W	2	operculum	6.4777
	66°18'N	33°17'E	23	operculum	7.5029
	65°545'N	38°15'E	90	operculum	7.6015
<i>Bushiella (J.) kofiadii</i>	17°30'N	17°30'E	230	operculum	0.8426
	78°05'N	149°30'E	58	operculum	6.1644
	75°15'N	170°45'W	390	operculum	6.4025
	70°26'N	17°56'E	120	operculum	6.4876
	75°15'N	171°15'W	455	operculum	6.5842
	69°2'N	33°32'E	280	operculum	6.656
	78°15'N	15°52'W	165	operculum	6.8077
	71°3'N	30°00'E	330	operculum	6.8269
	74°3'N	32°30'E	387	operculum	6.8816
	48°14'N	49°45'W	220	operculum	6.9043
	81°04'N	53°32'E	422	operculum	6.9188
	71°1'N	33°15'E	340	operculum	6.9793
	54°00'N	54°47'W	220	operculum	6.9799
	72°3'N	33°30'E	287	operculum	7.1269
	81°11'N	75°20'E	124	operculum	7.1478
	80°00'N	10°00'E	550	operculum	7.1821
	79°1'N	40°30'E	380	operculum	7.192
	77°03'N	13°24'E	420	operculum	7.2015
78°01'N	13°07'W	136	operculum	7.2094	
78°08'N	73°47'E	426	operculum	7.3719	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Bushiella (J.) kofiadii</i>	80°58'N	80°26'E	74	operculum	7.4159
	80°45'N	69°46'E	560	operculum	7.4302
	77°58'N	71°43'E	365	operculum	7.4395
	78°34'N	110°09'E	364	operculum	7.5066
<i>Bushiella (J.) quadrangularis</i>	22°29'N	56°40'W	0	operculum	4.6924
	52°53'N	160°09'E	176	operculum	4.9657
	56°45'N	145°50'E	218	operculum	5.0475
	57°45'N	159°55'E	115	operculum	6.1871
	60°07'N	160°46'E	100	operculum	6.4239
	71°30'N	171°54'W	58	operculum	6.5165
	48°24'N	45°59'W	92	operculum	6.5376
	54°19'N	140°22'E	60	operculum	6.5878
	55°34'N	161°18'W	46	operculum	6.6371
	63°4'N	10°50'E	100	operculum	6.6589
	43°20'N	50°15'W	65	operculum	6.6677
	48°00'N	139°46'E	58	operculum	6.723
	58°41'N	151°09'E	89	operculum	6.8463
	69°12'N	36°10'E	114	operculum	6.8735
	45°49'N	55°34'W	70	operculum	6.9073
	42°38'N	130°45'E	10	operculum	6.9256
	45°25'N	56°13'W	70	operculum	6.9441
	69°34'N	32°12'E	70	operculum	6.9574
	70°47'N	47°15'E	150	operculum	6.9655
	44°26'N	50°50'W	72	operculum	6.993
	68°55'N	37°37'E	167	operculum	7.019
	74°35'N	75°26'E	32	operculum	7.0423
	74°3'N	20°1'E	90	operculum	7.0666
	62°05'N	179°19'E	72	operculum	7.0847
	70°07'N	37°12'E	172	operculum	7.0978
	80°19'N	34°33'E	115	operculum	7.1331
77°07'N	13°37'E	200	operculum	7.2061	
71°06'N	42°40'E	127	operculum	7.2083	
54°14'N	160°29'E	80	operculum	7.2557	
69°12'N	35°47'E	30	operculum	7.3072	
66°18'N	33°17'E	12.5	operculum	7.3448	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Bushiella (J.) quadrangularis</i>	54°52'N	162°11'E	78	operculum	7.3544
	44°5'N	50°20'W	46	operculum	7.3562
	45°00'N	147°42'E	0	operculum	7.3615
	43°5'N	146°42'E	0	operculum	7.3693
	70°23'N	64°00'E	158	operculum	7.4077
	43°44'N	145°32'E	13	operculum	7.4561
	71°32'N	52°14'E	9	operculum	7.4618
	77°07'N	156°37'E	30	operculum	7.4649
	47°09'N	152°15'E	15	operculum	7.4714
	57°33'N	156°37'E	38	operculum	7.5108
	79°17'N	76°08'E	54	operculum	7.5324
	79°17'N	76°08'E	54	operculum	7.5324
	73°77'N	53°00'E	145	operculum	7.5487
	47°03'N	56°07'W	70	operculum	7.5612
	52°54'N	159°27'E	92	operculum	7.5941
	78°3'N	50°00'E	230	operculum	7.6751
	56°11'N	163°23'E	14.5	operculum	7.7053
	75°54'N	92°59'E	16	operculum	7.7401
	76°00'N	92°4'E	20	operculum	7.7401
	57°5'N	162°25'E	13	operculum	7.7786
	58°58'N	164°29'E	53	operculum	7.8253
	50°52'N	156°40'E	13	operculum	7.8324
	69°42'N	60°03'E	7	operculum	7.8722
	46°44'N	142°42'E	35	operculum	7.8742
	53°05'N	160°03'E	18	operculum	7.9267
	69°46'N	60°35'E	20	operculum	7.9553
	59°33'N	150°43'E	5	operculum	7.9602
	59°31'N	150°34'E	10	operculum	7.963
	69°42'N	170°16'E	7	operculum	8.0051
	53°16'N	159°58'E	10	operculum	8.0503
80°41'N	78°37'E	32	operculum	8.076	
52°57'N	158°29'E	6	operculum	8.1005	
80°21'N	52°16'E	73	operculum	8.1636	
71°24'N	156°29'W	50.4	operculum	8.2035	
79°24'N	91°13'E	24	operculum	8.493	
78°4'N	104°30'E	7	operculum	8.5248	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Bushiella (J.) similis</i>	56°00'N	149°29'E	397	operculum	3.0755
	56°1'N	149°23'E	284	operculum	3.2626
	46°14'N	138°33'E	630	operculum	5.5418
	37°41'N	122°18'W	28	operculum	5.6473
	54°19'N	140°22'E	60	operculum	6.5878
	59°31'N	156°29'E	42	operculum	6.628
	53°46'N	160°17'E	135	operculum	6.7168
	48°00'N	139°46'E	58	operculum	6.723
	45°49'N	55°34'W	70	operculum	6.9073
	52°53'N	159°39'E	125	operculum	7.3194
	43°44'N	145°32'E	0	operculum	7.3693
	80°26'N	85°36'E	313	operculum	7.3719
	78°22'N	15°05'E	20	operculum	7.5234
	59°33'N	150°43'E	27	operculum	7.5598
	47°03'N	56°08'W	70	operculum	7.5612
	53°16'N	159°58'E	19	operculum	7.9267
	52°57'N	158°29'E	6	operculum	8.1005
80°21'N	52°16'E	73	operculum	8.1636	
<i>Neodexiospira alveolata</i>	42°50'N	132°35'E	0	operculum	6.6205
	42°54'N	132°44'E	2	operculum	6.6205
	42°39'N	130°45'E	1	operculum	6.7595
	42°50'N	132°35'E	10	operculum	6.7777
	42°54'N	132°44'E	8	operculum	6.7777
	43°01'N	144°50'E	?	operculum	7.2469
	42°39'N	130°45'E	22	operculum	7.2897
	43°44'N	145°32'E	3	operculum	7.3693
	43°37'N	146°19'E	6	operculum	7.4561
43°44'N	145°32'E	9	operculum	7.4561	
<i>Neodexiospira foraminosa</i>	19°37'N	37°14'E	4	operculum	4.2598
	17°24'S	177°43'E	2.5	operculum	4.7144
	25°50'N	80°10'W	0	operculum	4.7152
	21°10'S	175°09'W	0	operculum	4.7379
	16°45'N	169°32'W	3.5	operculum	4.7387
	21°10'S	175°09'W	16	operculum	4.7536
	21°24'N	158°11'W	8	operculum	4.8093
	34°17'N	136°49'E	1	operculum	5.1355



Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Neodexiospira lamellosa</i>	34°05'S	151°08'E	?	operculum	5.0714
	35°01'S	138°30'E	?	operculum	5.6582
<i>Neodexiospira mannarensis</i>	08°58'N	79°55'E	0.5	operculum	4.522
	22°45'N	41°35'W	1	operculum	4.797
	22°59'S	43°03'W	1	operculum	4.8842
	38°35'S	58°40'W	1	operculum	6.3667
<i>Neodexiospira preacuta</i>	19°37'N	37°14'E	40	operculum	4.2666
	17°24'S	177°43'E	15	operculum	4.6816
	21°10'S	175°09'W	3	operculum	4.7379
	19°44'N	155°05'W	0	operculum	4.9549
<i>Paradexiospira (S.) violacea</i>	55°34'N	161°18'W	72	tube	6.1184
	45°20'N	53°17'W	88	tube	6.6811
	56°24'N	143°22'E	50	tube	6.689
	55°34'N	161°18'W	27	tube	6.8248
	45°49'N	55°34'W	70	tube	6.9073
	69°35'N	31°18'E	0	tube	7.0461
	60°35'N	147°25'W	?	tube	7.0478
	69°06'N	36°03'E	0	tube	7.0764
	62°05'N	179°19'E	72	tube	7.0847
	76°26'N	25°30'E	110	tube	7.0874
	59°06'N	163°31'E	1	tube	7.1035
	75°30'N	23°30'E	70	tube	7.156
	69°06'N	36°03'E	55	tube	7.2261
	51°54'N	177°24'E	18	tube	7.2348
	59°09'N	163°16'E	9	tube	7.4404
	59°09'N	163°16'E	15	tube	7.4404
	54°45'N	167°43'E	0	tube	7.4408
	58°50'N	170°22'E	75	tube	7.5034
	50°51'N	155°41'E	40	tube	7.5047
	55°11'N	165°56'E	0	tube	7.5149
78°22'N	15°05'E	25	tube	7.5234	
78°22'N	15°05'E	3	tube	7.5725	
55°11'N	165°56'E	30	tube	7.6484	
50°51'N	155°41'E	12	tube	7.6678	
46°47'N	56°16'W	55	tube	7.7106	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Paradexiospira (S.) violacea</i>	60°06'N	165°10'E	3	tube	7.7808
	65°54'N	169°41'W	48	tube	7.8076
	50°44'N	156°10'E	14	tube	7.8324
	50°52'N	156°40'E	10	tube	7.8324
	50°52'N	156°40'E	15	tube	7.8324
	50°44'N	156°10'E	3	tube	7.8559
	53°05'N	160°03'E	18	tube	7.9267
	52°49'N	158°38'E	10	tube	8.1005
	52°49'N	158°38'E	12	tube	8.1005
	72°57'N	55°54'E	25	tube	8.2805
<i>Paradexiospira (S.) cancellata</i>	45°49'N	55°34'E	70	tube	3.8231
	56°11'N	163°23'E	118	tube	5.4482
	49°43'N	156°16'E	172.5	tube	6.3014
	56°24'N	143°22'E	76	tube	6.5351
	57°50'N	162°25'E	120	tube	6.5559
	45°20'N	53°17'W	88	tube	6.6811
	56°24'N	143°22'E	50	tube	6.689
	59°04'N	154°01'E	62	tube	6.8908
	57°46'N	156°48'E	76	tube	7.0372
	62°95'N	179°19'E	72	tube	7.0847
	61°50'N	170°30'E	72	tube	7.0915
	59°09'N	163°16'E	3	tube	7.1035
	46°42'N	56°10'W	90	tube	7.2165
	69°06'N	36°03'E	61	tube	7.2261
	59°55'N	172°25'E	75	tube	7.2998
	60°55'N	172°25'E	60	tube	7.3001
	59°09'N	163°16'E	15	tube	7.4404
	54°49'N	167°33'E	20	tube	7.4851
	66°18'N	33°17'E	25	tube	7.5029
	47°03'N	56°07'W	70	tube	7.5612
78°22'N	15°05'E	?	tube	7.5725	
66°18'N	33°17'E	28	tube	7.5768	
53°16'N	159°58'E	25	tube	7.9267	
69°46'N	60°35'E	20	tube	7.9553	
<i>Paradexiospira (S.) vitrea</i>	50°41'N	157°30'E	217	tube	5.3666
	56°06'N	137°34'E	62	tube	5.797

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Paradexiospira (S.) vitrea</i>	59°00'N	142°35'E	62	tube	5.8186
	43°38'N	146°58'E	150	tube	5.9227
	49°28'N	02°31'W	25	tube	5.9652
	35°25'N	120°53'W	0	tube	6.0217
	50°09'N	155°01'E	242	tube	6.0398
	49°55'N	06°17'W	25	tube	6.0676
	50°22'N	04°09'W	15	tube	6.0751
	49°55'N	06°17'W	0	tube	6.0842
	36°38'N	121°56'W	0	tube	6.1164
	50°22'N	04°09'W	0	tube	6.1259
	49°28'N	02°31'W	0	tube	6.1738
	49°53'N	155°38'E	140	tube	6.2859
	49°43'N	156°16'E	172.5	tube	6.3014
	49°51'N	156°18'E	151	tube	6.3014
	44°37'N	124°5'W	0	tube	6.4075
	54°33'N	142°40'E	67	tube	6.6084
	59°16'N	10°36'E	40	tube	6.6115
	56°24'N	143°22'E	50	tube	6.689
	42°18'N	141°00'E	0	tube	6.7034
	42°18'N	141°00'E	15	tube	6.7343
	42°27'N	130°56'E	5	tube	6.7595
	42°38'N	130°45'E	5	tube	6.7595
	48°00'N	123°00'E	0	tube	6.7595
	42°27'N	130°56'E	10	tube	6.9256
	42°38'N	130°45'E	10	tube	6.9256
	68°55'N	37°37'E	167	tube	7.019
	49°52'N	155°56'E	106	tube	7.0434
	60°35'N	147°25'W	?	tube	7.0478
	69°06'N	36°03'E	3	tube	7.0764
	62°05'N	179°19'E	72	tube	7.0847
	59°09'N	163°16'E	2	tube	7.1035
	58°59'N	154°01'E	36	tube	7.1448
71°06'N	42°40'E	127.5	tube	7.2083	
69°06'N	36°03'E	55	tube	7.2261	
50°06'N	140°33'E	20	tube	7.2391	
43°01'N	144°50'E	0	tube	7.2469	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
	53°32'N	160°03'E	80	tube	7.2557
	43°01'N	144°50'E	15	tube	7.3171
	52°50'N	172°45'E	11	tube	7.3291
	43°44'N	145°32'E	3	tube	7.3693
	72°00'N	48°10'E	95	tube	7.44
	59°09'N	163°16'E	6	tube	7.4404
	43°46'N	145°54'E	26	tube	7.446
	47°09'N	152°15'E	0	tube	7.4598
	47°09'N	152°15'E	20	tube	7.4614
	66°18'N	33°17'E	25	tube	7.5029
	50°51'N	155°41'E	40	tube	7.5047
	57°33'N	156°37'E	38	tube	7.5108
	55°11'N	165°56'E	0	tube	7.5149
	78°22'N	15°05'E	25	tube	7.5234
	73°77'N	53°00'E	145	tube	7.5487
	54°46'N	137°14'E	40	tube	7.5501
	78°22'N	15°05'E	2	tube	7.5725
<i>Paradexiospira (S.) vitrea</i>	53°16'N	159°58'E	1	tube	7.5795
	55°11'N	165°56'E	20	tube	7.6612
	50°51'N	155°41'E	10	tube	7.6678
	56°11'N	163°23'E	14.5	tube	7.7053
	50°52'N	156°40'E	40	tube	7.7069
	52°57'N	158°29'E	4	tube	7.7705
	60°06'N	165°10'E	3	tube	7.7808
	65°54'N	169°14'W	48	tube	7.8076
	54°46'N	137°14'E	8	tube	7.8133
	50°52'N	156°40'E	15	tube	7.8324
	60°21'N	167°04'E	2.5	tube	7.8738
	56°06'N	137°34'E	10	tube	7.9463
	59°31'N	150°44'E	0	tube	7.9602
	59°31'N	150°44'E	10	tube	7.963
	64°21'N	173°22'W	8	tube	8.0382
	53°16'N	159°58'E	10	tube	8.0503
	64°21'N	173°22'W	4	tube	8.0905
	52°57'N	158°29'E	10	tube	8.1005
	72°57'N	55°54'E	25	tube	8.2805

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Paradexiospira (S.) vitrea</i>	79°24'N	91°13'E	24	tube	8.493
<i>Spirorbis tridentatus</i>	79°34'N	10°59'E	44	tube	7.3089
	42°39'N	130°47'E	0	operculum	6.7595
	42°39'N	130°47'E	4	operculum	6.7595
	47°08'N	130°47'E	0.5	operculum	6.8488
	47°08'N	130°47'E	0	operculum	6.8488
	47°08'N	130°47'E	3	operculum	6.8488
	47°08'N	130°47'E	0	operculum	6.8488
	47°08'N	130°47'E	4	operculum	6.8488
	42°27'N	130°56'E	7	operculum	6.9256
	42°27'N	130°56'E	17	operculum	7.2897
	43°27'N	145°54'E	9	operculum	7.4561
	33°14'S	118°10'W	1	operculum	5.6744
	36°19'S	174°48'E	0	operculum	5.5975
<i>Neodexiospira brasiliensis</i>	33°05'N	138°50'E	20	operculum	5.0568
	43°12'N	140°51'E	0	operculum	6.3087
	42°20'N	141°02'E	0	operculum	6.7034
	33°56'S	25°37'E	0	operculum	5.0501
	33°54'S	18°29'E	0	operculum	5.7905
	11°25'N	162°22'E	0	operculum	4.4933
	30°23'N	88°54'W	1	operculum	4.8049
	19°39'N	37°14'E	1	operculum	4.2598
	50°49'N	01°07'W	1	operculum	6.3038
	27°37'S	48°33'W	1	operculum	4.7628
	19°07'S	146°51'E	?	operculum	4.5635
	43°09'S	147°51'E	?	operculum	5.7379
	33°57'S	151°10'E	?	operculum	5.0714
	22°29'N	56°40'W	0	operculum	4.6924
	24°46'N	48°08'W	0	operculum	4.7735
	39°07'N	70°24'W	0	operculum	5.8926
	03°22'S	39°58'E	0.5	operculum	4.6705
<i>Neodexiospira formosa</i>	09°41'N	80°00'E	1	operculum	4.522
	08°00'N	79°49'E	1	operculum	4.3906
	34°01'N	76°05'W	0	operculum	4.7193
	12°10'N	68°18'W	1	operculum	4.4731
	33°51'S	151°17'E	0	operculum	5.0714

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Neodexiospira kayi</i>	03°22'S	39°58'E	2	operculum	4.6705
	08°00'N	79°49'E	1	operculum	4.3906
	29°43'N	47°44'E	0	operculum	5.048
<i>Neodexiospira pseudocorugata</i>	42°38'N	130°45'E	10	operculum	6.9256
	36°38'N	121°56'W	0	operculum	6.1164
	33°24'N	118°21'W	0	operculum	5.6744
	21°08'S	176°09'W	1	operculum	4.7376
	21°08'S	176°09'W	7	operculum	4.7427
	44°38'N	33°33'E	3	operculum	6.4392
	44°50'N	34°59'E	4	operculum	6.4288
	44°50'N	34°59'E	12	operculum	6.6237
	33°51'S	151°17'E	0	operculum	5.0714
	36°03'S	136°42'E	0	operculum	5.5984
	14°41'S	145°27'E	0	operculum	4.6827
	19°07'S	146°51'E	0	operculum	4.5635
	23°31'S	152°05'E	0	operculum	4.8571
	27°30'S	153°24'E	0	operculum	4.8485
	30°02'S	153°12'E	0	operculum	4.9201
	30°02'S	152°04'E	0	operculum	4.9201
	35°12'S	150°41'E	0	operculum	5.1145
	37°16'S	150°03'E	0	operculum	5.3425
	38°29'S	145.18'E	0	operculum	5.629
	40°58'S	145°44'E	0	operculum	5.7052
	43°09'S	147°51'E	0	operculum	5.7379
	43°12'N	140°51'E	0	operculum	6.3087
	42°20'N	41°02'E	0	operculum	6.2105
	32°38'N	16°55'W	0	operculum	5.1635
	32°38'N	16°55'W	15	operculum	5.1528
	25°43'N	79°18'W	1	operculum	4.7152
	10°30'N	61°02'W	1	operculum	4.7185
	50°21'N	4°10'W	12	operculum	6.0751
	49°55'N	06°19'W	5	operculum	6.0842
	49°55'N	06°19'W	20	operculum	6.0676
53°09'N	09°07'W	0	operculum	6.1176	
48°43'N	04°00'W	0	operculum	6.0992	

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3	4	5	6
<i>Neodexiospira pseudocorugata</i>	49°11'N	02°08'W	0	operculum	6.1738
	23°41'S	35°21'E	1	operculum	4.8626
	33°56'S	25°37'E	0.5	operculum	5.0501

Table 2. Results of Tukey HSD test for 10 spirorbin species.  
Таблица 2. Результаты теста Тукей для 10 родов спирорбин.

Species (incubation type)	N	Subset		
		1	2	3
<i>N. foraminosa</i> (opercular)	9	4.80060		
<i>N. pseudocorugata</i> (opercular)	35	5.52796	5.52796	
<i>N. brasiliensis</i> (opercular)	25		5.98453	
<i>B. similis</i> (opercular)	20			6.74617
<i>P. cancellata</i> (tube)	24			6.97104
<i>N. alveolata</i> (opercular)	11			7.00704
<i>B. kofiadii</i> (opercular)	24			7.06628
<i>P. vitrea</i> (tube)	75			7.11541
<i>B. quadrangularis</i> (opercular)	72			7.22555
<i>P. violacea</i> (tube)	35			7.41715

Table 3. The list of morphological characters used in the phylogenetic analysis.  
Таблица 3. Список морфологических данных, использовавшихся в филогенетическом анализе.

Characters	Character states
1	2
1. Incubation	1 — embryo string attached by a filament to inside of tube, 2 — embryos adhering to tube, 3 — embryos attached to body, 4 — embryo in cup formed by invagination of operculum, 5 — embryos in cuticular cup outside of operculum, 6 — free in tube, 7 — no incubation
2. Tube white opaque	no — 0, yes — 1
3. Tube white porcellanous	no — 0, yes — 1
4. Tube semitransparent porcellanous	no — 0, yes — 1
5. Tube transparent vitreous	no — 0, yes — 1
6. Tube uncoiled	no — 0, yes — 1
7. Tube coiling dextral	no — 0, yes — 1
8. Tube coiling sinistral	no — 0, yes — 1
9. Number of thoracic chaetigers	3 — 3, 4 — 4, 5 — 5, about 7 — 7

Table 3 (continued).  
Таблица 3 (продолжение).

1	2
10. Thoracic membrane length	to end of thorax, no apron — 0, up to 8th abdominal chaetiger on convex side — 1, to end of thorax forming apron — 3
11. Thoracic membrane margins	free — 0, fused — 1
12. Opercular position	in radiolar crown — 0, outside of radiolar crown — 1
13. Crystalline patches present in thorax	no — 0, yes — 1
14. Crystalline patches absent	no — 0, yes — 1
15. Fin & blade collar chaetae	absent — 0, present — 1
16. Cross-striation of collar chaetae present	no — 0, yes — 1
17. Cross-striation of collar chaetae absent	no — 0, yes — 1
18. Typical geniculate collar chaetae	absent — 0, present — 1
19. Strong geniculate collar chaeta	absent — 0, present — 1
20. Sickle chaetae of 3rd chaetiger	no — 0, yes — 1
21. Simple chaetae of 3rd chaetiger	no — 0, yes — 1
22. Abdominal chaetae	usual — 0, brush-type — 1, wide — 2
23. Abdominal hooked chaeta on all chaetigers	no — 0, yes — 1
24. Abdominal hooked chaeta on last chaetigers	no — 0, yes — 1
25. Abdominal hooked chaeta absent	no — 0, yes — 1
26. Anterior fang of thoracic uncini blunt	no — 0, yes — 1
27. Anterior fang of thoracic uncini pointed	no — 0, yes — 1
28. Anterior peg of thoracic uncini trifurcate	no — 0, yes — 1
29. Anterior fang of thoracic uncini laterally pointed	no — 0, yes — 1
30. Anterior peg of thoracic uncini fluted	no — 0, yes — 1
31. Number teeth rows at largest thoracic uncini	narrow 1-3 — 0, median 3-5 — 1, wide 4-8 — 2, very wide 6 and more, up to 15 — 3
32. Abdominal uncini distribution	fairly symmetrical — 0, asymmetrical — 1
33. Larval abdominal glands absent	no — 0, yes — 1
34. Larval abdominal present	no — 0, yes — 1
35. Larval thoracic glands present	no — 0, yes — 1



Table 4. Data set for phylogenetic analysis of spirorbini genera.  
Таблица 4. Данные, использовавшиеся в филогенетическом анализе родов спирорбин.

Taxon	Characters
<i>Spirorbis</i> ( <i>Spirorbis</i> )	11010011300001101101101101000010010
<i>Spirorbis</i> ( <i>Velorbis</i> )	11000001301001101101100101000010010
<i>Circeis</i>	21011011300001011110100011000031100
<i>Paradexiospira</i>	20001010400001010101000011000031100
<i>Paradexiospira</i> ( <i>Spirorbides</i> )	20001011400001110101000011000031100
<i>Eulaeospira</i>	31010001300001101100110100000111100
<i>Helicosiphon</i>	31000001400001001100110101000001100
<i>Metalaeospira</i>	31100001400001001101110101000011100
<i>Protolaeospira</i>	31101011400001111101110111000001110
<i>Romanchella</i>	31010001301001001101111001000011100
<i>Amplificaria</i>	41000001500001101101100011000000010
<i>Vinearia</i> ( <i>Nidificaria</i> )	41000001300010110100100011000000010
<i>Bushiella</i>	41000001300001001101101001000000010
<i>Bushiella</i> ( <i>Jugaria</i> )	10000013000111111101101111000000010
<i>Pileolaria</i>	41000001300010110101100011000000010
<i>Protolaeodora</i>	41000001310101001101101001000000010
<i>Simplaria</i>	41000001300010110100100011000000010
<i>Janua</i>	51000011301001001101120010100020101
<i>Leodora</i>	51000001300001001100120010100020101
<i>Neodexiospira</i>	51010011301001011100120010110020101
<i>Pillaiospira</i>	51000010300001001100120010010020101
<i>Paralaeospira</i>	61000001400001101101100011000001100
<i>Anomalorbis</i>	?1000010500001001100100100001001???
<i>Crozetospira</i>	?0001001300001010101100011000011???
<i>Neomicrorbis</i>	?00011117?0001101101100011000000???
<i>Serpula</i> (outgroup)	71000100730001011100100010101000100
<i>Filigrana</i> (outgroup)	61000100730001110?00100010101110100

test whether significant differences exist among average oxygen contents in habitats of tube- and operculum-incubating spirorbids.

## Results

### Phylogenetic analysis

The heuristic searches yielded 8 equally parsimonious trees of 106 steps, with a consistency index (CI) of 0.425 (CI excluding uninformative characters is 0.419) and homoplasy index 0.575 (HI excluding uninformative characters is 0.581). The strict consensus of 8 trees (Fig. 1) shows a reasonably good resolution.

Pileolariini is paraphyletic and includes Spirorbini. There is a polytomy in the Pileolariini-Spirorbini clade. An uncertainty in the positions of *Amplificaria* results in polytomy within this clade on the consensus tree. Romanchiellini is monophyletic and Paralaeospirini is its sister taxon. The consensus tree shows a dichotomy between Romanchiellini-Paralaeospirini and Pileolariini-Spirorbini clades. The positions of *Crozetospira* and *Neomicrorbis* are uncertain, resulting in unresolved polytomy. Januini is monophyletic and is located close to the tree base.

Brooding characters were optimized on all eight trees to infer the direction of their evolu-

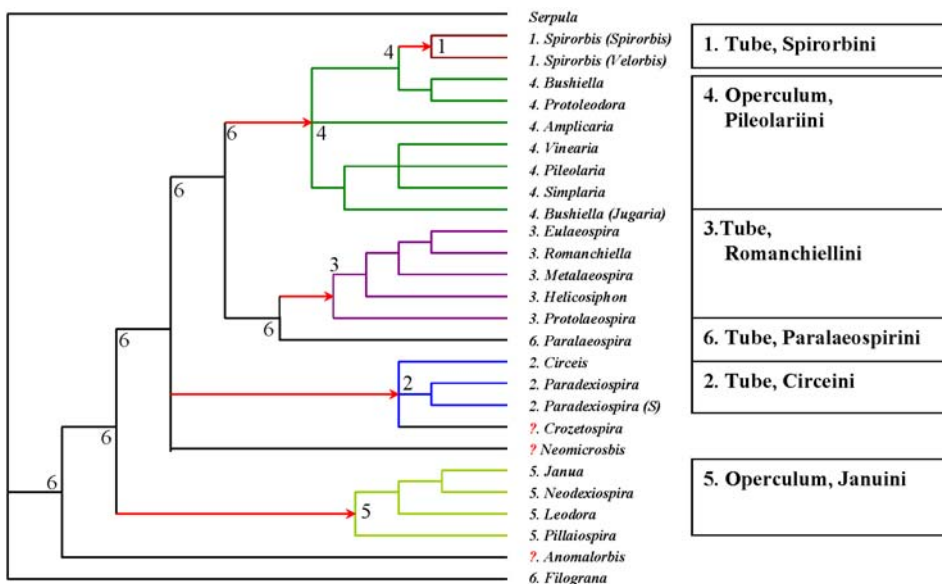


Fig. 1. Strict consensus of 8 equally parsimonious trees of spirorbin genera showing the transformations in the character 1 (type of incubation). Three transitions from tube incubation to opercular incubation ( $6 \rightarrow 5$ ,  $6 \rightarrow 2$ ,  $6 \rightarrow 3$ ,  $6 \rightarrow 4$ ) and one reversal to tube incubation ( $4 \rightarrow 1$ ) took place in the evolution of the group. Рис. 1. Строгий консенсус 8 одинаково парсимонных деревьев родов спиорбин, показывающий трансформацию признака 1 (тип инкубации). Два перехода от трубчатой к оперкулярной инкубации ( $6 \rightarrow 5$ ,  $6 \rightarrow 2$ ,  $6 \rightarrow 3$ ,  $6 \rightarrow 4$ ) один обратный переход к трубчатой инкубации ( $4 \rightarrow 1$ ) имели место в эволюции группы.

tion (Fig. 1). Character state = brooding free in tube is the most primitive mode and other brooding types originated from it. Two independent transitions from tube to opercular brooding occurred in the history of the group. One reversal is found in transition from the operculum brooding to the tube brooding with embryos attached to the body by a posterior filament.

### Distribution in relation to water oxygen content

Comparison of distribution of all opercular and tube brooders combined showed that tube brooders inhabit waters with higher dissolved oxygen concentration (ANOVA,  $F = 63.94$ ,  $P < 0.0001$ ). The similar results were obtained when distribution of the three genera (*Neodexiospira*, *Bushiella*, and *Paradexiospira*) was analysed independently (ANOVA,  $F = 106.87$ ,  $P < 0.001$ ). The Tukey HSD test revealed two significantly different ( $P < 0.05$ ) homogeneous subsets of

oxygen concentrations. The first subset included species of operculum-brooding genus *Neodexiospira*, and the second contained operculum-brooding *Bushiella* and tube-brooding *Paradexiospira*. More detailed multiple comparisons of 10 individual species (species with insufficient number of records were omitted) using ANOVA ( $F = 27.217$ ,  $P < 0.001$ ) and Tukey HSD test showed three homogeneous subsets (Table 3). The first and second subsets consisted of operculum-brooders, while the third subset consisted of a mixture of both brooding types.

### Discussion

The results of this study provide several important findings. First, the phylogenetic analysis of morphological characters confirmed the evolutionary schemes based on comparative morphology data (e.g., Gee, 1964; Thorp, 1975;

Knight-Jones, Thorp, 1984; Nishi, 1993) suggesting that opercular brooding is apomorphic and evolved from tube brooding. The results suggest that the two types of opercular brooding chambers (januini and pileolarii) originated independently from tube brooding. Brood chambers of Januini apparently originated early in the evolution of the group, whereas those of Pileolarii are very advanced and appeared much later. Such evolutionary scenario is well corroborated by observations that pileolarii brood chambers are structurally more complex and exhibit a wide range of forms (e.g., Thorp, 1975). The most doubtful result of the study is the reversal from the opercular brooding in Pileolarii to the tube brooding in Spirorbini.

The conclusion of evolutionary novelty of opercular brooding also agrees with those of another phylogenetic analysis of spirorbins (Macdonald, 2003). However, results of Macdonald (2003) suggest that the opercular brooding arose only once within the spirorbin clade, despite the dissimilar morphology that is exhibited by the two major opercular-brooding tribes. According to Macdonald (2003), the januini brood chamber represents a simplification of a more complex form of pileolarii one. From the evolution of development point of view, it is unclear how such evolutionary transformation could proceed, because pileolarii brooding opercula are not only more complex than, but are also very different morphogenetically from the januine operculum.

Both this study and Macdonald (2003) present preliminary, cladistics-based hypotheses of the evolution of brooding in Spirorbinae. Combined analyses of molecular and morphological data are clearly needed to resolve both the relationships within Spirorbinae as well as to address the evolution of brooding in this group. Despite the limitations of both phylogenetic analyses, these studies present an important step towards an understanding of the historical component in evolution of spirorbin brooding. However, even the best phylogeny provides little information on the mechanisms that drive evolutionary transitions in these characters.

Comparison of distribution in several selected operculum- and tube-brooding spirorbins relative to the dissolved oxygen concentration provided the second finding of this study. The results of this comparison partly support the idea that evolution of opercular brooding in spirorbids is related to the oxygen limitation experienced by tube brooders in poorly oxygenated waters. On average, tube brooders inhabit waters with higher oxygen content than operculum brooders do. That opercular brooders inhabit a wider range of oxygen concentrations suggests that they might be less restricted by oxygen content in their distribution.

However, the results do not allow any definite conclusion about validity of Harris (1972) hypothesis. Because of large interspecific variability and the large scale of this investigation, comparison of spirorbin distributions is not the best way to test the hypothesis. More importantly, the original formulation of the hypothesis is self-contradictory, thus not lending itself well to rigorous testing. Harris (1972) suggested that embryos of tube incubating species should have a low oxygen demand, whereas those of operculum incubating species should have high oxygen demand. However, at the same time, the hypothesis predicts that tube incubators (with low oxygen demand) species should inhabit highly-oxygenated waters, whereas operculum incubators (with high oxygen demand) should be found in low-oxygenated waters.

Oxygen demands referred to by Harris (1972) may be defined as oxygen consumption rates by embryos. These rates may differ between tube and operculum incubators if measured at the same temperature. However, oxygen consumption rates are temperature-dependent. An increase of oxygen consumption with increasing temperature has been well documented in marine invertebrates (e.g., Sedova, 2000: echinoderms; Pilditch, Grant, 1999: molluscs; Chen, Kou, 1996: crustaceans; Kupriyanova, Havenhand, 2005; Fritzsche, von Oertzen, 1995: polychaetes). At the same time, dissolved oxygen concentration declines with increasing water temperature. The combined effect of the increase in respiration rate and decrease of avail-

able dissolved oxygen may result in oxygen limitation for embryos of both tube and opercular incubating species with increasing temperature even if the original oxygen consumption rates are the same.

Further studies are required to compare oxygen consumption rates by embryos of tube- and opercular-incubating spirorbins and to quantify the effect of temperature on oxygen consumption in both. However, such data may not be sufficient to explain the selective advantage of operculum brooding over tube brooding in low-oxygenated waters. An implicit assumption of this hypothesis is that the gradient between the ambient water oxygen concentration and that inside brooding structures is higher for tube incubators than for operculum incubators. This seems unlikely given the small size of spirorbins. Small size is believed to be adaptive for brooders because it helps to overcome oxygen limitation due to constraints in oxygen diffusion in packed embryos (Chaffe, Strathmann, 1984; Strathmann, Strathmann, 1985; Cohen, Strathmann, 1996). Besides, this suggestion does not take into account any active parental role in brood ventilation.

In addition to passively holding embryos in brooding structures, some invertebrates show active brood care (Dick *et al.*, 1998, 2002; Fernandez *et al.*, 2000). A direct link exists between active brood care and oxygen provision in marine invertebrates, since oxygen limitation has been reported for many taxa. For example, amphipods *Crangonyx pseudogracilis* Bousfield, 1985 show a highly responsive form of active brood care involving ventilation of the brood pouch and the “cycling” of eggs therein. Both increased temperature and decreased oxygen concentration result in increased levels of brooding behaviour in this species. Females of amphipod *Apherusa jurinei* (H. Milne Edwards, 1830) show higher levels of brood care under lowered oxygen conditions, thus serving the changing metabolic demand of the brood (Dick *et al.*, 1998, 2002). Female brachyuran crabs show an active brooding behaviour that helps to provide oxygen to the embryo mass (Fernandez *et al.*, 2000). The simple physiolog-

ical constraint of oxygen provision in marine invertebrates may have important ecological and evolutionary consequences (Baeza, Fernandez, 2002).

The interaction of embryonic development with temperature and dissolved oxygen regime allows us to re-formulate the hypothesis of the role that oxygen limitation plays in evolution of brooding in spirorbins. As temperature increases and dissolved oxygen concentration decreases, because of an increase in oxygen consumption by embryos, more active parental care is required to meet those demands. Brood ventilation is likely to be more energetically expensive for tube (internal) incubators than for opercular (external) incubators. Thus, the constraints that are imposed on tube incubation in warmer waters are related to the increased energetic costs of parental brood ventilation. Removal of the brood from inside the tube and its positioning in operculum at the end of feeding radioles is an adaptation that allows spirorbins to decrease costs of active parental care in warm-water habitats.

A disadvantage of spirorbin opercular brooding is that fecundity is limited by space in the operculum. However, a lowered number of embryos per brood and potential higher susceptibility to predation may be offset by higher developmental rates of embryos in warm waters. Hess (1993) suggested that extended development of brooded spirorbin embryos can serve as size-related constraint on brooding. Larger egg masses often take longer to develop and oxygen limitation increases development time. Good oxygenation allows larger numbers of eggs per clutch without a significant increase in development time; therefore, larger broods are more beneficial in highly-oxygenated temperate waters, as the example of tube-incubating spirorbins. If opercular brooding provides better oxygenation and is a cheaper ventilation method in oxygen-deficient warm waters, it should also offer the advantage of shorter development time. Therefore, in warmer waters opercular brooding would allow producing more broods per reproductive period, thus increasing total number of offspring and balancing the

effects of lowered fecundity per brood. Total fecundity may be even higher as reproductive period is extended in low latitudes.

The hypothesis proposed here can be tested by measuring the oxygen consumption rates by spirorbin embryos and by tube- and opercular-incubating adults at various temperatures. Studies of effects of temperature and oxygen concentration on development time in spirorbins would allow testing whether lowered fecundity per brood in operculum incubators is indeed balanced by shorter generation time and increased number of broods per reproductive season.

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