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А.В. Жирмунского  
ДВО РАН



Происхождение заботы о потомстве у  
полихет спионид  
(ANNELIDA: SPIONIDAE)

## SEXUAL REPRODUCTIVE MODES IN POLYCHAETES: CLASSIFICATION AND DIVERSITY

*W. Herbert Wilson*

### ABSTRACT

A two-factor classification system for types of reproductive modes within the Polychaeta is described. The classification is based on the type of larval development and the fate of the female gametes (free-spawned or brooded in a variety of ways). A compilation of information from the literature allowed the classification of 306 species. The Orders Phyllodocida and Spionida show the greatest diversity of reproductive modes. The most common reproductive mode involves the free spawning of gametes and the development of planktotrophic larvae. It is apparent that there has been multiple evolution of many reproductive modes during the course of polychaete evolution. This plasticity is argued to exceed that of the Classes Gastropoda, Bivalvia and Malacostraca.

Table 1. List of the reproductive modes of polychaetes, based on the criteria of the fate of the ova and the type of larval development (Abbreviations for each mode are used throughout the text)

Abbreviation	Description
FS-PLK	Free spawning with planktotrophic larvae
FS-LEC	Free spawning with lecithotrophic larvae
FS-DIR	Free spawning with entirely benthic development
BR-EXT-PLK	Brooding on the outside of the body with release of planktotrophic larvae
BR-EXT-LEC	Brooding on the outside of the body with release of lecithotrophic larvae
BR-EXT-DIR	Brooding on the outside of the body with direct development
BR-INT-PLK	Brooding inside the body with release of planktotrophic larvae
BR-INT-LEC	Brooding inside the body with release of lecithotrophic larvae
BR-INT-DIR	Brooding inside the body with direct development
BR-TUBE-PLK	Brooding inside the tube with release of planktotrophic larvae
BR-TUBE-LEC	Brooding inside the tube with release of lecithotrophic larvae
BR-TUBE-DIR	Brooding inside the tube with direct development
BR-CAP-PLK	Brooding of encapsulated embryos inside the tube with release of planktotrophic larvae
BR-CAP-LEC	Brooding of encapsulated embryos inside the tube with release of lecithotrophic larvae
BR-CAP-DIR	Brooding of encapsulated embryos inside the tube with direct development
GEL-PLK	Encapsulation of embryos in a gelatinous mass with release of planktotrophic larvae
GEL-LEC	Encapsulation of embryos in a gelatinous mass with release of lecithotrophic larvae
GEL-DIR	Encapsulation of embryos in a gelatinous mass with direct development

6 типов нереста –  
свободный вымет и  
разные типы вынашивания.

3 типа личиночного развития –  
планктотрофное,  
лецитотрофное,  
прямое.

18 типов развития

## SEXUAL REPRODUCTIVE MODES IN POLYCHAETES: CLASSIFICATION AND DIVERSITY

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Table 3. The distribution of reproductive modes within the Polychaeta (Number of species, orders and families in which each mode occurs are given; data are compiled from Table 2)

Reproductive mode	Species	Orders	Families
FS-PLK	79	7	22
BR-TUBE-DIR	39	8	11
FS-LEC	34	8	16
BR-CAP-PLK	24	1	1
BR-INT-DIR	17	2	4
GEL-LEC	16	6	9
BR-EXT-DIR	15	1	1
BR-CAP-DIR	15	2	2
GEL-DIR	13	6	7
BR-TUBE-LEC	11	4	5
GEL-PLK	10	3	4
FS-DIR	10	4	6
BR-TUBE-PLK	7	2	2
BR-EXT-LEC	7	3	3
BR-EXT-PLK	6	2	3
BR-CAP-LEC	3	1	1
BR-INT-LEC	1	2	2
BR-INT-PLK	0	0	0

306 видов из  
36 семейств

1. Пластичность и разнообразие типов размножения полихет превышает таковое гастропод, двустворчатых моллюсков и высших ракообразных (Malacostraca). Эта пластичность, вероятно, была одним из основных факторов успешного развития полихет в донных сообществах Мирового океана.
2. В некоторых семействах (Nephtyidae и Sabellariidae) используется единый тип размножения.
3. В большинстве семейств типы размножения разнообразны даже в пределах одного рода.

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BR-EXT-LEC	7	3	3
BR-EXT-PLK	6	2	3
BR-CAP-LEC	3	1	1
BR-INT-LEC	1	2	2
BR-INT-PLK	0	0	0

306 видов из  
36 семейств

Wilson: Наиболее распространённый тип размножения – свободный вымет гамет и планктотрофное развитие.

Свободный вымет (FS) – 123 вида (40%)

Забота о потомстве (BR+Gel) – 184 вида (60%)

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BR-TUBE-PLK	7	2	2
BR-EXT-LEC	7	3	3
BR-EXT-PLK	6	2	3
BR-CAP-LEC	3	1	1
BR-INT-LEC	1	2	2
BR-INT-PLK	0	0	0

Самое высокое разнообразие типов размножения – 14 – в отряде Spionida  
(изучено 86 видов)

# Spionidae

Grube, 1850  
> 600 species  
~ 40 genera

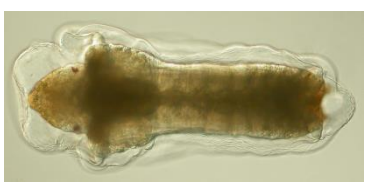
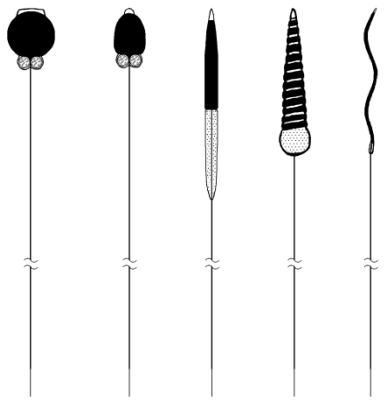
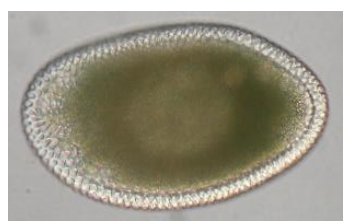
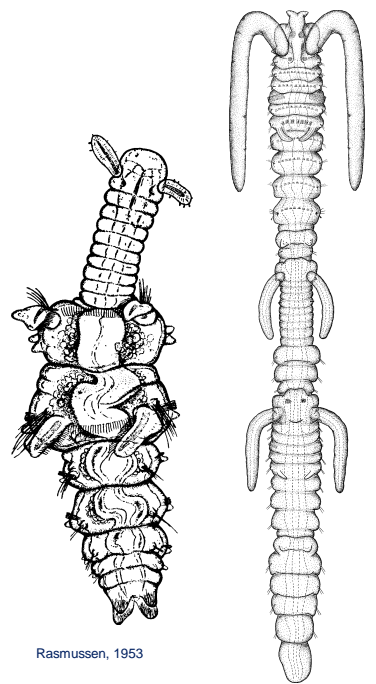
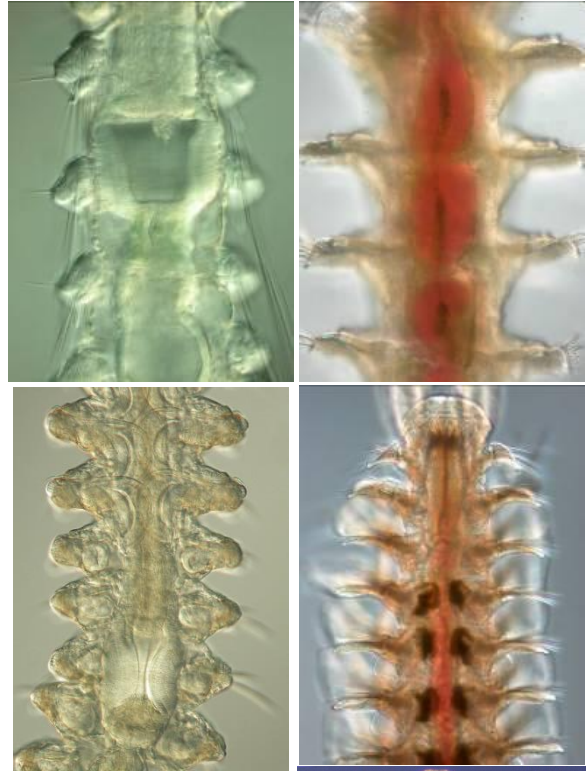
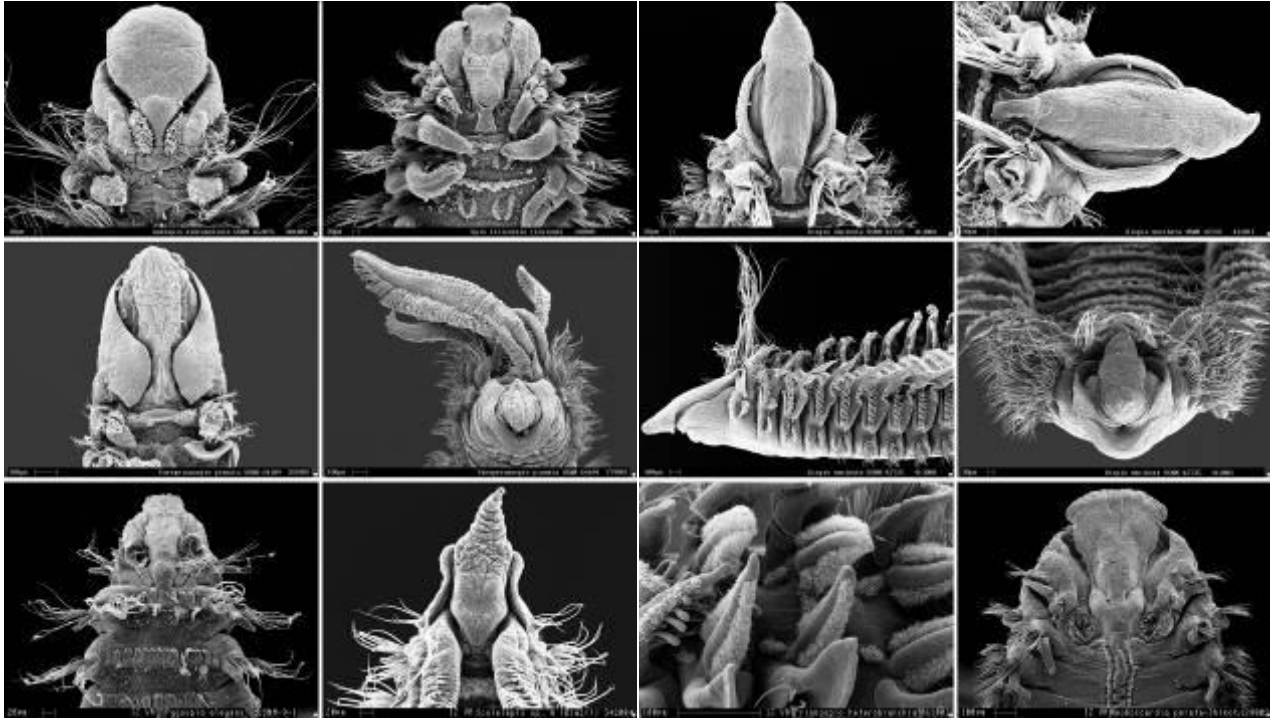


by Fredrik Pleijel



by Leslie Harris

by Fredrik Pleijel



Rasmussen, 1953

*Pseudopolydora paucibranchiata*

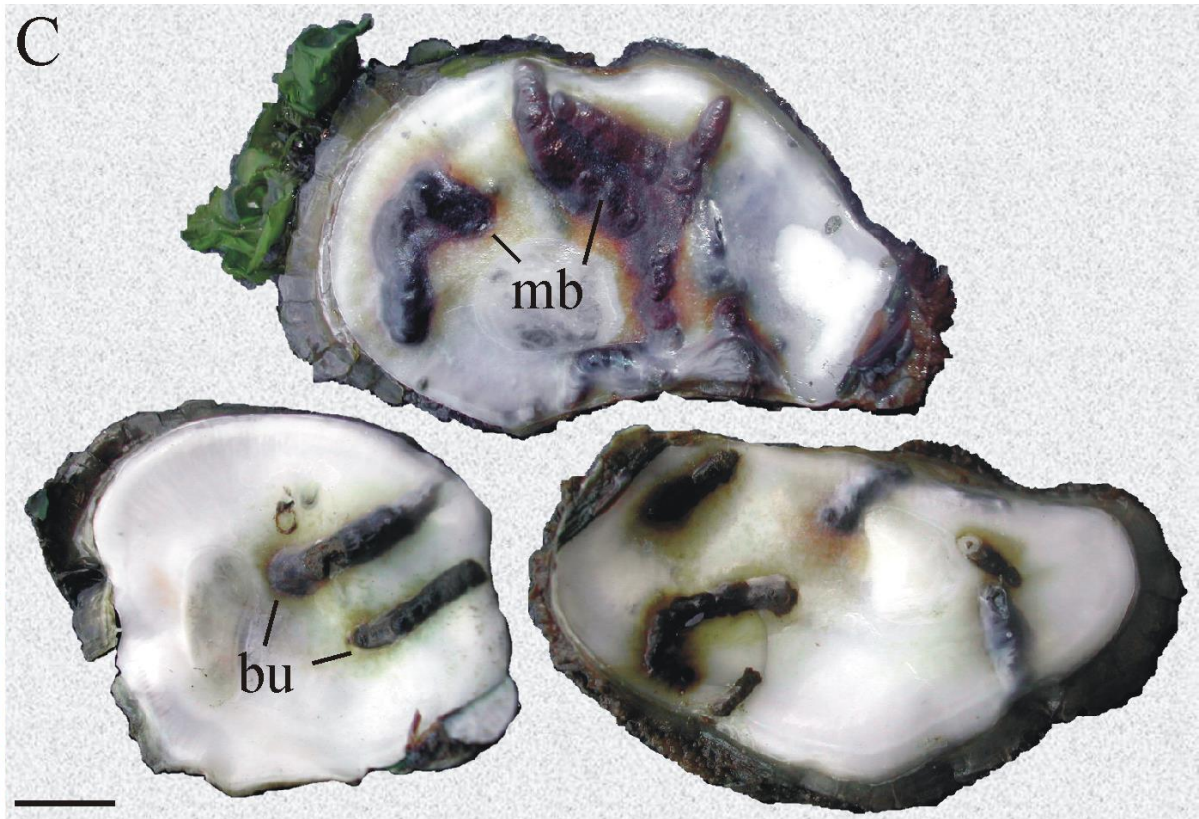
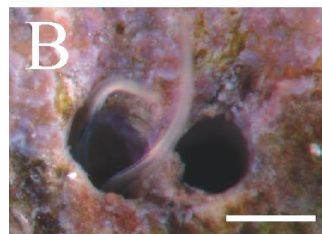


photo by Marco Faasse

Radashevsky, 2021

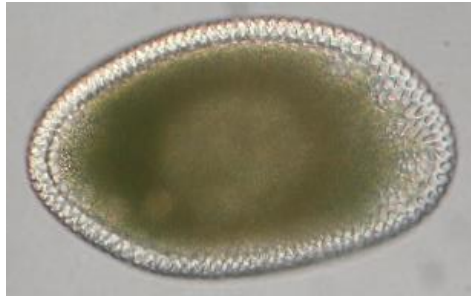
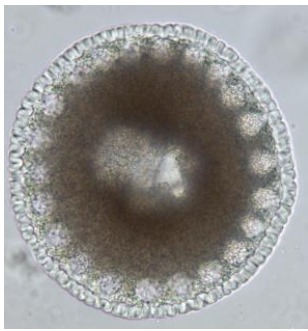


*Polydora ecuadoriana*

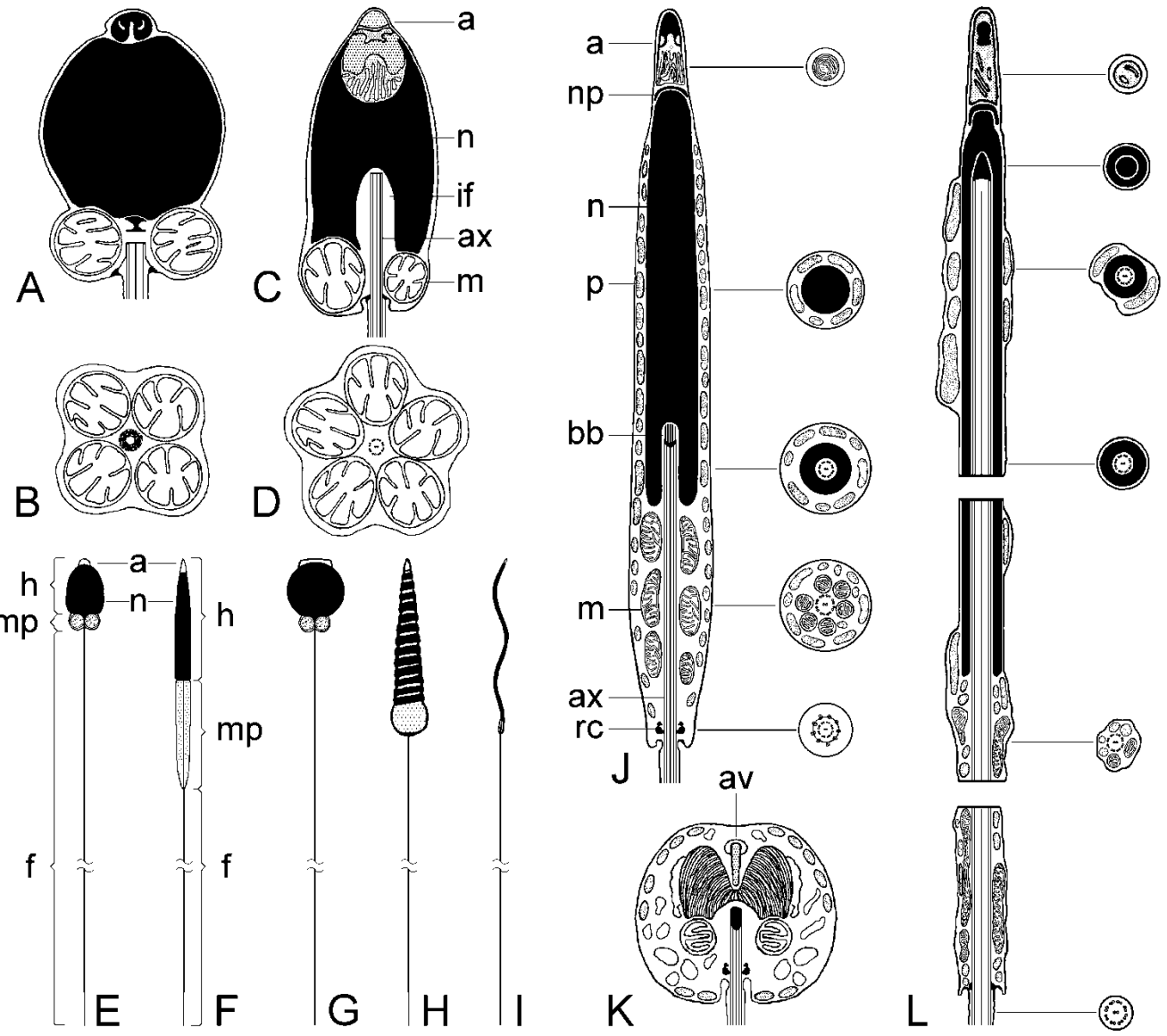


Radashevsky et al., 2006

толстые оболочки 5-30 μm



тонкие оболочки ~1 μm

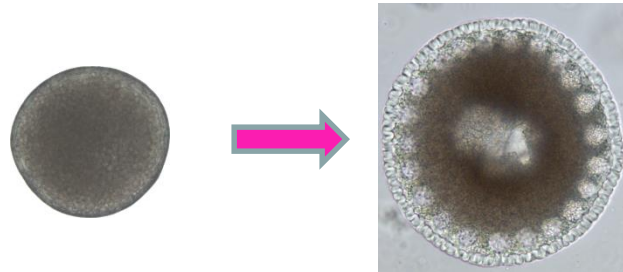


## Почему у одних спионид ооциты имеют тонкие оболочки, а у других спионид ооциты имеют толстые оболочки

Söderström (1920)

Oocytes with thin and smooth envelope is a plesiomorphic character shared by **Spioninae** members and many other polychaetes.

Oocytes with thick sculptured envelope is a derived character evolved within Spionidae



“Eggs with thin envelopes occur in several other ‘sedentary’ polychaete families such as Apistobranchidae, Capitellidae, Chaetopteridae, Cirratulidae, Orbiniidae, Magelonidae and Paraonidae, suggesting that it is the less common thick-enveloped eggs that are apomorphic. If so, **the spionids (subfamily Spioninae) having thin-enveloped eggs are plesiomorphic.** This hypothesis has been tested and supported as part of a phylogenetic analysis.”

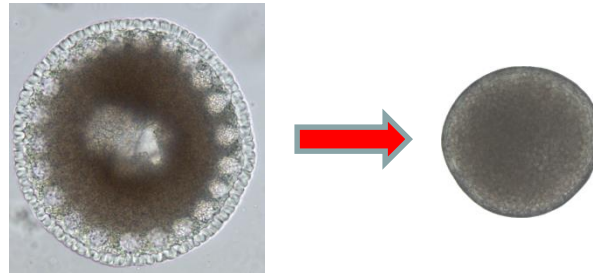
Blake & Arnofsky (1999: 60)

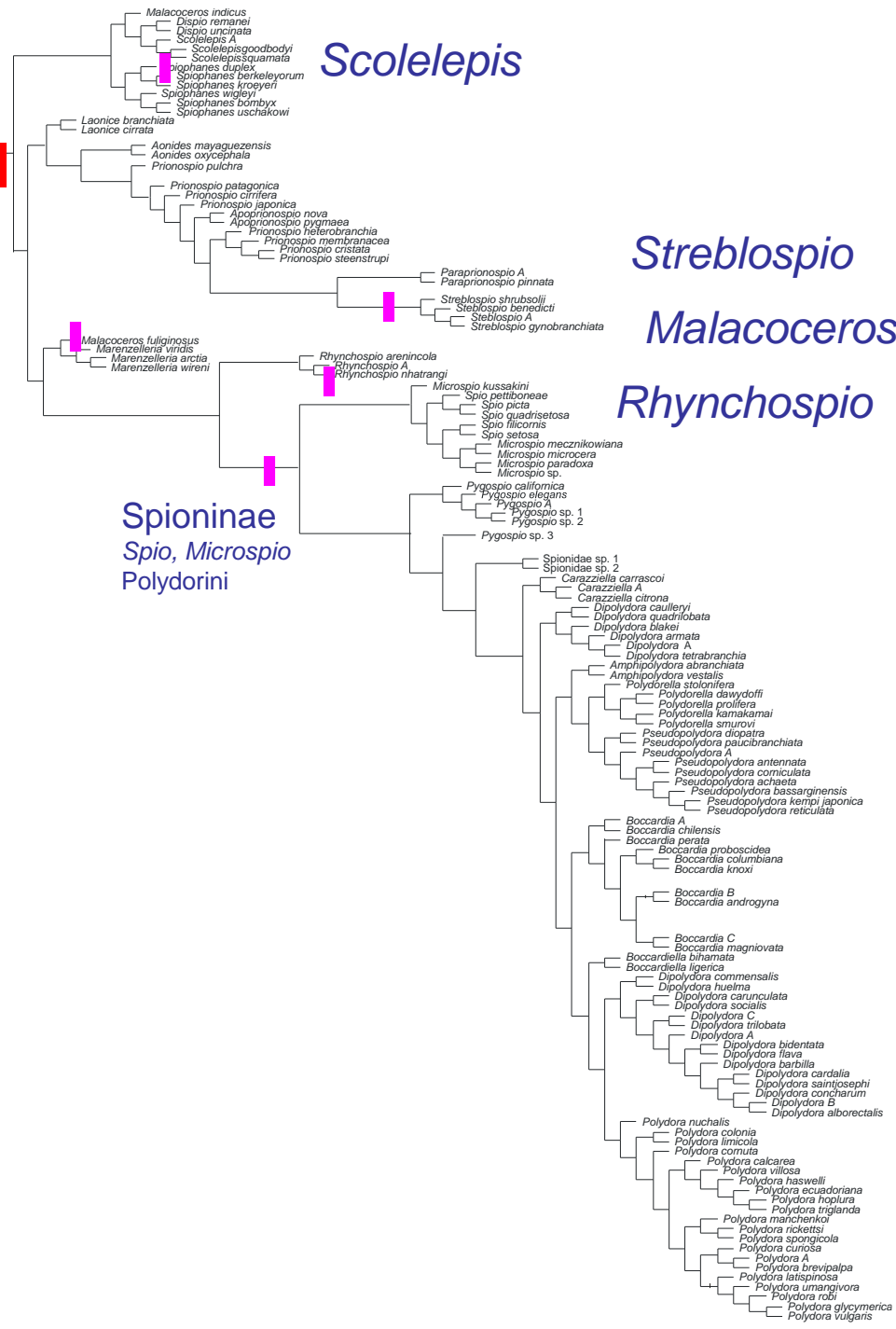
LARVAL DEVELOPMENT OF THE  
POLYCHAETE FAMILIES SPIONIDAE SARS,  
DISOMIDAE MESNIL, AND POECILO-  
CHAETIDAE N. FAM. IN THE GULLMAR  
FJORD (SWEDEN)

BY  
LENNART HANNERZ

“Development through brood protection is attended by reduction of the thickness of the egg-membrane and elimination of the “membrane vesicles”.”

Hannerz (1956)





Забота о потомстве возникла независимо среди видов 4-х родов и у общего предка подсемейства Spioninae

## ***Malacoceros***

**all gonochorists,  
most species free-spawners,  
some species brooders**

**Роение,  
Вымет в слизь, в которой  
происходит оплодотворение и  
начальные стадии личиночного  
развития**

# *Scolelepis*

all gonochorists,  
most species free-spawners,  
some species brooders

## *Scolelepis cf. tridentata*

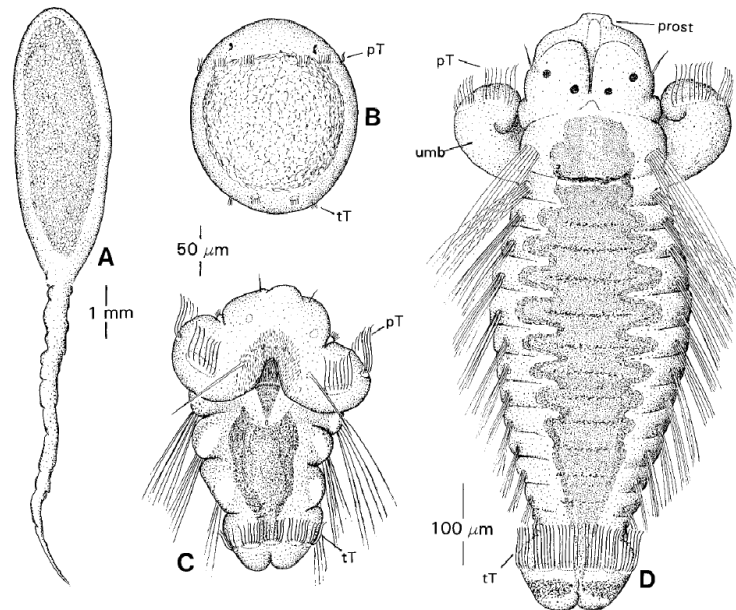


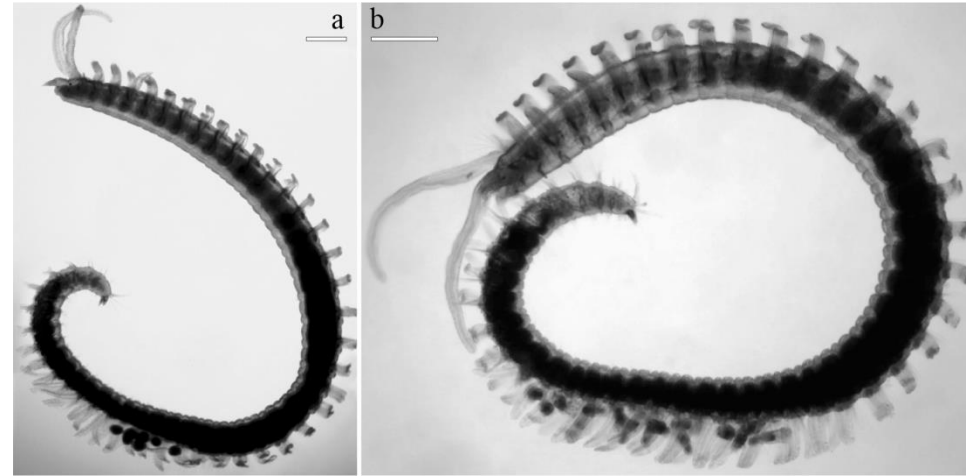
Figure 8. Egg mass and larvae of *Parascolelepis cf. tridentata* from northern California. (A) Egg mass. (B) Encapsulated trochophore. (C) 3-chaetiger hatching larva. (D) Planktotrophic 14-chaetiger larva. prost, prostonium; pT – prototroch; tT – telotroch.

Blake & Arnofsky, 1999

# Rhynchospio

all simultaneous hermaphrodites,  
 basal species free-spawner,  
 other species brooders on parent's dorsum

*Rhynchospio glandulosa*



*Rhynchospio nhatrangi*

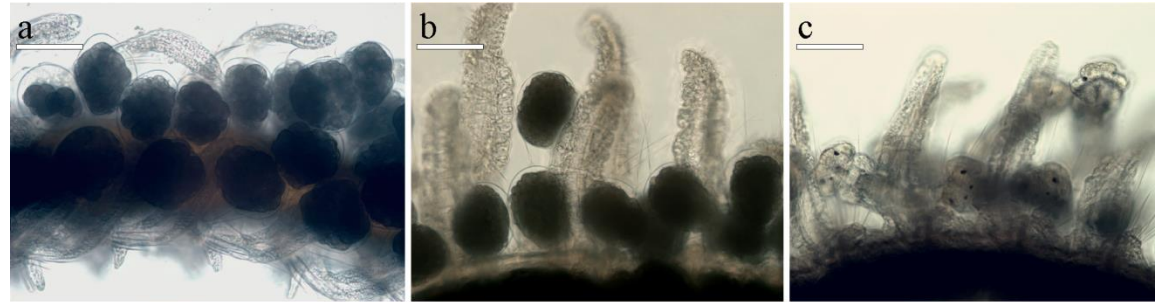
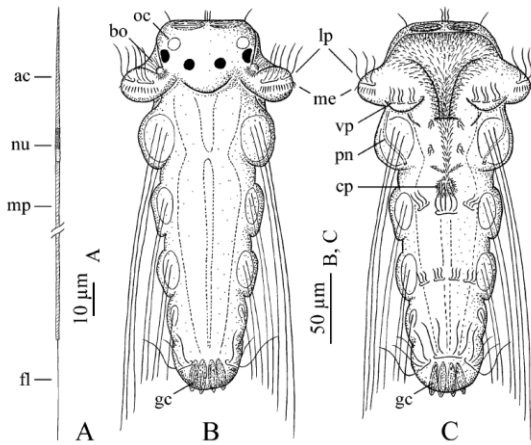
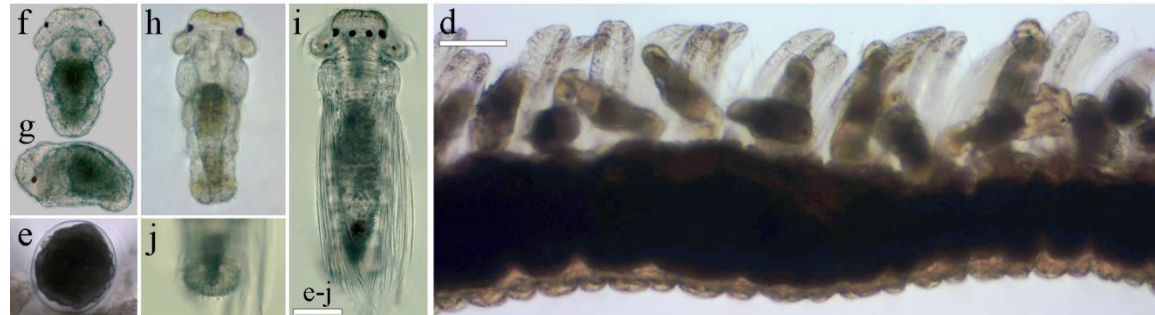


Figure 5. *Rhynchospio nhatrangi* sp. nov. sperm and larval morphology. (A) Spermatozoon with spiral acrosome (ac) 35 μm long, nucleus (nu) 10 μm, spiral middlepiece (mp) ca 200 μm long, and flagellum (fl) 35–60 μm long; (B) four-chaetiger larva escaped from hatchery on dorsal side of parent segments, dorsal view, showing unpigmented ocelli (oc), small bosses (bo) with fine non-motile cilia within nuchal ciliary patches, and large glandular cells (gc) with striated content in the pygidium; (C) same, ventral view, showing lateral (lp) and ventral (vp) parts of prototroch, metatroch (me), ventral ciliated pit (cp) on chaetiger 2, gastrotrich on chaetiger 3, telotroch, and one pair of protonephridia (pn) in chaetiger 1.

Radashevsky, 2007



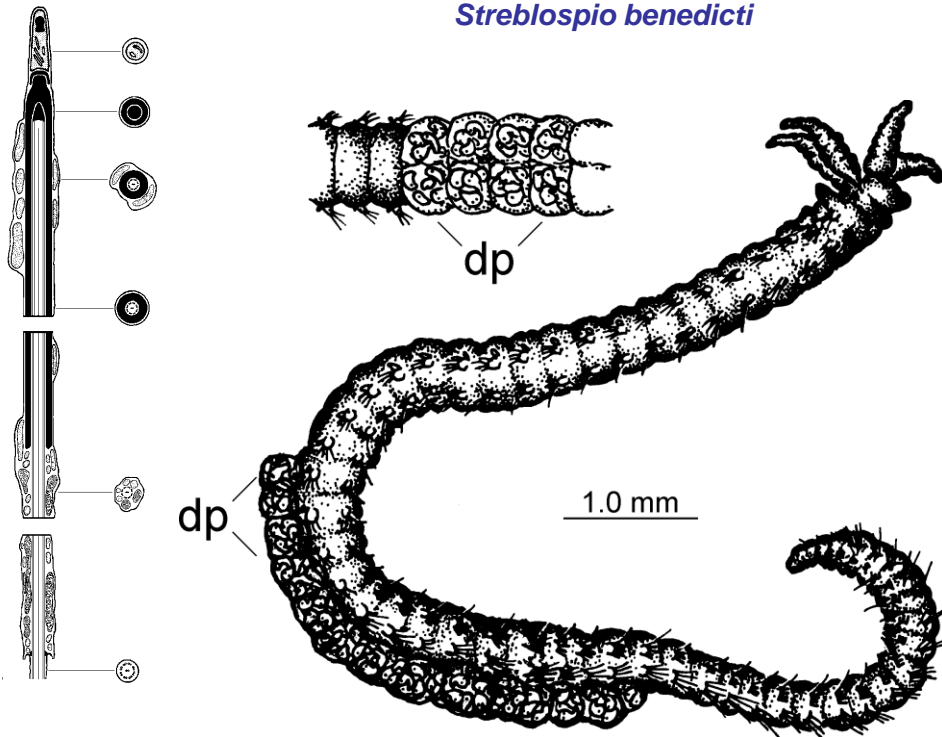
Radashevsky & Choi, 2021



# Streblospio

all gonochorists,  
basal species free-spawner,  
other species brooders

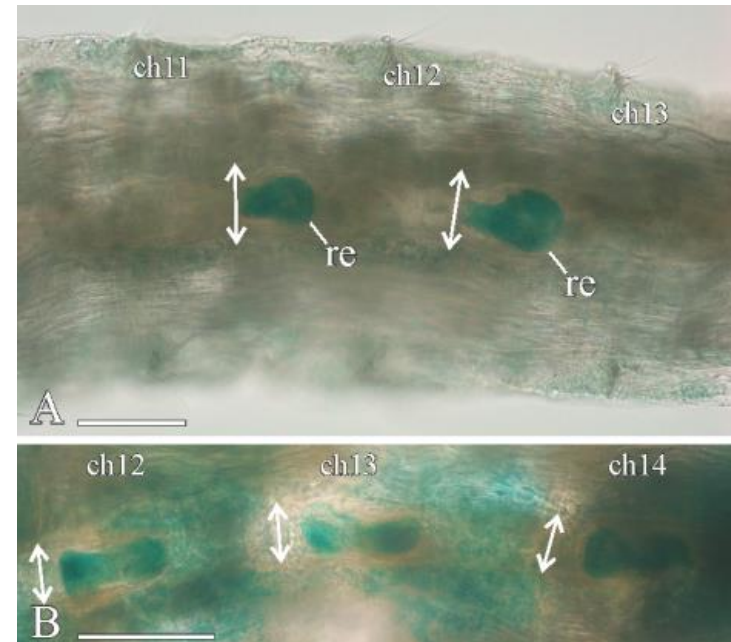
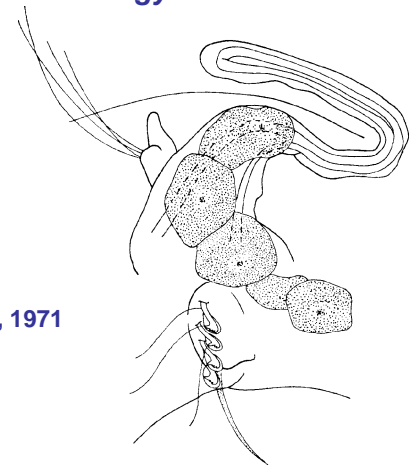
*Streblospio benedicti*



Fonsêca-Genevois & Cazaux, 1987

*Streblospio gynobranchiata*

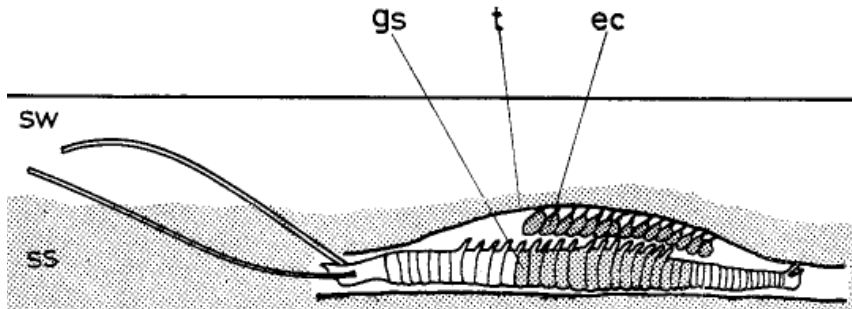
Foster, 1971



Radashevsky & Selifonova, 2013

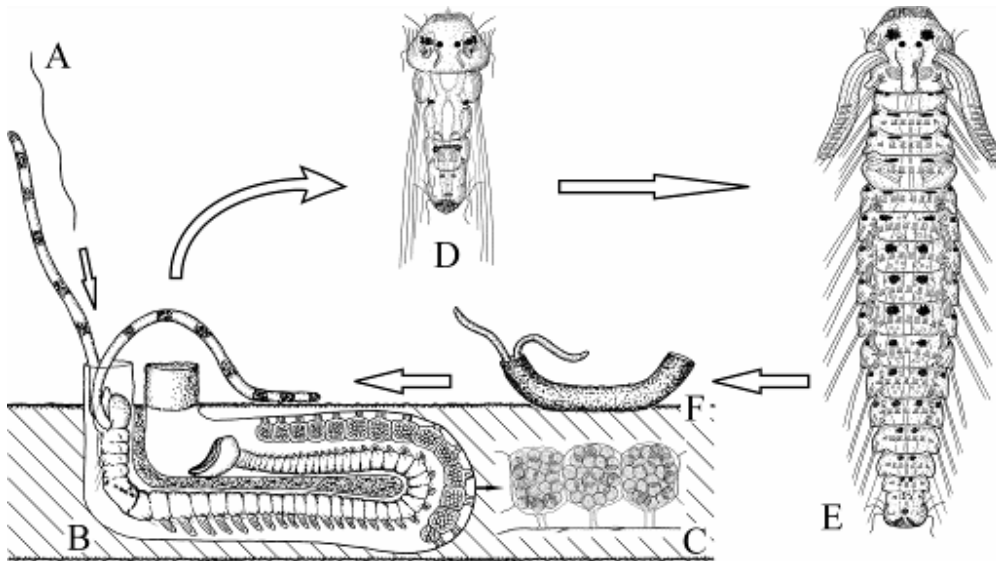
# п/сем. Spioninae Brooding in capsules

*Pseudopolydora kempii japonica*



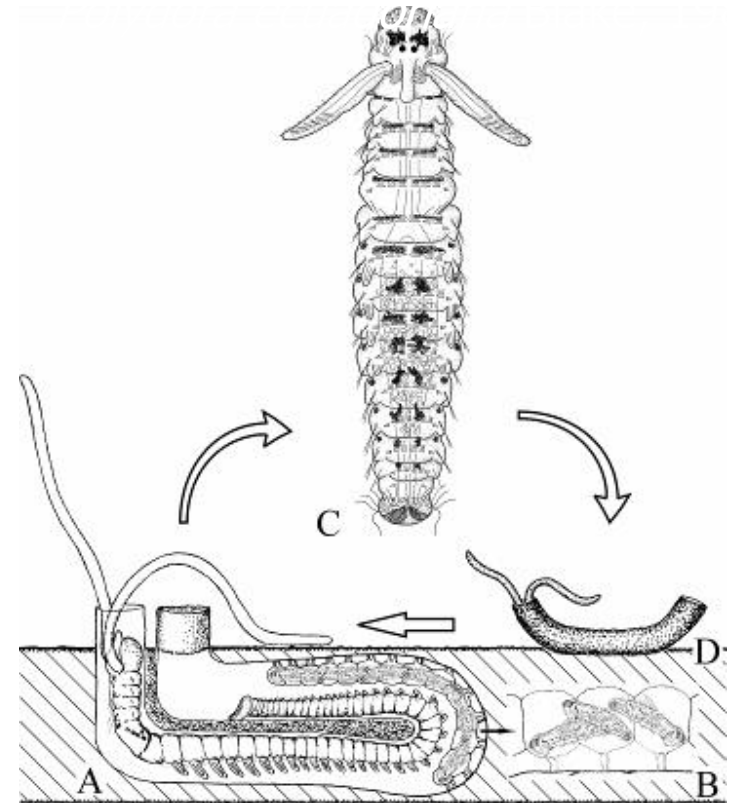
Myohara, 1979

*Polydora ecuadoriana*



Radashevsky et al., 2006

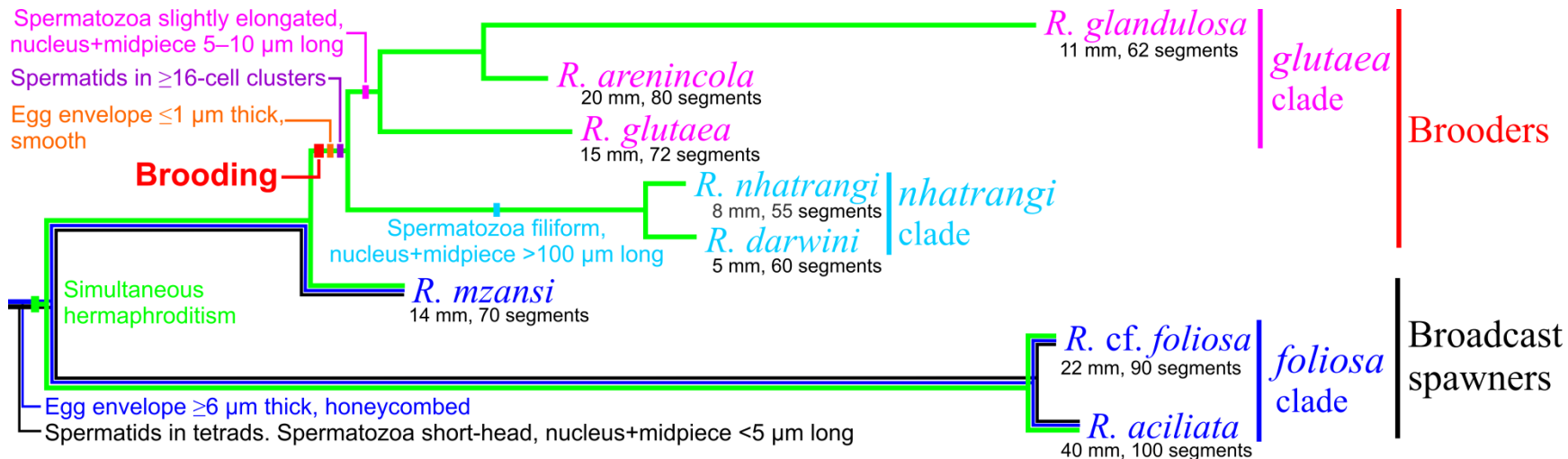
*Polydora carinhosa*

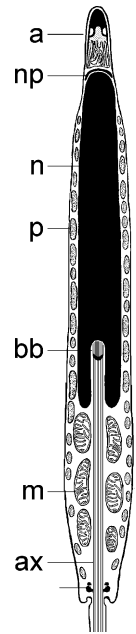
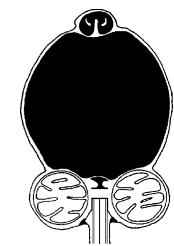
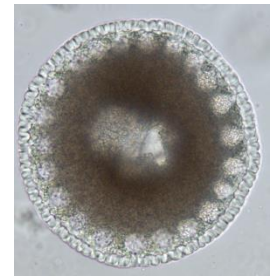
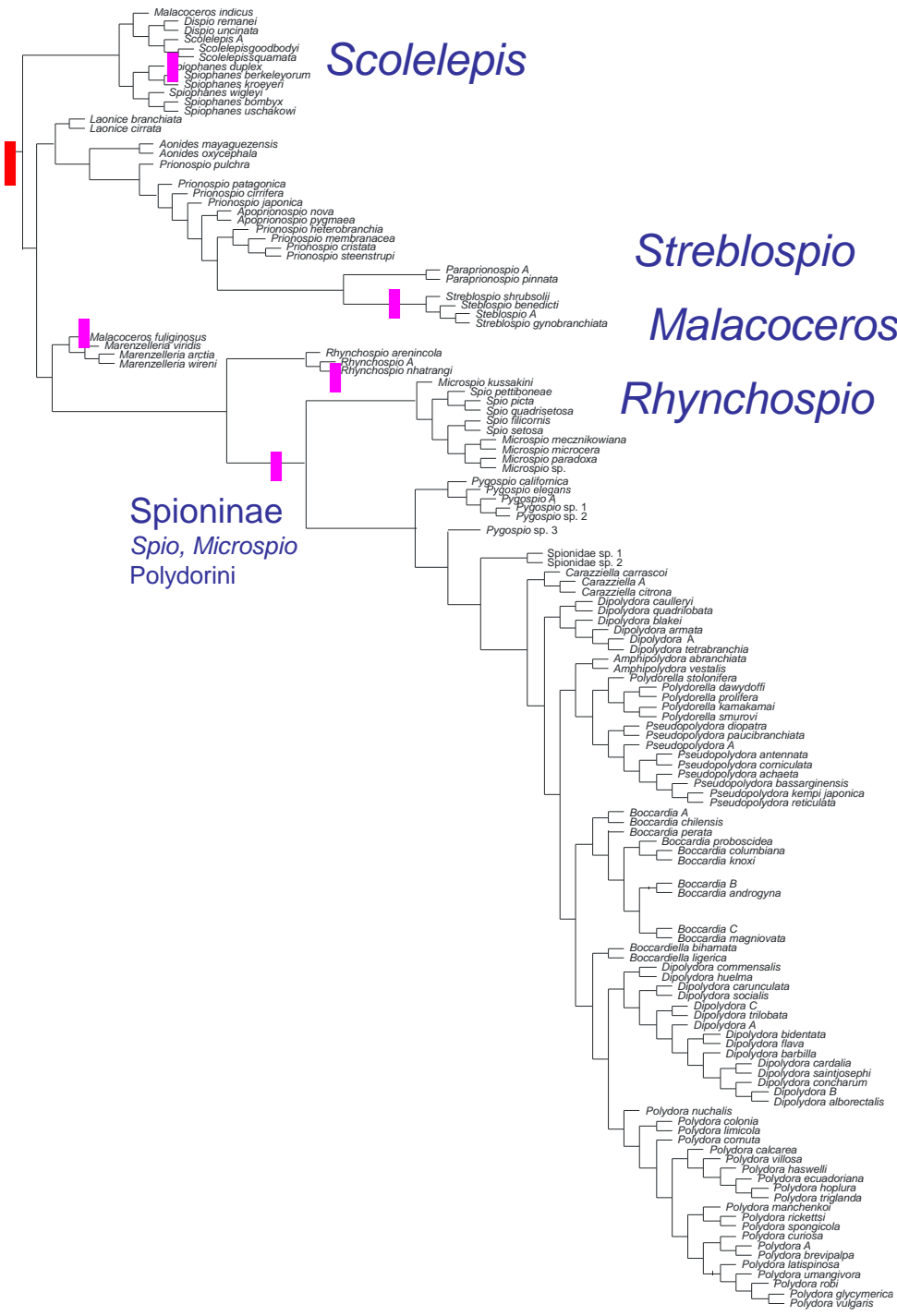


Radashevsky et al., 2006

# Rhynchospio

all simultaneous hermaphrodites,  
 basal species free-spawner,  
 other species brooders on parent's dorsum

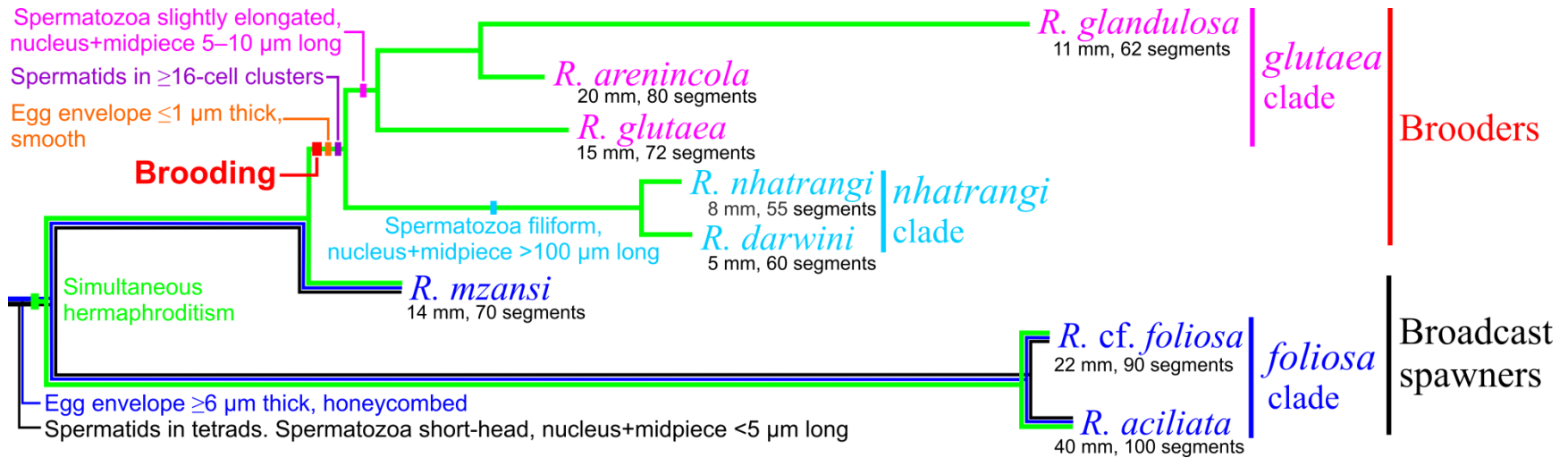




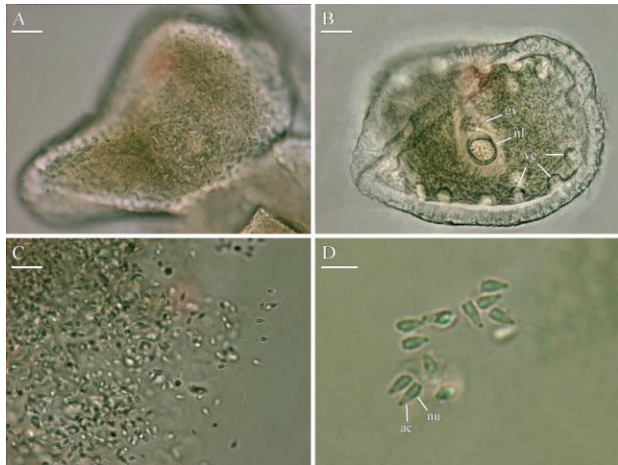
Забота о потомстве возникла независимо среди видов 4-х родов и у общего предка подсемейства Spioninae.

# Rhynchospio

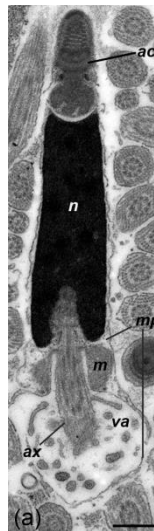
all simultaneous hermaphrodites,  
 basal species free-spawner,  
 other species brooders on parent's dorsum



## *Rhynchospio cf. foliosa*

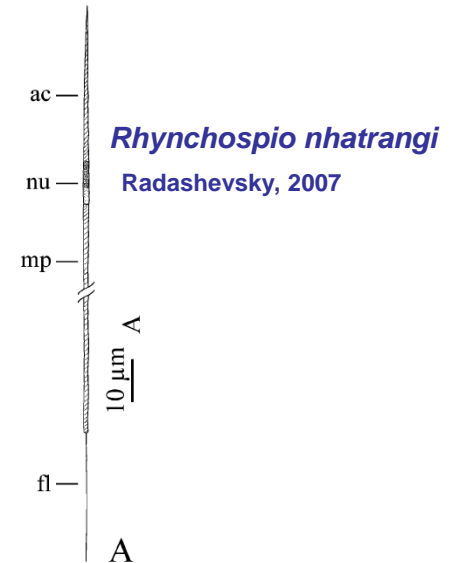


Radashevsky et al., 2016

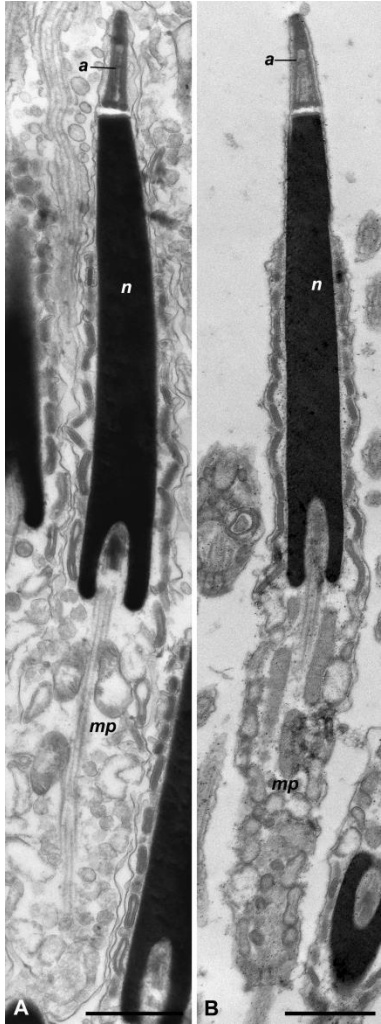


## *Rhynchospio glandulosa*

Radashevsky & Yurchenko, 2023

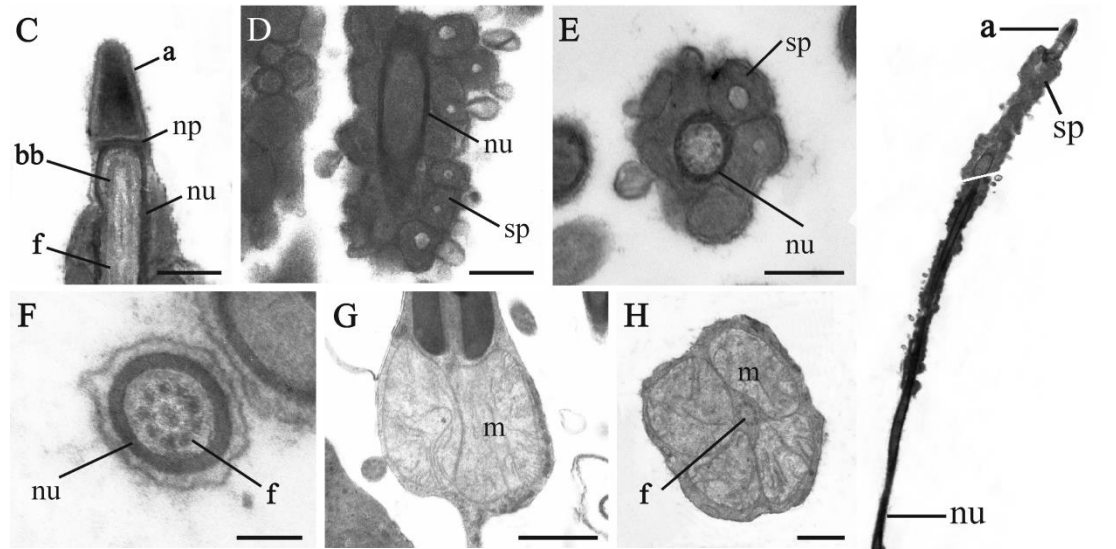


*Dipolydora bidentata*



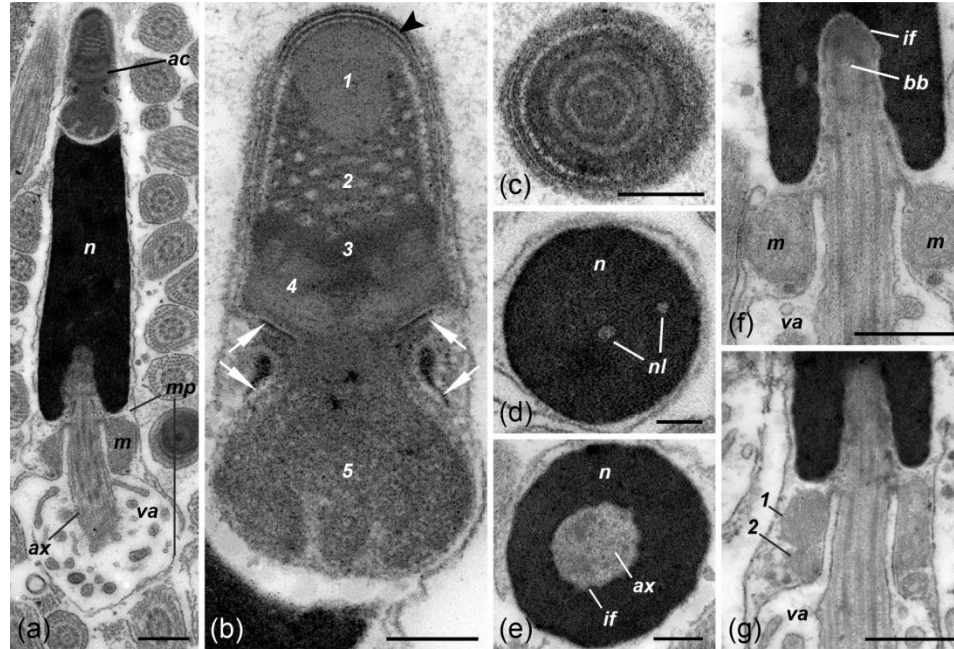
Radashevsky et al., 2015

*Boccardiella hamata*



Reunov et al., 2010

*Rhynchospio glandulosa*



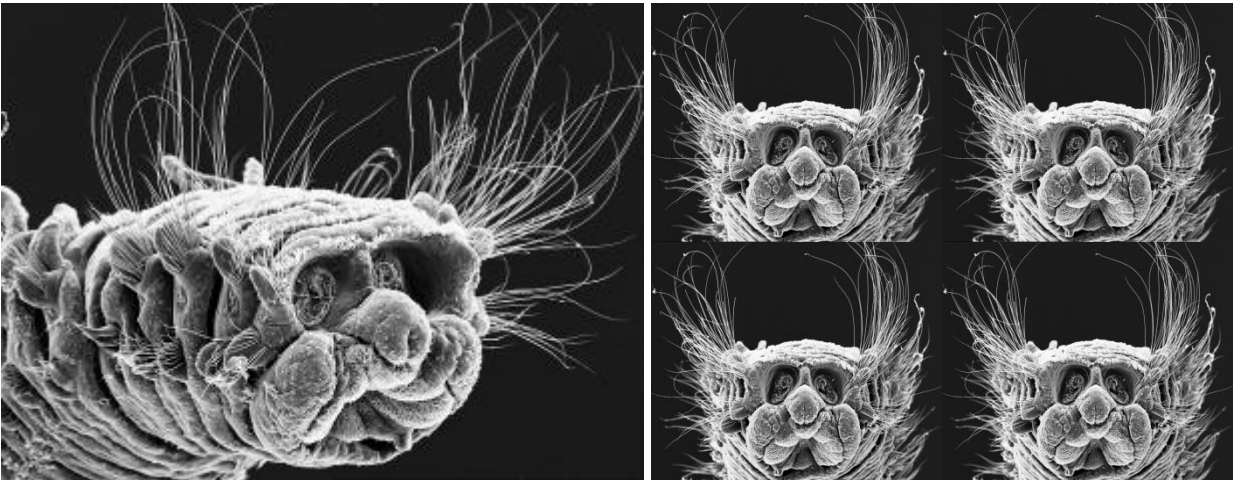
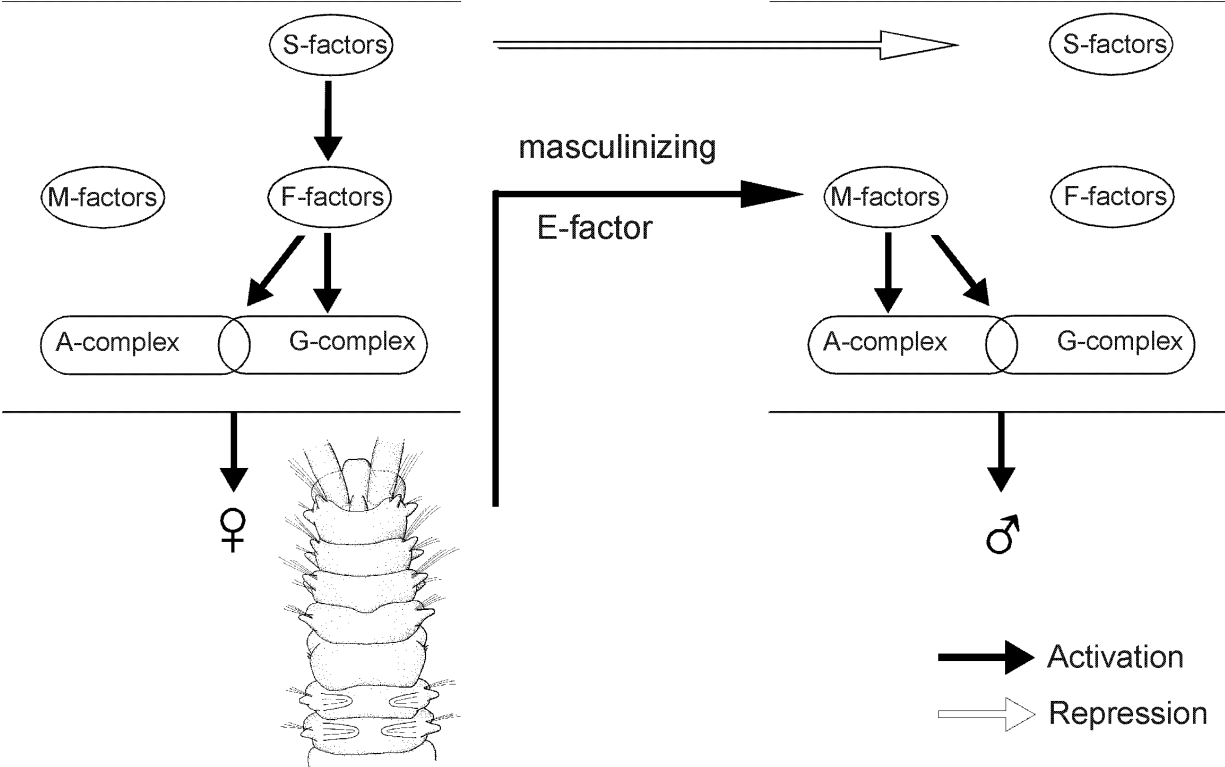
Radashevsky & Yurchenko, 2023

Спасибо за внимание!

Происхождение  
и эволюция  
**SPIONIDÆ**

# Environmental sex determination

*Dipolydora commensalis*





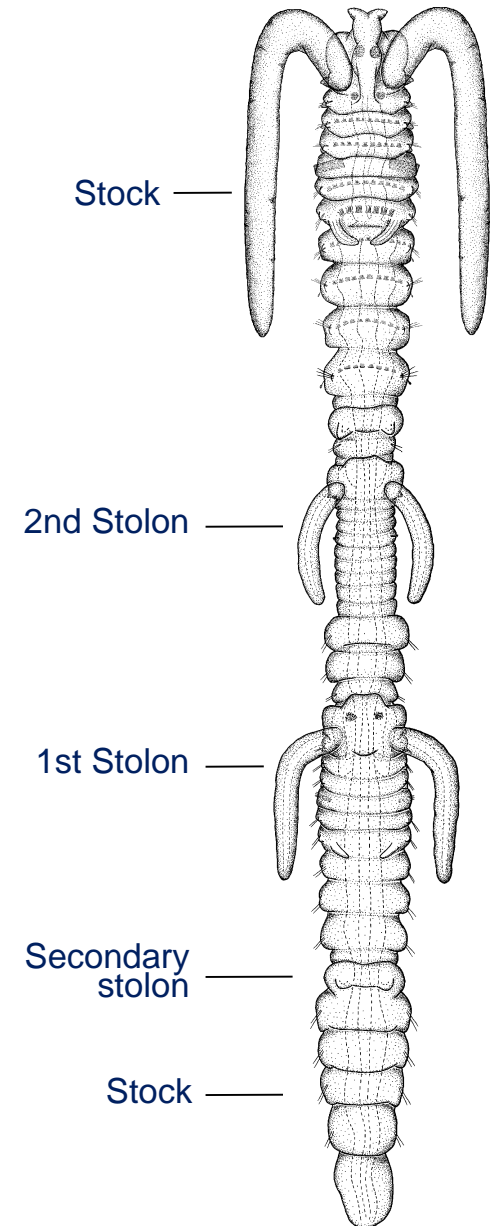
# *Polydorella*

- miniaturization 1-2 mm long,
- living on sponge surface,
- asexual reproduction by paratomy.

*Polydorella prolifera*

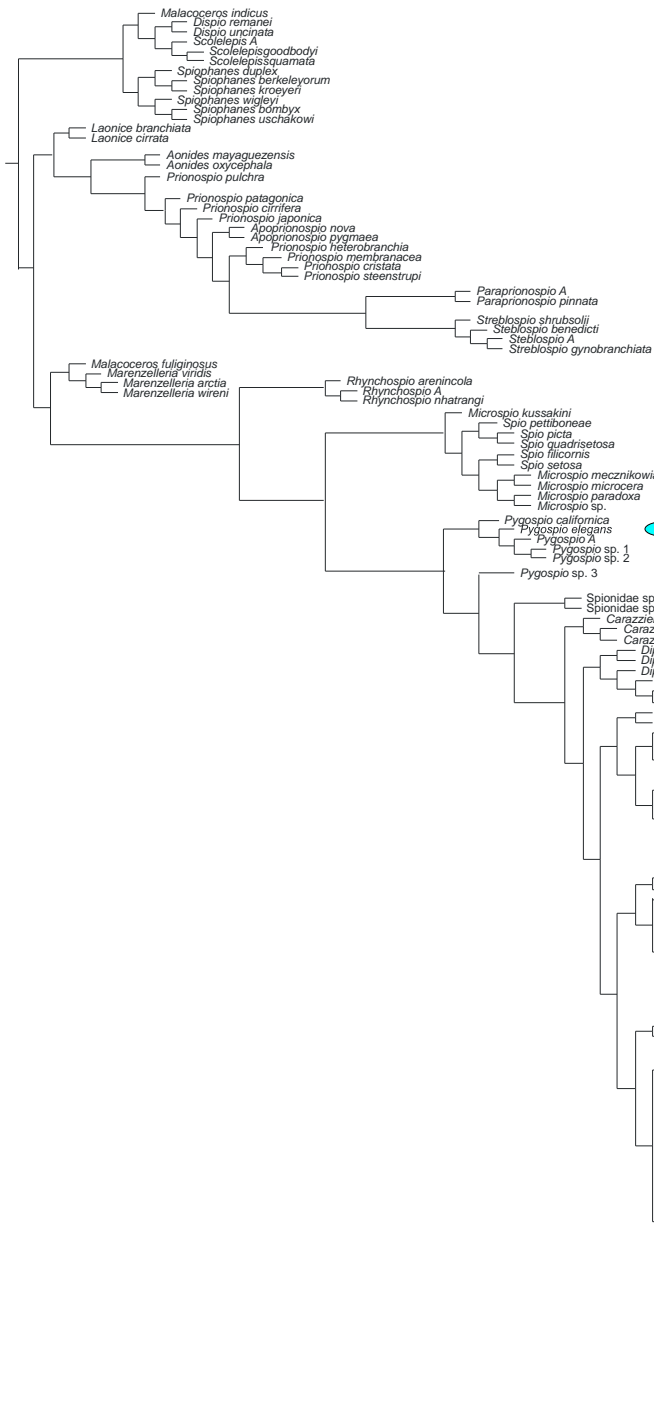


Radashevsky, 2015



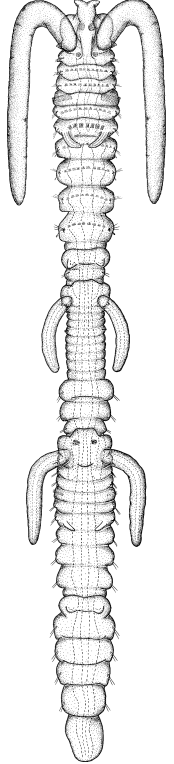
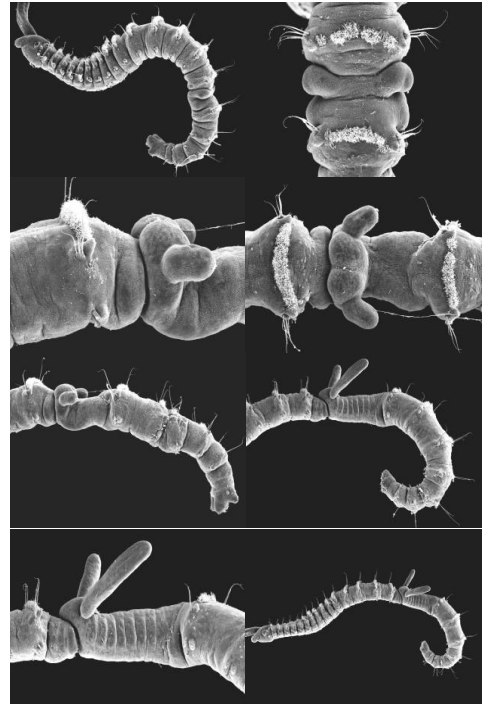
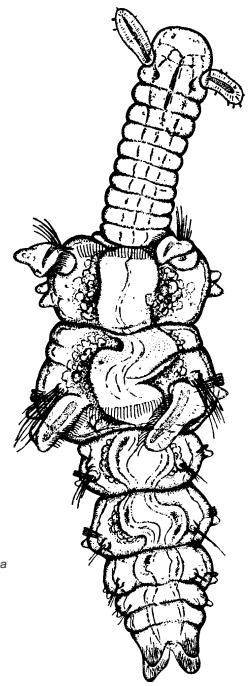
Radashevsky, 1996

# Бесполое размножение



Architomy

Paratomy



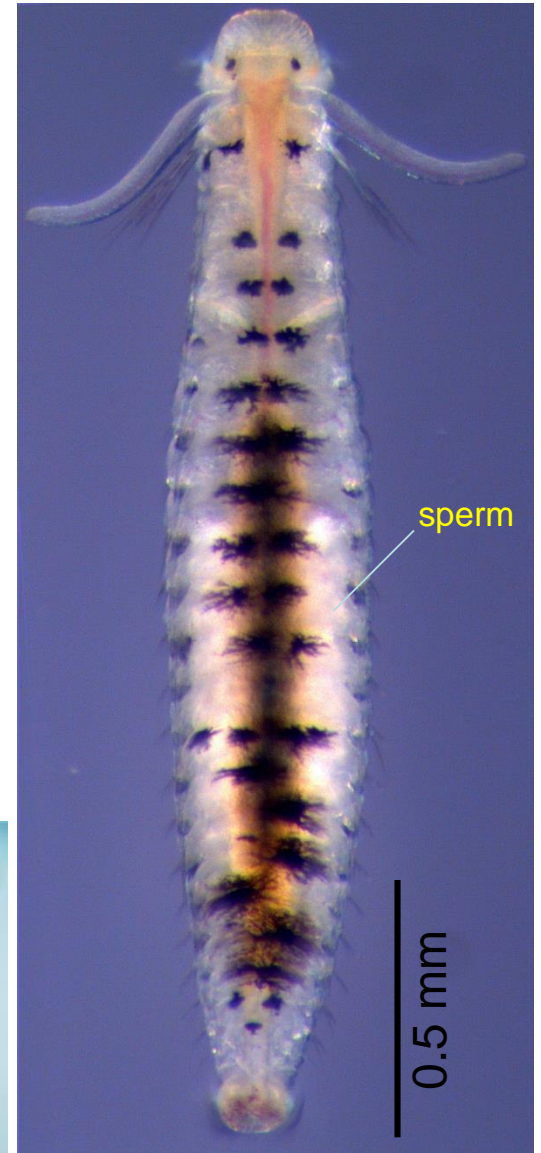
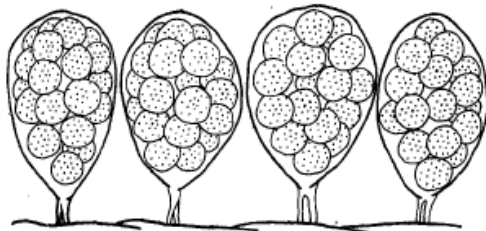
# Партеногенез



*Pseudopolydora rosebelae*  
Radashevsky & Migotto, 2009

Simultaneous hermaphroditism  
Male neoteny

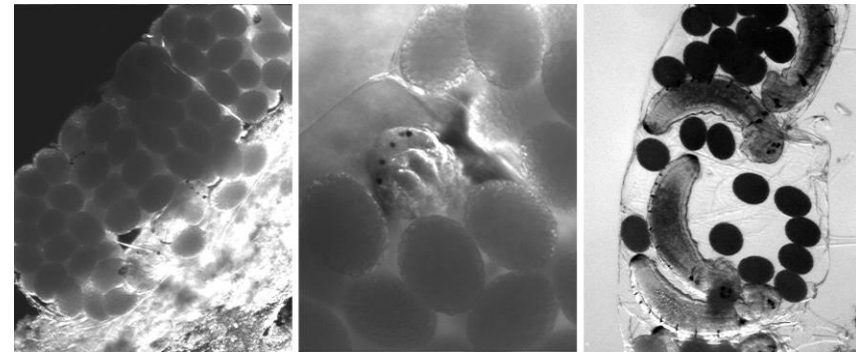
*Polydora glycymerica* Radashevsky, 1989



# Lecithotrophic larval development

Exolecithotrophy  
(adelphophagy, oophagy)

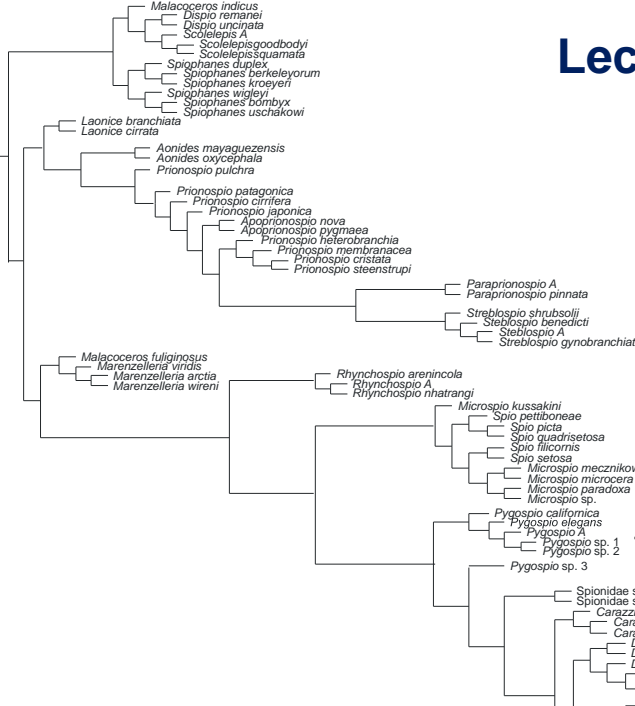
*Polydora hoplura*



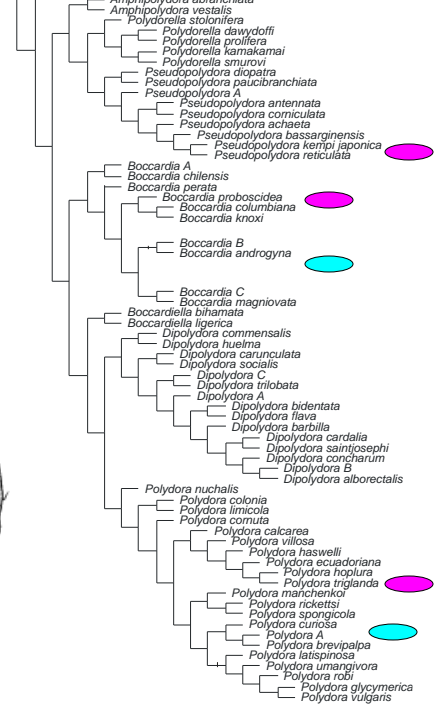
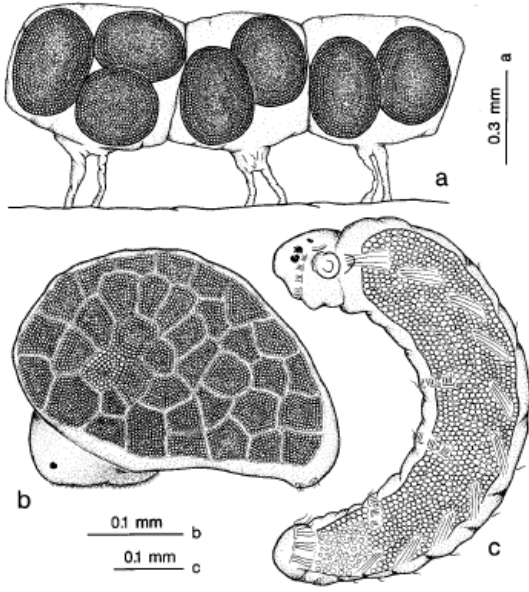
Radashevsky & Olivares, 2005



Radashevsky & Migotto, 2017



Endolecithotrophy



# *Pygospio elegans*

## Poecilogony

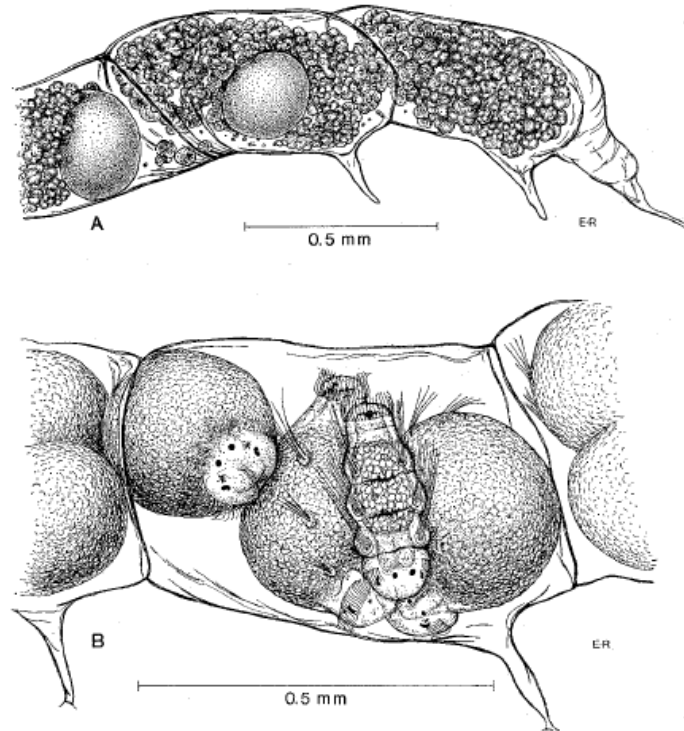
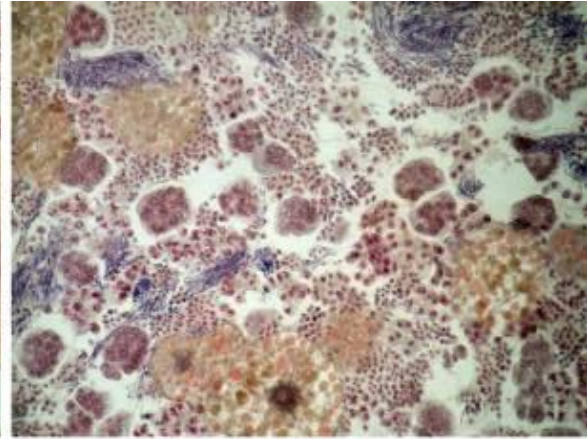
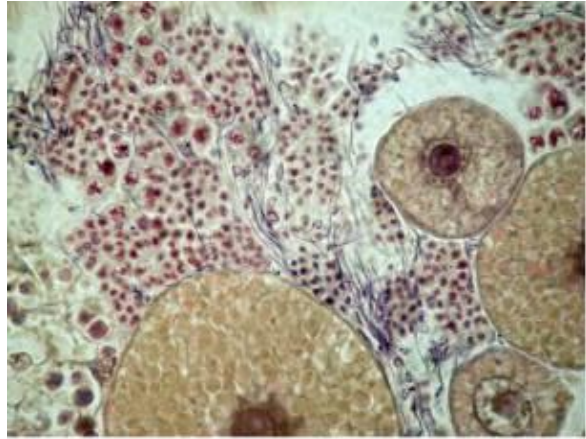
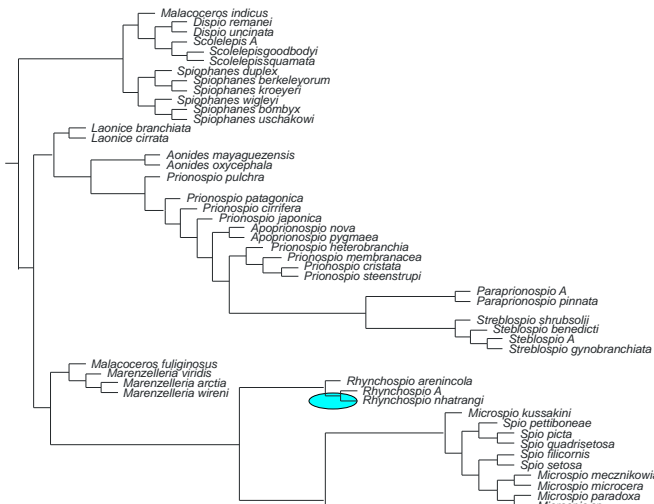


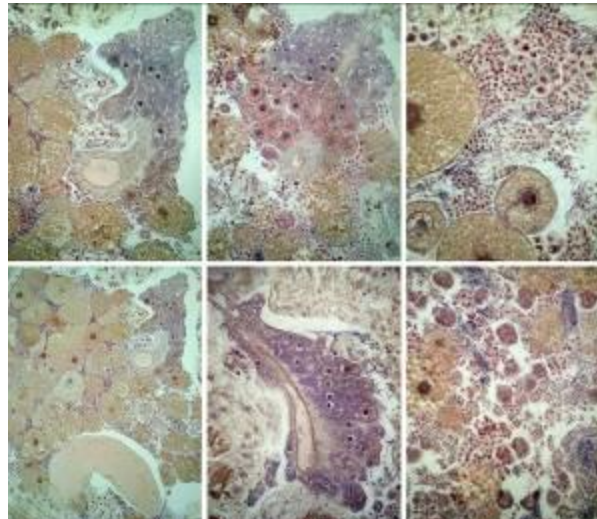
FIG. 30. *Pygospio elegans*. A, part of egg string showing hunchbacked embryos feeding on nurse egg particles; B, single capsule from another egg string showing the normal difference in development. The small stage has ingested a smaller amount of nurse eggs and may have a pelagic life before metamorphosis. Both from Vellerup Vig, 28.vi.1944, and drawn from life with the aid of a camera lucida.

Rasmussen, 1973



*Boccardia* sp.

*Boccardia* sp.



## Hermaphroditism

simultaneous

sequential

Hermaphroditism and environmental sex determination evolved independently in various commensal species as a strategy to provide reproductive couples in condition of limited space and, consequently, small limited size of worm colonies.

