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REDESCRIPTION OF *ALLENCOTYLA MCINTOSHI* PRICE, 1962 (MONOGENEA), WITH AN EMENDED DIAGNOSIS OF *ALLENCOTYLA* PRICE, 1962

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ABSTRACT: The original description of the type species of *Allencotyla*, *A. mcintoshi* Price, 1962, was based on 5 specimens collected from 1 amberjack *Seriola lalandi* in Florida. In this study, *A. mcintoshi* is redescribed based on new specimens collected from juvenile greater amberjacks *S. dumerili* captured off the Spanish Mediterranean coast and maintained in experimental culture tanks. Except for a slightly smaller size, individuals of *S. dumerili* were morphologically similar to the type specimens. However, reexamination of the type material and examination of the new specimens revealed the following discrepancies with respect to the original description: (1) the vaginal pore is unarmed and covered with pointed folds with a spinelike appearance; (2) the cirrus is armed, but spines are frequently lost (e.g., in the type specimens); (3) the esophagus is long with 3 or 4 pairs of diverticula and branches into cecae at the level of the genital atrium; and (4) the genital atrium is surrounded by 8 concentric crowns of spines, not 11 or 12 as reported in the original description. An emended diagnosis of *Allencotyla* is presented.

Two species are currently included within *Allencotyla* Price, 1962, i.e., *A. mcintoshi* Price, 1962 and *A. pricei* Kritsky, Noble, and Moser, 1978. The original description of *A. mcintoshi* was based on 5 specimens collected from the gills of 1 amberjack *Seriola lalandi* Valenciennes, 1833 in Florida. During a parasitological analysis of juvenile greater amberjacks, *S. dumerili* (Risso, 1810), captured off the Spanish Mediterranean coast and maintained in experimental culture tanks, a number of monogenean specimens, tentatively identified as *A. mcintoshi*, were collected. A comparison of this material with the type specimens of *A. mcintoshi* confirmed this possibility but revealed some important discrepancies between the characters observed in all specimens and those reported in the original description by Price (1962). Therefore, the aim of this study is 2-fold. First, *A. mcintoshi* is redescribed based on a careful reexamination of the type material and on a large sample of specimens from *S. dumerili*. Second, the current status of *Allencotyla* within the Heteraxininae is briefly discussed, and the diagnosis of *Allencotyla* is emended.

MATERIALS AND METHODS

Juveniles of *S. dumerili* were captured off Puerto de Mazarrón, Murcia, Spain (37°29′–37°34′N, 1°9′–1°15′W), in 1997. Fish were maintained in tanks at the Spanish Institute of Oceanography (I.E.O.) in Puerto de Mazarrón. A total of 137 fish less than 1 yr old were killed with an overdose of benzocaine administered by bath exposure. Specimens of *A. mcintoshi* were found dead on the gills, with the body relaxed due to the effect of the anesthetic. Thirty-nine mature specimens from 10 hosts were selected for the taxonomic study. Parasites were fixed and preserved in AFA, stained with alum carmine, and mounted in Canada balsam. Voucher specimens are deposited in the USNPC (nos. 90915/16/17). We also examined the 5 specimens of the type series of *A. mcintoshi* obtained from 1 specimen of *S. lalandi* from Florida (Price, 1962). Morphometric measurements were taken using an ocular micrometer or from drawings made with the aid of a camera lucida. Total number of spines of the genital atrium was counted in 5 specimens from *S. lalandi* and 5 specimens from *S. dumerili*.

To clarify the nature of spinelike structures of the genital pore of *A. mcintoshi*, 2 methods were followed. First, the genital pore of the type specimens, and of the specimens from *S. dumerili*, was compared with that of other closely related species of the Heteraxininae in which similar structures have been described, namely, *A. pricei* (USNPC nos. 74633, 76473, 80952/3 and Harold W. Manter Laboratory Collection nos. 20861, 31150/2), *Heteraxine heterocerca* (Goto, 1894) and *Zeuxapta japonica* Yamaguti, 1963 from Dr. K. Ogawa's collection, and *Z. japonica* from the collection of the Meguro Parasitological Museum (no. 22874). Second, 2 specimens of *A. mcintoshi* from *S. dumerili*, previously stained with alum carmine and mounted in Canada balsam, were cut with a razor blade. The resulting sections were remounted in Canada balsam. This method allowed an observation of a transverse section of the pore.

Ecological information follows the recommendations provided by Bush et al. (1997).

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DESCRIPTION

Allencotyla mcintoshi Price, 1962

(Figs. 1, 2)

Body lanceolate, widest at the anterior region of haptor. Tegument smooth. Anterior end forming subapical ventral cavity, with transverse glandular ledge (''sticky convoluted tegument'', according to Rohde's [1981] terminology), 2 open, subelliptical suckers. Two subtriangular areas of glandular cells behind each sucker. Haptor asymmetric, with short side at right in 22 of 39 individuals examined. Clamps microcotyle-type, with middorsal trident sclerite. Clamps of long side more numerous and notably larger than those of short side. Largest clamps occur in the median zone.

Mouth within the haptoral cavity. Pharynx small, elliptical, posterior to haptoral suckers. Esophagus with 3 or 4 pairs of lateral branches, bifurcated into intestinal cecae at the level of beginning of genital atrium. Cecae profusely ramified; outer branches occurring along the length of cecae, inner branches from level of ovary to posterior end of cecae. Digestive tract ending close to posterior end of body. Neural junction posterior to pharynx.

Testes small, numerous. Testicular zone between intestinal cecae extending from the level of end of ovary to haptor. Vas deferens median, sinuous narrow, running from testes to genital atrium. Genital atrium midventral, armed with 8 concentric crowns of numerous (321–456) elongated spines with hooked tip. Ejaculatory bulb wide, connected with genital atrium. Muscular cirrus in anterior part of genital atrium, sometimes (34.7% of individuals collected from *S. dumerili*) armed with long, thin, hooked spines (1–13). Ovary pretesticular, elongated, with posterior globular germinal zone (proximal ovary), followed by narrow, longer U-shaped zone (distal ovary). Seminal receptacle placed over germinal ovary. Oviduct connected with genito-intestinal duct at right side of body. Spindle-shaped ootype surrounded by numerous shell glands, connected to oviduct by sphincter. Uterus wide, specially after ovarian area. Vagina single, middorsal, posterior to genital atrium. Vaginal pore unarmed, covered by pointed folds. Vitellaria follicles extending along entire body. Vitelline ducts joining anterior to ovary, forming single, wide duct ending in oviduct. Eggs elliptical; opposite end to operculum pointed, continued by long polar filament ending in conical structure.

Morphometric measurements (mean ± SD with the range in brackets) of *A. mcintoshi* from *S. lalandi*, *A. mcintoshi* from *S. dumerili*, and both hosts together, respectively, are as follows (all morphometric data in micrometers): total length 10,869 ± 2,238 (8,336–14,320), 7,229 ± 1,130 (5,080–9,776), 7,578 ± 1,648 (5,080–14,320); body maximum

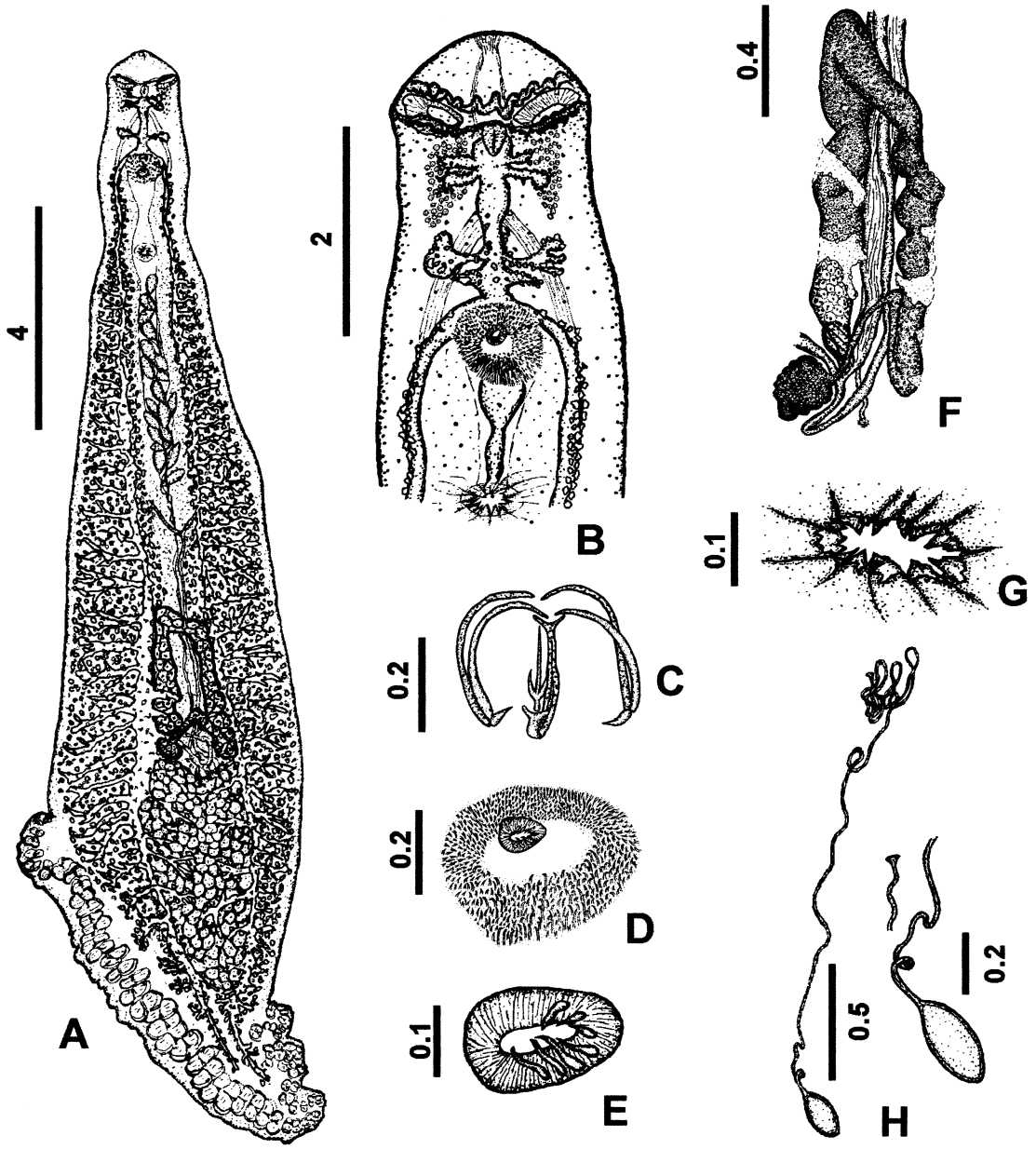

FIGURE 1. *Allencotyla mcintoshi* Price, 1962 from greater amberjacks, *Seriola dumerili*, in the Spanish Mediterranean. **A.** Whole specimen, ventral view. **B.** Anterior end, ventral view. **C.** Clamp, dorsal view. **D.** Genital atrium, ventral view. **E.** Cirrus. **G.** Ovary, ventral view. **H.** Egg. Bar in millimeters.

width 1,773 ± 276 (1,472–2,224), 1,333 ± 310 (800–2,048), 1,376 ± 331 (800–2,224); body maximum width without haptor 1,354 ± 162 (1,152–1,568), 1,020 ± 160 (752–1,440), 1,072 ± 200 (752–1,568); sucker length 88 ± 7 (81–98), 82 ± 19 (24–125), 83 ± 17 (24–125); sucker width 178 ± 8 (171–189), 127 ± 31 (34–192), 132 ± 33 (34–192) (values of the 2 suckers averaged); haptor length 2,829 ± 359 (2,352–3,232), 2,179 ± 342 (1,616–3,184), 2,241 ± 392 (1,616–3,232); number of clamps (long side) 34 ± 5 (27–38), 37 ± 2 (34–41), 36 ± 3 (27–41); number of clamps (short side) 20 ± 2 (17–22), 21 ± 2 (17–29), 20 ± 2 (17–29); clamp maximum length (long side) 175 ± 51 (86–208), 138 ± 29 (96–192), 150 ± 40 (86–208); clamp maximum width (long side) 309 ± 22 (282–339), 251 ± 31 (176–298), 257 ± 35 (176–339); clamp maximum length (short side) 129 ± 30 (96–157), 99 ± 32 (25–144), 102 ± 37 (25–157); clamp maximum width (short side) 186 ± 49 (109–243), 120 ± 22 (80–189), 127 ± 31 (80–243); pharynx length 61 ± 5 (54–67), 56 ± 9 (35–74), 57 ± 9 (35–74); pharynx width 43 ± 4 (38–48), 43 ± 5 (29–51), 43 ± 5 (29–51); esophagus length 459 ± 44 (421–534), 304 ± 56 (170–404), 319 ± 72 (170–534); testicular area length 1,770 ± 203 (1,520–1,968), 1,346 ± 269 (848–2,032), 1,387 ± 290 (848–2,032); testicular area width 566 ± 48 (496–624), 414 ± 72 (320–520), 465 ± 98 (320–624); testis maximum diameter (average obtained from 20 testes for each individual) 84 ± 10 (67–91), 79 ± 11 (47–105), 79 ± 11 (47–105); number of testes 190 ± 27 (165–229), 119 ± 24 (79–170), 130 ± 36 (79–229); distance from posterior end of testicular area to posterior end of body 1,773 ± 174 (1,504–1,968), 1,403 ± 266 (1,120–1,904), 1,526 ± 295 (1,120–1,968); atrium length 173 ± 25 (144–205), 177 ± 28 (115–240), 176 ± 27 (115–240); atrium width 213 ± 17 (195–238), 180 ± 25 (128–208), 191 ± 27 (128–238); number of atrium spines in external crown 87 ± 11 (70–100), 81 ± 8 (66–97), 82 ± 9 (66–100); atrium spine length 36 ± 4 (29–38), 35 ± 4 (28–42), 35 ± 4 (28–42); atrium to body anterior end distance 805 ± 81 (712–912), 604 ± 104 (256–848),

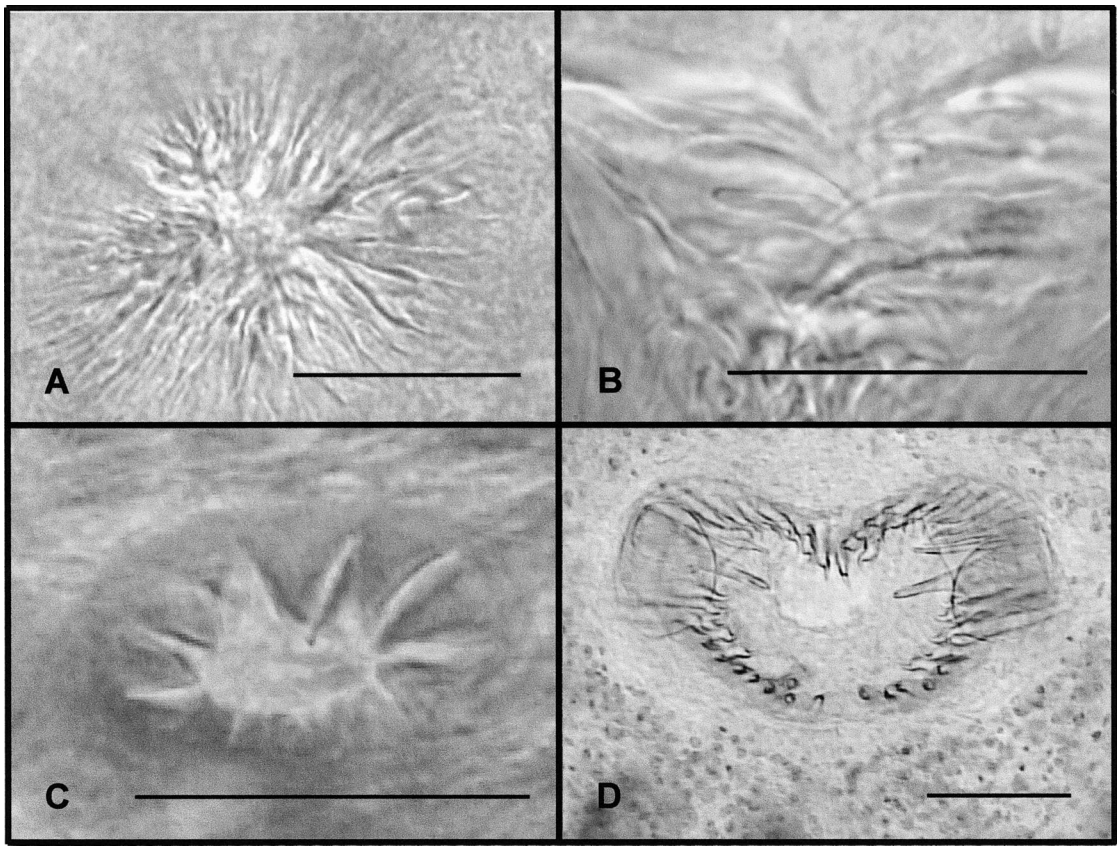

FIGURE 2. Vaginal pores of some species of the Heteraxininae. **A.** *Allencotyla mcintoshi*, dorsal view. **B.** *A. mcintoshi*, transversal view. **C.** *Heteraxine heterocerca*, dorsal view. **D.** *A. pricei*, ventral view. Bar = 50 μm.

624 ± 118 (256–912); atrium to vagina distance 514 ± 109 (368–672), 482 ± 108 (256–960), 485 ± 107 (256–960); cirrus length 35 ± 5 (27–42), 43 ± 6 (29–58), 43 ± 6 (27–58); cirrus width 43 ± 7 (35–53), 38 ± 6 (26–50), 40 ± 7 (26–53); ovary length 2,174 ± 316 (1,806–2,588), 2,054 ± 449 (932–2,980), 2,066 ± 436 (932–2,980); proximal ovary width 147 ± 14 (137–170), 95 ± 48 (26–228), 100 ± 48 (26–228); distal ovary width 90 ± 26 (59–124), 76 ± 19 (52–117), 80 ± 22 (52–124); egg length 161 ± 6 (156–169), 156 ± 13 (136–188), 157 ± 12 (136–188); egg width 77 ± 6 (70–86), 81 ± 16 (66–121), 80 ± 15 (66–121) (for each individual, a single value obtained using 10 eggs when available).

Taxonomic summary

Localities: Gulf Stream near Miami, Florida (type specimens); Puerto de Mazarrón, Murcia, Spain (37°29′–37°34′N, 1°9′–1°15′W).

Hosts: Amberjack, *S. lalandi* Valenciennes, 1833 (weight 20,412 g) (type host); greater amberjack, *S. dumerili* (Risso, 1810) (range of weight 362–1,250 g; range of length 32–45 cm) (Osteichthyes; Carangidae).

Infection site: Gill filaments.

Infection parameters (in S. dumerili): Number of hosts examined, 137; intensity, 1–72 (mean ± SD, 12.2 ± 17.2; median, 3); prevalence, 21.9% (95% CI, 14.0–29.0).

Specimens: Holotype, USNPC no. 37730; paratypes, no. 37731 from *S. lalandi*, deposited vouchers from *S. dumerili*, USNPC nos. 90915/16/17 (5 specimens); remaining material from *S. dumerili* in the parasitological collection of the Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Remarks

Except for a slightly smaller size, specimens of *A. mcintoshi* from *S. dumerili* were morphologically similar to the type specimens. Because the processing techniques were not reported for the type specimens (see Price, 1962), the extent to which the smaller size of worms from *S. dumerili* may result from differences in processing is not known. However, there is strong evidence that the size of *A. mcintoshi* individuals is dependant on host size (F.E. Montero, in prep.), and the type specimens were collected from a substantially larger host individual (Price, 1962). Incidentally, this observation makes it advisable to routinely include data on host size in taxonomic studies of monogeneans.

Reexamination of the type specimens of *A. mcintoshi* and examination of new specimens from *S. dumerili* indicate important discrepancies with the original description of *A. mcintoshi* (see Price, 1962). First, the vaginal pore is not armed. In all individuals examined, the epithelium surrounding the vaginal pore and the anterior part of the vaginal duct is covered by pointed folds (Figs. 1G, 2A, B). These folds are projections of integument without spines. Similar folds are observed, e.g., surrounding the vaginal pore and accessory vaginal pore of *H. heterocerca*, and were described by Ogawa and Egusa (1977) as ''frill-like structures'' (Fig. 2C). Numerous less developed projections of this type are also observed in the vaginal pore of *Z. japonica*. However, *A. pricei*, the other species of *Allencotyla*, has true spines surrounding the vaginal pore (Fig. 2D).

Second, the cirrus was reported to be unarmed in the original description of *A. mcintoshi*. In fact, spines were not observed in the cirrus of the type specimens but were seen in many individuals collected from *S. dumerili*. Cirral spines are shorter than those found in the genital atrium, but the morphology is similar (Fig. 1C). The number and distribution of cirral spines varied widely among specimens, suggesting that the absence of these spines might be due to natural intraspecific variability in spine growth or, most probably, to postmortem lose during the handling of specimens.

Third, there are apparent inconsistencies regarding the morphology of the digestive tract. In the original description, the esophagus was

described as a very short, nonramified duct that ended close to the pharynx without reaching the genital atrium. However, in all specimens examined in this study, the esophagus was long and branched into ceca at the level of the genital atrium (Fig. 1B). The bifurcation described by Price as being the end of the esophagus seems to be that of the nervous system. Moreover, in the present study, 3 or 4 pairs of diverticula, not described by Price (1962), were observed in the esophagus. This author neither described the internal diverticula of the intestinal ceca probably because they are less evident in specimens from *S. lalandi*.

Finally, Price (1962) described the genital atrium of *A. mcintoshi* as surrounded by concentric crowns of thin spines, hooked at the distal end. However, he reported 11 or 12 such crowns, although only 8 were found in all specimens examined in the present study (Fig. 1D).

The finding of *A. mcintoshi* in greater amberjacks from the Spanish Mediterranean extends both the geographical range and the host range of this parasite. There are other species of the Heteraxininae infecting more than 1 host species and throughout a wide geographical region: *A. pricei* was reported from several species of the Embiotocidae (Kritsky et al., 1978; Payne, 1990), and *Z. seriolae* (accepting the synonymization proposed in Rohde, 1978) infects carangid fishes in *Seriola* and *Caranx* from the Pacific and the Mediterranean (Montero, 2001).

DISCUSSION

The taxonomic status of *Allencotyla* has been controversial. A year after this genus was erected, Yamaguti (1963) included *A. mcintoshi* in Heteraxininae without explanation, and Unnithan (1971) agreed with this synonymy. However, Kritsky et al. (1978) argued that the characters of *A. mcintoshi* warranted consideration of *Allencotyla* as a separate genus. In fact, these authors included a second species within *Allencotyla*, *A. pricei*. Given that the major generic-level traits within the Heteraxininae are the presence and structure of genital pores (Tripathi, 1957; Unnithan, 1957; Price, 1962; Yamaguti, 1963; Mamaev, 1970, 1990; Ogawa and Egusa, 1977; Kritsky et al., 1978; Bravo-Hollis, 1983; Payne, 1990), we agree with Kritsky et al. (1978) that *Allencotyla* is a valid genus. However, in view of the new evidence about some key traits of the type species, i.e., an armed genital atrium and an unarmed vaginal pore, the following emended diagnosis for *Allencotyla* is proposed:

Genus *Allencotyla* Price, 1962

Emended diagnosis: Heteraxinidae Unnithan, 1957; Heteraxininae, Unnithan, 1957. Body elongated, with asymmetric haptor, without haptoral anchors and anchor-bearing lappet. Mouth in anterior subapical aperture. Suckers preceded by sticky convoluted tegument. Sessile clamps, those in short side considerably smaller than those in long side. Genital atrium postbifurcal, armed with concentric crowns of simple hooked spines. Cirrus armed (unarmed in some specimens). Vagina unarmed, covered with pointed folds. Egg with filament at 1 pole.

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