

A New, Disjunct Species of Triclad Flatworm (Turbellaria: Tricladida) From a Spring in Southern New England

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Abstract. An undescribed species of flatworm belonging to the genus *Polycelis* (family Planariidae) is reported from a spring in western Massachusetts. The new species represents the first recorded occurrence of *Polycelis* in eastern North America. The morphological uniqueness and geographical disjunction of the new species suggests that it has been isolated from congeneric forms for a considerable length of time. However, it is alternatively possible that the species' existence in western Massachusetts is the result of introduction from some as yet unknown "natural" range elsewhere. If in fact naturally occurring in New England, the new species could be a survivor of a pre-glacial fauna that survived glacial advances by living in groundwater habitats under the ice sheet.

Introduction

The freshwater flatworm genus *Polycelis*, as recently defined by Gourbault (1972) and Kenk (1973), is characterized by certain morphological features which vary little among described species. Within the genus, two subgenera are recognized (*Polycelis* and *Seidlia*), the basis of distinction being founded in the degree of musculature associated with the genital atrium (Kenk, 1953, 1973). Only a few species are presently assigned to *Seidlia*, in which the atrium is provided with an extensive and thick musculature. Apart from the differences in atrial musculature separating *Polycelis* (*sensu stricto*), without extensive atrial musculature, and *Seidlia*, the distinctions among the several known species in the genus are limited to differences in the shape and position of various com-

ponents of the male reproductive system and, to a lesser extent, the presence or absence of muscular prostatic organs also known as adenodactyls.

The distribution of *Polycelis* covers a large portion of the Northern Hemisphere (Kenk, 1953; Ball, 1975). In North America, the known species are restricted to the western third of the continent. Kenk (1953) proposed that the North American distribution of *Polycelis* is a result of pre-glacial dispersal from Asia across the Bering Strait when a land bridge existed during periods of lower sea stands. According to Kenk (1953), subsequent glaciations have controlled or adjusted the distribution of certain species. Kenk's (1953) synthesis of *Polycelis* distribution has been adopted by Ball (1975).

Recent investigations of springs in western Massachusetts, in the northeastern United States, have revealed the existence of an undescribed species of *Polycelis*. The new species possesses, among other distinctive morphological features, a specialized gland situated near the reproductive structures, termed the ventral gland, which is unlike that of any other described species of *Polycelis* or any other known North American triclad species. This paper provides a description of the new species and attempts to explain the disjunct occurrence of the new species in New England.

Materials and Methods

The spring in which the new species was found is in Sunderland, Franklin County, Massachusetts and represents the type locality. The spring is the principal source of water for a state-owned fish hatchery. Specimens were collected on 25 August, 22 September, 30 October, 1987,

and 13 January, 1988. One hundred and fifty specimens were collected and examined. Of the series, 34 animals had fully formed reproductive organs.

Most specimens were killed in 2% nitric acid and fixed in FAA. A few specimens were maintained in laboratory conditions for behavioral observations. Twelve specimens were serially sectioned using conventional techniques and stained with Delafield's or Ehrlich's hematoxylin and eosin. Though most sections were of the sagittal plane, cross sections were prepared in two cases. An additional three specimens were dissected. The Holotype and the Paratypes (all slides) and a series of whole specimens have been deposited into the collections of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. The remaining specimens and prepared slides have been deposited into the Museum of Zoology, University of Massachusetts, Amherst, Massachusetts.

Systematic Account and Results

Family Planariidae Stimpson, 1857

Genus *Polycelis* Ehrenberg, 1831

Polycelis remota, new species

Diagnosis

Polycelis remota is a medium sized species (maximum length, 17 mm) demonstrating characteristics representative of the genus, including the presence of an arc of eyespots following the anterior contour of the body of the animal, distinct cephalic auricles produced anterolaterally, testes situated ventrally, and pre-pharyngeal and paired oviducts uniting posteriorly of the penis bulb to form a common oviduct which descends to the genital atrium. Otherwise, it is distinct from all known species of *Polycelis* by the possession of a large, transverse muscular gland with a single exterior sucker-like organ situated always on the right ventral side of the animal, anterior and separate from the gonopore and its associated atrial cavities. The new species is further distinguished from all other known species of *Polycelis* by the peculiar seminal vesicle, by having a greatly elongated penis bulb, and by the position of the copulatory bursa which extends anterior of the posterior margin of the pharyngeal cavity.

Description

General characteristics of Holotype (living animal, 11.0 mm) (Fig. 1A, B). The anterior margin of the head forms a low inverted "V," and continues laterally with sub-triangular auricles. The neck region is posterior to auricles with slight constriction. The body widens posteriorly, reaching its greatest width in the region of phar-

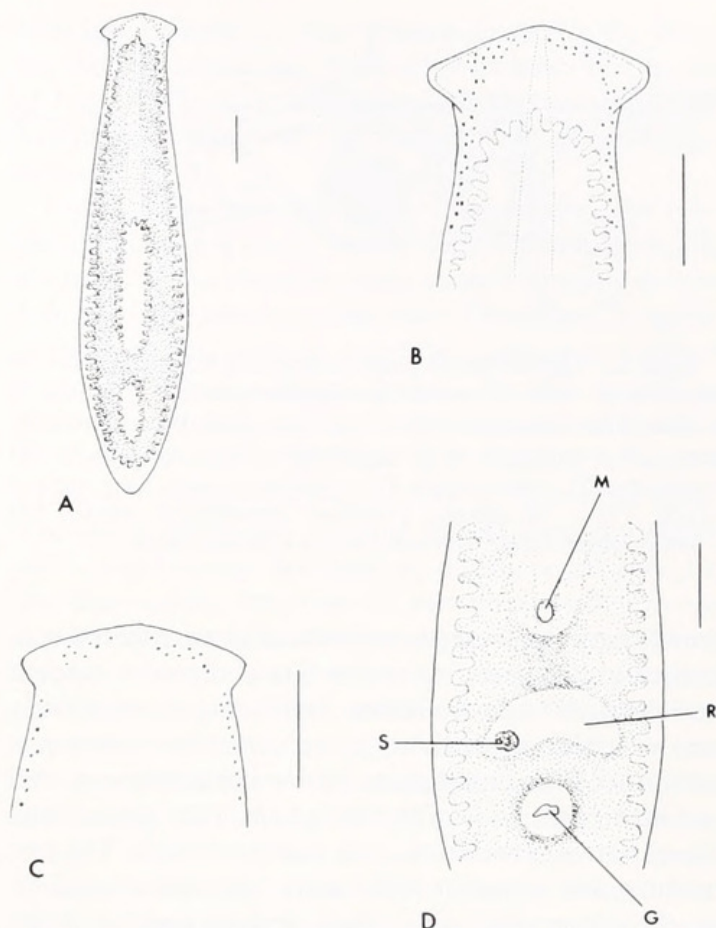


Figure 1. External characteristics of *Polycelis remota*: A, dorsal view of living animal; B, anterior end of living animal; C, anterior end of preserved animal; D, ventral view of posterior portion of preserved animal. Scale line equals 1 mm; G = gonopore, M = mouth pore, R = region of ventral gland, S = "sucker."

ynx. The posterior part of the animal tapers to a rounded point. Eyes are present and numerous, and extend across the margin of the head and along the lateral margins, exclusive of auricles, some distance posterior to auricles. The arc is interrupted at the midpoint of the anterior margin. The dorsal surface anterior to the pharyngeal region with the low median keel extending anteriorly to the apex of the anterior margin. The pharynx is single, medially placed, and occupies about one third of the length of the animal. The inner muscle layers of pharynx are composed of an outer, thin longitudinal layer and an inner, thick circular layer. Rhabdites are present along the margins of the animal. Both mouth and genital pores open ventrally on the midline. The color of the dorsal surface of animal, exclusive of the area of digestive caeca, is olive, and the digestive caeca are brown to yellowish-brown. The pharyngeal region is a lighter whitish-yellow. Ventrally, the animal is grayish-white, and the region of the atrium and gland is lighter. The pharynx is unpigmented.

Anatomy of the Holotype (Figs. 1D, 2, 3a-d). In the

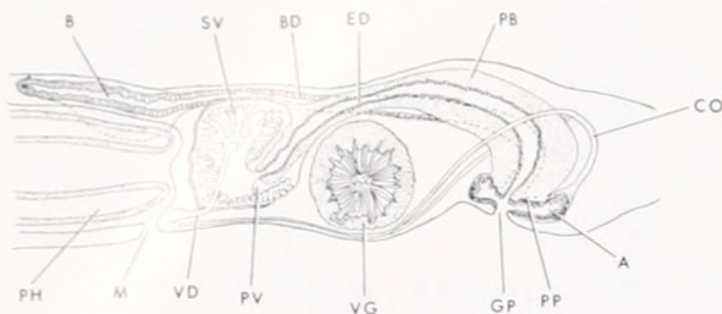


Figure 2. Sagittal view of posterior male and female reproductive structures of *Polycelis remota*, semi-diagrammatic: A = atrium, B = bursa, BD = bursa duct, CO = common oviduct, ED = ejaculatory duct, GP = gonopore, M = mouth pore, PB = penis bulb, PH = pharynx, PP = penis papilla, PV = papilla of vesicle, SV = seminal vesicle, VD = vas deferens (narrowed spermiductal vesicle), VG = ventral gland; stipple indicates presence of muscle tissue.

female reproductive system, the ovaries are situated ventrally and just posterior to first lateral digestive caecum and slightly to side of midline. Oviducts pass posteriorly and ventrally, medially to nerve cords, to a point just posterior of the ventral gland, under which they pass, and ascend on either side of the penis bulb. The right oviduct passes between the bursa duct and penis bulb. The two oviducts join posterior to the penis bulb to form a common oviduct which proceeds to female portion of the atrium. The copulatory bursa is a lobate, somewhat flattened sac placed dorsally and to right of the pharyngeal cavity. The bursa stalk or duct proceeds posteriorly from the bursa to the right of the penis bulb and joins the atrium ventrally along side the penis papilla. The histology of the bursa duct changes during its course. The duct wall is anteriorly similar to the bursa wall and contains a thick cellular lining composed of a tall, spacious, and densely staining columnar epithelium without a detectable muscle coat. The posterior portion of ventral gland is surrounded by a coat of connective tissue fibers; the inner epithelium is characterized by thin columnar cells which stain densely only at their bases.

The male reproductive system contains separate testes extending ventrally from between second and third digestive caeca posteriorly to near base of the pharynx. Up to eight testicular masses are evident at one time. The two vasa deferentia pass ventrally and posteriorly, and medially to the nerve cords near the distal third of the pharynx where the ducts enlarge to form spermiductal vesicles. The vesicles narrow somewhat and separately enter the seminal vesicle at approximately opposite lateral points on the vesicle. The seminal vesicle is large, oval, and situated immediately posterior to the pharyngeal cavity and has a spacious lumen. The vesicle wall is thinly lined with connective tissue, but a distinct muscle layer is not evident. The lumen is penetrated by lobes of

villus-like tissue containing large, vacuolated cells presumed to be secretory. Ventrally, the lumen extends through a broad papilla into the ejaculatory duct, which is enclosed in a long and thickly muscularized penis bulb. The penis bulb extends posteriorly over the ventral gland and terminates in an expanded tip of a very short, conical, and unarmed penis papilla. The distal portion of the penial apparatus veers to the right, ending with the papilla facing and in close proximity to the opening of the bursa duct and near site of the gonopore. The genital atrium is narrow but cavernous; the region of the penis papilla has muscular walls. Glandular cells occupy deep pockets of the atrium to either side of penis papilla.

A structure, herein termed the ventral gland, occupies a position anterior of midpoint between the posterior pharyngeal cavity wall and the posterior tip of animal. The gland is large and crescent shaped; the apex of the crescent is pointed anteriorly. The structure is enclosed entirely by mesenchyme tissue. Its width equals about one half the body width of the animal. From left to right the gland is characterized by a thick muscle layer, at first opening dorsally, then closing to form a ring enclosing a nearly solid capsule. The muscle fibers are parallel to the long axis of the gland. The interior of the capsulated gland is comprised of bands of densely staining, apparent glandular cells arising in groups from the inner muscle margin and radiating inward, leaving a small, granule-filled lumen at the center. Invaginations are lined with large, cuboidal cells occasionally present on the inner muscle margin. Farther to the right of the animal, the dorsal musculature of gland capsule reopens, the ventral musculature splits, and the inner free portions of the ventral layer descend ventrally to form a secondary capsule communicating with the exterior. At the right extremity of gland, the secondary capsule, believed to represent a sucker-like organ, acquires an intrinsic thin musculature enclosing the sucker capsule and penetrating to basal papillae-like extensions that communicate with the exterior. Papillae-like extensions interrupt the epidermis and basement membrane of the body wall and contain, in addition to muscle fibers, intercellular spaces and elongated, apparent glandular cells.

Discussion

Variations

Lengths of animals collected ranged from 5 to 17 mm, however, only specimens 10 mm or greater in length had fully formed reproductive organs. The dorsal surface color, exclusive of the digestive caeca, varied from a very light olive in smaller specimens to brown in larger specimens. The area of the digestive caeca varied from reddish-brown to yellowish-brown, the color probably in-

fluenced by the contents of the caeca. Upon preservation, the anterior auricles become reduced and the eyes at the bases of the auricles become obscured (Fig. 1C). Within the female reproductive system, the ovaries are situated just slightly to the right or left of the midline. The size and the position of the copulatory bursa varies somewhat. The principal lobe is placed either to the left or right of the dorsal midline. The bursa duct passes either dorsally or laterally (right side) of the penis bulb. The male reproductive system of certain animals may have fewer testes, and lobes of the testes may occasionally extend dorsally. The posterior, enlarged vas deferens (spermiductal duct) sometimes continues a short distance posterior to the seminal vesicle before turning upward and anterior towards the point of union with the vesicle. Additional observations on cross sections of animals (Fig. 3e, f) confirm the position of the bursa duct on the right side of the penis bulb and the posterior orientation of the penis bulb and papilla. A single specimen contained two distinct penial complexes, neither functional, as the one embedded in the dorsal mesenchyme was connected to the single seminal vesicle whereas the one existing at the site of the gonopore originated blindly.

Ecology and habitat

The species was living in the spring and in the open stream and concrete lined raceways downstream from the spring for about 90 meters. Within this habitat the water temperature varied between 8.5° and 9.0°C on each collecting date. Specimens lived on the undersides of stones and cobbles and were more concentrated toward the spring itself. Farther downstream two other species of triclads were encountered. *Phagocata morgani morgani* (Stevens and Boring) was common in the 9.0° to 10.0°C zone and *Phagocata woodworthi* Hyman was found in the 10.0°C and higher zone. A certain amount of overlap was observed for all three species.

Living specimens moved by gliding over the substrate with their somewhat mobile auricles held slightly aloft. Copulation was not observed, however, unstalked cocoon-like structures were deposited by animals held in captivity. The capsules were bean shaped, translucent, and measured 0.3×0.7 mm.

Systematics and distribution

Little argument can be made to remove *P. remota* from *Polycelis* (*sensu lato*) as all the characters defining the genus are found without deviation in the described species. Similarities with other *Polycelis* species cease below the genus level, and *P. remota* can not be assigned to either of the recognized subgenera. Based on the mor-

phological characters of *P. remota* assessed in this study, the species stands apart from all other described species of *Polycelis* to such an extent as to make phylogenetic hypotheses regarding its intergeneric relationships difficult.

Concerning the male reproductive system, the morphology of the seminal vesicle and its connection with the penis bulb is distinctive and cannot be easily derived from any known *Polycelis* species. Generally, in species of *Polycelis*, the seminal vesicle is enclosed in a definite muscle coat and empties directly into the ejaculatory duct without first passing through a papilla as found in *P. remota*. Probably the most problematic character in terms of evolutionary relationships is the ventral gland. The ventral gland may function as both a secretory gland and a holdfast that is employed during copulation; but this assumption remains to be proven as neither *in vivo* nor *in vitro* copulation has been observed. The gland can not be easily homologized with a true adenodactyl, as described by Kenk (1930) and Hyman (1951), because it is not associated with a cavity of any sort nor does it contain an apical, conical style or papilla typical of the solid adenodactyls found in other *Polycelis* species. Of the species of *Polycelis* in which typical adenodactyls are found, *P. felina* is the only one with adenodactyls situated away from the reproductive atrial cavity. However, in *P. felina*, these organs are posterior of the reproductive complex (Vandel, 1921; Dahm, 1958), whereas in *P. remota* the ventral gland is anterior.

Histologically and morphologically the ventral gland appears similar to the frontal musculo-glandular adhesive organs of dendrocoelid triclads as described by Hyman (1951). The morphology of the capsulated adhesive organ of *P. remota* somewhat resembles the anterior adhesive organ of *Procotyla fluviatilis* (Hyman, 1951; Fig. 21D). Ball (1974) argued that adhesive organs are derived features within the Tricladida. If this is true then there is little reason to dispute the derived nature of the ventral gland in *P. remota*. Thus, assuming that the ventral gland has evolved secondarily, the extreme length of the penis bulb and the displacement of the bursa to a more anterior position may have been merely a morphological adjustment to accommodate the ventral gland. Additionally, the size and complexity of the ventral gland represents more than a simple aberration or modification of some previously existing organ such as an adenodactyl or similar gland. It must be concluded that *P. remota*, though retaining the basic suite of *Polycelis* characters, has nonetheless undergone specialization during a long period of isolation.

Regarding the female reproductive system, the Palearctic species *P. nigra* and *P. tenuis* contain a bilobed bursa (Lender, 1936), which overlaps the pharyngeal

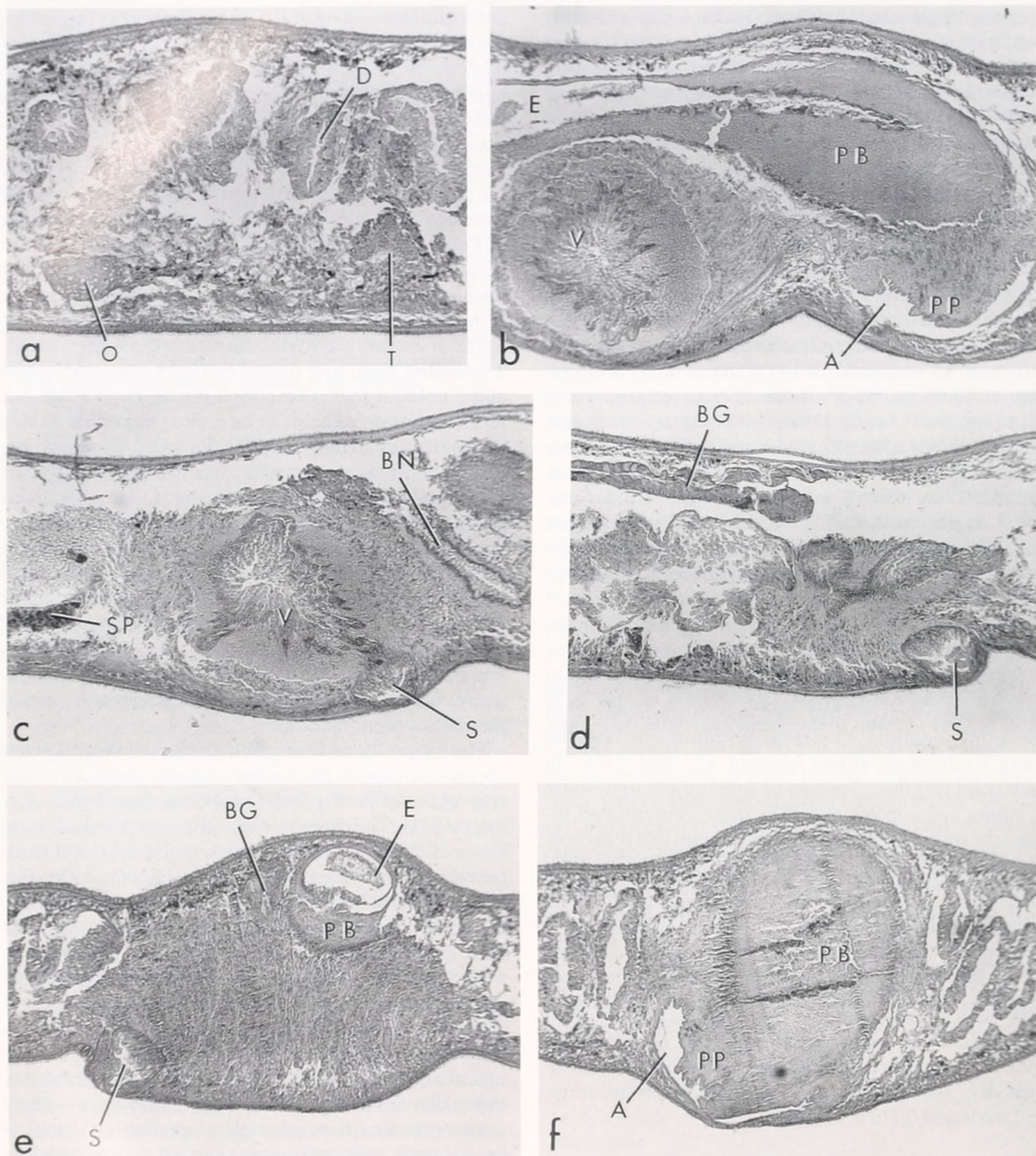


Figure 3. Reproductive anatomy of *Polycelis remota*; a-d, Holotype, sagittal view; a, anterior, left of midline; b, posterior, near midline; c, posterior, right of midline; d, posterior, right side; e-f, cross sections of adult specimen, posterior of pharynx, all figures $\times 95$: A = atrium, BG = glandular portion of bursa duct, BN = nonglandular portion of bursa duct, D = digestive caecum, E = ejaculatory duct, O = ovary, PB = penis bulb, PP = penis papilla, S = "sucker," SP = spermiductal vesicle, T = testes, V = ventral gland.

cavity, an apparently unique feature in Planariidae besides *P. remota*. Whether the overlap of the pharyngeal cavity by the bursa in *P. remota* and the two Palearctic forms indicates a relationship among the three species is debatable. In *P. remota*, the overlap can be attributed to the position of the ventral gland which has displaced the seminal vesicle and the bursa farther anteriorly. In fact, the position and shape of each component of the entire posterior male and female secondary reproductive complex has been no doubt affected to some extent by the presence of the ventral gland.

Understanding the zoogeographical history of *P. remota* is complicated by not only unclear relationships within the genus, but by the fact that the species is thus far known from only the type locality. As discussed earlier, the species exists in a geographical area not previously known to be inhabited by *Polycelis*. Its presence in New England, an area presumably well sampled for most animal groups, can be explained by introduction from some presently unknown area or indicative of a natural but very restricted distribution. With respect to the possibility of introduction, artificial transfers of freshwater triclad flatworms are generally considered rare (Reynoldson, 1966) and have occurred for only a few wide ranging, ecologically generalistic species. Furthermore, species known to have resistant cocoons have not been found outside of their natural range (Ball and Fernando, 1969; Ball, 1974). Nonetheless, the terricolan triclad *Bipalium kewense* was first described from introduced material (Hyman, 1951) and its natural distribution was not understood for many years (Winsor, 1981).

The *P. remota* locality is the source of water for a fish hatchery that for many years has reared exotic species of trout (*Salmo trutta* and *S. gairdneri*). The former trout species was originally imported from Europe while the latter came from western North America, both regions known to have *Polycelis* species. The possibility of introduction with trout species declines as details of the distribution of *P. remota* within the spring are revealed. *P. remota* occurs only in the coldest section of the hatchery drainage, at or near the spring source, where the water temperature is well below regimes in which trout are maintained. The trout pens, farther downstream, have *P. m. morgani* and *P. woodworthi* populations, but rarely is *P. remota* found, and this species only occasionally occurs at the upstream most portion of the first pens in the system. Although introduction from some area containing as yet undiscovered populations of *P. remota* remains possible, the natural distribution theory has equally attractive arguments.

As previously discussed, the distinctive morphology of the reproductive system of *P. remota* suggests that the species has existed outside of the main body of the distri-

bution of the genus for some time. Geographically, New England is situated far from regions where *Polycelis* spp. are found. Within North America, New England has been isolated hydrologically from other physiographic provinces for long periods of time by ancient boundary mountains of Paleozoic age. Species or species groups able to gain entry into provincial New England drainages during rare stream capture events could subsequently evolve independent of gene flow from contemporary forms elsewhere. In support of the prediction that the geographical and geological history of the New England province has favored the evolution of distinct forms is the presence of certain other freshwater invertebrate species apparently endemic to New England. The taxonomic and zoogeographic uniqueness of *P. remota* is characteristic of a group of relatively non-vagile endemic, plus a few non-endemic, invertebrates which have been hypothesized to have survived in the Pleistocene glaciers in subsurface environments (Holsinger, 1978, 1981; Smith, 1986) or periglacial refugia in southeastern New England (Smith, 1982, 1983). The species in this group that are geographically restricted to New England are likely relics of a preglacial fauna, possibly quite diverse, that was peculiar to the New England province. *Polycelis remota* is arguably a member of this group and survived the Pleistocene ice advances by existing in water laying near the surface or water continuously discharging from seepage environments beneath the glacial ice sheet.

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