ROMAN KENK

Freshwater Triclads (Turbellaria) of North America IV. The Polypharyngeal Species of Phagocata

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ABSTRACT

Kenk, Roman. Freshwater Triclads (Turbellaria) of North America. IV. The Polypharyngeal Species of *Phagocata*. *Smithsonian Contributions to Zoology*, 80:1–18, 1970.—Two polypharyngeal species of *Phagocata* are recognized: *P. gracilis* (Haldeman), which includes *P. subterranea* Hyman, and *P. woodworthi* Hyman. The distinguishing characteristics of the two species are described and illustrated. *P. gracilis* has a backward loop of each sperm duct before it enters the penial bulb, an elongated, pointed penis papilla, a fibrous layer below the epithelium of the papilla to which longitudinal muscles attach, a non-glandular antechamber to the glandular seminal vesicle, and lacks a sphincter on the bursal canal. In *P. woodworthi* the sperm ducts enter the bulb without forming a backward loop, the penis papilla is short and truncate, its outer muscle layer consists of alternating sheets of circular and longitudinal muscle fibers, the penial lumen is not differentiated into seminal vesicle and ejaculatory duct, and the bursal canal is very wide and is provided with a terminal sphincter. The morphology of the reproductive system, geographic distribution, ecology, and life cycle of the two species are discussed in detail.

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Introduction

Polypharyngy, or the development of multiple pharynges, has been observed in three genera of freshwater triclads: *Phagocata, Crenobia,* and *Sphalloplana.* The arrangement of the 3 to about 40 pharynges within the common pharyngeal cavity generally is such that one pharynx occupies the normal position in the midline of the body, attached to the anterior wall of the pharyngeal pouch and connected with the anterior ramus of the intestine, while the remaining pharynges are inserted on the lateral walls of the pouch, more or less serially alternating on the right and left and connected to the corresponding posterior intestinal rami. They may be separated from each other by partial septa formed by tissue projecting from the walls of the pouch. During the process of food ingestion several pharynges are extended through the single, very distensible mouth opening. The origin and phylogenetic significance of the polypharyngy have been amply discussed in the literature. The various hypotheses tendered on the basis of comparative morphological and experimental considerations have been reviewed by Steinmann (1917: 3293–3304) and need not be repeated here. True polypharyngy is a genetically stable condition, not to be confused with the occasional development of individual supernumerary pharynges which has been seen in several planarian species as an extraordinary occurrence, probably of traumatic origin. It is also different from the transverse duplication or triplication of structures (pharynx, eyes) reported by Stéphan (1963) and by Tar and Török (1967) for some clones of *Dugesia tigrina.*

From the taxonomical standpoint, polypharyngy is of very limited significance. The polypharyngeal forms of the European genus *Crenobia,* i.e., *C. montenigrina* (Mrázek) and *C. teratophila* (Steinmann), agree so closely in other characters with the more widely distributed *C. alpina* (Dana) that they are often considered subspecies of *C. alpina.* The tripharyngeal *C. anophthalma* (Mrázek) differs from *C. alpina* chiefly by the lack of body and eye pigment besides the presence of three pharynges. In the American genus *Sphalloplana,* comprising only subterranean planarians, polypharyngy is known to occur in *S. mohri* Hyman and related forms discovered in caves of Texas, which in other anatomical features entirely conform with the monopharyngeal species of this genus. The same may be said of the polypharyngeal forms of *Phagocata* which, by the anatomy of their reproductive systems, fit the design exhibited by other species of the genus which have only one pharynx. It is a coincidence that the generic (originally subgeneric) name *Phagocata* was first applied by Leidy (1847: 248) to the polypharyngeal *Planaria gracilis* Haldeman and that its derivation (from *phagein,* Greek, to eat, devour) apparently alludes to the mode of food ingestion. This seems to be one of the reasons

Roman Kenk, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

why some investigators, particularly in Europe, prefer the generic name *Fonticola* Komárek (1926: 9) which, however, is superseded by the older name *Phagocata*.

Within the genus *Phagocata*, polypharyngy occurs in the forms currently designated as *P. gracilis gracilis, P. gracilis woodworthi,* and *P. subterranea*. Examination of the anatomical characteristics of these three forms revealed, however, that their interrelationship has been misunderstood.

Acknowledgments

This study was supported by National Research Foundation Grant GB–6016 to the George Washington University. I wish to express my thanks to the many persons who have contributed to my efforts by furnishing materials or information or have served as guides and collaborators in the field: Dr. J. T. Baldwin, Jr. (College of William and Mary), Mr. Ian R. Ball, Dr. Thomas E. Bowman (National Museum of Natural History), Mr. Harold S. Feinberg (American Museum of Natural History), Dr. John R. Holsinger (Old Dominion College), Mr. Leslie Hubricht, Mr. Lyndon Jon Mayers, Dr. Marvin C. Meyer (University of Maine), Mr. Russell M. Norton, Dr. R. A. Raff (Massachusetts Institute of Technology), Mr. Dale Webb, Mr. Lawrence Weingartner, and Dr. Eliot C. Williams (Wabash College).

Phagocata gracilis (Haldeman)

FIGURES 1A–D, 2, 3, 5–8

Planaria gracilis, new species, Haldeman, 1840: 3.
Phagocata gracilis Leidy, 1847: 248.
Euplanaria (Euplanaria) (?) gracilis Kenk, 1930: 292.
Fonticola gracilis Castle and Hyman, 1934: 155.
Phagocata gracilis gracilis Hyman, 1945: 476.
Phagocata subterranea, new species, Hyman, 1937b: 474.
Fonticola subterranea Ball, 1969: 60.

HISTORICAL NOTES.—The species was first briefly described as *Planaria gracilis* by Haldeman (1840: 3), who indicated its geographic distribution as "springs in Eastern Pennsylvania." Leidy (1847: 248–249), who apparently obtained his material of the species either from Haldeman or from the same source as Haldeman, enlarged the original description, furnished some details concerning its anatomy and behavior, and placed the species in a new subgenus, *Phagocata*, on account of its polypharyngeal characteristic. With regard to its occurrence he stated: "The animal I have only found in abundance in the neighborhood of Prof. Haldeman's residence, near Columbia, Pa. In a spring in front of his house, thousands of them may be seen gliding along the bottom. . . ." In a later paper, Leidy (1885: 51) gives more details about the locality:

> My attention was first called to the singular creature by the late Prof. S. S. Haldeman, while I was a guest in his hospitable home at Chickis, on the Susquehanna river, in 1847. He had previously described it, in 1840, with the name of *Planaria gracilis*. In front of the house is a beautiful spring of water, which has its source in the neighboring cliff of Potsdam sandstone, and runs in a clear stream over a sandy bottom into the Susquehanna.

Thus, we may consider the spring at Chickis (present spelling Chickies), Lancaster County, Pennsylvania, to be the type locality of *Phagocata gracilis*.

EXTERNAL FEATURES (Figure 1A–D).—Descriptions of the external habit of *Phagocata gracilis* have been given by Haldeman (1840: 3), Leidy (1847: 248), Peaslee (1910: 5–6), and Hyman (1937a: 302). Sexually mature specimens are generally 8 to 20 mm long and 1.5 to 5 mm wide. Peaslee has observed individuals measuring up to 30 mm in length and 6 mm in width. As has been pointed out by Hyman, *P. gracilis* is a polytypic species, populations from various localities differing particularly in the shape of the head region. Within an individual locality, however, the animals are of rather uniform shape and color. The head is truncate, with a slight bulge in the median portion of the frontal margin. The variability of the head shape concerns mainly the development of lateral projections or auricles (Figure 2). Haldeman's original description ("head square in front, with a projecting appendage on each side: neck narrowed") and Leidy's notes stress the presence of prominent auricles. As the auricles are held slightly elevated when the animal is moving, and particularly during "feeling" or "searching" movements, the angle at which the observer sees the auricles may be such that they appear slender and pointed (Figure 1C). Such pointed auricles are shown in Girard's (1894, pl. 5: fig. 45) illustration. Specimens from Virginia and from the Washington, D.C., area (Figures 1D, 2C and D), however, may be devoid of auricular projections and may show only a very shallow incurving of the lateral margins behind the rounded

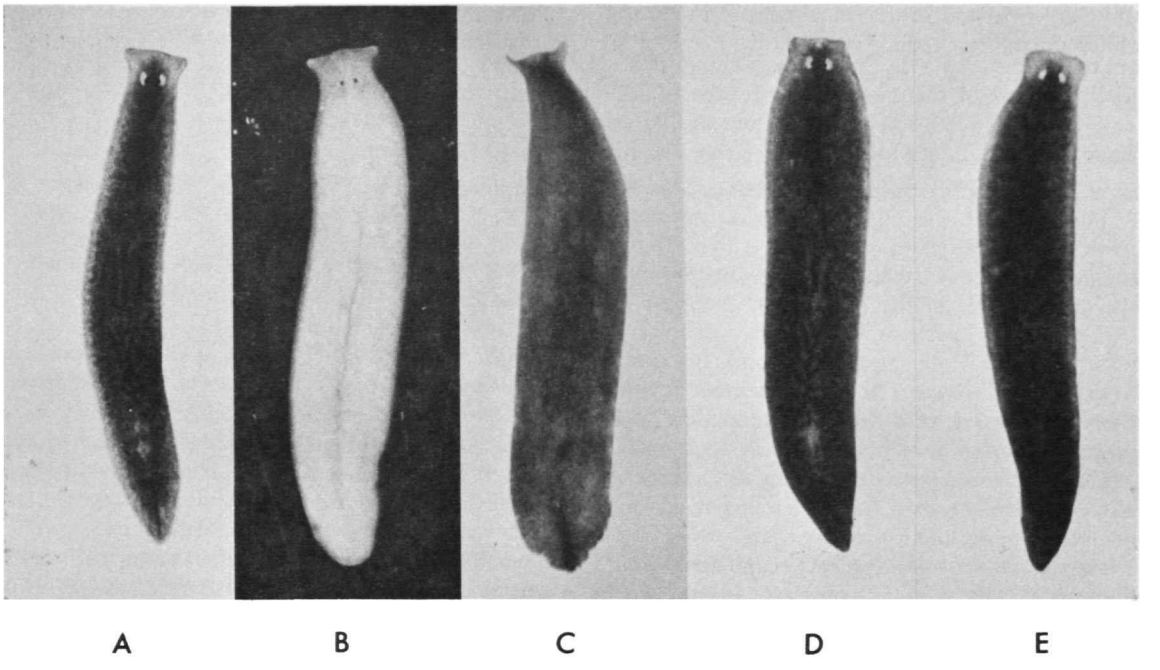


FIGURE 1.—Photographs of living specimens: A, *Phagocata gracilis* from Chickies, Pennsylvania. 6/1. B, *P. gracilis* from Bronsons Cave, Indiana. 8/1. C, *P. gracilis* from Leetown, West Virginia. 5/1. D, *P. gracilis* from Montrose Park, District of Columbia. 5/1. E, *P. woodworthi* from Ipswich River, Massachusetts. 6/1.

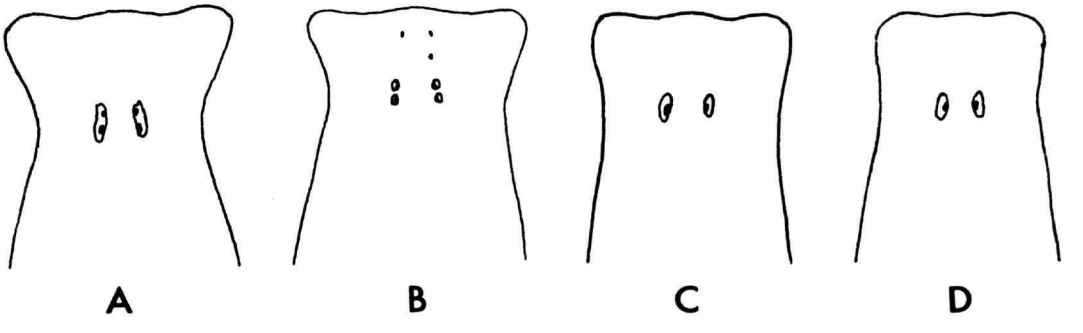


FIGURE 2.—*Phagocata gracilis,* outline drawings of anterior end, from life: A and B, specimens from Leetown, West Virginia; C, specimen from Gloucester, Virginia; D, specimen from Great Falls Park, Fairfax County, Virginia.

auricular edges of the head. There exist all intergrades between these two extreme conditions in animals from different localities. Behind the eye level, the lateral margins diverge gradually in the anterior third of the body, then run parallel, converge again in the postpharyngeal region, and meet at the bluntly pointed posterior end.

The color of the dorsal surface is generally a shade of gray or brown, often almost black, appearing uniform to the naked eye. Under magnification, the arrangement of the pigment may appear mottled or cloudy, without exhibiting a definite pattern. Two small oblong patches above the eyes are unpigmented, white. The ventral surface is lighter than the dorsal side, but also pigmented. The mouth opening is seen as a white spot and the genital aperture is located in a small circular or elongated lighter area. Animals living in caves are generally more lightly colored and may appear white. Such specimens have been described by Hyman (1937b: 474) as a separate species, *Phagocata subterranea*. Williams (1958 and personal communication) investigated the pigmentation of *P. subterranea* from its type locality (Donaldson's Cave, Lawrence County, Indiana) and found all gradations between the unpigmented cave form and the pigmented *P. gracilis* occurring in the same stream as it emerges from the cave. He also kept specimens of the cave form in laboratory cultures in the dark and in light and observed some difference in pigmentation between the two cultures after three months. I have examined living specimens from two caves (Banners Corner Cave, Russell County, Virginia; and Bronsons Cave, Lawrence County, Indiana) that would have been considered unpigmented if seen in the preserved state. Careful examination revealed, however, that the unpigmented eye patches were discernible against a very light cream or off-white background. When cultured in the laboratory, individuals from both localities developed a marked gray pigmentation. Freshly hatched young of the epigean pigmented form also lack pigment and acquire their typical color in the course of their further development.

Eyes are normally two, situated at a distance from each other amounting to one-fourth to one-third the width of the head at the level of the eyes. Their distance from the lateral margin is smaller than that from the frontal border. Accessory or supernumerary eyes are not infrequent, situated either within the same unpigmented eye patch or in a white spot of their own, generally in front of the principal eyes. In one specimen (Figure 2B), which had been kept in a laboratory culture for many months, a total of 7 pigment spots was observed, 3 on the left and 4 on the right side, arranged in a pair of longitudinal rows. Only the posterior two pairs were provided with pigmentless patches while the small anterior three spots lacked the white areas. Both Hyman (1937b: 474) and Williams (1958: 300) state that in some specimens of the cave form (*P. "subterranea"*) eye spots may be entirely lacking. I have observed complete eyelessness in specimens from The Hole Cave, West Virginia, and very small eyes in an individual from Salamander Cave, Indiana. Animals examined from other caves (Bronsons and Jim Ray caves, Indiana; Tom Moore Cave, Missouri; Veiled Lady Cave, Pennsylvania; and Banners Corner Cave, Virginia) proved to have well-developed eyes. In light-colored specimens the tip of the anterior intestinal ramus may be seen extending into the head between the eyes about halfway toward the frontal margin. The lateral branching of the intestine starts behind the eye level. The multiplicity of the pharynges is generally noticeable in the living animal.

The locomotion of *Phagocata gracilis* is generally a smooth gliding. Sustained "crawling" movements such as described by Peaslee (1910: 13) were rarely observed, even upon mechanical stimulation of the animal.

ANATOMY.—The reproductive system of *P. gracilis* has been studied with modern methods by Peaslee (1910: 22–32), Kenk (1935: 89–91), and Hyman (1937a: 303; and 1937b: 475 [*P. subterranea*]). It may be briefly reviewed here, with particular reference to characteristics which separate the species from *P. woodworthi* with which it has been confused by some investigators. The numerous testes are predominantly ventral, arranged in a pair of broad bands which extend from a level behind the head almost to the posterior end of the body. Hyman's (1937b) statement, that in *P. subterranea* the zone of testes reaches posteriorly only to the copulatory apparatus, is erroneous as could be verified on Hyman's slides of the type specimen of that form. The sperm ducts or vasa deferentia expand

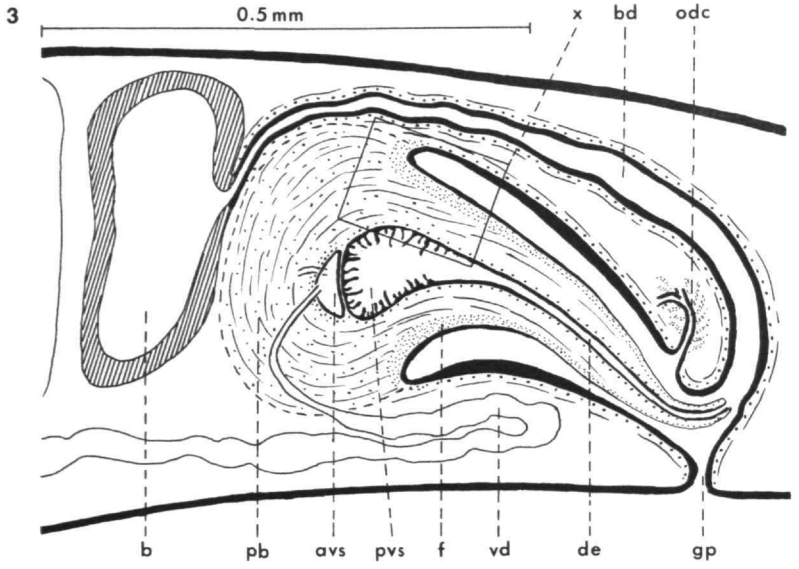
in the pharyngeal region to form the false vesicles (spermiductal vesicles), tortuous ducts filled with sperm. These ducts (Figure 3, *vd*) run posteriorly past the penial bulb (*pb*) to the level of the male atrium, then reverse their direction and enter the bulb ventrolaterally. This backward loop of the sperm ducts is characteristic for the species and is shown in the figures of the copulatory complex presented by most investigators. Only in Hyman's (1937b: 467) figure of *P. subterranea* is this loop not indicated. I have reexamined Hyman's slides of the type specimen of *P. subterranea* (deposited in the National Museum of Natural History) and have found that the sperm ducts, before entering the penis bulb, do extend backward to the sides of the atrium as is typical for *P. gracilis*.

The penis of *P. gracilis* consists of a highly muscular bulb (*pb*) and a conical or finger-shaped, pointed papilla. The size relations between bulb and papilla in preserved specimens are subject to great variation, depending in part on the state of contraction or extension of the organ and in part on characteristics of individual populations, with all intergrades existing between the two extremes (Figures 5 and 6). In the bulb the muscle fibers are arranged in concentric layers, running in various directions. Many of these fibers enter the papilla as longitudinal muscles and attach to the fibrous layer of the outer wall of the papilla. The histological details of the transitional area between bulb and papilla are shown in Figure 8. The papilla is generally long and often bent in various directions, sigmoid, or turned upon itself. Its outer surface is covered with a flattened epithelium (*ep*), below which there is a layer of fine fibers (*f*) which stain only faintly with eosin (as opposed to the strongly eosinophilic muscle fibers). At the base of the papilla this layer is the continuation of the circular muscle layer of the atrial wall. Hyman (1937a: 303) believed that this layer is of a muscular nature although it does not stain typically. It obviously is homologous to the circular muscular layer of the penis papilla of other planarians. In the early stages of the differentiation of the copulatory complex there is indeed no tinctorial difference between this layer and the muscular tissue. At full maturity, however, the fibrous layer may be very conspicuous and clearly distinct from muscles. In sagittal sections through the penis papilla the direction of its fibers appears to be circular, but in tangential sections of a well-extended papilla they are seen running in two diagonally crossed directions.

The configuration of the penial lumen in preserved specimens varies considerably according to the state of muscular contraction. There is a large cavity (Figure 3, *pvs*) lined with an epithelium of apocrine glandular cells, usually filled with secretion. In the retracted penis, this cavity is located in the penial bulb. In specimens with extended penis, the cavity is drawn into the papilla and may be rather far removed from the bulbous part (Figures 5 and 6). The vasa deferentia, which enter the bulb ventrolaterally, do not open directly into this cavity, but enter, separately or united, a smaller cavity (Figure 3, *avs*) more or less anterior to the principal lumen, often anteroposteriorly compressed. This cavity is usually empty or contains sperm. Its lining consists of a flattened epithelium of non-glandular nature. We may call the smaller cavity the anterior seminal vesicle (*avs*), the larger one the posterior seminal vesicle (*pvs*). In most of the sectioned specimens there is no open connection seen between the two vesicles, although they undoubtedly communicate through a temporary orifice which may be normally closed.

From the posterior seminal vesicle a narrower duct proceeds along the axis of the penis papilla to open at its tip, the ejaculatory duct (*de*). The outline of this duct may be smooth or may show some local irregular enlargements (such as the "posterior seminal chamber" mentioned by Peaslee, 1910: 30).

The ovaries, situated on the medial side of the ventral nerve cords at the level of the first or second lateral branch of the anterior intestinal ramus, show no peculiarities. Parovaria are present and may form voluminous, often lobate, masses extending from the ovaries dorsolaterally in specimens at full female maturity (in which the yolk glands or vitellaria are fully developed). The two oviducts or ovovitelline ducts unite after approaching the midline in the space between the wall of the male atrium and the duct of the copulatory sac (*bd*). The united or common oviduct (*odc*) opens into the posterior part of the male atrium from the dorsal side. The end sections of the paired oviducts and the common oviduct are amply supplied with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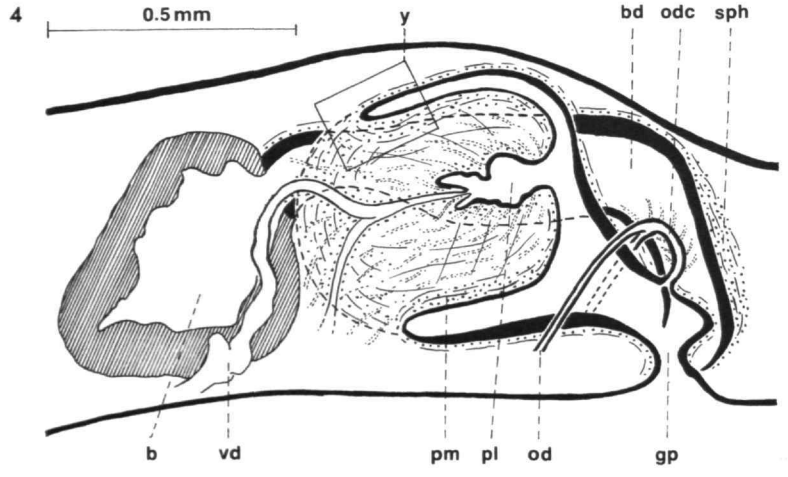
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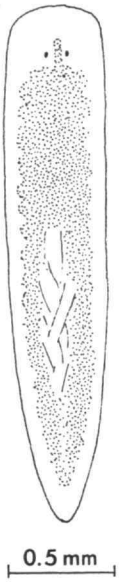
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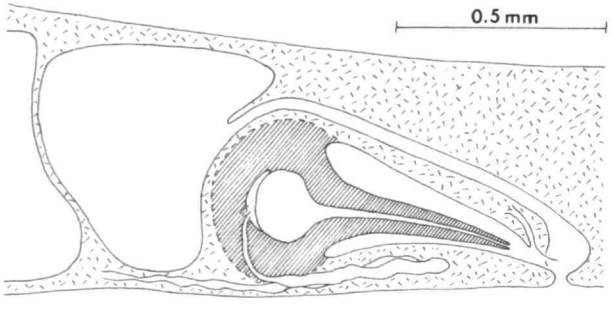
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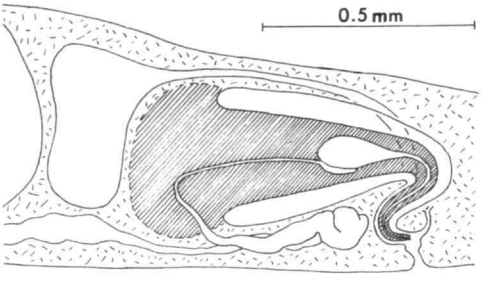
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eosinophilic gland ducts entering from the surrounding mesenchyme.

The copulatory bursa (*b*) is a rather large sac lying anterior to the penis bulb. Its outlet, the bursa duct (*bd*), proceeds dorsally to the penis or to one side (right, more rarely left) of the midline. It is of moderate width, widening only gradually as it runs posteriorly and bends to the ventral side behind the atrium, where it joins the atrial cavity close to the gonopore (*gp*). Its muscular cover consists of a layer of circular fibers adjoining the epithelium and an outer layer of longitudinal muscles. There is no intermingling of the fibers of these two layers, nor a thickening or sphincter in the terminal section of the duct.

REPRODUCTION AND DEVELOPMENT.—Sexually mature specimens of *Phagocata gracilis* were collected in the field at all seasons of the year. Hyman (1937a: 303) assumed that maturity occurred only from late fall through winter and spring. Chandler (1966: 19–24) studied the seasonal abundance and age or size composition of populations of the species in two localities near Bloomington, Indiana, and concluded that breeding appears to be most pronounced from April through August, although it may occur the year round. The same author also collected egg capsules or cocoons in the field and described them as unstalked, reddish brown to almost black, spherical, and with a diameter of 0.75 to 1.25 mm. Cocoons were also laid in my cultures and were either spherical, 1.0 to 1.6 mm in diameter, or, in three cases, ellipsoidal, measuring 0.8×0.9, 1.2×1.5, and 1.4×1.7 mm, respectively. In the cultures kept at a temperature of 14° C, the cocoons hatched in approximately four weeks, individual capsules releasing 2 to 7 young. The young (Figure 7) are 2.0 to 2.5 mm long, unpigmented (white), and have a truncate or more rounded head without auricular expansions. At the time of hatching they possess 3 to 5 (average, 4) pharynges. Hyman (1937a: 303 and 305) stated that young *P. gracilis* have only one pharynx and that accessory pharynges, up to 30, are added in the course of further development and growth. It appears that her conclusion was based on the examination of a mixed planarian population which contained, besides mature *P. gracilis*, an asexual, monopharyngeal species similar to *P. gracilis* in shape and coloration.

No asexual reproduction by fission was observed in my cultures of *P. gracilis*. The "encystment" of animals kept under unfavorable conditions, described by Peaslee (1910: 12), seems to be a pathological reaction rather than a regular occurrence or form of asexual reproduction.

During further growth, the young of *Phagocata gracilis* acquire their typical pigmentation and undergo gradual changes in the shape of the anterior end to reach the shape of the adult (i.e., develop auricular appendages in populations with flared heads). The number of pharynges increases by the development of additional ones in the posterior section of the pharyngeal region. Reproductive structures appear rather late when the animals have reached a length of about 7 mm.

GEOGRAPHIC DISTRIBUTION.—Hyman (1937a and later papers) indicated the geographic range of *Phagocata gracilis* as extending from Pennsylvania and Virginia westward to Missouri, while *P. woodworthi* occupies the New England states, New York, and New Jersey. She considered the Delaware River to be the dividing line between the two ranges. Since Hyman's studies, few reliable identifications have been made by later investigators, so that some records of *"Phagocata gracilis"* may actually refer to *P. woodworthi*. On the other hand, no overlapping of the ranges of the two species has been demonstrated, and we may, for the present, assume that the two species are allopatric. In the following I am presenting a list of the literature data and of my own findings concerning the occurrence of *P. gracilis*, indicating with asterisks (*) those cases in which the identifications of the species have been made on the basis of anatomical characters. Two

FIGURES 3 and 4.—Semidiagrammatic views of copulatory complex in sagittal section: 3, *Phagocata gracilis* from Bronsons Cave, Indiana. 4, *P. woodworthi* from Orland, Maine. *avs*, anterior seminal vesicle; *b*, copulatory bursa; *bd*, bursa duct; *de*, ejaculatory duct; *f*, fibrous layer; *gp*, gonopore; *od*, oviduct; *odc*, common oviduct; *pb*, penis bulb; *pl*, penis lumen; *pm*, muscle layer of penis papilla; *pvs*, posterior seminal vesicle; *sph*, sphincter of bursal duct; *vd*, vas deferens; *x*, area corresponding to photomicrograph Figure 8; *y*, area corresponding to photomicrograph Figure 9.

FIGURES 5 and 6.—*Phagocata gracilis*, shape of copulatory organ: 5, penis retracted (specimen from Tom Moore Cave, Missouri); 6, penis extended (specimen from Great Falls Park, Fairfax County, Virginia).

FIGURE 7.—*Phagocata gracilis*, freshly hatched young. The shaded area indicates the extent of the intestinal branches.

somewhat dubious records have not been included in this list: Stringer's (1918: 359) record of *P. gracilis* from Wisconsin and the finding of Longest (1966: 34), who states that in *P. gracilis gracilis* from Louisiana "the penis papilla is not as elongated as that shown by Kenk and Hyman." These two records need further confirmation before they can be attributed to one or the other of the two species.

DISTRICT OF COLUMBIA. GLOVER-ARCHBOLD PARK: (1) • Wetzels Spring, near W border of the park, 6 October 1969, clear water, temperature 13.6° C, 3 specimens under stones, some mature (besides *Phagocata morgani*). (2) Foundry Branch, 6 October 1969, moderate current, 14.9° C, one mature specimen under stone. MONTROSE PARK: (1) Spring and stream on W edge of the park, 6 October 1969, 3 specimens collected by Dr. T. E. Bowman, one mature. •Same locality, 21 December 1969, 3.7° C, many individuals under stones, some mature (besides *Phagocata morgani*). ROCK CREEK PARK: (1) Rock Creek (Girard, 1856: 80), now polluted and without planarians. (2) •Piney Branch, tributary of Rock Creek, 3 April 1936 (USNM 20235); this locality is now without planarians. TIBER CREEK (Girard, 1856: 80); this creek, at the site of the present Mall, is now covered up. WHITEHAVEN PARKWAY property (adjoining Glover-Archbold Park): (1) Spring near N edge of the property, 6 October 1969, 14.6° C, several individuals, some mature, under fallen leaves (besides *Phagocata morgani*).

ILLINOIS. MONROE COUNTY: (1) •Spring on bluff 2 miles N of Fountain Gap, 30 January 1943, many specimens, mostly mature, collected by L. Hubricht (USNM 20936). (2) Stream near the Carbondale Reservoir (Beatty, 1966: 10). UNION COUNTY: (1) Two springs in the Pine Hills (Beatty, 1966: 10). (2) •Elm Spring, in Pine Hills area of Shawnee National Forest (this is probably one of the springs mentioned by Beatty in the preceding record), moderate current, 13.2° C, pH 7.3. Under stones many specimens, some mature, besides less numerous *Procotyla fluviatilis*.

INDIANA. LAWRENCE COUNTY: (1) Donaldsons Cave, in Spring Mill State Park (•Hyman, 1937b: 474, type locality of *Phagocata subterranea;* Williams, 1958: 300). (2) • Stream outside Donaldsons Cave, 13 November 1965, 6 specimens, some mature, collected by R. M. Norton. (3) • Bronsons Cave, in Spring Mill State Park, 13 November 1965, 2 mature individuals collected by R. M. Norton. •Same locality, 15 August 1969, 12 specimens (some pigmented, some almost white), collected by L. Weingartner. MONROE COUNTY: (1) Mayfields Cave, NW of Bloomington (Banta, 1907: 82; Hyman, 1937b: 474). (2) Near Bloomington (Lansing, 1942: 393; • Chandler, 1966: 1; Reynierse, 1966: 246; 1967a: 366; 1967b: 270). (3) • Salamander Cave, 2 August 1967, one mature specimen collected by R. M. Norton. FLOYD COUNTY: (1) • Spring near Edwardsville, 12 June 1965, 18 specimens, some mature, collected by R. M. Norton. GREENE COUNTY: (1) • Jim Ray Cave, 18 June 1965, 7 individuals, not fully mature, collected by R. M. Norton.

KENTUCKY. MEADE COUNTY: (1) Morgan's Creek (Minshall, 1967: 144 and 1968: 318).

MISSOURI. "MISSOURI" (Hyman, 1937a: 303; • 1951: 161). PERRY COUNTY: (1) • Tom Moore Cave, 3 miles N of Perryville, 16 September 1969, several light-brown specimens collected by L. Hubricht, some mature. SAINTE GENEVIEVE COUNTY: (1) • Valley Spring at St. Genevieve, 4 October 1967, one mature specimen under a stone (besides one *Dugesia dorotocephala*).

OHIO. Near CINCINNATI (Hamilton County?) (• Hyman, 1937a: 303). ATHENS COUNTY: (1) One mile E of Athens (Stehr and Branson, 1938: 297). JEFFERSON COUNTY: Springs, creeks, and lake in the county (Stokely et al., 1965: 312–315).

PENNSYLVANIA. Near CARLISLE (Cumberland County?) (Eddy and Gleim, 1932: 28). Near PHILADELPHIA (Philadelphia County?) Leidy, 1885: 52). Near PITTSBURGH (Allegheny County?) (Griffard, 1963: 598; Griffard and Peirce, 1964: 1472). CENTRE COUNTY: (1) Veiled Lady Cave (Dearolf, 1937: 46 and 1941: 170; • Hyman, 1939: 280). LANCASTER COUNTY: (1) Spring and stream at Chickies, 1½ miles NW of Columbia, type locality of *Planaria gracilis* (Haldeman, 1840: 3; Leidy, 1847: 248 and 1885: 51; • stream crossing State Road 441, 12 December 1969, fast current, water somewhat turbid after rain, 6.4° C, under stones 8 specimens, majority mature. (2) Lancaster (• Hyman, 1937a: 302, 303). MIFFLIN COUNTY: (1) Goss Cave (Holsinger, 1963: 28). PERRY COUNTY: (1) Newport (Leidy, 1885: 52; his locality is probably in Perry County, although there is another Newport in Lawrence County, Pennsylvania). PHILADELPHIA COUNTY: (1) Woodlands Cemetery, Philadelphia (• Hyman, 1937a: 300).

TENNESSEE. "EAST TENNESSEE" (Longest, 1966: 35). DECATUR COUNTY: (1) Near Scott's Hill (Chandler, 1968: 103). HAMILTON COUNTY: (1) Chattanooga (Hyman, 1931: 327, 1937a: 305). OBION COUNTY: (1) "Various points in Obion County" (Bolen, 1938: 164). SHELBY COUNTY: (1) Shelby Forest State Park (Horne and Darlington, 1967: 268). WEAKLEY COUNTY (1) Spring in Weakley County (Chandler, 1968: 103).

VIRGINIA. ALEXANDRIA: (1) Stream along S side of Windsor Avenue, between Russell and Braddock roads. Water clear, fast, bottom stones and mud. Under stones sexual and immature specimens collected 25 May 1952 and repeatedly between 23 February and 26 June 1953, at water temperatures varying between 9.1° and 18.8° C. The stream is now covered up. FAIRFAX COUNTY: (1) • Great Falls Park, in stream below ruins of old mill, bottom stones and mud. Under stones and among leaf litter several specimens collected on various occasions between 31 August 1965 and October 1968, at water temperatures varying between 12.8° and 24.5° C. (2) • Small seepage spring on property of M. M. Bratter on Olley Lane, Burke, one specimen collected 5 April 1967. GILES COUNTY: (1) Shallow pool on left bank of Walker Creek (tributary of New River), about 300 m above bridge, 1 mile E of Bane, altitude about 1,650 ft. Water clear, under stones 7 specimens collected 22 July 1941. GLOUCESTER COUNTY: (1) Outflow of spring-fed pond on Sam Janney's farm, about 1½ miles N of Gloucester, off County Road 616. 14 July 1960, 31 March 1963, and 30 August 1965 (21.5° C) many specimens taken under fallen leaves, stones, etc. JAMES CITY COUNTY: (1) • Green Springs, off County Road 614, 0.2 mile N of junction with State Road 5; 5 July 1960, water clear, 15.9° C; many

specimens taken under stones and on watercress. (2) • Spring at Centerville, W of County Road 614, between junctions with roads 612 and 633: 12 July 1960, clear, fast water, 13.7° C; under stones many young and mature specimens. (3) Small spring and stream at Five Forks, in the woods off State Road 5, about 0.2 mile E of bridge over Powhatan Swamp, 0.1 mile S of the road; 12 July 1960, water clear, 17.2° C; under fallen leaves 7 immature individuals. (4) Buck Spring at Ewell, E of County Road 603, N of Williamsburg Airport; 17 July 1960, water clear, fast, 14.7° C; under fallen leaves and branches several specimens, mature and young. (5) Bubbling Spring (one of the sources of Chisel Run), W of U.S. Road 60, S of Ewell, and W of Williamsburg Airport; 17 July 1960, water clear, fast, 14.0° C; under leaves, sticks, etc. numerous individuals, mostly mature. (6) Tributaries of Bassett Hall Pond (or Rockefeller Pond), SE of Williamsburg; 28 July 1960, water clear, temperature in various places 13.9° to 16.1°C; several specimens, mature and young. (7) Kingsmill Spring, SE of Williamsburg; at remains of old colonial spring house, 28 July 1960, water clear, fast, 15.3° C; numerous spetimens, mostly mature, under stones and fallen leaves. MONTGOMERY COUNTY: (1) Heath Spring at Radford (• Kenk, 1935: 91; • Abbott, 1960: 2). NORFOLK: (1) South Norfolk (Ferguson and Jones, 1949: 439). (2) Willoughy Bay, at Ocean View (Ferguson and Jones, 1949: 439). ROCKINGHAM COUNTY: (1) Spring near Endless Caverns (• Kenk, 1935: 92). (2) Lacey Spring (• Kenk, 1935: 92). RUSSELL COUNTY: (1) Banners Corner Cave (• Holsinger, 1963: 28 and 1966: 75; • additional material obtained by the writer from R. M. Norton and Dr. J. R. Holsinger). WILLIAMSBURG: (1) Small spring at 304 Indian Spring Road, 29 June 1960, 20.3° C, 6 specimens, mature and immature. (2) Seepage spring on campus of College of William and Mary, at western end of Sunken Gardens, above the Lily Pond; 30 June and 1 July 1960 (20.8° and 20.2° C, respectively), several specimens on watercress. (3) Stream in the College Woods, tributary of the outflow of Lily Pond, 18 July 1960, water clear, 18.6° C; one immature individual. (4) Spring and stream, tributary of Tutters Neck Pond, about 300 m SE of the spillway of the pond; 26 July 1960, 14.8° C, under stones and leaves mature and young individuals. (5) Stream E of Williamsburg golf course, 27 July 1960; water clear, 22.0° C; one mature specimen.

WEST VIRGINIA. Near BETHANY (Brooke County?) (• Hyman, 1937a: 305; Weimer et al., 1938: 159). GREENBRIER COUNTY: (1) The Hole Cave; 5 immature specimens collected 26 November 1966 by J. Rutherford, all eyeless; • 7 blind specimens, some of them mature, collected by Dr. J. R. Holsinger and others, 22 June 1968. HANCOCK COUNTY: (1) Tomlinson Run (Rose and Shostak, 1968: 554). JEFFERSON COUNTY: (1) • Outflow of experimental tanks, Leetown National Fish Hatchery, Leetown; 12 November 1967, water clear, 11.7° C, pH 7.8; under leaves many specimens, some mature. MONONGALIA COUNTY: (1) Falling Run at Morgantown (Weimer, 1918: 111). PENDLETON COUNTY: (1) • Seneca Creek, along S side of U.S. Road 33, 1.6 miles NW of Onego; 11 October 1969, water clear, fast, 14.3° C, pH 8.2; mature and young individuals.

At first glance, the distribution of *Phagocata gracilis* appears to be rather uneven, the District of Columbia and the state of Virginia showing a great preponderance in the number of habitats of the species. Actually, this unevenness reflects only a difference in the collecting activity in the distributional area. The species will, undoubtedly, be found in a number of additional states as well, such as in Maryland and in the still little-explored southern states.

ECOLOGY.—*Phagocata gracilis* is principally an inhabitant of springs and the upper reaches of creeks, more rarely of cool stagnant bodies of water (ponds and lakes). It is frequently met with in subterranean waters, in caves of Indiana, Missouri, Pennsylvania, Virginia, and West Virginia, where it may lose its dark pigmentation and appear almost white (*P. "subterranea"*). Physico-chemical analyses of its habitats have been presented by Abbott (1960), Stokeley et al. (1965), Chandler (1966), and Minshall (1968) for epigean and by Holsinger (1966) for hypogean populations of the species. Chandler found that its distribution in an Indiana locality is apparently not related to the chloride or magnesium content or to the specific conductance of the water, although calcium content and the nature of the substrate (presence of stones) may favor its occurrence. Ferguson and Jones (1949: 439) observed the species in brackish water in Willoughby Bay, Norfolk, Virginia. As *P. gracilis* is chiefly an inhabitant of springs, it is generally found in clean, unpolluted water. Nevertheless, it cannot be considered an indicator of water purity since it tolerates a considerable amount of organic pollution if other environmental factors are favorable. Holsinger (1966) reports that in Banners Corner Cave (Russell County, Virginia) *P. gracilis* (quoted as *P. subterranea*) is very abundant in pools heavily polluted with sewage from the overflow of septic tanks. It occurs there in the company of such notorious sewage organisms as *Tubifex tubifex* in water containing coliform bacteria.

The principal factor correlated with the distribution of *P. gracilis* is the temperature of the water, specifically the amplitude of its daily and seasonal fluctuations. Although the species may survive relatively high temperatures (25° C) for brief periods, it decidedly prefers low temperatures (0° to 9.5° C) when placed in a thermal gradient apparatus (Eddy and Gleim, 1932). In my own col-

lections, the species was taken in waters of a temperature range from 3.7° to 24.5° C, with an average of 15.3° C (38 measurements). It must be kept in mind, however, that most collections were made in the warmer months of the year and that during the cold season the temperature at some of the localities may be considerably lower. The preference for cold temperatures is also confirmed by the occasional occurrence in the same habitat of *Phagocata morgani*, known to be a cold-stenothermic species. Chandler (1966: 16) observed that *P. gracilis* occupied the headwaters of a stream, and downstream was gradually replaced by *Dugesia dorotocephala*.

Planarians are generally, though not exclusively, carnivores preying upon intact, injured, or dead invertebrates. Minshall (1967: 145) observed that in Morgan's Creek in Kentucky, *Gammarus* is the most important food item of *P. gracilis*. Holsinger (1966: 85) speculates that the preferred food of the species in Banners Corner Cave may be organic detritus, but does not exclude the possibility that living Metazoa such as isopods *(Asellus)*, aquatic oligochaetes *(Tubifex)*, and even small copepods, rotifers, etc., may serve as food. In the laboratory, the species takes readily dead tissues (beef liver) and living organisms *(Tubifex)*.

Little is known about the natural enemies of *P. gracilis*. Freshwater triclads are generally considered to be unpalatable to most predators. Holsinger (1966: 86) reported, however, that the spring salamander *(Gyrinophilus porphyriticus)* was observed to feed on the flatworm, and Minshall (1967: 145) stated that crayfish *(Cambarus)* and caddisfly larvae *(Rhyacophila)* ingest *P. gracilis*.

Phagocata woodworthi Hyman

FIGURES 1E, 4, 9

Planaria gracilis Girard, 1850a: 264 (not Haldeman).
Phagocata gracilis Girard, 1850b: 364, and other authors before 1937.
Euplanaria gracilis Hyman, 1931, in part.
Phagocata woodworthi, new species, Hyman 1937a: 305.
Phagocata gracilis woodworthi Hyman, 1951: 161.
Fonticola gracilis woodworthi Ball, 1969a: 60.

HISTORICAL NOTES.—*Phagocata woodworthi* has been for many years confused with *P. gracilis* which it resembles externally and with which it shares its polypharyngeal characteristic which, up to 1904, was a unique feature among freshwater triclads. The first extensive discussion of *P. woodworthi* was presented by Woodworth (1891) under the name of *P. gracilis*. It was only after Hyman (1937a) compared New England specimens with worms collected in Pennsylvania that the two species were separated and the new name *P. woodworthi* was introduced for the northeastern species. In a later paper, Hyman (1951) reduced *P. woodworthi* to a subspecies of *P. gracilis* on the basis of an alleged intermediary specimen from New Jersey.

EXTERNAL FEATURES (Figure 1E).—Adult individuals of *Phagocata woodworthi* generally are 15 to 20 mm long and 2 to 2.5 mm wide when the animals are quietly gliding. Woodworth (1891: 3) reports to have observed specimens measuring up to 30 mm in length and 4½ mm in breadth. The anterior end is truncate, the frontal margin assuming a straight, convex, slightly waved, or even concave shape when the animal is in motion. The lateral edges of the head are rounded, without lateral auricular projections. There is no distinct, at most a very shallow, narrowing or neck behind the head (in this regard *P. woodworthi* resembles the Virginia form of *P. gracilis* rather than that from the type locality in Pennsylvania). Behind the head region, the body gradually widens, soon reaches its greatest width, then the body margins run parallel up to the post-pharyngeal region where the body narrows again to form a bluntly pointed posterior end.

The color of the dorsal surface is dark gray or brown to almost black, that of the ventral surface somewhat lighter. The two eyes are situated at a distance from each other amounting to about one-third the width of the head at the level of the eyes. The distance of each eye from the frontal margin is greater than that from the lateral edge of the body.

As may be seen from this description, *P. woodworthi* cannot be distinguished from *P. gracilis* by its external appearance.

ANATOMY.—A good description of the anatomical features of *P. woodworthi* has been given by Woodworth (1891). Hyman (1937a: 306) has added to the analysis of the reproductive system and has corrected some of Woodworth's inaccurate inter-

pretations. As in *P. gracilis,* the numerous testes extend as a pair of broad bands from the level of the ovaries to the posterior end, their location being ventral and dorsal to the intestine and in the spaces between the intestinal branches, the ventral position predominating. The sperm ducts or vasa deferentia, which on either side of the pharyngeal chamber form the usual false seminal vesicles or spermiductal vesicles, proceed posteriorly to the level of the penial bulb, which they enter without having formed the backward loop characteristic of *P. gracilis.* Their entrance into the bulb is usually asymmetrical, anterodorsal for the left and anterolateral for the right sperm duct. Within the bulb they unite to a short common vas deferens which opens into the penial lumen (Figure 4, *pl*).

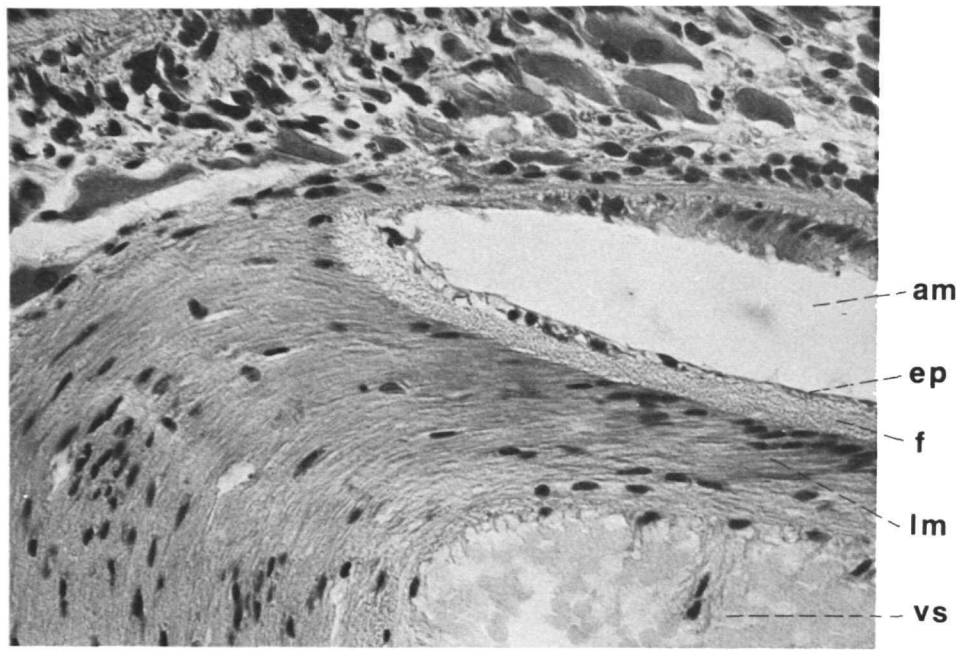
The penis consists of a rather feebly developed bulb and a stout, short, truncate or pluglike papilla. The muscle fibers of the bulb are, as is usual, arranged in concentric layers. The papilla is covered by a flattened epithelium, below which is a muscular layer (well described by Woodworth) consisting of alternating sheets of circular and longitudinal fibers (Figure 4, *pm*). Such an arrangement of the penial musculature is quite exceptional among the freshwater triclads and contrasts with the conditions obtaining in *P. gracilis,* as a comparison of Figures 8 and 9 demonstrates. The penial lumen (Figure 4, *pl*) is a rather wide tube of irregular outline which anteriorly receives the mouth of the common vas deferens and posteriorly opens into the atrium at the blunt end of the papilla. It is best interpreted as a combination of a seminal vesicle and an ejaculatory duct of other planarians. It has its own coat of circular muscle fibers. Between the outer and inner muscle layers of the papilla there are also radial and longitudinal fibers scattered through the parenchyma. Many gland ducts enter the penis bulb from the surrounding mesenchyme and traverse the tissues of the penis to open into the penial lumen. The lining of the lumen also consists of cuboidal or cylindrical glandular cells of an apocrine nature.

The female gonads and gonoducts conform with the general pattern observed in the genus *Phagocata:* a pair of ovaries, with parovaria of variable size and shape (depending on the maturity of the individuals), a pair of ovovitelline ducts or oviducts which unite above the posterior part of the male atrium after the right one has passed through the space between the atrium and the canal of the copulatory bursa, with many eosinophilic gland ducts opening into the posterior sections of the paired oviducts (*od*) and into the common oviduct (*odc*).

The copulatory bursa (*b*), Woodworth's "uterus," is a large sac lying between the pharyngeal pouch and the bulb of the penis. Its outlet or duct (*bd*) is very wide and is displaced from the midline to the right side of the male atrium. The greater part of the duct consists of an epithelial lining of tall, glandular cells surrounded by the usual two layers of muscle fibers, a circular and a longitudinal one. The posterior part of the duct, as it bends ventrally to approach the atrium near the gonopore, is equipped with a very thick muscular coat forming a sphincter consisting of several alternating layers of circular and longitudinal muscle fibers.

REPRODUCTION AND DEVELOPMENT.—I have kept several specimens of *P. woodworthi* in a laboratory culture (in spring water at 14° C) for over 12 months without observing either asexual reproduction or deposition of cocoons. In worms gathered in the field collections I have not seen any evidence of recent fission, such as regenerating anterior or posterior ends. Lillie (1901b: 134), who studied the regenerative abilities of the species, likewise states that it apparently does not reproduce by fission. Such statements as that by Girard (1850b: 364, and 1894: 171–172), that the supernumerary pharynges are young specimens formed by a process of budding, are, of course, obsolete as polypharyngy is not a reproductive process. According to Teal (1957: 293), the species at Concord, Massachusetts, reproduces throughout the year. In the laboratory, egg capsules are deposited in late winter (Buchanan, 1933: 186). So far we have no information on the cocoon and on the number and appearance of the young. Hyman's (1937a: 305) assumption that the young are monopharyngeal is probably erroneous.

GEOGRAPHIC DISTRIBUTION.—The distributional range of *P. woodworthi* is given by Hyman (1937a: 305) as comprising the New England states, New York and New Jersey, the southwestern boundary being the Delaware River. To this may be added the Canadian Maritime Provinces and the provinces of Quebec and Ontario. In the following compilation of the known habitats of the species, those



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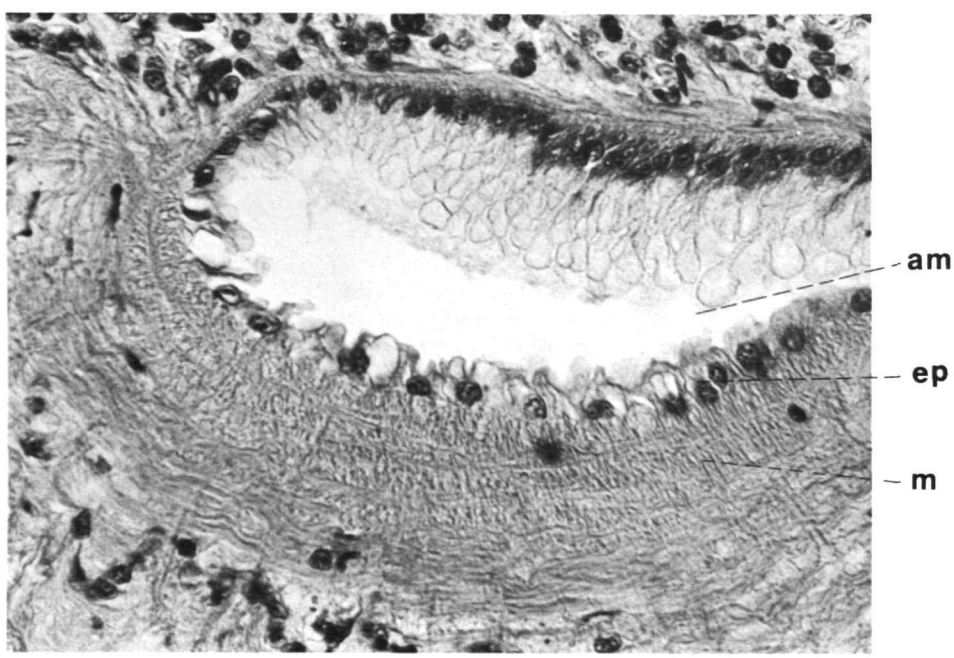

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records which are based on identifications made by examination of the anatomy are marked with asterisks (*).

CONNECTICUT. NEW HAVEN COUNTY: (1) New Haven (Buchanan, 1933: 186; * Hyman, 1937a: 299, 305).

MAINE. HANCOCK COUNTY: (1) Mount Desert Island (Blake, 1933: 128; Hyman, 1938: 25). (2) Swan's Island (* Hyman, 1931: 327; 1937a: 299, 305). (3) * Powerhouse Brook near Orland, at entrance of road to Craig Brook National Fish Hatchery, 1.4 miles E of the hatchery, in a dammed-up pond above the bridge on the road; 28 August 1968, water temperature 21.3° C, 7 specimens under stones and pieces of wood (besides these, *Dugesia tigrina*). PENOBSCOT COUNTY: (1) * Stillwater River (side arm of Penobscot River), below the dam at Stillwater; 28 August 1968, moderate current, 20.8° C, several specimens (some mature) collected under stones (besides *Procotyla fluviatilis*).

MASSACHUSETTS. Near BOSTON and CAMBRIDGE (Middlesex or Suffolk Counties?) (Girard, 1850a: 264; 1850b: 364; 1894: 171; * Hyman, 1937a: 305). Near SOMERVILLE (Middlesex County?) (* Woodworth, 1891: 1). BARNSTABLE COUNTY: (1) Falmouth (Lillie, 1901a: 1026; T. H. Morgan, 1904: 159; L. V. Morgan, 1906: 270; Walter, 1907: 46; Wilhelmi, 1908: 392; 1909: 6; Šivickis, 1931: 438). (2) Woods Hole (T. H. Morgan, 1900: 58; Wilhelmi, 1908: 392; 1909: 6; Child, 1913: 134). BRISTOL COUNTY: (1) Seekonk (Castle, 1941: 88). ESSEX COUNTY: (1) * Ipswich River at B. W. Palmer State Park, January 1970, 2 mature specimens collected by Dr. R. A. Raff. MIDDLESEX COUNTY: (1) Spring in Concord, together with *Phagocata morgani* (Teal, 1957: 285).

NEW JERSEY. Near PRINCETON (Mercer County?) (* Hyman, 1937a: 299, 305).

NEW YORK. Near YONKERS (Westchester County?), in a spring-fed stream (* Hyman, 1937a: 299, 305).

NEW BRUNSWICK. "New Brunswick" (Ball, 1969a: 60, and personal communication).

NEWFOUNDLAND. "Newfoundland" (* Ball, personal communication). Port-aux-Basques and Table Mountains (Luther, 1952: 79).

NOVA SCOTIA. "Nova Scotia" (Ball, personal communication).

ONTARIO. St. Lawrence River (* Ball, 1969b: 224, and personal communication).

QUEBEC. Anticosti Island (Ball and Fernando, 1970:333).

ECOLOGY.—Little is known about the ecological requirements of *P. woodworthi*. It is generally taken in ponds and rivers, more rarely in cold streams and springs. The fact that it often shares its habitat with such eurythermic species as *Dugesia tigrina* (Girard) and *Procotyla fluviatilis* Leidy suggests that it tolerates greater temperature fluctuations than does *P. gracilis*. Some physical and chemical characteristics of a spring containing *P. woodworthi* have been studied by Teal (1957). Wilhelmi (1909: 2 and 368) found the species in several ponds with brackish water in the vicinity of Falmouth, Massachusetts.

TAXONOMIC POSITION.—Hyman (1937: 306), in her description of *Phagocata woodworthi*, states that the species differs from *P. gracilis* in many details of the reproductive system. She mentions specifically the presence of a large parovarium; the fact that the vasa deferentia unite within the penis bulb forming an ejaculatory duct which in the distal part of the penis enlarges into a broader tube that she interprets as presumably representing the seminal vesicle; the truncate, pluglike shape of the short penis papilla which has a thick layer of muscle fibers under the surface epithelium; and the extraordinarily wide bursa stalk which in its posterior part is provided with a thick muscular sphincter.

Most of these characters are clearly recognizable and are not dependent on the state of contraction of muscular organs or the phase of the development of the various structures of the reproductive system. Only the size of the parovaria is not tenable as a distinguishing feature, since it is variable and depends to a great extent on the state of sexual maturity. The term "parovaria" was introduced by Woodworth (1891: 33) for the "two prominent compact cell masses with deeply stained nuclei" which adjoin the ovaries anteriorly, dorsally, and laterally. Woodworth considers them to be the organs which give rise to the yolk glands. A detailed discussion of the parovaria of the triclads and of their relation to the ovaries and yolk glands has been given by Graff (1912–1917: 2995–3000). Such parovaria occur also in *P. gracilis* and are quite conspicuous and voluminous in specimens that are in that phase of maturity in which the yolk glands or vitellaria are well developed.

The course of the vasa deferentia in *P. woodworthi* differs from the conditions obtaining in *P. gracilis*. The false seminal vesicles (or spermiductal

FIGURES 8 and 9.—Photomicrographs of base of penis papilla: 8, *Phagocata gracilis* (see area marked *x* in Figure 3), specimen from Pine Hills, Union County, Illinois. 404/1. 9, *P. woodworthi* (see area marked *y* in Figure 4), specimen from Orland, Maine. 404/1. *am*, male atrium; *ep*, epithelium of penis papilla; *f*, fibrous layer; *lm*, longitudinal muscles; *m*, muscle layer consisting of circular and longitudinal fibers; *vs*, seminal vesicle.

vesicles) running posteriorly along the sides of the pharyngeal pouch bend inward and dorsally as soon as they reach the level of the penis bulb and enter the bulb, generally asymmetrically; in *P. gracilis,* each spermiductal vesicle first bypasses the penis bulb, proceeding posteriorly to the level of the male atrium, then abruptly turns forward again to penetrate the penis from the ventrolateral side, thus making a characteristic backward loop. Within the bulb the vasa deferentia in *P. woodworthi* unite, forming a common vas deferens which opens into the wide penis lumen that shows no histological differentiation into seminal vesicle and ejaculatory duct; in *P. gracilis* the two vasa deferentia, separately or united, open into a small cavity which connects with the wide and highly glandular seminal vesicle; this tapers posteriorly forming a narrower canal, with often irregular diameter, the ejaculatory duct.

The shape of the penis papilla, short and truncate in *P. woodworthi* and long and pointed in *P. gracilis,* is generally sufficient to separate the two species. In view of the great pliability of this organ and its variable aspect in preserved specimens, histological differences are more valid in the ultimate identification. *P. woodworthi* has a thick layer of intermingled circular and longitudinal muscles below the surface epithelium of the papilla, while in *P. gracilis* the layer adjoining the epithelium is a fibrous layer to which longitudinal muscle fibers attach.

The stalk of the copulatory bursa of *P. woodworthi* is very wide, displaced to the right of the midline, and equipped with a terminal sphincter, consisting of alternating circular and longitudinal muscle layers; in *P. gracilis* the bursal canal is narrower and has no terminal sphincter, and its muscle coat consists of a circular and a longitudinal layer throughout its length.

Thus, the characteristic features of the anatomy of the copulatory complex of *P. woodworthi* may be summed up as follows: (1) lack of a backward loop of the vas deferens before entering the penis bulb; (2) common vas deferens entering the seminal vesicle directly, without opening first into a separate small cavity; (3) outer wall of the short penis papilla with a thick layer of intermingled circular and longitudinal muscles, lacking a fibrous layer; and (4) wide bursal stalk with terminal sphincter consisting of circular and longitudinal muscles arranged in several alternating layers.

Conclusion

In summary, there are at present two distinct polypharyngeal species of *Phagocata* known from North America: *P. gracilis* (Haldeman) (which also includes *P. subterranea* Hyman) and *P. woodworthi* Hyman. A discussion of the taxonomic position of a monopharyngeal form described by Hyman (1945: 475) as *P. gracilis monopharyngea* from Haskins (about 8 miles northeast of Washington, Washington County), Iowa, and its relation to *P. gracilis* must await further investigation.

The characteristics enumerated justify a clear specific separation of *P. woodworthi* from *P. gracilis,* as Hyman (1937a) had originally proposed. In a later paper (1945: 476) she reduced *P. woodworthi* to a subspecies of *P. gracilis* on the basis of having found a transitional form in material from New Jersey (". . . one of the Princeton specimens has a penis-papilla which is somewhat intermediate in shape between the two species" [Hyman, 1937a: 306]). If this atypical character concerns only the shape of the penis papilla of one specimen, it may not even represent a transitional feature but simply a transitory phase of muscular contraction of the penis, which should not be given much weight in the absence of differences in the other specific characteristics separating the two species. Through the courtesy of the American Museum of Natural History I had the opportunity of examining the problematic Princeton specimen in the slide collection of the late Dr. Hyman. The shape of the penis proved to be conical, though rather short, with the penis lumen opening into the atrium ventrally to the tip of the papilla. All other distinguishing features clearly identified the specimen as *P. woodworthi:* intermingled circular and longitudinal fibers in the muscle coat of the papilla and in the sphincter of the bursa duct, lack of the backward loops of the sperm ducts, and extraordinarily wide bursal canal displaced from the midline. Another set of sections, apparently of an individual of the same Princeton population, conformed with *P. woodworthi* in all relevant characteristics.

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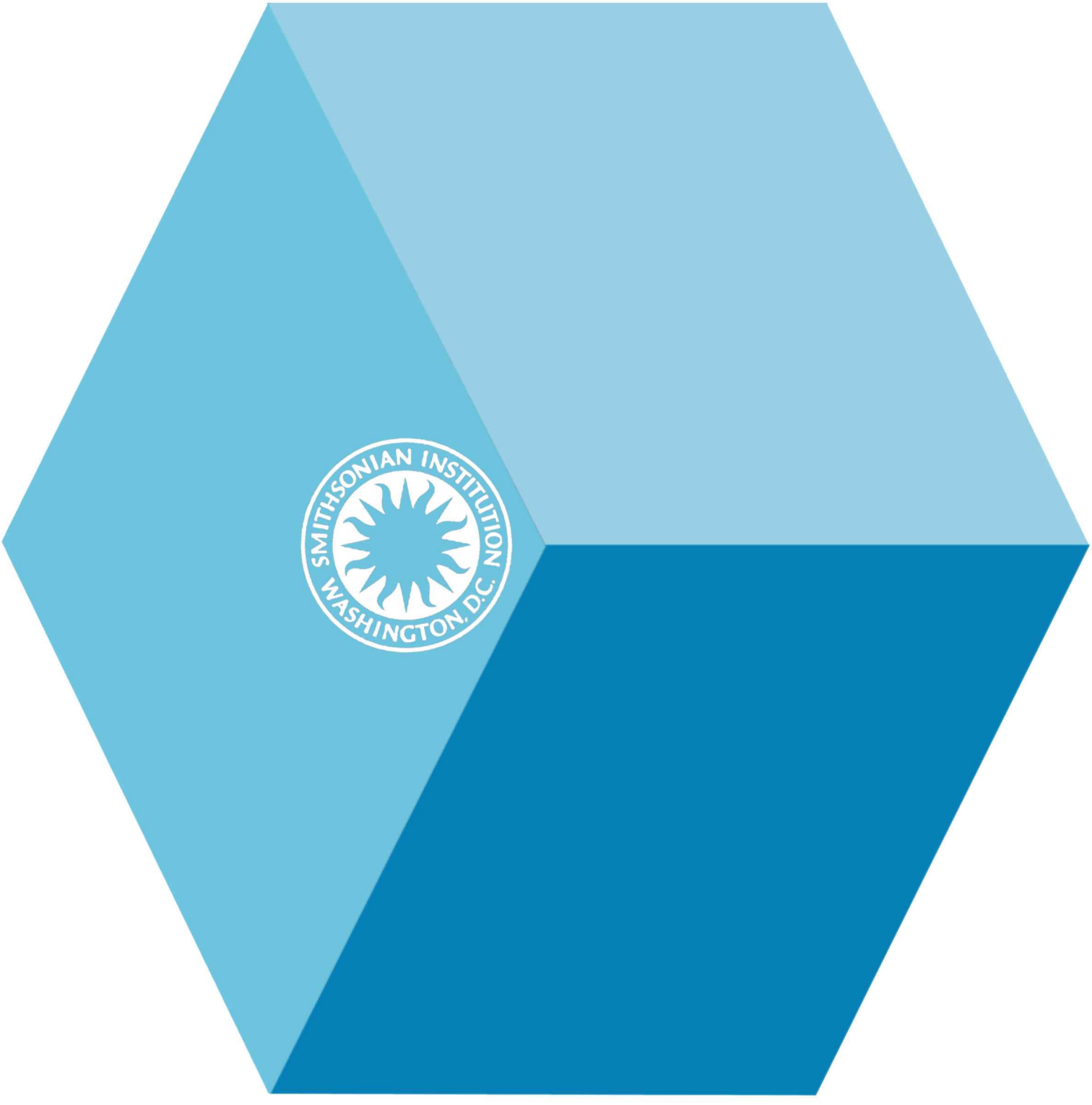
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