Freshwater Triclads (Turbellaria) of North America, IX: The Genus *Sphalloplana*

ROMAN KENK

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 246

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 246

Freshwater Triclads (Turbellaria) of North America, IX: The Genus *Sphalloplana*

Roman Kenk

SMITHSONIAN INSTITUTION PRESS
City of Washington
1977

ABSTRACT

Kenk, Roman. Freshwater Triclads (Turbellaria) of North America, IX: The Genus *Sphalloplana*. *Smithsonian Contributions to Zoology*, number 246, 38 pages, 62 figures, 1 table.—A revision of the North American species of the genus *Sphalloplana* is presented. Apart from the nine species already known (*S. percoeca, S. georgiana, S. kansensis, S. virginiana, S. weingartneri, S. buchanani, S. pricei, S. hubrichti,* and *S. mohri*), seven new species are introduced and described: *S. evaginata, S. californica, S. culveri, S. consimilis, S. subtilis, S. holsingeri,* and *S. chandleri.*

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Kenk, Roman, 1898–
Freshwater triclads (Turbellaria) of North America, IX, the genus Sphalloplana.
(Smithsonian contributions to zoology ; no. 246)
Bibliography: p.
1. Sphalloplana. 2. Platyhelminthes—North America. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 246.
QL1.S54 no. 246 [QL391.P7] 591'.08s [595'.123] 76-44832

Contents

Freshwater Triclads (Turbellaria) of North America, IX: The Genus *Sphalloplana*

Roman Kenk

Introduction

The genus *Sphalloplana* was established by Beauchamp (1931:321) for a white, blind planarian from Mammoth Cave in Kentucky, reported earlier by Packard (1879:142) from the same locality under the name of *Dendrocoelum percoecum,* new species. Beauchamp stressed the fact that the species has the external appearance of a dendrocoelid, particularly by the undulated body margins of the preserved specimens. Anatomically, however, it could not be placed in the family Dendrocoelidae, as its internal pharyngeal musculature consisted of two distinct layers, an inner circular and an outer longitudinal one, while in the dendrocoelids it is composed of one layer of intermingled circular and longitudinal muscle fibers.

Additional species of *Sphalloplana* were described by Hyman in several papers, all collected in caves or springs and placed into a new family, Kenkiidae. Hyman (1937:473) also introduced a related genus, *Speophila,* which differed from *Sphalloplana* by having a more highly developed adhesive organ. In a later paper, however, she (1945:481) stated that "it is probable that all gradations in the development of the adhesive organ exist among the Kenkiidae, and hence that eventually it will be impossible to draw any definite line between the two genera. I therefore anticipate that when our cavernicolous planarians are sufficiently known, *Speophila* will become a synonym of *Sphalloplana.*" This union of the two genera was finally proposed by Mitchell (1968:614–615) and has been accepted by Kawakatsu (1969:76), Carpenter (1970), and myself (1972:13).

The genus *Sphalloplana* may be defined as Kenkiidae, in which the internal pharyngeal muscle zone consists of two layers arranged as in the Planariidae, an internal layer of circular fibers surrounded by a layer of longitudinal muscles. In the other two genera of the family, the outer zone of the internal pharyngeal muscles has an intermingled network of longitudinal and circular fibers. This is known for the genus *Macrocotyla* (Kenk, 1975:326). Kawakatsu, who had an opportunity of examining *Kenkia rhynchida* Hyman from its type-locality, informed me (pers. comm.) that *Kenkia* has the same muscular condition as *Macrocotyla.*

Sphalloplana may be divided into subgenera as proposed by Carpenter (1971:1284): subgenus *Sphalloplana* (type-species, *Dendrocoelum percoecum* Packard) with weak adhesive organ, and subgenus *Speophila* (type-species, *Speophila pricei* Hyman) with highly differentiated, deeply invaginated adhesive organ (with some gradations between the two subgenera). The third subgenus proposed by Carpenter, *Polypharyngea* (type-species, *Sphalloplana mohri* Hyman), based on the presence of many pharynges, is of doubtful value, since polypharyngy occurs in other genera (*Phagocata, Crenobia*) as a specific or even subspecific charac-

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

teristic. Therefore I place *S. mohri* in the subgenus *Speophila.*

Concerning the distinguishing characteristics of the species of *Sphalloplana,* Carpenter (1970) assumes that they are subject to great variation. Nevertheless, in worms preserved by a proper technique there is a great uniformity in the characters of specimens from the same locality, with only little variability. Kenkiid planarians are rather difficult to preserve. The usual methods of relaxation (by anesthetics) or extension (e.g., with diluted nitric acid), which are appropriate for many planariids, frequently result in great distortions of the internal muscular organs (pharynx, penis, etc.). The same is true for Carpenter's (1969) rapid freeze technique that, however, preserves the external shape of the animals beautifully (see also Kawakatsu and Miyazaki, 1972:87–88, and the photographs in Carpenter, 1970).

I have obtained the best and most uniform results by instantaneous killing of the worms with a hot fixative. A worm is placed in a small dish with only a few drops of water. When it is well extended, a hot (almost boiling) fixative is rapidly poured over it. I use as fixative a saturated (about 7%) solution of corrosive sublimate ($HgCl_2$) in water or physiological saline solution. After killing, the fixative is acidulated with a few drops of diluted acetic acid. After several hours, the specimen is washed in water for one hour, then transferred to increasing concentrations of ethyl alcohol. The last traces of the sublimate are removed by adding small quantities of tincture of iodine to the alcohol.

The characters used for the differentiation of the species of *Sphalloplana* are both external and anatomical ones. Externally, the shape of the anterior end is very characteristic, some species bearing anterolateral auricular projections, others no auricles. The anterior border of the intestinal area is either rounded or shows anterior extensions along both sides, with a median recess, producing the shape of the letter V, as is seen in some of the species with well-developed adhesive organ. Anatomically, the location of the essentially prepharyngeal testes, whether dorsal, ventral, or both, is important. In the copulatory apparatus, the shape of the penis, the proportional size between the penis bulb and penis papilla, the shape and histology of the penial lumen, and the location of the mouth of the ejaculatory duct are to be noted. The vasa deferentia in some species enter the penis bulb anteroventrally or laterally, in others they curve upward and enter the bulb posterodorsally. The presence or absence of a distinct vagina on the bursal duct and the location of the mouth of the common oviduct are other distinguishing features. Some species show a characteristic distribution of infranucleate epithelia in the copulatory complex.

The present report deals chiefly with those species of *Sphalloplana* that I have been able to obtain alive. There are, in all, 19 species of the genus reported in the literature, of which 15 occur in the United States, two in Japan, and one each in South Korea and Siberia. Five of the North American species are considered to be identical and one, *S. hoffmasteri* (Hyman), has been transferred to the genus *Macrocotyla* (Kenk, 1975:333). The Siberian species, *S. ductosacculata* Livanov and Zabusova (1940), has the testicular zone extending to the posterior end and may not belong to this genus. One of the two undescribed Japanese species, *S.* sp. from the Yatsu-gadake Mountains (Ichikawa and Kawakatsu, 1967:512), is a two-eyed, darkly pigmented planarian and has not been studied anatomically. In addition to the valid nine species of *Sphalloplana* of the United States, seven new species are described in the present paper.

A comparison of the American cavernicolous triclad fauna with that of Europe is very interesting from the zoogeographical standpoint. The American Kenkiidae, split into many closely related species, occupy the same ecological niches as do the numerous subterranean species of *Dendrocoelum* and related genera in Europe (see particularly Beauchamp, 1932, and Gourbault, 1972). The differentiation of both faunas apparently is of relatively recent geological origin. There is no kenkiid known to occur in Europe and no *Dendrocoelum* in the Americas.

ACKNOWLEDGMENTS.—My study of the genus *Sphalloplana* would not have been possible without the generous aid of many collaborators, particularly speleologists who kindly provided me with materials from various caves. I wish to express to them my deep appreciation of their valuable cooperation. It would be difficult to list all persons who have sent me specimens. They are mentioned under the collection data for the individual species. I may name here only the most outstanding contrib-

utors: Dr. John R. Holsinger (Old Dominion University), Mr. Jerry Lewis (Southern Illinois University), Dr. Russell M. Norton (Yale University), Mr. Arnold Norden, and Mr. William W. Torode. Dr. John C. Harshbarger (Smithsonian Institution) kindly permitted me the use of his laboratory facilities for the preparation of photographic illustrations. Thanks are due to the American Museum of Natural History, which kindly lent me some of L. H. Hyman's slides for examination. I also wish to express my gratitude to various publishers who permitted me to reproduce some, in part copyrighted, figures from their publications: McGraw-Hill Book Company, American Microscopical Society, Biological Society of Washington, and the publishers of American Midland Naturalist.

The location of the type materials of the individual species is indicated by the following abbreviations: AMNH for American Museum of Natural History, New York; and USNM (former United States National Museum), for materials in National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Sphalloplana (Sphalloplana) percoeca (Packard, 1879)

FIGURES 1, 11, 30, 45

Dendrocoelum percoecum Packard, 1879:141.
Fonticola percoecum.—Hyman, 1931:328.
Sphalloplana percaeca.—Beauchamp, 1931:321.
Dendrocoelum percaecum.—Giovannoli, 1933:622.
Sphalloplana percaeca.—Castle and Hyman, 1934:156.
Fonticola percaeca.—Hyman, 1935:345.
Sphalloplana percoeca.—Hyman, 1937:469.
Sphalloplana (Sphalloplana) percoeca.—Carpenter, 1971:1284.
Sphalloplana alabamensis Hyman, 1945:476.

TYPE MATERIAL.—Packard's original material apparently is not preserved. Hyman's syntypes of *S. alabamensis,* one whole mount and two slides of sagittal sections (USNM 20639).

HISTORY.—The early history of the discovery and description of the species has been reviewed by Buchanan (1936:194). It was first depicted by Packard (1879:141) in a small, rather primitive illustration that was also reproduced in later publications of the same author (1880:141 and later editions of his *Zoology;* 1888:28). Illustrations of preserved specimens were furnished by Beauchamp (1931:322) and drawings and photographs of living animals by Buchanan (1936:196) and Carpenter (1970, fig. 11). Descriptions of the species were given by Packard (1888:28), Beauchamp (1931), Buchanan (1936:195–196), Hyman (1937:470–471), and Carpenter (1970:69–75). Hyman's description of *S. alabamensis* is based on badly preserved materials and contains several inaccuracies. In the following, only the essential characters of the species will be discussed.

EXTERNAL FEATURES (Figures 1, 11).—*Sphalloplana percoeca* is a purely white species, without any pigmentation. Mature animals generally are about 10–12 mm long and about 2 mm wide, but may reach a length of 16 mm. The anterior end has a bulging frontal margin and conspicuous rounded auricles projecting anterolaterally. The situation of the adhesive organ is seen as an opaque spot behind the center of the frontal margin. Behind the auricles, the lateral margins of the body narrow to some extent, then widen again. Characteristic is the outline of the anterior border of the intestinal area that is rounded and not forming the two lateral extensions seen in some species with more highly developed adhesive organs.

ANATOMY.—The adhesive organ (Figure 30) is a shallow subterminal pit lined with an infranucleate epithelium that is pierced by many eosinophilic gland ducts and equipped with a system of muscle fibers (see Beauchamp, 1931:323–325; Hyman, 1937:470).

In the reproductive system, examined by me in four sets of sagittal serial sections, the ovaries are situated at the level of the second or third lateral branch of the anterior intestinal ramus. The testes, in moderate number, are dorsal and prepharyngeal, occupying on either side a longitudinal zone. The copulatory complex (Figure 45) has been described and illustrated by Beauchamp (1931, fig. 8) and Hyman (1937, fig. 13), but needs further analysis. The genital atrium is divided distinctly into an anterior male atrium (*am*) surrounding the penis papilla and a posterior chamber that appears to be a combination of the common atrium (*ac*) and the expanded terminal part of the bursal duct or vagina (*v*). The penis has a rather small bulb (*bp*) with weak musculature and a large, generally rounded, plug-shaped papilla (*pp*). This corresponds to the penis shape illustrated by Beauchamp (1931, fig. 8) rather than to Hyman's (1937, fig. 13) diagram of the copulatory apparatus.

The papilla is covered with a cuboidal epithelium with an underlying coat of muscle fibers, circular ones adjoining the epithelium and longitudinal ones below them. The bulb contains a small cavity, the seminal vesicle (*vs*), of rounded shape in a medial section, but extending laterally to both sides. From this cavity originates a duct (*de*) passing into the papilla, rather narrow in its anterior part and of variable diameter posteriorly, sometimes widening in a funnel-like fashion, and opening at the tip of the papilla. This lumen apparently corresponds to an ejaculatory duct. It is surrounded by a muscle layer consisting chiefly of longitudinal fibers. The sperm ducts or vasa deferentia (*vd*) approach the sides of the penis bulb, enter the bulb laterally, and open into the lateral extensions of the seminal vesicle. Eosinophilic gland ducts enter the penis bulb from the surrounding mesenchyme, traverse the penis, and open on the outer surface of the papilla. The two oviducts unite above the male atrium and the common oviduct (*odc*) thus formed opens into the dorsal roof of the male atrium, far removed from the gonopore (*gp*). The copulatory bursa (*b*) is a sac of variable shape located between the posterior wall of the pharyngeal chamber and the penial bulb. Its outlet, the bursal duct (*bd*), starts as a rather narrow, straight canal running posteriorly above the penis and male atrium to a level behind the gonopore. There it turns ventrally and expands into a voluminous cavity, the vagina (*v*), which is in wide connection with the cavity of the common genital atrium (*ac*). The vagina has a thick muscle coat of intermingled circular and longitudinal fibers. It was not possible to analyze the musculature of the anterior, thin part of the bursal duct.

All epithelia of the copulatory apparatus are nucleate except, perhaps, the lining of the male atrium, which appears to be, at least in part, infranucleate in some of the specimens studied.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana percoeca* is a troglobitic species and appears to be widely distributed in the states of Kentucky, Tennessee, and Alabama, possibly extending also into West Virginia and Georgia. Localities that need verification are preceded by a question mark (?) in the following list.

ALABAMA. JACKSON COUNTY: (1) Dinky Pit, Alabama Cave Survey No. 756 (Carpenter, 1970:71). (2) Fern Cave, Survey No. 597, located just above the town of Paint Rock; about 25 specimens collected by William W. Torode, many mature, 14 December 1975. (3) Graham Pit, Survey No. 943 (Carpenter, 1970:71). (4) "Old Saltee Cave" (= Sauta Cave), Survey No. 50, near town of Lim Rock, type-locality of *S. alabamensis* (Hyman, 1945:477; Carpenter, 1970:71; Holsinger, 1966:85). (5) Williams Saltpeter Cave, Survey No. 590, located about 20 miles east of Huntsville; 30 specimens collected by W. W. Torode, some mature, 27 October 1975.

KENTUCKY. CALDWELL COUNTY: (1) ?Lisanby Cave (Carpenter, 1970:69). CARTER COUNTY: (1) ?Cascade Cave (Dearolf, 1953:226). EDMONSON COUNTY: (1) ?Diamond Cave (Packard, 1888:28). (2) ?Ganter Cave (Dearolf, 1953:226). (3) Great Onyx Cave (Carpenter, 1970:71); specimens kindly sent to me by J. H. Carpenter in February 1971. (4) Mammoth Cave, type-locality of *Dendrocoelum percoecum*, in Shaler's Brook, Gothic Avenue, Richardson's Spring, Annette's Dome, Audubon Avenue, and Rafinesque Hall (Packard, 1888:28; Bolivar and Jeannel, 1931:308; Beauchamp, 1931: 317; Giovannoli, 1933:622; Buchanan, 1936:194; Barr, 1968: 155); one specimen collected by the writer in Annette's Dome, August 1933. (5) ?White Cave (Dearolf, 1953:226; Carpenter, 1970:71; Barr and Kuehne, 1971:71). ESTILL COUNTY: (1) Pearson Cave (Carpenter, 1970:71). HART COUNTY: (1) ?Mammoth Onyx Cave (Dearolf, 1953:226). JACKSON COUNTY: (1) Clemons Cave, (2) John Rogers Cave, (3) Morning Hole Cave, and (4) Wind Cave (Carpenter, 1970:71). WAYNE COUNTY: (1) Jesse Cave (Carpenter, 1970:71).

TENNESSEE (all records need verification). CAMPBELL COUNTY: (1) Meredith Cave (Barr, 1961:31). DAVIDSON COUNTY: (1) Mill Creek Cave (McRitchie, 1959:31). PUTNAM COUNTY: (1) Harve Petty Cave (Barr, 1961:31). RUTHERFORD COUNTY: (1) Herring Cave (McRitchie, 1959:31). VAN BUREN COUNTY: (1) Creeping Cave (Barr, 1961:31). WHITE COUNTY: Indian Cave (Carpenter, 1970:71).

WEST VIRGINIA. PENDELTON COUNTY: (1) ?Blowhole Cave (Carpenter, 1970:69).

Sphalloplana georgiana, a problematic species, may also be identical with *S. percoeca*. The localities of that species are listed under *S. georgiana*.

Some ecological data for *S. percoeca* were presented by Buchanan (1936): The temperature of the waters in Mammoth Cave was in the range of 12°C to 14°C, the pH, 7.6. Holsinger (1966:85) observed a large population of *"S. alabamensis"* in Sauta Cave in a rimstone pool where large amounts of decaying wood had accumulated; he speculated that the flatworms may be able to feed on particulate organic matter or on smaller organisms that inhabit such pools or on both types of food. Barr (1968:155) and Barr and Duehne (1971:71) reported that the species in White Cave occurred in temporary rimstone pools soon after the pools filled with water dripping from stalactites or trickling down and concluded that they had survived in the silts of the dried pools by encysting in the layers of the hygroscopic deposits at the bottom of the

pools. A similar survival of cave planarians had been reported by Ginet and Puglisi (1964) for *Phagocata notadena* (Beauchamp) and by Gourbault (1965:477) for *Dendrocoelopsis chattoni* (Beauchamp) in two caves in France. The same mode of survival during the desiccation of the habitat is known also for some epigean planarians (see, for example, Lascombe, 1971:31–32). Carpenter (1970 and 1973) reported that cocoons of *S. percoeca* were found in the caves in spring and summer and hatched in the laboratory at 13°C in about three months, each cocoon yielding 2–17 young.

PHYSIOLOGICAL STUDIES.—Buchanan (1935 and 1936) studied the behavior of the species in the cave and the laboratory, its locomotion, reactions to light, tolerance of acidity and alkalinity (pH 6.6 to 8.0) and of temperature (it may tolerate 24°C for hours), and its limited regenerative ability. Wells and Harris (1954) reported briefly on its sensitivity to ultraviolet irradiation.

TAXONOMIC POSITION.—The weakly developed adhesive organ places *S. percoeca* in the subgenus *Sphalloplana* of which it is the type-species. Other specific characteristics are the presence of conspicuous auricles, the rounded anterior border of the intestinal area, the dorsal position of the testes, the shape of the penis (with small bulb and large, plug-shaped papilla), the lateral entry of the vasa deferentia, the opening of the penis lumen on the tip of the papilla, the confluence of the common genital atrium and the vagina of the bursal duct, and the location of the mouth of the common oviduct, far removed from the genital aperture. From the externally similar *S. consimilis* it differs by its penial structure, from *S. evaginata* by the absence of diverticula on the common genital atrium, and from *S. holsingeri* by the dorsal position of the testes and the anatomy of the copulatory complex.

Sphalloplana (Sphalloplana) georgiana Hyman, 1954

FIGURE 46

Sphalloplana georgiana Hyman, 1954:566.
Sphalloplana (Sphalloplana) georgiana.—Carpenter, 1971:1284.

TYPE MATERIAL.—Holotype, one whole mount (USNM 24614). Paratypes, one whole mount of anterior part of the body (USNM 24614) and four sets of sections on 16 slides (AMNH 705).

The species is known for certain only from the type-locality and Hyman's (1954:566–570) description.

EXTERNAL CHARACTERS.—A blind, white species, rather slender, with truncate anterior end bearing a central adhesive organ. Size of preserved specimen, about 8 mm long.

ANATOMY.—Hyman states that the four specimens studied were in a very bad histological condition. The small adhesive organ is rather simple, forming a cuplike depression with eosinophilic glands and attached retractor muscles.

The testes are small, arranged on either side in a rather short band anterior to the pharynx. Hyman indicates that they are ventral; however, they seem to me to be in a dorsal position if I interpret Hyman's paratype slides correctly. In the copulatory organs (Figure 46), the penis has a rounded, muscular bulb (*bp*) and a conical papilla covered with a tall epithelium. The two sperm ducts (*vd*) enter the bulb anterolaterally and open separately into the sides of the rounded bulbar cavity (seminal vesicle, *vs*), from which an ejaculatory duct (*de*) proceeds to open at the tip of the papilla. The common oviduct (*odc*), surrounded by esosinophilic shell glands, opens into the roof of the male atrium, far removed from the gonopore (*gp*). The copulatory bursa was not observed. The bursal duct (*bd*) runs as a slender canal dorsally to the male atrium to behind the level of the gonopore, then curves downward and anteroventrally and expands into a large vagina (*v*) with thick walls, which is not separated from the common genital atrium.

DISTRIBUTION AND ECOLOGY.—The type-locality of *S. georgiana* is Howard's Waterfall Cave, Dade County, Georgia, where it was collected by C. E. Mohr on 8 December 1950. J. H. Carpenter (1970: 76) visited this locality again in 1969 and collected two sickly, immature specimens that could not be used for closer examination, but appeared externally identical with *S. percoeca*.

Dr. J. R. Holsinger transmitted to me planarians from two caves located in Dade County near the type-locality of *S. georgiana:* Byers Cave (1.5 miles southwest of Rising Fawn) and Johnson Crook Cave (near Rising Fawn), collected on 18 and 19 June 1967 by J. R. Holsinger, S. Peck, A. Fiske, and R. Barody (see Holsinger and Peck, 1971:28). Unfortunately, the specimens were not properly preserved. Their recognizable anatomical charac-

ters (weak adhesive organ, predominantly dorsal testes, far dorsal entry of the common oviduct, general configuration of the penis and bursal duct) are identical with the features observed in *S. percoeca.*

TAXONOMIC POSITION.—Because of the bad condition of the type specimens, the exact position of the species cannot be determined. All characters of the copulatory apparatus are compatible with *S. percoeca* (which occurs also in the neighboring state of Alabama). The only essential difference appears to be in the location of the testes, which in *S. percoeca* are dorsal and in *S. georgiana,* according to Hyman's description, ventral. Hyman's statement, however, is probably erroneous. The identity of the two species has already been suspected by Carpenter (1970:77).

Sphalloplana (Sphalloplana) evaginata, new species

FIGURES 2, 12, 20, 31, 47

TYPE MATERIAL.—Holotype, series of sagittal sections of anterior region (6 slides) and of posterior region (12 slides), USNM 53427. Paratypes, three sets of sagittal and transverse sections on 41 slides, USNM 53428–53430; one whole mount, USNM 53431.

EXTERNAL FEATURES (Figures 2, 12).—*Sphalloplana evaginata* is a blind, rather large and plump species, measuring up to 30 mm in length and 6 mm in width when fully extended. The truncate anterior end has a convex frontal margin and bears a pair of rather prominent rounded auricular lobes protruding anterolaterally. Behind the head is an insignificant narrowing or neck, then the lateral body margins diverge, run parallel up to the level of the mouth, then narrow again in the postpharyngeal region. The tail end is bluntly pointed. The root of the pharynx lies at about the middle of the body and its length amounts to one-sixth the body length. The copulatory complex is situated in the anterior half of the postpharyngeal region. The intestinal system ends anteriorly in an arc (Figure 20) without forming the V-shaped extension of the lateral branches which is characteristic of some species of the subgenus *Speophila.*

The color of the living specimens is a light pink, due to a diffuse nongranular pigment permeating the subepidermal tissues. This pigment is not evenly distributed but is more concentrated in the head, the pharynx, the copulatory organs, and in a pair of longitudinal bands along both sides of the midline in the posterior two-thirds of the prepharyngeal region (corresponding to the site of the testes). A similar pinkish tint of the body is seen in *Macrocotyla glandulosa* Hyman, which, however, shows the denser organs (adhesive organ, pharynx, and copulatory apparatus) in a lighter hue than the general body coloration.

The movements of the worm are rather sluggish. Upon mechanical stimulation, the adhesive organ may be protruded temporarily as a pointed, conical projection in the center of the frontal margin.

ANATOMY.—The marginal zone with tall epidermal cells and long rhabdites is developed typically. The adhesive organ (Figure 31) appears in the slides as a subterminal shallow depression in the middle of the frontal margin. The central part of the organ may be invaginated, but not as deeply as is seen in representatives of the subgenus *Speophila.* The epidermis lining the depression is infranucleate, free of rhabdites, and pierced by numerous gland ducts containing a granular eosinophilic secretion. The glands forming this secretion are located in the mesenchyme some distance behind the organ. A network of muscle fibers is attached to the epithelium, functioning as retractors. The anatomy of the pharynx shows no peculiarities.

The two ovaries are situated behind or below the first to third lateral branches of the anterior intestinal ramus. In fully mature animals the zone of yolk glands or vitellaria begins a certain distance anterior to the ovaries. The testes are numerous and small, located dorsally, arranged in a pair of broad longitudinal rows, beginning some distance behind the ovaries and extending to the level of the pharyngeal root or somewhat behind it. In the zone of the testes, the thin sperm ducts or vasa deferentia run on top of the ventral nerve cords, generally medial to the oviducts or, in some places, lateral to them. They connect with the testes by long efferent ductules. At the level of the pharynx and behind it, the vasa deferentia form the usual expanded, tortuous spermiductal vesicles or false seminal vesicles.

The copulatory complex (Figure 47) was studied in series of sagittal sections of nine individuals. The gonopore (*gp*) leads into a voluminous com-

mon atrium (*ac*), which connects anteriorly with the male atrium (*am*) and posteriorly with the widely expanded terminal part of the bursal duct or vagina (*v*). The wall of the ventral section of the common atrium forms 8–19 (average, 13) cylindrical diverticula or evaginations (*da*), which project into the surrounding mesenchyme in all directions, but predominantly laterally. The lining of the genital atria is generally a cuboidal epithelium underlaid with a thin layer of circular muscle fibers followed by a layer of longitudinal muscles. Only the dorsal part of the common atrium has a muscle coat of interlaced circular and longitudinal fibers.

The penis has a rather small bulb (*bp*) and a large, generally plug-shaped, papilla (*pp*) of variable outline, subject to contraction and distortion when the animal is being preserved. The papilla has a very feeble musculature, confined chiefly to the rather thin layers of circular and longitudinal muscles underlying its cuboidal epithelial cover, and circular muscles surrounding the penial lumen, while its general tissue is parenchymal, with considerable plasticity. The lumen of the penis (*pl*), also variable in shape, is uniform both morphologically and histologically, not differentiated into a seminal vesicle and an ejaculatory duct. It begins in the ventral part of the penis bulb, proceeds first dorsally, then arches posteriorly toward the papilla. In some of the slides, this lumen appears funnel-shaped, narrow anteriorly and enlarging toward the papilla, with a wide opening into the male atrium. In the specimen depicted in Figure 47, the distal part of the lumen was compressed dorsoventrally, simulating a canal in the sagittal section. The two vasa deferentia (*vd*), enlarged as spermiductal vesicles, approach the base of the penis bulb, enter it ventrolaterally, diminish in diameter, and acquire a distinct layer of circular muscles. They penetrate the bulb, unite in the midline, and connect with the anterior end of the penial lumen.

The two oviducts unite in the space between the genital atrium and the bursal duct to form a rather short common oviduct (*odc*) that opens into the atrium from the dorsal side near the transition between the male and common atria. The copulatory bursa (*b*), variable in size, is a rounded sac in the usual position between the pharyngeal pouch and the penial bulb. Its outlet, the bursal duct (*bd*) runs first as a narrow straight canal in the midline above the penis to a level behind the gonopore. Then it curves sharply anteroventrally and expands into a voluminous cavity, the vagina (*v*), which fuses with the common atrium. The anterior part of the duct has a rather thin muscular layer, whereas the covering of the vagina consists of a thicker, but rather loose, coat of intermingled circular and longitudinal muscle fibers. The epithelium of the duct is cuboidal and nucleate. None of the epithelia of the entire copulatory apparatus are infranucleate.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana evaginata* is known to occur in four caves in Perry County, Missouri:

Klump Cave (type-locality), situated east of Perryville; 3 February 1968, 2 specimens collected in still pools in the stream bed in shallow water, given to me by Dr. Joseph A. Beatty of Southern Illinois University; 8 April and 30 September 1973, 17 specimens collected by Jerry Lewis and Brent Opell, together with the isopod, *Asellus antricolus* (Creaser), and the amphipod, *Gammarus troglophilus* Hubricht and Mackin.

Crevice Cave, near Perryville; 23 September 1961 and 9 June 1964, 8 specimens collected by Stewart Peck and others, transmitted to me by Russell M. Norton.

Berome Moore Cave, 4 October 1964, 3 specimens collected by R. A. Brandon and A. Altig, sent to me by Russell M. Norton.

Garbage Hole Cave, part of the Rimstone Cave System, southeast of Perryville; 3 February 1973, 2 specimens collected by Jerry Lewis, together with amphipods and isopods, sent to me alive.

TAXONOMIC POSITION.—*Sphalloplana evaginata* is placed in Carpenter's subgenus *Sphalloplana* on account of its feebly developed adhesive organ, although the occasional appearance of a short invagination in the center of the adhesive pit indicates a transition to the subgenus *Speophila*. It shares other distinctive characters, such as the dorsal location of the testes, the configuration of the anterior border of the intestinal system, the development of a common genital atrium, etc., with other species of both subgenera. The most conspicuous feature of the species is the presence of cylindrical coeca or evaginations on the wall of the common genital atrium, which is expressed also in the specific name *evaginata*. Similar differentiations have been reported only in *S. kansensis*

Hyman (1945:479), where the evaginations are described and depicted as "irregular epithelial outgrowths." In other details (shape of the penis, length of the common oviduct, etc.) *S. kansensis* differs from *S. evaginata.*

Sphalloplana (Sphalloplana) kansensis Hyman, 1945

FIGURE 48

Sphalloplana kansensis Hyman, 1945:478.
Sphalloplana (Sphalloplana) kansensis.—Carpenter, 1971:1284.

TYPE MATERIAL.—Holotype, set of serial sections on 3 slides, AMNH 311–313.

The species was described by Hyman (1945:478–479) from one preserved specimen. An examination of her slides showed that the worm was badly contorted and not suitable for a detailed anatomical analysis. Another specimen was sent to the writer by Russell M. Norton, unfortunately also in a badly preserved state, which made its exact study impossible. The following description must, therefore, be based on the data presented by Hyman.

EXTERNAL FEATURES.—No illustration of the living animal is available. It is a rather large (20 mm long), broad, and thin planarian, white and eyeless, with a truncate anterior end.

ANATOMY.—The adhesive organ is a depression equipped with eosinophilic glands and a moderate musculature. It is deeper than is generally seen in species of the subgenus *Sphalloplana,* but not as highly differentiated as in representatives of the subgenus *Speophila,* a feature which has been noticed also by Carpenter (1970:81). Hyman states that the rhabdites in the marginal zone are only little larger than elsewhere.

The testes are dorsal. The penis has a slightly developed bulb and a short, rounded papilla (Figure 48, *pp*). The vasa deferentia unite outside the bulb to form the ejaculatory duct (*de*) that first ascends dorsally, then bends posteriorly and opens at the tip of the papilla. The male atrium (*am*) is elongated and lined with a very tall epithelium, the common atrium very small and its wall bears irregular small blind epithelial outgrowths (*da*) that are very characteristic of the species. The bursal canal (*bd*) is very long and slender, the bursa (*b*) being separated from the penis bulb by a considerable distance, as is the case also in my specimen. The terminal portion of the bursal duct turns ventrally and is considerably widened. The long common oviduct (*odc*) enters the roof of the male atrium.

DISTRIBUTION.—*Sphalloplana kansensis* is known only from the type-locality, Purity Springs, a walled spring located about 4 miles east of Augusta, Butler County, Kansas. Hyman's specimen was collected there on 18 March 1942 by Leslie Hubricht, another specimen by Russell M. Norton on 12 June 1964. I visited this locality on 22 May and 13 July 1967 and again on 10 June 1970 without finding any planarians. Jerry Lewis was so kind as to expose in the spring traps baited with fresh shrimp in August 1973, also without results.

TAXONOMIC POSITION.—By its moderately developed adhesive organ *S. kansensis* is a species intermediate between the subgenera *Sphalloplana* and *Speophila,* as Carpenter (1970:81) pointed out. Many aspects of its morphology are unclear, and Hyman's slides show a great deal of distortion of the structures of the copulatory complex due to muscular contractions and possibly some artifacts. The epithelial outgrowths on the wall of the common atrium are reminiscent of the atrial diverticula of *S. evaginata,* but their shape appears to be quite different. A clearer picture will ensue only upon reexamination of properly preserved specimens.

Sphalloplana (Sphalloplana) californica, new species

FIGURES 4, 21, 32, 39, 49

TYPE MATERIAL.—Holotype, set of sagittal sections on 5 slides, USNM 53432. Paratypes, two sets of sagittal and transverse sections on 8 slides, USNM 53433–53434.

EXTERNAL FEATURES (Figures 4, 21).—The largest specimen, when quietly gliding, measured 17 mm in length and 2.5 mm in width. The anterior end is bluntly truncate, with a conspicuous indentation in the center of the frontal margin. The lateral edges of the head are rounded, without auricular projections. No distinct constriction or neck is seen behind the head, at most a very slight transitory narrowing during locomotion. Then the body gradually widens and the lateral margins become parallel up to the postpharyngeal region. The posterior end may appear rounded or bluntly pointed during gliding locomotion. The pharynx

is rather short, about one-eighth the body length, and its root lies somewhat posterior to the middle of the body. The motion of the animal is either a smooth gliding or, upon mechanical stimulation, "crawling." During gliding movement, the central part of the frontal margin is rather sharply elevated above the substrate. The worm is purely white, rather transparent. The intestinal area ends anteriorly with a rounded outline, not showing any V-shaped extensions of the gut branches.

ANATOMY.—The adhesive organ (Figure 32) appears in the sections as a slightly depressed, subterminal field of infranucleate epithelium, pierced by numerous eosinophilic gland ducts and provided with a moderate number of muscle fibers (retractors). There is no invagination of the adhesive epithelium into the mesenchyme, which places the species in the subgenus *Sphalloplana*.

The testes (Figure 39) are numerous, essentially ventral, some of them extending into the mesenchymal spaces between the intestinal branches or bridging the entire dorsoventral diameter of the body. They occupy, on either side, a longitudinal zone beginning behind the third or fourth pair of lateral intestinal branches and reaching to a level some distance anterior to the insertion of the pharynx, located mainly medially to the ventral nerve cord. The testes are in wide communication with the thin anterior vas deferens that runs along the medial side of the nerve cord. The ovaries are positioned below the second pair of intestinal branches. In the testicular region, the vitellaria or yolk glands lie mainly in the lateral regions of the mesenchyme.

The copulatory apparatus (Figure 49) was studied in two sets of serial sections, one cut longitudinally, the other transversely. The gonopore (*gp*) leads directly into the male atrium (*am*) and into the expanded terminal portion of the outlet of the copulatory bursa, the vagina (*v*). There is no common atrium developed. The lining of the atrium is a flattened epithelium with the usual two muscle layers, a circular and a longitudinal one.

The penis has a large, spherical, highly muscular bulb (*bp*) and a rather long, conical papilla (*pp*). The papilla is covered by a flattened epithelium underlaid by a layer of fine circular fibers (*f*) followed by longitudinal muscles. The fibrous layer is particularly thick at the base of the papilla, where it forms a continuation of the circular muscle layer of the atrial wall. The penis lumen consists of a rounded cavity (*pr*) in the bulb, lined with tall secretory cells filled with an eosinophilic secretion. From this cavity a narrow canal, the ejaculatory duct (*de*) runs posteriorly through the penis papilla and opens at its tip. The vasa deferentia (*vd*) enter the penis bulb posteroventrally, proceed within the bulb anterodorsally, and open, on either side, into a rounded cavity (*vs*) that empties into the anterior part of the ejaculatory duct. This pair of cavities apparently functions as seminal vesicles, although morphologically it does not correspond to the unpaired seminal vesicle of other species of the genus. The latter is represented in our species by the glandular lumen of the penis bulb which may have the function of a prostate, since no sperm passes through it but it apparently adds some secretions to the sperm fluid.

The two oviducts unite in the space between the male atrium and the bursal duct, the common oviduct (*odc*) proceeding ventrally and opening into the posterior part of the male atrium, very close to the gonopore. The copulatory bursa (*b*) is a rounded sac, somewhat compressed in the specimen studied. The bursal duct (*bd*) runs above the penis and genital atrium as a narrow, straight canal, then bends ventrally and expands considerably into a vagina (*v*) that histologically, however, does not differ from the narrow part of the duct. The rather thin muscle coat of the duct, not clearly analyzable, appears to consist of an inner circular and an outer longitudinal layer.

All epithelia of the copulatory apparatus are nucleate.

DISTRIBUTION AND ECOLOGY.—The material of *S. californica* was furnished to me by the courtesy of a group of enthusiastic cave explorers, calling themselves the "Bower Cave Diving Group." The collections were made in the lake, which fills the greater part of Bower Cave, by scuba diving, chiefly by Messrs. Paul Hara, Bill Kruse, and Steven J. Shimek.

Bower Cave, 8 miles east of Coulterville, Mariposa County, California (type-locality). 16 and 18 July 1971: 4 specimens collected and shipped to me (only one, immature, arrived alive). 22 October 1971: water temperature 52°F (11°C), 3 immature worms collected at a depth of about 70 feet (21 m). 2 April 1972: 1 sexually mature specimen from about 70 feet (21 m) depth. 10 October 1973: 1

specimen collected at depth of 100 feet (30 m), disintegrated in transit. 11 August 1974: 2 specimens, one of them semimature, collected at depth of 30 feet (9 m).

The species lives in the cave together with amphipods (*Stygobromus wengerorum* Holsinger), which apparently are its natural food. Mr. Hara informed me that in laboratory cultures the worm does not accept liver as food, but ingests dead amphipods and, very eagerly, crayfish meat. He was able to maintain animals in a culture for over one year and to raise one specimen to maturity.

TAXONOMIC POSITION.—*Sphalloplana californica* is characterized by a very feebly developed adhesive organ and a somewhat aberrant structure of its copulatory apparatus, particularly the anatomy of the penis. The paired seminal vesicles opening into the ejaculatory duct and the development of a prostatic cavity are unique within the genus as far as we know today. Other characteristics, such as the differentiation of a marginal zone with thickened epithelium and large rhabdites, and the prepharyngeal location of the testes are typical features of the genus *Sphalloplana*.

Sphalloplana (*Sphalloplana*) *culveri*, new species

FIGURES 17, 33, 40, 50

TYPE MATERIAL.—Holotype, set of sagittal serial sections on 5 slides, USNM 53435.

EXTERNAL FEATURES.—I had only one sexually mature specimen at my disposal, which measured, in the preserved state, 5.5 mm in length and 1.9 mm in width. In life, the animal must have been somewhat larger. Unfortunately, I had no opportunity of photographing or drawing the living worm, only making a few notes on its external appearance. The anterior end (Figure 17) was truncate, with a slightly convex frontal margin, showing occasionally a small median notch when gliding. The lateral corners had small rounded auricles projecting anterolaterally. Behind the auricles was an insignificant narrowing of the body, then the lateral margins diverged as is usually the case in related species. The animal was unpigmented, white. The pharynx was inserted at about the middle of the body and measured approximately one-sixth the body length.

ANATOMY.—The marginal epithelium with large rhabdites is typically developed. The adhesive organ (Figure 33) is a rather shallow subterminal pit lined with an infranucleate epithelium, with eosinophilic gland ducts opening through the bottom of the pit. The muscles attached to the organ are chiefly longitudinal retractor muscles.

The ovaries are situated at the level of the second or third lateral branch of the intestine. The testes (Figure 40) are arranged in two longitudinal rows, beginning a certain distance behind the ovaries and ending at about the level of the pharynx root. They are ventral, located above and medially to the ventral nerve cords, opening widely into the anterior vas deferens. The expanded and tortuous spermiductal vesicles on the sides of the pharynx are typically developed.

In the copulatory apparatus (Figure 50), the gonopore (*gp*) leads into a small common genital atrium (*ac*) that connects anteriorly with the male atrium (*am*) and posteriorly with the vaginal end portion (*v*) of the bursal duct. The penis consists of a relatively small bulb (*bp*) with weak musculature and a large, plug-shaped papilla (*pp*) with rounded tip. Near the tip is a rounded depression that may or may not be an artifact caused by a muscular contraction at the time of preservation. The papilla has a coat of muscles at the periphery, below the outer epithelium, a sheet of circular fibers underlaid by a layer of longitudinal muscles. Only a few longitudinal fibers run through the center of the papilla from the penis bulb. The epithelial cover of the papilla is infranucleate, except for a ring of normal nucleate epithelium at the base of the papilla. The bulbar lumen is a seminal vesicle (*vs*), appearing rather small and dorsoventrally compressed in the median section, but transversely elongated and provided with a muscular coat. It is lined with a cylindrical epithelium, apparently of secretory nature, and receives the outlets of faintly eosinophilic glands. From its median portion extends a narrow, nonglandular duct, the ejaculatory duct (*de*), with cuboidal epithelium, which opens on the dorsal side of the papilla close to its base. This duct also has a coat of chiefly longitudinal muscle fibers. The two vasa deferentia (*vd*) approach the penis bulb from its sides, bend upward, enter the bulb laterally, diminishing in diameter, and open each into the lateral extensions of the seminal vesicle.

The male atrium (*am*) duplicates the shape of the penis papilla. It narrows posteriorly and connects with the common atrium (*ac*). The two oviducts unite in the space between the male atrium and the bursal duct to form a common oviduct (*odc*), which opens into the atrium from the dorsal side close to the connection between the male and common atria. The copulatory bursa (*b*) is of moderate size. Its outlet, the bursal stalk (*bd*), proceeds posteriorly to a level behind the gonopore. It widens gradually, arches anteroventrally, and expands to a voluminous cavity, the vagina (*v*), which narrows again and opens into the common atrium from the left side. The anterior part of the bursal duct up to the level of the gonopore is lined with a normal, nucleate epithelium, while the posterior portion, including the vagina, has an infranucleate lining. The muscular coat of the bursal duct consists of intermingled circular and longitudinal fibers.

Remarkable is the great extent of infranucleate epithelia in the copulatory complex. Such epithelia are seen in the greater part of the cover of the penis papilla, the terminal portion of the busal stalk, and the lining of the oviduct. The male and common genital atria and the penial lumen have normal nucleate linings.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana culveri* is known from only one locality, Harper Cave in Tucker County, West Virginia, located 5 miles southeast of Hendricks. One sexually mature specimen was collected by John R. Holsinger and David C. Culver on 19 May 1973, together with two *Macrocotyla hoffmasteri* (Hyman) and several specimens of a white *Phagocata* sp. Another specimen, small and immature, was taken in the same cave 2 January 1974 by Arnold Norden and Beth Ball.

TAXONOMIC POSITION.—The principal characters of *S. culveri* are the feeble development of the adhesive organ, presence of small auricles, ventral position of the testes, dorsal mouth of the ejaculatory duct, and presence of a distinct vagina. It shares some of these characters with *S. holsingeri* from Virginia, which, however, differs by having a more highly developed, deeply invaginated adhesive organ with different histological structure. The species is named in honor of one of its collectors, Dr. David C. Culver of Northwestern University, Evanston, Illinois.

Sphalloplana (Sphalloplana) consimilis, new species

FIGURES 5, 22, 34, 41, 51

TYPE MATERIALS.—Holotype, set of sagittal sections on 7 slides, USNM 53407. Paratypes, eight sets of sagittal sections on 46 slides, USNM 53408–53415.

EXTERNAL FEATURES (Figures 5, 22).—Fully grown specimens are up to 14 mm long and 2 mm wide. The head has a bulging frontal margin and rather well-developed rounded auricles projecting anteriorly and laterally. In the center of the frontal margin, a moderately developed adhesive organ is discernible, which may be protruded as a conical, pointed projection. Behind the auricles, the body narrows somewhat, forming a necklike constriction, then widens again. In the greater part of the body, the lateral margins run parallel, tapering again in the postpharyngeal region to meet at the more or less pointed posterior end. The rather long pharynx, measuring about one-sixth of the body length, is inserted behind the middle of the body. The copulatory complex occupies the anterior half of the postpharyngeal region. The color of the worm is purely white in most specimens. Animals from Buis Saltpeter Cave, however, showed a light pinkish hue in the neck region and in the area of the copulatory organs. The anterior margin of the intestinal area does not form the V-shaped lateral extensions seen in some species that have a more pronounced adhesive organ.

ANATOMY.—The thickened marginal epithelium is typically developed. The adhesive organ (Figure 34) appears in the slides as a shallow subterminal pit, part of which is invaginated, but not as deeply as in representatives of the subgenus *Speophila*. Both the pit and the invagination receive numerous eosinophilic gland ducts and are connected with muscle fibers that presumably act as retractors.

In the reproductive system, the ovaries are located behind or below the second to fourth lateral branches of the anterior intestinal trunk. The rather numerous testes (Figure 41), of moderate size, are in a strictly dorsal position. They occupy, on either side of the midline, a longitudinal zone beginning at a considerable distance posterior to the ovaries (behind the sixth to eighth lateral intestinal branches) and extending to the level of the pharynx root. The thin anterior vasa deferentia

run parallel to the ventral nerve cords, somewhat removed from them, medially to the oviducts.

The copulatory apparatus (Figure 51) was analyzed in sagittal sections of 10 specimens. The genital atrium is divided into an anterior male atrium (*am*) containing the penis and a posterior common atrium that receives the outlet of the copulatory bursa. Below the infranucleate atrial epithelium are the usual two muscle layers, a circular one and a longitudinal one. The penis has a weakly developed, not very muscular bulb and a short, rounded or plug-shaped papilla, which is covered by a flattened to cuboidal, infranucleate epithelium with an underlying very feeble muscle layer. Faintly eosinophilic gland ducts (*gl*) enter the penis bulb from the surrounding mesenchyme and penetrate the penial tissues to open on the surface of the penis papilla. The two vasa deferentia (*vd*), after widening in the pharyngeal region to form the usual spermiductal vesicles, approach the ventral side of the penis bulb, proceed medially, and open into the anterior end of the tubular penis lumen. There is no seminal vesicle developed. The lumen consists of a short canal (*de*), surrounded by a muscle coat, which begins in the anteroventral portion of the penis bulb, proceeds first posterodorsally, then arches posteroventrally and opens on the ventral side of the penis papilla very near its base. It apparently acts as an ejaculatory duct.

The common oviduct (*odc*), provided with numerous eosinophilic shell glands, opens into the atrium from the dorsal side near the transition between the two atria, rather far removed from the gonopore (*gp*). The copulatory bursa (*b*) is round or ovoid. Its outlet, the bursal duct (*bd*), first runs posteriorly, above the penis, as a rather narrow canal, then bends ventrally and sometimes expands into a very wide compartment, the vagina (*v*). The musculature surrounding the duct consists of intermingled circular and longitudinal fibers.

Remarkable is the wide occurrence of infranucleate epithelia in the copulatory complex of the species at full sexual maturity. The covering of the penis papilla and the linings of the atria, the bursal canal (including the vagina), and the common oviduct are all infranucleate.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana consimilis* has been collected in several caves in western Virginia and northeastern Tennessee.

TENNESSEE. CLAIBORNE COUNTY: (1) Buis Saltpeter Cave, northeast of Tazewell, 3 specimens collected 19 August 1972 by J. R. Holsinger and D. C. Culver and sent to me alive.

VIRGINIA. LEE COUNTY: (1) Bowling Cave, east of Ben Hur, 1 specimen collected 28 July 1967 by J. R. Holsinger. (2) Cope Cave, south-southeast of Jonesville, 6 specimens collected 23 August 1969 by J. R. Holsinger. (3) Gallohan Cave No. 1, type-locality, 8 specimens collected 26 August 1971 by J. R. Holsinger, D. C. Culver, and J. M. Beck and sent to me alive; they were associated with the isopods, *Asellus recurvatus* and *Lirceus usdagalun*, the amphipod, *Crangonyx antennatus*, and the snail, *Fontigens* sp. (see Holsinger and Bowman, 1973:267). (4) Gregory's Cave, east-southeast of Rose Hill, several specimens collected 27 October 1967 by J. R. Holsinger. (5) McClure's Cave, west of Jonesville, 9 August 1973, 5 specimens; 31 July 1974, about 50 specimens collected by J. R. Holsinger and D. C. Culver from a huge population of perhaps 300 worms, sent to me alive.

TAXONOMIC POSITION.—By the anatomy of the moderately developed adhesive organ, *S. consimilis* forms a transition between the subgenera *Sphalloplana* and *Speophila*. The most outstanding characteristic of the species is the configuration of the penis, specifically the lack of a seminal vesicle and the opening of the ejaculatory duct on the ventral side near the base of the short, pluglike papilla. A similar feature is seen in *S. virginiana*, which species, however, has the testes positioned ventrally, while in *S. consimilis* they are located on the dorsal side. The species name, *consimilis* (Latin, similar), refers to the great similarity of the copulatory complex with that of *S. virginiana*.

Sphalloplana (Sphalloplana) subtilis, new species

FIGURES 6, 13, 27–29, 35, 42, 52

TYPE MATERIAL.—Holotype, set of sagittal sections on 5 slides, USNM 53444. Paratypes, two sets of sagittal and transverse sections on 9 slides, USNM 53445–53446.

EXTERNAL FEATURES (Figures 6, 13).—This is a very slender, unpigmented species, up to 16 mm long and 1 mm wide when extended. The head end is truncated, with almost straight or slightly convex frontal margin and rounded lateral edges, which may extend very little anteriorly and laterally. There is no conspicuous adhesive organ discernible in life. In the quietly gliding animal, no necklike construction is seen behind the head, at most a very insignificant narrowing. The lateral margins of the body run almost parallel for the greater part of the body length, tapering behind the level of the

copulatory complex to meet at the posterior end. The short pharynx, measuring about one-ninth of the length of the body, is inserted far back at about the beginning of the third fifth of the body length. The copulatory apparatus is located in the anterior half of the postpharyngeal region.

ANATOMY.—The marginal zone with thickened epithelium and large rhabdites, characteristic of the genus, is developed typically (Figure 29). The adhesive organ (Figure 35) appears in the sections as a small subterminal pit in the center of the frontal margin, lined with an infranucleate epithelium pierced by numerous eosinophilic gland ducts. It has a very feeble musculature, principally fibers that may act as retractors. No protrusion of the organ has been observed in living specimens upon stimulation, such as is seen in many other representatives of the genus.

The anterior ramus of the intestine bears over 20 pairs of lateral branches, each posterior ramus about 25 short branches. The anterior border of the intestinal area is rounded. Behind the copulatory apparatus, the two posterior rami unite to a single trunk.

The two ovaries are located behind the third to fifth lateral branches of the anterior intestinal ramus. The testes, in moderate number, form a pair of longitudinal rows extending through the posterior three-fifths of the prepharyngeal region. They are ventral, lying below the intestinal branches (Figure 42), above and medial to the ventral nerve cords. Many testicular follicles are connected directly to the thin anterior vasa deferentia that run along the upper border of the nerve cords, medial to the oviducts.

The copulatory apparatus (Figure 52) was analyzed in two series of sagittal sections. It occupies the anterior half of the postpharyngeal region. The genital aperture (*gp*) leads into two cavities, anteriorly into the male atrium (*am*) and posteriorly into the expanded outlet of the copulatory bursa or vagina (*v*). The penis consists of a rather small bulb (*bp*) embedded in the mesenchyme and a larger, plug-shaped papilla (*pp*). Its lumen (*pl*) forms an arched canal, histologically rather uniform, without a differentiation into a seminal vesicle and an ejaculatory duct. This canal, lined with a cuboidal epithelium, opens into the atrium on the ventral side of the penis papilla. The two sperm ducts or vasa deferentia (*vd*), which at the level of the pharynx expand to form the spermiductal vesicles, approach the penis bulb and enter it anterolaterally, diminish in diameter, acquire each a muscle coat, and open into the anterior part of the penial lumen independently from the sides. The musculature of the penis is very weakly developed. That of the penis bulb consists of a loose network of muscle fibers, while the papilla has a thin muscle layer developed below the external epithelium. The penial lumen is enclosed in a coat of circular muscle fibers. Many faintly eosinophilic gland ducts enter the bulb from the surrounding mesenchyme and empty into the penis lumen as well as into the atrium in a field on the dorsal side of the penis papilla.

The two oviducts or ovovitelline ducts unite in the space between the male atrium and the bursal duct, forming a common oviduct (*odc*), which runs ventrally and opens into the posterior part of the male atrium. As is usual, the terminal parts of the paired oviducts and the common oviduct receive the outlets of strongly eosinophilic so-called shell glands. The copulatory bursa (*b*) is a voluminous sac lying anterior to the penis bulb. Its outlet, the bursal duct (*bd*), begins as a rather narrow, straight canal passing posteriorly above the penis and male atrium to a level posterior to the gonopore. There it bends abruptly anteroventrally and widens into a large expansion, the vagina (*v*). Close to the gonopore, the vagina narrows again and joins the atrial outlet. The epithelial lining of the vaginal sac is infranucleate, while the epithelia of the narrow proximal bursal canal and the narrow terminal parts of the vagina contain nuclei. The vagina has a coating of muscles consisting of intermingled circular and longitudinal fibers, the circular ones predominating. The musculature of the thin anterior part of the bursal canal is very feeble and could not be analyzed in my preparations.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana subtilis* is known only from a spring on the property of J. W. Biggers at 6278 East Edsall Road, Fairfax County, Virginia, close to the Alexandria city line. The spring (Figures 27, 28) is enclosed in a brick structure with a removable concrete cover. The water is 6 feet (1.8 m) deep, its level reaching to 2 feet (0.6 m) below the rim of the casing. The species was obtained by J. R. Holsinger, W. Biggers, and the writer by baiting with fresh marine shrimp on

several occasions between 18 March and 12 August 1973. The water temperature on 25 March was 8.6°C, on 12 August 17.7°C (while the temperature of the surface layer was 22.1°C), the pH 5.4 on both dates. A total of 10 specimens were collected, three of them sexually mature. Besides *S. subtilis,* the spring contained another species of *Sphalloplana, S. holsingeri,* which was much more abundant (over 80 specimens were collected).

TAXONOMIC POSITION.—The weakly developed adhesive organ of *S. subtilis* places the species in the subgenus *Sphalloplana.* The testes are ventral as they are in some other species of the genus. The most important specific characters are in the configuration of the copulatory organs. The short penis with very weak bulb and plug-shaped papilla and the ventral opening of the penial lumen show some similarity with *S. consimilis* (which has dorsal testes) and *S. virginiana* (which has a more highly developed adhesive organ). Another outstanding character, the development of a voluminous vagina with infranucleate epithelium, is shared with *S. holsingeri,* from which it differs by the anatomy of the penis and of the adhesive organ. The specific name, *subtilis* (Latin, slender) alludes to the elongated shape of the species.

Sphalloplana (Speophila) virginiana Hyman, 1945

FIGURE 53

Sphalloplana virginiana Hyman, 1945:477.
Sphalloplana (Sphalloplana) virginiana.—Carpenter, 1971: 1284.

TYPE MATERIAL.—Holotype, whole mount of one specimen, AMNH 314. Paratypes, set of sagittal sections on 5 slides, MNH 315–319, and whole mount of three specimens on one slide, AMNH 706.

The following discussion is based on Hyman's (1945:477–478) description and a reexamination of Hyman's paratype sections.

EXTERNAL FEATURES.—A slender, white species, preserved specimens measuring to 12 mm in length.

ANATOMY.—The adhesive organ, according to Hyman, consists of an irregular depression lined with eosinophilic gland cells, from which a small band of retractor muscles proceed dorsally to join the dorsal subepidermal muscle layers. The paratype slide, however, shows a distinct invagination of the organ, as has already been noticed by Carpenter (1970:79).

In the reproductive system, the numerous testes are subventral, lying below the intestinal branches or extending into the mesenchymal spaces between the branches. Carpenter (1970:78) stated that the testes appeared to him to be dorsal rather than ventral on Hyman's slides; however, I see them there clearly in a ventral position.

The copulatory complex (Figure 53) is located at a considerable distance posterior to the pharyngeal pouch. The penis has a slightly developed bulb and a papilla (*pp*) of moderate size, somewhat more elongated than shown in Hyman's figure. The penial lumen lacks a distinct seminal vesicle and consists of a short, rather wide canal, the ejaculatory duct (*de*), which begins in the penis bulb, runs posteroventrally, and opens on the ventral side of the papilla close to its base. The two sperm ducts (*vd*) enter the penis bulb anteriorly and connect with the anterior end of the ejaculatory duct. The mouth of the common oviduct (*odc*) is on the posterodorsal roof of the male atrium (*am*). The rather small copulatory bursa (*b*) is situated above the penis bulb, with its outlet, the bursal duct (*bd*), running posteriorly and curving ventrally to connect with the common atrium (*ac*).

DISTRIBUTION AND ECOLOGY.—The type-locality of *S. virginiana* is Showalter's Cave in Rockbridge County, Virginia, where numerous specimens were collected in a pool on 30 October 1943 (Hyman, 1945:478). Carpenter (1970:80) visited this locality in 1969 and J. R. Holsinger at several occasions, both without finding any planarians.

TAXONOMIC POSITION.—*Sphalloplana virginiana* is here placed in the subgenus *Speophila* on account of its invaginated adhesive organ, as has already been suggested by Carpenter (1970:79). Its outstanding specific characteristics are the ventral position of the testes, the lack of a seminal vesicle, and, particularly, the ventral opening of the ejaculatory duct. The species appears to be rather close to *S. subtilis* (which, however, has a very weak adhesive organ) and to *S. consimilis* (which has the testes positioned dorsally). A closer comparison will be possible only after the reexamination of well-preserved specimens from the type-locality.

Sphalloplana (Speophila) holsingeri, new species

FIGURES 7, 14, 18, 27, 28, 36, 43, 54

TYPE MATERIAL.—Holotype, set of sagittal sec-

tions on 5 slides, USNM 53436. Paratypes, eight sets of sagittal and transverse sections on 35 slides, USNM 53437–53443, 53478.

EXTERNAL FEATURES (Figures 7, 14).—*Sphalloplana holsingeri* is a blind, white species, measuring, when gliding quietly, up to 15 mm in length and 1.5 mm in width. The anterior end is truncate, with a bulging frontal margin flanked by a pair of short, rounded auricles projecting anterolaterally. In the center of the frontal margin, the location of the adhesive organ is visible as an opaque spot. When protruded, the organ appears as a short conical projection. Behind the auricles, the body narrows slightly, then widens again to attain its greatest width a short distance behind the head. In the greater part of the body, the lateral margins run parallel up to the region of the copulatory complex, where they converge again to meet at the pointed posterior end. An opaque marginal rim, corresponding to the modified marginal epithelium, is conspicuous in the living animal. The pharynx is inserted behind the middle of the body and measures in length about one-seventh the length of the body. The copulatory apparatus occupies the anterior half of the postpharyngeal region. The anterior end of the intestine forms a median projection behind the adhesive organ (Figure 18); there is no V-shaped extension of the lateral branches to the sides of the organ such as is seen in some other species of the subgenus *Speophila,* e.g., *S. pricei* (Hyman) (Figure 19).

ANATOMY.—The epidermal epithelium of the lateral margins is thickened and contains rhabdites considerably larger than those of either the dorsal or ventral epidermis, as is seen generally in the genus *Sphalloplana.*

The adhesive organ (Figure 36) is well developed, consisting of a rounded subterminal depression, the central part of which forms a deep invagination when the organ is retracted. The muscular differentiations of the organ correspond to those described in other species of *Sphalloplana* with conspicuous adhesive organs, such as *S. pricei* (see Hyman, 1937:464–465), *S. mohri* Hyman (see Mitchell, 1968:611–613), and *S. weingartneri* Kenk (see Kenk, 1970:315). The glandular equipment of the organ, however, differs from the conditions seen in other species of the genus. Two kinds of glands open through the epithelial lining: eosinophilic gland ducts passing through the infranucleate epithelium of the invaginated portion and cyanophilic glands through the remaining field of the depression surrounding the inverted canal. The eosinophilic secretions are of a homogeneous or coarsely granular nature, while the cyanophilic secretions, staining deeply with hematoxylin, appear as threadlike or rod-shaped filaments. The gland cells producing these threads form voluminous masses occupying both the dorsal and ventral portions of the mesenchyme and the spaces between the intestinal branches in the medial part of the anterior two-thirds of the prepharyngeal region. In other species of *Sphalloplana,* only eosinophilic secretions are known to occur. It is difficult to interpret the functions of the two types of glands. The eosinophilic secretions in the central, eversible part of the organ presumably correspond to those described in other triclads that are equipped with adhesive organs, e. g., *Procotyla fluviatilis* Leidy, where the secretions dissolve into a sticky mucous mass that is used in the capture of living prey. The function of the cyanophilic secretions, so prominent in *S. holsingeri,* is not clear. It is interesting to note that a similar differentiation of the glands of the adhesive organ has been observed in a European planarian, *Dendrocoelum album* (Steinmann), where erythrophilic glands open through the epithelium of the adhesive pit and cyanophilic gland ducts at the peripheral rim of the organ (Steinmann, 1910:190).

The musculature of the pharynx follows the plan of the genus *Sphalloplana.* The internal pharyngeal epithelium is surrounded by a thick layer of circular muscle fibers, followed by a thinner layer of longitudinal muscles.

In the reproductive system, the two ovaries are situated on the medial sides of the ventral nerve cords, behind the third or fourth lateral branch of the anterior intestinal trunk. The numerous testes (Figure 43) are arranged in two longitudinal rows, one on either side of the midline, occupying the posterior half of the prepharyngeal region. They are located essentially ventral, medial to the nerve cord. Only a few testes may be pushed toward the dorsal side in the "septa" between the intestinal branches, or may extend through the entire dorsoventral diameter of the body. Many follicles are attached directly to the sperm ducts or vasa deferentia without the mediation of efferent ductules. In the region of the testes, the vasa deferentia run

parallel to the ventral nerve cords, somewhat removed from the ventral integumental muscle layers. At the level of the pharynx, they widen to form the sinuous spermiductal vesicles (or false seminal vesicles) that keep their expanded shape up to their entrance into the penis bulb.

The copulatory apparatus (Figure 54) was analyzed in 12 series of sagittal sections. The penis consists of a relatively small bulb (*bp*) with rather feeble musculature, embedded in the mesenchyme, and a larger, generally plug-shaped, papilla, sometimes constricted at its base, protruding into the genital atrium. The shape of the papilla is rather variable in the specimens studied, as it is easily distorted when the animal is being killed. It lacks any rigid supporting structures and its musculature is confined to two rather thin layers of muscle fibers, a circular layer underlying the external epithelium and a weak longitudinal layer below it. Only a few scattered longitudinal fibers run through the parenchyma of the papilla. The bulb contains an elongated cavity, the seminal vesicle (*vs*), lined with an epithelium pierced by gland ducts with a finely granular, faintly cyanophilic secretion that enter the bulb from the surrounding mesenchyme. Toward the penis papilla, the cavity continues as a narrow, nonglandular canal, the ejaculatory duct (*de*), which opens into the atrium on the dorsal side of the papilla, about halfway between its base and its tip.

The genital aperture or gonopore (*gp*) leads into two cavities, anteriorly the male atrium (*am*) and posteriorly the cavity of the large vagina (*v*). There is no common atrium developed.

The two vasa deferentia (*vd*), which approach the penis bulb as enlarged spermiductal vesicles, enter the bulb ventrolaterally, diminishing in diameter, and open separately into short lateral extensions of the anterior part of the seminal vesicle.

The two oviducts, in the region of the copulatory complex, ascend from their course above the ventral nerve cords, pass to the midline, and unite above the male atrium to form the common oviduct (*odc*), which arches ventrally and opens into the posterior part of the atrium. The copulatory bursa (*b*) is an elongated sac lying close to the anterior face of the penis bulb. Its outlet is a rather narrow, straight canal (*bd*) running in the midline dorsally to the penis and atrium and extending rather far posteriorly. Behind the level of the gonopore, the canal curves ventrally and widens into a voluminous cavity, the vagina (*v*). In the preserved specimens, the outline of the vagina is very variable, usually irregularly folded. In fully mature worms, the lining of the vagina is infranucleate while that of the narrow part of the bursal canal contains nuclei. In young specimens, however, nuclei are present in the vaginal epithelium; it appears, therefore, that the nuclei pass from the cellular lining only at the approach of full sexual maturity. The vagina is surrounded by a thick coat of interlaced circular and longitudinal muscle fibers. The musculature of the anterior, narrow part of the bursal canal is very feeble, probably also made up of intermingled longitudinal and circular muscles.

Distribution and Ecology.—*Sphalloplana holsingeri* is known from only one locality, the spring on the property of J. W. Biggers in Fairfax County, Virginia, the same spring where *S. subtilis* occurs (see above and Figures 27, 28). Two specimens, both mature, were collected first by Dr. John R. Holsinger on 23 May 1965 but were fixed in alcohol, which made an analysis of their anatomy rather difficult. Additional (over 80) specimens were obtained by Dr. Holsinger, Bill Biggers, and the writer by baiting with shrimp meat on 18 March, 25 March, 2 April, and 12 August 1973, among them many mature animals.

Taxonomic Position.—The presence of a deeply invaginated, protrusible adhesive organ places the species in the subgenus *Speophila*. Among the outstanding characteristics of the species is the differentiation of the glands of the adhesive organ, eosinophilic glands in the inverted part, surrounded by a field of cyanophilic gland openings. In the reproductive system, it shares the ventral position of the testes with several other species of the genus. The most important specific characters are in the anatomy of the copulatory complex: the opening of the ejaculatory duct on the dorsal side of the penis papilla and the development of a voluminous vagina in the terminal part of the bursal duct. The species is named in honor of my distinguished colleague, Dr. John R. Holsinger, who collected the first specimens and collaborated in the procurement of additional material of the species.

When the manuscript of this description was completed, I received notice that the American Museum of Natural History had, among the ma-

terials left by the late Libbie H. Hyman, a set of three slides of sagittal sections marked *"Sphalloplana holsingeri."* The condition of the sections is rather bad, so that no identification of the species can be made. Apparently, Hyman's *S. holsingeri* is an unpublished manuscript name and has no nomenclatorial standing.

Sphalloplana (Speophila) weingartneri Kenk, 1970

FIGURES 23, 55

TYPE MATERIAL.—One set of 2 slides of sagittal sections, USNM 41181.

A description of this species was given by Kenk (1970), based on a single specimen. The description will not be repeated here, only the essential characteristics may be listed.

EXTERNAL FEATURES (Figure 23).—This is a rather small species, 6 mm long and 1.2 mm wide, white. Anterior end truncate, without auricles. The anterior border of the intestinal zone is rounded, without a V-shaped median recess. The pharynx is inserted somewhat behind the middle of the body, measuring about one-seventh the body length. The region of the copulatory apparatus is visible in life as a transparent field with an opaque spot in the center.

ANATOMY.—The deeply invaginated adhesive organ and the tall marginal epidermal cells with long rhabdites are typically developed. The testes are located both dorsally and ventrally. In the copulatory apparatus (Figure 55), the penis consists of a large, spherical, very muscular bulb (*bp*) and a small, rather slender papilla (*pp*). The vasa deferentia (*vd*) enter the bulb ventrolaterally. The penis lumen is divided into an elongated seminal vesicle (*vs*) with a secretory epithelial lining and a narrow ejaculatory duct (*de*) that opens at the tip of the penis papilla. The common oviduct (*odc*) empties into the posterior part of the male atrium (*am*), close to the gonopore (*gp*).

DISTRIBUTION AND ECOLOGY.—One specimen was collected by Lawrence Weingartner in Bronsons Cave in Spring Mill State Park, Lawrence County, Indiana, on 15 August 1969. Dr. Jerry Carpenter informed me that he obtained additional material of the species from the type-locality at a later visit (in 1970) and kindly sent me photographs of a sexually mature specimen.

TAXONOMIC POSITION.—*Sphalloplana weingartneri* appears to be rather closely related to *S. pricei* of Pennsylvania. It resembles it by the shape of the anterior end (absence of auricles), the location of the testes (dorsal and ventral), and the ventrolateral entry of the vasa deferentia into the penis bulb. It differs from *S. pricei* by its smaller size, the configuration of the anterior intestinal border, and particularly by the size relation between the bulb and the papilla of the penis.

Sphalloplana (Speophila) buchanani (Hyman, 1937)

FIGURES 15, 56

Sphalloplana percoeca.—Beauchamp, 1931:321 [in part].
Speophila buchanani [nomen nudum] Hyman, 1936:129.
Speophila buchanani Hyman, 1937:468.
Sphalloplana buchanani.—Mitchell, 1968:615.
Sphalloplana (Speophila) pricei.—Carpenter, 1971:1283 [in part].

TYPE MATERIAL.—Syntypes, 6 specimens (2 whole mounts on one slide and 4 sets of serial sections on 11 slides), AMNH 648.

I had no opportunity of examining living specimens of this species, only Hyman's type slides that are histologically very poor, in part with badly faded stain. *Sphalloplana buchanani* was described originally by Hyman (1937:468–469) from preserved specimens obtained by Prof. J. W. Buchanan in Mammoth Cave in Kentucky. Carpenter (1970, 1971) considers the species to be identical with *S. pricei* from Pennsylvania. In the absence of an exact analysis of its anatomy, however, we may consider this identity to be still an open question. The following account is based chiefly on the literature data available.

EXTERNAL FEATURES (Figure 15).—Hyman (1937, fig. 16) published an illustration of the aspect of the species in life, prepared by Buchanan. It varies in length from 7 to 15 mm. The anterior end is shown to be truncate with rounded lateral edges, lacking auricular projections. The protrusible adhesive organ appears as a retracted conical structure. The intestinal area terminates anteriorly with a V-shaped outline. The pharynx, measuring about one-eighth of the body length, is inserted somewhat posterior to the middle of the body, and the copulatory complex occupies the anterior third of the postpharyngeal region. All these features are compatible with the conditions obtaining in *S. pricei*.

ANATOMY.—The deeply invaginated adhesive

organ and the lateral marginal zone with large rhabdites are developed typically. The testes, in moderate number, are prepharyngeal and dorsal (in *S. pricei* they are dorsal, ventral, and intermediate). Illustrations of the copulatory organs (Figure 56) have been given by Hyman (1937, fig. 19) and probably by Beauchamp (1931, fig. 6), who confused the species with the sympatric *S. percoeca*. Both figures show the aspect of the organs in dorsal view; however, Hyman's slide of horizontal sections, from which her figure is drawn, shows the bursal duct to be on the right side of the penis rather than on the left side. The penis has a rather muscular bulb (*pb*) and a cylindrical to conical papilla (*pp*). The vasa deferentia enter the bulb laterally, traverse its tissues, and unite to a rather narrow canal, the ejaculatory duct (*pl*), which runs through the center of the papilla and opens at its tip. There is no seminal vesicle developed, but in Hyman's figure a widening of the ejaculatory duct is shown near the tip of the papilla. Carpenter (1970:92) also stated that in his specimen of *"S. pricei"* from Mammoth Cave no dilated seminal vesicle was present. The common oviduct (*odc*) opens into the male atrium close to the entrance of the bursal stalk (*bd*), which is there enlarged to form a vagina (*v*) with somewhat muscular walls.

DISTRIBUTION AND ECOLOGY.—The only reliably documented habitat of *S. buchanani* is Mammoth Cave, Edmonson County, Kentucky, where it was collected first in 1928 (Bolivar and Jeannel, 1931: 38, in Audubon Avenue, together with *S. percoeca*), by Buchanan and others in October and November 1935 (in the less accessible and deeper parts of the cave, Hovey's Cathedral Domes, Fox's Alley, and Becky's Alley, see Hyman, 1937:469), and again by Carpenter (1970:92, 180).

Additional localities recorded in the literature need further confirmation. McRitchie (1959:24) reported *"Speophila buchanani"* from Mill Creek Cave, Davidson County, Tennessee. Carpenter (1970:92) found a *Sphalloplana* which he believed to be identical with the Mammoth Cave form in Cathedral Cave, Edmonson County, Kentucky, a few miles from Mammoth Cave. His specimens, however, had a well-developed seminal vesicle and the vasa deferentia entering the penis bulb posterodorsally (see his fig. 51). Finally, Barr and Kuehne (1971:70) observed *S. buchanani* in a stream in Great Onyx Cave, Edmonson County, Kentucky, a locality where Carpenter (1970:180) had collected only *S. percoeca*.

A few physicochemical parameters of the habitat of *S. buchanani* are given by Hyman (1937:469). The temperature of the water in Mammoth cave was 55°F [12.8°C], the pH, 7.6. Barr (1968:155) observed the species in temporary drip pools and assumes that it survives the periods of dryness by encystment in the hygroscopic deposits at the bottom of the pools, as does *S. percoeca*.

TAXONOMIC POSITION.—*Sphalloplana buchanani* appears to be very close to *S. pricei*, from which it differs by the location of the testes and the anatomy of the penis, particularly the absence of a seminal vesicle and the morphology of the ejaculatory duct.

Sphalloplana (Speophila) pricei (Hyman, 1937)

FIGURES 8, 19, 24, 37, 44, 57

Speophila pricei Hyman, 1937:462.
Sphalloplana pricei.—Mitchell, 1968:615.
Sphalloplana (Speophila) pricei.—Carpenter, 1971:1284 [in part].

TYPE MATERIAL.—Holotype, one set of 6 slides of sagittal sections, USNM 20228. Paratypes, 5 specimens in alcohol, USNM 20236. Six specimens (one whole mount and 5 sets of serial sections mounted on 31 slides), designated as syntypes, AMNH 649 (see Feinberg, 1970:49).

EXTERNAL FEATURES (Figures 8, 24).—Mature specimens are up to 28 mm long and 3.5 mm wide, but maturity is observed also in smaller individuals. The color in life is a pure white apart from the intestinal contents, which may shine through the body wall. The anterior end has a straight or very slightly bulging frontal margin, with a median notch frequently seen when the animal is gliding. No auricular projections are developed, as the rounded lateral edges of the head do not extend anteriorly. Behind the head, the body first narrows, forming a necklike constriction, then widens again. In the greater part of the body, the lateral margins run parallel, converging again behind the region of the pharynx and meeting in the rather pointed tail end.

The anterior intestinal border shows a V-shaped indentation, the lateral branches extending somewhat anteriorly to both sides of the adhesive organ (Figure 19). The pharynx is inserted at about the middle of the body, its length amounting to

approximately one-seventh the body length. The copulatory apparatus, visible in life as an elongated transparent field with a central opaque spot, is situated in the anterior half of the postpharyngeal section.

ANATOMY.—The structure of the adhesive organ (Figure 37), which in the retracted state forms a deep, folded invagination, is described well by Hyman (1937:464–465). No "snout-like" projection was visible, however, in specimens fixed with hot mercuric chloride solution. The modifications of the marginal epithelium with tall cells and large rhabdites are also analyzed by Hyman.

I have studied the reproductive organs of the species in eight sets of serial sections, including some of the type specimens. The ovaries are situated behind the third or fourth pair of lateral branches of the intestine. The numerous, rather small testes are not confined to the dorsal region, as Hyman indicates, but are located dorsally, ventrally, and in intermediate positions (Figure 44). The thin anterior vas deferens on either side runs along the ventral nerve cord, parallel to the oviduct and on the medial side of it. It expands at the pharyngeal level as the usual spermiductal vesicle. The copulatory apparatus appears rather much contracted in Hyman's figure 11. In specimens killed in the extended state by a hot fixative, the apparatus is generally more elongated (Figure 57). The genital aperture (*gp*) leads into a common atrium (*ac*), which communicates widely with the anterior male atrium (*am*). The penis has a muscular bulb of moderate size and a large, very pliable papilla (*pp*), which is very variable in appearance, from conical to finger-shaped, often bent in various directions. The constriction at the middle of the papilla, mentioned by Hyman, is not a regular occurrence. The papilla is provided with a very feeble musculature, chiefly two thin layers of muscle fibers, one circular, the other longitudinal, below the external epithelium of the papilla. The two vasa deferentia (*vd*) enter the penis bulb ventrolaterally and proceed posterodorsally toward the midline. They open into the penis lumen either separately and close together or after first uniting to a short common vas deferens. The penial lumen is an elongated cavity, arching from the bulb toward the papilla and opening at the tip of the latter. The anterior part of the cavity has a glandular epithelial lining, the cells of which, staining deeply with eosin, project in some of the specimens into the lumen in a villus-like fashion. This anterior part is frequently widened and corresponds to a seminal vesicle (*vs*). Posteriorly, the cavity continues as a canal with somewhat variable diameter, the ejaculatory duct (*de*). Gland ducts with a homogeneous, faintly cyanophilic secretion enter the penis bulb from the surrounding parenchyma and open into the anterior portion of the ejaculatory duct. The common oviduct (*odc*) opens from the dorsal side into the atrium near the junction of the male and common atria. The bursa copulatrix (*b*) shows no peculiarities. Its outlet, the bursal duct (*bd*), starts as a straight, narrow canal but widens considerably in its posterior section, forming sinuous convolutions and acquiring a thicker muscle coat. This widened terminal part may be termed a vagina (*v*).

None of the epithelia of the copulatory complex are infranucleate.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana pricei* inhabits several caves in Pennsylvania.

DAUPHIN COUNTY: Brownstone Cave: One specimen collected by John W. Price, 23 May 1936 (Hyman, 1937:466). LANCASTER COUNTY: Refton Cave (type-locality): several specimens collected by John W. Price, 20 January and 17 April 1936 (Hyman, 1937:466); several specimens collected by Jerry H. Carpenter, 20 May 1971; 10 specimens collected by Arnold Norden and Beth Ball, 4 February 1973. MIFFLIN COUNTY: Upper Johnson Cave: specimens collected by Charles E. Mohr and Kenneth Dearolf, 23 January and 27 February 1937 (Hyman, 1937:471; Dearolf, 1941:170).

TAXONOMIC POSITION.—The distinguishing characters of *S. pricei* are the following: Adhesive organ deeply invaginated, anterior intestinal border V-shaped, testes dorsal and ventral, penial papilla large with ejaculatory duct opening at tip, and entry of the vasa deferentia into the penis bulb ventrolateral. Carpenter (1970:85) considers *S. pricei* to include three more of Hyman's species of *Speophila, S. buchanani, S. hubrichti,* and *S. hoffmasteri,* which he lists as synonyms of *S. pricei.* An analysis of the morphological characters of these forms, however, justifies their standing as good separate species. *Sphalloplana buchanani* appears to have only dorsal testes (Hyman, 1937:469), but will need a more detailed reexamination; *S. hubrichti* differs from our species by having dorsal testes and not showing the V-shaped recess in the anterior border of the digestive system; *S. hoffmasteri,* by the arrangement of the muscles in the

interior pharyngeal muscle zone, is to be removed from the genus *Sphalloplana* and placed into *Macrocotyla* (Kenk, 1975:333).

Sphalloplana (Speophila) hubrichti (Hyman, 1945)

FIGURES 9, 25, 58, 59

Speophila hubrichti Hyman, 1945:479.
Sphalloplana hubrichti.—Mitchell, 1968:615.
Sphalloplana (Speophila) pricei.—Carpenter, 1971:1284 [in part].

TYPE MATERIAL.—Holotype, whole mount, AMNH 320. Paratypes, whole mount and sets of serial sections, AMNH 321–324 and 703 from Kolms Cave; whole mount and set of serial sections, AMNH 704, from Morrisons Cave.

EXTERNAL FEATURES (Figures 9, 25).—This is a rather large species, measuring up to 20 mm in length and 3 mm in width, in life of purely white color. The head is truncate, with slightly bulging frontal margin, frequently showing a median notch at the site of the adhesive organ. The lateral edges of the head are rounded, without auricular projections, but somewhat protruding laterally. The adhesive organ is visible in the living specimen as an opaque spot. The pharynx is situated behind the middle of the body and its length is about one-eighth the body length. The copulatory organs occupy the anterior half of the postpharyngeal region. The testes are visible in life as transparent spots, arranged in a pair of zones, several testes wide, to the right and left of the midline, each zone occupying the posterior half of the prepharyngeal region, extending posteriorly to the level of the anterior part of the pharynx. The intestinal zone ends anteriorly in a transversal border, not showing any V-shaped formation.

ANATOMY.—Apart from the materials of this species deposited in the American Museum of Natural History and in the United States National Museum, I had an opportunity of studying several live specimens from the type-locality in Missouri and from localities in Illinois.

The adhesive organ is a deep pit with irregularly folded walls and is provided with a complex musculature, as described by Hyman (1945:479).

The reproductive system was examined in the paratype slides and in 12 sets of serial sections preserved by a better method than that used by L. Hubricht for his original collection. The testes are of moderate size, dorsal or subdorsal. The ovaries are located usually at the level of the third or fourth lateral branch of the anterior intestinal ramus. Hyman's description of the copulatory complex needs some emendations. The genital pore (Figure 58, *gp*) leads into a rather small common genital atrium that connects anteriorly with the male atrium (*am*) and dorsally with the widened outlet (*v*) of the copulatory bursa. The penis consists of a rounded, muscular bulb and a large, generally finger-shaped papilla. Each vas deferens (*vd*), after expanding to form the convoluted spermiductal vesicle, enters the penial bulb ventrolaterally, proceeds toward the midline and opens into a rather large seminal vesicle (*vs*). What Hyman (1945:480) describes as "narrow ejaculatory duct" is actually the anteroposteriorly compressed, rather voluminous seminal vesicle that extends laterally to both sides. The epithelial lining of this vesicle is of a glandular nature, with club-shaped cells protruding into the lumen. In the median section, the vesicle generally arches from the anteroventral part of the bulb dorsally and posteriorly and, at the transition between bulb and papilla, connects with a duct that runs through the axis of the papilla to open at its tip. This canal, the true ejaculatory duct (*de*), is lined with a normal, nonglandular epithelium and varies considerably in its width and shape. It appears to have no surrounding muscular layer. The outer surface of the penis papilla is covered by a cuboidal epithelium, below which there is a well-developed layer of fine circular fibers, followed by a layer of coarser longitudinal muscles. In some specimens, the tip of the penis papilla was invaginated into the ejaculatory duct (Figure 59), so that the distal part of the duct showed the same muscular layers as the outer covering of the papilla. It is difficult to decide whether this invagination corresponds to the shape of the resting male organ that may extend at the moment of preservation by a contraction of the musculature of the penis papilla.

The spaceous male atrium (*am*) duplicates the shape of the penis. At its posterior end it narrows and connects with the small common atrium. The copulatory bursa (*b*) shows no peculiarities. Its outlet, the bursal duct or stalk (*bd*), begins as a narrow, straight canal running posteriorly above the penis bulb, then gradually widens, becomes more convoluted, and finally bends downward as an

expanded section (*v*) situated to the left of the midline.

The two oviducts or ovovitelline ducts, which accompany the ventral nerve cord, ascend dorsally and medially at the level of the copulatory complex, each giving off a short posterior vitelline duct running toward the yolk glands of the tail region. The oviducts unite in the space above the male atrium and proceed posteroventrally as common oviduct (*odc*), provided with the usual eosinophilic shell glands, which opens into the common atrium from the dorsal side.

None of the epithelia of the copulatory complex are infranucleate.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana hubrichti* inhabits a number of caves and springs in Missouri and Illinois. The following localities may be taken as habitats of the species.

MISSOURI. JEFFERSON COUNTY: Spring near Kimmswick and spring near Selma, collected by Leslie Hubricht in June 1937 (Hyman, 1945:480). SAINTE GENEVIEVE COUNTY: Kolms Cave (this is the correct spelling, rather than Kohn's Cave as Hyman indicates), type-locality of the species; many specimens collected by Leslie Hubricht in June 1937 (Hyman, 1945:480); about 35 specimens collected by Leslie Hubricht 13 September 1941 (alcohol material, USNM 50907); 6 specimens collected by Jerry Lewis and Margaret Meister 21 July 1974 and 12 April 1975.

ILLINOIS. JACKSON COUNTY: A walled spring in Happy Hollow, Fountain Bluff, south of Gorham, a total of 17 specimens collected by Jerry Lewis and Margaret Meister 10 February, 2 March, 14 April, 14 September, and 20 October 1974. MONROE COUNTY: Burksville Cave (also called Morrisons Cave, Eckerts Cave, Illinois Caverns, or Mammoth Cave of Illinois), collected by Leslie Hubricht, June 1937 (Hyman, 1945:480); about 25 specimens collected by Jerry Lewis 24 November 1974, occurring together with 2 species of *Asellus* and 4 species of amphipods. UNION COUNTY: Richs Cave, east of Cobden, 5 specimens, collected by Jerry Lewis, 2 February 1974, besides *Phagocata gracilis* (Haldeman).

Other distributional data for *S. hubrichti* given in the literature either need reexamination or are misidentifications caused by Hyman's defective description of the species. Beatty's (1966:10) "Cave near Cobden" is probably Richs Cave in Union County, Illinois, mentioned above. Beatty's Tom Moore Cave, Perry County, Missouri has *Macrocotyla lewisi* rather than *S. hubrichti* (see Kenk, 1975:333). McRitchie's (1959:20, 21) localities in Tennessee are probably all erroneous: the species occurring in the spring at Stokes Lane in Nashville is *S. chandleri,* described in this paper (p. 21). Specimens from the spring "at junction of U.S. routes 70N and 70S, Cheatham County," and from Herring Cave, near Lascassas, Rutherford County, are not further described by McRitchie; *S. chandleri* from the Stokes Lane spring in Nashville is also mentioned by Darlington and Chandler (1972: 160) and by Chandler (1972:62) as *"Speophila hubrichti."*

TAXONOMIC POSITION.—By the development of a conspicuous adhesive organ, *S. hubrichti* belongs to the subgenus *Speophila.* Carpenter (1970:85) placed the species in synonymy with *S. pricei,* from which it may be distinguished in life by a slightly different shape of the head and by the transverse or rounded anterior border of the intestinal zone (which in *S. pricei* shows a V-shaped formation) and in the anatomy by the location of the testes (dorsal in *S. hubrichti,* dorsal and ventral in *S. pricei*). From the very similar *S. chandleri* it differs by the shape of the anterior intestinal border and by the entry of the vasa deferentia into the penis bulb (ventrolateral in *S. hubrichti,* dorsal after recurving in *S. chandleri*). The remaining American species of the subgenus differ from *S. hubrichti* chiefly in the location of the testes and the configuration of the copulatory complex.

Sphalloplana (Speophila) chandleri, new species

FIGURES 10, 26, 38, 60, 61

Speophila hubrichti.—McRitchie, 1959:20 [misidentification].
Sphalloplana (Speophila) pricei.—Carpenter, 1970:96 [in part].

TYPE MATERIALS.—Holotype, set of sagittal sections on 7 slides, USNM 53416. Paratypes, 10 sets of sagittal and transverse sections on 62 slides, USNM 53417–53426.

EXTERNAL FEATURES (Figures 10, 26).—A purely white species of moderate size, up to 18 mm long and 3 mm wide. Smaller individuals (12 mm long) may also be sexually mature. The anterior end is truncated, with a somewhat convex frontal margin and rounded lateral corners lacking prominent auricular projections. The protrusible adhesive organ is seen as a slightly opaque area and its outlet may be noticeable as a small notch in the midline of the frontal margin when the animal is gliding quietly. There is no definite constriction or neck behind the anterior end, only a gentle narrowing of the body margins when the animal is in locomotion. Then the body widens gradually, to narrow

again in the postpharyngeal region to a rounded or bluntly pointed posterior end. The anterior portion of the intestinal area forms a V-shaped border, the lateral branches of the intestine reaching farther forward to both sides of the adhesive organ than the median intestinal trunk. The root of the pharynx is located at about the middle of the body length or slightly behind the middle. Its length is about one-eighth the length of the body.

ANATOMY.—The adhesive organ (Figure 38), in its retracted state, is a deep invagination with folded walls, as is typical for the subgenus *Speophila*. The zone of marginal epithelium is also typically developed.

The two ovaries are situated below or behind the first to third pair of lateral intestinal branches. The numerous, rather small, rounded testes are strictly dorsal, occupying, on either side of the midline, a longitudinal zone beginning some distance behind the level of the ovaries and ending near the pharyngeal root. The copulatory complex (Figure 60) was studied in 14 sets of serial sections. The genital aperture or gonopore (*gp*) leads into the common genital atrium (*ac*) that is not very clearly marked off from the terminal part of the outlet (*bd*) of the bursa copulatrix (*b*). Anteriorly, the common atrium connects with the male atrium (*am*) surrounding the penis papilla. The penis appears in the slides in various stages of muscular contraction indicating the great plasticity of this organ. The rounded, muscular penis bulb is of moderate size. The penis papilla, when extended (Figure 60), is long, finger-shaped, and larger than the bulb. In several of the specimens, however, the posterior part of the papilla is inverted into the penis lumen to a varying degree or even telescoped (Figure 61). The musculature of the penis papilla is restricted to a two-layered coat underlying the external epithelium, while the penis lumen seems to be devoid of a musculature of its own. The penial lumen consists of a rather large cavity, lined with a tall, secretory epithelium, the seminal vesicle (*vs*), located in the penis bulb and extending into the basal part of the penis papilla, and a canal (*de*) of variable diameter running through the rest of the papilla and opening at its tip. This canal, corresponding to an ejaculatory duct, has a nonglandular, cuboidal or flattened epithelial lining. The two vasa deferentia (*vd*) approach the copulatory apparatus as expanded, twisted spermiductal vesicles filled with masses of sperm, run posteriorly to the level of the male atrium, curve dorsally, enter the penis bulb posterodorsally, and open into the seminal vesicle. This recurving of the vasa deferentia is very characteristic and was seen in all specimens examined, regardless of the state of contraction of the muscular organs. The common oviduct (*odc*) opens into the posterior part of the male atrium from the dorsal side, generally at a considerable distance from the gonopore (in the specimens from Indiana and Virginia more closely to the gonopore). The copulatory bursa (*b*) is a rounded sac of variable size. Its outlet, the bursa stalk (*bd*), widens gradually as it proceeds posteriorly, then becomes contorted and thrown into loops, and bends ventrally to unite with the common atrium. The terminal part of the bursal stalk does not change its histological characteristics. The muscle layer surrounding the stalk consists of intermingled circular and longitudinal fibers.

None of the epithelia of the copulatory apparatus are infranucleate.

DISTRIBUTION AND ECOLOGY.—*Sphalloplana chandleri* was collected by Dr. Clay Chandler under rocks in a stream issuing from a cave near Stokes Lane in Nashville, Davidson County, Tennessee, on 22 August 1973 (water temperature, 16°C) and in May 1975. A total of about 35 specimens were sent to me alive. Some were placed in cultures maintained at about 14°C. Two cocoons were laid in the cultures soon after the collection dates. The cocoons are spherical, unstalked, 1½ mm in diameter. The locality has been known to turbellarian workers for some time. The presence of *"Speophila hubrichti"* in the Stokes Lane spring had been reported by McRitchie (1959:20) and by Darlington and Chandler (1972:60). McRitchie states that he collected a very large specimen, 3 cm in length, on 5 May 1959. Carpenter (1970:96), who considered *S. hubrichti* to to be a synonym of *S. pricei*, listed *S. pricei* for the same locality, collected in 1969. Other possible habitats of *"S. hubrichti"* in Tennessee, mentioned by McRitchie (1959:21) (spring at junction of U.S. routes 70N and 70S, Cheatham County, and Herring Cave, near Lascassas, Rutherford County), which also may refer to *S. chandleri*, need further examination.

INDIANA. Small spring next to the road on Edwardsville Hill, west of New Albany, Floyd County. One specimen col-

lected by Jerry Lewis on 22 December 1974 (besides *Phagocata gracilis*).

VIRGINIA. Fallen Rock Cave, Tazewell County, located 5 miles south-southeast of Pounding Mill. A total of 7 specimens collected by John R. Holsinger and others on 13 October 1973, 27 July and 27 November 1974, and on 24 July 1976.

One cocoon, laid in a culture (kept at 14°C) in June, hatched after about 12 weeks and nine young emerged.

McRitchie (1959:20, 36, 37) comments on the gliding and leechlike locomotion and on the sensitivity to light of the form from the Stokes Lane spring.

TAXONOMIC POSITION.—*Sphalloplana chandleri,* apart from its well-developed adhesive organ that places it in the subgenus *Speophila,* is characterized by the lack of auricles, the V-shaped anterior intestinal border, dorsal position of the testes, recurving of the sperm ducts before dorsal entry into the penial bulb, large penis papilla, nonmuscular penial lumen, and lack of a distinctive vagina. In life, it is very similar to *S. pricei* (lack of auricles, V-shaped intestinal border), but differs from it by the dorsal location of the testes and the recurving of the vasa deferentia. *Sphalloplana hubrichti,* which also has a similar outline of the anterior end, has a different intestinal border and configuration of the sperm ducts. It is interesting to note that Carpenter (1970:88, 96) was aware of some of these differences but did not consider them to be significant enough to be the basis of species separation.

The species is named in honor of the collector, Dr. Clay M. Chandler of the Middle Tennessee State University.

Sphalloplana (Speophila) mohri Hyman, 1938

FIGURES 16, 62

Sphalloplana mohri Hyman, 1938:137.
Sphalloplana kutscheri Mitchell, 1968:598.
Sphalloplana sloani Mitchell, 1968:600.
Sphalloplana zeschi Mitchell, 1968:604.
Sphalloplana reddelli Mitchell, 1968:607.
Sphalloplana (Polypharyngea) mohri.—Carpenter, 1971:1284.

TYPE MATERIAL.—*Sphalloplana mohri,* holotype, whole mount, AMNH 650; paratypes, two specimens (one whole mount and one set of serial sections on 24 slides), AMNH 651. *S. kutscheri,* holotype, set of serial sections on 35 slides, USNM 38982; two paratypes. *S. sloani,* holotype, set of serial sections on 36 slides, USNM 38980; three paratypes. *S. zeschi,* holotype, set of serial sections on 10 slides, USNM 38981; eight paratypes. *S. reddelli,* holotype, set of serial sections on 7 slides, USNM 38979; four paratypes. The paratypes of Mitchell's species are in the collection of Dr. R. W. Mitchell.

Sphalloplana mohri was first briefly mentioned by Hyman (1938:137) and later (1939:276–280) more fully described. Mitchell (1968) established four additional species on the basis of minor differences in the structure of the reproductive system, which in my opinion do not justify their specific differentiation from *S. mohri.* The published descriptions offer a sufficiently clear account of the external aspects and the anatomy of the species. The essential characters of the species are the following.

EXTERNAL FEATURES (Figure 16).—*Sphalloplana mohri* is the largest species of the genus, mature animals attaining a length of 20–30 mm and even 35 mm. Photographs of the species have been published by Mitchell (1974:413, a well-extended specimen, and pp. 415, 420, and 422, all "*S. zeschi*") and earlier by Mohr (1948:17, "planarian"), and outline drawings by Mitchell (1968:608). The anterior end is truncate, with a straight or slightly bulging frontal margin, the lateral edges bearing short auricular projections extending laterally and anteriorly. The adhesive organ in the center of the frontal margin may appear retracted or protruded as a pointed conical structure. Behind the auricles, the head narrows to some extent, then widens again gradually to reach its maximum width. The anterior border of the intestinal area appears to have a V-shaped outline as seen in Carpenter's (1970) figure 13. An important character of the species is its polypharyngy. Hyman (1939:276) gives the number of pharynges as being about 50, Mitchell (1968) as 40 for all his species. The elongated pharyngeal pouch, measuring about one-fourth to one-third the body length, begins at a level anterior to the middle of the body.

ANATOMY.—The adhesive organ, when retracted, forms a rather deep invagination with irregular, folded walls, as indicated by Mitchell (1968:612); when protruded, it appears as a broad, pointed, conical projection. Hyman (1939:276) states that the epidermis along the lateral margins of the body does not show the large rhabdites usually seen in

the species of *Sphalloplana*. The marginal epithelium is thicker than elsewhere, however, and tapers gradually toward the dorsal and ventral surfaces.

The testes, in moderate number, are arranged in a pair of longitudinal rows beginning some distance behind the head and ending at the level of the more anterior pharynges. In Mitchell's type slides they are seen in a predominantly dorsal position. The copulatory apparatus (Figure 62) in the various specimens studied by Mitchell appears to be subject to small variations, probably due to various states of muscular contraction. The penis has a small, not very muscular bulb and a larger, cylindrical or conical papilla with rounded or more or less pointed tip. The vasa deferentia (*vd*) enter the anterior side of the bulb, traverse it, and unite within the papilla to a straight canal, the ejaculatory duct (*de*), which opens at the tip of the papilla. There is no distinct seminal vesicle developed, although the ejaculatory duct may show some local widening such as that seen in Hyman's figure 4, which she interprets as a seminal vesicle. The common oviduct (*odc*) opens into the posterior part of the male atrium from the dorsal side. The bursal duct (*bd*) proceeds from the copulatory bursa (*b*) posteriorly above the penis as a straight, narrow canal, then bends ventrally at the level of the gonopore (*gp*), widens somewhat, and acquires a thick muscular coat. This terminal section of the duct (*v*) may be considered to be a vagina.

Distribution and Ecology.—*Sphalloplana mohri* has been reported from several caves in Texas. Ezell's Cave (type-locality) in Hays County, collected by Charles E. Mohr and Kenneth Dearolf, 19 June 1938 (Hyman, 1939:280), also recorded by Mitchell (1968:609). Mitchell's species are from four other caves of the Edwards Plateau of Texas (Mitchell, 1968: *S. kutscheri*, Spanish Wells Cave, Travis County, collected by Mitchell, 9 June 1967; *S. sloani*, Harrell's Cave, San Saba County, collected by Mitchell, 14 October 1967; *S. zeschi*, Zesch Ranch Cave, Mason County, collected by Mitchell, 10 June 1968 and other dates; and *S. reddelli*, Cascade Caverns, Kendall County, collected by James Reddell, 8 April 1966). Eigenmann (1900:229 and 1902:84–85) reported the finding of an unidentified flatworm in the outflow of an artesian well in San Marcos, Hays County. Dr. Glenn Longley brought me a preserved, slightly damaged specimen of a polypharyngeal *Sphalloplana* from this well, collected 28 October 1974 by Joe Kolb. The specimen was not fully mature sexually, but agreed in all recognizable characters with *S. mohri*.

A few data on the habitat of *S. mohri* have been presented by Hyman (1939:280), whose material was from a shallow pool in Ezell's Cave with a water temperature of 71°F–72°F [about 22°C]. Mitchell (1974) gives more data on the ecology of his *S. zeschi* in Zesch Ranch Cave. The worms occur there in an intermittent pool with a temperature of 21°C–21.5°C, together with the amphipod, *Stygonectes russelli* Holsinger, and an ostracod, *Candona* sp. Their natural food appears to consist of injured or moribund amphipods and of any other arthropods (cave crickets, flies, etc.) that may have fallen into the water.

Laboratory Studies.—Mitchell (1974) performed some very interesting experiments on *S. zeschi*. He analyzed the types and speed of movement, the righting time from an inverted position, attraction to food and mode of feeding, negative rheotaxis, responses to light, and temperature tolerance and preference.

Taxonomic Position.—The well-developed adhesive organ places *S. mohri* in the subgenus *Speophila*. It shows, however, certain characters that differ from the general features of this subgenus. The absence of distinct zone of tall epithelial cells on the lateral margins of the body appears to be unique within the genus *Sphalloplana*. The polypharyngy, also a unique character, should not be given great systematic value, as it occurs in other genera (*Phagocata, Crenobia*) as a specific or even subspecific feature. It is, however, a good distinguishing character of the species. The small differences in the anatomy of the forms described by Mitchell (1968) are, in the writer's judgment, well within the framework of the expected variations caused by contractions and distortions of muscular organs in the process of fixation, particularly when different methods of killing (nitric acid, formalin) are employed.

Literature Cited

Barr, T. C.

1961. Caves of Tennessee. *Tennessee Division of Geology Bulletin*, 64: 569 pages, 1 folding map.

1968. Ecological Studies in the Mammoth Cave System of Kentucky, I: The Biota. *International Journal of Speleology*, 3:147–204, plates 37–64.

Barr, T. C., and R. A. Kuehne

1971. Ecological Studies in the Mammoth Cave System of Kentucky, II: The Ecosystem. *Annales de Spéléologie*, 26:47–96.

Beatty, J. A.

1966. *Key to the Land and Fresh-Water Triclad Turbellaria of North America (for Living Specimens Only)*. 13 pages, 6 plates [unpublished, reproduced from typewritten copy].

Beauchamp, P. de

1931. Biospeologica, LVI: Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928), 2: Turbellariés triclades. *Archives de Zoologie Expérimentale et Générale*, 71:317–331.

1932. Biospeologica, LVI [correctly LVIII]: Turbellariés, Hirudinées, Branchiobdellidés, deuxième série. *Archives de Zoologie Expérimentale et Générale*, 73: 113–380, plates 6–8.

Bolivar, C., and R. Jeannel

1931. Biospeologica, LVI: Campagne spéologique dans l'Amérique du Nord en 1928 (première série). Énumération des grottes visitées. *Archives de Zoologie Expérimentale et Générale*, 71:294–316.

Buchanan, J. W.

1935. The Eyeless Cave Flatworm, *Sphalloplana percaeca*. *Anatomical Record*, 64(supplement 1):78.

1936. Notes on an American Cave Flatworm, *Sphalloplana percaeca* (Packard). *Ecology*, 17:194–211.

Carpenter, Jerry H.

1969. A New Killing and Fixing Technique for Small Animals. *Transactions of the American Microscopical Society*, 88:450–451.

1970. *Systematics and Ecology of Cave Planarians of the United States*. 213 pages. Ph.D. dissertation, University of Kentucky [unpublished, reproduced from typewritten copy].

1971. Systematics and Ecology of Cave Planarians of the United States. *Dissertation Abstracts International*, (B)32:1283–1284. [This is the published abstract of the above paper, Carpenter, 1970.]

1973. Systematics and Biogeography of Cave Flatworms. *Bulletin of the National Speleological Society*, 35:15.

Castle, W. A., and L. H. Hyman

1934. Observations on *Fonticola velata* (Stringer), including a Description of the Anatomy of the Reproductive System. *Transactions of the American Microscopical Society*, 53:154–171.

Chandler, C. M.

1972. Planarians of Tennessee. *Journal of the Tennessee Academy of Science*, 47:62.

Darlington, J. T., and C. M. Chandler

1972. A Survey of the Epigean Triclad Turbellarians of Tennessee. *American Midland Naturalist*, 88:158–166.

Dearolf, K.

1941. The Invertebrates of 35 Pennsylvania Caves. *Proceedings of the Pennsylvania Academy of Science*, 15:170–180.

1953. The Invertebrates of 75 Caves in the United States. *Proceedings of the Pennsylvania Academy of Science*, 27:225–241.

Eigenmann, C. H.

1900. A Contribution to the Fauna of the Caves of Texas. *Proceedings of the American Association for the Advancement of Science*, 49:228–230.

1902. *In* C. J. Ulrich, A Contribution to the Subterranean Fauna of Texas. *Transactions of the American Microscopical Society*, 23:84–85.

Feinberg, Harold S.

1970. *A Catalogue of Type Specimens in the Department of Living Invertebrates, The American Museum of Natural History, New York, New York, U.S.A. The Phyla Platyhelminthes and Gnathostomulida*. 66 pages. New York: American Museum of Natural History [reproduced from typewritten copy].

Ginet, R., and R. Puglisi

1964. Écologie de *Fonticola notadena* de Beauchamp (Turbellarié, Triclade) dans la grotte de La Balme (Isère, France); survie en période de sécheresse. *International Journal of Speleology*, 1:203–216.

Giovannoli, L.

1933. Invertebrate Life of Mammoth and Other Neighboring Caves. *In* V. Bailey, Cave Life of Kentucky, Mainly in the Mammoth Cave Region. *American Midland Naturalist*, 14:600–623.

Gourbault, N.

1965. *Amyadenium chattoni*, Triclade obscuricole: Données préliminaires sur la biologie et la durée de la régénération. *Annales de Spéléologie*, 20:477–481.

1972. Recherches sur les Triclades paludicoles hypogés. *Mémoires du Muséum National d'Histoire Naturelle* (Paris), nouvelle série, série A (Zoologie), 73:1–249, 1 folding map, plates 1–3.

Holsinger, J. R.

1966. A Preliminary Study on the Effects of Organic Pollution of Banners Corner Cave, Virginia. *International Journal of Speleology*, 2:75–89.

Holsinger, J. R., and T. E. Bowman

1973. A New Troglobitic Isopod of the Genus *Lirceus* (Asellidae) from Southwestern Virginia, with Notes

on Its Ecology and Additional Cave Records for the Genus in the Appalachians. *International Journal of Speleology*, 5:261–271.

Holsinger, J. R., and S. B. Beck

1971. The Invertebrate Cave Fauna of Georgia. *National Speleological Society Bulletin*, 33:23–44.

Hyman, L. H.

1931. Studies on the Morphology, Taxonomy, and Distribution of North American Triclad Turbellaria, IV: Recent European Revisions of the Triclads, and Their Application to the American Forms, with a Key to the Latter and New Notes on Distribution. *Transactions of the American Microscopical Society*, 50:316–335.

1935. Studies on the Morphology, Taxonomy, and Distribution of North American Triclad Turbellaria, VI: A New Dendrocoelid from Montana, *Dendrocoelopsis vaginatus* n. sp. *Transactions of the American Microscopical Society*, 54:338–345.

1936. Some Cave Planarians of the United States. *Anatomical Record*, 67, supplement 1:129.

1937. Studies on the Morphology, Taxonomy, and Distribution of North American Triclad Turbellaria, VIII: Some Cave Planarians of the United States. *Transactions of the American Microscopical Society*, 56: 457–477.

1938. Additional North American Cave Planarians. *Anatomical Record*, 72(4), supplement, page 137.

1939. North American Triclad Turbellaria, X: Additional Species of Cave Planarians. *Transactions of the American Microscopical Society*, 58:276–284.

1945. North American Triclad Turbellaria, XI: New, Chiefly Cavernicolous, Planarians. *American Midland Naturalist*, 34:475–484.

1954. North American Triclad Turbellaria, XIII: Three New Cave Planarians. *Proceedings of the United States National Museum*, 103(3333):563–573.

Ichikawa, A., and M. Kawakatsu

1967. Records of Two Planarian Species of the Family Kenkiidae from Japanese Subterranean Waters. *Archiv für Hydrobiologie*, 63:512–519.

Kawakatsu, M.

1969. An Illustrated List of Japanese Freshwater Planarians in Color. *Bulletin of Fuji Women's College* (Sapporo), series 2, 7:45–91.

Kawakatsu, M., and T. Miyazaki

1972. Effect of Different Fixatives on a Common Japanese Freshwater Planarian, *Dugesia japonica* Ichikawa et Kawakatsu. *Bulletin of Fuji Women's College* (Sapporo), series 2, 10:81–117.

Kenk, R.

1970. Freshwater Triclads (Turbellaria) of North America, III: *Sphalloplana weingartneri*, New Species, from a Cave in Indiana. *Proceedings of the Biological Society of Washington*, 83:313–320.

1972. Freshwater Planarians (Turbellaria) of North America. *Biota of Freshwater Ecosystems, Identification Manual*. Number 1, ix + 81 pages. Washington: Environmental Protection Agency.

1975. Freshwater Triclads (Turbellaria) of North America, VII: The Genus *Macrocotyla*. *Transactions of the American Microscopical Society*, 94:324–339.

Lascombe, Claude

1971. *Recherches écologiques et biogéographiques sur deux espèces jumelles de Planaires d'eau douce dans la région lyonnaise.* [vii] + 116 pages, 20 plates. Thesis, Université Claude Bernard (Lyon) [unpublished, reproduced from typewritten copy.]

Livanov, N. A., and Z. I. Zabusova

1940. Planarii basseĭna Teletskogo ozera i novye dannye o nekotorykh drugikh sibirskikh vidakh (Paludicoles du Lac Télétzkoë et nouvelles données sur quelques formes sibériennes). *Trudy Obshchestva Estestvoispytateleĭ pri Kazanskom Gosudarstvennom Universitete*, 56(3–4):83–159.

McRitchie, Robert Gerald

1959. *The Kenkiidae of the Nashville Area.* v + 43 pages, 10 plates. M.A. thesis, Vanderbilt University [unpublished, reproduced from typewritten copy].

Mitchell, R. W.

1968. New Species of *Sphalloplana* (Turbellaria: Paludicola) from the Caves of Texas and a Reexamination of the Genus *Speophila* and the Family Kenkiidae. *Annales de Spéléologie*, 23:597–620.

1974. The Cave-Adapted Flatworms of Texas: Systematics, Natural History, and Responses to Light and Temperature. Pages 402–430 *in* Riser and Morse, editors, *Biology of the Turbellaria*. New York, etc.: McGraw-Hill Book Company.

Mohr, C. E.

1948. Unique Animals Inhabit Subterranean Texas. *National Speleological Society Bulletin*, 10:15–21, 88.

Packard, A. S.

1879. *Zoology for Students and General Readers.* viii + 719 pages. New York: Henry Holt and Company.

1880. *Zoology for High Schools and Colleges.* Second edition, viii + 719 pages. New York: Henry Holt and Company. [Identical with the preceding publication, with changed title page.]

1888. The Cave Fauna of North America, with Remarks on the Anatomy of the Brain and Origin of the Blind Species. *Memoirs of the National Academy of Sciences* (Washington), 4(1):3–159, plates 1–27, 1 map.

Steinmann, P.

1910. Eine neue Gattung der paludicolen Tricladen aus der Umgebung von Basel (*Polycladodes alba* n. g. n. sp.). *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 21:186–196.

Wells, P. H., and C. O. Harris

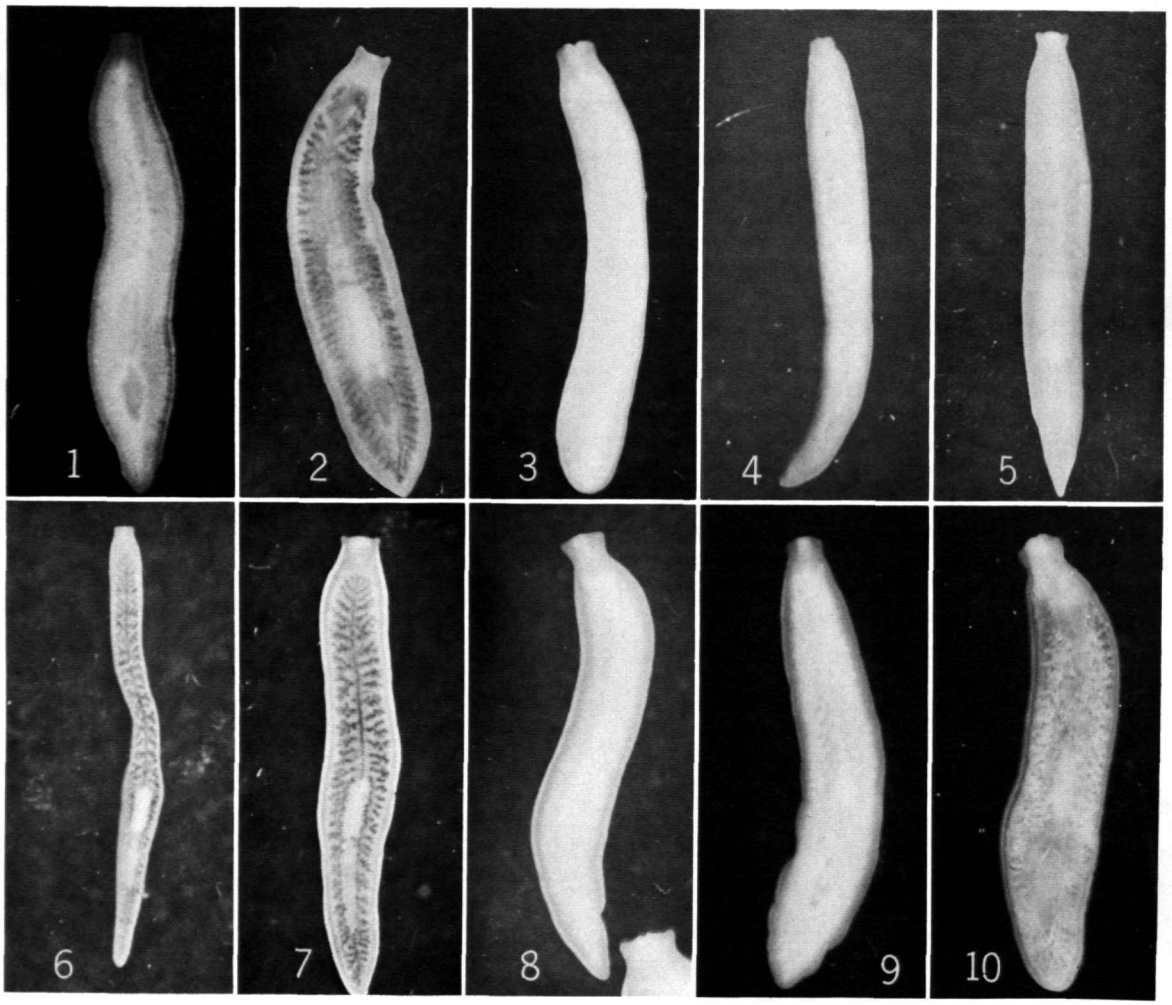
1954. Ultraviolet Sensitivities of Pigmented and Colorless Flatworm Species. *Anatomical Record*, 120:793.

TABLE 1.—Comparison of the North American species of *Sphalloplana*

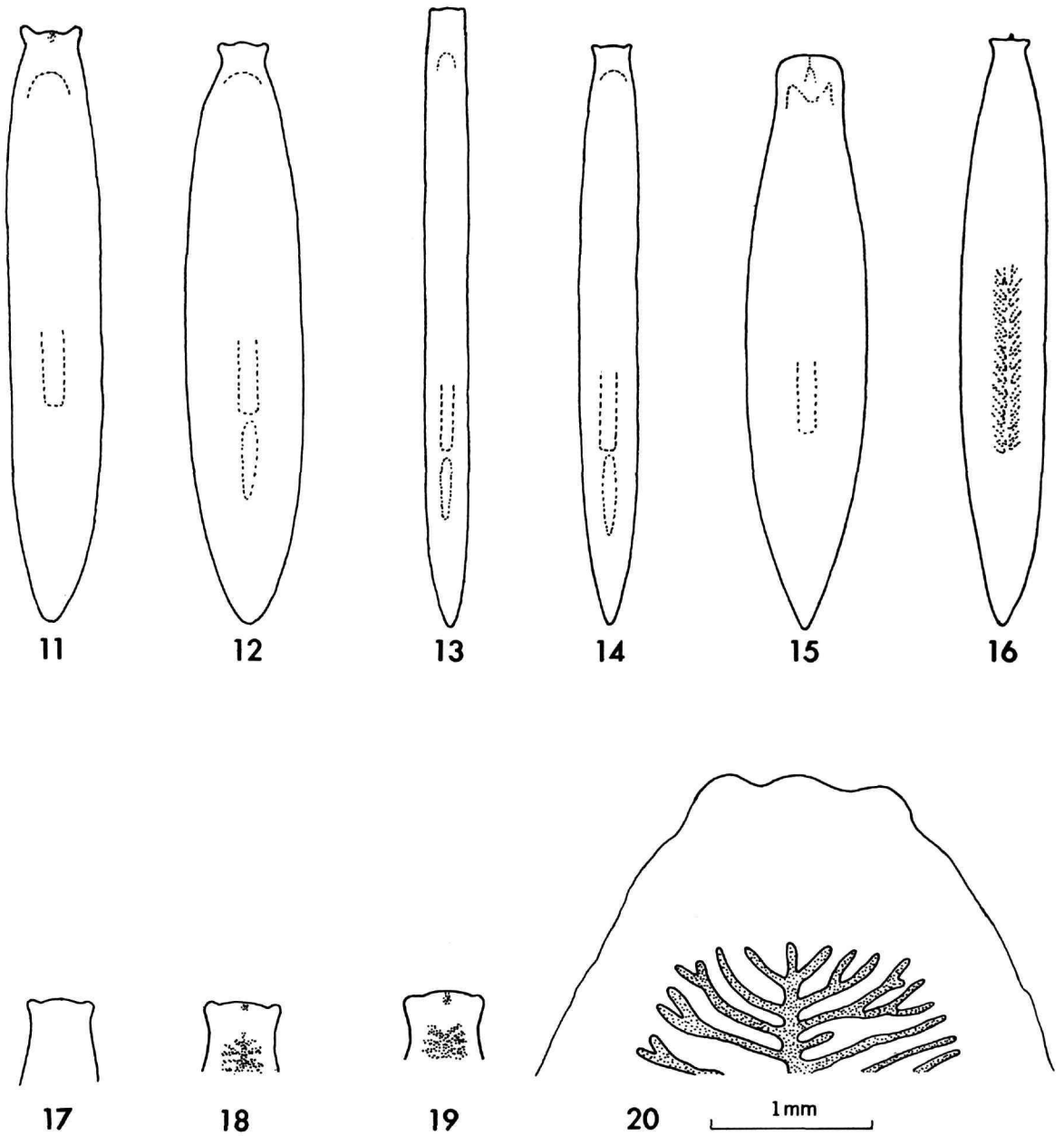
Sphalloplana	Distribution	Auricles	Adhesive organ	Intestinal border	Testes	Penis papilla	Seminal vesicle	Ejacul. duct	Oviduct opening	Vagina	Remarks
percoeca	KY, TN AL	prominent	weak	rounded	dorsal	plug-shaped	small	opens at tip	far dorsal	wide	
georgiana	GA	?	weak	?	dorsal?	conical	small	opens at tip	far dorsal	wide	
evaginata	MO	prominent	weak	rounded	dorsal	large, plug-shaped	absent	opens at tip	far dorsal	widening	pink color, cylindrical diverticula on common atrium
kansensis	KS	?	moderate	?	dorsal	small	absent	opens at tip	common ov.long	widening	irregular diverticula on common atrium
californica	CA	absent	weak	rounded	predom. ventral	long, conical	paired	opens at tip	close to gonopore	widening	prostate in penis bulb, double seminal vesicle
culveri	WV	small	weak	rounded?	ventral	large, plug-shaped	small	opening dorsal	intermediate	large	wide-spread infranucleate epithelia
consimilis	VA, TN	prominent	moderate	rounded	dorsal	plug-shaped	absent	opening ventral	intermediate	widening	
subtilis	VA	very small	weak	rounded	ventral	plug-shaped	absent	opening ventral	intermediate	prominent	very slender shape
virginiana	VA	?	moderate	?	ventral	plug-shaped	absent	opening ventral	dorsal	narrow	
holsingeri	VA	small	strong	rounded	ventral	plug-shaped	narrow	opening dorsal	close to gonopore	large	no common atrium
weingartneri	IN	absent	strong	rounded	dorsal & ventral	small, finger-shaped	present	opens at tip	close to gonopore	narrow	large penis bulb
buchanani	KY	absent	strong	V-shaped	dorsal	conical or cylin.	absent	opens at tip	?	widening	
pricei	PA	absent	strong	V-shaped	dorsal, ventr., & intermed.	long, finger-shaped	narrow	opens at tip	intermediate	convoluted	
hubrichti	MO, IL	absent	strong	square	predom. dorsal	long, finger-shaped	present	opens at tip	close to gonopore	convoluted	no common atrium
chandleri	TN, IN VA	absent	strong	V-shaped	dorsal	long, finger-shaped	present	opens at tip	intermediate	convoluted	vasa defer. recurve, enter bulb posterodorsally
mohri	TX	small	strong	?	predom. dorsal	conical or cylin.	absent	opens at tip	intermediate	narrow	large, polypharyngeal

ABBREVIATIONS USED IN ILLUSTRATIONS

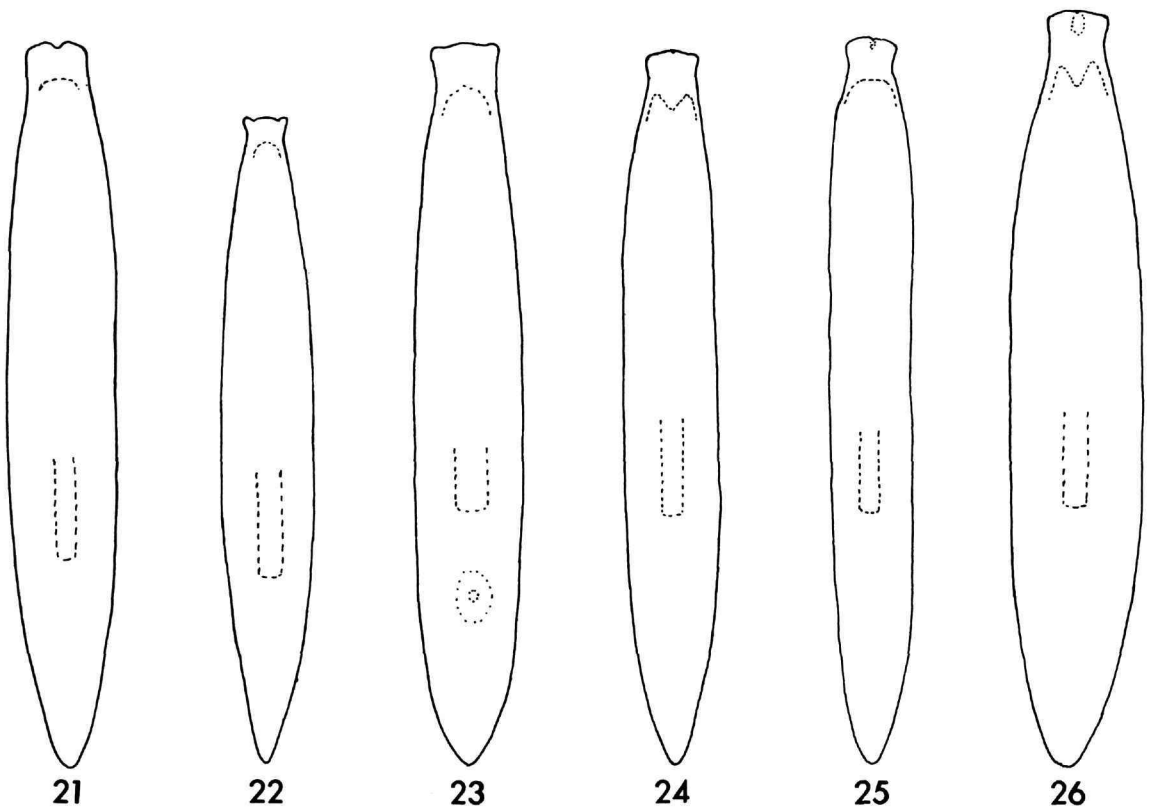
a	genital atrium
ac	common genital atrium
am	male atrium
b	copulatory bursa
bd	bursal duct
bp	penis bulb
da	atrial diverticulum
de	ejaculatory duct
f	fibrous layer
gl	gland duct
gp	gonopore
i	intestine
inv	invaginated part of penis papilla
m	mouth
me	marginal epithelium
od	oviduct
odc	common oviduct
pb	penis bulb
ph	pharynx or pharyngeal pouch
pl	penial lumen
pp	penis papilla
pr	prostate
t	testis
v	vagina
vd	vas deferens or sperm duct
ve	efferent ductule
vi	vitellarium or yolk gland
vs	seminal vesicle



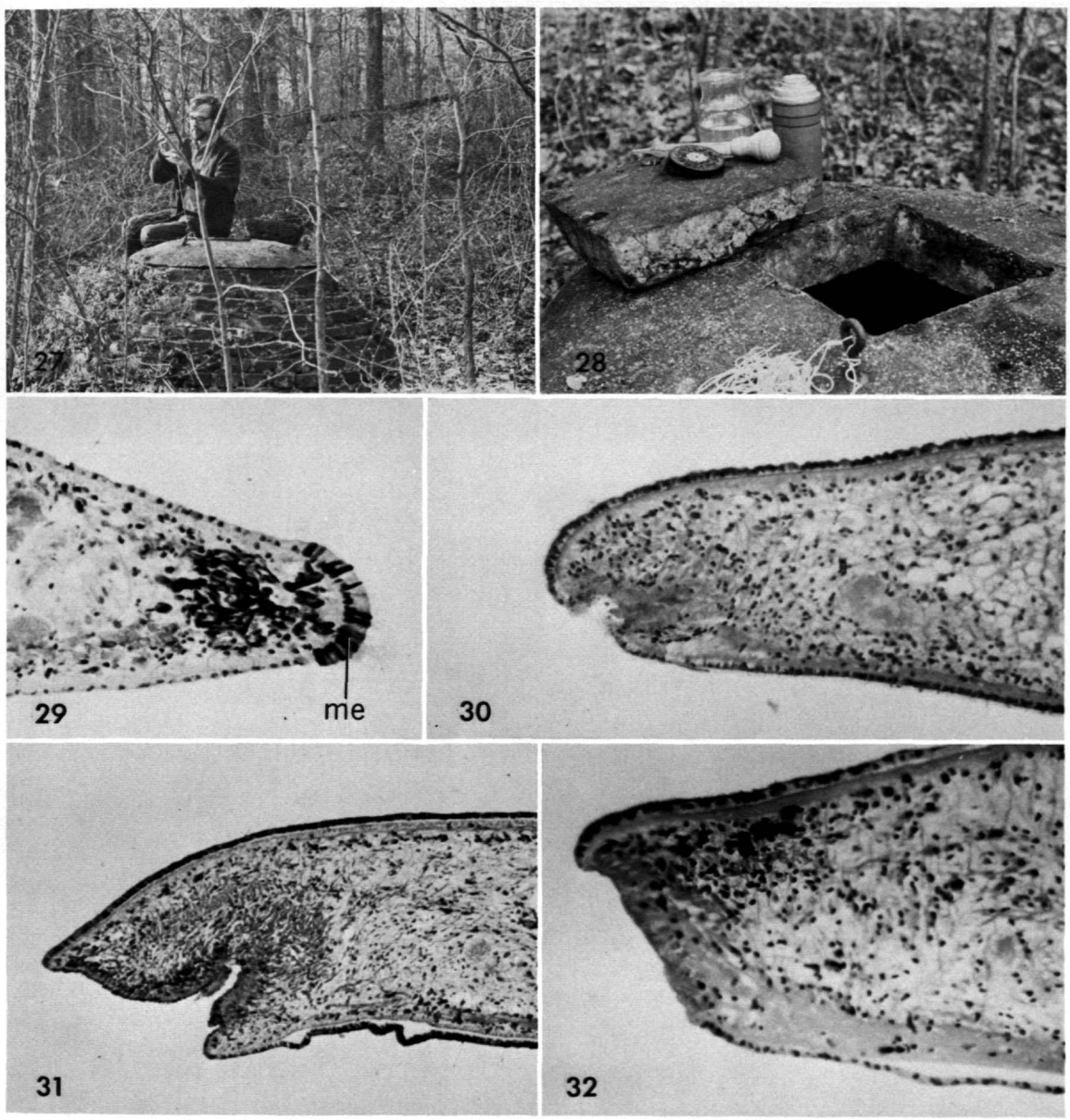
FIGURES 1–10.—*Sphalloplana,* photographs of living specimens: 1, *S. percoeca* from Williams Saltpeter Cave, Alabama, × 4.4; 2, *S. evaginata* from Garbage Hole Cave, Missouri, × 3.7; 3, *S. californica,* immature, from Bower Cave, California, × 4; 4, *S. californica,* mature, from Bower Cave, California, × 4.9; 5, *S. consimilis* from Gallohan Cave No. 1, Virginia, × 4.8; 6, *S. subtilis* from Biggers Spring, Virginia, × 4.4; 7, *S. holsingeri* from Biggers Spring, Virginia, × 4.9; 8, *S. pricei* from Refton Cave, Pennsylvania, × 3.5; 9, *S. hubrichti* from Kolms Cave, Missouri, × 3.6; 10, *S. chandleri* from Nashville, Tennessee, × 4.7.



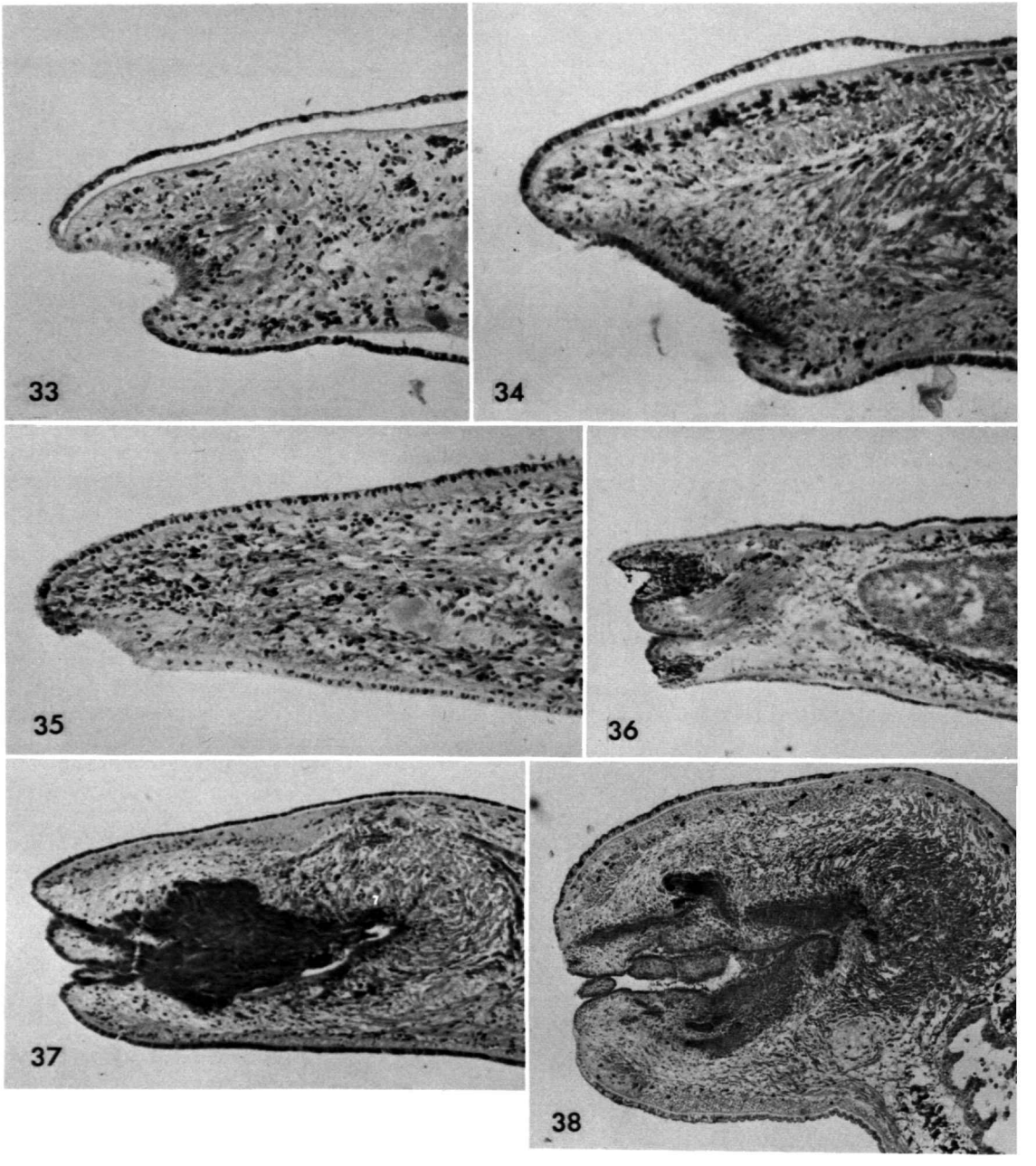
FIGURES 11–20.—*Sphalloplana,* outline drawings of living specimens, indications of pharynx and anterior intestinal border: 11, *S. percoeca,* redrawn from Buchanan (1936:196), × 6; 12, *S. evaginata,* × 3.6; 13, *S. subtilis,* × 6; 14, *S. holsingeri,* × 6; 15, *S. buchanani,* redrawn from Hyman (1937, fig. 16), × 7.3; 16, *S. mohri,* redrawn from Mitchell (1974:413, "*S. zeschi*"), used by permission of McGraw-Hill Book Company, × 3. 17, *S. culveri,* anterior end; 18, *S. holsingeri,* anterior end, showing intestinal area; 19, *S. pricei,* anterior end, showing intestinal area; 20, *S. evaginata,* anterior end, drawn from whole mount.



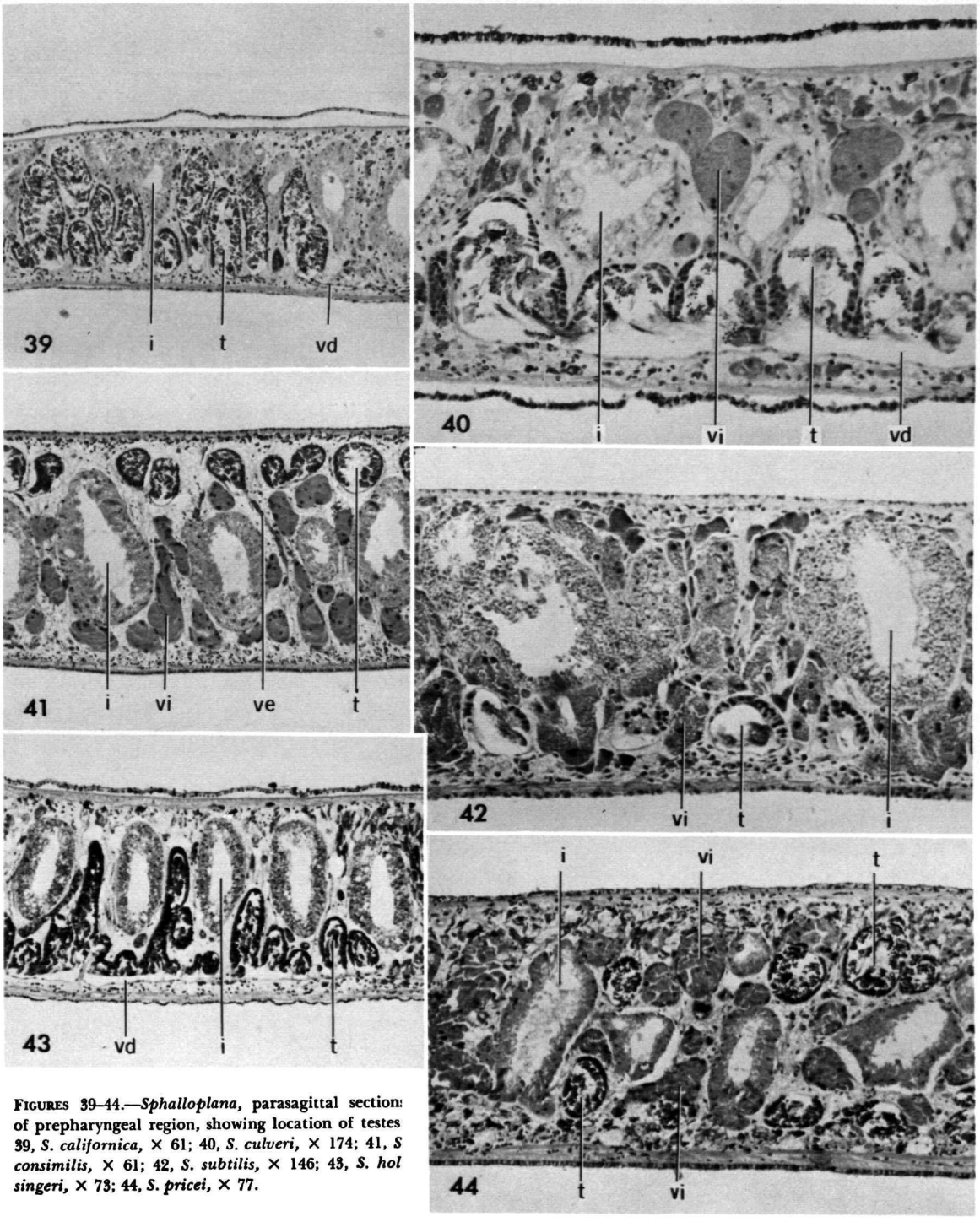
FIGURES 21–26.—*Sphalloplana*, outline drawings of living specimens, with indications of pharynx and anterior intestinal border: 21, *S. californica*, × 6; 22, *S. consimilis*, × 6.6; 23, *S. weingartneri* (redrawn from Carpenter's photograph), × 11.7; 24, *S. pricei*, × 4.3; 25, *S. hubrichti*, × 4.3; 26, *S. chandleri*, ×6.



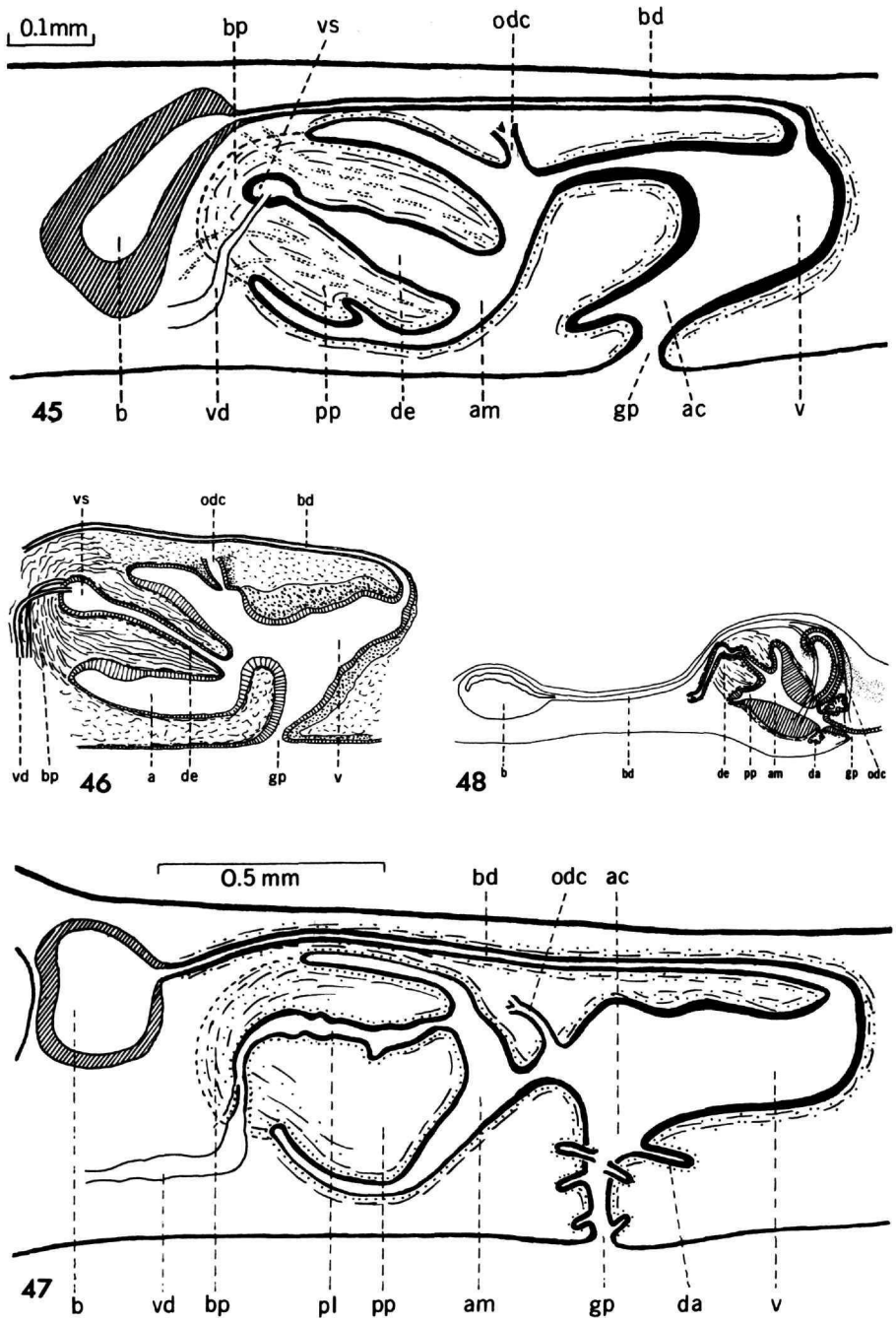
FIGURES 27–32.—Biggers Spring, Fairfax County, Virginia, type-locality: 27, 28, *Sphalloplana subtilis* and *S. holsingeri*. Transverse section of prepharyngeal region, showing differentiation of the marginal epithelium, × 186: 29, *Sphalloplana subtilis*. Adhesive organs in sagittal section: 30, *S. percoeca*, × 153; 31, *S. evaginata*, × 55; 32, *S. californica*, × 175.



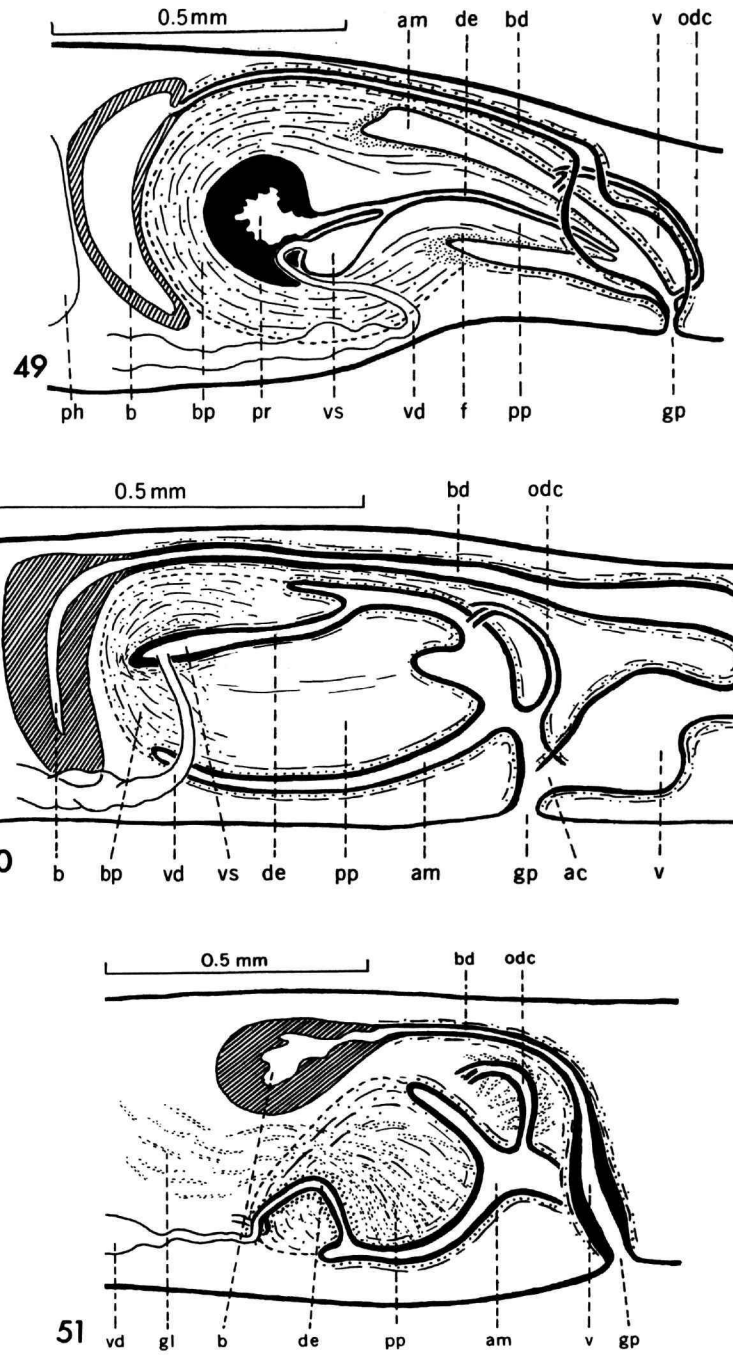
FIGURES 33–38.—Adhesive organs in sagittal section: 33, *S. culveri*, × 139; 34, *S. consimilis*, × 109; 35, *S. subtilis*, × 180; 36, *S. holsingeri*, not fully retracted, × 56; 37, *S. pricei*, × 62; 38, *S. chandleri*, × 64.



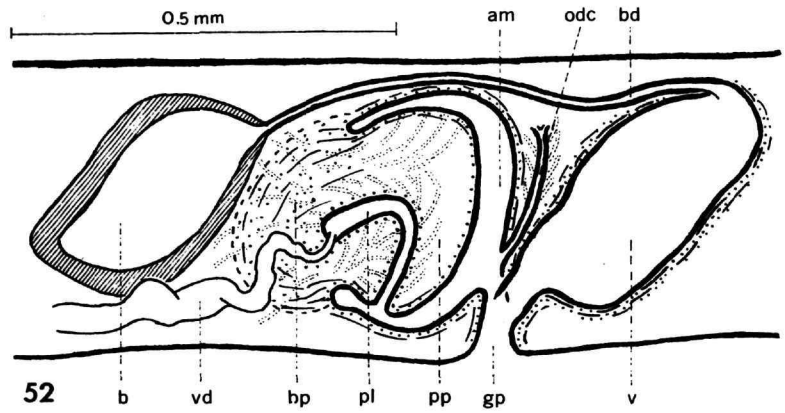
FIGURES 39–44.—*Sphalloplana*, parasagittal sections of prepharyngeal region, showing location of testes 39, *S. californica*, × 61; 40, *S. culveri*, × 174; 41, *S consimilis*, × 61; 42, *S. subtilis*, × 146; 43, *S. hol singeri*, × 73; 44, *S. pricei*, × 77.

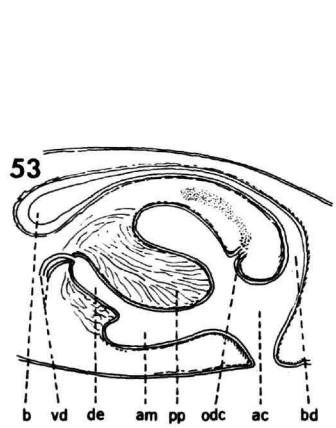


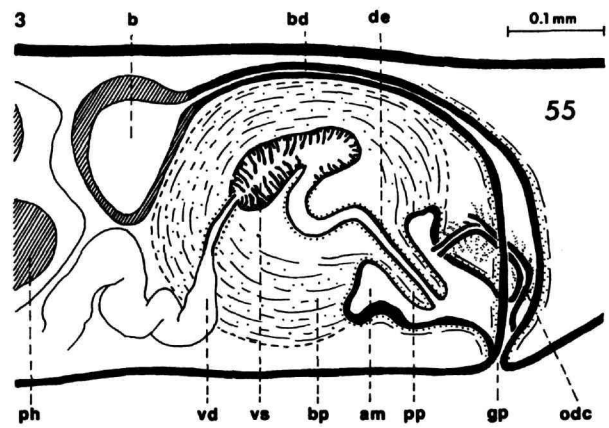
FIGURES 45–48.—Semidiagrammatic views of copulatory apparatus in sagittal section: 45, *S. percoeca* from Great Onyx Cave, Kentucky; 46, *S. georgiana*, after Hyman (1954:569), modified; 47, *S. evaginata* from Klump Cave, Missouri; 48, *S. kansensis*, after Hyman (1945:483), modified.

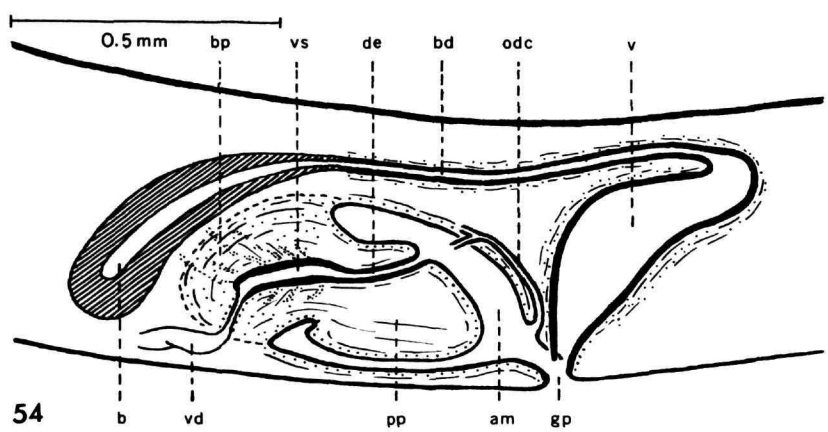


FIGURES 49–51.—Semidiagrammatic views of copulatory apparatus in sagittal section: 49, *S. californica* from Bower Cave, California; 50, *S. culveri* from Harper Cave, West Virginia; 51, *S. consimilis* from Gallohan Cave No. 1, Virginia.

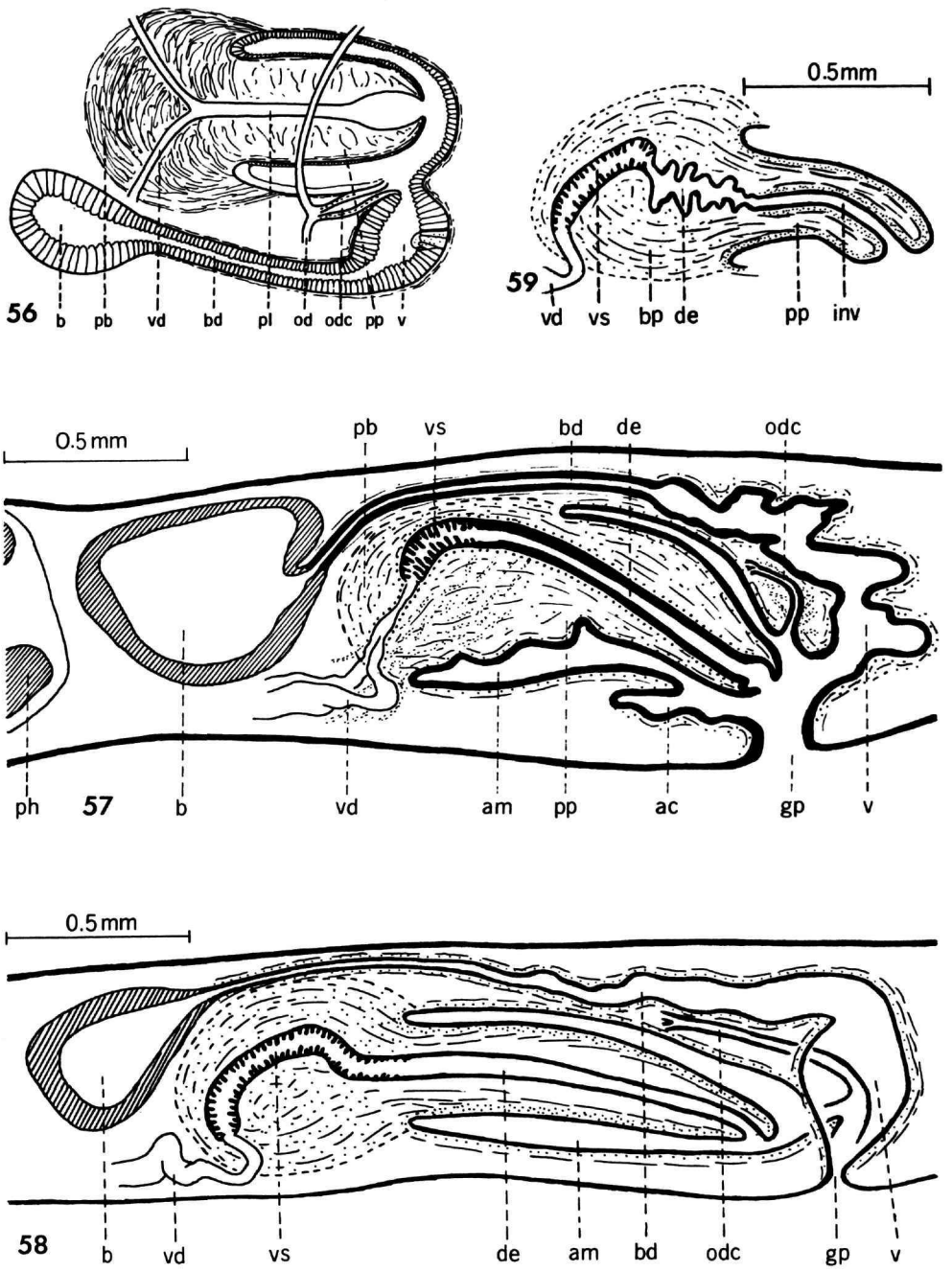




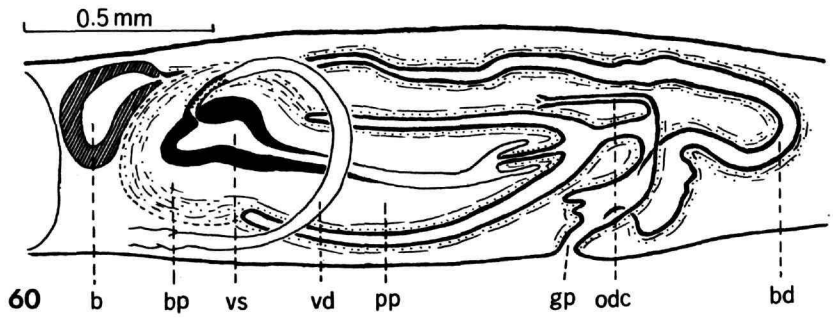


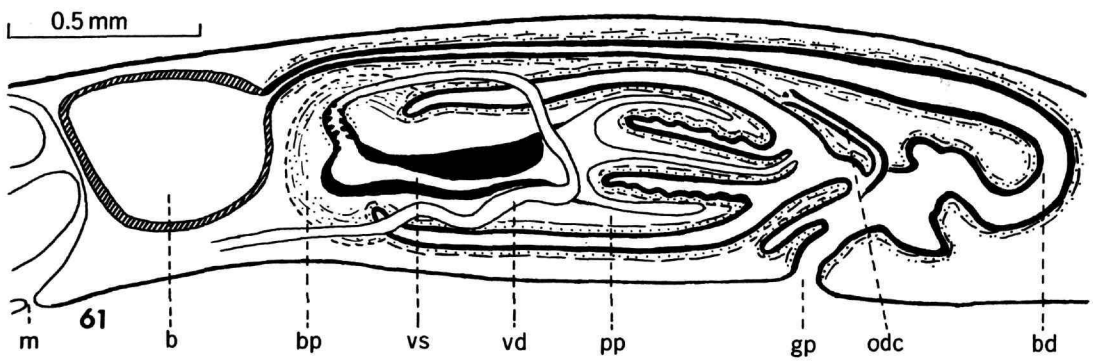


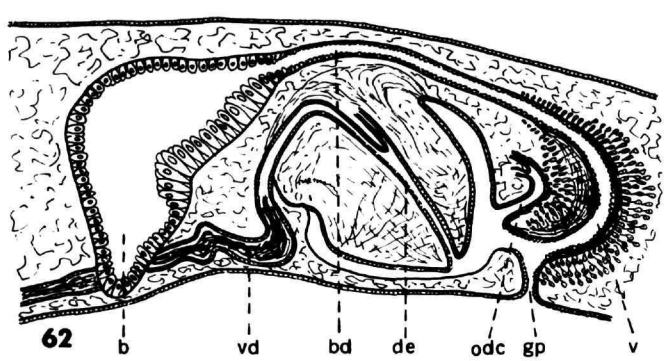
FIGURES 52–55.—Semidiagrammatic views of copulatory apparatus in sagittal section: 52, *S. subtilis* from Biggers Spring, Virginia; 53, *S. virginiana*, after Hyman (1945:483), modified; 54, *S. holsingeri* from Biggers Spring, Virginia; 55, *S. weingartneri*, after Kenk (1970:316).



FIGURES 56–59.—Semidiagrammatic views of copulatory apparatus: 56, *S. buchanani*, after Hyman (1937:467), dorsal view; 57, *S. pricei* from Refton Cave, Pennsylvania, sagittal section; 58, *S. hubrichti* from Richs Cave, Illinois, sagittal section; 59, *S. hubrichti* from Kolms Cave, Missouri, penis, sagittal.







FIGURES 60–62.—Semidiagrammatic views of copulatory apparatus in sagittal section: 60, *S. chandleri* from Nashville, Tennessee; 61, *S. chandleri* from Nashville, Tennessee; 62, *S. mohri*, after Mitchell (1968:606, *S. reddelli*), modified.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI–36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9b." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9b." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.