The Planarians (Turbellaria: Tricladida Paludicola) of Lake Ohrid in Macedonia

ROMAN KENK

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ABSTRACT

Kenk, Roman. The Planarians (Turbellaria: Tricladida Paludicola) of Lake Ohrid in Macedonia. *Smithsonian Contributions to Zoology,* number 280, 56 pages, 57 figures, 1978.—A revision is presented of the planarian fauna of the Lake Ohrid area, known for its richness in endemic species with limited distribution. Apart from the already known four endemic species of *Phagocata* and ten species of *Dendrocoelum,* six new species are described: *Dendrocoelum decoratum, D. dorsivittatum, D. minimum, D. albidum, D. sinisai,* and *D. translucidum.*

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Contents

The Planarians (Turbellaria: Tricladida Paludicola) of Lake Ohrid in Macedonia

Roman Kenk

Introduction

Lake Ohrid, situated in Macedonia astride the frontier between Yugoslavia and Albania, occupies a unique position among the lakes of Europe. It is a deep, ancient lake with an exceedingly rich endemic fauna of a relict nature, which has survived in the lake since the preglacial (Tertiary) period. A detailed discussion of the history, limnology, and biology of the lake has been presented by Siniša Stanković (1960) in his valuable monograph.

I studied the triclad fauna of the Ohrid region several weeks in the summers of 1935 and 1937. Samples of some of the species were also taken alive to my laboratory at the University of Ljubljana, Yugoslavia, and were kept and observed there in cultures maintained at a temperature of 10° C. Work on the accumulated materials was interrupted by my change of employment, first to the University of Puerto Rico and then to the Library of Congress in Washington, D. C. My appointment as Research Associate of the Smithsonian Institution enabled me to resume the long overdue work on the Lake Ohrid collections.

In the following discussion of the individual planarian species of the Ohrid region, I shall outline and illustrate the external and anatomical characters of each species, including those that already have been well described and analyzed in the previous literature, particularly in the classical paper by Stanković and Komárek (1927) and in later additions by Stanković (1938, 1969). Thus the essential features of this very interesting planarian fauna, now scattered in the literature, will be found combined in one paper, and the new observations will indicate possible variations in the appearance of the anatomical characters that are so important in the systematics of the group. The zoogeographic relations and the questions of the historical origin of the Ohrid fauna will not be repeated here, as they have already been discussed in detail by Komárek (1953a) and Stanković (1932, 1960).

My studies of the Ohrid planarians were made principally in the Bay of Ohrid in the northern part of the lake and in various tributary streams and their springs (see map, Figure 1).

With regard to the vertical distribution of the benthic fauna of Lake Ohrid, particularly in its northern part, the following ecological zones may be distinguished (Stanković, 1960:131–167): (1) an upper littoral zone or zone of water movement and/or emerging vegetation, from the water surface to a depth of 2–5 m; (2) a lower littoral zone, characterized chiefly by dense stands of several species of *Chara*, the Chara zone, at a depth of about 5–20 m; (3) the sublittoral zone or shell zone (mainly *Dreissena* shells), extending from 20 m to about 40–50 m; and (4) the profundal zone, below the shell zone to the bottom of the lake (286 m).

Specimens that are deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., are listed under the catalog numbers of the former United States National Museum (USNM).

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Roman Kenk, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D. C. 20560.

ably in the field collections. My thanks are due to Professor Siniša Stanković, then Director of the Hydrobiological Station Ohrid, who kindly extended to me the facilities of the station and permitted me the use of his personal boat in my work. Our stay at the station in 1937 was made even more enjoyable by the presence of our dear friend Dr. Walther Arndt of the Zoological Museum of Berlin, whose tragic death in 1944 shocked the worldwide community of his colleagues. Mr. Ivan Žnidaršič of Ljubljana prepared the watercolor paintings of living planarians reproduced in Figures 2–14. Dr. John C. Harshbarger and Mrs. Carolyn B. Gast of the Smithsonian Institution were helpful in the preparation and arrangement of the illustrations of the paper. Dr. Marian H. Pettibone kindly reviewed the paper for stylistic and topical errors. I am grateful also to the publishers who permitted me to reproduce some figures from their publications: Dr. W. Junk in The Hague, E. Schweizerbart's Verlagsbuchhandlung in Stuttgart, and Gustav Fischer Verlag in Jena.

Family DUGESIIDAE

The family Dugesiidae was first proposed by Ball (1971:24) in a section of his doctoral dissertation that was later (1974) published. The family is to include the genera *Dugesia, Cura, Bopsula,* and possibly *Rhodax,* which had previously been placed in the family Planariidae. The principal distinguishing character of the family is the opening of the oviducts, separately or after uniting, into the bursal stalk or rarely into the common atrium close to and posterior to the bursal stalk (Meixner's, 1928, types I and II). In the Planariidae, the common oviduct empties into the roof of the atrium (Meixner's type III). Ball (1974:376–378) subdivided the genus *Dugesia* into several subgenera that he later (1976) elevated to the rank of genera. I agree with Ball's separation of the family Dugesiidae from the Planariidae, but am not inclined to give the subgenera of *Dugesia* a full generic status.

Dugesia Girard

Dugesia gonocephala (Dugès)

MATERIAL DEPOSITED.—Sagittal serial sections of 1 specimen on 3 slides, USNM 55294.

This species, widely distributed in Europe, has been reported by Stanković (1960:248) as occurring in running waters in the Ohrid region. I observed it in the spring Elešec, about 2 km north of Peštani.

Dugesia lugubris (O. Schmidt)

Stanković (1960:248) states that this widely distributed European species occurs in stagnant waters in the Ohrid area. I collected it in a drainage ditch at Teferić, west of Struga.

Family PLANARIIDAE

Planaria Müller

Planaria torva (Müller)

This is another eurythermic species with a wide distribution in Europe. Stanković (1960:253) reports that one specimen was observed at the mouth of a brook at Studenčište, but none in the lake itself. I have not collected any mature specimens that could be assigned with certainty to this species.

Phagocata Leidy

The genus *Phagocata* in the wider sense, as indicated in my index (Kenk, 1974:40), is admittedly a very heterogeneous genus, widely distributed over the Northern Hemisphere. Most of the species of *Phagocata* described up to the early part of this century were placed by their authors in the genus *Planaria.* Komárek (1926a:9–10) was the first to attempt a subdivision of the European species of that genus when he arranged the representatives of *Planaria* into several genera and establish *Fonticola* and *Albiplanaria* for several white species of planariids in which the common oviduct opens into the genital atrium; the male atrium is not surrounded by radial muscle plates; and adenodactyls are lacking. Kenk (1930:293) and de Beauchamp (1932:272) did not accept *Albiplanaria* as a separate genus and included it in *Fonticola.* The genus, as defined above, today comprises a great number of species inhabiting Europe, Asia (including the Japanese islands), and North America. Hyman (1937:302) pointed out that one of the Ameri-

can species of the genus, *Planaria gracilis* Haldeman, had been placed by Leidy (1847:248) into a new subgenus, *Phagocata,* which predates Komárek's *Fonticola* and should therefore be applied to all species placed into *Fonticola.* This suggestion was followed by Dahm (1949), Gourbault (1972), and Kenk (1974) but was objected to by several European investigators, particularly Komárek (1953a: 275) and Reisinger (1960:289–290).

It is true that the about 50 species, now included in *Phagocata* because of the scheme of organization of their reproductive systems, represent a great variety of external features as well as specific anatomical characters. It would be very desirable if one could divide them at least into subgenera that would reflect natural (evolutionary) groups that would make sense also from a zoogeographical standpoint (see Ball, 1976:417–418). The three North American polypharyngeal species *(Phagocata gracilis, P. woodworthi,* and *P. nordeni)* with almost identical external habit but clearly different anatomical features, could be united in a subgenus *Phagocata* sensu stricto, as suggested by Reisinger (1960:290). *Fonticola* was used as a subgenus by Gourbault (1972:29) who, however, did not formally define it. *Atrioplanaria* de Beauchamp (1932:334), with five or six European species, may be considered a valid genus because of morphological as well as karyological peculiarities (Gourbault and Benazzi, 1977). Livanov and Zabusova (1940:96) established a separate genus *Penecurva* for four Asian species of different external aspects, in which the ejaculatory duct opens on the ventral side of the penis papilla rather than on its tip. Such a condition is observed also in several American species that have little else in common with the Asian forms. Thus, *Penecurva* is hardly tenable even as a subgenus.

When *Fonticola* is established formally as a subgenus or genus with a clear definition, it will comprise all *Phagocata* species of the Ohrid region, since the type-species of *Fonticola, Planaria olivacea* O. Schmidt, 1961, is a member of this species group.

The European species of *Phagocata,* generally designated under *Fonticola,* eliminating *Atrioplanaria,* are very similar in their external appearance: unpigmented (white, with one exception), two-eyed planariids with a truncate head, lacking prominent auricular appendages and anterior adhesive organs. The interspecific differences concern mainly their anatomical characters. Reisinger (1960: 289–291), a meticulous investigator of this group, lists the following features as distinctive attributes: presence or absence of a spermatopositor (a stiff tube attached to the spermatophore); number and arrangement of the excretory pores; epithelial conditions at the transition from the copulatory bursa to the bursa stalk; number of retinal clubs in the eyes; differences in the postembryonic development of the copulatory apparatus; and characteristic behavior of the animals in the search for food or for a copulatory mate. Not all these characters can be identified in preserved specimens; some must be investigated in living animals by special techniques.

The following species may be considered to be well established and readily distinguishable morphologically: *Phagocata vitta* (Dugès), *P. albissima* (Vejdovský), *P. olivacea* (Schmidt), *P. paravitta* (Reisinger), *P. bosniaca* (Stanković), *P. undulata* (Stanković), and *P. leptophallus* (Reisinger). On the other hand, the affinities of four species, distributed chiefly on the Balkan Peninsula, *P. macedonica* (Stanković), *P. dalmatica* (Stanković and Komárek), *P. ochridana* (Stanković and Komárek), and *P. illyrica* (Komárek), have been questioned, with good reason, by de Beauchamp (1932), Dahm (1958, 1967), and even by one of their authors, Komárek (1953a: 277; 1955:170). Not all the criteria enumerated by Reisinger can be applied to these species. I shall retain them for the time being until further detailed investigations can be carried out.

Phagocata ochridana (Stanković and Komárek)

FIGURES 15, 32

Fonticola ochridana Komárek, 1926a:9 [nomen nudum].
Fonticola ochridana Stanković and Komárek, 1927:643.
Fonticola ohridana.—Stanković, 1932:577.
Fonticola albissima var. *dalmatica.*—de Beauchamp, 1932:319 [in part].
Phagocata (?=*Fonticola*) *ochridana.*—Dahm, 1964:486.
Phagocata (*Fonticola*) *ochridana.*—Gourbault, 1972:32.
Phagocata ochridana.—Kenk, 1974:42.

MATERIAL DEPOSITED.—Sagittal serial sections of 7 specimens on 9 slides, USNM 55299–55305.

A good description of this species was given by Stanković and Komárek, based on materials from springs and streams in the Ohrid region.

EXTERNAL FEATURES (Figure 15).—This is a rather slender species, sexually mature specimens measuring up to 8 mm in length and 0.8 mm in width.

The anterior end is truncated, with a convex frontal margin and rounded lateral corners. There is no narrowing or neck behind the head. The lateral body margins diverge only slightly behind the anterior end, then run parallel up to the level of the copulatory complex where they begin to converge to form a bluntly pointed or nearly rounded tail end. The two eyes are far removed from the frontal margin and lie close together at a distance of one-fifth to one-fourth the width of the head. The body is unpigmented, white. The pharynx is inserted at about the middle of the body or slightly behind it and measures one-seventh the body length. The copulatory apparatus occupies the anterior two-fifths of the postpharyngeal region. The anterior ramus of the intestine ends at, or somewhat behind, the level of the eyes. The animals move by gliding only, never by "crawling."

ANATOMY.—The testes extend from the level of the ovaries backward to near the posterior end. They are situated, in general, nearer to the ventral than to the dorsal body wall, though a few testes may be placed in a more dorsal position and individual testes may occupy almost the entire dorsoventral diameter of the body. The structure and situation of the ovaries show no pecularities. Vitellaria or yolk glands are found in the mesenchyme of the entire body, except the head, and are particularly numerous in the spaces lateral to the zone of testes.

In the copulatory apparatus (Figure 32), the genital opening leads directly into the genital atrium which is not divided into the usual two chambers. In several specimens, however, histological differences were seen in the epithelium lining the atrial cavity. The anterior part, which would correspond to a male atrium, had a normal, cuboidal or cylindrical, nucleate epithelium, while in the posterior section, the common atrium, the epithelium was infranucleate.

The size, shape, and position of the male copulatory organ appear, in the majority of my specimens, as shown in Figure 32. The bulb of the penis is of moderate size and hemispherical. Its musculature is rather weak, the muscle fibers being densest near the periphery of the bulb. The free penis or penis papilla is conical or finger shaped, somewhat curved ventrally, its pointed tip reaching to the dilated genital pore. The papilla is covered with a cuboidal or flattened epithelium, beneath which is a well-developed layer of circular muscle fibers, followed by a thinner layer of longitudinal muscles. The two vasa deferentia enter the penis bulb laterally and acquire a coat of circular muscles. They first pass toward the midline of the organ, then turn posteriorly, enter the base of the penis papilla, and open closely together, but separately, into the penis lumen. This lumen is a straight canal, the ejaculatory duct, running in the axis of the papilla and opening at its tip. Histologically, it is differentiated into three sections. A short anterior portion is lined with very tall cells, the distal parts of which are bent posteriorly and form a villus or plug filling the lumen of the canal. This part has been likened to a seminal vesicle by Stanković and Komárek. The following section of the canal has a rather flattened epithelium, the cells of which are pierced by numerous gland ducts with a granular, strongly eosinophilic secretion. The third, most distal region of the penial lumen is usually somewhat widened and lined with taller cells with apparently secretory function. It narrows again at the tip of the papilla. At least the anterior two sections of the penis lumen have a thin coat of circular muscle fibers. A considerable variation in the length and shape of the penis was observed even in animals collected in the same locality. These differences are, undoubtedly, due to muscular contractions of the organ. The two main muscular systems of the penis, i.e., the peripheral layer of the penis bulb and the powerful circular muscles of the papilla, both effect, when contracted, an elongation of the penis and its protrusion through the gonopore; much of the soft parenchymal tissue of the bulb is pressed into the base of the penis papilla. On the other hand, a relaxed state of the muscles will result in a shorter and broader shape of the organ; such a retraced penis has a more voluminous bulb. The outer covering of the papilla appears to be a cuboidal epithelium in the shortened penis, a flattened one in the elongated organ. The histological differentiation of the penial lumen is related to its function of forming a spermatophore during (or before?) copulation. The most anterior section, though it is not widened in this species, may play the role of a seminal vesicle as Stanković and Komárek (1927: 625) assume. A comparison with closely related species indicates that the middle part of the lumen

produces the chitinoid stalk or spermatopositor, and the distal section the capsule of the spermatophore (cf. "*Fonticola albissima* var. *illyrica*" in de Beauchamp, 1932:317).

The two oviducts, running above the nerve cords, are equipped with accessory seminal receptacles or modified yolk funnels, as Reisinger (1963:686–687) has demonstrated. In the region of the copulatory complex they ascend dorsally and medially, the left one passing between the genital atrium and the bursal stalk. They unite dorsally to the atrium to form a rather long, somewhat curved common oviduct that opens into the posterior part of the atrium. The end parts of the paired oviducts and the greater part of the common oviduct are connected with numerous eosinophilic shell glands. The copulatory bursa varies in size and shape according to the state of maturity. Its lumen frequently contains remainders of one or more spermatophores and/or spermatopositors. The bursal stalk proceeds from the bursa dorsally to the penis, then shifts to the left of the midline, increasing gradually in its outer and inner diameters, and joins the genital atrium from the left side near the gonopore. Sometimes a differentiation of the epithelium lining of the duct is seen. The anterior part, adjoining the bursa, always has a normal, nucleate, cuboidal epithelium, while the posterior section, connecting with the atrium, may show partly or wholly infranucleate cells.

Numerous eosinophilic glands open into a large area of the epidermis surrounding the genital aperture, the function of which is not quite evident. Their secretions may serve for the attachment of the egg capsules (cement glands) or else may play a role during copulation.

DISTRIBUTION AND ECOLOGY.—*Phagocata ochridana* occurs in the Ohrid region in a great variety of habitats. Stanković and Komárek found it originally in springs near Sveti Naum and in the large limestone spring Šum. Later, Stanković (1934:167; 1938:9; 1955b:288) extended its known occurrence first to the littoral zone of Lake Ohrid and to littoral springs of Lake Janina (Ioannina) in the Greek Epirus, and then to the sublitoral and profundal zones of Lake Ohrid. Obviously, Stanković's interpretation of the species includes a form that was designated by Reisinger (1960:274) as a separate species, *P. stankovici*.

I collected *Phagocata ochridana* in the following localities: Studenčište, at the Hydrobiological Station, in cold springs and warmer pools, under stones, and also on water plants; Bej-Bunar, northeast of the station, where it is rare in the cold spring itself, more common in the creek and in ditches with warmer water, and under stones; a small spring near Elešec (north of the village of Peštani), together with *Dugesia gonocephala*; springs at the monastery of Sveti Naum; spring Šum (about 1 km south of Zagračani, near Struga), where the species is absent in the cold springs (8.2° C, 7 September 1935) but occurs in warmer parts (up to 11.7° C), under stones; an irrigation ditch at Teferić, west of Struga; in Lake Ohrid, the species was found in Ohrid Bay and near Kalište from the shoreline down to the shell zone.

A lot of *Phagocata ochridana* was cultured for two generations in the laboratory, with beef liver offered as food. No asexual reproduction was observed in the cultures.

TAXONOMIC POSITION.—*Phagocata ochridana* was first recorded by Stanković (1926:238) as a continental variety of *P. olivacea* (Schmidt). Stanković and Komárek (1927:643) described it as a separate species. De Beauchamp (1932:319) considered it to be a probable synonym of *P. dalmatica* (Stanković et Komárek), which he cited as "*Fonticola albissima* var. *dalmatica*." This assumption was accepted also by Komárek (1953a:278) and by the majority of later authors who made reference to the species. On the other hand, Stanković (1960:177) preferred to keep the species separate "for reasons of biogeographical order." Reisinger (1963:687) pointed out that accessory seminal receptacles on the oviducts have been found only in a few species of "*Fonticola*," *F. ochridana*, *F. maculata*, and *F. leptophallus* Reisinger, but apparently he did not examine *P. dalmatica* for their occurrence. Reisinger (1960:274) also separated from Stanković's *P. ochridana* a form inhabiting the deeper zones of Lake Ohrid, which he designated as a new species, *P. stankovici*.

Considering that these three forms are still open questions, for the time being I am keeping the common Ohrid *Phagocata* as a separate species to avoid a possible confusion when a more thorough comparison can be made, an investigation that should include experiments on the possibility of interbreeding. It seems to me quite probable that

all three will unltimately prove to be one species, *Phagocata dalmatica* (Stanković and Komárek).

Phagocata stankovici (Reisinger)

FIGURES 13, 16

Fonticola stankovici Reisinger, 1960:274
Phagocata stankovici.—Kenk, 1974:43.

MATERIAL DEPOSITED.—Sagittal serial sections of 3 specimens on 3 slides, USNM 55306–55308.

This species was briefly characterized by Reisinger as differing from *Phagocata ochridana* by having a precerebral extension of the intestine, without other morphological data being given.

EXTERNAL FEATURES (Figure 13).—*Phagocata stankovici* is externally very similar to *P. ochridana*. It is somewhat smaller than the latter species, 5 mm long and about 1 mm wide. The anterior end appears to be more rounded. The two eyes, separated from each other by about one-fourth the width of the head, are a little bigger than those of *P. ochridana*. The end of the anterior intestinal trunk forms an unbranched extension that reaches in the midline to a level anterior to the eyes. This seems to be the only essential external character that separates *P. stankovici* from *P. ochridana*. The length of the pharynx amounts to one-seventh the body length, and the copulatory complex lies in the anterior half of the postpharyngeal region.

ANATOMY.—All anatomical features recognizable in preserved specimens are identical with those of *Phagocata ochridana*. I see no differences between the two species in the configuration of the reproductive system, which makes a redescription here unnecessary.

DISTRIBUTION AND ECOLOGY.—Several specimens of *Phagocata stankovici* were collected in Ohrid Bay in the sublittoral (shell) zone at a depth of about 20 m, and one specimen was recovered from two samples of mud dredged from 67 and 90 m, respectively. The statement by Stanković (1955b: 288) that *P. ochridana* inhabits all vertical zones of the lake apparently includes *P. stankovici* under that species.

Phagocata stankovici was kept in the laboratory at 10° C on a diet of beef liver. The animals deposited many spherical or slightly ovoid unstalked egg capsules of 0.6–0.9 mm diameter.

TAXONOMIC POSITION.—It is with some reluctance that I list *Phagocata stankovici* as a separate species different from *P. ochridana*. If the sole distinguishing character is the extent of the anterior intestinal ramus, it would not justify giving the form the rank of a species. In the American *P. morgani* (Stevens et Boring), the ramus extends to in front of the eyes in young specimens but ends behind the eye level in the adults. It is true that the difference between *P. stankovici* and *P. ochridana* remains constant and unaltered in the laboratory cultures for several months. In *Hymanella retenuova* Castle, belonging to a genus closely related to *Phagocata*, individuals with precerebral and postcerebral gut trunks occur mixed in the same population. It will be necessary to study the behavior and possibly the karyological characters of the two forms before arriving at a definitive conclusion as to their status.

Phagocata maculata (Stanković)

FIGURES 12, 22, 33

Albiplanaria maculata Stanković, 1932:577.
Fonticola maculata.—Stanković, 1938:7.
Phagocata (?=*Fonticola*) *maculata*.—Dahm, 1964:487.
Phagocata (*Fonticola*) *maculata*.—Gourbault, 1972:33.
Phagocata maculata.—Kenk, 1974:42.

MATERIAL DEPOSITED.—Sagittal serial sections of 4 specimens on 5 slides, USNM 55295–55298.

EXTERNAL FEATURES (Figures 12, 22).—Species is rather small, mature individuals having a length of 3–5 mm and a width of 0.75–1 mm. Stanković (1938:7) estimated the size of living specimens from his preserved materials as being 6–8 mm, more than I measured in living animals. The general shape of the body is similar to that of *Phagocata ochridana*. The frontal margin is somewhat more pointed than in the latter species. It may be recalled that the outline of the head in the different species of *Phagocata*, as well as in other freshwater triclads, is subject to considerable variation according to the physiological state of the animals, the temperature, and other environmental factors. If a cold-stenothermic animal is examined in a dish with cold water that is gradually warming up during the time of observation, certain changes in the behavior of the animal may be noticed. It becomes rather active, glides around restlessly, performs searching movements, etc. During such increased activity, the anterior part

of the body is sometimes excessively elongated and narrowed. This fact makes it occasionally difficult to recognize the "normal" shape of the head and may account for certain discrepancies in the descriptions of one and the same species given by different observers or by the same observer at different times. In *P. maculata,* no narrowing or neck behind the head is seen. The two eyes lie close together at a mutual distance amounting to one-fourth to one-third the width of the head. The root of the pharynx is anterior to the middle of the body length.

The outstanding characteristic of the species is the pigmentation of the dorsal side. While the entire ventral surface, the head, and the marginal parts of the dorsal side are white, the middorsal area is pigmented in various ways. Usually there is one large spot of brown or almost black pigment some distance behind the eyes (Figure 22A,C,D). Toward the head and the lateral margins, the pigmentation gradually fades out, while a faintly brown middorsal pigment band extends toward the posterior end. Or, there may be a pair of spots in the prepharyngeal region, one on each side of the unpigmented midline (Figure 22B,E,F). The rest of the middorsal area behind the spots may show just a touch of pigment, with the midline remaining white. The pigmentation is granular, often cloudy or even spotty in appearance. Stanković (1938:7) indicated that the general color was light yellow and not white. His description, however, was made from specimens that had been preserved for about 12 years. The yellowish ground color possibly was not natural or may have been due to the pale brownish tint of the middorsal area.

ANATOMY.—The pigment of *Phagocata maculata* consists of fine granules enclosed in the cells of the mesenchyme underlying the layer of integumental muscles of the dorsal side. Only little pigment is seen between the muscle fibers.

The anatomy of the reproductive system links the species closely to the white phagocatas of the Balkan Peninsula. The distribution and arrangement of the testes are the same as in *P. ochridana* and *P. stankovici.* In fully mature specimens, many testes extend throughout the entire dorsoventral diameter of the mesenchyme, as in *P. stankovici.* According to Reisinger (1963:687), the oviducts in their anterior course have accessory seminal vesicles similar to those of *P. ochridana.*

The description and figure of the copulatory apparatus of *Phagocata maculata* by Stanković (1938: 7–8) are fairly accurate. There is no separate common genital atrium developed, as the male atrium reaches to the gonopore. The penis has a small bulb and a conical pointed papilla, somewhat curved ventrally (Figure 33). The layer of circular muscles underlying the external epithelium of the papilla is rather thick. The penial lumen is a straight tube in the axis of the papilla, formed by the union of the two vasa deferentia (*vd*) and showing the same three sections as in *P. ochridana*: an anterior section (*vs*), only slightly widened, filled with a plug of elongated cells, representing the seminal vesicle; a tubular middle section, receiving the outlets of eosinophilic gland ducts, presumably the section forming the spermatopositor of the spermatophore; and a distal section of somewhat wider diameter, lined with taller cells and opening at the tip of the papilla. I was not able to see a small diverticulum or cul-de-sac at the anterior end of the penial lumen as illustrated by Komárek (1953a, fig. $1B_2$).

The copulatory bursa (*b*) in some of my specimens contained remains of spermatophores. Its outlet, the bursal duct (*bd*), opens into the genital atrium from the left side, close to the genital pore. Its anterior section is lined with a normal nucleate epithelium, its posterior part with an infranucleate epithelium.

DISTRIBUTION AND ECOLOGY.—*Phagocata* is a comparatively rare species inhabiting the sublittoral shell zone of Lake Ohrid. Stanković originally collected 8 specimens in Ohrid Bay from depths of 25–35 m. My materials of about 20 specimens were dredged in the same locality at depths between 18 and 30 m. One immature individual, kept in a laboratory culture, reached sexual maturity.

TAXONOMIC POSITION.—Both Stanković (1938:7) and Komárek (1953a:277) stressed the similarity of the anatomy of *Phagocata maculata* with that of *P. macedonica* or *P. illyrica,* and Komárek expressed the opinion that *P. maculata* might be interpreted as being a small depth race ("Tiefenrasse") of the white *P. illyrica.* Since the extent and intensity of the pigmentation of *P. maculata* shows an exceedingly wide range of variation, I am inclined to attribute only a subordinate taxonomic value to this character. Nevertheless, in view of the gaps in our knowledge of its behavior, life history, and karyo-

logical and genetic conditions, I am keeping it tentatively as a separate species.

Phagocata undulata (Stanković)

FIGURES 23, 28A,B, 34

Fonticola undulata Stanković, 1960:178.
Phagocata (?=Fonticola) undulata.—Dahm, 1964:487.
Phagocata (Fonticola) undulata.—Gourbault, 1972:33.
Phagocata undulata.—Kenk, 1974:43.

MATERIAL DEPOSITED.—Sagittal serial sections of 3 specimens on 9 slides, USNM 55309-55311.

Phagocata undulata has been known only from a figure by Stanković (1960: 177, fig. $68b_2$).

EXTERNAL FEATURES (Figure 23).—Mature animals attain a length of 8 mm and a width of 2 mm. The species is characterized by a strikingly beautiful shape that is unique not only among the representatives of the genus *Phagocata,* but among the freshwater triclads in general. The lateral margins of the body are thrown into almost regular, wave-like curves and folds that give them a peculiar scalloped appearance. The number of folds on either side is from six to eight, in nearly symmetrical arrangement. The inner margins of the folds extend over the dorsal surface of the body. Except on the frontal outline of the head and the tip of the posterior end, the margin has a row of short conical papillae. The curves and folds are constant features and are distinct in resting as well as gliding animals. They should not be confused with the transitory wavy ruffles that appear in many planarians, particularly in dendrocoelids, when the body is contracted during "crawling" movement or at rest. The frontal margin of the head is more or less rounded or forms a blunt angle at the anterior tip. The body is widest at about the region of the pharynx. The posterior end is usually pointed during locomotion. The animal is unpigmented, white, and rather transparent. The two eyes are situated very close together at a distance of about one-sixth the width of the head, and removed from the frontal margin. The pharynx lies approximately at the middle of the body or somewhat behind it. The intestine is clearly visible in the living animal because of the transparency of the body. The anterior intestinal ramus ends at the level of the eyes and bears on each side four to five lateral branches, which themselves are ramified. Each posterior ramus has many small lateral branches and several short medial branches. The animal moves exclusively by "gliding," never by "crawling."

ANATOMY.—The usual smooth, ciliated epithelium is found only on the ventral surface of the body, covering the area that is in contact with the substrate (Figure 28B). The entire dorsal surface and the folds and papillae of the marginal region are covered with a modified epithelium consisting of conical or hemispherical cells lacking cilia (Figure 28A). Each cell contains a large number of small rhabdites surrounding the nucleus. Another type of epithelium occurs along the frontal margin of the head, forming a narrow strip to either side of the midline, immediately above the submarginal zone of adhesive cells. This epithelium is ciliated, infranucleate, and contains very few small rhabdites. Apparently the two strips represent the auricular sense organs.

In the reproductive system, the numerous testes lie predominantly close to the ventral side of the body. Only few are situated more dorsally, particularly in sections where the testes are very crowded. The testicular zone begins immediately behind the ovaries and extends posteriorly almost to the tail end.

The copulatory organs (Figure 34) correspond closely to the scheme characteristic of the Balkanic representatives of the genus *Phagocata.* The genital pore (*gp*) leads into a relatively small common atrium (*ac*) that connects anteriorly with the male atrium (*am*), the two chambers not being marked off distinctly. The penis consists of a rather small bulb and a conical papilla. The musculature of the bulb is weak, developed mainly near its periphery. The papilla, on the other hand, possesses powerful muscles arranged in a thick layer of circular fibers and a thinner one of longitudinal muscles beneath the outer epithelium. The two vasa deferentia (*vd*) approach the ventral part of the penis bulb, penetrate it in a medial direction, then turn dorsally and open into the moderately wide lumen of the penis. This lumen is divided histologically into three sections, as is the case also in *P. ochridana* and *P. maculata.* At the openings of the vasa deferentia, the epithelium of the lumen consists of very tall cells that are directed toward the papilla and form a plug filling the lumen. Posterior to the plug, the ejaculatory duct (*de*) is lined with a flatter epithelium that is pierced by numerous

eosinophilic gland ducts. Great masses of their secretion are found in the tissues surrounding this region, in the parenchyma of the penis bulb, and adjoining parts of the papilla, particularly in the ventral half of the organ. This secretion is apparently used in the formation of the spermatopositor of the spermatophore. The third section of the penial lumen is usually somewhat widened, lined with a taller epithelium, and opens into the atrium at the tip of the penis papilla.

The two oviducts unite dorsally to the male atrium forming the common oviduct (*odc*) that opens into the atrium. The end parts of the paired oviducts and the upper three-fourths of the common oviduct are equipped with shell glands. The copulatory bursa (*b*) sometimes contains remnants of spermatophores. The stalk of the bursa (*bd*) runs somewhat left of the penis, starting from the bursa as a narrow canal, then curving ventrally while gradually becoming wider, and opening into the common genital atrium from the left side. A large number of eosinophilic gland ducts (*gl*) open in the area surrounding the genital pore.

Ecology and Distribution.—A total of 32 specimens of *Phagocata undulata* were collected in August 1937 in Ohrid Bay by dredging at depths between 16 and 26 m in the shell zone of the sublittoral. All animals were small, generally about 3 mm long, and immature. They were placed in a culture maintained at a temperature of 10° C and fed beef liver. They grew and developed sexual structures after several months. Several cocoons were laid and many young hatched between January and May 1938, after which the culture was discontinued. No reproduction by fission occurred in the culture. The fact that only immature animals were collected in August may indicate that reproduction in the lake takes place at some other season, possibly in winter or spring.

Two specimens were observed in copula. They rested at the bottom of the culture dish, parallel to each other, both heads pointing in the same direction The anterior parts of their bodies were attached to the substrate, while the posterior parts were twisted in such a way that the ventral surfaces of the two animals were pressed against each other. When the animals were pulled apart, the two penes could be seen protruding from the genital pores.

Taxonomic Position.—The peculiar differentiation of permanent folds and papillae along the margin of the body is not duplicated in any other species of freshwater planarians so far known. *Phagocata papillifera* (Ijima and Kaburaki) of Japan has a linear series of 20 to 25 small papillae along the middorsal line. Numerous papillae spread over the dorsal surfaces are known to occur in two species of Lake Baikal in Siberia, *Sorocelis leucocephala* Zabusov and *Planaria papillosa* Korotnev, both now placed in the genus *Papilloplana* (= *Thysanoplana* Graff, not Plehn). In an earlier paper (Kenk, 1930: 148), I expressed my doubts as to the taxonomic value of projections on the body surface (papillae, etc.). *Phagocata undulata* fully confirms this opinion. The anatomical structure of the species entirely conforms with the scheme observed in the genus *Phagocata* and, moreover, the species is more closely related to the Balkanic representatives of the genus than to the remaining *Phagocata* species of the Eastern and Western Hemispheres. In particular, it is the detailed structure of the male copulatory organ that resembles closely that of *P. ochridana* and related forms. *Phagocata undulata* is, therefore, despite its striking external habit, a typical member of the genus *Phagocata.*

Crenobia Kenk

Crenobia alpina montenigrina (Mrázek)

Material Deposited.—Sagittal serial sections of 1 specimen on 3 slides, USNM 55252.

This polypharyngeal subspecies of the widely distributed alpine planarian, found in many places in the Balkan Peninsula, is a cold-stenothermic form inhabiting springs and streams in the Ohrid region. Stanković and Komárek (1927:647) found it in the large spring Šum and in the outlet of Lake Ohrid, the river Drim. It is very numerous in the spring Bej-Bunar, where it occurs in the company of *Dendrocoelum maculatum, D. sanctinaumi, D. adenodactylosum, D. jablanicense, Phagocata ochridana,* and *Polycelis tenuis.* I collected it also in Šum, together with four endemic Ohrid species of the genera *Dendrocoelum* and *Phagocata,* and in three small springs near Velestovo.

Polycelis Ehrenberg

Polycelis tenuis Ijima

Material Deposited.—Sagittal serial sections of 2 specimens on 3 slides, USNM 55312-55313.

This ubiquitous eurythermic European species, generally inhabiting stagnant waters, was observed in the Ohrid region in several streams (but never in Lake Ohrid): in the creek Kulinčivljik na Sinoru at the town of Ohrid, also in Bej-Bunar, and at Studenčište.

Family DENDROCOELIDAE

Dendrocoelum Örsted

The dendrocoelids of Lake Ohrid were first placed into a new genus, *Neodendrocoelum,* established by Komárek (1926a:7), who listed among their distinguishing characteristics the large size of the adenodactyl (which is larger than the penis) and the configuration of the atrial cavity. This cavity consists of two compartments: a long cavity named "atrum genitale," which contains the papilla of the penis and receives the mouth of the common oviduct in its posterior part; and a compartment designated as "atrium copulativum," enclosing the papilla of the adenodactyl and connecting with the opening of the bursal stalk. These two cavities unite only near the genital pore. No "atrium commune" is developed. The species have one pair of eyes and are either white or pigmented.

Stanković and Komárek (1927:596–598) mentioned the same characteristics of the genus and added that the penis has a wide lumen and that its papilla may be invaginated, resembling a flagellum.

Kenk (1930:300) included *Neodendrocoelum* in the genus *Dendrocoelum* and distinguished only two subgenera, *Dendocoelum* sensu stricto and *Paradendrocoelum,* which differ in the course of their oviducts.

Later authors have not accepted Kenk's subdivision of the genus *Dendrocoelum.* De Beauchamp (1931:157; 1932:207–208), who studied the genus most intensively based on copious material, divided it into eight subgenera. He accepted *Neodendrocoelum* as a subgenus of *Dendrocoelum* after some hesitation, but stated that it was not clearly separable from the subgenus *Dendrocoelides.* He added to the characteristics of the subgenus the presence of a glandular field around the genital opening and peculiarities in the histology of the oviducts. He excluded one of the Ohrid species, *N. jablanicense,* from *Neodendrocoelum* and placed it in the subgenus *Eudendrocoelum* with a question mark. Gourbault (1972), the latest reviser of the genus *Dendrocoelum,* followed essentially de Beauchamp's arrangement.

Komárek (1953a:303) accepted the status of *Neodendrocoelum* as a subgenus of *Dendrocoelum* and also included *Dendrocoelum subterraneum,* a blind species described earlier from a cave in Croatia.

Stanković (1960:178–179, 263), in evaluating the taxonomic rank of *Neodendrocoelum,* repeated the previously enumerated characters of the taxon and considered it "more prudent to keep *Neodendrocoelum* provisorily as a distinct genus precisely because of its peculiar geographic distribution."

Reisinger (1971:117–119) discussed the interrelationships of the various genera or subgenera of the *Dendrocoelum* group. He came to no conclusion about the definite rank of *Neodendrocoelum,* but was inclined to consider it an acceptable genus.

It is very difficult to establish clear criteria for the demarcation of *Neodendrocoelum* from other species groups of the *Dendrocoelum* complex. The division of the genital atrium into two compartments, the genital and copulatory atria, is seen also in other members of the subgenus *Dendrocoelides,* where the cavities are generally designated as the male and the common atria. The relative sizes of penis and adenodactyl are subject to great variation within the genus and cannot be used as an important systematic character. The glandular field around the gonopore may be seen also in other species of the genus, perhaps to a lesser degree, and it is also not prominent in all Ohrid species.

In view of this complex situation, I prefer to leave the question of the validity of *Neodendrocoelum,* even as a subgenus, open to further investigations. New criteria may possibly be found in the analysis of the chromosome morphology or in biochemical studies of the species concerned.

As has been pointed out very appropriately by Komárek (1953a:303; 1953b:269), the copulatory apparatus of a great number of the species of *Dendrocoelum* of the Ohrid region exhibits a surprising conformity, which would make it very difficult to identify the individual species by its anatomy alone. Variations within the apparatus are often only of a quantitative nature or are due to various states of muscular contraction, stages of sexual maturity, or employment of different fixing agents. It is, therefore, necessary to look for other charac-

ters as well, such as the general proportions of the body, the exact shape of the anterior end, the situation and arrangement of the testicles, the development of the subepidermal musculature, the behavior of the animal in life, and the pattern of pigmentation. Pigmentation is generally considered to be a rather variable and taxonomically not very reliable character. Nevertheless, it is the most obvious and most easily recognizable feature of the Ohrid species.

Species that were available to former workers and to the present writer in sufficient numbers to be observed and analyzed intimately are undoubtedly good species. Among these I would count *Dendrocoelum maculatum, D. sanctinaumi, D. jablanicense, D. magnum, D. ochridense, D. cruciferum, D. lacustre,* and *D. translucidum.* Of the unpigmented white species, *D. adenodactylosum* is obviously very near to *D. nausicaae,* which is more generally distributed in southwestern Europe but may be distinguished by karyological characters, according to Stanković (1969:427). *Dendrocoelum jablanicense* clearly differs from the rest of the Ohrid dendrocoelids by the deviating anatomy of its copulatory complex. The whitish *D. albidum* and *D. sinisai* differ from all other species of the Ohrid area by having a distinctive invaginated adhesive organ. Their mutual relationship, however, needs to be investigated on more material. Among the pigmented species of the lake, several forms inhabiting the sublittoral and profundal zones show a variable number of light spots arranged in a pair of rows on the dorsal surfaces, but have been examined in only a few specimens. They differ from each other chiefly by the number and outline of the spots. As we lack sufficient information on the effects of environmental parameters on the color pattern of these forms, it is possible that they may in part be referable to species occurring in the littoral or in the tributaries of the lake. Among these are *D. komareki, D. decoratum, D. dorsivittatum, "Neodendrocoelum* sp. 3" of Stanković (1955a, pl. 5: fig. 7), and a few other forms observed occasionally but not described in this paper. Two other species, *D. cruciferum* and *D. lacustre,* both from the shell zone of the lake, are somewhat similar in their color pattern, consisting of a median pigment stripe and a pair of dark spots on the dorsal surface. They differ, however, so markedly in the shape of the anterior end, their size, and behavior that their specific identity cannot be doubted.

Some of these open questions may be solvable by karyological, by biochemical studies, or by an investigation of the possibility of interbreeding of the forms concerned.

Dendrocoelum adenodactylosum (Stanković and Komárek)

FIGURES 5, 24, 26, 35, 52A,B

Neodendrocoelum adenodactylosum Stanković and Komárek, 1927:599.

Neodendocelum nausicae.—Stanković, 1930:168 [in part].

Dendrocoelum (Neodenrocoelum) adenodactylosum.—de Beauchamp, 1931:157.

MATERIAL DEPOSITED.—Sagittal and transverse serial sections of 7 specimens on 22 slides, USNM 55253–55259.

Dendrocoelum adenodactylosum is the most common triclad of the Ohrid region, occurring both in Lake Ohrid and in its tributary streams and sources. It was first described by Stanković and Komárek (1927:599–603). In later publications, beginning with 1930, Stanković considered the species to be identical with *D. nausicaae* O. Schmidt (1861), a species originally discovered in several localities on two Ionian islands, Corfu (Kerkyra) and Cephalonia (Kephallenia), off the west coast of Greece. Schmidt's figures and anatomical analysis of the copulatory organs of his species were surprisingly accurate for his time, considering that the observations were made on whole animals. Many years later, Wilhelmi (1909:4) collected additional specimens from Schmidt's original localities, which were examined by Komárek (1925:326–328), Stanković and Komárek (1927:617–620), and by de Beauchamp (1932:219–222). Komárek (1953a:305) himself collected the species again on the island of Corfu; *D. nausicaae* proved to be widely distributed in southeastern Europe (Balkan Peninsula, Austria, Italy) and even in Asia Minor. De Beauchamp (1932:208, 219) treated *D. adenodactylosum* and *D. nausicaae* as separate species and, in a later paper (1937:357), pointed out the differences between them (see also Gourbault, 1972). More recently, Stanković (1969:427) came to the same conclusion, chiefly on the basis of differences in the chromosome numbers of the two forms. Reisinger (1971:133) also

considered *D. adenodactylosum* to be a separate species, though closely related to *D. nausicaae.*

EXTERNAL FEATURES (Figures 5, 24).—The shape of the animal in life was discussed by Stanković and Komárek. The species is unpigmented, white, and its appearance is similar to that of *Dendrocoelum lacteum.* According to Stanković, the animals attain a length of 20 mm and a width of 3.5–5 mm. De Beauchamp reported that specimens from Šum measured less than 10 mm, but this obviously refers to preserved worms. I have seen sexually mature specimens that in life were only 16 mm long and 2.5 mm wide. The anterior end is truncated, the frontal margin bulging anteriorly. To either side of the frontal margin is a rounded lobe, projecting somewhat laterally. When the animal glides along undisturbed, a faint, but usually well discernible, narrowing or neck is seen, separating the head from the rest of the body.

There are normally two eyes, situated approximately at the level of the neck. The distance between them is slightly more than one-third the width of the neck and their distance from the frontal margin is greater than that from the lateral margins. Supernumerary eyes are not rare and may occur anteriorly as well as posteriorly to the principal eyes. Occasionally one finds specimens that have up to four eyes on each side, arranged in a curved longitudinal row (Figure 26), as has already been observed by de Beauchamp (1937:357).

The intestine is usually well visible in the living animal, particularly from the ventral side. The anterior ramus reaches up to the level of the eyes and bears 9–12 branches on each side. The two posterior rami, with up to 18 branches each, usually unite behind the copulatory apparatus.

The pharynx is inserted at about the middle of the body in sexually mature specimens, its length amounting to one-seventh the body length. The copulatory apparatus occupies the anterior half of the postpharyngeal region.

The animal moves generally by gliding. Upon stimulation, a "crawling" locomotion may be induced, in which the subterminal adhesive organ is used for successive attachment to the substrate. This crawling is less jerky than that of *D. lacteum* and is sustained only for a short time. During crawling and when the animal is at rest, the lateral margins of the body form wavy folds.

ANATOMY.—The anterior adhesive organ is moderately developed. It is situated in the midline on the ventral side of the frontal margin and consists of a well-circumscribed area of infranculeate epithelial cells pierced by eosinophilic gland ducts. Fibers of the ventral subepidermal longitudinal muscle layer attach to the adhesive area, but no special muscular differentiations are developed. The organ is larger than that of *D. jablanicense,* but far less conspicuous than the adhesive cushion of *D. lacteum.* The median diameter of the adhesive surface is about 150 μm.

The anatomy and histology of the reproductive system of *D. adenodactylosum* has been discussed in detail by Stanković and Komárek (1927:599–602) and by de Beauchamp (1932:208–211; 1937:357). I am giving here only the essential features of this system and am adding figures of the copulatory apparatus that will show the appearance of this complex in various states of contraction and relaxation of its organs. The testicles are numerous and essentially ventral. They occupy a broad zone on either side, which extends from the level of the ovaries to close to the posterior end. The widened anterior end or tuba of each oviduct, adjoining the ovary and functioning as a seminal receptacle, appears at full maturity as a large rounded sac with a tall epithelial lining, the tubal bursa, quite similar to that described by de Beauchamp (1932: 212) for *D. maculatum* (see also Reisinger, 1963: 684). This tubal bursa serves for the resorption of superfluous sperm and is found also in other species of dendrocoelids of Lake Ohrid.

In the copulatory apparatus (Figure 35), the adenodactyl (*ad*) is very large and situated to the left of the midline; the penis is smaller and located on the right side and rather far dorsal. The size and shape of the atria may vary considerably due to the state of contraction or expansion of the adenodactyl. The male atrium, designated by Stanković and Komárek as the genital atrium, is rather long and is lined with a thick epithelium, the inner border of which is packed with eosinophilic secretion granules. The penis may assume different shapes. In the majority of the preparations it appears as shown in Figure 35: a penis bulb of moderate size, enclosing a slightly widened cavity with a thick epithelial lining, the seminal vesicle (*vs*), receiving close to its anterior end the separate openings of the vasa deferentia (*vd*); the penis papilla shows a more or less distinct division into

two parts, a basal part with thick walls, covered by a rather tall surface epithelium, beneath which is a strong layer of circular muscles; and a distal, thin-walled part with hardly any muscle fibers, containing a usually rather wide lumen. In other specimens the penis may be completely extended (Figure 52A; see also de Beauchamp, 1932, fig. xxiv): in this case the bulb is extremely contracted, the seminal vesicle pushed into the base of the papilla, the papilla itself appearing tube shaped, tapering in diameter toward its tip. In the other extreme (Figure 52B), a complete introversion of the papilla into the bulb may occur: the bulb then appears expanded, its wall rather thin, its lumen voluminous, the openings of the vasa deferentia placed far apart, the papilla assuming the shape of an inverted pseudoflagellum. The statement by Reisinger (1971: 133) that *D. adenodactylosum* differs from *D. nausicaae* by the fact that it normally (in life) has no invaginated pseudoflagellum, while *D. nausicaae* regularly shows such an invagination, may be erroneous.

The two oviducts unite behind the copulatory apparatus after embracing the bursal duct. The common oviduct (*odc*) thus formed is rather short and opens into the caudal part of the male atrium. The bursa (*b*) and the bursal stalk (*bd*) show no peculiarities. De Beauchamp observed a connection of the bursa with intestinal caeca that approach it from both sides. He did not see any continuity of the cavities of the bursa and the caeca. Nevertheless he interpreted these connections as virtual genitointestinal communication. I have repeatedly seen intestinal branches approaching or even touching the bursa laterally. This is, however, by no means a constant feature. I would hesitate to consider this connection a functioning communication between bursa and intestine. The bursal duct (*bd*) proceeds from the bursa posteriorly above or slightly to the left of the penis and gradually widens, then turns ventrally and opens into the common atrium (Komárek's "copulatory atrium"). The anterior part has a very fine cover of muscle fibers, which thickens in the posterior part and becomes rather conspicuous just before the mouth of the duct. This terminal portion of the muscle coat, consisting principally of circular fibers, is the "sphincter" mentioned by de Beauchamp (1932: 211; 1937:357).

The adenodactyl (*ad*) is unusually large and contains a long lumen that may expand to a cavity of irregular outline in the bulb of the organ. Its shape varies from a long, slender, somewhat curved organ to a pear-shaped one with almost spherical bulb. It is obvious that these different shapes depend mainly on the state of contraction of its muscular systems. The papilla is always bent but may be pointing in various directions. When the organ is elongated, the papilla protrudes posteriorly and extends the wall of the common atrium abnormally (see Stanković and Komárek, 1927, text-figure 2); in other cases it is inserted into the end portion of the bursal duct (Figure 35), protrudes through the genital aperature (de Beauchamp, 1932, fig. xxiv), or may penetrate into the male atrium.

The glandular field of tall epidermal cells surrounding the gonopore, considered by de Beauchamp (1931:158) to be a distinguishing characteristic of the subgenus *Neodendrocoelum,* is well differentiated at full sexual maturity.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum adenodactylosum* is a very common inhabitant of cold springs and streams of the Ohrid region. I collected it in the spings of Studenčište, Bej-Bunar, Sveti Naum and Šum and in Kulinčivljik na Sinoru, a small stream near the western border of the town of Ohrid. Stanković and de Beauchamp likewise obtained most of their animals from springs, and expressly mention Studenčište, Sveti Naum, Šum, and Gradište, the latter being a small tributary of Drim River (which is the outlet of Lake Ohrid). Stanković and Komárek reported that the species is common also in the littoral zone of the lake. In a later paper, Stanković (1934:176) stated that the littoral animals are usually asexual during the summer. I found, however, both mature and immature specimens in the littoral zone, particularly among the dense vegetation of reeds near the Hydrobiological Station. Stanković and Komárek also reported the species from the profundal zone at a depth of 108 m. It is highly probable that this record concerns *D. sinisai* rather than *D. adenodactlyosum*. The latter species occurs also in Lake Prespa, a nearby lake southeast of Lake Ohrid (Stanković, 1969:428).

Dendrocoelum adenodactylosum can easily be kept in the laboratory. Beef liver is readily taken as food. In one culture, cocoons (spherical and unstalked) were deposited and young animals hatched.

TAXONOMIC POSITION.—The history of the dis-

covery of *D. adenodactylosum* has been discussed in the introductory paragraph to the species. Its close relationship to *D. nausicaae* is undeniable (see also Komárek, 1953a:305–306). Nevertheless, I agree with the opinion of de Beauchamp and of Reisinger: of keeping the two forms as separate species, particularly because of the karyological differences between them, as mentioned by Stanković (1969: 427). In a recent paper, Paunović (1977) established the chromosome number of *D. adenodactylosum* to be 2n = 32, while that of *D. nausicaae* is 2n = 14.

Dendrocoelum maculatum (Stanković and Komárek)

FIGURES 2, 36, 54

Neodendrocoelum maculatum Stanković and Komárek, 1927: 603.

Neodendrocoelum spec. (immaturum I) Stanković and Komárek, 1927:621.

Dendrocoelum (*Dendrocoelum*) *maculatum*.—Kenk, 1930:301.

Dendrocoelum (*Neodendrocoelum*) *maculatum*.—de Beauchamp, 1931:157.

Dendrocoelum maculatum.—Kenk, 1974:18.

MATERIAL DEPOSITED.—Sagittal and transverse serial sections of 6 specimens on 24 slides, USNM 55272–55277.

EXTERNAL FEATURES (Figure 2).—Illustrations of the external aspects of the species in life were given by Stanković and Komárek (1927:604) and by Stanković (1955a, pl. 4: fig. 1). Mature animals are 15 to 25 mm long and 3 to 4 mm wide. During undisturbed gliding, the frontal margin of the head shows three distinct lobes: a broad, curved, median lobe and a pair of smaller, rounded, lateral lobes well marked off from the median lobe. Behind the head, a slight constriction or neck is visible. Posteriorly to this, the lateral margins of the body diverge gradually until the greatest width is attained at about the middle of the body length or somewhat behind it, then converge again in the last quarter of the body and meet at the moderately pointed posterior end. In gliding locomotion, the margins are smooth, but during crawling movement they are thrown into folds and ruffles. The shape of the anterior end also changes constantly in the crawling animal, the median lobe being now retracted, now excessively protruded.

The two eyes are situated far apart, their distance from each other amounting to about one-half the width of the head at the level of the eyes. The mouth is situated somewhat behind the middle of the body and the genital aperture is closer to the mouth than to the tail end.

The most distinguished character of the species is the pattern of its coloration. The dorsal surface is a variable shade of brown (olive brown, reddish brown, chocolate brown, or almost black) with a lighter (yellowish or grayish) pattern. The light color forms a narrow rim along the lateral margins, except on the lateral lobes of the head; a triangular field on the head extends from the middle lobe backward beyond the level of the eyes; there are characteristic spots to each side of the midline in a longitudinal row of 6 to 8 that have an irregular lobed and branched outline. In the gliding animal, these spots appear elongated longitudinally. They frequently show a tendency to fuse to a netlike pattern. A pair of indistinct light dashes extends from the lateral lobes of the head obliquely backward and medially, which probably corresponds to the location of the auricular sense organs. Usually there is also a more or less marked light band in the middorsal line. On closer examination, it consists of a double row of small elongated splashes along the midline of the prepharyngeal region, a pale, somewhat broader spot above the pharynx and copulatory complex, and a distinct median band in the hindmost part of the body. The ventral surface is likewise pigmented, but much lighter, almost uniformly yellow or yellowish brown, with a lighter area below the pharynx and another surrounding the genital pore.

In young animals, the pattern of the dorsal surface is simpler, the lateral spots being less branched, often almost round. The shape of the anterior end, however, is typical and the characteristic light triangular field on the head is always distinct.

ANATOMY.—The pharynx is relatively long, about one-seventh the body length. The adhesive cushion, situated on the underside of the median frontal lobe, is a rather large field of modified epithelium with eosinophilic gland ducts, measuring 180–290 μm in median diameter.

The reproductive system of *Dendrocoelum maculatum* has been described well by Stanković and Komárek (1927:603–605) and de Beauchamp (1932: 212–215). I shall give here only the essential characters of the system.

The numerous small testes are located both dor-

sally and ventrally to the intestine and at immediate levels between the intestinal branches. The testicular zone extends from the region of the ovaries backward close to the posterior end.

The genital pore (Figure 36, *gp*) is surrounded by an area of very tall epithelial cells, characteristic of several related species of the Ohrid region. It measures 36–60 μm in thickness, while the general epithelium of the ventral surface is 17 μm and that of the dorsal surface 25 μm thick. The cells in this area lack rhabdites and are pierced by a great number of parallel gland ducts (*gl*), the cell bodies of which are situated in the mesenchyme of the ventral side, above the layers of the integumental muscles of the genital region. In preparations fixed by de Beauchamp's fluid (ethanol, formalin, and acetic acid), the secretions of the glands are dissolved and the gland ducts appear empty. Worms killed with mercuric chloride solution show the secretion in the canals to be homogeneous, staining pink with erythrosin. It is difficult to establish the homology of these peculiar glands, as de Beauchamp (1932:219) points out. They seem to correspond to glands found in various triclads and designated by Meixner (1928) as "Kittdrüsen" (cement glands), though this name might properly be restricted to glands that empty into the common atrium.

The genital pore leads into the common atrium (*ac*), which encloses the free papilla of the adenodactyl and connects with the stalk (*bd*) of the copulatory bursa and with the more or less elongated male atrium (*am*).

The penis lies to the right side of the midline. Its bulb is large, but not very muscular. When extended, the penis papilla is conical and somewhat irregular in outline (Figure 36). It is covered by a cubical or columnar epithelium pierced by numerous gland ducts that carry a grandular secretion staining in various shades of red with erythrosin. Beneath the epithelium is a layer of circular muscle fibers, strong and thick in the basal half of the papilla, but very thin in the distal part. The wide cavity in the penis bulb, the seminal vesicle (*vs*), is lined with an epithelium that forms villuslike projections. The two vasa deferentia (*vd*) open separately into the anterior part of the vesicle from the sides. The cavity continues into the penis papilla, forming a wide canal with uneven outline that opens at the tip of the papilla. Many gland ducts (pink after staining with erythrosin) empty into the penis lumen, at least into its anterior part. The penis papilla can be partly invaginated into the penis lumen. Then the penis bulb appears to be distended and the seminal vesicle very voluminous (Figure 54). Only the distal part of the papilla, that is the part lacking the thick muscle layer, is inversible, while the basal portion remains protruding into the atrium.

The two oviducts unite behind the copulatory apparatus, embracing the bursal duct. The long common oviduct (*odc*) runs, to the right side of the bursal stalk, almost horizontally forward and opens into the end part of the "male" atrium.

The copulatory bursa (*b*) is a large sac extending far laterally (however, not occupying the entire width of the body, as Stanković and Komárek indicate). The ratio between its transverse and anteroposterior diameters is approximately 3:1. The bursa is often lobate, with irregular outline. De Beauchamp stated that a pair of outgrowths of the bursa approach the vasa deferentia; these outgrowths, however, are not always present. In one case he also observed an open communication between the sperm ducts and the bursa, through which sperm were passing. I have never seen such a communication in my preparations and must assume that what de Beauchamp saw was an accidental rupture of the walls of the two organs.

The bursal stalk or duct (*bd*) starts from the posterior wall of the bursa as a rather narrow canal situated to the left of the penis, then widens transversally to a flat sac above the common atrium. From this flattened portion, a short wide canal proceeds ventrally and opens through the roof of the common atrium. This canal is surrounded by a thick layer of muscle fibers. The widening of the bursal stalk and the sharp bend it undergoes above the common atrium are particularly characteristic of the species.

The adenodactyl (*ad*) is large and usually exceeds the penis in size. It lies to the left side of the midline.

Distribution and Ecology.—*Dendrocoelum maculatum* was collected by Stanković and Komárek in several tributary streams of Lake Ohrid (at Studenčište and Sveti Naum) and in the large spring Šum (west of Struga). De Beauchamp examined animals from springs near Sveti Naum and near Tušeimište (Albania). Immature specimens were re-

ported from the littoral of the lake, particularly in the Bay of Ohrid. My own material was collected in Bej-Bunar, Studenčište, Sveti Naum, and Šum. In these cold habitats, the worms may be found in summer and probably the year round in all stages of development. They are more numerous in the quiet parts of the streams and rare or entirely absent in the springs themselves. The species is also very common in the littoral zone of the lake, under stones, among algae, and on high plants; however, no sexually mature animals can be found there during the summer months or in early autumn. As the color pattern of the young specimens is somewhat different from that of the adults, their identity with the animals living in cold streams was not recognized at first by Stanković and Komárek, who described the littoral form as "*Neodendrocoelum spec.*?–(immaturum I)." Mature specimens with typical coloration were found in the lake in winter, however (Stanković, 1938:6). I kept several individuals of the immature shore form in the laboratory at low temperature and they developed the typical spotted pattern of the adults. There can be no doubt that the animals from the two types of habitat are identical.

I collected *Dendrocoelum maculatum* in the lake in shallow water near the town of Ohrid (water temperature in August, 24.7°C), near Studenčište, near Velidab (in the vicinity of a submerged spring, 10.9°C), and at Kalište. De Beauchamp reports it also from Struga and Lin. It was occasionally found in the lower littoral (Chara zone) in Ohrid Bay, at a depth of 10 m, and at Kalište, 7–13 m.

Reisinger (1963:684–685) reports to have collected near Graz, Austria, a planarian that is anatomically identical with *D. maculatum,* particularly in the development of large tubal bursae and yolk funnels. The only difference from the Ohrid form is its complete lack of body pigment, though the eyes are developed normally. He referred to the species first as "*Neodendrocoelum ad maculatum,*" later as *N. maculatum,* and considered the lack of pigment to be no taxonomically valid characteristic. The identical species was reported later by An der Lan (1964:479) from the Danube River in Austria. If this form had been observed in the Ohrid area, it would undoubtedly have been described as a separate species, as it is well known that several species in that area can hardly be separated by anatomical characters (see Komárek,, 1953b:269), although they differ in their pigment patterns, behavior, and preferred type of habitats. In light of this situation, I would prefer to consider the unpigmented form preliminarily to be at least a separate subspecies for which I propose the name *Dendrocoelum maculatum candidum.* Further investigations will be necessary to determine its relation to the Ohrid form, such as a karyological analysis and, particularly, a study of the possibility of interbreeding of the two forms.

In the laboratory, *Dendrocoelum maculatum* may easily be kept in culture on a diet of beef liver. Cocoons laid in the aquaria were round or bluntly ellipsoidal and unstalked (smallest cocoon spherical, with a diameter of 1.7 mm; largest one ellipsoidal, with diameters 2.6 and 2.3 mm).

TAXONOMIC POSITION.—In the structure of the copulatory apparatus, *Dendrocoelum maculatum* is very similar to other pigmented species of the Ohrid region, *D. ochridense* and *D. lacustre,* which can easily be distinguished by their characteristic color patterns, body shape, some histological features, and behavior. From *D. sanctinaumi,* which shows a somewhat similar pigment design, *D. maculatum* differs by its slender proportions, the shape of the anterior end (the lateral lobes being marked off from the median lobe), the position of the eyes (farther apart), and by the shape of the dorsal spots. Preserved specimens of *D. maculatum* are usually elongated, frequently rolled in toward the ventral side, with the lateral margins ruffled, while in *D. sanctinaumi* the body remains broad and flat, with concave ventral and convex dorsal sides, and the body margins smooth (see also Stanković and Komárek, 1927:609, and de Beauchamp, 1932:216). Paunović and Rimsa (1968) and Paunović (1977) investigated the chromosome set in the testes and ovaries of *D. maculatum,* and they determined the chromosome numbers to be n=16, 2n=32.

Dendrocoelum magnum (Stanković)

FIGURES 10, 37

?*Neodendrocoelum* sp. 4 Stanković 1955a, pl. 5: fig. 8.

Neodendrocoelum grande Paunović and Rimsa, 1968:413 [nomen nudum].

Neodendrocoelum magnum Stanković, 1969:414.

Dendrocoelum (*Neodendrocoelum*) *magnum.*—Gourbault, 1972:70.

Dendrocoelum magnum.—Kenk, 1974:18.

MATERIAL DEPOSITED.—Sagittal serial sections of 2 specimens on 11 slides, USNM 55278–55279.

This is a rather common species of the shell zone of Lake Ohrid.

EXTERNAL FEATURES (Figure 10).—The species is characterized by having a thick and bulky body, not as flattened as the similar *D. sanctinaumi* or *D. maculatum*. My specimens measured up to 22 mm in length and 6 mm in width. According to Stanković, they may attain a length of 26 mm at full maturity. The anterior end is truncate with a very slightly bulging frontal margin and rounded lateral corners. Behind the head is only a slight indication of a neck constriction. The posterior end is rather bluntly pointed. The pigmentation of the dorsal side consists of a dark grayish-brown ground color, which fades out toward the body margins, and a pair of longitudinal rows of profusely branched whitish or light yellowish spots, 8–12 in each row. An indistinct light brown stripe runs along the dorsal midline, widening somewhat above the pharynx. On either side of the head is seen a short unpigmented streak, apparently corresponding to the auricular sense organs. The ventral surface is a dirty white or light yellow.

The two eyes are rather close together, at a distance of about one-fourth the width of the head. Their distance from the frontal margin is less than that from the lateral margins.

The locomotion of the animal is by a slow gliding, rarely by crawling movements.

ANATOMY.—The adhesive organ is a small (up to 170 μm in diameter) subterminal field of infranucleate epithelium in which the eosinophilic adhesive glands open and to which a few longitudinal fibers of the ventral subepidermal muscle layer are attached.

Unfortunately, I had no fully mature specimens of *Dendrocoelum magnum* at my disposal, only a few individuals in which the reproductive organs were in the anlage stage. For the analysis of the reproductive system we have, therefore, to rely on Stanković's (1969:414–417) detailed description. The zone of rather small testes extends from the level of the ovaries to the posterior end. The testes are indicated as being predominantly dorsal (however, I observe also many testicular anlagen in the ventral parts of the mesenchyme in my specimens). The oviducts are equipped with well-developed yolk funnels and their anterior enlargements adjoining the ovaries show large typical tubal bursae. The adenodactyl and bursal duct are situated to the left, the penis to the right of the midline. The genital pore is surrounded by a field of epidermis pierced by numerous eosinophilic glands. The penis is shown in Stanković's figure (see Figure 37) as a rounded bulb with a large spherical cavity, into which a rather folded penis papilla is completely invaginated. The long male atrium connects with the common atrium close to the gonopore, receiving the common oviduct in its terminal part.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum magnum* is a common species essentially confined to the sublittoral (shell zone) of Lake Ohrid. My specimens were dredged from depths between 19 and 30 m in Ohrid Bay, always associated with *Dreissena*, which appears to be their natural food. Stanković reported its occurrence at depths of 20–50 m and stated that it deposits its cocoons of 3.5–4 mm diameter on dead *Dreissena* shells. The species may be kept in the laboratory at 10°C on a diet of beef liver and also tolerates temperatures above 20°C, according to Stanković.

TAXONOMIC POSITION.—*Dendrocoelum magnum* agrees with the other pigmented species of *Dendrocoelum* of the Ohrid area in all its anatomical characters. From the similar *D. maculatum* and *D. sanctinaumi*, it differs by the bulkiness of its body and the pigmentation pattern of the dorsal side, as well as by the different ecological habitat. Paunović and Rimsa (1968) analyzed the chromosomes of "*Dendrocoelum grande*" and found their number to be 2n = 32. One of the authors (D. Paunović) informed me that the species was *D. magnum*, still undescribed at the time of their publication. A detailed analysis of the chromosome morphology was given by Paunović (1977).

Dendrocoelum sanctinaumi (Stanković and Komárek)

FIGURES 3, 38, 55

Neodendrocoelum St. Naumi Stanković and Komárek, 1927: 609.

Neodendrocoelum spec.—(immaturum II) Stanković and Komárek, 1927:622.

Dendrocoelum (Dendrocoelum) st.-naumi.—Kenk 1930:300.

Dendrocoelum (Neodendrocoelum) Sancti-Naumi.—de Beauchamp, 1931:157.

Neodendrocoelum Sancti Naumi.—Komárek, 1953a:303.

Neodendrocoelum svetinaumi.—Geus, 1967:253.

MATERIAL DEPOSITED.—Sagittal and transverse serial sections of 9 specimens on 29 slides, USNM 55285–55293.

Descriptions of *Dendrocoelum sanctinaumi* were presented by Stanković and Komárek (1927:609–613) and by de Beauchamp (1932:216–219).

EXTERNAL FEATURES (Figure 3).—The species is comparatively short and broad, mature individuals attaining a maximum length of 15 mm and a width of 4 mm. The anterior end is truncate, with a bulging frontal outline that forms an indistinct, very blunt, median point in the quietly gliding animal. The rounded lateral lobes are not marked off from the central region of the frontal margin. Behind the head is an indistinct trace of a neck constriction. The lateral margins then diverge very gradually to reach the maximum width at about the posterior third of the body length. The tail end is bluntly pointed. At rest, the animal assumes a broad, ovoid shape.

The two eyes lie rather close together at a distance of about one-third (or less) the width of the head. The mouth is situated a little behind the middle of the body, the genital pore halfway between the mouth and the posterior end.

The ground color of the dorsal surface is brown, varying in shade from a light grayish-brown to almost black. The light, yellowish color pattern resembles that of *Dendrocoelum maculatum:* it forms a rim along the margins of the body; a streak along the midline, beginning at the anterior point of the head, narrowing behind the eyes, widening again in the regions of the pharynx and the copulatory complex, and ending at the posterior tip; and a row of four to six lobed or irregularly branched spots in the lateral fields on each side of the midline. These spots are, in general, wider and less ramified than in *D. maculatum,* extending more in a transverse direction. They may, though rarely, show a tendency to fuse longitudinally. A pair of short oblique splashes above the lateral lobes of the head mark the position of the auricular sense organs. The ventral surface is uniformly gray.

Dendrocoelum sanctinaumi is slower and less active than *D. maculatum.* Its locomotion is either gliding or crawling. Already Stanković (1960:260) observed that *D. sanctinaumi* usually contracts and remains still upon mechanical stimulation, while *D. maculatum* tries to escape by rapid crawling movements.

ANATOMY.—The anterior adhesive organ is very weak, forming a small subterminal spot, 70–100 μm in diameter, no longer than the width of the lateral adhesive zone from which it is separated by a small gap on either side. The pharynx is short, its length amounting to one-ninth or one-eighth the length of the body in preserved specimens. The ratio between the width and the length of the pharynx is 1:1.1 or 1:1.6.

The reproductive system of *Dendrocoelum sanctinaumi* has been analyzed in detail by Stanković and Komárek and by de Beauchamp. The rather small testes are situated in the ventral, dorsal, and intermediate parts of the mesenchyme, extending from the level of the ovaries posteriorly to about midway between the gonopore and the tail end. The copulatory organs (Figure 38) are very similar to those of *D. maculatum,* with only some quantitative differences. The genital pore is surrounded by a circular area of modified epithelium with many gland ducts (*gl*), analogous to that described for *D. maculatum.* The general arrangement of the parts of the copulatory apparatus is the same as in the latter species, the adenodactyl and bursal stalk lying somewhat to the left and the penis and common oviduct to the right of the midline. The penis and the adenodactyl are of approximately equal size. In most specimens, the penis papilla (*pp*) is elongated, filling the entire male atrium (*am*), sometimes reaching down to the genital aperture. The penial lumen is a wide duct running from the bulb to the tip of the papilla. Its anterior portion may be somewhat expanded and is lined with a taller epithelium through which gland ducts open. This portion receives the separate openings of the two vasa deferentia (*vd*) and corresponds to a seminal vesicle (*vs*). The posterior part of the lumen, lined with a more flattened epithelium, may be considered to be a modified ejaculatory duct. In one of the eight animals examined, however, the distal part of the papilla was inverted into the lumen of the penis (Figure 55). It is possible that the inverted position is the normal condition in the living animal and that the eversion and elongation of the penis is brought about by a contraction of the muscles in the wall of the penis bulb when the animal is being killed. The arrangement of the muscles and glands of the penis is similar to that of *D. maculatum.*

From the junction of the two oviducts behind the

copulatory complex the common oviduct (*odc*) passes anteriorly to the right of the bursal stalk and connects with the posterior part of the male atrium (*am*). The copulatory bursa (*b*) has a rounded or more or less lobate outline. The bursal duct or stalk (*bd*) widens somewhat above the common atrium (*ac*) but is not as excessively broadened and flattened as in *D. maculatum*. It curves ventrally to open into the common atrium.

ECOLOGY AND DISTRIBUTION.—Stanković and Komárek collected mature specimens of *Dendrocoelum sanctinaumi* only in running water, in springs near the monastery of Sveti Naum. Immature animals were found also in the littoral zone of the lake but were rarer than *D. maculatum*. De Beauchamp's material also comprised mature individuals from Sveti Naum and a few immature specimens collected near the shore of the lake at the towns of Ohrid and Struga. In later papers, Stanković (1955a:491; 1969:430) reported its occurrence also in the sublittoral zone. I found *D. sanctinaumi* to be fairly common in cold streams along the east side of the lake: Bej-Bunar, Studenčište, and Sveti Naum. It occurs usually under stones, frequently in a strong current, often resting (feeding?) on small snails. As a rule, it is absent in the springs themselves and appears in the streams at some distance from their source. In the lake itself, the species occurs from the littoral zone down to the shell zone but is nowhere common. Some specimens collected in summer in the shell zone of Ohrid Bay (at depth from 16 to 26 m) were sexually mature. From these data we may conclude that *D. sanctinaumi* attains maturity in the cold habitats (streams, deeper zone of the lake) at any time of the year; in the littoral waters, which warm up considerably in the summer months, it apparently develops genital organs only during the colder season (see also Stanković, 1969:430). It is, however, a eurythermal species and may be maintained in the laboratory for months at a temperature above 25°C (Stanković, 1934:175).

I have kept *D. sanctinaumi* in laboratory culture for prolonged periods at 10°C. The animals refused to take beef liver as food and diminished in size. It is possible that aquatic snails are their normal food, as they are often associated with them in their natural habitat. No experiments were made to verify this assumption.

TAXONOMIC POSITION.—*Dendrocoelum sanctinaumi* fits well into the group of pigmented planarians of the Ohrid region. Its differences from *D. maculatum*, which resembles it superficially by its pigment pattern, are discussed under that species. According to Paunović (1977), the chromosome numbers are the same in both species, 2n = 32.

Dendrocoelum komareki (Stanković)

FIGURES 17, 39

Neodendrocoelum sp. 2 Stanković, 1955a, pl. 5: fig. 6.
Neodendrocoelum komarkei Stanković, 1969:421.
Dendrocoelum (*Neodendrocoelum*) *komareki*.—Gourbault, 1972:67.
Dendrocoelum komareki.—Kenk, 1974:17.

I had in my collections no specimens that I could assign to this species. Stanković (1969:421) himself was hesitant in describing it as a new species. The following data are excerpted from Stanković's description.

EXTERNAL FEATURES (Figure 17).—The body size is 11–13 mm by 3 mm. The frontal margin is slightly convex, without distinct lateral lobes. The dorsal surface is brown, with a lighter median band and a pair of longitudinal rows of 5–6 unbranched light spots of different sizes. The distance of the two eyes from each other is about one-third the width of the head. The movements of the animal are slow. When it is at rest, the lateral body margins are smooth and unruffled.

ANATOMY.—The adhesive organ is weak, similar to that of *Dendrocoelum sanctinaumi*. The subepidermal musculature is feeble. The tubal bursae of the oviducts are less developed than in other species of Lake Ohrid. The testes are numerous, dorsal and ventral, their zone extending to the posterior end. The copulatory apparatus (Figure 39) is similar to that of *D. sanctinaumi*. The penis bulb is muscular, the penis papilla very long and reaching to the gonopore when extended, its distal part resembling an inversible pseudoflagellum. The common oviduct opens into the posterior part of the male atrium. The bursal duct bends to the left of the penis and opens with a slightly widened terminal portion into the small common atrium. The adenodactyl is smaller than the penis. The modified epidermis surrounding the gonopore seems to be less distinctly developed than in *D. sanctinaumi*.

DISTRIBUTION AND ECOLOGY.—Stanković obtained only a few specimens of *Dendrocoelum komareki* from the sublittoral of the lake near the mouth of a small tributary, Daljanska, west of the town of Ohrid.

TAXONOMIC POSITION.—*Dendrocoelum komareki* differs externally from other pigmented species of *Dendrocoelum* by the color design of the dorsal surface; it differs anatomically chiefly by the very long penis papilla.

Dendrocoelum decoratum, new species

FIGURES 6, 40

TYPE MATERIAL.—Holotype, set of serial sagittal sections on 5 slides, USNM 55236; paratypes, sagittal sections of 2 specimens on 9 slides, USNM 55237–55238.

EXTERNAL FEATURES (Figure 6).—This pigmented form resembles, to some extent, *Dendrocoelum sanctinaumi;* it is a short, rather broad species attaining in the mature state a length of 8 mm and a width of 3 mm. During gliding locomotion, the general outline of the body is ovoid, the widest region being behind the middle of the body. The anterior end is truncate with a moderately bulging frontal margin and rounded lateral edges. There is no distinct narrowing behind the head. The posterior end is bluntly pointed.

The distance between the two eyes is somewhat less than one-third the width of the head and is about equal to the distance from the eyes to the frontal margin. The mouth is situated behind the middle of the body. The genital aperture is closer to the posterior end than to the mouth opening.

The central area of the dorsal side is pigmented in a brownish hue (light chocolate brown, reddish brown, or grayish brown). The pigment fades out laterally, leaving a rather wide light rim along the margin. The brown pigment is darkest near the anterior end where it forms a deeply colored area behind the eyes, covering one-fifth to one-fourth of the length of the body. This dark anterior spot gives the animal its characteristic appearance. A more or less distinct light yellowish-brown band extends along the midline throughout the pigmented area. Along each side of the median band are from two to four, rarely five, light spots with irregular outline, often branched, usually extending transversely or obliquely. The arrangement of the spots on both sides is asymmetrical. The ventral surface appears whitish, but has a very light tinge of pigment.

The animal moves rather slowly, usually in a gliding fashion.

ANATOMY.—The anterior end bears a weakly developed median subterminal adhesive field, consisting mainly of a small area of infranucleate epithelium perforated by eosinophilic gland ducts. There are no particular muscular differentiations connected with it. The adhesive area is small (median diameter, 35–65 μm) and separated from the marginal adhesive zones by wide gaps on each side of the head. The length of the pharynx amounts to one-sixth or one-seventh the length of the body in preserved specimens. The ratio between the width and length of the pharynx is 1:1.7 to 1:2.5.

In the reproductive system, *Dendrocoelum decoratum* conforms very closely with *D. sanctinaumi.* In fact, it would be difficult to distinguish the two species with certainty based on the anatomy of the genital organs alone. The testes are scattered in the mesenchyme of the ventral and dorsal sides as well as in intermediate locations between the branches of the intestine. They are more numerous ventrally than dorsally. The most anterior testes are situated anterior to the ovaries, the posterior ones behind the copulatory complex.

The genital aperture (Figure 40, *gp*) lies within an area of tall epithelium pierced by many gland ducts (*gl*), as is the case also in related species. Here again, the adenodactyl and the bursal stalk are situated on the left side, the penis and the common oviduct on the right side of the midline. Penis and adenodactyl (*ad*) are of about equal size. The penis has a moderately muscular bulb that contains a cavity with somewhat irregular outline, the seminal vesicle (*vs*). The two vasa deferentia (*vd*) open into this cavity separately from the anterolateral sides. The papilla of the penis (*pp*) may have a shape as shown in Figure 40, where it consists of a thick-walled basal part with narrow lumen and an expanded distal portion with thin walls. Between the two parts may be a circular constriction. In one specimen, however, the penis papilla was extended, with the tip reaching close to the gonopore (a similar shape is frequently observed in *D. sanctinaumi*). The detailed histology of the organ is the same as in *D. maculatum.* The male atrium (*am*) is shown in

Figure 40 as being composed of a widened anterior portion enclosing the penis papilla and a posterior narrower duct connecting with the common genital atrium. The anterior part is lined with a rather flattened epithelium, while the posterior duct has a lining of tall, columnar cells. This separation of the two portions, however, is dependent on the state of contraction of the copulatory organ. When the penis papilla is extended and reaches throughout the length of the male atrium, the posterior duct widens and its epithelium becomes flatter; the male atrium then appears as a uniform cavity.

The oviducts unite posterior to the copulatory apparatus to form the common oviduct (*odc*), which passes forward to the right of the bursal stalk and opens into the end part of the male atrium. Both the end portions of the separate oviducts and the greater part of the common oviduct receive numerous outlets of eosinophilic shell glands. The copulatory bursa (*b*) is of medium size. Its outlet, the bursal duct (*bd*), is slightly widened posteriorly and opens into the common atrium from the dorsal side.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum decoratum* lives in the sublittoral (shell zone) and profundal zones of Lake Ohrid. A total of about 25 specimens were collected in the summers of 1935 and 1937, all in Ohrid Bay. Five individuals had sexual structures developed, but only three were fully mature. Most of the animals collected in the shell zone were obtained by dredging at depths from 16 to 36 m; one individual was taken on meat bait at 22 m. In the profundal zone, animals were dredged from depths between 37 and 90 m.

Attempts to rear young specimens to maturity in the laboratory were unsuccessful. The animals did not take beef liver as food and died within a few months.

TAXONOMIC POSITION.—In some ways, *Dendrocoelum decoratum* resembles *D. sanctinaumi* very closely. It differs by its smaller size and particularly by the pattern of its dorsal pigmentation: the presence of a pair of dark brown fields posterior to the eyes, the greater width of the light rim along the body margins, and the smaller number of light spots along both sides of the midline. Anatomically, the two species are very similar, the main difference being the smaller size of the penis papilla. Another species that might be confused with *D. decoratum* is *D. komareki,* for which, however, Stanković (1969:421) indicates a more slender shape and a uniformly brown dorsal ground pigmentation. The name of the species, *decoratum* (*decoratus,* Latin, adorned), makes reference to the characteristic color design of the dorsal surface.

Dendrocoelum lacustre (Stanković)

FIGURES 20, 41

Neodendrocoelum lacustre Stanković, 1932:577 [nomen nudum].

Neodendrocoelum lacustre Stanković, 1938:1.

Dendrocoelum (Neodendrocoelum) lacustre.—Gourbault, 1972: 67.

Dendrocoelum lacustre.—Kenk, 1974:18.

Dendrocoelum lacustre, a rare species of the sublittoral zone of Lake Ohrid, was first mentioned by Stanković (1942:577) without indication of its specific characters. In a later paper, Stanković (1938:1, 2, 10) presented a description of the external features of the species, based on the examination of a considerable number of specimens, none of which were mature, however. An analysis of the anatomy of the reproductive organs was published by Stanković in 1969 (pages 425–427).

EXTERNAL FEATURES (Figure 20).—To this species I refer one single, immature specimen that was dredged in September 1935 from the shell zone of Ohrid Bay, at a depth of about 25 m. Unfortunately, the specimen was not in a good physiological condition and could not be reared to maturity. A rough sketch was made of the living, contracted animal (Figure 20). For the normal aspect of the living specimens we must rely on Stanković's description. The shape of the body is similar to that of *Dendrocoelum sanctinaumi,* the outline of the head showing three lobes resembling that of *D. ochridense.* Characteristic is the pigment pattern. In my specimen, the central area of the dorsal side showed a yellowish-brown tint, with a thin, unpigmented stripe along the midline. One large dark brown spot was placed transversely in the prepharyngeal region and another smaller and paler spot above the pharynx. In the postpharyngeal part, the white midline was bordered by a pair of darker lines on both sides.

ANATOMY.—The description of the reproductive system by Stanković (1969:426) mentions the dorsal and ventral position of the testes and presents a diagram of the copulatory apparatus. Komárek

(1953a:269), who must have examined Stanković's slides, states that the apparatus appears to be identical with those of *D. maculatum* and *D. sanctinaumi*. Stanković's figure 15 shows the papilla of the penis partly invaginated into the bulbar lumen, giving the impression of a pseudoflagellum, a condition that may also occur in the related species.

DISTRIBUTION AND ECOLOGY.—Stanković reported the occurrence of *Dendrocoelum lacustre* in the sublittoral zone of the lake, at depths of 20–50 m.

TAXONOMIC POSITION.—*Dendrocoelum lacustre*, together with *D. sanctinaumi* and *D. decoratum*, forms a very closely related group of species that differ chiefly in their pigment patterns. Paunović (1977) studied the chromosomes of *D. lacustre* and found them to be 2n = 32.

Dendrocoelum dorsivittatum, new species

FIGURES 18, 42

TYPE MATERIAL.—Holotype, set of serial sagittal sections on 10 slides, USNM 55239; paratype, sagittal sections of 1 specimen on 4 slides, USNM 55240.

Only two specimens of this species were collected in the profundal zone of Lake Ohrid, one sexually mature, the other not fully differentiated.

EXTERNAL FEATURES (Figure 18).—The larger specimen measured in life 13 mm long and 4 mm wide, the smaller one 10 and 2.5 mm, respectively. Unfortunately, the larger individual had an injured head. The anterior end of the smaller animal was broad and truncated, with an indistinct angular projection in the midline, to the sides of which the frontal margin sloped gently backward to the rounded lateral corners. There was no distinct narrowing behind the heatd. Posteriorly, the body ended in a blunt point.

The distance between the two eyes amounted to one-third, or a little more, of the width of the head. Their distance from the frontal margin was smaller than that from the lateral margins of the head.

The most characteristic feature of the species is its pigment pattern. The dorsal surface has a light yellowish-brown or grayish-brown ground color, which fades out toward the margins of the body. A dark brown band extends along the midline from a level behind the eyes to about the middle of the body (in the larger individual) or to close to the posterior end (in the smaller one). This band is less distinct than Figure 18 would suggest. To either side of the midline is a longitudinal row of from 6 to 10 unpigmented spots of different sizes and irregular shapes. The ventral side is lighter, whitish.

The locomotion of *Dendrocoelum dorsivittatum* is gliding, upon stimulation also crawling.

ANATOMY.—The anterior adhesive organ is a moderately developed field of adhesive epithelium, without special muscular differentiations. The pharynx is comparatively long and slender. In the two preserved specimens, its length amounts to 1.7 and 1.1 mm, corresponding to approximately one-seventh the length of the body.

The anatomy of the reproductive system places the species in close relationship to the remaining spotted species of *Dendrocoelum*. Only one fully mature specimen was available for the study of the genital organs. The testes are situated ventrally, dorsally, and at intermediate heights, extending from the level of the ovaries to close to the posterior end.

In the copulatory apparatus (Figure 42), the penis is located to the right, the bursal stalk and the adenodactyl to the left of the midline. The glandular area of thick epidermis around the genital aperture is typically developed. The penis has a rather large bulb enclosing a voluminous seminal vesicle (*vs*) into which the vasa deferentia (*vd*) empty separately from the anterolateral sides. The penis papilla consists of a thick-walled basal portion with a well-differentiated external circular muscle layer and a distal part with thin walls and a wide lumen. The two parts are separated externally by a circular groove.

The anterior enlargements or seminal receptacles of the oviducts are equipped with large tubal bursae. An outstanding feature is the great length of the common oviduct (*odc*) which is formed by the union of the two oviducts at a considerable distance behind the copulatory complex. The common oviduct runs anteriorly in an almost straight line and opens into the end part of the male atrium. The posterior two-thirds of the common oviduct and the terminal parts of the separate oviducts are connected with shell glands. The copulatory bursa (*b*) shows no peculiarities. Its outlet, the bursal duct (*bd*), starts as a narrow canal and gradually widens as it runs posteriorly, turning

abruptly to the ventral side above the genital pore, and connecting with the common atrium. The adenodactyl (*ad*) is larger than the penis and has a very long lumen.

DISTRIBUTION AND ECOLOGY.—The two individuals of *Dendrocoelum dorsivittatum* were dredged in September 1935 in the profundal zone of Lake Ohrid, in Ohrid Bay, at depths between 47 and 55 m, on a bottom consisting of soft and hardened mud with few empty *Dreissena* shells.

TAXONOMIC POSITION.—I am establishing this new species with some hesitation, because we know so little about the variability of the color pattern of the undoubtedly closely allied forms of the Ohrid region. From related spotted species of *Dendrocoelum*, the new species differs mainly by the presence of the dark middorsal band. In the others (*D. maculatum, D. sanctinaumi, D. ochridense, D. magnum, D. komareki,* and *D. decoratum*), the dorsal midline has a color lighter than the ground shade of the dorsal surface. The dark midline shown in the figures for *D. ochridense* and young specimens of *D. maculatum* by Stanković and Komárek (1927, text-fig. 5, 13) is erroneous. This was corrected in a later paper by Stanković (1938, fig. 3, 4, 7). The great length of the common oviduct is perhaps the most remarkable anatomical characteristic of the species (which it shares with *D. ochridense*).

The name of the species, *dorsivittatum* (*dorsum*, Latin, back; *vitta*, Latin, band or stripe), alludes to the presence of the dark middorsal stripe.

Dendrocoelum lychnidicum (Stanković)

FIGURES 8, 43, 57

Neodendrocoelum sp. 1 Stanković, 1955a, pl. 5: fig. 5.
Neodendrocoelum lychnidicum Stanković, 1969:148.
Dendrocoelum (Neodendrocoelum) lychnidicum.—Gourbault, 1972:66.
Dendrocoelum lychnidicum.—Kenk, 1974:18.

MATERIAL DEPOSITED.—Sagittal serial sections of 3 specimens on 4 slides, USNM 55269–55271.

Dendrocoelum lychnidicum was first mentioned and illustrated by Stanković (1955a:491) as an undescribed "spec. 1" of *Neodendrocoelum*, inhabiting the sublittoral zone of Lake Ohrid. A description of the external aspect and the anatomy of the species was given by the same author in 1969 (pages 418–419). Based on my material, the following supplements the original description and indicates some of the variability of the species.

EXTERNAL FEATURES (Figure 8).—This rather rare form is the smallest of the pigmented *Dendrocoelum* species of Lake Ohrid. Mature animals attain a length of 6 mm and a width of 1 mm. The anterior end is truncated, with a slightly bulging frontal margin and moderately rounded lateral corners. There is no distinct narrowing or neck behind the head. The body has a more or less ovoid outline, the greatest width being at approximately the middle of the body. The posterior end is bluntly pointed.

The distance of the two eyes from each other is about one-third, or less, of the transverse diameter of the head, and their distance from the frontal margin approximately equal to that from the lateral margins.

The central area of the dorsal surface has a rather light chocolate brown ground color of somewhat cloudy appearance. Toward the head and the margins of the body, the brown pigment fades out, leaving a broad marginal rim free of pigment. There is an indistinct light band along the midline. Very characteristic is one large rectangular or more rounded spot of light yellowish color placed transversely in the brown area, at about the middle of the back in young animals, more anterior in adult specimens. Occasionally two small round spots in the midline, one behind the other, are present in mature specimens above the copulatory organs. The ventral surface has a light yellowish-brown hue.

The animal moves principally by gliding.

ANATOMY.—A small adhesive area is situated on the underside of the frontal margin, sometimes appearing as a shallow central depression. Many eosinophilic glands open in this area and a few muscle fibers, running mainly in a longitudinal direction, are attached to it. The infranucleate epithelium and the glands show the same structure as those of the marginal adhesive zone from which they are separated on each side by a gap. The pharynx is short and wide, measuring about one-seventh the length of the body (in preserved animals); the ratio between its width and length is about 1:1.7, but may change to 1:1 when the body is contracted.

In the three mature specimens at my disposal for the study of the reproductive system, the copulatory apparatus was well differentiated. One of the speci-

mens laid a cocoon shortly before it was preserved. Apparently the animals had already passed the peak of their reproductive function, as no testes could be found in the three specimens, though sperm were present in the spermiductal vesicles and also in the tubae of the oviducts (indicating that the animals had copulated). The complete reduction of the testes may be a sign of a pronounced protandry such as has been observed also in some other freshwater triclads. Stanković (1969:418) indicates that in his specimens the numerous small testes were located predominantly on the ventral side. The ovaries were situated far posteriorly, about midway between the head end and the root of the pharynx.

The thickened glandular area surrounding the genital aperture (Figure 43, *gp*) is rather small. In the general arrangement of the copulatory apparatus, *Dendrocoelum lychnidicum* agrees with its pigmented relatives from the lake. The penis is small and has a remarkably weak musculature. When the organ is extended (Figure 43), the lumen of the penis bulb (*bp*) is a rather small cavity (seminal vesicle), receiving the two vasa deferentia (*vd*) from the right and left sides. From this cavity, a narrow, almost straight canal extends through the papilla (*pp*) to open at its tip. The penis papilla is constricted at its base, where a subepithelial layer of circular muscle fibers is developed. In the other two specimens, however, the penis was retracted and the papilla partly inverted into the widened seminal vesicle (Figure 57). The inversion or invagination occurred at the basis of the papilla and not, as is usually the case in the genus *Dendrocoelum*, at the free end of the papilla. The tissues of both the bulb and papilla of the penis are traversed by many gland ducts, at least part of them opening through the epithelial covering of the papilla.

The male atrium is lined with a tall columnar epithelium. The distal parts of the cells, bordering the lumen of the atrium, are closely packed with granular, strongly eosinophilic inclusions. The same differentiation is observed also in related species, but here it is more conspicuous due to the great thickness of the epithelium, which reduces the atrial lumen to a narrow canal with irregular outline.

The oviducts run, in the typical way, as a pair of narrow tubes (outer diameter, 12 to 14 μm) above the ventral nerve cords to a level posterior to the copulatory complex. There they converge medially, increasing in thickness (diameter, 20 to 35 μm) and unite in the midline. The long common oviduct (*odc*) extends anteriorly in a slight curve and opens into the posterior part of the male atrium. The diameter of this duct is very large (43 to 50 μm) compared to the dimensions of the atrial organs. The end parts of the paired oviducts and the common oviduct are equipped with eosinophilic shell glands. The copulatory bursa (*b*) is of moderate size. Its outlet, the bursal duct (*bd*), passes on the left side of the penis, starting as a narrow canal but expanding considerably in its posterior half; above the genital pore, it curves ventrally and connects, from the dorsal side, with the common atrium (*ac*). The adenodactyl (*ad*), situated ventrally and to the left of the midline, is long and slender, exceeding the pharynx in length, with an elongated lumen extending through the greater part of the organ.

DISTRIBUTION AND ECOLOGY.—About 10 specimens of *Dendrocoelum lychnidicum* were collected in August 1937 in Ohrid Bay by dredging in the shell zone of the sublittoral at depths between 16 and 26 m. The animals are comparatively rare and can easily be overlooked because of their small size and slow movements. An attempt to rear immature individuals to maturity in the laboratory was unsuccessful. They kept sufficiently well at a temperature of 10°C, but refused to take beef liver offered as food and died after a few months. One of the mature specimens deposited a cocoon in the laboratory culture; it was spherical, reddish-brown, unstaked, but adhered to the substrate by a mucous secretion.

TAXONOMIC POSITION.—Externally, *Dendrocoelum* differs from related species of the Ohrid region mainly by its small size and by the characteristic saddle-shaped light spot of the dorsal side. Anatomically, it conforms well with its pigmented relatives. Its chromosome numbers are 2n = 32 (Paunović, 1977).

Dendrocoelum ochridense (Stanković and Komárek)

FIGURES 4, 27, 30, 44

Neodendrocoelum ochridense Stanković and Komárek, 1927: 605.

Neodendrocoelum ohridense.—Stanković, 1932:578.

Dendrocoelum (Neodendrocoelum?) ochridense.—de Beauchamp, 1931:157.
Dendrocoelum (Neodendrocoelum) ohridense.—Gourbault, 1972:68.
Dendrocoelum ochridense.—Kenk, 1974:18.

MATERIAL DEPOSITED.—Sagittal and horizontal serial sections of 5 specimens on 25 slides, USNM 55280–55284.

This well-defined species of the lower littoral, sublittoral, and profundal zones of Lake Ohrid was first described by Stanković and Komárek (1927: 605–609) from a single specimen dredged from a depth of 40 m. Unfortunately, the description of the external characters and the accompanying illustration (fig. 5) were inaccurate. The original description was corrected and supplemented in a later paper by Stanković (1938:3–5). The anatomical data given in both papers are sufficient to identify the species with certainty.

EXTERNAL FEATURES (Figure 4).—Mature specimens attain a length of 16–20 mm and a width of 3–4 mm. Compared with related species, *D. ochridense* is a rather slender form. The head is only a little narrower than the body and is separated from the latter by a slight, hardly noticeable constriction or neck. In the quietly gliding animal, the frontal margin of the head has a small, bluntly pointed, anterior projection in the midline. The lateral edges of the head are likewise more pointed than those of other *Dendrocoelum* species of the same region. Behind the neck, the lateral body margins first diverge gradually, then run parallel, and, beginning at the level of the copulatory organs, converge to form a distinctly pointed posterior end. The body is considerably flattened dorsoventrally.

The two eyes are situated close to the midline, their distance from each other amounting to about one-fifth the transverse diameter of the head at the level of the eyes; their distance from the frontal margin is two to three times as large as their mutual distance. The root of the pharynx lies at about the middle of the body or somewhat anterior to it in mature animals. The mouth and the genital opening divide the posterior half of the body into approximately equal thirds.

The color pattern of the dorsal surface is very characteristic, composed of two colors, light yellowish and dark brown. The yellowish background color forms a distinct median band extending from the anterior margin of the head to the posterior end of the body. Lateral to this band on either side is a longitudinal row of six to ten large dark spots of triangular or trapezoidal shape. The most anterior spots are situated a short distance behind the eyes. The arrangement of the spots is rather regular. In some individuals the pattern may be almost symmetrical on both sides, particularly in the anterior part of the body. More frequently, however, the spots of the two sides are placed at different levels. The spots are connected with each other by a thin line bordering the light median band. A similar line may join the lateral margins of the spots; usually, however, the spots fade out laterally midway between the median line and the lateral margin of the body. There is always a rather broad, light border along the margins, usually paler than the yellow ground color of the middorsal surface. A pair of indistinct unpigmented strips is visible on the head at the site of the auricular sense organs.

The ventral surface is whitish or yellowish. When the intestine is not filled excessively, the color pattern of the dorsal surface may shine through ventrally.

The locomotion of the animal is normally gliding, occasionally "crawling." Upon strong stimuli, the animal detaches from the substrate and swims freely in the water for a short distance. This particular reaction will be discussed below in connection with the ecology of the species.

ANATOMY.—The anterior adhesive organ of *Dendrocoelum ochridense* is feebly developed, consisting of a small field of epidermis in which numerous adhesive gland ducts open, measuring about 100 μm in median diameter (Figure 30). The extraordinary thick subepidermal muscle layers (Figure 27) of the species have already been mentioned by Stanković and Komárek (1927:608) and by Stanković (1969:429).

The numerous testes (Figure 27, *te*) are arranged in two broad longitudinal zones, one on either side of the midline, extending from the region of the ovaries to close to the posterior end. They are comparatively small and are situated in the mesenchyme ventrally to the intestine and between the intestinal branches, leaving the dorsal parts of the mesenchyme free. The dorsal and lateral regions of the mesenchyme are occupied chiefly by yolk glands. Tubal bursae at the beginning of each oviduct are well developed.

The general anatomy of the copulatory apparatus (Figure 44) resembles closely that of *Dendrocoelum maculatum*. The penis lies somewhat to the right of the midline, the adenodactyl and the posterior portion of the bursal duct to the left of the penis. The genital aperture (*gp*) is surrounded by a small circular area of modified surface epithelium, as in *D. maculatum*. The spaceous common atrium (*ac*), enclosing the large papilla of the adenodactyl, has a very characteristic shape; it forms a long, conical extension posterior to the gonopore, which may reach about halfway between the genital pore and the hind end of the body in fully mature individuals.

The penis is smaller than the adenodactyl and consists of a spherical, moderately muscular bulb and a short, conical or gland-shaped papilla. The bulb has a wide central cavity, the seminal vesicle (*vs*), lined with a glandular epithelium, the cells of which protrude irregularly into the lumen. The two vasa deferentia (*vd*) open separately into the anterolateral parts of the vesicle. A wide canal, lined with a flattened epithelium, proceeds to the tip of the papilla, where it opens through a somewhat narrowed aperture. The wall of the penis papilla is thin and contains a layer of circular muscles beneath the outer epithelium, rather thick in the basal part of the papilla, but tapering off distally. Gland ducts, containing a granular secretion, open through the surface epithelium of the papilla.

The long common oviduct (*odc*) connects with the end part of the male atrium. The duct (*bd*) of the copulatory bursa opens into the common atrium from the dorsal side. The adenodactyl (*ad*) has a voluminous bulb and a long, slender, straight papilla. Its glandular lumen is either confined to the papilla or extends through both the bulb and the papilla, particularly in fully mature animals. It may be noted that the papilla of the adenodactyl lies in the posterior extension of the common atrium in all four individuals examined by me and in the two specimens that Stanković and Komárek (1927:606) and Stanković (1938:4) used for their illustrations. In other species, the papilla is frequently curved ventrally and tends to protrude through the gonopore. The action of the killing fluid apparently causes a contraction of the musculature of the adenodactyl, accompanied by an elongation of the papilla. This appears to occur also in *Dendrocoelum ochridense*; however, as the papilla is not bent downward, it pushes the wall of the common atrium posteriorly. It is possible that the shape of the common atrium in the living animal is not as elongated as it appears to be in the slides. The posterior extension of the atrium may well be caused, or at least greatly exaggerated, by the expanding adenodactyl.

DISTRIBUTION AND ECOLOGY.—Stanković and Komárek (1927:606) and Stanković (1938:5; 1955a: 491) collected *Dendrocoelum ochridense* in the lower littoral and the sublittoral zones of Lake Ohrid; they found single specimens even at greater depths, down to 120 m. Individuals taken in the Chara zone (5–20 m) were always immature and sexual specimens were found only in the shell zone (25–35 m). Stanković assumes that the animals migrate from the littoral zone to the sublittoral when they approach sexual maturity.

I collected the species during the summer months in Ohrid Bay on Chara (10–15 m depth) and in the shell zone (15–36 m) by dredging and using meat bait; off Kale, below the shell zone (at about 45 m); and near Kalište, at the lower boundary of the Chara zone (7–13 m). All specimens were immature except for one sexual individual from the shell zone. Many immature worms were reared in the laboratory at 10°C and fed beef liver. They attained sexual maturity and laid fertile cocoons.

Contrary to Stanković's opinion, I believe that in nature the life cycle of *Dendrocoelum ochridense* is dependent primarly on the temperature of the water: the animals become sexual at low temperatures. Accordingly, mature individuals will be found in the deeper (cooler) habitats the year round, while in the littoral region the animals are immature in the warm season and develop sex organs probably in winter. A seasonal migration from one zone to another is not probable.

The peculiar swimming reaction of *Dendrocoelum ochridense* was mentioned above. It may be induced by strong stimuli, such as shaking the aquarium, teasing the animal with a needle, etc. The animal detaches itself from the substrate, bending the body violently upward and downward in quick succession. Suspended in the water, it swims by wavy movements of the entire body, head first, for a short distance and finally sinks to the bottom, similar to the swimming of certain leeches. This swimming ability is undoubtedly correlated with the extraordinary development of the integu-

mental muscles, especially the thick layers of dorsal and ventral longitudinal fibers. It is interesting to note that the swimming reaction took place regularly when the animal touched an individual of *Dendrocoelum cruciferum,* a species occurring in the same habitat. In this case, apparently a chemical stimulus brought about the reaction. Toward other species living in Lake Ohrid (*D. lacteum, D. magnum, D. adenodactylosum,* etc.), also toward *Polycelis tenuis,* the species was entirely indifferent. *D. cruciferum* is a rapacious species, preying upon other triclads. There is no doubt that *D. ochridense* occasionally is capable of escaping an attack of *D. cruciferum* by this peculiar reaction. It does not, however, afford a complete protection: of 11 individuals of *D. ochridense* kept in the same aquarium with three specimens of *D. cruciferum,* nine were eaten within a period of 20 days.

The swimming locomotion of *D. ochridense* is quite unique among the triclads of the Ohrid region. A comparable reaction has been reported so far only in one other freshwater triclad, a species of the *Phagocata dalmatica* group (from the cave Logarček in Slovenia; see Kenk, 1936:15, 20 *"Fonticola dalmatica"*). *Dendrocoelum translucidum* also shows a similar reaction to stimuli but does not lift itself above the substrate.

TAXONOMIC POSITION.—Stanković and Komárek (1927:606, 621) originally suspected that an immature form designated as *"Neodendrocoelum spec.?–(immaturum I)"* of the upper littoral zone of Lake Ohrid might be identical with *Dendrocoelum ochridense,* but later Stanković (1938:6) realized that it was the young stage of *D. maculatum.* De Beauchamp (1932:211), who had no opportunity of examining the species, listed *D. ochridense* as a questionable synonym of *D. maculatum. Dendrocoelum ochridense* differs from related species by its pattern of pigmentation, the shape of the head, the position of the eyes (very close together), the ventral location of the testes, the extraordinary development of the subepidermal muscle layers, and its behavior upon stimulation. In the anatomy of the copulatory apparatus, it is very close to other species of the lake, such as *D. adenodactylosum* and *D. maculatum.* Paunović (1977), who studied the chromosome set of the species, found the chromosome number to be the same as in many of its relatives, 2n=32.

Dendrocoelum minimum, new species

FIGURES 21, 45

TYPE MATERIAL.—Holotype, set of serial sagittal sections on 2 slides, USNM 55241; paratypes, sagittal sections of 2 specimens on 4 slides, USNM 55242–55243.

A very small, rather rare, white species inhabiting the profundal zone of Lake Ohrid.

EXTERNAL FEATURES (Figure 21).—*Dendrocoelum minimum* is the smallest triclad occurring in Lake Ohrid and in general ranks among the smallest species of the genus *Dendrocoelum.* Mature specimens have a length of 4–6 mm. The few individuals that I was able to procure did not permit a detailed analysis of the external habit of the species, since they were not in good physiological condition and had, in part, suffered damages in the process of collecting. The anterior end appeared more or less rounded, without outstanding characters. No adhesive organ could be detected in the living animals. The posterior end had an obtusely rounded shape. The two eyes were placed at a mutual distance of about one-third the width of the head. The pharynx was situated behind the middle of the body, and the copulatory organs occupied the anterior half of the postpharyngeal region. The animals were devoid of body pigment, white, and with the profusely ramified intestine well discernible from both the dorsal and the ventral sides.

ANATOMY.—The anterior end has no distinct adhesive organ. The few outlets of eosinophilic glands that open in the midline of the frontal subterminal surface are insignificant. There is no special muscular differentiation in this region.

The pharynx is very short, its length amounting to one-tenth to one-thirteenth the length of the body.

For the study of the reproductive system I had only four mature specimens, some of which were not in the best histological shape. The testes are found in both the dorsal and ventral parts of the mesenchyme in a zone extending from the ovaries posteriorly to about the level of the gonopore; none were seen in the hindmost part of the body. The copulatory apparatus (Figure 45) resembles closely that of other species of the *Dendrocoelum adenodactylosum* group. The male genital atrium and the penis are somewhat to the right, the adeno-

dactyl and the bursal stalk to the left of the midline. No particular differentiation of the epidermis surrounding the genital aperture could be seen in three of the animals examined. One individual, however, had a thicker epithelium covering a wide area beneath the copulatory apparatus and even enclosing the mouth opening. It appears, from differentiations seen in the underlying mesenchyme, that many gland ducts open in that area. Unfortunately, most specimens had been treated with a fixing agent that dissolves rhabdites and certain glandular secretions (ethanol-formalin-acetic acid), so that no detailed analysis of these structures was possible.

The penis is small and of rather variable shape. In the specimen from which Figure 45 was drawn, it has a small bulbar part (*bp*) with only feeble musculature and a more or less cylindrical papilla. The basal part of the papilla is equipped with a strong circular muscle layer beneath the outer epithelium. The lumen of the penis is greatly reduced, consisting of a small seminal vesicle in the anterior part of the bulb that receives the openings of the two vasa deferentia, a thin canal running posteriorly, and a widened portion near the tip of the papilla that opens into the male atrium. In another individual, however, the cavity of the penis is rather voluminous and the distal part of the papilla is inserted into the cavity. The variability of the penis shape, as seen in the preserved animals, is obviously due to differences in the physiological condition of the animals while they were killed and to the action of the fixing agents. The male atrium consists of an anterior widened part enclosing the penis papilla and a narrow canal leading obliquely in a posteroventral direction into the common genital atrium. The canal is lined with the usual thick epithelium and coated with a very strong muscular layer of circular and longitudinal fibers.

The two oviducts unite behind the copulatory apparatus to form the common oviduct (*odc*) that runs anteriorly to the right of the bursal stalk and opens into the end part of the male atrium.

The copulatory bursa (*b*) is sac shaped, with no peculiarities. Its outlet, the bursal duct (*bd*), starts as a narrow tube proceeding posteriorly to the left of the penis, widening gradually, then turning ventrally to connect with the common atrium, and forming usually a posterior caecum of variable size.

The adenodactyl (*ad*) is larger than the penis and is situated to the left of the midline. Its conical papilla is inserted into the end part of the bursal duct in most preparations.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum minimum* appears to be a rather uncommon species, though it may easily be overlooked on account of its small size. Only four mature specimens were taken, all in Ohrid Bay, below the shell zone at depths between 30 and 52 m. No attempt was made to culture the species under laboratory conditions.

TAXONOMIC POSITION.—By the arrangement of the organs of the copulatory complex, *Dendrocoelum minimum* fits well into the group of *D. adenodactylosum* and related species of the Ohrid area. Apart from its small size, it differs from its relatives by having the testicular zone extending posteriorly only to the level of the gonopore, lacking testes behind that level. It is easily separated from the similar white species, *D. albidum* and *D. sinisai*, by lacking a well-developed adhesive organ.

The name of the species, *minimum* (*minimus*, Latin, smallest), refers to its minute size.

Dendrocoelum albidum, new species

FIGURES 14, 19, 29, 46, 53

TYPE MATERIAL.—Holotype, set of serial sagittal sections on 2 slides, USNM 55233; paratypes, sagittal sections of 2 specimens on 6 slides, USNM 55234–55235.

This is a small, whitish *Dendrocoelum* inhabiting the shell zone of Lake Ohrid.

EXTERNAL FEATURES (Figures 14, 19).—Mature specimens are 7–9 mm long and 1–1.5 mm wide. The truncated head has a straight or slightly bulging frontal margin and rounded lateral edges not projecting laterally. During locomotion, the frontal contour may vary and a transitory short projection may appear in the midline, corresponding to the site of the adhesive organ, which may be recognized in life as a small opaque spot. There is no narrowing or neck behind the head. The lateral margins diverge for a short distance behind the anterior end, converge again in the posterior region, and meet at the rather pointed posterior end.

Eyes are normally two, separated from each other by about one-third, or slightly more, the transverse diameter of the head; their distance from the frontal

margin is about equal to, or a little greater than, their distance from each other. A division of the principal eyes into two or three cups is frequently observed. The median trunk of the intestine reaches anteriorly almost to the level of the eyes.

The general color is usually whitish, with the darker intestine shining through when filled. Many specimens, however, show a light reddish-brown pigmentation on the dorsal side. This pigmentation may be easily discernible or it may appear as a very light tint visible only in the starving animal when it is not obscured by the color of the intestinal contents. There are all intergrades between purely white and distinctly pigmented individuals. In a group of white specimens collected at one time and kept under observation for about three months, several animals developed different degrees of pigment while others remained white. When it occurs, the pigment is arranged in two broad longitudinal stripes, one on each side of the midline (Figure 19). Each stripe has a sharp medial border, while laterally it fades out toward the margin. No pigment is present on the head, along the midline, and in a rather broad rim along the margins of the body. The ventral surface is always unpigmented.

The pharynx is situated approximately in the middle of the body. The copulatory complex occupies up to one-half of the postpharyngeal region.

Dendrocoelum albidum is in life easily recognized by its peculiar pigment pattern. Unpigmented specimens, however, cannot be readily distinguished from other small white species of Lake Ohrid, such as *D. minimum, D. sinisai,* and even *Phagocata ochridana.*

ANATOMY.—The adhesive organ (Figure 29) consists of a deep tubular pit (*ao*) opening on the underside of the head close to the frontal margin. It is lined with an infranucleate epithelium pierced by gland ducts containing an eosinophilic secretion. The same secretion also fills the cavity of the pit. The musculature of the organ consists mainly of fibers belonging to the longitudinal layer of the ventral subepidermal muscles. In a median section, these fibers are seen adhering to the wall of the pit and running backward, in more or less curved lines, passing below the cerebral commissure (*cc*) to enter the ventral muscle layer. The ventral layers of circular and diagonal fibers (*mvc*) are not modified in the region of the adhesive organ, while the inner layer of transversal muscles (*mt*) is absent in that region. The cell bodies of the adhesive glands are situated at a considerable distance behind the anterior end. Their outlets (*gl*) pass above the cerebral commissure.

In the reproductive system, the numerous testes occupy both the dorsal and ventral parts of the mesenchyme extending from the level of the ovaries to near the posterior end. The ovaries and yolk glands show no peculiarities.

The anatomy of the copulatory complex (Figure 46) conforms, in general, with that of related species of the *Dendrocoelum adenodactylosum* group. The bursal duct (*bd*) is located to the left of the midline, the adenodactyl (*ad*) beneath, or somewhat to the left of, the penis. The genital pore (*gp*) is surrounded by an epithelium somewhat thicker than the general surface epithelium of the ventral side. The cells of the thickened area contain no typical rhabdites and are apparently of a glandular nature.

The penis is of moderate size and has an inversible papilla (*ppi*). When the papilla is inverted, the penis bulb appears large and contains an expanded lumen (*vs*) into which the two vasa deferentia (*vd*) empty. On the other hand, when the papilla is completely everted (Figure 53A), the bulb is contracted and the lumen is reduced in size. The papilla consists of a basal portion with a thick wall and a strong musculature (particularly a layer of circular muscles underlying the outer epithelium) and a thin-walled distal part of variable shape. The male atrium (*am*) is lined by a thick, glandular epithelium and is surrounded by a strong coat of circular and longitudinal muscle fibers.

The common oviduct opens into the end part of the male atrium. Both the terminal portions of the paired oviducts and the greater part of the common oviduct connect with numerous eosinophilic shell glands. The copulatory bursa (*b*) is a rounded or more irregularly shaped sac of moderate to rather small size. The bursal duct (*bd*) is at first a narrow canal running posteriorly to the left of the penis. In its posterior part it widens considerably and then opens into the common atrium from the dorsal side. Before its opening it forms a well-developed, rather characteristic, posterior caecum (*cbd*). The adenodactyl is of moderate size, about as large as the penis or somewhat larger. It has a conical papilla and a long lumen.

ECOLOGY AND DISTRIBUTION.—*Dendrocoelum al-*

bidum was dredged in the shell zone of Lake Ohrid, in Ohrid Bay, at depths ranging from 16 to 30 m. Both mature and young individuals were taken. The species seems to be rather common in the shell zone but is easily overlooked on account of its small size. Several young animals were reared to maturity in aquaria on a diet of fresh beef liver.

TAXONOMIC POSITION.—*Dendrocoelum albidum* is undoubtedly a member of the *D. adenodactylosum* group, considering the anatomy of its reproductive system. Among its outstanding characteristics is the frequent development of a specific pigment pattern and the presence of a rather highly differentiated adhesive organ. It shares the latter characteristic with a closely allied species of the profundal zone, *D. sinisai,* from which it differs externally by having the eyes situated more closely together and by the fact that its intestinal area reaches anteriorly to the level of the eyes.

The name of the species, *albidum* (*albidus,* Latin, whitish), refers to the white or near-white color of the animal.

Dendrocoelum sinisai, new species

FIGURES 11, 47

?Neodendrocoelum adenodactylosum Stanković and Komárek, 1927:602 [in part].
?Neodendrocoelum sp. (immaturum album) Stanković, 1938:2.
?Neodendrocoelum album.—Komárek, 1953a:304.
[Not *Dendrocoelum album* (Steinmann, 1910:188).]

TYPE MATERIAL.—Holotype, set of serial sagittal sections on 3 slides, USNM 55244; paratypes, sagittal sections of 2 specimens on 5 slides, USNM 55245–55246.

This is a rather rare white species inhabiting the profundal zone of Lake Ohrid.

EXTERNAL FEATURES (Figure 11).—Mature specimens are about 10 mm long and 1.7 mm wide. The head is not marked off from the rest of the body by any narrowing or neck. The anterior end is truncate, the frontal margin bulging only slightly. In the middle of the frontal margin is a small depression or opening, clearly visible in the living animal, the entrance to the adhesive organ. The lateral corners of the head are rounded and do not project laterally or anteriorly. Behind the head, the lateral body margins diverge posteriorly for a short distance, then run parallel up to the level of the copulatory complex, where they narrow again to form a sharply pointed tail end.

The two eyes are remarkably small and placed far apart, their mutual distance amounting to about one-half the width of the head. The distance of each eye from the lateral margin is about equal to that from the frontal margin.

The body is unpigmented, white. The pharynx is rather long, attaining about one-sixth the length of the animal. Its root is situated behind the middle of the body. A broad, rather delicate, transparent border along the lateral margins is left free of branches of the intestinal system. This border is well marked off from the area covered by the intestine. Anteriorly, the intestine ends at a considerable distance behind the level of the eyes.

The locomotion of the animal is a slow gliding. I observed no crawling movements. The margins of the body are not thrown into folds during movement.

ANATOMY.—The anterior subterminal adhesive organ resembles very closely that of *Dendrocoelum albidum.* Here again is a deep tubular depression into which the adhesive glands open. The arrangement of the muscle layers of the organ is the same in both species: fibers of the ventral subepidermal longitudinal muscle layer attach to the adhesive epithelium.

The testes are situated at dorsal, ventral, and intermediate levels in a zone extending from the ovaries to the tail end. Of the five mature specimens examined, only three contained functioning testes, in the other two no testes were found, but there was an abundant accumulation of sperm in the enlarged vasa deferentia (spermiductal vesicles) on both sides of the pharynx.

The copulatory apparatus (Figure 47) is very similar to that of related species of *Dendrocoelum* of the Lake Ohrid area. The adenodactyl (*ad*) and the posterior part of the bursal duct (*bd*) are slightly to the left of the penis, and the common oviduct passes on the right side of the bursal duct. The genital aperture (*gp*) is more or less obstructed by a plug formed by the tall cells lining the common atrium in my specimens. There seems to be no distinct glandular area surrounding the genital pore, although the epidermis in this area is somewhat thicker than the general ventral epidermis. The common atrium is rather small, encloses the short papilla of the adenodactyl, and connects on

the right side with the male atrium and dorsally or posteriorly with the outlet of the copulatory bursa. The male atrium (*am*) is long, tubular, and has a strong muscular coat composed of a thick layer of circular fibers and a thinner layer of longitudinal fibers. It extends rather far ventrally, opening into the common atrium very close to the genital aperture. The moderately developed penis bulb (*bp*) contains a rather small seminal vesicle (*vs*), the walls of which form irregular folds. The two vasa deferentia (*vd*) traverse the bulb and open separately, though not far apart, into the anterolateral part of the vesicle. The papilla of the penis consists of a thick-walled basal portion and a thin-walled distal part. The epithelium covering the papilla is rather thick and glandular. In the basal portion is a strong layer of circular muscles beneath the outer epithelium, while the distal part practically lacks any muscular differentiation. The lumen of the papilla expands considerably in the distal part and opens through a narrow aperture at the tip of the papilla. The penis papilla is expanded into the male atrium in all the specimens examined. Nevertheless it may be assumed that it can be inverted into the penis bulb, as observed in organs of similar structure in related species.

The two oviducts (*od*) unite behind the copulatory apparatus, embracing the bursal stalk. The common oviduct opens into the posterior part of the male atrium. Shell glands connect, as usually, with the end parts of the paired oviducts and with the common oviduct. The duct (*bd*) of the copulatory bursa runs posteriorly, somewhat to the left of the penis. It gradually widens and becomes rather broad at the level of the common atrium, then narrowing again and opening into the atrium from the posterodorsal side. The adenodactyl (*ad*), a little larger than the penis, has a rather short conical papilla pointing more or less straight posteriorly.

Ecology and Distribution.—*Dendrocoelum sinisai* was obtained by dredging from the profundal zone of Lake Ohrid, at depths ranging from 40 to 90 m. A total of 20 animals were taken, 8 of which had sexual structures developed. The majority of the specimens were collected in Ohrid Bay, the remainder off Velidab (between Peštani and Trpezica, on the east shore of the lake). The white triclad reported by Stanković and Komárek (1927:602) from a depth of 108 m and considered to be "*Neodendrocoelum adenodactylosum*" was presumably *D. sinisai*. It is highly probable that the immature white species collected by Stanković (1938:2) at a depth of 65 m in Ohrid Bay, designated by him as "*Neodendrocoelum* sp. (immaturum album)" and cited by Komárek (1953a:304) as "*Neodendrocoelum album*," also belongs to this species.

No attempt was made to rear the animals in the laboratory.

Taxonomic Position.—*Dendrocoelum sinisai* resembles the other local species of the group of *D. adenodactylosum* by many anatomical characters. It differs from most of them by having a well-developed anterior subterminal adhesive organ and by having the testes located both dorsally and ventrally, while they are predominantly ventral in some of the other forms. Its nearest relative is *D. albidum* of the shell zone of the lake, both species possessing an analogous adhesive organ. In life, the two species differ in the position of the eyes and in the location of the anterior border of the intestinal area.

The new species is named in honor of Professor Siniša Stanković, the meritorious investigator of the limnology and biology of Lake Ohrid.

Dendrocoelum translucidum, new species

Figures 7, 48, 56

Type Material.—Holotype, set of serial sagittal sections on 7 slides, USNM 55247; paratypes, sagittal and transverse sections of 4 specimens on 25 slides, USNM 55248–55251.

This species is fairly common in the profundal zone of Lake Ohrid.

External Features (Figure 7).—Mature specimens of *Dendrocoelum translucidum* attain a length of 7 mm or slightly more, and a maximum width of 2¼ mm. The general aspect of the animal resembles a planariid rather than a dendrocoelid triclad. The anterior end is broad, truncated, and with a small projection in the midline, to the sides of which the frontal margins slant backward to the rounded lateral corners. Behind the head the lateral margins of the body diverge gradually and reach the greatest width at about the middle of the body. There is no neck constriction behind the head. The posterior end is rather sharply pointed.

The color of the animal appears whitish when seen against a dark background. Upon closer examination of the living animal, however, a very light touch of nongranular brown pigment can be seen, somewhat denser near the midline than toward the sides of the body. The distance between the two eyes is about one-third the width of the head. Their distance from the frontal margin is smaller than that from the lateral margins.

The body is rather flattened and, in living specimens, unusually translucent, more so than in unpigmented species. Not only can the intestinal branches be clearly seen, but the outlines of the pharynx and the copulatory complex, the two swollen vasa deferentia (spermiductal vesicles) on both sides of the pharynx, and even the opaque yolk glands filling the spaces between the gut branches can be discerned wtih a hand-lens.

The undisturbed animal moves by a very slow gliding. Upon stimulation it detaches from the substrate and twists the body violently upward and downward. This very characteristic reaction has a certain resemblance to the swimming reaction of *Dendrocoelum ochridense,* but here the animal is not lifted above the substrate. It apparently is correlated with the extraordinary development of the integumental muscle layers.

ANATOMY.—The combined thickness of the subepidermal muscle layers of the dorsal and ventral sides may amount to one-sixth the total dorsoventral diameter of the body.

The anterior end has a feebly developed subterminal adhesive organ in the form of a transverse strip of infranucleate epithelium perforated by eosinophilic gland ducts but lacking special muscular differentiations. The width of the organ in the midline is 30 to 60 μm.

The pharynx is comparatively small (both short and narrow). In preserved specimens its length amounts to one-ninth to one-twelfth the length of the body. The branching of the intestine can be clearly seen in the living animal (Figure 7). The anterior intestinal ramus begins at about the level of the eyes and bears 5 to 8 branches on each side; each of the two posterior rami has 9 to 14 branches. The branches themselves are only slightly ramified.

In the reproductive system, the testes are arranged in a zone extending from a level anterior to the ovaries backward to close to the tail end. They are located in both the dorsal and ventral portions of the mesenchyme. A large tubal bursa, with tall epithelium, is attached to each ovary.

The general arrangement of the various parts of the copulatory apparatus (Figure 48) of *Dendrocoelum translucidum* resembles that of the spotted species of the genus occurring in the lake. There is, however, no pronounced development of a glandular field of tall epidermal cells surrounding the gonopore, such as is characteristic for *D. maculatum*, etc. The adenodactyl and the bursal stalk are on the left side, the penis and the common oviduct on the right side of the midline. The genital atrium shows the usual differentiation into a common atrium (*ac*) enclosing the papilla of the adenodactyl (*ad*) and connecting with the male atrium (*am*), the bursal stalk (*bd*), and the genital pore (*gp*); and a male atrium (*am*) consisting of an elongated cavity that tapers posteriorly to a tubular section opening into the common atrium from the right side. The male atrium is lined with a tall glandular epithelium and is surrounded by a strong circular and a thinner longitudinal muscle layers.

In four of the five specimens examined, the penis appears as shown in Figure 48: it has a spherical bulb enclosing a voluminous seminal vesicle (*vs*) and a rather small papilla that is more or less retracted into the lumen of the bulb. According to the degree of retraction, it either appears as a thick circular fold or perforated diaphragm, separating the seminal vesicle from the cavity of the male atrium, or it has the shape of an inverted pseudoflagellum. In one specimen, the papilla was everted and formed a short, conical projection, the seminal vesicle was contracted and opened through a narrow straight canal (comparable to an ejaculatory duct) at the tip of the papilla (Figure 56). The two vasa deferentia (*vd*) empty separately into the seminal vesicle from the anterolateral sides, rather far dorsally.

The oviducts unite behind the copulatory complex, embracing the bursal stalk. The long common oviduct (*odc*) opens into the male atrium close to its junction with the common atrium. The end portions of the separate oviducts and the posterior two-thirds of the common oviduct are connected with shell glands. The copulatory bursa (*b*) is rather large, sac shaped, with a smooth outline. The bursal stalk (*bd*) widens somewhat as it runs posteriorly and opens from the dorsal side into the common atrium; in its posterior section, the muscular coat

attains a considerable thickness. The adenodactyl (*ad*) is larger than the penis; its papilla either points posteriorly or is bent ventrally and protrudes through the genital pore.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum translucidum* lives in the profundal zone of Lake Ohrid. A total of about 60 specimens, the majority of them sexually mature, were dredged in September 1935 in Ohrid Bay, from depths varying between 40 and 90 m. All the localities were below the zone of living *Dreissena*. The bottom deposits were soft or hard mud, often with fragments of *Dreissena* shells.

TAXONOMIC POSITION.—*Dendrocoelum translucidum*, an almost white species, is well characterized by its planariid-like habit, the shape of its anterior end, and its general transparency. From another species of the profundal zone, *Dendrocoelum sinisai*, it differs by the shape of its head and the absence of an anterior adhesive organ discernible in the live animal.

The species name, *translucidum* (Latin, transparent), refers to the remarkable transparency of its body.

Dendrocoelum cruciferum (Stanković)

FIGURES 9, 31, 49

Neodendrocoelum cruciferum Stanković, 1969:419.
Dendrocoelum cruciferum.—Kenk, 1974:16.

MATERIAL DEPOSITED.—Sagittal serial sections of 2 specimens, on 21 slides USNM 55260–55261.

This large, well-defined species of the shell zone of Lake Ohrid was accurately described by Stanković (1969:419–421). It can easily be recognized by its very characteristic pigment pattern.

EXTERNAL FEATURES (Figure 9).—Mature specimens are oblong-oval in shape, 15–28 mm long, and 5–8 mm wide. The broad anterior end is not marked off by any constriction from the rest of the body. During undisturbed gliding, the head appears truncated, with rather angular lateral corners. The central part of the frontal margin, about one-third the width of the head, is occupied by a well-differentiated grasping organ that forms a distinct, almost rectangular, anterior projection. The shape of this organ varies greatly in the different motor activities of the animal. In quiet gliding it is convex on the dorsal and concave on the ventral surfaces. Behind the head, the body widens gradually up to about the middle of its length, then narrows again, with the posterior end bluntly pointed.

The distance between the two eyes is a little less than one-third the width of the head; their distance from the lateral margins is greater than that from the frontal margin. In mature specimens, the mouth is situated behind the middle of the body, dividing the body length in the ratio 3:2. The genital pore is closer to the mouth than to the posterior end.

The ground color of the dorsal side is a light yellowish or grayish brown, frequently with an olive-green tint. A rather broad rim along the margins is lighter and almost colorless and transparent. There is an indistinct dark line on the boundary between the marginal rim and the central area. A distinct, grayish-black stripe runs along the midline of the central area, beginning behind the eyes and extending posteriorly to the marginal rim. A pair of rectangular, or more rounded, spots of the same dark color are placed transversely above the region of the pharynx (closely behind the middle of the body in mature specimens, farther back in young animals). These spots reach laterally about halfway between the midline and the marginal rim. Between the two spots, the dark medial stripe is interrupted. In mature animals, the median stripe may split for a short distance into two parallel lines above the copulatory apparatus. In the resting contracted animal, the median stripe and the transverse spots form a peculiar crosslike pattern, which has given the species its name. The ventral surface is unpigmented, whitish.

The locomotion of *Dendrocoelum cruciferum* is either gliding or, more frequently, crawling. In quiet gliding, the margins of the body are smooth. Crawling movement can easily be induced by even slight stimulation. The animal then alternately, in quick succession, extends the anterior end and attaches it to the substrate by means of the grasping organ, while contraction waves run backward along the body and the lateral margins are thrown into fine irregular folds. The animal progresses more rapidly by crawling than by gliding.

ANATOMY.—In fully grown specimens, the surface epithelium of the dorsal side is markedly thicker than that of the ventral side (42 μm and 20 μm, respectively, in one specimen; 67 μm and 25 μm in another). The distal parts of the dorsal epidermal cells are densely packed with rhabdites. Numerous subepidermal rhabdite-forming cells are seen below

the integumental muscle layers of the dorsal side.

The highly developed grasping or adhesive organ (Figure 31) has the shape of a hollow cup in the preserved animal. The adhesive surface lining the cavity is formed by an infranucleate epithelium pierced by numerous gland ducts filled with a granular, strongly eosinophilic secretion. It is difficult to analyze the muscular differentiations of the organ because of the deeply stained glandular structures. However, bundles of mucle fibers, parting from the ventral integumental layers, approach the organ in the direction toward the adhesive surface. There is no muscular sheet separating the organ from the surrounding mesenchyme; therefore the name "sucker" cannot be applied to it.

The pharynx is comparatively short and wide. Its muscle systems conform with the scheme characteristic of the family Dendrocoelidae, that is, the circular and longitudinal fibers of the internal muscle zone are intermingled. There are, however, remarkably few longitudinal fibers in that layer and the circular muscles predominate by far.

The ramification of the intestine may easily be seen in the living animals from the ventral side after they have ingested some darkly colored food. The anterior ramus bears from 8 to 12 branches on each side and each posterior ramus from 14 to 16 lateral branches. The branches are only little ramified.

For the study of the reproductive system, I had two mature and two semimature specimens at my disposal. The relatively small testes are situated in both the prepharyngeal and postpharyngeal parts of the mesenchyme, the majority being ventral at different levels, with only few distinctly dorsal (mainly in the prepharyngeal region). Each ovary connects with a large oviductal tuba.

The copulatory apparatus (Figure 49) is voluminous and occupies somewhat less than the anterior half of the postpharyngeal region. The genital pore (*gp*) lies in the center of a circular area formed by an exceedingly thick columnar epithelium. In the two fully mature specimens, the length of the cells amounted to 125 μm and 92 μm. Numerous eosinophilic gland ducts (*gl*) open in this area, the cell bodies of which are situated in the adjoining mesenchyme. In the semimature specimens, this glandular field was not yet differentiated. The genital pore leads into the common atrium, which contains the papilla of the adenodactyl and connects in the usual way with the end portion of the male atrium (*am*) and with the outlet of the copulatory bursa.

The penis has a large, spherical bulb and a short, blunt papilla (*pp*). The wide cavity of the bulb, the seminal vesicle (*vs*), receives the vasa deferentia (*vd*) separately from the anterolateral sides. The vesicle connects with the atrium through a wide canal of irregular contour, corresponding to an ejaculatory duct. At the transition between the seminal vesicle and the duct is a well-differentiated circular fold (*fl*) hanging into the bulbar lumen. This is a true flagellum as Komárek (1926a:4; 1926b:4) defines it, that is, a fold attached to the inner surface of the penial lumen, quite comparable to the flagellum of *Dendrocoelum lacteum* and related species. The musculature of the penis bulb is moderately developed. The papilla has a well-differentiated layer of circular fibers underlying the epithelium of the outer surface as well as that of the ejaculatory duct. In all specimens examined, the flagellum was introverted into the lumen of the penis. It is obvious that this structure has the same function as the flagellum of *D. lacteum,* which is everted during the act of copulation. Behind the penis, the male atrium narrows to a long tube, runs posteriorly to the right of the adenodactyl, and opens into the common atrium.

The two oviducts unite behind the copulatory complex. The rather long, somewhat curved, unpaired or common oviduct (*odc*) runs anteriorly on the right side of the common atrium and opens into the end portion of the male atrium close to its junction with the common atrium. Both the end parts of the paired oviducts and the common oviduct receives numerous eosinophilic shell glands. The copulatory bursa (*b*) is of moderate size. The bursal duct (*bd*) starts as a narrow canal, coated with a feeble muscle layer, and runs posteriorly on the left side of the penis; behind the level of the penis, the canal widens gradually or more abruptly; the terminal portion, opening into the common atrium from the dorsal side, is again narrowed, bent ventrally, and surrounded by a strong sphicter (*sph*). The adenodactyl (*ad*) lies to the left of the midline and exceeds the penis in size. In fully mature specimens, its lumen is lined with a very thick epithelium, as indicated also by Stanković.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum cruciferm* is a rather rare inhabitant of the shell zone

of Lake Ohrid. Only 11 specimens (9 immature and 2 mature) were collected in Ohrid Bay by dredging at depths ranging from 16 to 29 m, and on bait (meat and a dead fish) at 28 m. The species is rapaceous and presumably preys on other triclads that abound in the sublittoral zone. At first, when its feeding habits were not realized, I kept three specimens of *D. cruciferum* in an aquarium together with 11 specimens of *D. ochridense*. Within a few weeks, only two *D. ochridense* were left. The two species were then separated and five specimens of a darkly pigmented planarian, *Polycelis tenuis,* were introduced into the culture of *D. cruciferum*. The next day, only four individuals of *Polycelis* were in the dish and one specimen of *D. cruciferum* had its intestine darkly stained. Another lot of *D. cruciferum,* six immature animals, was kept in a refrigerator at 10° C and fed *Polycelis tenuis;* in due time they grew to maturity.

Ingestion of food was not actually observed; however, there is reason to believe that *D. cruciferum* uses its grasping organ to catch its prey, similar to *D. lacteum, Procotyla fluviatilis,* etc.

TAXONOMIC POSITION.—*Dendrocoelum cruciferum* stands somewhat apart from the great majority of the species of this genus occurring in Lake Ohrid and approaches *D. lacteum* to some extent. This is seen particularly in the anatomy of the male copulatory organ, in the presence of a flagellum. It differs from *D. lacteum* clearly by its external appearance. An outstanding feature is the large, though apparently histologically simple, adhesive organ. The pigment pattern of the species is very characteristic and resembles superficially that of *D. lacustre*. According to Paunović (1977), the chromosome number of *D. cruciferum* is 2n = 32.

Dendrocoelum lacteum (Müller)

FIGURE 50

MATERIAL DEPOSITED.—Sagittal serial sections of 3 specimens on 23 slides, USNM 55266–55268.

Stanković and Komárek (1927:661) and later Stanković (in several papers) reported the occurrenc of this common European species in Lake Ohrid. Arndt (1938:52) also found an individual of this species on a specimen of a sponge, *Ochridaspongia rotunda,* dredged in Ohrid Bay. The lake form differs from the typical species, however, in some constant characters.

EXTERNAL FEATURES.—The animals in the lake attain a length of 25 mm and a width of 4–5 mm at maturity. The general shape of the body and the configuration of the head are the same as in the typical species. The head is truncate and is flanked by a pair of rounded auricular lobes that project laterally. The greater part of the frontal margin is differentiated into a large, somewhat lobed and folded adhesive cushion. The eyes are far apart from each other at a distance of about three-fifths the transverse diameter of the head. In mature animals, the pharynx lies approximately in the middle of the body, and the copulatory apparatus occupies the anterior third of the postpharyngeal region.

The lake form is characterized by a light, but distinct, reddish-brown coloration, distributed almost evenly over both the dorsal and ventral surfaces of the body. Only a very thin, white middorsal line remains free of pigment. This line is not always well distinguishable when the gut is filled, as the color of the intestinal contents may shine through on the dorsal side. In the fasting animal, however, it is clearly visible.

ANATOMY.—The lake form agrees with the typical species in all essential anatomical characters. The testes are situated in both the dorsal and ventral parts of the mesenchyme, in the prepharyngeal as well as the postpharyngeal regions. In the copulatory complex (Figure 50), the adenodactyl (*ad*) lies slightly to the left of the midline and is smaller than the penis. The bursal duct (*bd*) opens into the common atrium rather far dorsally, above the base of the papilla of the adenodactyl. The shape of the penis shows a wide range of variation in the four specimens examined. The penis bulb is generally of ellipsoidal shape and contains a seminal vesicle (*vs*), the walls of which have villus-like projections protruding into the cavity. The size of the vesicle varies within wide limits. In the specimen depicted in Figure 50, the vesicle was very voluminous and did not extend posteriorly beyond the penis bulb. In another case, the bulb was more contracted, the cavity narrower and situated for the greater part within the papilla of the penis. The two vasa deferentia (*vd*) open separately, generally far apart from each other, into the anterolateral sides of the seminal vesicle. The outlet of the vesicle, or ejaculatory duct, is rather short. At the transition between this outlet and the vesicle is

seen the flagellum (*fl*). In two of the specimens, the flagellum was inverted into the vesicle, in the other two it projected into the male atrium. The flagellum is perhaps a trifle smaller than that of the typical species. A similar wide variation in the relative size of the penis bulb, the papilla, and the seminal vesicle, as we encounter in the lake form, is observed also in the typical *Dendrocoelum lacteum* (see particularly Gelei, 1928:10–11). The greater part of these apparent modifications is doubtlessly due to different states of contraction of the muscular systems of the organs, particularly that of the penis bulb. When the muscles of the bulb are relaxed, the bulb appears large, its cavity voluminous, and the penis papilla short. A contraction of the muscles, on the other hand, will reduce the size of the bulb, constrict the seminal vesicle, and push a considerable part of the penis tissues posteriorly; the papilla will then appear comparatively larger and will contain part or all of the seminal vesicle.

One of the four specimens examined showed a definite glandular area surrounding the genital pore. The epithelium was thicker than that of the general ventral surface and was pierced by many gland ducts filled with an eosinophilic secretion. The other three specimens showed no such marked glandular differentiation, although the epithelium was here also thicker and crowded with tall rhabdites. Only very few gland ducts were seen approaching the area. It may be that the glands develop only in a certain physiological stage of the reproductive cycle and function only a short time. In the typical *Dendrocoelum lacteum* I have occasionally observed a similar glandular field, and Iijima (1884:367, 371) has noticed a thicker epithelium with numerous long rhabdites in the vicinity of the genital pore. De Beauchamp (1932: 138), however, states that in the genus *Dendrocoelum* only representatives of the subgenus *Neodendrocoelum* have glands around the genital aperture. The glandular field of *D. lacteum* differs from that of other Ohrid species by the presence of rhabdites in the thickened epithelium, while in *D. maculatum* and relatives the cells of the glandular field lack rhabdite inclusions.

Distribution and Ecology.—*Dendrocoelum lacteum* is rather common in the sublittoral zone (shell zone) of Lake Ohrid. It was collected in Ohrid Bay at depths ranging from 16–30 m and near Kalište at depths from 7 to 13 m. It also occurs in the profundal region (Ohrid Bay, 47–90 m), but was rarely taken in the littoral zone (near Kalište, above the Chara zone). Cocoons of this species were found repeatedly; they are unstalked, spherical, with a diameter of 3–3.5 mm. Three cocoons that I opened contained 5 to 8 embryos each. The hatching young were rather large (6 mm) and unpigmented. Specimens were kept in laboratory cultures for several weeks and accepted beef liver as food, but did not remain in good condition; they gradually reduced their pigmentation, and in many individuals the head region disintegrated. Apparently the food offered them was not adequate, as the species normally feeds on amphipods, isopods, and oligochaetes (Reynoldson and Davies, 1970). No cocoons were deposited in the aquaria.

Taxonomic Position.—The lake form of *Dendrocoelum lacteum* differs from the typical form principally by its pigmentation. Several older authors have described and even named "colored" varieties of *D. lacteum* in which, however, the color was due to the intestinal contents: *Fasciola crenata* Müller (1774:64); *Planaria lactea* var. *crocea* Baer (1827:728); four color varieties of *D. lacteum* named by Spoof (1889:7). The only true, genetically stable, colored subspecies known is *Dendrocoelum lacteum verbanense,* described by Benazzi (1945: 31–33) and again mentioned by Mirolli (1961:976), inhabiting the littoral zone of Lake Maggiore in northern Italy. In the Lake Ohrid form, there is also a true, almost uniform pigmentation present not only in the area covered by the intestine, but also in the head region and the margins of the body. Moreover, a very thin middorsal white line, free of pigment, is seen in starving specimens.

A white form of *Dendrocoelum lacteum, D. l. bathycola* (Steinmann), is known to occur in the profundal zones of several lakes in the Swiss and Austrian Alps, in a lake (Madüsee) in Pomerania, and possibly in Sweden (Vättern). It is characterized by a reduced size (7 mm), by a tendency to eye reduction, by a small number of intestinal branches, and by a relatively well-developed reproductive system (for a more comprehensive account, see Zschokke, 1911:82–84). It is disputable whether the characters of the subspecies *bathycola* are genetically fixed or are the result of the profundal environment that differs considerably from the usual littoral habitat of *D. lacteum*. The discon-

tinuous distribution of the form would rather suggest that it originated from the typical species independently in the individual lakes and that it should be considered merely an ecological modification. The Lake Ohrid form of *D. lacteum* has little in common with the subspecies *bathycola:* its size is above the average size of the typical species; the eyes are well developed; and the body is opaque (in *bathycola* rather translucent).

No transitional specimens that would bridge the gap between the typical *D. lacteum* and the Ohrid form have been found. Nevertheless, I refrain from considering the lake form to be a separate subspecies until its relation to the typical species can be studied more intimately.

Dendrocoelum jablanicense (Stanković and Komárek)

FIGURES 25, 51

Neodendrocoelum jablanicense Stanković and Kamárek, 1927: 613.
Dendrocoelum (Dendrocoelum) jablanicense.—Kenk, 1930:301.
Dendrocoelum (Eudendrocoelum?) jablanicense.—de Beauchamp, 1931:158.
Dendrocoelum (Neodendrocoelum?) jablanicense.—Gourbault, 1972:68.
Dendrocoelum jablanicense.—Kenk, 1974:17.

MATERIAL DEPOSITED.—Sagittal, transverse, and horizontal serial sections of 4 specimens on 9 slides, USNM 55262–55265.

Dendrocoelum jablanicense was described by Stanković and Komárek (1927:613–616) from specimens collected in Šum, a large limestone spring west of Struga, on the northern bank of Lake Ohrid, so far the only known habitat of this interesting species. From the same locality, de Beauchamp (1937:357) obtained a single specimen that conformed to some extent with the description by Stanković and Komárek, as well as several samples of *D. adenodactylosum*. De Beauchamp considered the specimen to be a somewhat deviate form of *D. adenodactylosum*. I also collected the species in Šum but have found it to be more common in some tributaries of Lake Ohrid.

EXTERNAL FEATURES (Figure 25).—Because of the very similar outward appearance of *Dendrocoelum jablanicense* and *D. adenodactylosum,* I did not differentiate between the two species in the field, nor did I analyze the detailed habit of *D. jablanicense* in the laboratory. For the external aspect of the living animals we must, therefore, rely on the description given by Stanković and Komárek. According to these authors, *D. jablanicense* is somewhat smaller than *D. adenodactylosum* (the length of mature animals being 10–15 mm and 20 mm, respectively) and has a more slender shape. The truncate head is only little narrower than the body and not separated from it by any constriction. The frontal margin does not show the well-marked lateral lobes seen in *D. adenodactylosum;* only a slight hint of such lobes is indicated by the wavy outline of the margin. The distance between the two eyes is about one-third the diameter of the head, while in *D. adenodactylosum* the eyes are farther apart. In my preserved material, the average size of *D. jablanicense* is smaller than that of *D. adenodactylosum,* though the difference is certainly not significant. Small mature specimens of *D. adenodactylosum* may be no larger than large specimens of *D. jablanicense.*

ANATOMY.—The subterminal adhesive organ is rather weak. It consists of a small area of a median diameter of 40 μm, which has either a shallow concave or a bulging surface in the preserved animal. It connects with numerous eosinophilic gland ducts but apparently has no special muscular differentiations.

The testes are situated ventrally and form a broad zone extending from the level of the ovaries to the tail end on either side of the midline. The zones meet and unite in the midline only behind the copulatory complex.

The arrangement of the organs of the copulatory apparatus is very characteristic for the species, as pointed out by Stanković and Komárek and again by Stanković (1969:428). The adenodactyl (*ad*) lies to the right side of the midline and not to the left side as in all other species of *Dendrocoelum* from the Ohrid region. The duct of the copulatory bursa (*bd*) is markedly expanded and has a strictly lateral position to the left of both the penis and the adenodactyl.

The genital aperture (Figure 51, *gp*) is situated in an area of modified epithelium that is pierced by many gland ducts (*gl*). It leads into a moderately large chamber, the common atrium, that encloses the papilla of the adenodactyl. Dorsally, this cavity connects with the male atrium (*am*) by a short,

narrow canal. Laterally on the left side, it communicates with the bursal duct by one or two rather small openings (*bdo*). The male atrium (*am*) is more or less conical and extends posteriorly beyond its connection with the common atrium, to receive, at its end, the mouth of the common oviduct (*odc*).

The penis is of moderate size, smaller than the adenodactyl, and consists of a muscular bulb and a rather short papilla. A more or less marked constriction separates the basal part of the papilla from the somewhat expanded distal portion or glans. The outer wall of the papilla has a well-differentiated layer of circular muscles. Beneath these, in the parenchyma of the papilla, are longitudinal muscles fibers. The lumen of the penis is variable in shape, depending on the state of contraction of the muscles of the penis bulb. It may form a voluminous cavity or seminal vesicle within the bulb and open through a narrow canal at the tip of the papilla as shown by Stanković and Komárek (1927, text-figs. 10, 11) and found in one of my specimens. In other specimens, the cavity may appear constricted, assuming a more tubular shape, and extending throughout the length of the organ. Upon extreme contraction of the penis bulb, the lumen and the tissues surrounding it may be pushed posteriorly into the papilla. The penis is traversed by numerous gland ducts containing a finely granular, weakly eosinophilic secretion and opening into the penial cavity. The two vasa deferentia (*vd*) enter the penis bulb separately, converge toward the midline of the organ, and unite to form a common vas deferens that connects with the penis lumen from the ventral side. This union of the two sperm ducts is very characteristic, as it has so far been observed in only two other species of the genus *Dendrocoelum* (*D. puteale* Kenk and *D. kenki* de Beauchamp), which in other regards show no close relationship to *D. jablanicense*.

The two oviducts unite behind the copulatory apparatus, embracing the bursal stalk. The moderately long common oviduct (*odc*) runs anteriorly and opens into the posterior extension of male atrium. Both the end parts of the paired oviducts and the greater portion of the common oviduct are connected with eosinophilic shell glands. The sac-shaped copulatory bursa (*b*) shows no peculiarities. Its outlet or duct (*bd*), however, has a remarkable shape and position: it starts as a rather narrow canal, proceeding posteriorly to the left of the penis, then gradually widens to form a laterally compressed sac that occupies about one-half the dorsoventral diameter of the body at the level of the adenodactyl and connects with the common atrium by one or two rather narrow openings (*bdo*). This double communication between the bursal duct and common atrium is unique among the freshwater triclads. The adenodactyl (*ad*) is larger than the penis but is not excessive in size. It contains a rather long, tubular lumen.

DISTRIBUTION AND ECOLOGY.—*Dendrocoelum jablanicense* is an inhabitant of cold springs. All literature records (Stanković and Komárek, 1927:616; de Beauchamp, 1937:357; Stanković 1969:428) list the source of Šum, a large spring west of Struga, as the only known habitat of the species. I visited that locality and besides collecting *D. jablanicense*, I also collected *D. adenodactylosum*, *D. maculatum*, *Crenobia alpina montenigrina*, and *Phagocata ochridana*. Most of my material of *D. jablanicense* was taken in the cold springs at Studenčište and at Bej-Bunar, where the animals are found on the undersides of stones together with other triclad species. It is possible that its distribution in springs of the Ohrid region is much wider than is known at present, as the animals are easily confused with *D. adenodactylosum*. Stanković (1960:179) reported that in Šum the species is found also in the cave from which the spring issues, and he assumed that it might be a troglophile in spite of its well-developed eyes. I made no attempt to rear the species in laboratory culture, as I had not expected to find it among the materials collected in the more eastern springs. It was recognized only when analyzing the anatomy of the preserved specimens.

TAXONOMIC POSITION.—*Dendrocoelum jablanicense* stands somewhat apart from the other species of *Dendrocoelum* of the Ohrid region in several anatomical characters. In the field it is easily confused with another white spring planarian, *D. adenodactylosum*. The principal differences between the two species in life have been pointed out by Stanković (1969:428): *D. jablanicense* has a different shape of the head, the eyes are closer together, and the intestinal branches less ramified than in *D. adenodactylosum*. Among the anatomical characters, the spatial arrangement of the parts of the copulatory complex does not conform with the general scheme observed in the genus: the bursal duct is

situated to the left and the adenodactyl to the right of the penis, while in most related species the bursal duct and adenodactyl are placed on the same side, generally left of the penis. The union of the two vasa deferentia before they open into the seminal vesicle is also exceptional. The peculiar communication between the common atrium and the duct of the copulatory bursa, by one or two short canals or narrow openings, is another character not known in other freshwater triclads. Paunović (1977) found the chromosome number of the species to be $2n = 32$.

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ABBREVIATIONS USED IN ILLUSTRATIONS

ac	common genital atrium
ad	adenodactyl
am	male atrium
ao	adhesive organ
b	copulatory bursa
bd	bursal duct or stalk
bdo	opening between bursal duct and common atrium
bp	penis bulb
cbd	caecum of bursal duct
cc	cerebral commissure
de	ejaculatory duct
ed	dorsal epidermis
ev	ventral epidermis
fl	flagellum
gl	gland ducts
gp	gonopore
i	intestine
m	mouth
md	dorsal integumental muscle layer
mdc	dorsal circular and diagonal muscles
mdl	dorsal longitudinal muscles
mdv	dorsoventral muscles
me	mesenchyme
mt	transversal muscles
mv	ventral integumental muscle layer
mvc	ventral circular and diagonal muscles
mvl	ventral longitudinal muscles
od	oviduct
odc	common oviduct
pg	penial glands
ph	pharynx
pp	penis papilla
ppi	inverted penis papilla
sph	sphincter
te	testis
vd	vas deferens or sperm duct
vi	vitellaria or yolk glands
vs	seminal vesicle

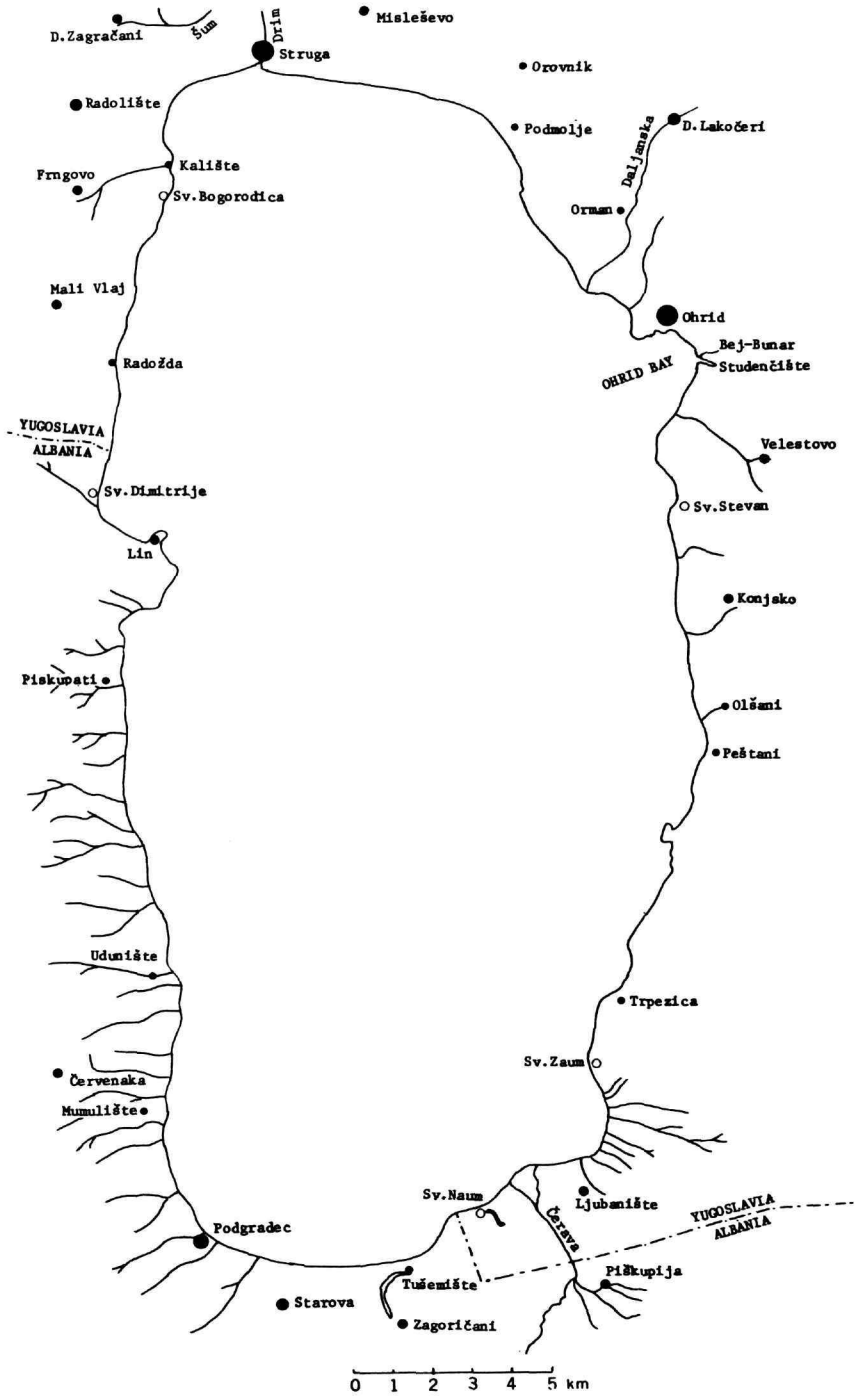
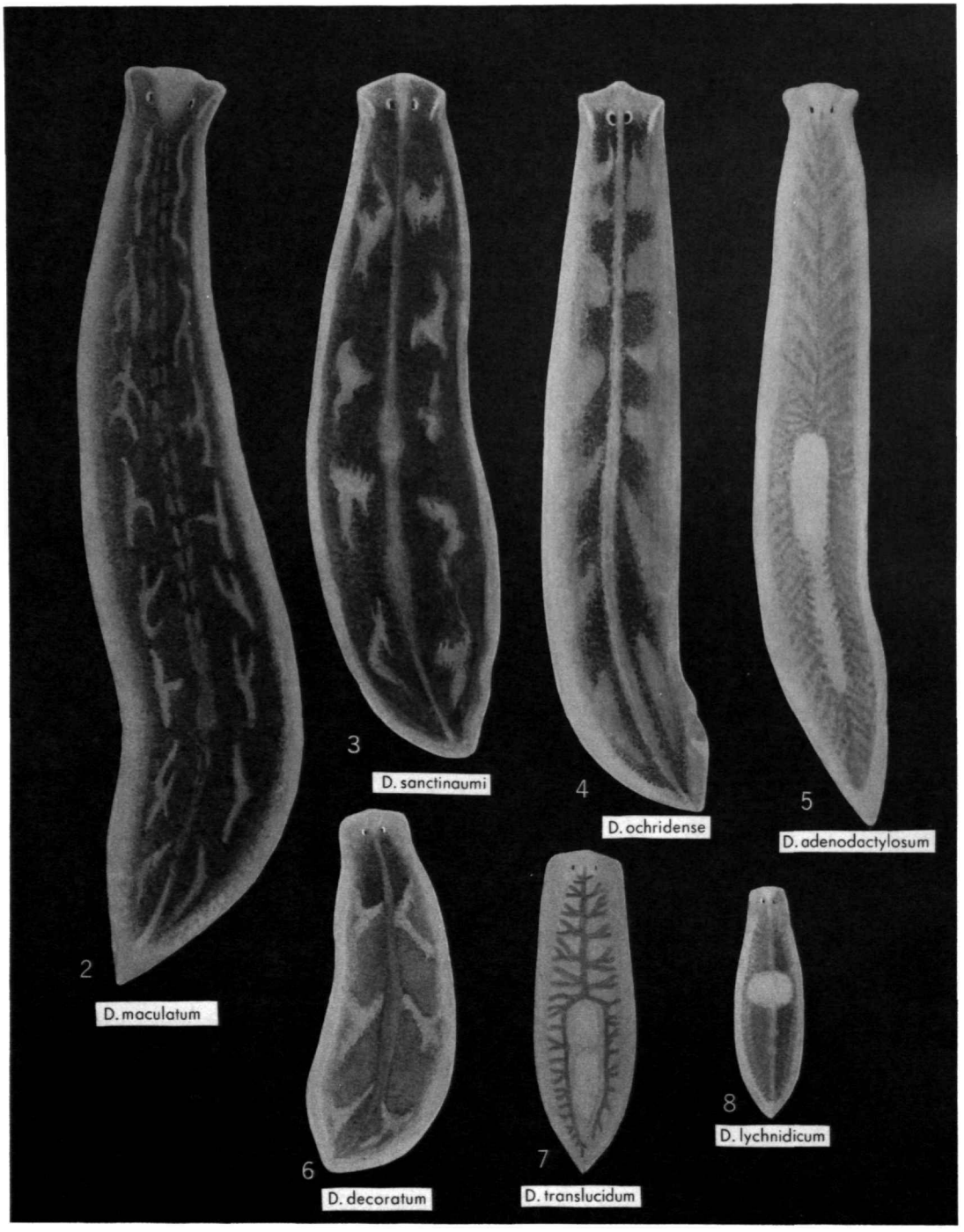
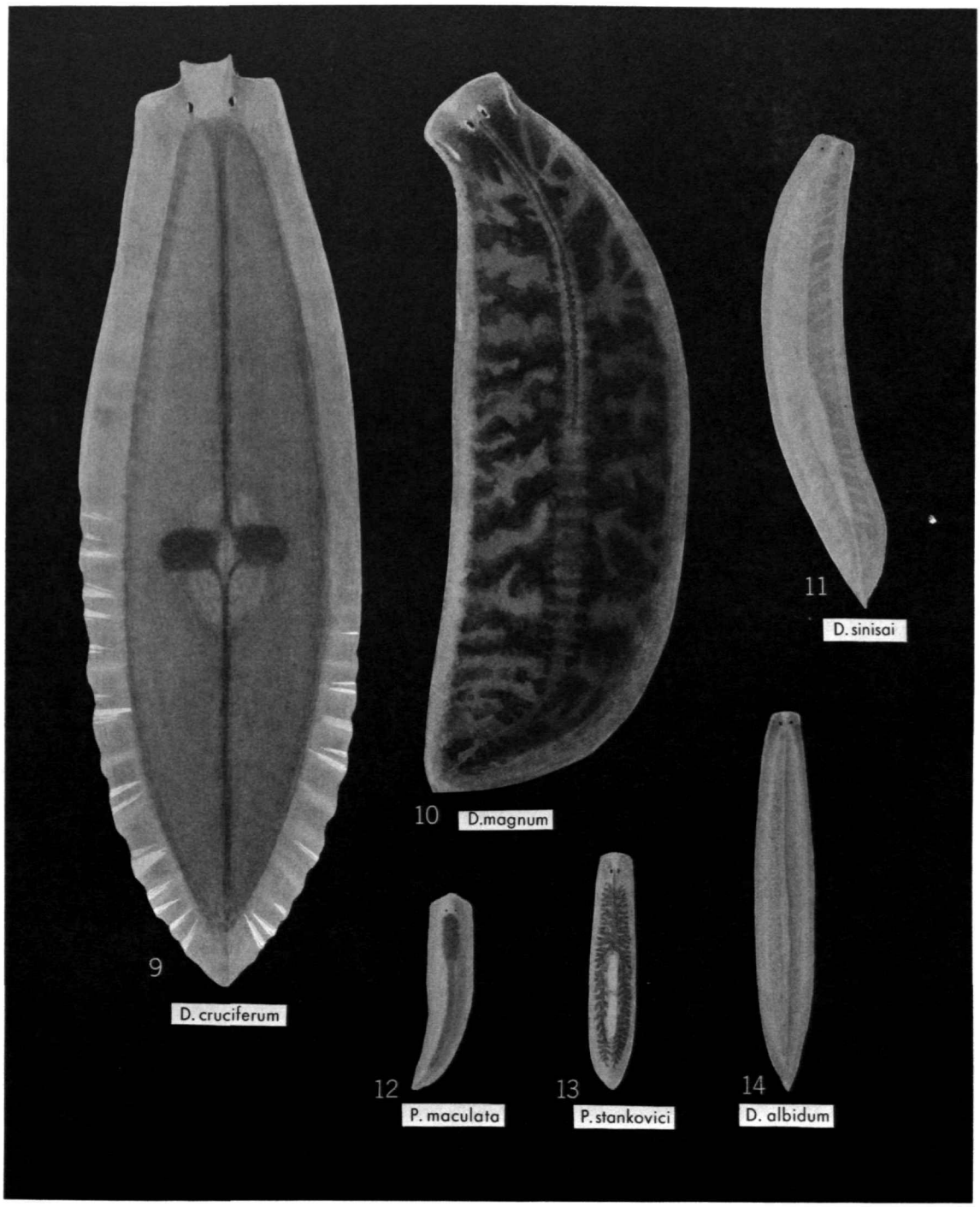


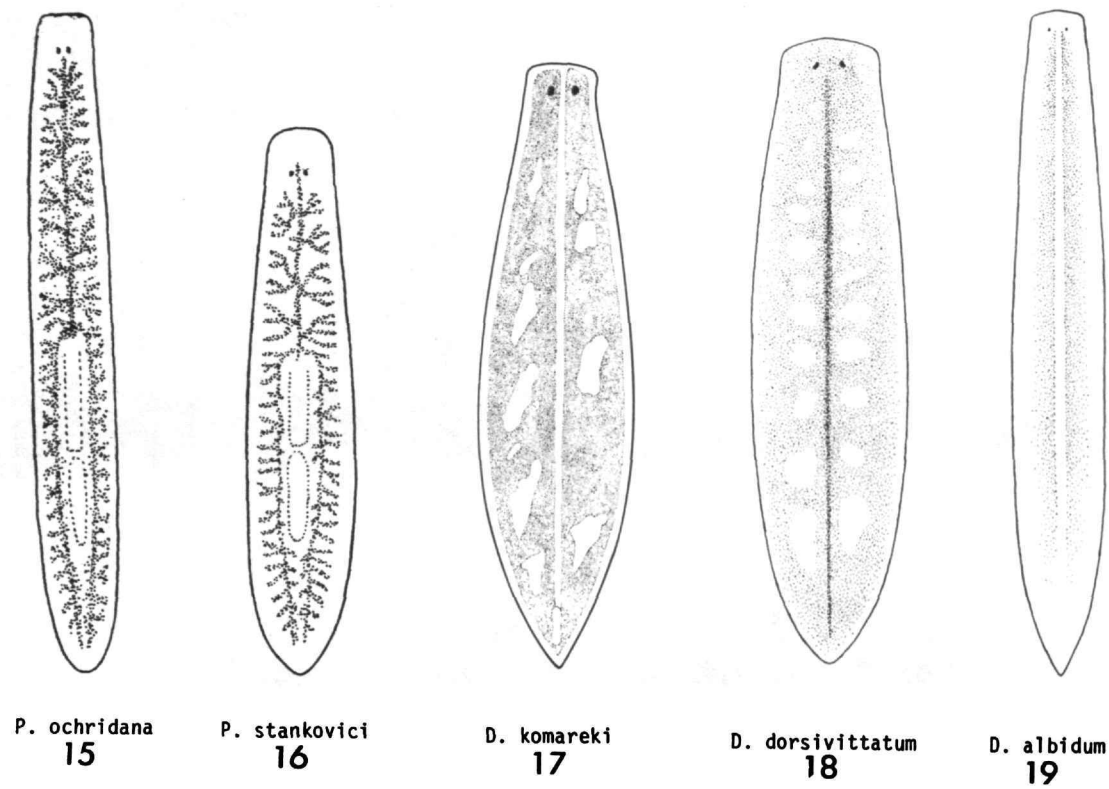
FIGURE 1.—Map of Lake Ohrid and surroundings.



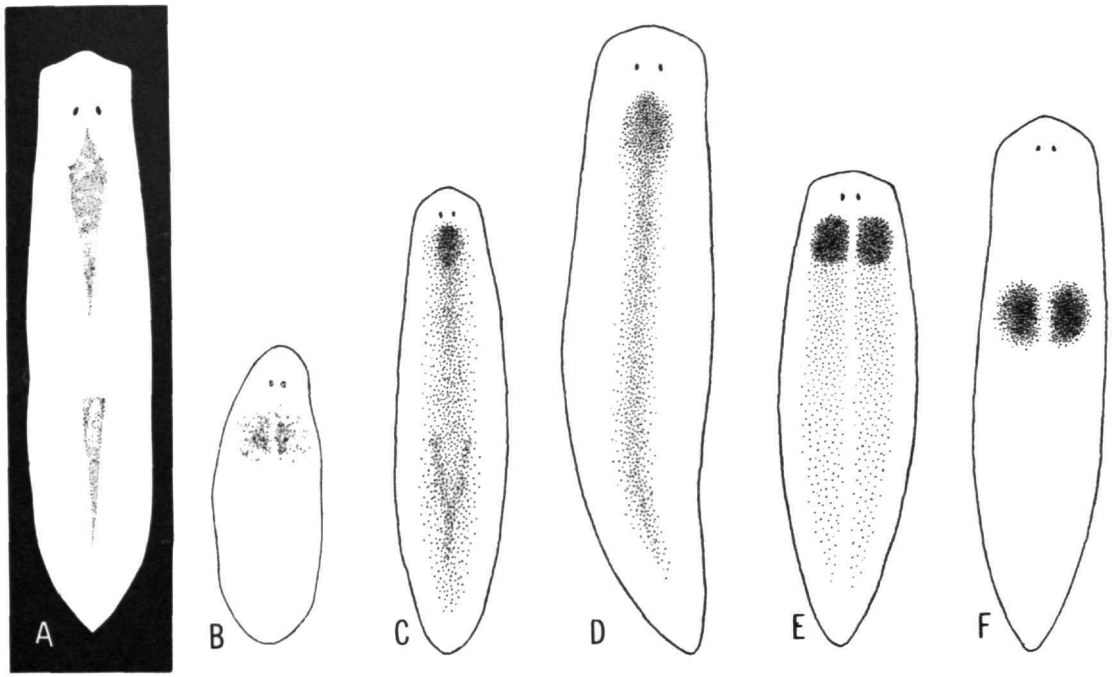
FIGURES 2–8.—Ohrid planarians, from life (paintings by Žnidaršič), all ×8.



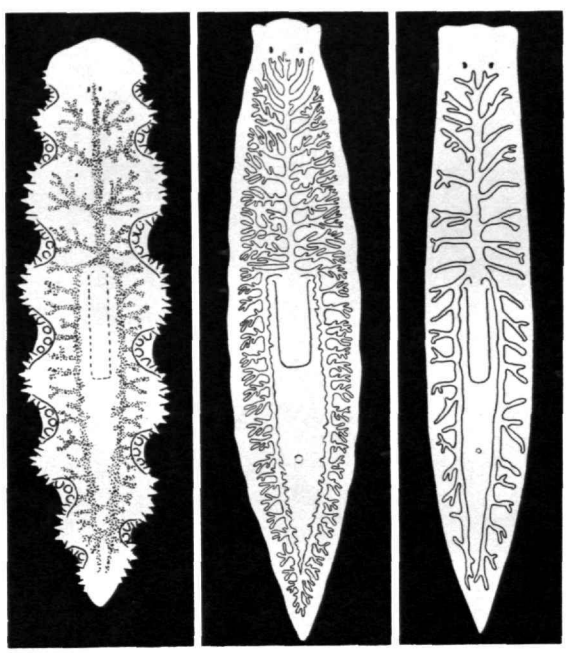
FIGURES 9–14.—Ohrid planarians, from life (paintings by Ivan Žnidaršič), all ×8.



FIGURES 15–21.—Ohrid planarians, sketches from life: 15, ×16; 16, ×16; 17, after Stanković, 1969; 18, ×9; 19, ×12; 20, magnification not recorded; 21, ×16.



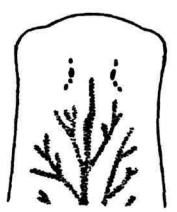
22 P. maculata



P. undulata 23

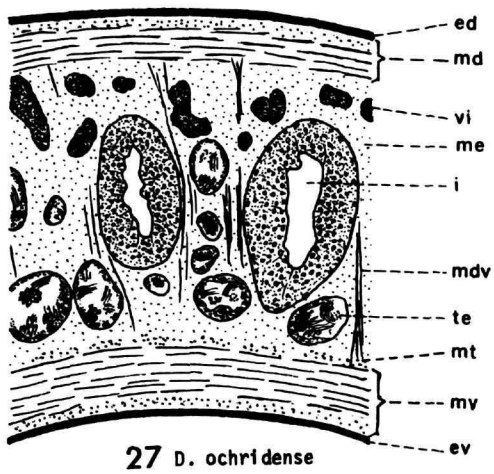
D. adenodactylosum 24

D. jablanicense 25

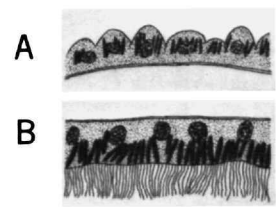


D. adenodactylosum 26

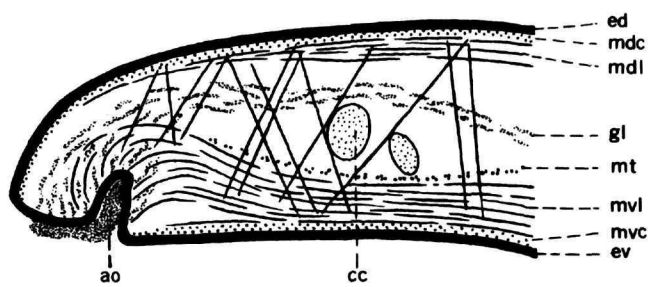
FIGURES 22–26.—Ohrid planarians, sketches from life: 22, variation of pigment pattern (A, after Stanković, 1960; B, after Stanković, 1938; C–F, ×23); 23, ×10; 24–25, after Stanković and Komárek, 1927; 26, specimen with supernumerary eyes, anterior end, ×15.



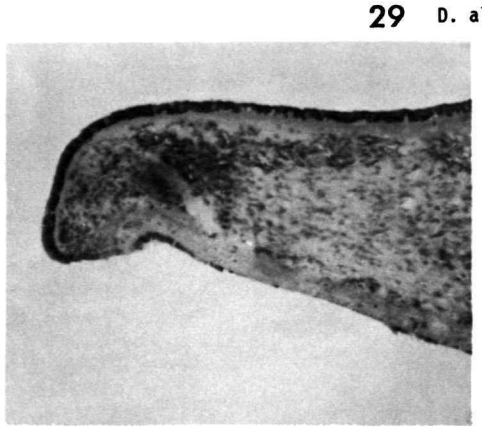
27 D. ochridense



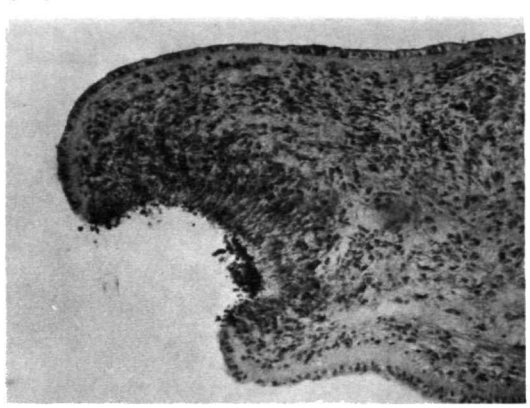
28 P. undulata



29 D. albidum

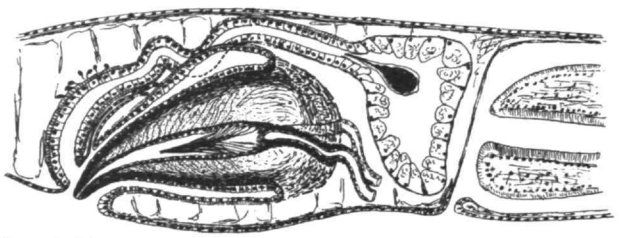


30 D. ochridense

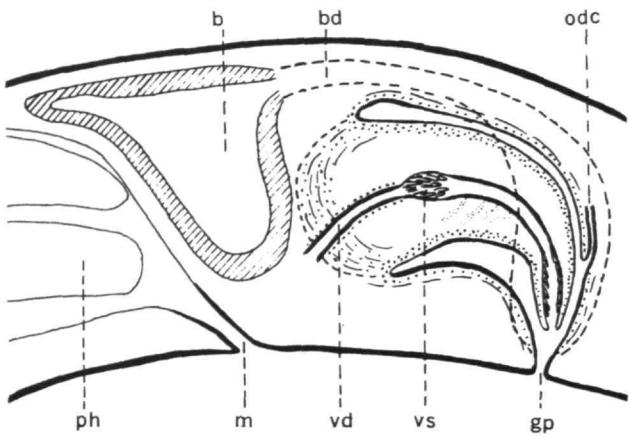


31 D. cruciferum

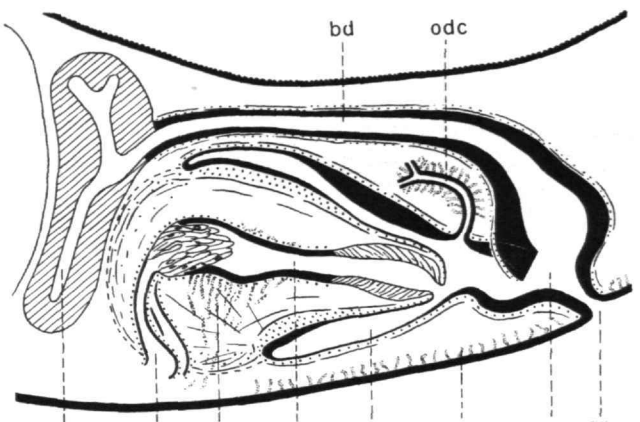
FIGURES 27–31.—27, Parasagittal section showing subepidermal muscle layers, ×71. 28, Epidermis, ×656 (A, dorsal surface; B, ventral surface). 29, Sagittal section of anterior end, showing adhesive organ, ×134. 30–31, Adhesive organs in sagittal section, ×101.



32 P. ochridana

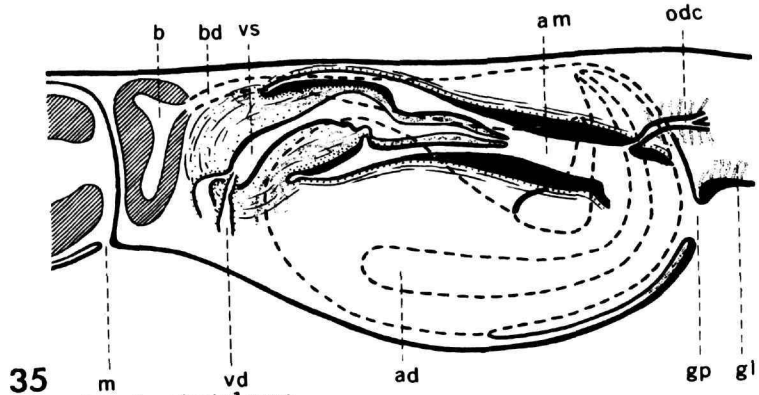


33 P. maculata

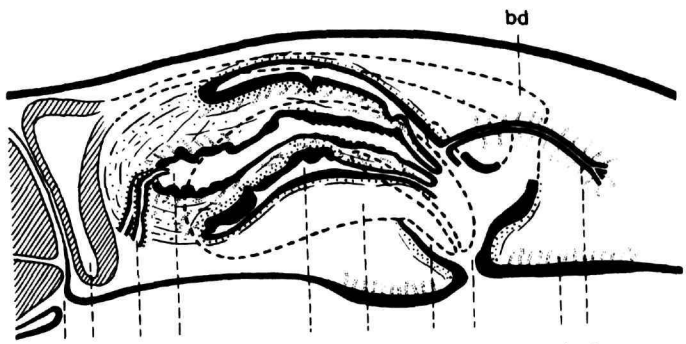


34 P. undulata

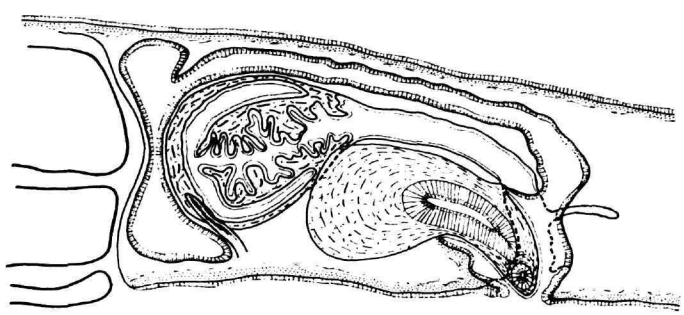
FIGURES 32–34.—Semidiagrammatic views of copulatory apparatus in sagittal section: 32, after Stanković and Komárek, 1927; 33, ×123; 34, ×119.



35 D. adenodactylosum

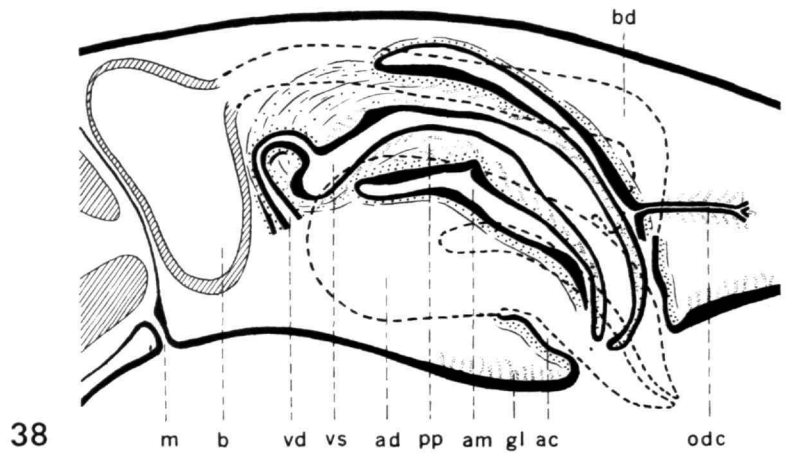


36 D. maculatum

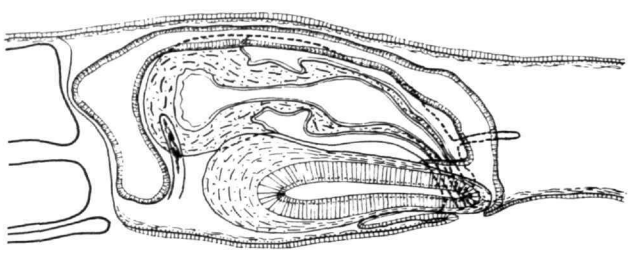


37 D. magnum

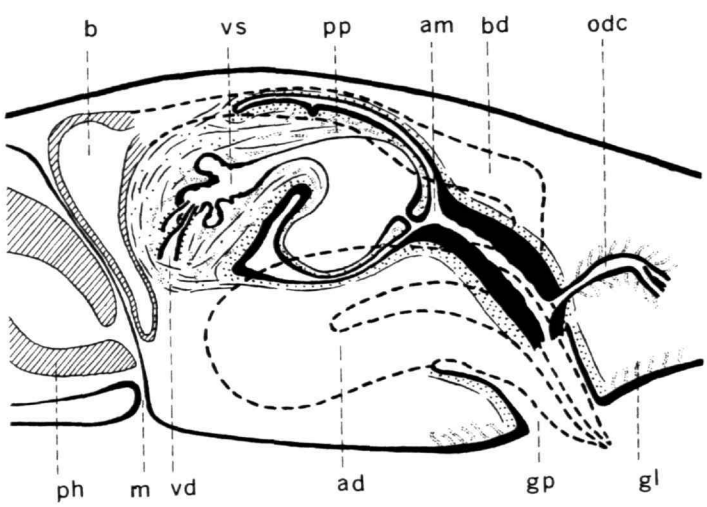
FIGURES 35–37.—Semidiagrammatic views of copulatory apparatus in sagittal section: 35, ×49; 36, ×40; 37, after Stankovič. 1969.



38 D. sanctinaumi

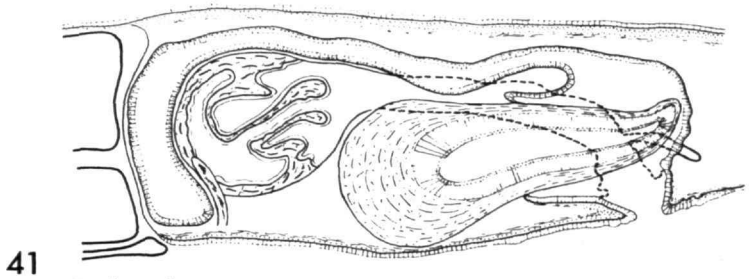


39 D. komareki

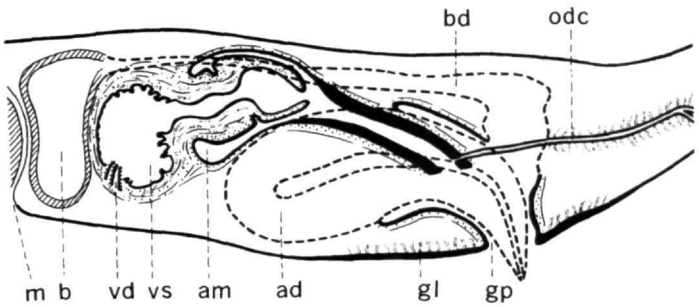


40 D. decoratum

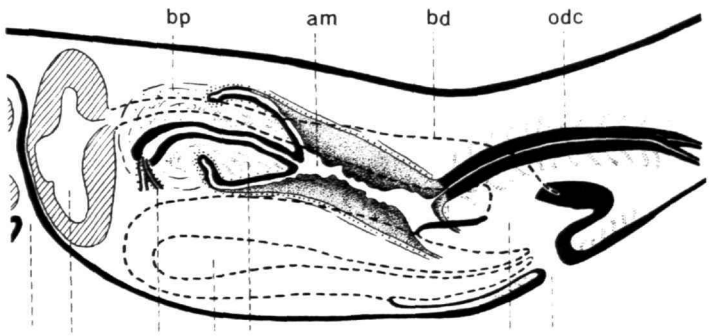
FIGURES 38–40.—Semidiagrammatic views of copulatory apparatus in sagittal section: 38, ×52; 39, after Stanković, 1969; 40, ×61.



41 D. lacustre

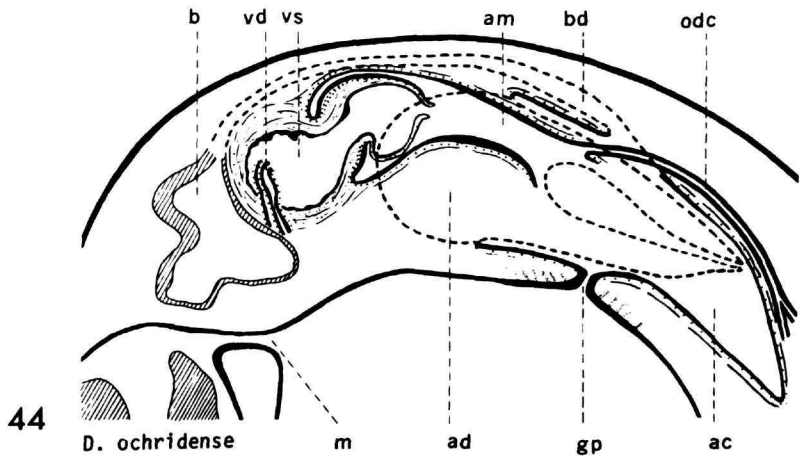


42 D. dorsivittatum

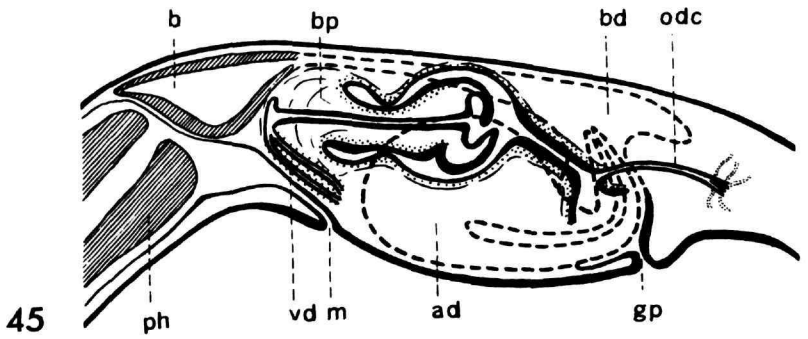


43 D. lychnidicum

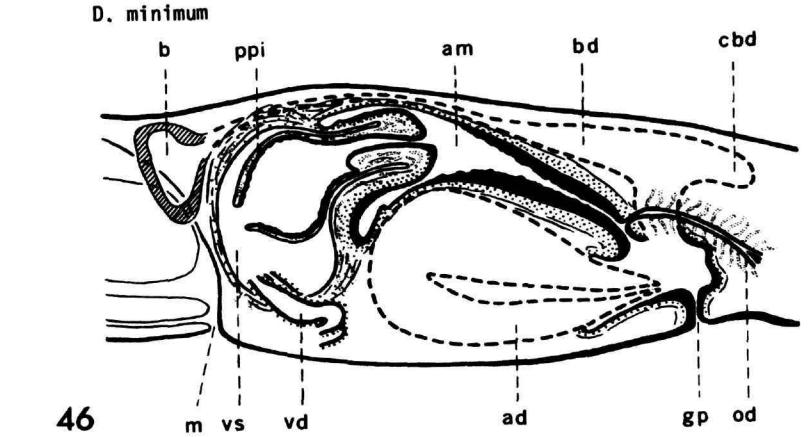
FIGURES 41–43.—Semidiagrammatic views of copulatory apparatus in sagittal section: 41, after Stanković, 1969; 42, ×32; 43, ×87.



44 D. ochridense

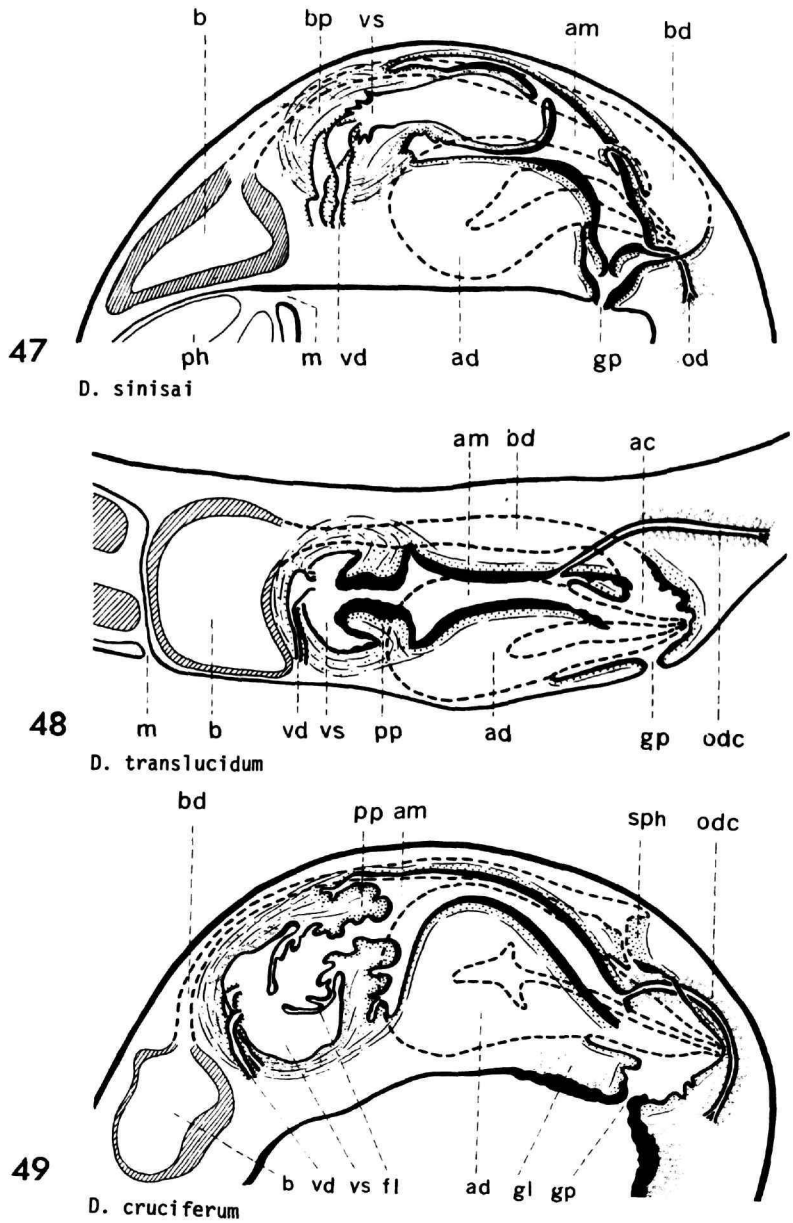


45 D. minimum

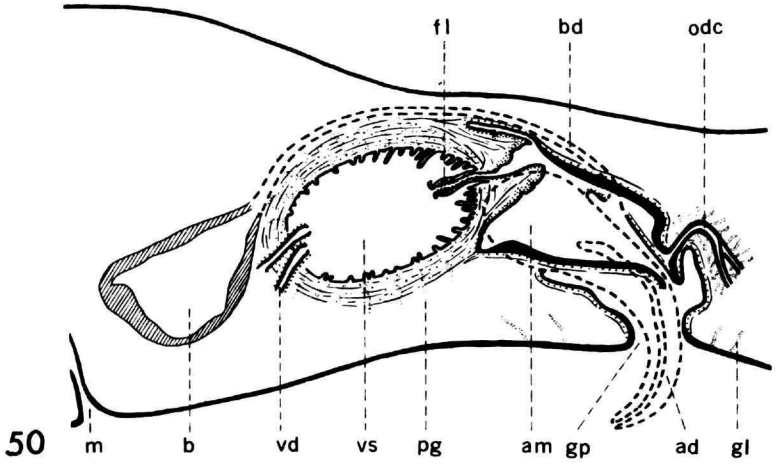


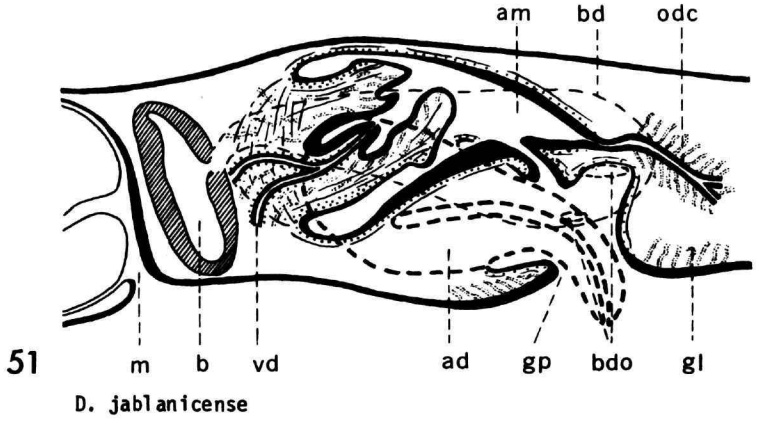
46 D. albidum

FIGURES 44–46.—Semidiagrammatic views of copulatory apparatus in sagittal section: 44, ×37; 45, ×108; 46, ×61.

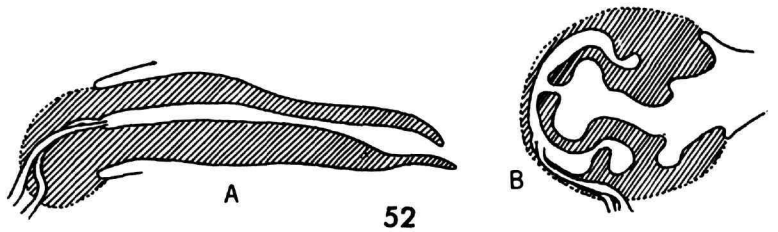


FIGURES 47–49.—Semidiagrammatic views of copulatory apparatus in sagittal section: 47, ×51; 48, ×52; 49, ×26.

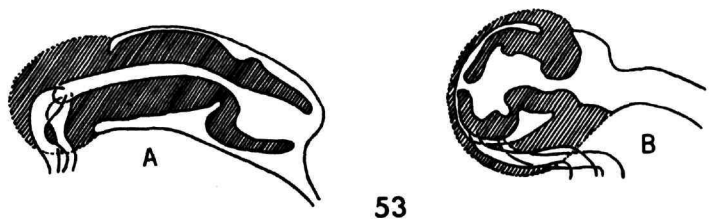




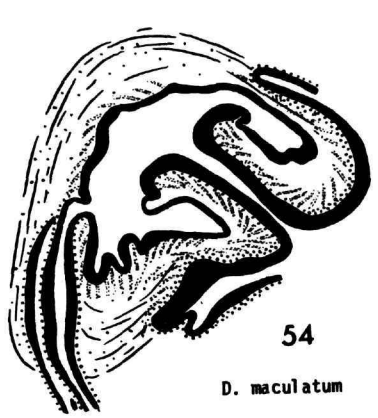
FIGURES 50–51.—Semidiagrammatic views of copulatory apparatus in sagittal section: 50, ×39; 51, ×68.



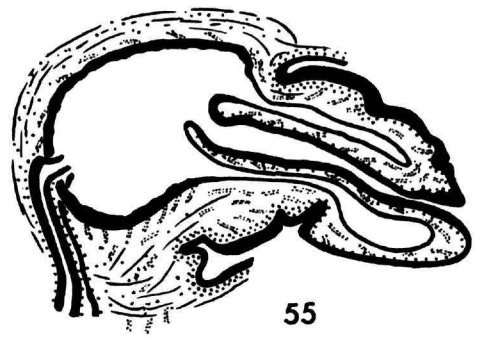
52
D. adenodactylosum



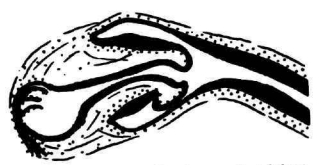
53
D. albidum



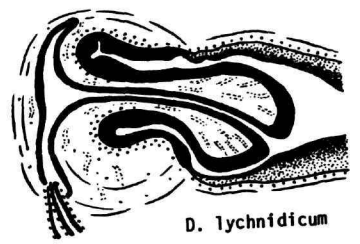
54
D. maculatum



55
D. sanctinaumi



D. translucidum
56



D. lychnidicum
57

FIGURES 52–57.—Alternate shapes of penis: 52, ×66; 53, ×67; 54, ×52; 55, ×67; 56, ×67; 57, ×130.

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