

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2472

OCTOBER 13, 1971

Systematic and Biogeographical Relationships of Some *Dugesia* Species (Tricladida, Paludicola) from Central and South America

BY IAN R. BALL¹

INTRODUCTION

The genus *Dugesia* achieves its greatest diversity in the New World, an area from which no fewer than 22 species are currently recognized (Ball, 1969a). The New World *Dugesia* species form a well-defined group within the genus (de Beauchamp, 1939) and often the differences between the species are small (Eveline Marcus, 1953). Indeed, de Beauchamp (*op. cit.*) refused to accept the validity of a number of forms, including one from North America, and placed a large number in synonymy with *Dugesia aurita* (Kennel, 1888) described from Trinidad. De Beauchamp's opinion, if correct, would be of great importance to the taxonomist and to the biogeographer who is dependent upon an adequate natural classification.

Although most taxonomists have declined to follow de Beauchamp, only Hyman attempted to collect *D. aurita* from Trinidad in order to clarify his conclusions (Hyman, 1957). She was unsuccessful, and the only sexual specimen she obtained was described as a new species, *D. arimana*.

In December, 1969 H. B. N. Hynes of the University of Waterloo made several collections on Trinidad, on my behalf, near Kennel's original

¹ Department of Biology, University of Waterloo, Ontario.

localities. No forms unequivocally referable to *D. aurita* were obtained. One sample, however, yielded several sexually mature individuals of *D. arimana*. These show features that help to clarify some of the systematic and biogeographical relationships of the Caribbean fresh-water triclads, and the fairly abundant material has enabled me to propose some corrections and additions to Hyman's original description. The proper evaluation of this material has led to a general review of the genus *Dugesia* in Central America, which forms the substance of the present paper.

ACKNOWLEDGMENTS

I thank Dr. H. B. N. Hynes and Dr. A. D. Harrison, both of the University of Waterloo, for kindly placing their collections of fresh-water triclads from the Caribbean region at my disposal, and for critically reading the final draft of this paper. I am also indebted to Dr. Roman Kenk of the United States National Museum, Smithsonian Institution, for lending me the holotype and paratypes of *Dugesia antillana*, and to Mr. Harold S. Feinberg of the American Museum of Natural History for so generously responding to my request for the loan of comparative material of various *Dugesia* species.

MATERIALS AND METHODS

Details concerning the specimens examined in this study are given under the appropriate species headings below.

The newly collected specimens were killed in Steinmann's fluid and transferred to 70 per cent alcohol. Selected specimens were serially sectioned at 8 μ m. intervals in the sagittal, frontal, or transverse plane. The sections were stained with Mallory-Heidenhain (Gurr, 1963) or with Phosphotungstic Acid Haematoxylin (Drury and Wallington, 1967) and mounted in neutralized DePeX.

The present dispositions of the various specimens examined are indicated by the following abbreviations:

AMNH, the American Museum of Natural History
USNM, United States National Museum, Smithsonian Institution
NMC, National Museum of Natural Sciences, Ottawa

FIGURE ABBREVIATIONS

bc, bursa copulatrix
bs, bursal stalk

ca, common atrium
cg, cement glands

cm, circular muscle	ma, male atrium
di, diverticulum of common atrium	nu, nucleus
ed, ejaculatory duct	od, oviduct
go, gonopore	pe, penis
id, intestinal diverticulum	sg, shell glands
lm, longitudinal muscle	vd, vasa deferentia

Dugesia arimana Hyman, 1957

MATERIAL EXAMINED: AMNH 465, holotype, sagittal sections, collected by L. H. Hyman, Arima River, between Simla and Arima, Trinidad, February 14, 1956; AMNH 739, sagittal and frontal sections, collected by H. B. N. Hynes, St. Joseph River, elevation 300 ft., east of Port-of-Spain, Trinidad, December 16, 1969; transverse, frontal, and sagittal sections of specimens collected by Hynes and retained in my private collection.

This species was described by Hyman from a single mature specimen. It is undoubtedly valid, but Hyman's description is mistaken in some important details and thus her assessment of its relationships is not acceptable. In particular, after a re-examination of the holotype, I disagree with Hyman's figure and description of the courses of the oviducts and the bursal stalk, and of the size of the penis papilla. Further, many histological details which are of taxonomic importance are not described.

In view of these considerations it seems desirable to provide a re-description of the species. The holotype and the new material collected by Hynes agree in all important respects, with a notable exception discussed below, and there can be no doubt that they all belong to a single species.

EXTERNAL FEATURES (FIG. 1; *cf.* HYMAN, 1957, FIG. 1): These are well described by Hyman. The proportions of the specimens collected by Hynes are more elongate than those seen by Hyman. The length to breadth ratio may be as high as 14/1, with a maximum length of 10–12 mm. Figure 1 is a drawing of a fixed specimen, which therefore is somewhat contracted, and serves to emphasize the unusual proportions. In this respect the species may be compared with *D. antillana* Kenk, 1941, from Puerto Rico. Kenk noted that younger specimens of the latter species were less elongate than mature adults. As most of Hyman's material was immature this may explain the discrepancy.

The auricles are also longer and more pointed than indicated by Hyman. Possibly these vary in size; if they do, it is likely that the long auricled asexual forms described from Trinidad by Hyman are also *D. arimana*.

ALIMENTARY SYSTEM: This shows no special peculiarities. The musculature of the pharynx, from outside inward, consists of outer longitudinal

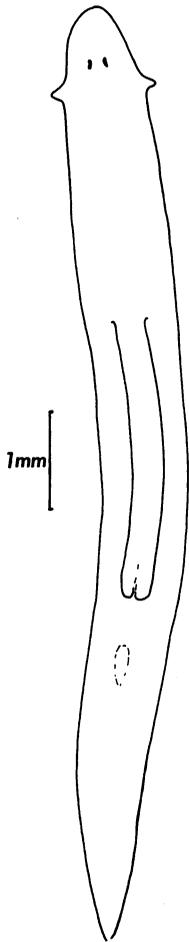


FIG. 1. *Dugesia arimana*. External features of preserved specimen from St. Joseph River, Trinidad.

fibers (4–5 μm .), outer circular fibers (6–8 μm .), inner longitudinal fibers (4–5 μm .), and inner circular fibers (8–12 μm .). The two muscle zones are separated by a parenchymatous layer, 50–60 μm . thick, which contains various glandular and nervous elements, as well as numerous nuclei. The thinness of the circular muscle layers is noteworthy.

FEMALE REPRODUCTIVE SYSTEM (FIGS. 2–4; cf. HYMAN, 1957, FIG. 2): The paired ovaries are simple, and ventrally situated in the usual place immediately posterior to the brain. The oviducts run ventrally caudad to the level of the copulatory apparatus and then curve upward, recurving slightly to enter the bursal stalk, quite high, at the point where the bursal stalk makes its pronounced downward bend to the atrium.

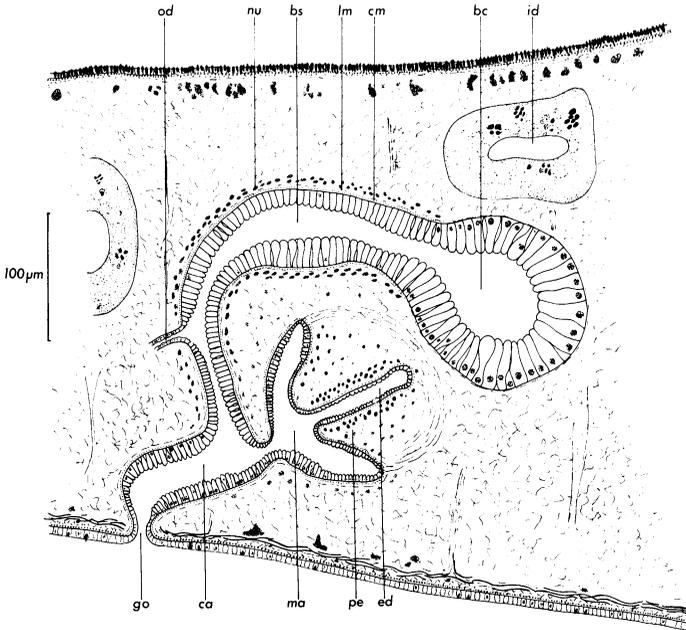


FIG. 2. *Dugesia arimana*. Holotype. AMNH 465. Reconstructed sagittal section of copulatory organs, viewed from right side.

Contrary to the description by Hyman, the oviducts never enter the bursal stalk near the atrium just above the gonopore. Hyman also described a short common oviduct. It is difficult to be sure of this from examination of the holotype. In some of my specimens the oviducts enter the bursal stalk separately, but very close together. In others there is a short common oviduct. The walls of the oviducts are nucleate.

The bursa copulatrix is a relatively small spherical sac situated dorsally between the penis and the pharynx. It has the usual nucleate columnar epithelium. The bursal stalk is a wide duct passing over the copulatory apparatus, perhaps a little to the right, and immediately posterior to the penis it bends downward and enters the atrium at the atrial fold (see below). The point of entry is thus much more anterior to the gonopore than is indicated by Hyman. The bursal stalk is lined with a tall, sometimes papillate, epithelium which is infranucleate (insunk, "ingesenkt," see Kenk, 1970). This is covered with a thin layer of circular muscle fibers overlain by a thin layer of longitudinal fibers. Numerous, and extensive, shell glands open into the bursal stalk just below the entrance of the oviducts (fig. 3).

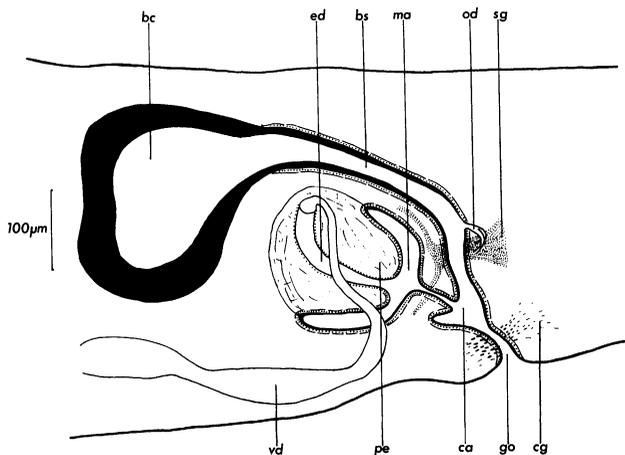


FIG. 3. *Dugesia arimana*. St. Joseph River, Trinidad. Diagrammatic sagittal section of copulatory organs, viewed from left side.

The vitellaria occur throughout the body length, dorsal and ventral to the intestinal diverticula, but mostly ventral.

MALE REPRODUCTIVE SYSTEM (FIGS. 2-4; cf. HYMAN, 1957, FIG. 2): The moderately numerous testes occur throughout the body length in a predominantly dorsal position. A few testes may occur ventrally to the intestinal diverticula, and the largest ones fill the entire dorsoventral space. The testes lie singly, not in groups, and are not as numerous as those of, for example, *D. antillana*, or the common North American forms, *D. tigrina* and *D. dorotocephala*. Some small testes may be situated anteriorly to the ovaries.

The penis consists of a poorly developed, muscular, hemispherical bulb, and a small thick papilla. The latter projects into a small male atrium that extends posteriorly into a common atrium, which opens to the exterior via the gonopore. Histologically, the male and common atria are identical, both being lined by a high nucleate epithelium bordered by a muscle coat similar to that of the bursal stalk. They are separated clearly, however, by a fold or diaphragm projecting from the atrial wall. The bursal stalk enters the atrium immediately posterior to the dorsal lip of this fold.

The vasa deferentia enlarge about halfway along the pharynx to form the usual sperm-filled false seminal vesicles. These travel past the penis bulb almost to the level of the tip of the penis. Here they turn upward, far anterior to the upward curvature of the oviducts, become thinner,

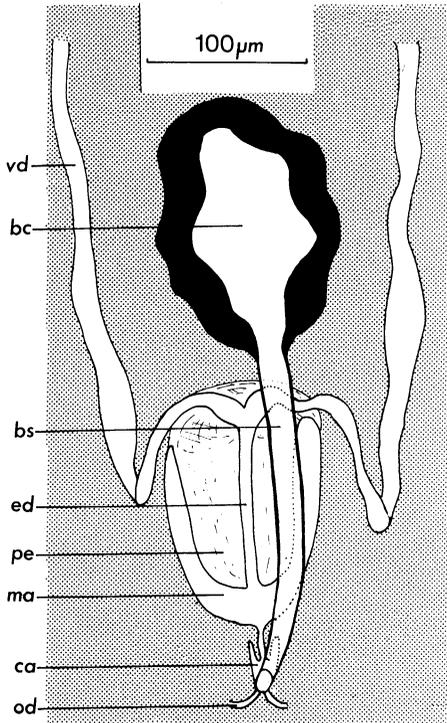


FIG. 4. *Dugesia arimana*. AMNH 739. St. Joseph River, Trinidad. Diagrammatic frontal section of copulatory organs, viewed from dorsal aspect.

and recurve anteriorly to the level of the anterior dorsal part of the penis bulb. They then turn mediad, and as thin tubes enter the penis bulb separately. Within the bulb they travel ventroposteriad, unite without forming an expanded vesicle, and form an unusually wide ejaculatory duct which opens at the tip of the penis. This unusual course of the vasa deferentia was not noted by Hyman. Generally, the courses of the two vasa deferentia are similar, but occasionally asymmetry occurs in which one of them enters the bulb more anteriorly, or more ventrally than the other. The ejaculatory duct is lined with a flat infranucleate epithelium, outside of which sparse circular muscle fibers may be discerned. The penis papilla is covered with an epithelium which is infranucleate for the most part.

The cement glands, in the region of the gonopore, are poorly developed in most specimens.

DISTRIBUTION AND HABITAT: Type locality, Arima River, Trinidad;

otherwise definitely known only from the St. Joseph River, Trinidad. Hynes also collected many asexual *Dugesia* species in Trinidad, including some from the Arima River, which he described as being of the same elongate shape as the sexual specimens from the St. Joseph River. These localities are listed in the discussion of the Caribbean fresh-water triclads given below. Hynes's notes on the collections stated that "at all the sites the worms were scarce and could only be taken with a net by stirring up the gravel. I found only one small one by lifting stones. They were astonishingly active, and could extend into a long narrow shape." It is possible that this unusual shape and activity is related to their unusual habitat, which appears to be within the bed of the stream.

DIFFERENTIAL DIAGNOSIS: *Dugesia arimana* may be distinguished from all other known *Dugesia* species by the following combination of characters: Pigmented, of thin, elongate shape, head of high triangular form with long thin auricles. Testes fairly numerous, predominantly dorsal, occurring throughout body. Penis bulb and papilla small, papilla bluntly conical. Vasa deferentia extend posteriorly to penis bulb, then recurve to it, entering it separately from sides. Expanded seminal vesicle(s) absent. Diverticula of ejaculatory duct absent. Male atrium clearly separated from common atrium by fold or diaphragm. Bursa copulatrix small and roughly spherical. Bursal stalk wide, with infranucleate epithelium, and covered with muscle coat consisting of inner circular, and outer longitudinal fibers. Oviducts entering bursal stalk, separately or united, in usual position at point where bursal stalk curves smoothly ventrad.

TAXONOMIC RELATIONSHIPS: Hyman (1957, p. 2) considered *D. arimana* to be very closely related to *D. aurita* (Kennel, 1888) as both were considered to have the entrance of the oviducts at or near the atrium, much more ventrally than usual. "It would seem that there is in the general Caribbean region a group of *Dugesia* species with the mentioned peculiarity of the ovovitelline ducts" (Hyman, 1957, p. 4). Marcus (1960) has accepted this relationship but the corrections given above to the course of the oviducts of *D. arimana* invalidate this conclusion. *Dugesia aurita* differs from *D. arimana* in several important respects, viz., its ventral testes, undivided atrium, low opening of the oviducts, more elongate and pointed penis papilla, and by the nucleate epithelium of its smoothly curved bursal stalk (Kennel, 1888, fig. 21).

In the form of the penis papilla, the divided atrium, and the course of the vasa deferentia, *D. arimana* approaches most closely *D. antillana* Kenk. Both are of similar slender proportions, by which they may be distinguished from *D. aurita*. *Dugesia arimana* may be readily distinguished from *D. antillana* in that it lacks the diverticula of the ejaculatory duct

which are characteristic of the latter species. In addition, the bursal stalk of *D. arimana* is infranucleate, whereas that of Kenk's species is nucleate (see below), and the common atrium is much larger.

Dugesia antillana Kenk, 1941

MATERIAL EXAMINED: USNM 43110, holotype, sagittal sections; USNM 43111, paratype, transverse sections; USNM 43113, paratype, whole-mount; USNM 43114, paratypes, sagittal sections. All from El Yunque, Puerto Rico, collected by R. Kenk, August 18, 1939.

Kenk has given his usual detailed and reliable description of this species, which is known only from Puerto Rico. I wish to add only a few histological details which now seem to be of taxonomic or diagnostic significance and to comment on the vasa deferentia.

The outer muscle zone of the pharynx consists of a subepithelial layer of longitudinal muscle fibers (3–5 μm .), inside which is a layer of circular fibers (10–12 μm .). Then follows a parenchymatous zone (40–55 μm .) containing the usual glandular and nervous elements. The inner muscle zone comprises a layer of longitudinal fibers (ca. 6 μm .) and subepithelial circular fibers (20–30 μm .). The circular layers are thus thicker than the corresponding layers of *D. arimana*.

The epithelia of the sexual apparatus are all nucleate, whereas the bursal stalk of *D. arimana* is infranucleate, and are similar in structure to those of the latter species. The musculature of the atria, and of the bursal stalk, is also similar in both species.

The vasa deferentia of *D. antillana* show a recurved course quite similar to that of *D. arimana*. However, since the entire copulatory complex is shorter in the former species, the upward curve of the male ducts toward the penis bulb occurs immediately anterior to the upward curve of the oviducts. In *D. arimana* the courses of these male and female ducts are quite distant from each other.

Kenk (1941, p. 5) has pointed out that the ejaculatory duct of his species lacks a distinct muscle coat, another feature which distinguishes it from *D. arimana*, and commented upon the uniqueness of the peculiar diverticula of the ejaculatory duct.

Dugesia aurita (Kennel, 1888)

TYPE MATERIAL: Present location unknown. Original localities, stony pool on the Savannah, Port-of-Spain, Trinidad; several small streams in the vicinity of Port-of-Spain, and the Arima River. Known only from the type material.

No species of *Dugesia* has caused so much confusion as this one. Kennel's description seems clear enough, but attempts to rediscover the species by Hyman (1957) and by Hynes have proved unsuccessful. These have yielded only specimens of *D. arimana* which differs from *D. aurita* in so many details that its specific separation is surely justified.

Concerning the two important characteristics Kennel is quite clear. Of the testes he said (1888 p. 467): "Die sehr zahlreichen Hoden nehmen die Ventralseite des ganzen Körpers vor und hinter der Geschlechtsöffnung ein." Concerning the oviducts and the bursal stalk he wrote: "Der Gang des Receptaculum seminis vereinigt sich mit dem Geschlechtsantrum ganz in der Nähe der äusseren Geschlechtsöffnung, und eben dort münden von den Seiten her die Oviducte ein." Kennel's figure 22 also shows the oviducts as opening very close to the gonopore.

The unusual course of the oviducts is as puzzling as are the repeated failures to recover more specimens with the same peculiarity from the Caribbean region. It is worth noting, however, the early date of Kennel's description. Around that time it was only the European triclads which were well known, numerous studies culminating in the monographic works of Böhmig (1909) and Steinmann and Bresslau (1913). The oviducts of *Dugesia gonocephala*, probably one of the best known species, were invariably misinterpreted and incorrectly described as being more ventral at the entrance of the bursal stalk than in fact they were. This was first noted by Meixner (1928, p. 575, note 3) who had re-examined some of the early sections. It is also instructive to compare the figure by Böhmig (1909, p. 163, fig. 271) with those of Meixner (1928, p. 573, fig. 2) and Marcus (1953, p. 8, fig. 7). The record of *D. gonocephala* from Illinois, in which the oviducts are said to "open separately into the vagina immediately before it enters the genital atrium" (Woodworth, 1897, p. 7) remains an enigma; the species does not occur in the New World. If Kennel described the oviducts of *D. aurita* inaccurately then the principal difference between this species and *D. dorotocephala* disappears.

Most taxonomists have agreed that the position of the testes, whether dorsal or ventral, is a useful taxonomic character. De Beauchamp (1939, p. 66), however, studying abundant material from Lake Titicaca, which he believed to be identical with *D. aurita*, has cast doubt upon the reliability of this feature. The testes of his material are described as follows (in translation): "The testes show remarkable variability. In most of the specimens they are exclusively ventral, occasionally very numerous and distributed along the body length in two or three rows on each side, as far as the level of the ovaries (which they extend beyond in *dorotocephala* and *paramensis*); in these specimens the vitellaria are poorly developed,

sometimes almost invisible, although the copulatory apparatus appears to be normally developed, or just about so. In others, on the contrary, the testes are exclusively dorsal and spacious, and occasionally part empty or with degenerating spermatozooids. In all of them the vitellaria are very well developed and full of inclusions. In one specimen in this condition the testes were apparently ventral, but the sections were frontal and it is difficult to be precise about this relationship. It appears, therefore, that we are dealing with two successive stages of development, and with a migration of the testes at the time of maturation of the vitellaria (which may be subsequent to copulation), although the latter develop dorsally and ventrally at the same time."

Thus, de Beauchamp did not accept the position of the testes as being of taxonomic importance. From this and other similarities between his Lake Titicaca material and other New World species, differences being dismissed as due to varying stages of development or methods of preservation, he assigned his material to *D. aurita* as described by Kennel, and relegated no fewer than eight South American forms to synonymy. At the same time he declared the widespread North American form *D. dorotocephala* (Woodworth) to be identical with *D. aurita*, the latter name having priority.

Evidence that the testes may migrate during maturation has been provided for only one other species, *Dugesia nonatoi* Marcus, 1946 from Brazil, but in this case they originate dorsally and then move to a ventral location. This is the reverse of the situation postulated by de Beauchamp, and it may also occur in *D. festai* (Marcus, 1960).

An interesting anomaly is provided by two of the specimens collected for me by Hynes, and ascribed to *D. arimana*. In the first the testes on the right side are predominantly ventral, elsewhere they are dorsal, and the vitellaria are correspondingly principally dorsal on the right side. In all other respects the specimen (AMNH 739) is referable to *D. arimana*.

The second specimen was unfortunately selected for transverse sections, hence sagittal reconstruction of the copulatory complex is difficult. However, in this specimen the testes are situated ventrally throughout, and the weakly developed vitellaria lie more dorsally. The testes exhibit advanced spermatogenesis and the vasa deferentia are full of sperm. Further evidence for the full maturity of the specimen is evidenced by the well-developed shell glands. All this is quite consistent with de Beauchamp's hypothesis. The fact that the ampullae of the oviducts contain sperm, indicating that copulation has taken place, does not detract from this since it is impossible to say how long before fixation copulation had taken place. If it was recent then there may not have been sufficient

time for the testes to migrate dorsally. The specimen is also unusual in that the epithelium of the lumen of the bursal stalk is normal, not infranucleate. It appears that this is a specimen in which the male system is mature, but the female system is as yet not fully developed.

Despite these *D. aurita*-like characters, I am unwilling to assign this specimen to that species. In other important respects, notably the course of the vasa deferentia, the high openings of the oviducts, and the clear diaphragm or fold dividing the male and common atria, the specimen approaches closely the typical *D. arimana*.

Nevertheless, it must be remembered that not only is de Beauchamp a careful observer, but he worked from an abundance of material from a single locality. His morphological and physiological conclusions are worthy of serious consideration and reinvestigation, especially in view of the data provided above, and by Marcus (1946) concerning *D. nonatoi*. The taxonomic conclusions he reaches are another matter entirely.

It is an undeniable fact that most *Dugesia* species known throughout the world have been described as possessing dorsal testes, and consistently described thus. This is true of the Palearctic species, and a recent review indicates that it is also true of the 10 species known from the Oriental Region (Ball, 1970). Species with ventral testes are most numerous in South America, and all the North American species of the genus have been repeatedly described as possessing ventral testes. Outside the New World the only form described with ventral testes is *Dugesia schauinslandi* (Neppi, 1904) (see also Nurse, 1950, under *Spathula limicola*) from Australasia, and I have been able to confirm this from specimens kindly sent to me by Mrs. F. R. Allison (née Nurse). In the closely related genus *Cura*, which typically has few, small, prepharyngeal dorsal testes there are two species described as having them ventrally situated, viz., *Cura pinguis* (Weiss, 1910) from Australasia, and *Cura tinga* Marcus, 1955 from South Africa. Perhaps the latter should be transferred to *Dugesia* as it shows other features which are unusual for a species of *Cura*.

It seems clear to me that the distinction between dorsally and ventrally situated testes is real, and that ventral testes are confined to an otherwise well-defined, morphologically and biogeographically, group of planarians. The New World *Dugesia* species have in common their markedly triangular heads with pointed auricles, a bursal stalk musculature in which the outer muscle layer is longitudinal (*cf.* Ball, 1970), a bifid seminal vesicle, or none at all, and the lack of a diaphragm in the ejaculatory duct. De Beauchamp himself (1939) has noted the uniformity of the American forms. His contribution lies in emphasizing that an

assessment of the position of the testes should be made on fully mature animals.

The conclusion from this review must be that de Beauchamp's synonymies are unacceptable on present knowledge. *Dugesia aurita* is a valid species, well characterized by Kennel, but is known only from Trinidad. De Beauchamp's identification of his Lake Titicaca material is erroneous and I agree with Eveline Marcus (1953) and Hyman (1951, 1957) that it is *Dugesia festai* (Borelli, 1898), which is otherwise known to occur in Lake Titicaca, and which, strangely enough, is one of the few species not placed in synonymy with *D. aurita* by de Beauchamp. It may also be noted that the figure in *Traité de Zoologie* (de Beauchamp, 1961, p. 82, fig. 39) is also of *D. festai* and not *D. aurita*.

De Beauchamp's conclusions concerning synonymy are most likely a result of his a priori assumption that the Americas would contain a single widespread species comparable with *D. gonocephala* of the Old World. At the time of his review this species was held to be distributed throughout the Palearctic, extending into the Oriental Region, and even Australasia. We know now that this is not true, largely as a result of the work of Marcus (1953), Porfirjeva (1960) and Ichikawa and Kawakatsu (1964). There is certainly no reliable evidence that the species occurs in the Oriental Region (Ball 1970). De Beauchamp's comparison of the distributional ranges of *D. aurita* and *D. gonocephala*, both taken in his broad sense, is misleading.

There is no doubt that there are many similarities between *D. aurita* and *D. dorotocephala*, including the very numerous ventral testes, but I agree with Kenk (1944) and others in maintaining the species separate for the present. Only the rediscovery from Trinidad of material fully matching Kennel's original description can settle this matter. For the benefit of future workers I provide below a differential diagnosis of *D. aurita*, based upon Kennel's detailed description and figures:

Pigmented, of normal proportions, head of high triangular form with long thin auricles. Testes very numerous, ventral. Penis bulb and papilla normal, papilla pointed cone-shaped, filling male atrium. Vasa deferentia enter penis bulb separately, without recurving, enlarge slightly, forming bifid seminal vesicle upon union, and ejaculatory duct which opens terminally. Atrium undivided. Bursa copulatrix normal, bursal stalk a wide duct curving smoothly opening into atrium just above gonopore. Entire copulatory apparatus lined with nucleate epithelium. Oviducts entering bursal stalk separately, very near junction with atrium.

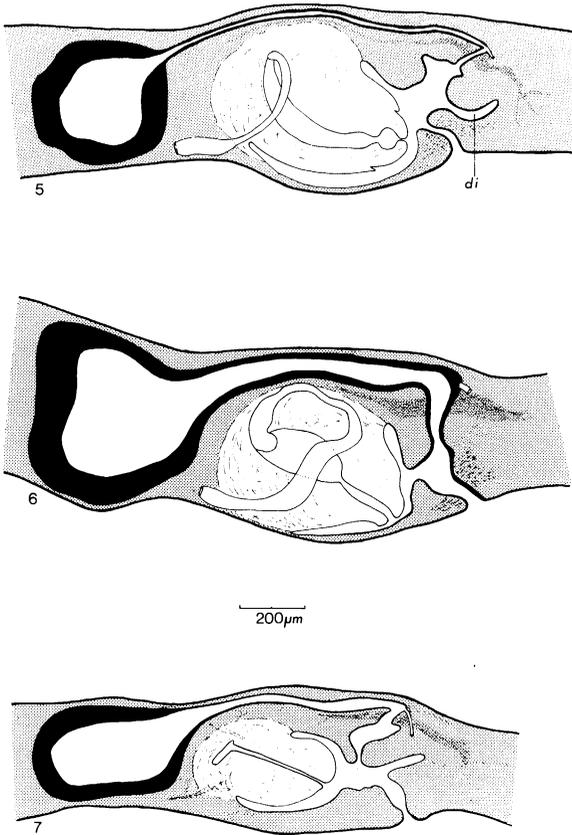
Dugesia dorotocephala (Woodworth, 1897)

MATERIAL EXAMINED: Sagittal sections by L. H. Hyman, as follows: AMNH 609, Oklahoma, two series; AMNH 734, Boiling Spring, Oklahoma; AMNH 735, Ft. Davis, Texas; AMNH 736 Spring near Milwaukee, Wisconsin; AMNH 737, Fish Tanks, AMNH, Mexico? (and two wholemounts); AMNH 468, Devils Cave, Nevada, as holotype of *Dugesia diabolis* Hyman, 1956; newly prepared sagittal sections of AMNH material, as AMNH 352 Los Angeles, California.

In her last general review of the triclads of North America, Hyman (1959) gave the distribution of this species as Pennsylvania and Virginia, westward to the Pacific coast. From the specimens listed above the range may be extended southward to Texas (see also Kenk, 1944, p. 21), and it also appears that it may reach Mexico. In addition, Hynes has collected for me a number of triclads from a spring stream at El Salto Finca, near Escuintla, about 30 miles southwest of Guatemala City. The water temperature was 21–23° C., the date March 9, 1970. He also informed me that triclads could be found in other spring streams and seepages in Guatemala, and that they were quite different in appearance from the specimens from Trinidad. Regrettably, none of the specimens were mature, but the possibility that all were *D. dorotocephala* exists, and a detailed investigation of this part of the continent would yield interesting results.

Dugesia dorotocephala has been described in detail by Hyman (1925) with later corrections of her interpretation of the shell glands and cement glands (Hyman, 1931). The close relationship of this species to *D. aurita* has already been discussed. For the present *D. dorotocephala* may be distinguished from *D. aurita* by the high openings of the oviducts, the shorter penis papilla (*cf.* Hyman, 1925, figs. 12 and 15 with Kennel, 1888, fig. 21), and the slight tendency for the vasa deferentia to recurve to the penis bulb. Those of *D. aurita* travel directly to the seminal vesicle (*cf.* Hyman, 1925, fig. 11 with Kennel, 1888, fig. 22).

It also seems appropriate to mention here that I consider *Dugesia diabolis* Hyman, 1956 to be conspecific with *D. dorotocephala*. Hyman (1956, p. 8) listed three features which she regarded as characteristic of *D. diabolis*: weakly developed penis bulb and papilla, single cavity of penis bulb, and asymmetrical entry of vasa deferentia into penis bulb. In my view the penis shows no special peculiarities not paralleled in the other material of *D. dorotocephala* that cannot be ascribed to the different sizes of the specimens. Asymmetry of the vasa deferentia occurs so frequently in the genus (as in *D. arimana*, *D. antillana*, and many specimens of *D. tigrina* which I have examined) that I attach little importance to this character. Similarly the single cavity of the penis bulb is an in-



FIGS. 5-7. Diagrammatic sagittal sections of copulatory organs, viewed from left side. 5. *Dugesia tigrina*. NMC 64. St. Lawrence River, Ontario. 6. *Dugesia dorocephala*. AMNH 352. 7. *Dugesia tigrina*. AMNH 353.

adequate character in this case. Although it is true that the North American *Dugesia* species usually have a bifid seminal vesicle, secondary enlargement is not unknown in *Dugesia tigrina* (Kenk, 1935, 1944) and *D. dorocephala* (AMNH 735). The "web-like tissue" filling the bulbar cavity (Hyman, 1956, p. 8) appears to be a secretion of some sort, and may also be seen in the specimens of *D. dorocephala* from Wisconsin (AMNH 736), Oklahoma (AMNH 609) and Texas (AMNH 735).

As I can find no real differences between the two forms I propose that *Dugesia diabolis* be considered a synonym of *D. dorocephala*.

Dugesia dorocephala is also very similar to the other widespread North

American form, *D. tigrina*. No detailed comparison of these two species has ever been made but Kenk (1944) has summarized the diagnostic differences as being the angled bursal stalk, close openings of the oviducts, and infranucleate epithelium of the copulatory apparatus of *D. tigrina*, compared with the smoothly curved bursal stalk, clearly separate openings of the oviducts, and nucleate epithelium of *D. dorotocephala*. The last cited character is variable, however, since at least one specimen of *D. dorotocephala* from ?Mexico (AMNH 737) is infranucleate. Marcus (1946) has drawn attention to similar variation in *D. tigrina*.

A useful character seems to be the blind diverticulum of the posterior wall of the common atrium of *D. tigrina*, which clearly shows in the figures of Sivickis (1923), Kenk (1935), Marcus (1946) and on my slides of eastern Canadian material, and which is absent from all the specimens of *D. dorotocephala* that I have examined. I also suggest that the bursal stalk of the latter is generally wider and lined by a taller epithelium, and that the common atrium is less well developed than in *D. tigrina*. All these differences can be seen by comparing figure 5 (*D. tigrina*) with figure 6 (*D. dorotocephala*), both of which were drawn from actual specimens. The atrial diverticulum of the former is exceptionally well developed; usually it is much smaller. Figure 7 was drawn from newly prepared sections of material from Caurchan River, British Columbia (AMNH 353), originally identified by Hyman as *D. dorotocephala*. By all the above criteria the three specimens which were sectioned are *D. tigrina*. It seems that occasionally Hyman may have confused these two species.

Dugesia dorotocephala thus extends from central and western North America to Texas and possibly Mexico and the central American states. It does not extend into South America although a number of South American forms are undoubtedly closely related to it as emphasized by de Beauchamp (1939). On the other hand *D. tigrina* is known throughout North America and from Brazil, but there are no records from intermediate areas. Nonetheless, Marcus (1946) was of the opinion that its occurrence in Brazil is a natural phenomenon.

REVIEW OF THE GENUS *DUGESIA* IN THE CARIBBEAN ISLANDS

The *Dugesia* species of the Caribbean Islands may be summarized as follows:

Dugesia antillana Kenk, 1941. Puerto Rico.

Dugesia species undetermined. Upper Buccament River, St. Vincent, British West Indies. Numerous specimens collected by A. D. Harrison of the University of Waterloo, June 2, 1970. Harrison informed me that in life these

were of the same elongate form as *D. antillana* and *D. arimana*. None of the specimens were mature.

Dugesia aurita (Kennel, 1888). Trinidad.

Dugesia arimana Hyman, 1957. Trinidad.

Dugesia species undetermined (*cf. D. arimana*). All collected H. B. N. Hynes in Trinidad: Tacarigua River, near Port-of-Spain, December 14, 1969, 24° C.; Caura River, near Port-of-Spain, December 17, 1969, 24° C., elevation 450 ft.; Arima River, Buena Vista, December 23, 1969, 25° C., at elevations from 100–1800 ft., but not at 1200, 400, and 55 ft.

Dugesia festai (Borelli, 1898). Curaçao; also known from Colombia, Peru, and Ecuador (Marcus, 1960).

Thus triclads appear to be widely distributed in the Caribbean area, even if only two or three species are well known.

A detailed analysis of the origin and relationships of *D. aurita* must await its rediscovery. As we have seen previously its closest relative seems to be *D. dorotocephala* of the Nearctic. Its relationship with northern Andean forms needs clarification, but as Trinidad belongs to the Caribbean mountains that are connected with the Andes, close relationships would not be entirely unexpected (Eveline Marcus, 1953).

There seems to be little doubt that *D. arimana* and *D. antillana* are very closely related species. They also show some striking similarities with *D. hypoglauca* Marcus, 1948 from Brazil. These include the dorsal testes, absence of expanded seminal vesicle(s), clearly divided atrium, and marked recurvature of the vasa deferentia. The three species are also similar in outward appearance (Marcus, 1948). *Dugesia hypoglauca* differs from the Antillean species in its more highly developed atrial fold, and by the bursal stalk that is acutely angled at the entrance of the oviducts.

The fact that the architecture of the copulatory apparatus of these eastern Neotropical species with dorsal testes is so distinctive, and their external features so similar, justifies the use of the term *Dugesia antillana*-group to contain them. I would also suggest that *Cura schubarti* (Marcus, 1946) be transferred to this genus and species group. The genus *Cura* is defined by the number and distribution of the testes (Marcus, 1955); in most species they are very few and prepharyngeal. In the Brazilian species they are numerous and extend to the copulatory apparatus, but not to the tail. In this character it is thus intermediate between *Dugesia* and the other species of *Cura*. In all other respects, notably the possession of long thin auricles which are unknown in any other species of *Cura*, it is a typical *Dugesia*. Apart from its dorsal testes, unusual in New World *Dugesia* species, it also shows a sharply divided atrium, and recurved vasa deferentia, the loops of which extend posteriorly to the tip of the penis.

Of the remaining South American species that possess dorsal testes,

Dugesia chilla Marcus, 1954 (AMNH 738) and *D. andina* (Borelli, 1895) are the best known. Both have a divided atrium, the common part of which is quite long, and a very short penis papilla comparable with that of *D. antillana* and *D. arimana*. They differ from the Brazilian and Antillean species in having the vasa deferentia normal, and in possessing seminal vesicles. Relationship to the *D. antillana* group appears to be more distant, although undoubtedly closer than it is to the other New World forms.

The eastern distributional range of the *D. antillana* group, from Brazil (São Paulo) to the Greater Antilles, has numerous parallels in other organisms which are amply discussed in Croizat's monumental work (1958, especially chapter 7). The group is almost certainly represented in Venezuela, and further collecting will no doubt dispel the apparent disjunctions. That the group reaches its northern limit in the Greater Antilles is interesting. Its distribution and relationships do not support Schmidt's (1954) contention, not accepted by Simpson (1956) and Fittkau (1969), that the Greater Antilles belong with North America in the Holarctic.

The faunal relationships of the Greater Antilles have been the subject of a number of reviews (Darlington, 1938; Simpson, 1956) but, regrettably, the Lesser Antilles have received less attention. The general conclusions appear to be that the Antillean fauna is best explained by over-water dispersal rather than by land bridges. Simpson (1956, p. 11) concludes: "On the basis of present evidence, the over-water theory is so much the more probable that the land bridge theory is not worthy of further serious consideration except in the unlikely event of the discovery of wholly new evidence favoring it." According to him, groups for which any form of over-water transport is improbable are indeed absent from the West Indies.

It is generally accepted that fresh-water triclads disperse by their own activity and that passive dispersal is rare in the group (de Beauchamp, 1940; Reynoldson, 1966). They have not been recorded in the aerial plankton and their resistance to salinity and to extremes of temperature is very low, so that drift across seas is very unlikely. Even within single fresh-water bodies they appear to disperse mainly by their own activities, unless man intervenes; there are few records, for example, of triclads occurring in invertebrate drift in streams (Minshall and Winger, 1968).

Comparisons of the triclad faunas on opposite sides of some narrow sea straits that were subjected to Pleistocene glaciation add valuable information to our knowledge of triclad vagility. Reynoldson (1966) has argued cogently that the differences in the triclad faunas of the fresh

waters on either side of the Irish Sea, English Channel, Menai Straits (North Wales), and Skaggerak and Kattegat all testify to the poor ability of fresh-water triclads to cross even narrow sea passages, including those that carry a large volume of shipping. A similar situation occurs in the Gulf of St. Lawrence where it has been shown that the triclad fauna of Anticosti Island, which was entirely glaciated, shows little relationship with that of the neighboring mainlands. In this case it was concluded that the fresh-water triclads of this island were introduced by man, a contention for which there is historical support (Ball and Fernando, 1970).

There are only two authenticated cases on record of passive trans-oceanic dispersal of fresh-water triclads, and in both cases these can be attributed unequivocally to the activities of modern man. *Dugesia tigrina* has been introduced from North America into Europe, where it is now widely distributed (Gourbault, 1969), probably by means of the trade in aquarium plants. It has also been introduced into Japan (Kawakatsu and Hirai, 1968). In addition, *D. polychroa* has been introduced into the St. Lawrence River and Lake Champlain in North America from Europe, probably with shipping (Ball, 1969b). That dispersal in this fashion is a rare phenomenon is illustrated by the fact that, despite the numerous examples provided by Lindroth (1957) of the introduction of European faunal elements into the Canadian Maritime Provinces by traders in the last two or three hundred years, no European triclad is known from this area. In fact the triclad fauna of the Maritime Provinces is fairly restricted and typical of eastern North America.

Thus, there is a great deal of evidence to support the view that fresh-water triclads do not disperse readily, if at all, across even narrow sea barriers, and the contention that present-day distribution patterns may be reliable guides to paleogeographical relations (Ball and Fernando, 1969) seems well founded. The presence of these organisms on several of the Caribbean Islands, therefore, is of great interest.

Fresh-water triclad occurrence on Trinidad presents no special problem. The fauna of this island is richer than that of the Greater Antilles, and shows close relationships with that of the nearby South American mainland (de Beaufort, 1951). This is true of the terrestrial organisms and also the fresh-water fishes (Darlington, 1938). That Trinidad has been accessible for long periods of time by a land (fresh-water ?) route is probable from faunistic evidence, and such a connection existing to the beginning of the Cretaceous is shown in the paleogeographic maps of Eardley (1954). Subsequent intermittent connections cannot be ruled out as the Gulf of Paria and the Serpents Mouth do not exceed 20 and 55 meters in depth respectively, and the lowering of the sea level during the Pleistocene

would have been sufficient to expose a land connection in these areas (Emery, 1969).

The occurrence on both Puerto Rico and St. Vincent of triclads which show clear relationships with the triclads of Brazil is a different question. The possibility of land bridge origins for the Greater Antillean fauna has been proposed by Schuchert (1935), but it must be acknowledged that his opinions were based mainly on faunistic, not geological evidence. Further, the proponents of a land bridge theory generally think in terms of a connection with Central, not South America, if only because the fauna of the Greater Antilles is closest to that of Central America (Schmidt, 1954). The triclads of the *Dugesia antillana*-group conflict with this supposition.

Eardley (1951) has proposed that much of the present-day Caribbean Sea was land, at least in the Cretaceous (1951, p. 594, fig. 341), and later he suggested that the eastern Caribbean Basin was due to middle and late Tertiary subsidence, and the western Caribbean Basin to Cretaceous and early Tertiary subsidence (Eardley, 1954). This view has not remained unchallenged (Ewing et al., 1957), and recently Barr (1958) has concluded that the present trend of geophysical evidence is opposed to a major continental mass in this area. It seems that the matter is still not fully resolved, and there remains much to be learned concerning the geological history of the Antilles.

That the Caribbean has been a site of intense geosynclinal activity with concomitant orogenic changes in land forms is an established fact. Woodring (1954) emphasized that it is quite evident on ordinary geological grounds that much of the Caribbean Sea was land during the Cretaceous, and some possibly during the Eocene. The question remains, however, as to how extensive the land was and for how long it endured. That the chronology of geological events in this area is equivocal is also stressed by Barr (1958).

From the biogeographical point of view a continuous land connection at any given point in time is not essential. It is only necessary that refugia should persist while various connections are made and broken. The importance of tectonics to the biogeographer has been repeatedly stressed by Croizat (1958, 1962), and he has amassed a great deal of evidence to indicate that the nature and origin of insular faunas may be as much a result of the tectonic history of the area as of chance dispersal over seas.

From the evidence discussed earlier I believe that any theory of the origin of the Caribbean fresh-water triclads relying on hydrochore and anemochore dispersal is unrealistic. It seems much more plausible that

present-day systematic and distributional relationships result from the fragmentation of a previously widespread parent population existing in the fresh waters of former Caribbean lands. A similar view is expressed by Ross (1967) to explain the distribution and endemism of certain Trichoptera (Insecta) in this area, and he added that the geotectonic oscillations of the Caribbean region may well have had a profound effect upon the rate of speciation. Additional support comes from the distribution pattern of certain fresh-water molluscs which are obligate rheophiles. Species of the operculate gastropod genus *Hemisinus* (Thiaridae) are distributed in northern South America, Cuba, and Jamaica, but are absent from Antigua, which possesses no suitable habitats, except as fossils. De Beaufort (1951) reasoned that such a distribution indicates former connections with South America and later restriction of the distribution when the sea transgressed.

It must be admitted, however, that a great deal more evidence is required before a definitive solution to the problem of the origin of the Antillean fauna is forthcoming. Nevertheless, I am unable to agree with Simpson as quoted earlier in the present paper (p. 18). The question of land bridge theories for the origin of the Antillean fauna is still open both geologically and biologically.

LITERATURE CITED

BALL, IAN R.

- 1969a. An annotated checklist of the freshwater Tricladida of the Nearctic and Neotropical Regions. *Canadian Jour. Zool.*, vol. 47, pp. 59-64.
- 1969b. *Dugesia lugubris* (Tricladida: Paludicola), a European immigrant into North American fresh waters. *Jour. Fish. Res. Bd. Canada*, vol. 26, pp. 221-228.
- 1970. Freshwater triclads (Platyhelminthes, Turbellaria) from the Oriental Region. *Zool. Jour. Linnean Soc.*, vol. 49, pp. 271-284.

BALL, IAN R., AND C. H. FERNANDO

- 1969. Freshwater triclads (Platyhelminthes, Turbellaria) and continental drift. *Nature*, London, vol. 221, pp. 1143-1144.
- 1970. Freshwater triclads (Platyhelminthes, Turbellaria) from Anticosti Island. *Nat. Canadien*, vol. 97, pp. 331-336.

BARR, K. W.

- 1958. The structural framework of the Caribbean region. Demarara, Rept. First Meeting Caribbean Geol. Conf. Antigua, B.W.I. 1955, pp. 30-32.

BEAUCHAMP, P. DE

- 1939. Results of the Percy Sladen Trust Expedition to Lake Titicaca V. Rotifères et Turbellariés. *Trans. Linnean Soc. London*, vol. 1, pp. 51-79.
- 1940. Sur les triclades paludicoles de l'hémisphère sud. *Compt. Rendus Soc. Biogéogr.*, vol. 17, pp. 7-9.

1961. Ordre des Turbellariés. In Grassé, Pierre-P. (ed.), *Traité de zoologie. Anatomie, systématique, biologie.* Paris, Masson et Cie., pp. 37-123.
- BEAUFORT, L. F. DE
1951. Zoogeography of the Land and Inland Waters. London, Sidgwick and Jackson Ltd.
- BÖHMIG, L.
1909. Tricladida. Süsswasserfauna Deutschlands, vol. 19, 141-176.
- BORELLI, A.
1895. Viaggio del Dott. Alfredo Borelli nella Republica Argentina e nel Paraguay 13. Planarie d'acqua dolce. Boll. Mus. Zool. Anat. Comp. Torino, vol. 10, pp. 1-6.
1898. Viaggio del Dr. Enrico Festa nel'Ecuador etc. IX. Planarie d'acqua dolce. *Ibid.*, vol. 13, pp. 1-6.
- CROIZAT, LÉON
1958. Panbiogeography. Caracas, Venezuela, Léon Croizat.
1962. Space, time, form: the biological synthesis. Caracas, Venezuela, Léon Croizat.
- DARLINGTON, P. J.
1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. *Quart. Rev. Biol.*, vol. 13, pp. 274-300.
- DRURY, R. A. B., AND E. A. WALLINGTON
1967. Carleton's histological technique. Toronto, Oxford Univ. Press.
- EARDLEY, A. J.
1951. Structural geology of North America. New York, Harper and Brothers.
1954. Tectonic relationships of North and South America. *Bull. Amer. Assoc. Petrol. Geol.*, vol. 38, pp. 707-773.
- EMERY, K. O.
1969. The Continental Shelves. *Sci. Amer.*, vol. 221, pp. 107-122.
- EWING, J. I., C. B. OFFICER, H. R. JOHNSON, AND R. S. EDWARDS
1957. Geophysical investigations in the eastern Caribbean: Trinidad Shelf, Tobago Trough, Barbados Ridge, Atlantic Ocean. *Bull. Geol. Soc. Amer.*, vol. 68, pp. 897-912.
- FITTKAU, E. J.
1969. The fauna of South America. Biogeography and ecology in South America, vol. 2, pp. 624-658. The Hague, W. Junk N.V.
- GIRARD, C.
1850. A brief account of the freshwater planariae of the United States. *Proc. Boston Soc. Nat. Hist.*, vol. 3, pp. 264-265.
- GOURBAULT, NICOLE
1969. Expansion de *Dugesia tigrina* (Girard), planaire americaine introduite en Europe. *Ann. Limnol.*, vol. 5, pp. 3-7.
- GURR, G. T.
1963. Biological staining methods. London, G. T. Gurr Ltd.
- HYMAN, LIBBIE H.
1925. The reproductive system and other characters of *Planaria dorotocephala* Woodworth. *Trans. Amer. Micros. Soc.*, vol. 44, pp. 51-89.
1931. Studies on the morphology, taxonomy and distribution of North

American triclad Turbellaria. IV. Recent European revisions of the triclads, and their application to American forms, with a key to the latter and new notes on distribution. *Ibid.*, vol. 48, pp. 316-335.

1951. North American triclad Turbellaria. XII. Synopsis of the known species of freshwater planarians of North America. *Ibid.*, vol. 70, pp. 154-167.
1956. North American triclad Turbellaria. 15. Three new species. *Amer. Mus. Novitates*, no. 1808, pp. 1-14.
1957. A few turbellarians from Trinidad and the Canal Zone, with corrective remarks. *Ibid.*, no. 1862, pp. 1-8.
1959. Turbellaria, Tricladida. In Edmonson, W. T. (ed.), *Freshwater biology*. New York, Wiley.
- ICHIKAWA, A., AND M. KAWAKATSU
1964. A new freshwater planarian, *Dugesia japonica*, commonly but erroneously known as *Dugesia gonocephala* (Dugès). *Annot. Zool. Japan*, vol. 37, pp. 185-194.
- KAWAKATSU, M., AND T. HIRAI
1968. On a foreign freshwater planaria, *Dugesia tigrina*, found in an aquarium of tropical fishes in Sapporo. *The Heredity*, vol. 22, pp. 31-32 (in Japanese).
- KENK, ROMAN
1935. Studies on Virginian triclads. *Jour. Elisha Mitchell Sci. Soc.*, vol. 51, pp. 79-125.
1941. A freshwater triclad from Puerto Rico, *Dugesia antillana* new species. *Occas. Papers Mus. Zool. Univ. Michigan*, no. 436, pp. 1-9.
1944. The freshwater triclads of Michigan. *Misc. Publ. Mus. Zool. Univ. Michigan*, no. 60, pp. 1-44.
1970. Freshwater triclads (Turbellaria) of North America. II. New or little known species of *Phagocata*. *Proc. Biol. Soc. Washington*, vol. 83, pp. 13-33.
- KENNEL, J. VON
1888. Untersuchungen an neuen Turbellarien. *Zool. Jahrb. Anat. Ontog. Tiere*, vol. 3, pp. 447-486.
- LINDROTH, C. H.
1957. The faunal connections between Europe and North America. Stockholm, Almqvist and Wiksell.
- MARCUS, ERNESTO
1946. Sobre Turbellaria Brasileiros. *Bol. Fac. Fil. Ciên. Univ. São Paulo*, vol. 11, pp. 5-254.
1948. Turbellaria do Brasil. *Ibid.*, vol. 13, pp. 111-243.
1953. Turbellaria Tricladida. Exploration du Parc National de l'Upemba, Fascicule 21, pp. 1-62. Institut des Parcs Nationaux du Congo Belge.
1954. Reports of the Lund University Chile Expedition 1948-49. 11 Turbellaria. *Lund Univ. Årsskr.*, vol. 49, pp. 3-115.
1955. Turbellaria. In Hanstrom, B., P. Brinck, and G. Rudebeck (eds.), *South African animal life*, vol. 1, pp. 101-151. Stockholm, Almqvist and Wiksell.
1960. Turbellaria from Curaçao. *Studies Fauna Curaçao*, vol. 10, pp. 41-51.

MARCUS, EVELINE

1953. Some South American triclads. *An. Acad. Brasileira Cien.*, vol. 25, pp. 65-78.

MEIXNER, JOSEF

1928. Der Genitalapparat der Tricladen und seine Beziehungen zu ihrer allgemeinen Morphologie, Phylogenie, Ökologie und Verbreitung. *Zeitschr. Morph. Ökol. Tiere*, vol. 11, pp. 570-612.

MINSHALL, G. WAYNE, AND PARLEY V. WINGER

1968. The effect of reduction in stream flow on invertebrate drift. *Ecology*, vol. 49, pp. 580-582.

NEPPI, VALERIA

1904. Über einige exotische Turbellarien. *Zool. Jahrb. (Syst.)*, vol. 21, pp. 303-326.

NURSE, FRANCES R.

1950. Freshwater triclads new to the fauna of New Zealand. *Trans. Roy. Soc. New Zealand*, vol. 78, pp. 410-417.

PORFIRJEVA, N. A.

1960. On the zoogeography of planarians in U.S.S.R. *Zool. Zhur.*, vol. 40, pp. 454-456. (In Russian, English translation in the Library of the National Museum of Natural Sciences, Ottawa, Canada).

PURRETT, L.

1971. The birth of the Caribbean. *Science News*, vol. 99, pp. 169-170.

REYNOLDS, T. B.

1966. The distribution and abundance of lake-dwelling triclads—towards a hypothesis. *Advances in Ecological Research*, vol. 3, pp. 1-71. New York, Academic Press, Inc.

ROSS, HERBERT H.

1967. The evolution and past dispersal of the Trichoptera. *Ann. Rev. Ent.*, vol. 12, pp. 169-206.

SCHMIDT, K. P.

1954. Faunal realms, regions and provinces. *Quart. Rev. Biol.*, vol. 29, pp. 322-331.

SCHUCHERT, C.

1935. Historical geology of the Antillean-Caribbean region. New York, John Wiley and Sons, Inc.

SIMPSON, GEORGE GAYLORD

1956. Zoogeography of West Indian land mammals. *Amer. Mus. Novitates*, no. 1759, pp. 1-28.

SIVICKIS, P. B.

1923. Studies on the physiology of reconstitution of *Planaria lata* with a description of the species. *Biol. Bull. Marine Biol. Lab., Woods Hole*, vol. 44, pp. 113-152.

STEINMANN, PAUL, AND E. BRESSLAU

1913. Die Strudelwürmer (Turbellaria). Leipzig, Klinkhardt Verlag.

WOODRING, W. P.

1954. Caribbean land and sea through the ages. *Bull. Geol. Soc. Amer.*, vol. 65, pp. 719-732.

WOODWORTH, W. MCM.

1897. Contributions to the morphology of the Turbellaria. II. On some Turbellaria from Illinois. *Bull. Mus. Comp. Zool. Harvard*, vol. 31, pp. 1-16.

ADDENDUM

Very recent geological evidence (Purrett, 1971) suggests that the Caribbean basin is a former continental land mass which has undergone post-Cretaceous disruption, i.e., subsequent to Continental Drift.

