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SYNOPSIS OF THE FRESHWATER TRICLADS OF THE CARIBBEAN (PLATYHELMINTHES, TRICLADIDA, PALUDICOLA)

by

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ABSTRACT

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An account is given of the five species of freshwater triclads which are known from the Caribbean region, including taxonomic descriptions, karyological, ecological, and biogeographic information, supplemented with remarks on observations of previous workers and comparisons with similar species. Records of unidentified specimens are summarized. Caribbean freshwater planarians belong to the genus *Girardia*; the phylogenetic relationships within this genus remain to be resolved. It is argued that present distributional patterns in Caribbean *Girardia's* may be the result of vicariance caused by a changing geology.

Key words: **Platyhelminthes, Tricladida, Paludicola, *Girardia*, Caribbean, taxonomy, phylogeny, biogeography.**

INTRODUCTION

The historical biogeography of the Caribbean Islands has attracted much attention in recent years in relation to the question whether dispersal or vicariance hypotheses should be invoked to account for the present-day

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faunal elements of the archipelago (Rosen 1975; Savage 1982; Tolson 1987).

Vicariance hypotheses are most easily handled in biogeographic studies, whereas dispersal hypotheses are relatively immune to falsification. Freshwater triclads form a potentially useful group for testing and erecting vicariance hypotheses because these animals in general are poor dispersers and when they do disperse then it is only through contiguous freshwater bodies.

In recent years our limited knowledge on the freshwater triclads of the Caribbean has been enlarged through some collections made on islands from which previously no records were available (Codreanu & Balcesco 1973; Gourbault 1980). However, the triclad fauna of the large island Hispaniola remained unknown. Therefore it was fortunate that material from Hispaniola became available as a result of collections made in Haiti by Prof. Dr. J.H. Stock, Dr. L. Botosaneanu (Institute of Taxonomic Zoology, Amsterdam), and Dr. Ir. J. Notenboom (RIVM, Bilthoven, The Netherlands) during several of the Amsterdam Expeditions to the West Indian Islands. Furthermore, Prof. Stock also made collections of paludicolans on Margarita, Curaçao, and Guadeloupe. The planarian fauna of Jamaica, among others, remains to be studied.

Meaningful hypotheses on historical biogeography depend on good taxonomy and adequate information on the distribution of taxa. The present paper contributes to both these premises by presenting a synopsis of all paludicolans from the Caribbean known to date.

Because the present paper only aims at a synopsis of the freshwater triclads of the Caribbean, the species descriptions – based on literature study and specimen examination – are kept as concise as possible, and the emphasis is on diagnostic features.

MATERIAL AND METHODS

Serial sections were made at intervals of 8 µm and were stained in Mallory-Heidenhain or in PTAH. The material used is listed under the appropriate species headings and is deposited in the Zoölogisch Museum, Amsterdam (ZMA). Additional material examined consisted of specimens of *Girardia tigrina* (ZMA), and type specimens of *G. antillana*, obtained from the Smithsonian Institution, Washington (USNM).

Abbrevations used in the figures

bc	copulatory bursa
bs	bursal canal
ca	common atrium

cod	common oviduct
ed	ejaculatory duct
gl	gland
ma	male atrium
od	oviduct
pg	penial gland
pp	penis papilla
sg	shell gland
sv	seminal vesicle
vd	vas deferens

KEY TO SPECIES OF GIRARDIA

1. Oviducts separately opening into bursal canal 2
    Common oviduct 6
2. Angled bursal canal 3
    Smoothly curved bursal canal 5
3. Mouth opening at posterior end pharyngeal cavity 4
    Mouth anterior to posterior end pharyngeal pocket 7
4. Common atrium receives secretion shell glands. ....*G. festai*
    Shell glands open into bursal canal ....*G. cubana*
5. Ejaculatory duct with blindly ending accessory seminal vesicle in penis bulb ....*G. antillana*
    Ejaculatory duct without accessory seminal vesicle ....*G. aurita*
6. Testes ventral ....*G. festai*
    Testes dorsal, or dorso-ventral ....*G. arimana*
7. Penis papilla, ejaculatory duct, and bursal canal lined with an infranucleated epithelium ....*G. arimana*
    These structures lined with a nucleated epithelium ......*G. antillana*

SYSTEMATIC ACCOUNT

TRICLADIDA PALUDICOLA

Genus **Girardia** Ball, 1974

Head typically high triangular, but may be truncate. Seminal vesicle absent or of the bifid nonmuscular type. Diaphragm absent. Bursal canal musculature of inner circular muscles surrounded by longitudinal fibres, or intermingled. Testes numerous, ventral, dorsal, or occupying the entire space between dorsal and ventral body surface. Pharynx usually pigmented. (After BALL 1974, modified).

Girardia aurita (Kennel, 1888)

(Fig. 1)

Planaria aurita KENNEL, 1888

Description: High triangular head. Dorsal surface yellow-brown, or brown with pale mid-dorsal stripe and lateral margins. Pharynx pigmented.

Numerous ventral testes extend throughout the body length. The vasa

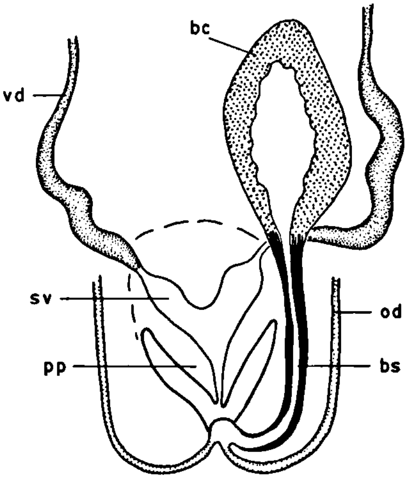

FIGURE 1. *Girardia aurita*. Diagrammatic, horizontal reconstruction of the copulatory apparatus (after KENNEL 1888).

deferentia separately penetrate the penis bulb and, subsequently, expand to broad seminal vesicles. The latter unite to a bifid seminal vesicle which tapers to form the ejaculatory duct, which opens at the tip of the penis papilla. The papilla is a short and broad cone, covered with a nucleated epithelium and provided with circular and longitudinal muscles. The penis bulb is well developed.

From its opening into the undivided atrium the bursal canal smoothly curves anteriad to communicate with a rounded copulatory bursa. The bursal canal is lined with a nucleated epithelium and receives the separate openings of the oviducts close to its junction with the atrium.

Localities and Ecology: The species is only known from the type material, which appears to be unavailable. Specimens were collected from pools and small rivers near Port of Spain, as well as from the Arima River on Trinidad.

Remarks: The description provided above is based on Kennel's (1888) account of the species.

Ball (1971) already discussed at length the taxonomic confusion around Kennel's *Planaria aurita* and provided ample arguments for maintaining its separate specific status. No new information has become available since Ball's publication which should make necessary a re-evaluation of Kennel's description and Ball's arguments.

Characteristic features of *G. aurita* are the ventral testes and the separate openings of the oviducts close to the gonopore.

Girardia festai (Borelli, 1898)

(Figs. 2-3)

Dugesia festae Borelli, 1898.
Planaria dimorpha Böhmig, 1902 new synonymy.
Planaria polyorchis Fuhrmann, 1914.
Euplanaria aurita – De Beauchamp, 1939.
Dugesia polyorchis – Kenk, 1941.
Dugesia sanchezi Hyman, 1959 new synonymy.
Dugesia titicana – Kenk, 1974.
Dugesia (Girardia) polyorchis – Ball, 1974.

Material examined: Curaçao: ZMA: V.Pl. 837, springs of San Pedro, 21.11.1958, sagittal sections on 3 slides; V.Pl. 838, springs of San Pedro, (12° 15'32"N 69° 02'36"W), 14.05.1978, sagittal sections on 2 slides; V.Pl. 839.1, Boca de Léon, Hofje van Hato (12° 11'05"N 68° 56'54"W), 15.05.1978, sagittal sections on 2 slides; V.Pl. 839.2, sagittal sections on 2 slides; V.Pl. 839.3, sagittal sections on 2 slides.

Description: Live specimens with high triangular head and pointed auricles, up to 20 mm long. Preserved specimens up to 15 mm long and 2.5 mm wide. Pattern of pigmentation rather variable. The ground colour of the dorsal surface varies between black and light brown and may show a pale, middorsal line; the lateral regions of the dorsal surface may be provided with numerous light spots; the auricles are unpigmented. Ventral surface black, grey, or white.

The anterior intestinal gut trunk gives off about 17 pairs of lateral diverticula, while each of the posterior rami gives rise to about 14 lateral diverticula. The pharynx is pigmented.

The ovaries are situated at a short distance behind the brain. The numerous ventral testes extend from directly behind the ovaries to almost the posterior end of the body.

The copulatory apparatus is highly variable between specimens from allopatric populations as well as between individuals from the same sampling locality. The great range of morphological variation in the copulatory apparatus may be gleaned from Marcus' (1960) diagrammatic reconstructions concerning specimens from Curaçao. The penis papilla may have the shape of a (1) broad and short cone, (2) long and slender cone, (3) short retracted cone, with an annular valve at its base, (4) blunt cone, with about half-way an annular constriction. The course of the vasa deferentia is charac-

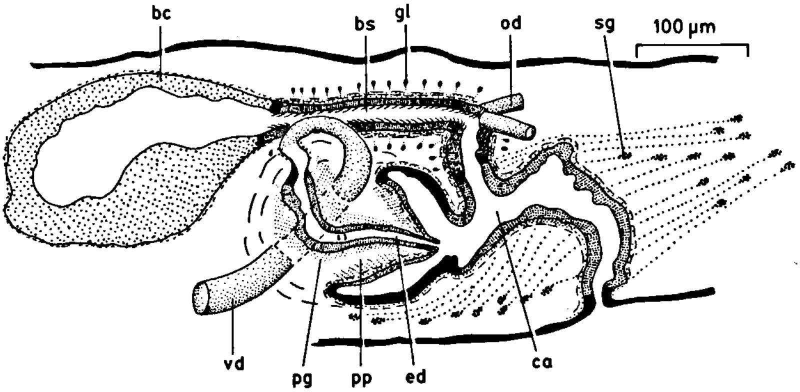

Figure 2. *Girardia festai*. ZMA V. Pl. 839.1. Sagittal reconstruction of the copulatory apparatus.

teristic because the ducts recurve considerably before separately penetrating the penis bulb. Within the bulb each vas deferens expands to a seminal vesicle, which is lined with a tall epithelium. These seminal vesicles eventually unite to form the ejaculatory duct, which shows a lining epithelium similar to that of the vesicles. The epithelium of the ejaculatory duct is penetrated by numerous openings of penial glands. In specimens with a highly contracted penis papilla the vasa deferentia may open into a single, intrabulbar seminal vesicle. A characteristic feature of *G. festai* is that the nucleated lining epithelium of the penis papilla is penetrated by the numerous openings of erythrophilic glands.

The male atrium is usually separated from the common atrium by a constriction that is developed to greater or lesser extent. The shape of the common atrium is rather variable because its posterior wall may be provided with one or two indentations. Characteristic for *G. festai* is that the tall lining epithelium of the entire common atrium is penetrated by numerous openings of highly abundant shell glands, which also discharge into the distal section of the bursal canal, just before the latter opens into the atrium.

The angled bursal canal is lined with cuboidal, nucleated cells which are provided with long cilia. The bursal canal receives the separate or combined openings of the oviducts at the point where the canal makes a sharp anterior bend. Numerous unicellular glands discharge a fine-grained secretion into the bursal canal, the latter being surrounded by layers of intermingled circular and longitudinal muscles. The rather large copulatory bursa is lined with tall, vacuolated cells.

Karyology: BENAZZI (1978) studied the chromosome portrait of alleged *D. sanchezi* specimens from Chile, in which the diploid complement consisted of 16 meta- and submetacentric chromosomes.

Localities and Ecology: The geographical distribution of *G. festai* is given in Fig. 3, which is based on the map provided by KAWAKATSU & MITCHELL (1984b), supplemented with the sampling localities of *D. sanchezi*.

It is interesting to note that present information suggests that *G. festai* remains west of the Andean belt, but only future field work may reveal to what extent the distribution presently known is the result of a collector's artifact.

G. festai has been collected from streams, lakes, and natural springs at altitudes ranging from almost sea level (HYMAN 1959) to 4800 m (DU BOIS-REYMOND MARCUS 1953).

Remarks: According to DU BOIS-REYMOND MARCUS (1953) BORELLI already stressed that *G. festai* resembles *G. tigrina*, which is evident indeed from its external appearance and the gross morphology of the reproductive apparatus. That these two species are very closely related is apparent also from a number of features previously not taken into consideration.

For example, in both species the bursal canal is surrounded by a zone of intermingled layers of circular and longitudinal muscles. Further, both species are unusual in that their common atrium is penetrated by numerous openings of shell glands. With respect to *G. festai*, the highly glandular nature of the copulatory apparatus was described in the above. Previous workers

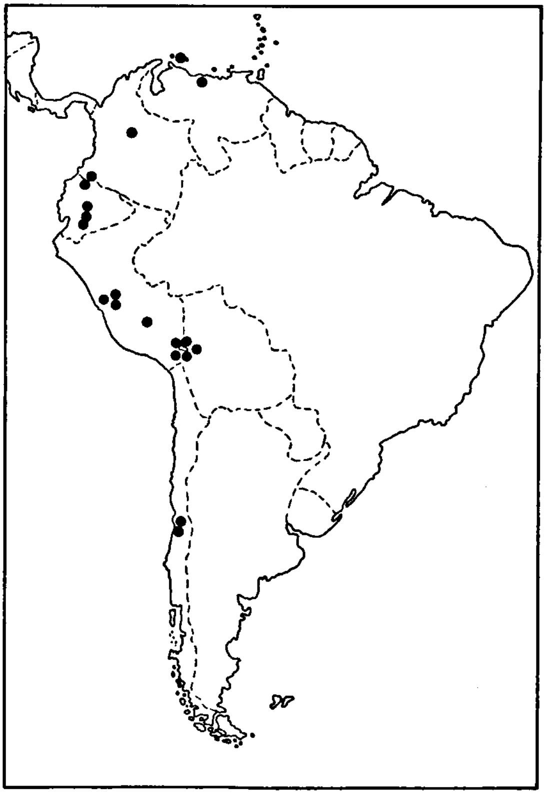

FIGURE 3. Geographical distribution of *Girardia festai*.

failed to describe the glands or did not differentiate between the various types of gland involved. HYMAN (1933) mentioned "cement glands of the atrium", DU BOIS-REYMOND MARCUS (1953) described abundant cement glands, HYMAN (1959) observed numerous "eosinophilous or fuchsinophilous glands", and KAWAKATSU & MITCHELL (1984b) mentioned the glandular epithelium of the common atrium. My microscopic slides show that the abundant, coarse secretion that is discharged into the common atrium of *G. festai* is similar in texture and colouration to the secretion produced by shell glands in other species of triclad. Another type of secretion, more fine-grained, is discharged into the bursal canal of *G. festai*, a situation already observed by HYMAN (1959) for the allegedly new species *D. sanchezi*.

The glandularization of the copulatory apparatus of *G. festai* is different from the situation in *G. tigrina*, as described in the literature. However, after examination of the histological slides of *G. tigrina* I am compelled to conclude that the existing literature (cf. BALL 1971; KENK 1976; BALL & REYNOLDSON 1981; KAWAKATSU *et al.* 1981) fails to recognize the different types of gland associated with the female copulatory apparatus. In *G. tigrina* the common atrium receives a coarse, orange secretion from abundant glands around the atrium, while the differently stained secretion of cement glands is discharged into the gonopore. This orange secretion is similar to the secretion produced by shell glands in other triclads. Furthermore, the bursal canal of *G. tigrina* receives a fine-grained secretion just ectally to the separate openings of the oviducts. The glands which produce this secretion are invariably referred to in the literature as shell glands. However, I find this secretion to be of a different composition because it stains either light blue or deeply red, and is much finer grained than the secretion usually produced by shell glands. Perhaps this type of secretion is homologous with the secretion that penetrates the entire bursal canal of *G. festai*. MARTINS (1970) observed the glandular nature of the common atrium in *Dugesia jimi* (= *G. tigrina*) but failed to distinguish between the various types of gland described above.

In conclusion: *G. festai* and *G. tigrina* also show a high degree of similarity in the abundant shell glands which discharge their secretion into the common atrium.

It is interesting to note that the ever meticulous BÖHMIG (1902) described *Girardia anceps* (Kenk 1930) and *G. dimorpha* (Böhmig 1902) with highly glandular atria. He distinguished three types of gland, *viz.* (1) glands opening just ectally to the openings of the oviducts, (2) glands discharging into the atrium, and (3) glands that open into the gonopore. The external features and anatomy of these two species are very similar to that of *G. festai* and *G. tigrina*. It may be that *G. anceps* is a junior synonym of *G. tigrina* and the *G. dimorpha* is a junior synonym of *G. festai*. The latter assumption is supported by the fact that HYMAN (1959) described *D. sanchezi* (= *G. festai*) from localities in Chile in the proximity of one of BÖHMIG's sampling localities.

It could well be that the kind of glandularization of the female copulatory apparatus as described above for *G. festai* and *G. tigrina*, forms a characteristic feature of a restricted group of *Girardia's*. In *G. jenkinsae* (BENAZZI & GOURBAULT 1977) the shell glands also appear to open into the atrium instead of the bursal canal (BENAZZI & GOURBAULT 1977); in *G. chilla* (MARCUS 1954) the common atrium is penetrated by numerous openings of eosinophilous glands (*cf.* MARCUS, 1954; HYMAN, 1959), and the same situation is present in *G. nonatoi* (MARCUS, 1946) (see MARCUS, 1946, fig. 168). Future study of well stained preparations (preferably in Mallory-Heidenhain) of species of the genus *Girardia* may be able to reveal the distribution of the character concerning the glandular common atrium.

Girardia antillana (Kenk, 1941)

(Figs. 4-5)

Dugesia antillana KENK, 1941.

Material examined: HAITI ZMA: V.Pl. 840.1, Spring Gongon (18° 38'54"N 72° 02'06"W), 21.11.1979, sagittal sections on 3 slides; V.Pl. 840.2, sagittal sections on 2 slides; V.Pl. 840.3, horizontal sections on 3 slides; V.Pl. 840.4, transverse sections on 9 slides; V.Pl. 840.5, sagittal sections on 4 slides; V.Pl. 840.6, sagittal sections on 2 slides; V.Pl. 841.1, Etang Saumâtre, Fond Parisien (18° 29'19"N 75° 56'25"W), 7.05.1978, sagittal sections on 4 slides; V.Pl. 841.2, transverse sections on 5 slides; V.Pl. 841.3, horizontal sections on 2 slides; V.Pl. 841.4, sagittal sections on 3 slides; V.Pl. 842.1, Etang Saumâtre, 7.05.1978, transverse sections on 9 slides; V.Pl. 842.2, sagittal sections on 2 slides; V.Pl. 842.3, sagittal sections on 2 slides; V.Pl. 843.1, springs at Fond Parisien (18° 29'19"N 71° 56'25"W), 7.05.1978, sagittal sections on 4 slides; V.Pl. 843.2, sagittal sections on 6 slides; V.Pl. 843.3, sagittal sections on 4 slides.

Other material examined: holotype (sagittal sections on 1 slide; USNM 43110), and a paratype (transverse sections on 1 slide; USNM 43111).

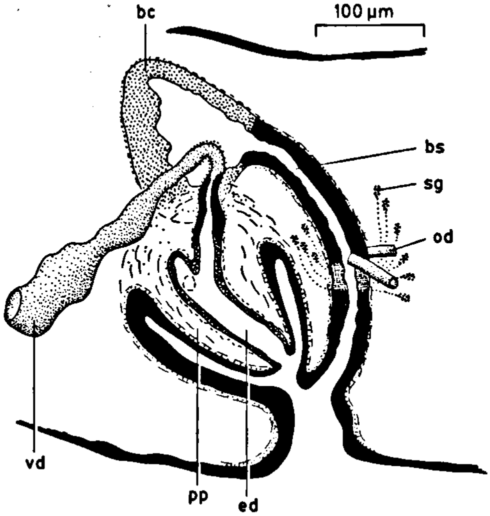

FIGURE 4. *Girardia antillana.* ZMA V.Pl. 840.1. Sagittal reconstruction of the copulatory apparatus.

Description: Preserved specimens up to 9 mm long and 1 mm wide. Body elongate, with high triangular head and prominent auricles. Dorsal surface brownish, ventral surface paler. The eyes are set in pigment-free spots.

The anterior intestinal trunk terminates behind the eyes and gives off about 18 pairs of ramified lateral diverticula. Each of the posterior intestinal rami gives rise to about 30 lateral diverticula. The pharynx is between one-fifth and one-fourth of the body length and may either be pigmented or unpigmented. The mouth opening is situated at one-third, sometimes one-half, of the distance between the posterior end of the pharyngeal cavity and the root of the pharynx.

Numerous dorsal, or almost dorso-ventral testes extend from directly behind the ovaries far into the posterior end of the body, where follicles also occur between the posterior gut branches.

The vasa deferentia separately penetrate the well developed penis bulb. Within the bulb each vas deferens expands to form an elongate vesicle which, subsequently, communicates with the nucleated ejaculatory duct. The subterminal openings of these vesicles into the ejaculatory duct make that the latter ends blindly in the penis bulb, forming an accessory seminal vesicle.

The short, conical penis papilla is covered with a nucleated epithelium.

The ovaries lie at a short distance behind the brain. The oviducts open separately into the smoothly curved bursal canal, which is lined with a nucleated epithelium and is surrounded by a layer of intermingled circular and longitudinal muscles. Shell glands open into the bursal canal, ectally to the oviducal openings.

The rounded copulatory bursa has a thin muscle coat.

Localities and Ecology: Specimens of *G. antillana* were obtained from several freshwater springs in the vicinity of Etang Saumâtre on Haïti, and on one occasion (sample ZMA V. Pl. 842.1-3) planarians were sampled from a brackish locality (3250 Cl mg/l) on the shore of the lake. Further, specimens have been reported from several streams and springs on Puerto Rico (KENK 1941).

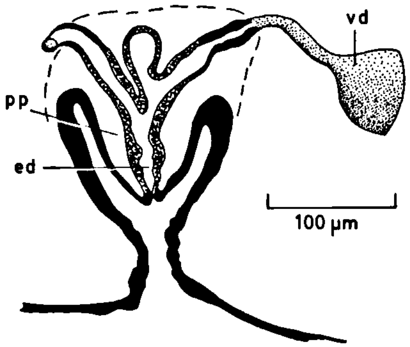

FIGURE 5. *Girardia antillana*. ZMA V.Pl. 844.1. Transverse section through penis.

Remarks: According to KENK (1941) the ejaculatory duct of *G. antillana* would have two blindly ending tubes or accessory seminal vesicles, while the expanded portions of the vasa deferentia would open into the ejaculatory duct distally to the tubes. However, in the type specimens examined and in the material from Haiti I found the situation to differ somewhat from KENK's interpretation, i.e. there is one blindly ending accessory seminal vesicle, close to the separate openings of the expanded portions of the vasa deferentia. KENK already noticed that this part of the anatomy of the species may have different appearances among specimens, due to muscular contraction.

KENK (1941) described the bursal canal with a subepithelial layer of circular muscles and a layer of longitudinal fibres, whereas I found the canal to be surrounded by a zone of intermingled muscle fibres, both in the type specimens and in animals from Haiti.

Girardia arimana (Hyman, 1957)

(Fig. 6)

Dugesia arimana Hyman, 1957.
Dugesia miltgeni Gourbault, 1980 new synonymy.

Material examined: Guadeloupe: ZMA: V.Pl. 844.1, Préf. de Basse-Terre, sources Pérou (16° 03'10"N 61° 33'47"W), 6.04.1978, sagittal sections on 4 slides; V.Pl. 844.2, sagittal sections on 5 slides; Margarita: V.Pl. 845.1, Galeria del Rio Tacariguas (11° 02'24"N 63° 53'36"W), 22.02.1982, sagittal sections on 2 slides; V.Pl. 845.2, sagittal sections on 2 slides; V.Pl. 845.3, sagittal sections on 2 slides; V.Pl. 845.6-10, several whole mounts on 5 slides.

Description: Preserved specimens up to 15 mm long and 2.5 mm wide. Body elongate, with high triangular head and well developed, pointed auricles; posterior end of body pointed.

Dorsal surface black, greyish brown, or pale brown, whereas the ventral surface is paler.

The anterior intestinal gut trunk extends anterior to between the eyes, while it gives off 13-20 pairs of lateral diverticula; each posterior gut trunk gives rise to 15-20 lateral diverticula. The long, pigmented pharynx is situated in the middle of the body and is between one-fourth and one-third of the body length.

The moderately numerous testes extend from directly behind the ovaries to almost the posterior end of the body. The relatively large follicles occupy the entire space between dorsal and ventral body surface, or have a dorsal position; the testes are located laterally to the vitellaria.

The vasa deferentia separately penetrate the penis bulb and, subsequently, unite to a wide ejaculatory duct, which follows a ventral course in the penis papilla. The ejaculatory duct is lined with a cuboidal, infranucleated epithelium; the duct is surrounded by a well developed, subepithelial layer of circular muscles and a thin layer of longitudinal muscle fibres.

The penis papilla is a broad and plump cone, which is covered with an infranucleated epithelium. The shallow penis bulb is well developed, while many muscle fibres radiate into the papilla.

The narrow male atrium is lined with a nucleated epithelium and shows a characteristic narrowing before communicating with the common atrium and bursal canal.

The ovaries are located at some distance behind the brain, while the vitellaria extend from anterior to the ovaries into the posterior end of the body. The oviducts arise from the antero-ventral surface of the ovaries. Posterior to the gonopore the oviducts unite to a long common oviduct, which penetrates the rear wall of the bursal canal. The latter is lined with an infranucleated epithelium and surrounded by circular and longitudinal muscles, respectively. The sac-shaped or rounded copulatory bursa is surrounded by a layer of intermingled muscle fibres.

Karyology: The haploid complement consists of four metacentric chromosomes which gradually decrease in size (GOURBAULT, 1980).

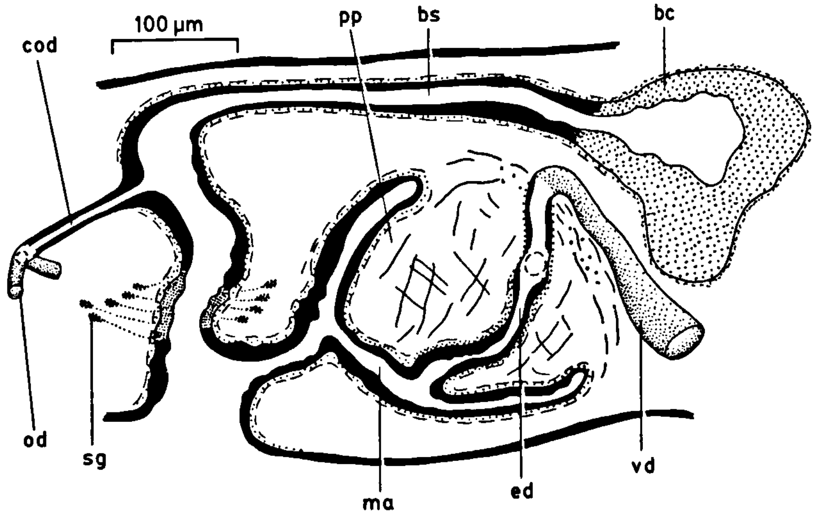

FIGURE 6. *Girardia arimana*. ZMA V.Pl. 844.1. Sagittal reconstruction of the copulatory apparatus.

Localities and Ecology: *G. arimana* is known from (1) various localities on Trinidad (HYMAN 1957; BALL 1971; KAWAKATSU & MITCHELL 1984a), (2) St. Vincent (HARRISON & RANKIN 1976; KAWAKATSU & MITCHELL 1984a), (3) Caracas, Venezuela (KAWAKATSU & MITCHELL 1984a), (4) Guadeloupe (GOURBAULT 1980; this paper), and (5) Margarita (this paper).

The species has been collected from under stones in rivers (HYMAN 1957; BALL 1971; HARRISON & RANKIN 1976), in springs (this paper), from subterranean localities (KAWAKATSU & MITCHELL 1984a; this paper), and from marshes (HARRISON & RANKIN 1976).

Remarks: According to GOURBAULT (1980) *G. arimana* differs from *D. miltgeni* in that the former has recurved vasa deferentia and a smaller number of testes. However, she did not provide an adequate comparison between the number of testes present in both species. Furthermore, recurved vasa deferentia appeared to be present in the newly collected paludicolans from Guadeloupe. These specimens also clearly showed the narrowing of the male atrium, the infranucleated lining of the penis papilla, ejaculatory duct, and bursal canal, as well as the circular and longitudinal muscles around the wide ejaculatory duct. GOURBAULT (1980) specifically mentioned for *D. miltgeni* the divided atrium, infranucleated lining of the bursal canal, and the longitudinal and circular muscles around the ejaculatory duct; she made no specific statements on the epithelium of the penis papilla and the ejaculatory duct. Similarities in the above-mentioned characters already suggest that *miltgeni* is the junior synonym of *arimana*, while other features point in the same direction.

GOURBAULT (1980) described *D. miltgeni* with a long common oviduct, and BALL (1971) described separate and combined openings for *G. arimana*. KAWAKATSU & MITCHELL (1984a) examined specimens of *G. arimana* obtained from four different localities, among which BALL's sample from St. Joseph Rivier, Trinidad. For the specimens from all four localities these workers described a relatively long common oviduct. Therefore, it may safely be concluded that fully mature specimens of *G. arimana* are characterized by a distinct common oviduct, a feature which is present also in the specimens from Guadeloupe described in this paper, and in the supposedly new *D. miltgeni*.

One other character that points to the synonymy of *D. miltgeni* and *G. arimana* is the ventral ejaculatory duct, which is present in GOURBAULT's (1980) specimens from Guadeloupe, as well as in the specimens from that island described in this paper, and in the animals studied by KAWAKATSU & MITCHELL (1984a).

Girardia cubana (Codreanu & Balcesco, 1973)

(Fig. 7)

Dugesia cubana Codreanu & Balcesco, 1973.

Material Examined: Cuba: Private collection I. R. Ball: N61-a, Gran Caverna de Santo Thomas, Provincia Pinar del Rio, sagittal sections on 2 slides; N61-b, horizontal sections on 1 slide; N61-c, sagittal sections on 2 slides.

Description: High triangular head with distinct, pointed auricles; dorsal surface grey and ventral surface pale, or the body being completely devoid of pigment. Preserved specimens up to 13 mm in length and 2.5 mm in maximum width (Codreanu & Balcesco 1973; Gourbault 1979).

The subepidermal musculature is provided with an extra, outer layer of longitudinal muscle fibres (cf. Sluys 1989).

The anterior intestinal gut trunk terminates behind the brain and gives off 9-15 pairs of lateral diverticula, while each of the posterior gut trunks gives rise to 20-30 lateral diverticula, as well as a number of short median diverticula; the posterior branches do not meet in the posterior end of the body. The pigmented pharynx is situated in the middle of the body and measures one-sixth to one-fifth of the body length.

In a single specimen the testes are situated in the dorsal as well as the ventral body region, while some of the larger follicles may occupy the entire space between ventral and dorsal body surface. The testes extend from directly behind the ovaries into the posterior end of the body, where the follicles are situated also between the posterior gut branches.

The vasa deferentia enlarge to false seminal vesicles, but decrease considerably in diameter before they separately penetrate the penis bulb. Within the bulb the vasa deferentia expand to large seminal vesicles, which fuse, thus giving rise to the ejaculatory duct.

In different animals the penis papilla may have a very different appearance. The papilla may be a broad and short cone, projecting obliquely or almost vertically into the male atrium (cf. Codreanu & Balcesco 1973, fig. 2; Gourbault 1979, fig. 1). The dorsal side of this cone is rather short and much reduced. In other specimens a penis papilla virtually seems to be absent, at first sight. In these animals the papilla is retracted to such an extent that the combined seminal vesicles appear to open into the male atrium through a kind of valve, the latter actually being the highly reduced penis papilla (Fig. 7; Codreanu Balcesco 1973, fig. 14).

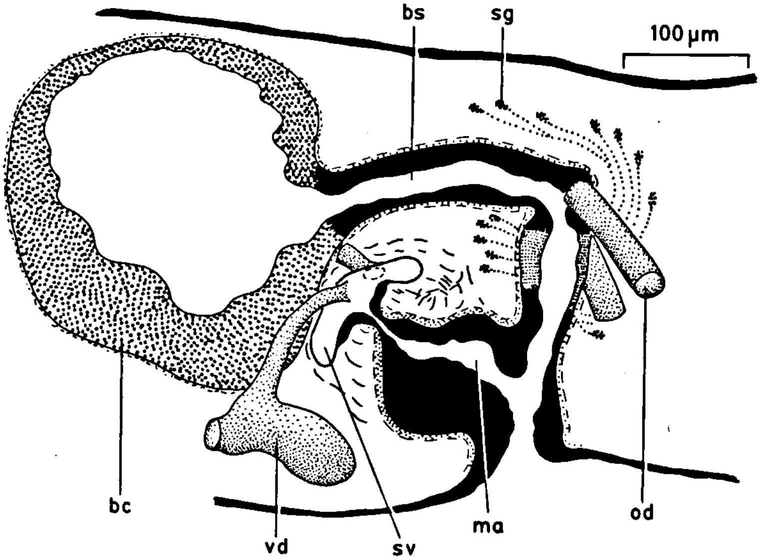

Figure 7. *Girardia cubana*. IRB N61-a. Sagittal reconstruction of the copulatory apparatus.

The ovaries are located at a short distance behind the brain, and the vitellaria extend from anterior to the ovaries into the posterior end of the body. The oviducts, which arise from the lateral wall of the ovaries, open separately into the bursal canal.

The bursal canal consists of a more or less horizontally running part, and an almost vertically oriented section, which communicates with the atrium. The bursal canal is lined with tall, nucleated cells and is surrounded by a layer of circular and longitudinal muscles, respectively. Shell glands open into the bursal canal ectally to the openings of the oviducts.

The large, rounded copulatory bursa is surrounded by a thin layer of interwoven muscle fibres.

Karyology: The diploid complement consists of nine pairs of chromosomes which gradually decrease in size. There are seven pairs of metacentric chromosomes, one submetacentric, and one pair of subtelocentric chromosomes (Gourbault 1979).

Localities and Ecology: Specimens of *G. cubana* have obtained from three epigean (Codreanu & Balcesco 1973), one hyporheic (Codreanu & Balcesco 1973), and one cave locality (Gourbault 1979) on Cuba.

UNIDENTIFIED SPECIMENS OF GIRARDIA

Unidentified freshwater planarians, probably *Girardia* species, have been reported from the following localities in the Caribbean region: Sto. Domingo (Kenk 1941), Barro Colorado Island, Panama (Hyman 1957), St. Vincent (Ball 1971), Trinidad (Hyman 1957; Ball 1971), Dominican Republic (Codreanu & Balcesco 1973, ZMA), southern peninsula of Haiti (ZMA) (see Fig. 8). It is not unlikely that the specimens from St. Vincent represent *G. arimana* and that the animals from Hispaniola are *G. antillana.*

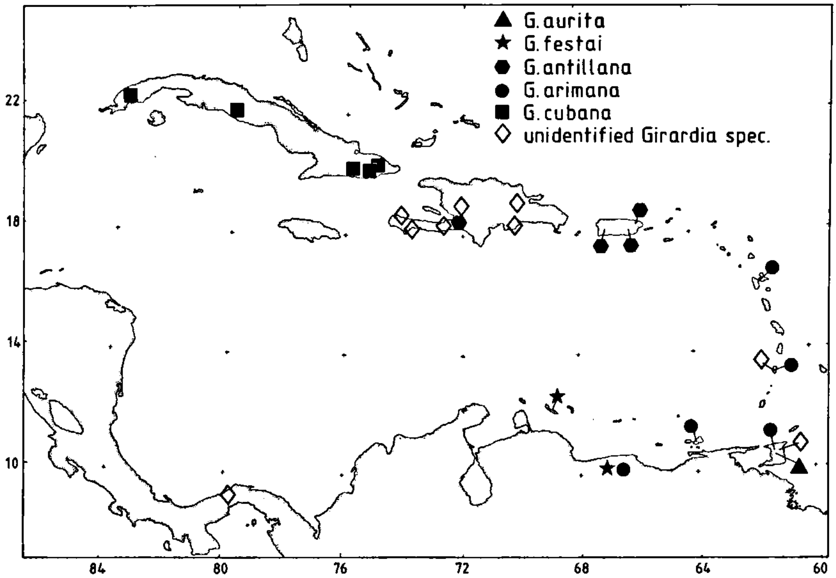

Figure 8. Distribution of *Girardia* species in the Carribean.

DISCUSSION

Taxonomy and Phylogeny: An historical biogeographic analysis depends on good taxonomy and should, preferably, be based on a phylogenetic analysis of the species. In that respect several workers confuse the issue in recent publications (cf. KAWAKATSU & MITCHELL 1984a, b) by still assigning Caribbean paludicolans to the genus *Dugesia*, although BALL (1974), among others, already pointed out that a large number of the New World species actually belong to a different phyletic lineage. BALL (1974) proposed the subgenus *Girardia* for this group of dugesids, while a recent study of DE VRIES & SLUYS (1991) showed that this subgenus should be elevated to the rank of genus.

Species of *Girardia* differ from members of the genus *Dugesia* sensu stricto in several, phylogenetically important characters (see DE VRIES & SLUYS 1991). The separate taxonomic status of *Girardia* is indicated by two presumed synapomorphies, *viz.* a pigmented pharynx, and a high triangular head. The genus *Dugesia* is characterized by two apomorphies, which are primitively absent in species of *Girardia*, *viz.* the presence of a diaphragm, and anterior extension of the ectal reinforcement around the bursal canal (DE VRIES & SLUYS 1991). Furthermore, species of *Dugesia* belong to a phyletic lineage which is characterized by a reversed bursal canal musculature, whereas *Girardia* has the primitive type of musculature around the bursal canal (DE VRIES & SLUYS 1991).

The improved concept that we now have of the various genera within the Dugesiidae reveals that all of the Caribbean paludicolans, and many South American species belong to the genus *Girardia*. This genus is represented with over 30 species on continental North America, Central and South America, and in the Caribbean.

Unfortunately, the systematic relationships of the Caribbean species with other members of the genus *Girardia* remain a matter of speculation in the absence of a comprehensive phylogenetic analysis of the entire genus. Such an analysis should be based on a revisionary study of the entire genus and on examination of specimens. Preliminary ideas based on published data may be flawed due to incorrect representation of character states. For example, BALL (1980) listed a number of *Girardia* species with dorsal testes and discussed the distribution of the character states concerning the divided/undivided atrium, and the angled/smooth course of the bursal canal. However, it turns out that published species descriptions may be poor indicators of these character states. For example, CODREANU & BALCESCO (1973) and GOURBAULT (1980) described a smooth bursal canal for *G. cubana* and *D. miltgeni* (= *G. arimana*), respectively. However, the present study shows that both species have an angled bursal canal.

Although for the present precise phylogenetic relationships within *Girardia* remain unknown, the available data already suggest that Caribbean species are not necessarily each other's closest relatives. In the above, for example, mention was already made of the glandular common atrium of *G. festai*. Such a glandular common atrium is absent in other Caribbean species and suggests that *G. festai* is more closely related to a group of mainland species to which at least *G. tigrina* belongs.

BALL (1980) already pointed out that a potentially important phylogenetic character is the presence of a divided atrium, which relates to the pronounced narrowing through which common and male atrium communicate. A clearly divided atrium is unusual among *Girardia* species and presumably represents an apomorphic character state, uniting *G. arimana*, *G. cameliae* (FUHRMANN 1914), *G. hypoglauca* (MARCUS 1948), *G. arizonensis* (KENK 1975), *G. festai*, and *G. nonatoi* (MARCUS 1946). Within this group *G. arimana*, *G. hypoglauca*, and *G. cameliae* may be more closely related to each other than each of them is to the other species because they share the ventral ejaculatory duct, and the infranucleated lining epithelia of the penis papilla, ejaculatory duct, and bursal canal.

Historical Biogeography: One of the main assumptions of the present paper is that biogeographic patterns in freshwater planarians in first instance may be explained best by vicariance hypotheses invoking a changing geology, thus de-emphasizing transoceanic hydrochore, biochore, or anthropochore dispersal.

CROIZAT (1958) has strongly argued against the idea that the fauna of the Lesser and Greater Antilles would be the result of waif dispersal. According to this worker the biogeographic patterns between the Caribbean and the mainland fauna are highly repetitive and show a regularity that belies accidental colonization. With respect to freshwater organisms HARRISON & RANKIN (1976) have pointed out that "...the bulk of the freshwater fauna of these islands... are neither hardy nor are they strong fliers, nor do they possess drought-resistent stages." In other words: under the Swim-Fly paradigm an ad hoc dispersal hypothesis has to be postulated for almost every component of the freshwater fauna. It appears to be appropriate to search for a more parsimonious explanation for the biotal relationships in the Caribbean, one that relates to the tectonic history of the area.

Ball (1971, 1974) has argued cogently that there is ample evidence suggesting that freshwater triclads are unable to cross even narrow sea straits on their own efforts. Therefore, freshwater triclads may indeed be considered reliable indicators of past paleogeographical connections.

Rosen (1985) distinguished eight fragmentation and seven accretionary events in the geological history of the Caribbean. In that perspective, and also considering the lack of a phylogenetic analysis, it cannot be expected that the historical biogeography of Caribbean paludicolans is fully understood and may shed light on the vexed geological problems in the Caribbean region. However, some biogeographic patterns do emerge from the present synopsis.

Present data suggest that single-island endemism is not the rule among freshwater planarians, in contrast to the suggestion made by Ball (1983: 414). Furthermore, there are clear links with South America, resulting (1) from species which occur on both the Lesser Antilles and the mainland, or (2) from biogeographic tracks linking the areas of endemism of presumed close relatives, e.g. *G. arimana*, *G. cameliae* (Colombia), and *G. hypoglauca* (Brazil) (see above); *G. antillana* and *G. veneranda* (Martins 1970), the latter from São Paulo.

It could be argued that the occurrence of *G. arimana* on Guadeloupe, St. Vincent, Trinidad, and Margarita resulted from dispersal of the mainland stock of this species in the Pleistocene, when several of the islands supposedly were connected due to the lowering of the sea level (Pregill & Olson 1981). However, recent information suggests that regressions were not large enough to interconnect the Lesser Antillean Islands, at least not those in the centre of the island arc (Donnelly 1988). Furthermore, Donnelly cites a publication in which it is suggested that throughout the Cenozoic the Lesser Antilles were farther from the mainland than at present, thus making dispersal from South America even more difficult.

The Lesser Antillean islands mostly consist of relatively young volcanoes, but this does not imply that the islands cannot be inhabited by an old fauna. It may well be that these islands were once very close to an ancient block or fragment from which faunal elements could 'diffuse' (Pielou 1979: 243) to the newly formed emergent volcanoes, or to their predecessors, e.g. the Aves Ridge or proto-Lesser Antilles (cf. Rosen 1985).

Paucity of data may lead to a great number of guesses. Therefore, meaningful scenarios or hypotheses on the historical biogeography of Caribbean planarians must await a comprehensive phylogenetic analysis of the genus *Girardia* as well as collections from still unsampled areas.

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