STUDIES ON THE FAUNA OF SURINAME AND OTHER GUYANAS: No. 7.

RIVULID FISHES OF SURINAME AND OTHER GUYANAS,

WITH A PRELININARY REVIEW OF THE GENUS RIVULUS

by

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1. Introduction and Acknowledgements

The present paper embodies the results of a study of 362 specimens of the genus *Rivulus* from Suriname and the other Guyanas.

So far, 58 species names (morphological species or subspecies) have been proposed, by a great many authors; these names are listed on pages 52–53. Of the 58, topotypical specimens have been examined in 8 instances. In order to facilitate a future review of the genus, which is in great need of revision, short remarks are made on the morphology and ecology of a number of specimens, from various localities, belonging to distinct species.

The samples studied were chiefly collected in Suriname by (1) Dr. D. C. Geijskes in 1938 and 1943; (2) Dr. D. C. Geijskes and Mr. P. Creutzberg, Suriname Expeditie, 1949; and on the (3) Blijdorp Zoo collecting trips in 1951 and 1952.

I wish to express my sincere thanks Dr. K. H. Voous, Zoological Museum, Amsterdam, and to Dr. P. Wagenaar Hummelinck, Zoological Laboratory, Utrecht, for their friendly aid and advice; to Dr. Ethelwynn Trewavas of the British Museum (Natural History), London, for her kind cooperation in taking counts and measurements for me on ten of Boulenger's types of *Rivulus harti*, and for sending in exchange one specimen of *Rivulus urophthalmus;* and to Dr. M. Boeseman, State Museum of Natural History, Leiden, who kindly lent me the entire *Rivulus* collection in his care.

2. Definitions of Terms applied

Measurements and proportions are all derived from lengths determined under the stereo-binocular dissecting microscope in the way indicated in figure 22. The proportion rates are expressed in thousandths of the standard length.

The terms used are as follows:

(a) *total length* (*tot. l.*), distance from the tip of the snout to the end of the caudal fin;

(b) *standard length* (*st.l.*), distance from the tip of the snout to the vertical from the rear end of the hypural plate;

(c) *predorsal length* (*prdl*), distance from the tip of the snout to the vertical from the base of the first dorsal ray;

(d) *preanal length* (*pral*), distance from the tip of the snout to the vertical from the base of the first anal ray;

(e) *interdorsal anal space* (*idas*), distance between the verticals from the first anal and dorsal rays;

(f) *head*, distance from the tip of the snout to the rear end of the fleshy opercle;

(g) *eye*, diameter of the eye, from anterior to posterior walls;

(h) *snout* (*snt*), distance from the tip of the snout to the front margin of the orbit;

(i) *depth of body* (*dpth*), greatest depth of the body;

(j) *depth caudal peduncle* (*dcp*), least depth of the caudal peduncle.

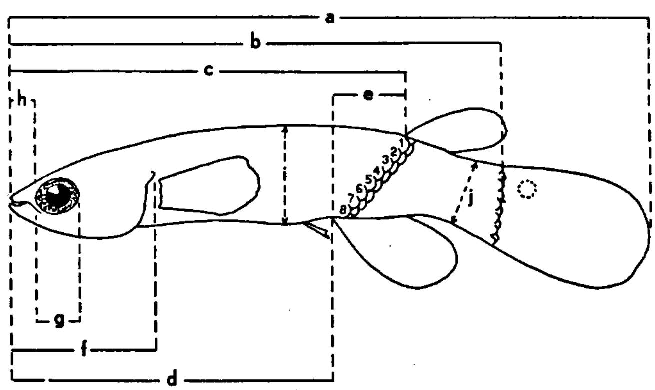

Fig. 22. Outline sketch of *Rivulus* showing the method in which the measurements have been taken. – a = total length, b = standard length, c = predorsal length, d = preanal length, e = inter dorsal/anal space, f = length of head, g = diameter of eye, h = length of snout, i = greatest depth of body, and j = least depth of caudal peduncle.

Counts have all been taken under the microscope.

Fin ray counts are all expressed in arabic numerals, and include all (even half) branched and unbranched rays; the last branched ray is counted as two if split to near the base; any rudimentary ray is counted as one. No roman numerals have been used for the simple unbranched rays, nor are the two types of rays given separately, in view of the fact that in many specimens, especially small and juvenile ones, the second ray of the fins may appear simple and unbranched (in many cases this ray is only beginning to fork), while, moreover, it is often not clear in specimens in which the fins are partly damaged.

Scale counts include all scales, to the extent of interpolating full and half scales near fin bases. Counts are taken in the following way:

(1) rows in lateral series are counted from the rear end of the opercle (upper edge of gill opening) to the end of the hypural plate, while the scales on the caudal fin are added after a + sign, in cases where it appears to be of importance to give these caudal scales.

(2) predorsal scales are counted on a median or zigzag row, from scale *b* of the frontal scale pattern (which is the first scale posterior to the pineal or central scale of the head) to the scale just in front of the dorsal fin, including – if present – scale with notch to receive this fin,

(3) transverse series are counted from the first full or half scale at the base of the dorsal fin, anteriorly downwards to the base of the anal fin,

(4) circumpeduncular scales are counted in a zigzag row around the narrowest part of the caudal peduncle, thus including all longitudinal rows.

3. Definition of the genus *Rivulus*

Rivulus Poey, 1861 p. 307 (genotype by monotypy *Rivulus cylindraceus* Poey), Cuba.

Cynodonichthys Meek, 1904, p. 101 (type by monotypy *Cynodonichthys tenuis* Meek), Oaxacá, Mexico; name corrected to *Cynodontichthys* by Meek, 1907, p. 145, footnote.

Slender elongate Cyprinodont fishes, small or of moderate size; body subcylindrical, compressed posteriorly; head flattened above or slightly depressed, deeper than wide; snout usually very short, blunt, with lower jaw slightly projecting; lateral gape of mouth short, horizontal; vertical cleft in front of eye marks the posterior edge of the lower lip; preorbital narrow; teeth in jaws, some conical teeth usually present on vomer, often obsolete or indistinct.

The fins are not very large, except for the caudal fin, which is the most important means of locomotion; dorsal and anal fins set far posteriorly; the dorsal is small, slightly more posteriorly than the anal, which is also small but has a few more rays and longer base; pectorals obtuse, distinct, inserted in the middle of the depth; ventrals obsolete; the caudal fin is rounded, truncate, or slightly pointed.

Body and head, and base of caudal, covered with thin cycloid Cyprinodont scales; the scalation of the head consists of a constant number of enlarged frontal scales, arranged round a large central scale which covers the pineal eye (organ); the exposed margins of the scales in front of the pineal scale are directed anteriorly; the margins of one lateral pair of these frontal scales are fully exposed.

The lateral line system is chiefly confined to the head, and is rudimentary or entirely absent on the sides; in several specimens the head pores and canals are most prominent. The pineal organ probably remains undeveloped in forms living in habitats where it is of no use, and develops in typical surface-dwellers and forms inhabiting running water. The system of pores and tracks on the head may be highly developed, but even if this is not so, obvious remains of it are present (at least in the specimens studied).

The present genus *Rivulus* can be distinguished from related South American and African genera of the family *Cyprinodontidae* by the insertion of the dorsal fin (behind anal origin), the rounded fins, and the subcylindrical body. It differs from the morphologically similar representatives of the strictly Ethiopian genus *Aphyosemion* chiefly in the absence of filamentous fin rays, and in a different pattern of the frontal scales.

4. Historical Review

1811 *Fundulus brasiliensis* from Brasil, the first species referable to the present genus *Rivulus*, became known to science from VALENCIENNES' description and figure. Status obscure. The type locality was restricted to Pará by GÜNTHER, 1866.

1861 *Rivulus cylindraceus* from Cuba, described by POEY as the type species of the genus *Rivulus* as established by him. The history of the genus proper therefore starts here.

1863 *Fundulus micropus* from the Rio Negro, Brasil, described by STEINDACHNER from a small collection secured in that river system.

1866 The first brief account of the genus appears in GÜNTHER's catalogue. In addition to a generic diagnosis – which still holds good for this genus, except as regards the absence of an air bladder – three species are listed: *Rivulus cylindraceus* from Cuba, *micropus* from the Rio Negro and Trinidad, and as a new form, *urophthalmus* from Pará, Brasil. *Rivulus brasiliensis* is referred to the genus *Haplochilus*, and its locality restricted to Pará.

1868 *Rivulus ocellatus* from Rio de Janeiro, described by HENSEL. This is the most southerly collecting place of the genus.

1877 *Rivulus poeyi* from Pará, Brasil, described by STEINDACHNER; but according to GARMAN, 1895, this name is synonymous with *urophthalmus*.

1880 *Rivulus marmoratus* from Cuba, described by POEY, as a second species of the genus from this island. Since GARMAN (1895), generally synonymized with *cylindraceus*. Quite recently RIVAS (1945) showed that *cylindraceus* and *marmoratus* are sympatric species. Ecological distribution unfortunately unknown. In most of its characters. *Rivulus marmoratus* resembles *ocellatus* from Rio de Janeiro.

1880 *Rivulus elegans* from the Cauca basin, Colombia, described by STEINDACHNER. Affinity discussed by GARMAN (1895), who believes it to be a variant of *micropus* from Rio Negro, Brasil.

1890 *Rivulus harti* from the island of Trinidad, described by BOULENGER.

1895 GARMAN's monumental review of the Cyprinodonts contains the first complete treatment of the genus *Rivulus:* ten forms are listed and diagnosed, four of them being new, viz. *Rivulus ornatus* from Silva and Cudajas, Amazonas, *obscurus* from Lake Hyanuary, Amazonas, *atratus* from Jutahy, Amazonas, and *isthmensis* from Costa Rica.
The Cuban forms *cylindraceus* and *marmoratus* are mixed up, while *urophthalmus* and *poeyi* are placed in synonymy with *brasiliensis*. *Rivulus ocellatus* is said to be hardly distinguishable from *brasiliensis*.

1899 *Rivulus geayi* from Carsevenne, French Guyana, described by VAILLANT. The first record of a species of *Rivulus* from the Guyanas.

1903 *Haplochilus peruanus* from Perim, Peru, described by REGAN. The first record of a species of *Rivulus* from Peru.

1904 *Cynodonichthys tenuis* from Oaxacá, Mexico, described by MEEK. This is the most northerly collecting place of the genus.

1907 *Rivulus flabellicauda* from Costa Rica, and *godmani* from Guatemala, described by REGAN. In his Biologia Centrali Americana of the same year REGAN lists these two forms in addition to *tenuis* and *isthmensis*.

1908 Distributional history of the genus *Rivulus* discussed by REGAN in the same account of Central American fishes, it is considered to be an offshoot of holarctic *Cyprinodontidae* that have spread southward into South America.

1909 *Rivulus breviceps* from Shrimp Creek, *holmiae* from Holmia, *waimacui* from Shrimp Creek, *stagnatus* from Christianburg, *lanceolatus* from Rockstone, and (as nomen nudum) *frenatus* from Gluck Island, all British Guiana, described by EIGENMANN. They represent the first records of the genus from British Guiana. Specimens of *breviceps* and *waimacui* are said to have been secured together, and these two must therefore be considered sympatric species.

1912 Reprint of EIGENMANN, 1909, with additional diagnosis and description of *frenatus*, and photographs of all forms described by the author in 1909.

1912 Revision of the genus *Rivulus* by REGAN; 22 species are described and keyed out, 2 of them being new, viz. *Rivulus strigatus* from the Amazon (restricted to Cudajas in the present paper), and *brevis* from Colombia (restricted here to Soplaviento, Rio Magdalena). REGAN's key long remained the most important means of recognizing the various forms described.

1913 *Rivulus brunneus* from Toro Point, Panama, described by MEEK & HILDEBRAND.

1914 *Rivulus flabellicauda*, synonymized with *isthmensis* by MEEK on account of an apparent error in the original description of *isthmensis*.

1914 *Rivulus heyi* from Saona island, Haïti, described by NICHOLS, is said to be probably a subspecies of the Cuban form *cylindraceus*.

1916 *Rivulus magdalenae* Eigenmann & Henn, from the Magdalena Basin, and *compressus* Henn, from Manaos, Amazon, described in HENN's account of the fishes collected in central South America. *Rivulus compressus* is a clear synonym of *micropus*.

1924 *Rivulus dorni* from Rio de Janeiro, and *mazaruni* from the Mazaruni river, British Guiana, described by MYERS.

1925 *Rivulus chucunaque*, with subspecies *chucunaque* from the lower Rio Chucunaque and *sucubti* from the upper Rio Chucunaque, Panama, are described by BREDER.

1926 *Rivulus xanthonotus*, locality unknown (? Amazonas), described by AHL from aquarium specimens.

1927 Review of the genus *Rivulus* by MYERS. The genus is divided into three genera: *Rivulus* (type *cylindraceus*), *Rivulichthys* (type *rondoni*), and *Rachovia* (type *brevis*). Descriptions of four new species are given: *Rivulus compactus* from Porto Nacional, Rio Tocantins, Brasil; *dibaphus* from Igarapé do Ajamuri, Brasil; *hildebrandi* from Boquete, Chiriqui, Panama; and *zygonectes* from Vereda, Brasil.

1926 *Rivulus beniensis* from Rio Beni, Bolivia, described by MYERS.

1936 *Rivulus myersi* from Progresso, Yucatan, described by HUBBS.

1938 *Rivulus volcanus* from Boquete, Panama, and *montium* from the Chagres basin, Panama, described by HILDEBRAND. The other known forms from Panama (*hildebrandi*, *brunneus*, and *chucunaque*) are also discussed, and the sympatric occurrence of at least *volcanus* and *hildebrandi* (general vicinity Boquete) is indicated.

1938 Rivulid species from San Domingo, described by ROLOFF, named *Rivulus roloffi* by TREWAVAS in 1948.

1941 *Rivulus milesi* from Honda, Colombia, described by FOWLER.

1944 *Rivulus* (*Vomerivulus*) *leucurus* from the Rio Jurado, Colombia, described by

FOWLER. A new subgeneric name is established on account of the presence of vomerine teeth. However, all specimens of *Rivulus* examined by the present author possessed toothed vomera.

1945 Rediscovery and redescription of the types of *Rivulus marmoratus* by RIVAS. *Rivulus marmoratus* is shown to be distinct from the other Cuban form *Rivulus cylindraceus*, with which it had been erroneously synonymized since GARMAN, 1895.

1945 *Rivulus taeniatus* from the Rio Caqueta drainage area, Colombia, described by FOWLER, is stated to be closely related to *strigatus* REGAN, from the Amazon.

1949 *Rivulus bondi* from La Florida, Caracas, Venezuela, described by SCHULTZ, and listed together with *harti* from Caripito.

1952 *Rivulus hendrichsi* from S. E. Mexico, described by ALVAREZ & CARRANZA.

1953 *Rivulus zygonectes* from Rio Tocantins, Amazonas, figured for the first time by ARLE in Aquarium Journal, MYERS p. 244.

1954 *Rivulus agilae* from Agila, Suriname, described by HOEDEMAN.

1958 *Rivulus marmoratus bonairensis* from Curaçao, Bonaire and Los Roques, described by HOEDEMAN.

5. DISTRIBUTION OF THE GENUS *Rivulus*

This genus has a wide range which comprises South America from Matto Grosso to the Venezuelan Islands, and Central America

Fig. 23. Map showing the type localities of the forms of *Rivulus* described. – The numbers correspond to those in column 3 of the alphabetical list.

including the West Indies. *Rivulus* can be found throughout virtually the whole of tropical South America, in the lowlands as well as in the more elevated parts of the continent. The map (figure 23) shows the type localities of all forms of *Rivulus*, as listed in alphabetical order on pages 52 and 53. The numbers on the map correspond to those in the third column of this list.

6. Alphabetical List of Species Names of the Genus *Rivulus*

Name, author and year:	Type locality:	No. on map at fig. 23:	Name in this paper:	Complex:
Rivulus agilae Hoedeman, 1954	Agila, Suriname	38	*agilae*	*breviceps*
Rivulus atratus Garman, 1895	Jutahy, Amazon	11	*atratus*	*breviceps*
Haplochilus balzanii Perugia, 1891	—		= *Rivulichthys*	
Rivulus beniensis Myers, 1927	Rio Beni, Bolivia	25	*beniensis*	*breviceps*
Rivulus bondi Schultz, 1949	Caracas, Venezuela	37	*bondi*	*micropus*
Rivulus breviceps Eigenmann, 1909	Shrimp Creek, Br. Guiana	17	*breviceps*	*breviceps*
Rivulus brevis Regan, 1912	—		= *Rachovia*	
Rivulus brunneus Meek & Hildebrand, 1913	Toro Point, Panama	19	*brunneus* ssp.	*elegans*
Rivulus chucunaque sspp. Breder, 1925	Rio Chucunaque, Panama	24	*b. chucunaque*	*elegans*
Rivulus compactus Myers, 1927	Rio Tocantins, Brasil	26	*compactus*	*breviceps*
Rivulus compressus Henn, 1916	Manaos, Amazonas	10	*micropus*	*micropus*
Rivulus cylindraceus Poey, 1861	Cuba	1	*cylindraceus*	*cylindraceus*
Rivulus dibaphus Myers, 1927	Igarapé do Ajamuri, Brasil	27	*dibaphus*	*breviceps*
Rivulus dorni Myers, 1924	Rio de Janeiro, Brasil	22	*dorni*	*breviceps*
Rivulus elegans Steindachner, 1880	Rio Cauca, Colombia	6	*elegans*	*elegans*
Rivulus elegans var. *santensis* Köhler, 1906	here restricted to Santos, Brasil	4	*santensis*	*urophthalmus*
Rivulus flabellicauda Regan, 1907	Costa Rica	—	= *isthmensis*	*isthmensis*
Rivulus frenatus Eigenmann, 1909/1912	Gluck Island, Br. Guiana	17	*frenatus*	*breviceps*
Rivulus geayi Vaillant, 1899	Carsevenne, Fr. Guiana	13	*geayi*	*breviceps*
Rivulus godmani Regan, 1907	Guatemala	16	*tenuis godmani*	*elegans*
Haplochilus hartii Boulenger, 1890	Trinidad	7	*harti*	*micropus*
Rivulus hendrichsi Alvarez & Carranza, 1952	Salto de Agua, Chiapas, S.E. Mexico	15		*elegans*
Rivulus heyi Nichols, 1914	Saona, Haïti	20	*heyi*	*cylindraceus*
Rivulus hildebrandi Myers, 1927	Boquete, Panama	28	*isthmensis*	*isthmensis*
Rivulus holmiae Eigenmann, 1909	Holmia, Br. Guiana	17	*holmiae*	*micropus*
Rivulus isthmensis Garman, 1895	Costa Rica	9	*isthmensis*	*isthmensis*
Rivulus lanceolatus Eigenmann, 1909	Rockstone, Br. Guiana	17	*lanceolatus*	*urophthalmus*
Rivulus (*Vomerivulus*) *leucurus* Fowler, 1944	Rio Jurado, Colombia	35	*leucurus*	*elegans*
Rivulus magdalenae Eigenmann & Henn, 1916	Magdalena basin, Colombia	21	*magdalenae*	*elegans*
Rivulus marmoratus Poey, 1880	Cuba	5	*marmoratus*	*marmoratus*
Rivulus m. bonairensis Hoedeman, 1958	Bonaire	39	*m. bonairensis*	*marmoratus*
Rivulus mazaruni Myers, 1924	Mazaruni R., Br. Guiana	23	*mazaruni*	*urophthalmus*
Fundulus micropus Steindachner, 1863	Rio Negro, Brasil, restricted to Maroa	2	*micropus*	*micropus*
Rivulus milesi Fowler, 1941	Honda, Colombia	34	*milesi*	*elegans*
Rivulus montium Hildebrand, 1938	Chagres basin, Panama	31	*montium*	*elegans*
Rivulus myersi Hubbs, 1936	Progreso, Yucatan	30	*myersi*	*marmoratus*
Rivulus obscurus Garman, 1895	Lake Hyanuary, Amazon	10	*obscurus*	*breviceps*
Rivulus ocellatus Hensel, 1868	Rio de Janeiro, Brasil	22	*ocellatus*	*marmoratus*
Rivulus ommatus Jordan, 1887	—	—	= *Leptolucania*	
Rivulus ornatus Garman, 1895	Silva, Cudajas, restricted to Silva	8	*ornatus*	*breviceps*
Haplochilus peruanus Regan, 1903	Perim, Peru	14	*peruanus*	*isthmensis*
Rivulus poeyi Steindachner, 1877	Pará, Brasil	—	= *urophthalmus*	*urophthalmus*
Rivulus punctatus Boulenger, 1895	Matto Grosso	12	*punctatus*	*breviceps*
Rivulus rachovii Ahl, 1923 (1925)	?	—	= *santensis*	*urophthalmus*
Rivulus rondoni Ribeiro, 1920 (1922)	—	—	= *Rivulichthys*	
Rivulus rogoague Pearson & Myers, 1924	—	—	= *Rivulichthys*	
Rivulus roloffi Roloff, 1938	San Domingo, Haïti	33	*roloffi*	*breviceps*
Rivulus stagnatus Eigenmann, 1909	Christianburg, Br. Guiana	17	*stagnatus*	*urophthalmus*
Rivulus strigatus Regan, 1912	Amazon, here restricted to Cudajas	18	*strigatus*	*breviceps*

Name, author and year:	Type locality:	No. on map at fig. 23:	Name in this paper:	Complex:
Rivulus taeniatus Fowler, 1945	Morelia, Rio Caqueta, Colombia	36	*taeniatus*	*breviceps*
Cynodonichthys tenuis Meek, 1904	Oaxaca, Mexico	15	*tenuis* ssp.	*elegans*
Rivulus urophthalmus Günther, 1866	Pará, Brasil	3	*urophthalmus*	*urophthalmus*
Rivulus volcanus Hildebrand, 1938	Chiriqui, Panama	32	*volcanus*	*isthmensis*
Rivulus waimacui Eigenmann, 1909	Shrimp Creek, Br. Guiana	17	*waimacui*	*micropus*
Rivulus xanthonotus Ahl, 1926	Amazon, here restricted to Obidos	8	*xanthonotus*	*urophthalmus*
Rivulus zygonectes Myers, 1927	Vereda, Brasil	29	*zygonectes*	*cylindraceus*

7. SURINAME RECORDS

Most of the samples under discussion originated from Suriname waters. Additional samples came from the drainage systems indicated in table 1. From this table it may be concluded that the genus *Rivulus* is fairly well represented in Suriname, particularly in the lowlands. The same can be said of the lowlands of British Guiana.

The fresh-water fauna of Suriname is only fragmentarily known, and the map (fig. 24) indicates that lowland forms of *Rivulus* have not yet been secured in the highlands. This, however, may be a normal circumstance caused by watersheds, just as in British Guiana. For the reasons given by EIGENMANN (1909, 1912) with regard to lowland and upstream forms, the same regions, viz., lowlands and plateau, are recognized in Suriname.

The Suriname lowland forms prompt recognition of at least two sympatric species, if, for the present, any possible ecological barriers are excluded. This kind of micro-geographical isolation however, occur, with respect to some of the *Rivuli* under report, as I shall point out later on.

The first ecological combination of forms among the samples came from Gold Placer (locality 2 on map, fig. 24), viz., *breviceps* collected together with *waimacui*. Sympatry of the same two species was reported by EIGENMANN (1909, p. 49) from Shrimp Creek, Upper Potaro river, British Guiana.

Secondly, sympatry is also obvious at Cable station (locality 7), where *holmiae* occurs together with *urophthalmus*.

Of equal importance are probable records of interbreeding found in samples from Gold Placer (2), Cable station (7), Nassau mountains (9), Table Mountain (14), referable to either *holmiae* or *waimacui*.

The forms *breviceps*, *frenatus*, *harti*, *holmiae*, *urophthalmus* and *waimacui* have been recorded as new for Suriname by BOESEMAN (1952). His record of *harti*, based on a sample collected by VAN HEURN at Paramaribo, can more suitably be referred to *urophthalmus* (s.l.). There is no indication of a distribution of *harti* farther east than Trinidad.

Rivulus urophthalmus is represented in Suriname waters by at least three forms, only one of which agrees well with the typical form from Pará, Brasil, whereas about half the samples conform quite well to the description of *stagnatus*. Two specimens are regarded as representing a subspecies, *Rivulus urophthalmus lanceolatus*.

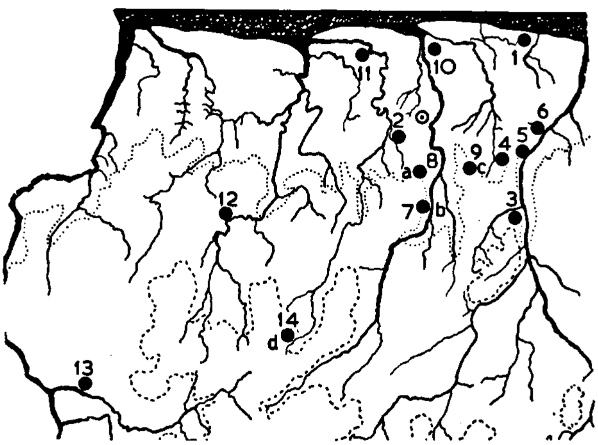

Fig. 24. Map of Suriname, showing localities in which samples of *Rivulus*, reported on in this paper have been collected. – Doubtful records have been omited. – The dotted line indicates the 200 m elevation level, the broken line the 500 m level. The letters a, b, c, and d refer to the localities of the 4 samples discussed on page 76 and graphs figs. 31, 33, and 34. – ⊙ Agila, type locality of *agilae;* 1 = Wia Wia, 2 = Gold Placer, 3 = Maroni system, 4 = Nassau mountains, 5 = Maroni district, 6 = Bush creek, 7 = Cable station, 8 = Railroad km 106, 9 = Nassau mountains, 10 = Paramaribo, 11 = Post Groningen, 12 = Langa Sula, 13 = Lucie river, 14 = Table mountain.

TABLE 1

Distribution of the forms of the genus *Rivulus* Poey, compiled from the samples under review (marked +) and from pertinent literature (marked ×). The last column refers to the type localities as given in the general map, fig. 23.

Drainage system	Cuba	Curaçao Bonaire, Roques	Haïti, Saona	St. Martin, Barbuda	Yucatan	Mexico	Guatemala-Costa Rica	Panama	Pacific slope Cordilleras	Cauca system	Magdalena system	Orinoco syst.-Trinidad, etc.	Rio Negro	Upper Brasilian Amazon	Peruvian Amazon	Br. Guiana (lowlands)	Suriname (lowlands)	Fr. Guiana (lowlands)	Br. Guiana (plateau)	Suriname (plateau)	Fr. Guiana (plateau)	Lower Amazon	Tocantins system	Matto Grosso	Eastern Brasil	Rio de Janeiro	Santos	Bolivian Amazon	Colombian Amazon	Type localities
Rivulus species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	map
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geayi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	13
dibaphus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	27
ornatus	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
strigatus	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
beniensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	25
taeniatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	36
compactus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	26
punctatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	12
obscurus	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
atratus	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
ocellatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	4
marmoratus	+	+	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
myersi	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
isthmensis	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
volcanus	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	32
hildebrandi	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	28
peruanus	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
urophthalmus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	+	+	.	.	.	×	.	.	×	.	.	.	.	3
stagnatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	+	.	.	.	.	.	.	.	.	.	.	.	.	17
lanceolatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	+	.	.	.	.	.	.	.	.	.	.	.	.	17
santensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	?
xanthonotus	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	?
mazaruni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	23
cylindraceus	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
heyei	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
zygonectes	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	29
tenuis	.	.	.	.	.	×	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15/16
brunneus	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
montium	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31
elegans	.	.	.	.	.	.	.	.	×	×	×	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6/34
leucurus	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35
magdalenae	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
micropus	.	.	.	.	.	.	.	.	.	.	.	.	+	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
bondi	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
harti	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
holmiae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	+	.	.	.	.	.	.	.	.	.	17
waimacui	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	+	.	.	.	.	.	.	.	.	.	.	.	.	17
Total number of forms described	2	1	2	1	1	1	2	4	3	1	2	3	4	2	2	6	7	2	1	2	0	2	2	1	2	3	1	1	1	62

8. The Problem

The main difficulty in carrying out any systematic study of the genus *Rivulus* is the poor quality of most of the descriptions and diagnoses made by previous authors. Even in the first revision of the genus by Regan (1912), the descriptions are insufficient for proper recognition of the forms. I shall therefore endeavour to summarize the various characters of each of the Guiana forms. This is the more necessary since the status of *Rivulus urophthalmus* from Pará is obscure, in spite of (or perhaps thanks to, in view of their divergence) the various diagnoses by Günther (1866), Garman (1895), Regan (1912), Myers (1927), and others.

In table 2, I have gathered together the diagnostic features of the four sympatric forms from Suriname. The two ecologically combined forms *breviceps* and *waimacui* (?), captured together at Gold Placer (locality 2 in fig. 24), differ greatly in all counts of the fin rays and scale rows. Not one of the proportion rates readily differentiates these two forms, unless large samples are available. The other two forms, *holmiae* and *urophthalmus*, differ from each other in about the same way – i.e. in fin ray and scale row figures. We may conclude that the Suriname forms *breviceps* and *waimacui* on the one hand, and *holmiae* and *urophthalmus* on the other, are sympatric species. From the data in table 2 it is not possible to decide easily whether these two ecological combinations of sympatric forms are identical. The question arises as to whether or not one or both forms of the second combination could be identical with one or both forms of the first combination. The Suriname *holmiae* samples differ from *breviceps* particularly in anal ray and scale counts, and in snout lengths. On the other hand, *holmiae* and *waimacui* have most

Table 2

Variation range of characters of the four sympatric Suriname *Rivulus* forms.

Species name	max. mm st.l.	D	A	prdl	pral	head	dpth	dcp	snt	eye	iob	Scales		
												lateral/ trans.	prd	cpcf
breviceps . . .	30	8–9	10–12	71–73	60–62	24–28	18–23	12–15	4–5	7–8.5	10–14	30–34/ 9–10	21–23	14–16
waimacui(?) .	55	10–12	15–18	70–76	59–66	25–28	19–25	11–14	4–7	7–10	12–17	40–52/11–14	28–35	16–21
holmiae . . .	65	9–11	15–18	72–77	59–63	24–28	19–25	11–14	5–9	6–9.5	12–16	38–49/10–12	28–38	15–20
urophthalmus.	40	7–8	11–13	75–80	61–67	20–26	18–21	12–15	3–5	6–7.5	9–13	34–40/ 9–10	28–30	17–18

characteristics in common, and these forms cannot be differentiated by these conventional characters only.

It has been shown that in this genus specific differences in behaviour pattern and ecological preference also exist; I shall discuss this to some extent later.

In view of the fact that in the Guyanan *Rivulus* populations not only morphological characters, but also ethological and ecological characters, may be considered as acting to establish or to maintain specific reproduction barriers, it will be necessary to deal separately with the following problems, viz. the morphology, ethology and ecology of Guyanan Rivulids.

9. Systematic Studies of the Suriname Rivulids

For the purpose of evaluating the characters generally used in describing this genus, the main source of information has been the above-mentioned samples from Guyana.

(1) *Morphology*

I have tried to make use of the following morphological characters:

(a) scalation of the head (frontal pattern),
(b) colour pattern of body and fins (particularly the caudal fin).

From aquarium experiments I noticed that, for instance, higher temperatures (from normal 18–20, to 24–28°C), from one generation to another, caused an increase in proportion rates of the head and in the number of transverse scale rows. The depth and head characters (length of head, length of snout, diameter of eye, and interorbital width) vary considerably with age and growth. I therefore consider the following conventional characters to be more or less adaptive and of secondary importance only. For these reasons they should be used with care:

(c) predorsal and preanal lengths, and interdorsal/anal space,
(d) number of lateral and predorsal scales,
(e) number of fin rays,
(f) number of transverse scale rows,
(g) number of circumpeduncular scale rows,
(h) proportion rates of the head, depth of body and of caudal peduncle.

(a) Scalation of head (frontal pattern)

While working on specimens from Suriname identified as ***holmiae*** by BOESEMAN, I found characters agreeing with those of both ***micropus*** and ***harti***. I was, therefore, forced to look for additional characters that might possibly reveal specific distinctness. In searching for these I was struck by the pattern of the scales on the head, covering the frontal bones, and surrounding the pineal organ (cf. fig. 25).

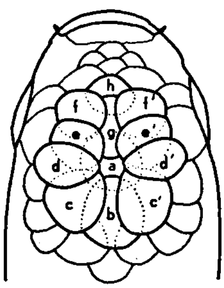

Fig. 25.

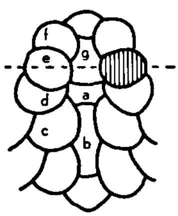

Fig. 26.

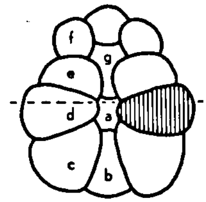

Fig. 27.

Fig. 25. Basic idealized pattern of the frontal scalation in *Rivulus*.
Fig. 26. Typical frontal pattern of the ***urophthalmus*** forms; see also plate Ia.
Fig. 27. Typical frontal pattern of Surinam ***holmiae;*** see also plate IIa.

Only once previously an other author had scalations of the head used and illustrated in this genus (FOWLER, 1944, p. 343), and then obviously on the basis of a damaged specimen, since the pattern illustrated was more irregular than any I have ever found in my specimens, except when some of the principal scales were missing. After close study of over 300 photographs of *Rivulus* heads I am convinced that this character can be of substantial assistance in separating various sympatric forms morphologically.

The scales on the body of *Rivulus* are very regularly arranged. They are rather large, smaller on the caudal and belly, and usually greatly enlarged (especially in older specimens) on top of the head. The generalized scales from the middle of the side are of normal Cyprinodontid type, with the apical field of the scales gently rounded, the lateral and basal margins meeting at an angle of nearly 90°; the basal margin is nearly straight to slightly curved; numerous fine circuli run parallel with the outer margin of the scale; the nucleus lies centrally; there are about 25 radii in the basal field, diverging but not all beginning in the centre of the scale.

The frontal scales are enlarged scales on top of the head. They are grouped round a scale ***a*** (cf. fig. 25), covering the pineal organ. In all 12 scales participate in forming the basic pattern, thus giving the pattern shown in idealized form in fig. 25. These 12 scales are arranged in three rows, i.e. one median row of scales ***a***, ***b***, ***g***, ***h***, and two lateral rows of scales ***c***, ***d***, ***e***, ***f***, and ***c'***, ***d'***, ***e'***, ***f'***, respectively. As will be clear from fig. 25, the scales situated in front of ***a*** have the outer (exposed) margin directed anteriorly. It is interesting to observe that in these frontal scales (i.e., those lying anterior to *a*) the apical field of the scales, which, in the normal body scales, is always directed towards the caudal (exposed portion), points away from the caudal; in the lateral scales *d* and *d'* the apical field is directed towards the lateral sides of the fish. Furthermore, in very young specimens, in which the scalation is not yet fully developed, I have always found these frontal scales present and arranged in accordance with their parental relations. The smallest specimens studied in this respect measured 12.3 mm in total length.

The central scale *a* has no exposed margin, and there is not even a clear indication of an apical or basal margin to it. Moreover this scale is covered by the surrounding scales of the pattern throughout its greater part (the entire margin). Two scales, normally forming one pair, are fully exposed, lying ON the others (*dd'* in fig. 25), thus closing the pattern. It will be understood that these fully exposed scales are often torn off in badly preserved specimens, but their impression can usually still be seen.

As far as I have been able to conclude at present from the material studied, there are three possibilities, each succeptible of some variation: viz., the exposed pair of scales can be the one named *ff'*, *ee'* or *dd'* in fig. 25. The way in which the scales overlie each other is illustrated in fig. 25. In order to facilitate comparison in scalation pattern I have named three main types of scalation after these exposed pairs of scales, viz. the pattern types *d*, *e*, and *f* (cf. figs. 26, 27, 36).

Irregularities in the pattern are ascribed either to the loss of one or more of the principal scales, and subsequent regeneration during life, or to interbreeding, when the pattern may appear asymmetrical but otherwise quite regular.

The scalation patterns in the seven Suriname forms are of three types, the three typical patterns discussed above. The forms *agilae*, *breviceps* and *frenatus* have the *f*-type pattern; *urophthalmus*, *lanceolatus* and *waimacui* the *e*-type pattern; and *holmiae* has the *d*-type pattern. In each of these seven forms the pattern is fully constant in the samples studied, showing nothing but a very slight individual variation. The asymmetry of the pattern found in some specimens should perhaps be ascribed to interbreeding; this point will be discussed in a special chapter.

(b) Colour pattern of body and fins

The seven Suriname forms differ pronouncedly in colour pattern of body and fins, particularly as regards the caudal fin. Four main types can be recognized:

1. *agilae*, *breviceps* and *frenatus* have no prominent markings on the sides, except that juveniles sometimes exhibit a number of oblique markings on the caudal peduncle; the caudal fin has a dark lower edge in males, and vertical rows of dots in females; no real caudal ocellus is present in either sex, but a bean-shaped dark spot is often visible on the females.
2. *waimacui* has more or less prominently marbled sides, with a broad dark band from the snout to the end of the mid-caudal-rays; no caudal ocellus is present in either sex.
3. *urophthalmus* and *lanceolatus* have almost plain sides, without dark markings in either sex (in life, carmine dots in the centre of each scale); in males entire outer margin of caudal fin (i.e., not only upper and lower edges) is darker, otherwise plain or finely mottled; females have definite caudal ocellus, and plain caudal fin.
4. *holmiae*, has dark spots arranged in longitudinal rows on the sides in both sexes;

caudal fin in male has black upper and lower margin and white intramarginal stripe; caudal fin in females plain or finely speckled; a prominent caudal ocellus in females only.

(c) Predorsal and preanal lengths, and interdorsal/anal space

In tabulating the ranges of predorsal and preanal proportion rates in each of the seven Surinam forms, we arrive at the following grouping:

form	prdl	pral	interdorsal anal space	index
1. *agilae*	70–72	60–63	10–11	286
2. *breviceps*	71–73	60–62	11	288
3. *frenatus*	72–73	61–62	11	290
4. *waimacui*	68–76	59–69	6–15	293
5. *urophthalmus*	75–80	61–67	13–14	310
6. *lanceolatus*	80–82	63–64	17–18	324
7. *holmiae*	72–77	59–63	13–14	298

agilae, *breviceps*, and *frenatus* all have about the same range;
waimacui comes very close to them, however, with a much wider range of the above characters (due to interbreeding?);
in *holmiae*, *urophthalmus* and *lanceolatus* the dorsal fin is situated considerably farther posterior.

The position of the vertical fins, dorsal and anal, expressed in predorsal and preanal lengths, and their relation to one another, expressed in interdorsal/anal space, are characters which have unfortunately been neglected by most previous authors. From my material I found that these proportion rates readily show specific distinction.

(d) Number of lateral and predorsal scales

Scalation is of great assistance in defining the groups and forms within the genus; this is especially true of the lateral and predorsal numbers. The seven Surinam forms can be roughly divided into two main groups: the coarse-scaled forms with 30 to 35 transverse rows of scales between opercle and caudal base, *agilae*, *breviceps*, and *frenatus;* and the fine-scaled forms with 40 to 50 transverse rows, *waimacui*, *urophthalmus*, *lanceolatus* and *holmiae*.

	lateral scales	predorsal sc.	index	transverse	circumped.	index
1. *agilae*	31–35 (av. 33)	19–23 (av. 21)	54	9–10 (10)	14–16 (15)	25
2. *breviceps*	30–34 (av. 32)	20–23 (av. 22)	54	9	14–16 (15)	24
3. *frenatus*	31–32 (av. 31)	22–24 (av. 23)	54	8–9 (9)	13	22
4. *waimacui*	39–52 (av. 47)	28–38 (av. 34)	81	11–12 (11)	16–21 (19)	30
5. *urophthalmus*	34–46 (av. 42)	27–35 (av. 33)	75	9–10 (10)	16–18 (17)	27
6. *lanceolatus*	43–45 (av. 44)	32	76	9	14	23
7. *holmiae*	38–49 (av. 43)	28–37 (av. 32)	75	10–12 (11)	15–20 (18)	29

(e) Number of fin rays

The number of fin rays exhibits very little variation, especially in the dorsal and anal fins, which yield rather low counts anyway; the number of caudal, pectoral, and ventral fin rays is almost uniform throughout the genus. As I observed the number of rays may be more or less adaptable to environmental influences.

In the seven Suriname forms the range of the number of pectoral rays is from 15 to 16 only, and this character is therefore of no systematic value within these forms. The dorsal rays range in number from 7 to 12, the anal rays from 10 to 18.

	dorsal rays	anal rays	index
1. *agilae*	8–9 (av. 8.2)	11–12 (av. 11.7)	199
2. *breviceps*	8–9 (av. 8.6)	10–12 (av. 11.2)	198
3. *frenatus*	7	10	170
4. *waimacui*	10–12 (av. 10.8)	15–18 (av. 16.9)	277
5. *urophthalmus*	7–8 (av. 7.6)	11–13 (av. 12.7)	203
6. *lanceolatus*	7	13	200
7. *holmiae*	9–11 (av. 10.2)	15–18 (av. 16.3)	265

These characters overlap to such an extent that only two groups can be recognized, i.e. those with small dorsal and anal fins, viz. *agilae, breviceps, frenatus, urophthalmus,* and *lanceolatus*, and those with a broader base to these fins, viz. *waimacui* and *holmiae*.

(f) Number of transverse scale rows

The transverse scale rows of the seven Suriname forms, as given above, see compilation under (d), show the same division of the forms as under (e).

(g) Number of circumpeduncular scales

The number of circumpeduncular scale rows in the seven Suriname forms are summarized above (see sub (d)); these numbers appear to be of some importance as a systematic character, and can probably also serve as a guide to the location of interbreeding forms.

(h) Proportion rates of head, depth of body, and caudal peduncle

The body proportions are considered to be very valuable, but they should be used with caution. Several forms exhibit similar proportions; these may have been affected by environmental factors. On the other hand, specimens from one single sample of a population of a certain form may show considerable differences, especially in the length of the head and in the derived measurements (snout, eye, interorbital width), and in the depths of both body and caudal peduncle, which differences may have been caused by such factors as temperature and availability of food. In various instances this susceptibility has been proved by aquarium experiments. Aquarists have noticed that even the brood of one pair of fishes show considerable individual variation in these respects.

Proportion rates in 1000ths of the standard length, with means in parentheses.

	head length	body depth	depth cp.	snout	diam. eye	interorb.	index
1. *agilae*	248–282 (260)	153–201 (190)	115–140 (126)	42–63 (51)	57–82 (73)	107–131 (124)	824
2. *breviceps*	248–277 (258)	176–228 (197)	121–150 (140)	36–51 (40)	60–86 (80)	94–145 (116)	831
3. *frenatus*	243–272 (261)	± 200	± 130	36–64 (50)	74–92 (84)	128–130 (129)	854
4. *waimacui*	242–282 (268)	178–252 (228)	110–138 (129)	45–72 (61)	76–106 (80)	113–171 (142)	908
5. *urophthalmus* . .	201–274 (246)	178–238 (202)	114–148 (134)	31–71 (52)	56–88 (70)	85–155 (117)	821
6. *lanceolatus* . . .	196	181	114	27	57	133	708
7. *holmiae*	241–282 (267)	193–251 (233)	104–135 (128)	47–72 (62)	62–96 (83)	113–141 (134)	907

A grouping based on the above characters is rather unsatisfactory because of the wide range of most of them, while moreover there is a considerable overlap in each. However, they may serve for subspecific recognition. The depth of the body shows two types, the slender-bodied and more robust forms, i.e., on the one hand *agilae, breviceps, frenatus, urophthalmus* and *lanceolatus,* with about 180 to 200, and on the other hand *waimacui* and *holmiae,* with about 230 thousandths of the standard length.

Summarising the characters of each of the seven Suriname forms discussed above, it is possible to draw up the following table, in which I have given the characters in their presumed sequence of importance.

	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
1. *agilae*	f	1	286	54	199	10	15	824
2. *breviceps*	f	1	288	54	198	9	15	831
3. *frenatus*	f	1	290	54	170	9	13	854
4. *waimacui*	e	2	293	81	277	11	19	908
5. *urophthalmus*	e	3	310	75	203	10	17	821
6. *lanceolatus*	e	3	324	76	200	9	14	708
7. *holmiae*	d	4	298	76	265	11	18	907

The forms *agilae, breviceps,* and *frenatus* differ pronouncedly from all other Suriname forms in having the *f*-type frontal pattern, and also in most other characters; these three forms clearly constitute a natural assemblage.

All three of the forms *waimacui, urophthalmus* and *lanceolatus* possess the *e*-type pattern, but an essential difference in this pattern is obvious, setting *waimacui* apart from *urophthalmus* and *lanceolatus.* This difference is, moreover, reinforced by some of the characters dealt with above (see under (b), (c), (d), (e), and (h)).

The last form, *holmiae,* distinguished from all the other six by its *d*-type pattern, also differs sharply from them in colour pattern. In several characters it seems to come close to *waimacui*, which, as will be seen, is strongly influenced by presumed interbreds. It is, moreover, difficult to determine whether or not *waimacui* really is a distinct form, and not merely a conglomerate of hybrids between *holmiae* and perhaps *urophthalmus*. This point will have to be decided. The samples under discussion do not contain any regular pure-strain *waimacui* series, while it is also questionable whether our presumed *waimacui* specimens are identical with EIGENMANN's British Guyanan *waimacui*.

The various sympatrically living morphological groups from Suriname are indubitably linked in one instance only, viz. *urophthalmus* × *holmiae* in the Cable station sample; but the *waimacui* specimens probably represent another link. The first case does not seem to be one of regular intermediates; the specimens show noteworthy asymmetry in the frontal pattern, and in other characters. They are considered hybrids. Some of the *waimacui* specimens show a quite regular frontal pattern, but several specimens have an irregular pattern. These may or may not be hybrids.

(2) *Ecology* and *ethology*

For more than eight years I have had the opportunity of studying alive in the home aquarium specimens of *agilae, cylindraceus, harti, holmiae, marmoratus* and *urophthalmus*, of which *agilae, holmiae* and *urophthalmus* came from Suriname waters. Practically nothing is known about the ecology of Rivulids (cf. also description of habitats of *Rivulus marmoratus* in HOEDEMAN, 1958a); and consequently the aquarium presents a highly advantageous way of becoming familiar with a group of animals in which coloration, behaviour and feeding habits could, in various instances, give hints towards a solution of problems of a systematic or geographical nature.

For example, the behaviour of *harti* and *holmiae* is quite similar, but is very different from that of *agilae* and *marmoratus*. When kept in the same large tank (450 litres) adult and even half-grown males of *harti* and *holmiae* behave as one species (form), and recognize other males as competitors; they join in defending their own territory. Neither *harti* nor *holmiae* seem to recognize specimens of *agilae* as intruders, though all other fishes of any kind are always kept at some distance from their territory. The same applies to *cylindraceus* as to *agilae*, but is has been observed that males of *urophthalmus* have been attacked by *holmiae* males when approaching the latter's territory, though, as a rule, *urophthalmus* certainly do not defend any territory. I shall deal with this subject more fully elsewhere; but the behaviour of *Rivulus* forms in the aquarium exhibits such prominent characters of an apparently specific nature that it is useful to mention them briefly here. Unfortunately, the behaviour of only a very limited number of forms has been observed and described.

When kept together or separately in large tanks (home aquaria), the tiny forms *agilae* and *marmoratus* prefer to live near the bottom of the tank, though they are not real bottom-dwellers like, for instance, certain *Cynolebias* forms. The robust forms such as *harti* and *holmiae* prefer running water, and are surface-dwellers. The resting attitude of the first group is sloping, tail downwards (cf. plate IVf), preferably between clusters of water plants but never right at the surface. The second group, the swift swimmers, rest at the surface in an almost straight position, with the flat head pressed against the air above, and watching everything above them. Moreover, the pineal organ seems to be much more sensitive to light in these forms; the central scale of the frontal pattern (scale *a*) is exposed to a greater extent than in the other forms, and is large and paper-thin. They are apt to leap out of the water, jumping at any insect in the air above them, and never missing. The other group feeds on insect larvae and micro-food nipped from plants.

A third group could be established, consisting of forms somewhat intermediate between these two, viz. *urophthalmus* and allies.

10. Supposed cases of Hybridization in Suriname Rivulids

In the present material, I observed irregularities and asymmetry in the frontal pattern of various specimens that might have been caused by the interbreeding of two distinct forms. Many more and larger samples from various localities are required in order to obtain values from which conclusions can be drawn regarding the parental forms of these presumed hybrids, the degree of hybridization, the actual zone of crossing and the causes of it. It is difficult at present to decide whether or not hydridization is indiscriminate in the samples under review. However, it is assumed that the features typical of the known forms occur in combination in the supposed hybrids; this is at the moment the only possible way of approaching the question.

The samples in which probable hybrids have been observed are:

(1) *urophthalmus* × *holmiae*, *urophthalmus* dominating: Paramaribo (10 in locality map, fig. 24), ZMA 100447, RML 18463, RML 18464; Cable station (7), RML 18425; Langa Sula (12), RML 18426; Post Groningen (11), RML 18465.
(2) *urophthalmus* × *holmiae*, *holmiae* dominating: Cable station (7), RML 18255–57; Rail-road km 106 (8), RML 19499; Nassau mountains (9), RML 19516.
(3) *waimacui* ?, *urophthalmus* × *holmiae*, and/or *breviceps* × *holmiae:* Gold Placer (2), RML 18462; Table mountain (14), RML 18427 and 18255–57,

(1) In most characters the presumed *urophthalmus* hybrids agree with the description of that form. The frontal pattern in the hybrid specimens seems to be the only ready indication of interbreeding. In order to define the outward appearance of regular Surinam *urophthalmus* and *holmiae*, I have thought it advisable to discuss the samples referable to them first.

a. Material of forms included in *urophthalmus* s.l.

The following samples have been referred to the three *urophthalmus* forms, and, for the sake of convenience, have been ranged under these headings in table 3. The samples from outside Suriname which have been studied for comparison have also been included.

Suriname: PARAMARIBO, Blijdorp exp., III. 1952, 4 ♂♂, 3 ♀♀ (ZMA 100447); surroundings, van Heurn, VII–VIII. 1911, 1 ♂, 1 ♀ (RML 18463); 3 ♂♂ (RML 18464); van Heurn, X. 1911, 1 ♂, 2 juvs. (RML no number); v.d. Hoek, XII. 1896, 1 ♀ (RML 18511); Blijdorp exp. 1952, 1 ♂, 3 ♀♀, 4 half decayed (RML 20–2–53); surroundings, ibid. 1 ♂ (RML 1–4–53); surroundings, 1 ♂ (ZMA 100434); 1 ♀ (ZMA 100438). POST GRONINGEN, Saramacca river, van Heurn, IX. 1911, 2 ♀♀ (RML 18465). CABLE STATION, Suriname river, Geijskes, 21–28, IX. 1938, 1 ♂, 2 ♀♀ (RML 18425). LANGA SULA, Coppename river, in bush in small pool, Geijskes, 25.VII.1943, 1 ♂ (RML 19426). LUCIE RIVER, van Hulk, Corantyne exp., 30.XI.1910, 1 ♂, 1 ♀ (RML 18319),
British Guiana: UPPER CUYUNI RIVER, Carter, exchange Br. Mus. (N.H.) Jan.1955, 1 ♂ (ZMA 101046).

As regards the early-described forms, *Rivulus urophthalmus* is one of the ill-defined ones, and needs thorough examination. Owing to the kindness of Dr. TREWAVAS I have been able to include data taken from the types. Most samples to hand have been identified by Dr. BOESEMAN as *urophthalmus*, but I have found it justifiable to consider revaluation of the forms *stagnatus* and *lanceolatus*, both from British Guiana, which are usually synonymized with it. Many of the present specimens agree with the original description of *stagnatus*, rather than with *urophthalmus*. All forms are no doubt very closely related, and I can hardly believe them to represent more than one distinct species; yet *lanceolatus* is most peculiar in its very low circumpeduncular scale count, and its quite different caudal fin.

There appears to be a constant difference between the specimens referred to *urophthalmus* proper and the *stagnatus* form as regards predorsal length and number of circumpeduncular scale rows, but the variation may be due to local circumstances. Since it is unlikely that *stagnatus* is anything other than a geographical representative of *urophthalmus*, it is equally unlikely that more than one of these forms occurs near Paramaribo.

A certain degree of hybridization (perhaps in all samples) with *holmiae* from the same vicinities might have caused the deviation from the normal type in the direction of *stagnatus*.

As regards *lanceolatus* I believe EIGENMANN (1909, 1912) was perfectly right in thus naming his aberrant specimen; two of my specimens from the Lucie river fully agree with his description and diagnosis, in combination with data from the excellent photograph of the type.

b. Discussion of the *urophthalmus* samples

The last column of table 3 refers to the photographs of the specimens in the *urophthalmus* samples. Fig. 26 (and pl. Ia) represent a normal regular pattern of this form, as seen in all specimens listed in table 3 except the aberrant specimens discussed below.

I should not have noticed any probable hybridization if deviations in the frontal pattern in some of the specimens had not attracted my attention. At present these irregularities seem to be the only means of recognizing specimens of probably hybrid origin. I was unable to recognize specimens of probably hybrid origin from the meristicals in table 3. In the case of the present aberrant specimens some deviation from the average could be traced afterwards.

The first aberrant specimen (ZMA 100447, 39.4 mm, ♂, from Paramaribo, pl. Ib) shows a pattern with, on the left side, scale *d* fully exposed (as in *holmiae*), while on the right side scales *d* and *e* seem to have struggled for supremacy, as *d* is checked halfway in a notch of *e*. The specimen differs from *urophthalmus* in having rather high scale counts, especially in the lateral series (42, as opposed to an average of 38), very much as in *holmiae*.

The second specimen (RML 18463, 34.6 mm, ♂, from Paramaribo, pl. Ic) is likewise hardly distinguishable from *urophthalmus* except in the peculiar way in which the scales are embedded. They are covered with a rather thick layer, which forms ridges and furrows at the borders of the exposed portions of the scales. I have only found a similar situation in a specimen of *marmoratus* from Curaçao (1958a), and in some smaller specimens of *holmiae* from Paramaribo. It might be due to the method of preservation. Anyhow, I am not able to ascribe any significance to it at present.

The third aberrant specimen (RML 18464, 26.7 mm, ♂, from Paramaribo) also

TABLE 3

Proportion rates in 1000ths of the standard length, and counts, of the samples referred to the *urophthalmus* forms. – The figures in parentheses in front of the localities relate to the map of Suriname, fig. 24. The figures in the last column relate to the illustrations. Data in *italics* have been taken from original illustrations.

Forms, authors and samples	mm st.l.	sex	D	A	prdl	pral	head	dpth	dcp	snt	eye	iob	scales			Plate
													lat/tr	prd	cpcf	
urophthalmus, Pará	38–52	—	6–7	9	780	620	222	182	?	55	60	110	38+?/11	?	?	—
GÜNTHER, 1866	37.5	♂	8	—	746	640	252	187	134	—	—	—	35–36/?	—	—	—
TREWAVAS, 1955, from types [1])	37.0	♀	8	12	797	675	257	203	134	—	—	—	38/?	—	—	—
(10) Paramaribo																
ZMA 100447	41.3	♀	7	13	780	640	236	212	143	49	75	99	36+2/10	28	18	—
	39.4	♂	8	13	775	630	226	203	134	40	69	106	42+3/9	30	17	Ib
	37.8	♂	8	13	761	610	219	191	130	34	69	90	40+2/10	33	18	—
	36.8	♀	?	13	782	633	235	202	135	41	63	110	34+3/9	31	17	—
	34.2	♀	7	13	771	599	223	192	133	44	73	108	38+3/9	30	18	—
	32.0	♂	7	13	780	623	201	206	148	31	66	115	37+2/10	29	18	—
	29.4	♂	7	13	774	628	242	192	146	34	78	85	39+3/9	28	17	—
RML 18463	36.9	♀	7	12	788	622	239	198	124	52	68	132	37+2/10	29	18	—
	34.6	♂	7	12	797	621	219	202	126	54	64	135	37+3/10	29	18	Ic
RML 18464	30.7	♂	8	12	788	632	238	202	127	56	65	132	35+4/9	29	17	—
	26.7	♂	8	11	786	636	232	195	135	49	75	124	37+3/9	30	18	—
	20.9	♂	8	12	786	650	248	?	?	?	?	?	34+4/9	29	17	—
(?) no locality																
RML 18511	29.9	♀	7	13	796	640	258	187	143	57	72	128	38+3/10	28	18	—
stagnatus, Christianburg, Br. G.																
EIGENMANN, 1909,	41	♂	7	11	*812*	*630*	220	182	*140*	*30*	*65*	?	42+3/9	30	*16*	—
types	46	♀	6	11	*805*	*625*	222	180	*140*	*30*	*65*	?	43+3/10	30	*16*	—
TREWAVAS, 1955,	28.8	♀	7	13	796	625	268	196	125	—	—	—	37+?/?	—	16	—
from cotypes [1])	25.5	♂	7	13	834	608	274	216	137	—	—	—	37+?/?	—	16	—
(7) Cable station																
RML 18425	31.7	♀	7	12	818	642	231	202	123	44	66	113	45+3/10	35	16	Id
	30.7	♀	7	11	822	639	255	189	117	43	77	117	44+2/9	34	16	—
	23.2	♂	7	11	815	631	238	200	124	52	79	111	43+3/9	33	16	—
(12) Langa Sula																
RML 18426	36.8	♀	8	12	800	636	250	182	125	49	63	133	41+3/10	32	16	Ie
(11) Post Groningen																
RML 18465	25.9	♀	7	11	799	630	270	223	141	71	86	141	37+3/9	29	16	If
	18.9	♀	6	11	789	618	265	?	?	66	88	155	34+4/10	27	15	—
(10) Paramaribo																
RML 20-2-53	39.2	♂	7	13	800	642	263	191	123	52	64	102	46+3/9	33	16	—
	37.8	♀	7	13	810	648	222	189	127	53	61	116	43+4/9	32	16	—
	37.1	♀	7	13	797	646	218	186	114	51	79	118	42+3/9	31	16	—
	33.7	♀	8	13	820	625	226	190	121	53	62	112	43+4/10	32	16	—
RML 1-4-53	29.7	♂	7	12	782	654	236	178	128	47	74	120	41+3/10	30	17	—
RML no number	31.1	♂	9	13	820	643	257	206	132	55	68	145	40+3/10	30	16	—
	17.9	juv	9	12	815	659	249	201	115	35	87	?	39+?/10	30	16	—
	17.3	juv	8	12	823	670	257	180	123	39	95	?	37+2/9	29	16	—
ZMA 100434	50.0	♂	9	13	800	664	232	238	150	48	72	132	40+4/11	29	16	—
ZMA 100438	54.0	♀	8	13	821	666	249	222	148	43	67	129	39+3/10	30	16	Ia
lanceolatus, Rockstone, Br. G.																
EIGENMANN, 1909	—	—	7	13	*800*	*650*	222	*200*	*110*	*40*	60	?	42+*4/9*	*30*	*14*	—
(13) Lucie river																
RML 18319	28.8	♀	7	12	800	632	195	181	108	28	59	134	45+4/9	32	14	Ig
	25.8	♂	7	12	822	635	197	182	119	26	56	133	43+4/9	32	14	—

[1]) In a letter (August 17, 1955) Dr Trewavas supplied me with these data, taken from the types of *urophthalmus* and cotypes of *stagnatus*. There are 22 scales round the body in two type specimens of *urophthalmus;* 24, 26, and 28 in three others; 26 and 28 respectively in the cotypes of *stagnatus*.

shows all the characters of *urophthalmus*, except that the occipital pair of scales lies under instead of over scale *b* of the pattern. This situation is normal in *breviceps*, and *marmoratus*, and also occurs in several specimens of *harti* and *holmiae*.

The next three aberrant specimens fall within the taxonomic limits of *stagnatus*, but correspond with *urophthalmus* in general appearance and colouration. In the home aquarium I observed several specimens of this *stagnatus* form, where they could not be distinguished from *urophthalmus* proper, even in behaviour. They mated freely with *urophthalmus*.

The first of these *stagnatus* specimens (RML 18425, 31.7 mm, ♀, from Cable station pl. Id) is asymmetric in pattern, being *urophthalmus* on the left side, and corresponding to *holmiae* on the right side. *Rivulus holmiae* influences probably caused the higher meristicals throughout the entire sample.

The second specimen (RML 18426, 36.8 mm, ♀, from Langa Sula, pl. Ie) is like the preceding one, except that here the left side corresponds to *holmiae* (the fully exposed scale *d* is missing, but its impression is still clearly visible), whereas the right side is *urophthalmus*.

The last specimen (RML 18465, 25.9 mm, ♀, from Post Groningen, pl. If) has the normal regular pattern typical of *urophthalmus*, and most of its characters, but is strikingly different in the high proportion rates of snout, eye, and interorbital width, and the head. In these respects it could be *holmiae*.

In conclusion it may be said that hybridization of the various samples of the *urophthalmus* series with (probably) *holmiae* is obvious. We shall now have to see what Suriname *urophthalmus* and *holmiae* look like.

Suriname *urophthalmus* can be recognized by the *e*-type pattern of the frontal scalation, which is as in fig. 26, with scale *b* laterally covered by the scales *cc'* and the occipital pair. Scale *g* has a narrow anterior and broad posterior exposed portion. Any deviation from this normal pattern, which is quite symmetrical, is to be ascribed to interbreeding with *holmiae*.

In table 3 I have listed a sample from the Lucie river (locality 13 in fig. 24), belonging to the *urophthalmus* series and agreeing in detail with Eigenmann's description of *lanceolatus*. The two specimens concerned show the typical *urophthalmus* frontal pattern, differing from both *urophthalmus* and *stagnatus* in the low circumpeduncular scale count. Furthermore, these two specimens differ strikingly from all others in their peculiar caudal fin and its basal scalation (cf. pl. Ig). I must disagree with Regan (1912), who synonymized *lanceolatus* with *urophthalmus* on account of "the different form of the caudal to be only due to the fact that it is less expanded". It is quite clear that this fin is unlike the more or less broadly rounded fins in the other specimens. Moreover, the scalation on the basal part of the fin is also quite different. If *lanceolatus* should be referred to *urophthalmus* s.l., as is indicated by the various features it has in common with that form, it surely deserves subspecific rank.

(2) The presumed *holmiae* hybrids agree in most respects with *holmiae* (Suriname form), and differ especially from the hybrids discussed before in general appearance, and particularly in the frontal pattern. There is obviously a difference between the hybrids in a *urophthalmus* population and those in a *holmiae* population, and therefore for the present I shall refer to these hybrids as *urophthalmus* × *holmiae* in the first case, and *holmiae* × *urophthalmus* in the second.

c. Material of forms included in Suriname *holmiae*

The following samples have been referred to *holmiae*, despite some irregularities.
CABLE STATION, Geijskes, 21–28.IX.1938, 8 ♂♂, 3 ♀♀ (RML 18255–57); RAILROAD KM 106, Geijskes & Creutzberg, 22.IV.1949, 16 ♀♀ (RML 19499); NASSAU MOUNTAINS, km 3.6 in creek, Geijskes & Creutzberg, 11.III.1949, 1 ♂, 4 ♀♀ (RML 19436); Geijskes & Creutzberg, 21.II.1949, 1 ♂ (RML 19458); creek, Geijskes & Creutzberg, 15.III.1949, 62 ♂♂, of which 55 half decayed (RML 19516).

d. Discussion of the *holmiae* samples

Material of *Rivulus harti* from the island of Margarita is referred to *holmiae* by SCHULTZ (1940, p. 90), whereas specimens of Suriname *holmiae* have been referred to *R. harti* by BOESEMAN (1952, p. 194).

As I have been able to show (1958a), *holmiae* does not occur on Trinidad or Margarita, or any of the other islands, and *harti* does not occur in British or Dutch Guiana.

The samples enumerated above and listed in table 4 have the frontal pattern outlined in fig. 27. It is a *d*-type pattern, built up from the same scales as in *urophthalmus* (cf. fig. 26). The scales are again enlarged, the lateral pairs covering the midrow scale margins almost entirely. Midrow scale *b* is, however, exposed posteriorly, overlying the occipital pair. This situation is different from that found in *urophthalmus*, where the occipital pair covers the lateral apical edges of scale *b*. The rather great essential difference between these two patterns is obvious from the outline sketches and photographs (plate II).

The frontal pattern in *holmiae* is rosette- shaped and regular, and the scales are generally well imbricated in a solid slime-skin, which accentuates the exposed margins in forming tiny ridges. The central scale *a*, which covers the pineal organ, is very thin and translucent, in life showing the 'third eye' as a whitish spot.

In plate II, photographs are given of the frontal patterns of 1 normal and 8 aberrant specimens of *holmiae*, the latter probably indicating various phases of interbreeding with *urophthalmus* and (?)*waimacui*. The specimens in table 4 have been referred to *holmiae* more because they look like this species (see fig. 28) than on account of morphological features.

The first sample, RML 18255–57, originally consisted of 22 specimens, 11 of which have been provisionally referred to *waimacui*, v.et. The other 11 can be classified in two groups.

The first group (first 3 specimens of table 4, 2 ♂♂ and 1 ♀) readily fall within the limits of typical *holmiae*, apart from their greater interorbital width. This broader interorbital is, incidentally, a remarkable feature in all Suriname *holmiae*. The largest male specimen (65.0 mm) shows a normal pattern like the one illustrated in fig. 27. The second male and the female differ slightly, and show the same fine regular *holmiae* pattern (pl. IIb), except that the occipital pair overlies scale *b* instead of lying under it. This may be the result of *urophthalmus* influence. The colour pattern is much as in *holmiae;* males show a purplish caudal with pale upper and lower margins, females have a definite caudal ocellus.

The second group, of 5 specimens, has a normal *holmiae* frontal pattern, except as regards the 45.3 and 43.3 mm males, which have an asymmetric pattern as illus-

TABLE 4

Proportion rates in 1000ths of the standard length, and counts, of the samples of Suriname *holmiae*. – The figures in parentheses before the localities refer to the map of Suriname, fig. 24. The figures in the last column refer to the illustrations. Data in *italics* have been taken from original illustrations.

Forms, authors and samples	mm st.l.	sex	D	A	prdl	pral	head	dpth	dcp	snt	eye	iob	scales			Plate
													lat/tr	prd	cpcf	
holmiae, Holmia, Br. G. EIGENMANN, 1909	–	–	8–10	15–17	*750–790*	*620–640*	220–250	200	*135*	60–70	60–70	100–110	43–44/9–10	29–33	*18–20*	–
(7) Cable station RML 18255–57	65.0	♂	10	17	763	600	241	248	129	55	86	137	39+4/11	30	20	–
	50.3	♂	9	16	751	601	254	225	130	59	74	130	42+3/11	30	20	IIb
	34.6	♀	10	17	770	626	282	193	113	58	69	138	41+5/11	31	19	–
	45.3	♂	10	16	772	630	260	216	130	57	84	136	47+3/10	34	18	IIc
	43.8	♀	9	16	760	610	270	205	116	64	89	133	49+4/11	36	19	–
	43.3	♂	10	16	750	598	263	209	131	46	70	138	49+2/11	37	19	–
	41.4	♂	9	16	752	620	262	193	125	51	75	130	47+5/11	30	17	–
	39.7	♂	10	16	756	607	252	211	131	55	65	136	46+4/11	38	18	IIa
	52.7	♀	10	17	750	611	250	225	135	62	73	151	48+4/12	35	18	–
	46.9	♂	11	15	732	593	240	214	122	47	77	132	48+3/11	35	19	IIe
	44.6	♂	11	15	773	622	245	207	128	42	74	140	46+4/11	30	20	IId
(8) Railroad km 106 RML 19499	47.4	♀	10	17	760	622	263	196	117	62	65	135	46+3/11	34	16	IIf
	31.2	♀	10	17	763	616	248	207	109	58	62	141	47+2/11	31	16	–
	24.5	♀	10	15	761	623	251	204	111	57	66	137	44+3/10	31	15	–
	20.0	♀	9	16	763	625	248	198	104	63	69	132	47+3/10	32	15	–
	33.8	♀	10	16	760	610	281	237	127	68	83	130	46+3/11	36	18	–
	33.2	♀	10	16	769	614	265	218	131	71	79	125	48+3/11	34	18	IIg
	28.2	♀	10	16	760	620	272	242	131	70	86	127	44+3/11	32	18	–
	27.4	♀	10	15	754	615	281	244	131	65	86	134	46+2/11	34	18	–
	25.0	♀	10	16	761	616	278	222	129	69	83	131	48+3/11	37	18	–
	23.2	♀	10	15	764	610	267	241	141	68	84	130	46+3/11	36	17	–
	22.7	♀	10	17	760	617	267	233	117	72	78	128	45+3/10	34	18	–
	21.4	♀	10	16	762	621	260	251	?	71	77	129	48+4/11	36	18	–
	19.2	♀	10	16	770	613	?	216	?	?	?	?	47+2/11	32	18	–
	18.6	♀	9	16	761	628	?	208	?	?	?	?	45+2/11	34	?	–
	14.9	♀	10	16	762	617	?	214	?	?	?	?	46+3/11	37	18	–
	14.2	♀	10	16	764	610	?	232	?	?	?	?	44+2/11	36	18	–
(9) Nassau mountains RML 19436	45.4	♂	11	17	735	603	253	205	117	53	73	121	38+3/11	29	17	IIh
	31.1	♀	9	16	736	606	263	224	125	48	96	128	39+3/11	28	17	–
	29.4	♀	10	16	734	604	276	204	125	57	82	125	39+2/11	30	18	–
	27.8	♀	10	17	734	600	273	195	119	54	90	113	39+3/11	28	17	–
	24.3	♀	10	16	732	604	269	201	117	55	89	118	39+3/11	29	17	–
RML 19458	53.6	♂	10	18	738	592	252	195	122	69	73	136	46+4/10	31	16	–
RML 19516	51.3	♂	11	17	720	585	?	?	?	?	?	?	43+3/10	30	?	–
	51.0	♂	11	17	758	612	266	208	119	65	74	135	44+6/11	35	17	IIi
	49.8	♂	11	17	746	609	248	198	123	66	67	135	45+4/10	32	17	–
	46.7	♂	11	16	736	598	261	200	122	65	70	129	45+2/11	29	17	–
	41.7	♂	11	17	728	586	255	198	118	59	66	119	41+4/11	33	17	–
	39.4	♂	11	17	735	604	255	206	123	67	69	120	44+3/11	34	17	–

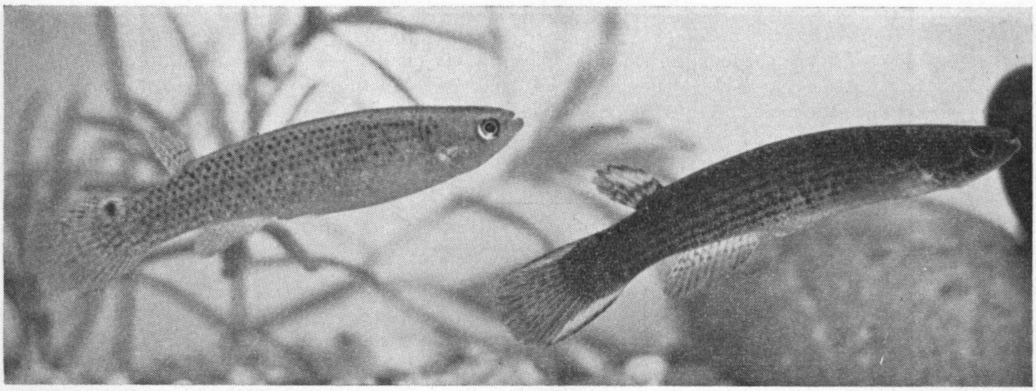

Fig. 28. A pair of *Rivulus holmiae* from Suriname district. – Photograph of living specimens by G. J. M. TIMMERMAN, reproduced through courtesy of 'Het Aquarium'.

trated in pl. IIc. The only irregularity is the exposed portion of scale *b*, which, in the 43.3 mm male, is just the other way round, i.e. the left occipital scale covers scale *b*, not the right one as in the photo of the 45.3 mm specimen. All 5 specimens in this group have a relatively high lateral scale count; both sexes resemble *holmiae*. The smallest specimen, the 39.7 mm male, is an example of the perfect frontal pattern found in Suriname *holmiae* (see fig. 27 and pl. IIa).

The third group of specimens resembles *holmiae*, except, again, in the high lateral scale count; the frontal pattern of the 52.7 mm female is quite normal, those of the two other specimens are illustrated in pl. IId. The general shape of these patterns is typical of *holmiae*, but with scales *ee'* fully exposed instead of *dd'*. Slight aberrations in the position of the occipital scales again point towards probable *urophthalmus* influences. In the 46.9 mm ♂ specimen, scales *d* and *e* of the left side seem to have struggled for supremacy, and receive each other in a notch (pl. IIe).

The Railroad km 106-sample, RML 19499, oddly enough, consists of females only, or at any rate of specimens showing external female characteristics (caudal ocellus, etc.). The sample comprises two groups.

Four females have normal *holmiae* morphological characters, with high lateral and rather low circumpeduncular scale counts. The frontal pattern (pl. IIf) is regular *holmiae*, but the lateral scales *ee'* meet dorsally, interrupting the midrow of unpaired scales.

The other twelve females have larger heads, greater depths, larger eyes, and again rather high lateral scale counts. In all cases the anal and caudal fins have a black margin. The frontal pattern (pl. IIg) resembles that of *holmiae* in general appearance, despite its seeming difference. It is, however, a *d*-type pattern, with an extra lateral pair interpolated between the regular pairs *cc'* and *dd'*, and is quite distinct from a regular *e*-type pattern (cf. fig. 26).

The next three samples originate from the Maroni district, and differ consistently from the preceding Suriname-district samples in having a shorter predorsal and preanal length, smaller depth of body, smaller snout, and narrower interorbital.

The first sample, RML 19436, resembles *holmiae* in frontal pattern and other features; the only male has a pale lower margin to the dark caudal fin, the anal is dark-edged; in the females, the outer margin of the caudal is blackish, and the lower edge of the anal dark. Although, as has been said, the frontal pattern (pl. IIh) is *holmiae*, the male specimen again shows an irregular occipital overlap of scale *b*. In all three samples the exposed portion of scale *g* is remarkably broad, probably indicating interbreeding.

The single specimen of RML 19458 is a perfect *holmiae*. It has 6 rows of flecks on the dorsal fin, and the caudal fin is speckled, with pale intramarginal stripe and black outer margin on the lower edge.

Finally, sample RML 19516 is of pure *holmiae* strain, except for the 51.0 mm male (pl. IIi), which shows the probable affinity of this sample with some *urophthalmus* or (?)*waimacui* population. The non-*holmiae* pattern in the one male specimen is quite regular, even in the occipital region, except that scales *ee'* are fully exposed, instead of *dd'* as in *holmiae*. This is the pattern found in the presumed *waimacui* specimens.

The coloration in the Suriname *holmiae* is much as in this last fine sample, and agrees with the photograph, fig. 28. The body is brownish, darker in the males, with 6 to 8 longitudinal rows of carmine dots. The caudal is dark purplish-brown with white outer margin; dorsal and anal also have a pale margin. Females have a definite caudal ocellus.

(3) The last group of probable hybrids consists of samples and specimens, some of which have been referred to *waimacui* as first described from British Guiana. However, they differ constantly from that form in having much greater numbers of dorsal and anal rays (see table 5), greater head and body depth, larger eye and interorbital width. We shall have to decide whether or not these important differences can be ascribed to distributional (local) variation. In general appearance these hybrids certainly resemble *waimacui* proper, in spite of the possibility that Suriname *waimacui* might be just a regular hybrid population of *holmiae* and *urophthalmus*.

e. Material of forms included in Suriname *waimacui*

Table mountain, Geijskes, 6.XI.1943, 2 ♂♂, 4 ♀♀ (RML 18427); same data, 3 ♂♂, 8 ♀♀ (RML 18255–57); Gold Placer, W. C. van Heurn, XI.1911, 2 ♀♀ (RML 18462).

f. Discussion of the presumed *waimacui* samples

Some of the *waimacui* samples have been referred to *holmiae* by Boeseman (1952, p. 192), but they all differ sharply from that form in the much higher transverse number of scales, (cf. graph, fig. 30). Most remarkable, however, is the frontal pattern in these presumed *waimacui* specimens (cf. fig. 29, compare with fig. 27). All specimens listed in table 5 have a pattern as in pl. IIIe, which is thus quite unlike the pattern of *urophthalmus* (fig. 26) and of *holmiae*. On the other hand, the construction of this *waimacui* pattern is much the same as in *holmiae*, the only real difference being the fully exposed pair of scales, which is *dd'* in *holmiae* and *ee'* in *waimacui*. Since *ee'* is also the pair that is fully exposed in *urophthalmus* it seems at first sight logical to ascribe a certain influence of this form to the pattern now found in our

TABLE 5

Proportion rates in 1000ths of the standard length, and counts of the samples referred to Suriname *waimacui*. – The figures in parentheses before the localities refer to the map of Suriname, fig. 24. The figures in the last column refer to the illustrations.

Localities and samples	mm st.l.	sex	D	A	prdl	pral	head	dpth	dcp	snt	eye	iob	scales lat/tr	scales prd	scales cpcf	Plate
waimacui, Shrimp Creek, Br. Guiana EIGENMANN, 1909	88	–	8–9	11–12	750	650	220	180	125	43	55	100	46–52/11	33–38	19	–
(14) Table Mountain RML 18427	40.0	♀	11	18	750	691	260	201	110	72	78	120	50+3/11	35	20	IIIe
	36.0	♂	10	17	750	631	257	195	122	–	–	–	50+2/11	34	19	IIIf
	32.4	♂	10	17	742	621	251	198	127	–	–	–	49+3/11	35	19	–
	24.0	♀	10	17	765	684	–	–	–	–	–	–	50+2/11	32	19	–
	14.3	juv	10	16	748	634	–	–	–	–	–	–	49+2/11	33	19	–
	13.7	juv	10	16	737	652	–	–	–	–	–	–	47+3/11	30	18	–
RML 18255–57	53.2	♀	11	16	731	623	242	240	131	51	66	124	46+2/12	33	21	IIIg
	51.4	♀	10	16	730	615	264	240	138	58	74	135	43+3/12	30	19	–
	44.4	♀	11	17	760	616	272	241	132	68	78	134	46+5/13	33	21	–
	41.5	♀	11	15	721	606	252	230	123	61	77	141	43+3/14	29	21	–
	34.0	♀	11	18	714	612	265	221	118	53	91	171	43+3/11	30	19	–
	27.8	♀	11	18	751	590	260	241	126	51	90	151	45+3/11	30	18	–
	26.9	♀	12	17	735	602	257	227	115	45	93	150	43+?/11	29	18	–
	18.8	juv	11	17	734	662	282	–	–	48	106	140	42+?/11	29	16	–
RML 18255–57	37.8	♂	12	16	717	646	264	252	127	62	80	113	39+4/11	28	18	–
	25.8	♂	12	16	680	583	255	236	120	–	–	–	39+4/12	29	19	–
	24.2	♂	12	15	–	597	–	–	–	–	–	–	40+?/11	30	19	–
(2) Gold Placer RML 18462	45.9	♀	10	15	742	590	247	178	118	48	72	116	52+4/11	37	20	–
	42.0	♀	10	15	740	595	252	183	123	52	77	123	50+5/11	38	20	–

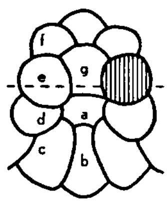

Fig. 29. Typical frontal pattern of Suriname *waimacui;* see also plate IIIe–g.

waimacui. There is, however, another possibility, i.e. a hybridization of some *breviceps* form with *holmiae;* the *ff'* pattern of *breviceps* × the *dd'* pattern of *holmiae* might also result in the *ee'* pattern of *waimacui*. There is, moreover, a close resemblance between *breviceps* and *waimacui* in several characters (cf. table 2). Our presumed *waimacui* is roughly like *holmiae* in fin ray and scale counts, and like *breviceps* in most proportion rates; the frontal pattern is intermediate.

Samples RML 18427 and 18462 answer rather well to the diagnosis of *waimacui* from British Guiana (cf. table 5), and though there is an indication of hybridization in the frontal pattern and in some other characters in some of the specimens, they all resemble this form rather than *holmiae*. The colouration in particular, is perfectly in agreement with that of typical *waimacui;* sides with rather large dark blotches, males with light lateral band bordered above and below by blackish stripes, females with dark lateral band bordered by pale streaks, no caudal ocellus in either sex (just as in the *breviceps* complex). The specimens in sample RML 18462 (2 females ?), have a pale blotch on the upper part of the tail root, in the place where the caudal ocellus is situated in *holmiae;* the caudal fin is subtruncate, with basal scalation extending about halfway up the fin; dorsal, anal, and caudal in males have a broad, dark outer margin, often extending halfway over the fin; dorsal in females with 4 rows of vertical dots, caudal shows scattered flecks, anal is dark-edged but otherwise plain.

g. Discussion of hybridization in Suriname Rivulids

The graphs below (fig. 30) show the range and means of the diagnostic morphological characters of 10 specimens of each of the three forms *urophthalmus*, *holmiae*, and *waimacui*. In Suriname the forms *urophthalmus* and *holmiae* have only been captured together, at any rate, in one locality, Cable station (7 in map, fig. 24).

From the preceding discussion, and their different habitats and ethology, we may conclude that they are distinct species. *Rivulus urophthalmus* ranges from Pará along the coastal lowlands of the Guyanas to the Essequibo river. The records of Peruvian *urophthalmus* (Myers, 1927, and Allen in Eigenmann & Allen, 1942) may or may not relate to this species. Anyhow, *urophthalmus* has not yet been found in the Guyanas, above the 200 m contour level). *Rivulus holmiae* is not a lowland form; at

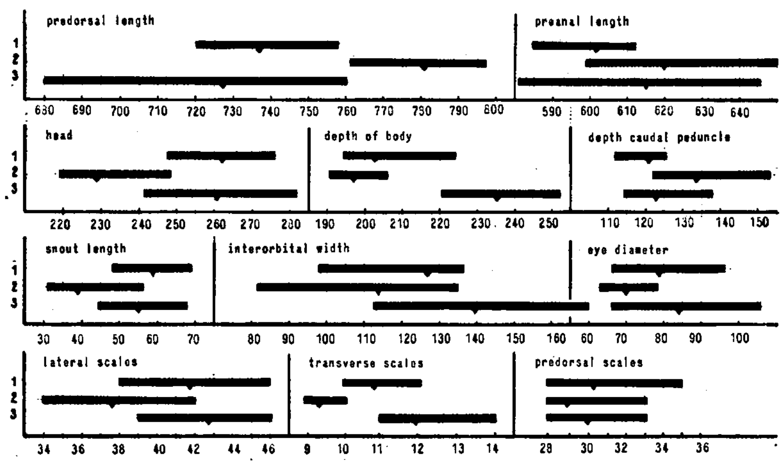

Fig. 30. The range and means of the important morphological characters in Surinam *Rivulus* in which hybridization has been observed. 1 = *holmiae*, 2 = *urophthalmus*, and 3 = *waimacui*. The figures in the abscis are 1000ths of the standard length. The graphs are based on 10 regular specimens of each form (*holmiae* from samples RML 19436, 19458, and 19516 (first 4 specimens), *urophthalmus* from samples ZMA 100447 (except first and fourth specimen), RML 18463, and 18464; *waimacui* from samples RML 18255–57 See also tables 3, 4, and 5).

any rate it has not yet been captured below the 200 m level, but has been found in the region between the last watersheds and the 500 m level.

The distribution in Suriname waters, according to the elevation of the sampling places and their distance from the coast, has been summarized in table 6. From this roughly sketched picture (based on a rather small number of samples) it may be provisionally concluded that the *breviceps* series (*agilae*, *breviceps* and *frenatus*) inhabits waters from quite near the coast (Wia Wia, locality 1 in map, fig. 24) to an elevation of about 250 m above sea-level, and at a distance from the coast of up to about 150 km. This complex is therefore apparently confined to swiftly flowing to stagnant waters; it is obviously capable of tolerating brackish water, but also occurs in fresh water. In most habitats or water systems it is found together with *urophthalmus* below the 200 m level, and with *holmiae* above the 200 m level. Hybrids may therefore result from both, but must be considered accidents, in view of the differences in ethology.

Rivulus urophthalmus is the strictly lowland species which ranges farthest inland, i.e. up to about 300 km from the coast, along the Corantyne river (e.g. the *lanceolatus* subspecies from the Lucie river, locality 13 in map, fig. 24). Most of the specimens from above the 100 m level are referable to the *stagnatus* form (cf. table 3). The zone of hybridization with *holmiae* is in the 150–200 m level region.

Rivulus holmiae has only been secured in localities at 100 to 150 km from the coast, at an elevation of 150 to 550 m above sea-level. It is a hill-stream species, and hybridization may occur with both *urophthalmus* (in the lowlands) and *breviceps* (in lowlands and lower hill-streams).

TABLE 6

Distribution of *Rivulus* in Suriname according to elevation of sampling places and their distance from the coast.

Elevation above sea-level	less than 100 m	100 to 200 m	200 to 250 m	250 to 500 m	above 500 m
breviceps series	———	———	———		
urophthalmus s.l.	———	———			
holmiae		———	———	———	———
?waimacui		——— 1)	——— 2)		———

Distance from coast	less than 50 km	50 to 100 km	100 to 150 km	150 to 200 km	200 to 300 km
breviceps series	———	———	———		
urophthalmus s.l.	———	———	———	———	———
holmiae			———		
?waimacui		——— 1)		——— 2)	———

1) sample RML 18462, *waimacui* in appearance, but may be a hybrid of *breviceps* × *urophthalmus* (locality 2 in map, fig. 24).

2) specimen with *waimacui* frontal pattern, referred to *holmiae*, may be a hybrid of *breviceps* × *holmiae* (locality 9 in map, fig. 24).

The presumed *waimacui* is found in three places at three different distances from the coast, and is but fragmentarily known. It looks as if the Suriname *waimacui* is a combination of hybrids that frequently result in various places (perhaps also in British Guiana) from accidental fertilization of eggs of *breviceps*, *urophthalmus* and *holmiae* by each other.

(*1*) We have seen that the samples of *urophthalmus* from the Suriname lowlands hardly show any deviation from the normal regular type; in other samples, from Paramaribo and district, *holmiae* influences yield an irregularity percentage of only 4 (1 specimen out of 23 shows a *holmiae* frontal pattern on the left side only). In these habitats the water is slightly oligohaline.

In samples from a little higher elevation this *holmiae* influence is greater, and, though the samples are small, the percentage may be estimated at about 30 (cf table 3 and discussion of *urophthalmus* samples).

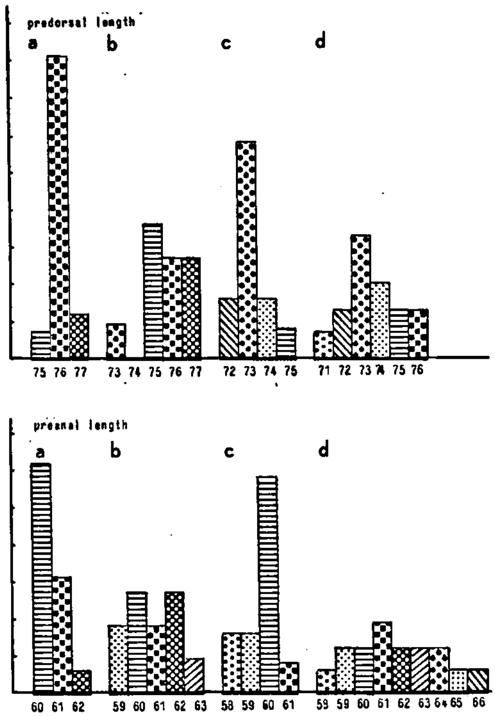

Fig. 31. Percentage frequencies of predorsal and preanal lengths in Suriname *Rivulus*. Comparison of samples of *holmiae*, a = RML 19499, b = RML 18255–57, and c = RML 19436 (cf. table 4), and d = *waimacui*, all specimens of table 5. – Proportion rates in the graphs are expressed in 100ths of the standard length (see map, fig. 24 for localities).

(*2*) The ***holmiae*** samples from the watershed region, for instance Cable station, show a ***urophthalmus*** influence of about 18% (in 2 of 11 specimens the scales *ee'* are exposed, as in ***urophthalmus***). In the Rail-road km 106 sample, this figure is about 68% (11 of 16 specimens show ***urophthalmus*** influences). These samples are, of course far too small to give a proper picture of the situation, but the percentages may give a preliminary idea, and will undoubtedly be helpful in estimating the proper zone of hybridization.

The hybrids of ***urophthalmus*** × ***holmiae*** are not perfect intermediates, but show either a ***urophthalmus*** or a ***holmiae*** configuration, whilst the proportion rates and fin ray and scale counts are either as in the one or as in the other species. However, in the ***holmiae*** sample from the lowland/watershed region (Railroad km 106, RML 19499, in table 4) the characters of all specimens show a tendency to approximate more closely to ***urophthalmus*** characters, especially in predorsal and preanal lengths, and depth of caudal peduncle. The same tendency is found in the Cable station sample (RML 18255–57, table 4), but a little less so. The percentage frequencies for these characters in the samples from the presumed zone of hybridization are given in the graphs below (fig. 31). The localities of these 4 samples concerned are marked *a*, *b*, *c*, and *d* respectively (see also map, fig. 24).

(*3*) As I have already pointed out, the *waimacui* samples greatly differ, not only from the British Guiana (typical) *waimacui*, but also from each other (cf. fig. 32). These differences are so considerable that recognition of local races or subspecies would seem to be warranted, were it not for the fact that hybridization obviously plays a role here. All three samples may prove to belong to one widespread and greatly diverging population, but this seems highly improbable. The question as to whether or not hybridization is indiscriminate, and which are the parental forms, will have to be decided.

The graphs of fig. 30 show that *waimacui* (?) resembles ***holmiae*** very closely, and that the differences between *waimacui* and ***urophthalmus*** seem to be of specific nature. In fig. 32, the various ***holmiae*** samples have been compared with the *waimacui* samples (tables 4 and 5). The ***urophthalmus*** samples differ greatly in the posterior insertion of the dorsal fin (greater predorsal length); the Paramaribo samples (2 in graphs) approximate closely to the extremes of ***holmiae*** in some specimens, which are obviously of hybrid origin. The three *waimacui* samples show extreme values of so wide a range that they must be ascribed to hybridization between distinct populations or populations of hybrid nature. Even the two larger samples (8 and 9 in fig. 32) differ greatly in all three characters.

Until further sampling has been done, and larger and more samples from various localities and unexplored districts, and from the probable zone of hybridization become available for study, I think that the presumed *waimacui* samples can best be referred to hybrid populations of ***holmiae*** with either ***urophthalmus*** or ***breviceps***. They cannot be referred to *waimacui* proper, though the possibility remains that in Suriname a pure strain of British Guiana *waimacui* (admittedly, this is not a hybrid either) inhabits the region of the hill streams, and that the hybrids are a result of the meeting of this form with ***holmiae***.

A *waimacui* pattern, which has not yet been checked against that of typical *waimacui*, has also been found in the Maroni district (Nassau mountains, locality 9 in map, fig. 24), in a specimen that, as regards all other characters, could only be referred to ***holmiae***. Consequently, possible hybridization between ***holmiae*** and ***breviceps*** must also be taken into consideration, as ***urophthalmus*** does not occur so high up in the mountains.

Another remarkable point is that British Guiana *waimacui* inhabits the region below the falls, occurring together with *breviceps*, almost in the same vicinities where *holmiae* is also found, i.e. at the border of the lowlands, whereas Suriname *waimacui* is found in the lowlands, the midlands and the hills. Comparison with the types of *waimacui*, especially with reference to the frontal pattern, would be helpful in solving this problem.

From the data gathered in the tables and graphs concerning *urophthalmus*, *holmiae*, and *waimacui* populations, it is possible to deduce that certain meristics vary with elevation and latitude. Other characters do not appear to correlate with elevation or latitude. See also under 'Vertical distribution' (page 83).

From the percentage frequencies for predorsal and preanal lengths (fig. 31), dorsal and anal ray numbers (fig. 33), and predorsal and lateral scale numbers (fig. 34), it

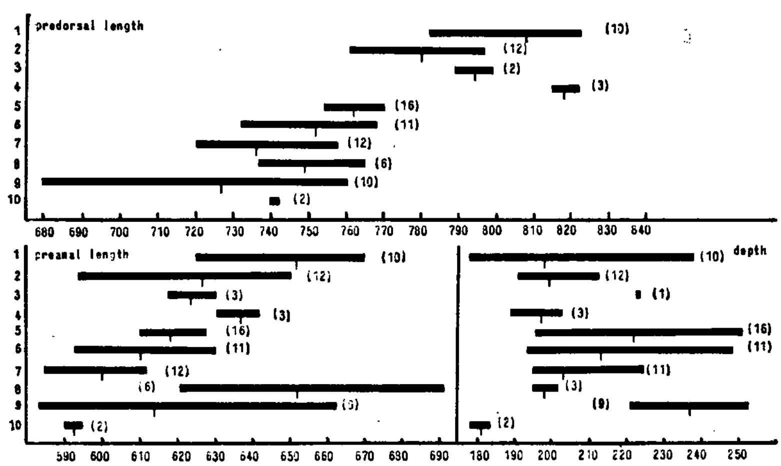

Fig. 32. The range and means of predorsal, preanal, and body depth proportion rates in 10 samples of Suriname *Rivulus*. 1–4 = *urophtalmus*, 1 = RML 20-2-53 + RML no number + ZMA 100434 + ZMA 100438, all Paramaribo (cf. table 3); 2 = ZMA 100447 + RML 18463 + RML 18464, all Paramaribo and surroundings (cf. table 3); 3 = RML 18465, Post Groningen (table 3); 4 = RML 18425, Cable station (table 3); 5–7 = *holmiae*, 5 = RML 19499, Railroad km 106 (table 4), 6 = RML 18255–57, Cable station (table 4); 7 = RML 19436 + RML 19458 + RML 19516, all Nassau mountains (table 4); 8–10 = *waimacui*, 8 = RML 18427, Table mountain (table 5); 9 = RML 18255–57, Table mountain (table 5); 10 = RML 18462, Gold Placer (table 5). – The figures in parentheses at the end of each black bar indicate the number of specimens in the sample. The figures in the abscis are proportion rates expressed in 1000ths of the standard length.

can be seen that the vertical fins are situated slightly farther backwards in the lowland specimens (the samples have been arranged from left to right, in order of increasing elevation), and also that in these specimens the number of rays in the vertical fins is less than in the hillstream specimens. The number of scale rows in predorsal and lateral series decreases with elevation, and consequently with increasing rapidity of the streams the fishes inhabit.

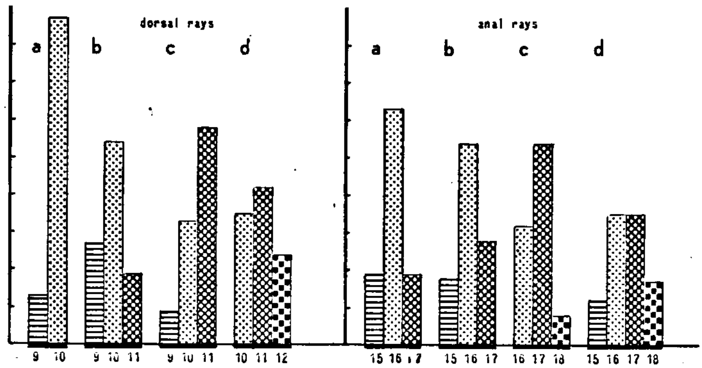

Fig. 33. Percentage frequencies of the dorsal and anal rays in Suriname *Rivulus*. Comparison of *holmiae* and *waimacui*. The samples are the same as in fig. 30. – Abscis = number of finrays.

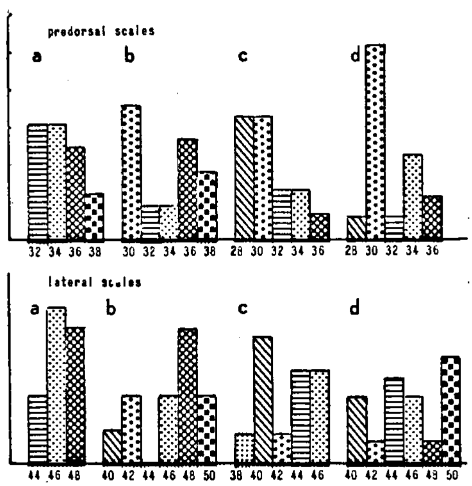

Fig. 34. Percentage frequencies of predorsal and lateral scale numbers in Suriname *Rivulus*. Comparison of *holmiae* and *waimacui*. The samples are the same as in fig. 31. – Abscis = number of scales; the figures 32, 34 and on, include 31, 33, etc. respectively.

The hybrid nature of our *waimacui* samples is again emphasized by the various graphs (figs. 30–34), particularly as regards the proportion rates of predorsal and preanal lengths. These are by far the most important characters, next to the frontal scalation pattern.

h. Conclusions from the hybrid samples

From the hybrids discussed above it may be concluded that:

a. there is every reason to ascribe most of the irregularities observed in the frontal patterns to hybridization of *urophthalmus* of the lowlands with *holmiae* of the midlands and watershed region.

b. Suriname *waimacui* specimens are not identical with British Guiana *waimacui;* they resemble the latter only in having a similar general appearance and coloration.

c. the frontal scalation pattern is a ready indication of hybridization, being invariable within populations of a distinct species.

d. the only constant morphological specific characters are the frontal scalation pattern and the general coloration of body and fins; these characters are influenced only by the interbreeding of distinct forms or species.

e. Suriname *waimacui* is apparently built up of three groups (in the samples); a lowland sample that might have been resulted from *holmiae* × *urophthalmus* or *holmiae* × *breviceps;* a lower mountain sample with indication of hybridization between *holmiae* and *breviceps;* and a higher mountain sample, obviously the result of interbreeding of a *holmiae* population with some undeterminable form (*urophthalmus*, *breviceps*, or (?)*waimacui* proper).

f. hybridization between *holmiae* and *urophthalmus* in most samples is only traceable from the irregularities in the frontal pattern.

g. from aquarium or laboratory experiments with these forms it will doubtless be possible to demonstrate the results of interbreeding. But fertilization will probably have to be artificial, since the parental species or forms will not bread freely in the case of *holmiae* × *urophthalmus*.

h. in spite of the hybrids observed, the conclusion to draw from the study is that *breviceps* and *urophthalmus* behave like distinct species; they are sympatric; *breviceps* and *holmiae* are also sympatric, and

urophthalmus and *holmiae* are morphologically different and normally reproductively isolated; they may also be looked upon as distinct species of allopatric nature. Only in the presumed zone of hybridization are they partly not reproductively isolated, and may prove to behave like subspecies.
i. waimacui from Suriname must be considered a hybrid form which, in some places, behaves like a distinct form or species.

Study of the material discussed has revealed the occurrence of at least two sympatric species in the lowlands (*urophthalmus* and the *breviceps* forms *agilae*, *breviceps* and *frenatus*), and a similar ecological combination of *holmiae* with the *breviceps* forms in the more elevated regions. The samples are too small to enable me to determine whether or not hybridization takes place only occasionally or frequently.

It will now be necessary to study the total range and geographical variation of each of the forms. For the most part the forms present a bewildering array of local populations reminiscent of the type of variation characteristic of such plastic groups as the Characids or Silurids. Since the samples available are small, and drawn from scattered localities, we may feel certain that we are dealing with distinct species. Closer study of the various forms, including observations of living specimens, leads to the conclusion that only three groups (superspecies) or evolutionary lines can be recognized in Guyana, and perhaps a fourth, if *waimacui* turns out to be a distinct species and not a hybrid form as considered here.

Three forms, *agilae*, *breviceps* and *frenatus*, show considerable intraspecific variation, and some of the differences may have a genetic basis, at least in part. Such populations may represent distinct races, or incipient subspecies or even species, but they may also result from environmental circumstances. Their status can only be clarified by thorough sampling and by study of behaviour patterns.

11. Extralimital Distribution of Suriname species of Rivulus

The preceding pages have shown that in Suriname at least three groups of forms, or species complexes, can be recognized, distinguished by the following characters, in sequence of importance:

1. the complex including the small forms, coarsely scaled, and especially typified by the *f*-type frontal pattern. Here this is called the *breviceps* complex.
2. the complex including larger-sized forms, finely scaled and with low fin ray counts, especially typified by the *e*-type pattern. This is called the *urophthalmus* complex.
3. the complex including the rather robust forms, also finely scaled, with rather high fin ray counts, especially typified by the *d*-type frontal pattern. This is called the *micropus* complex.

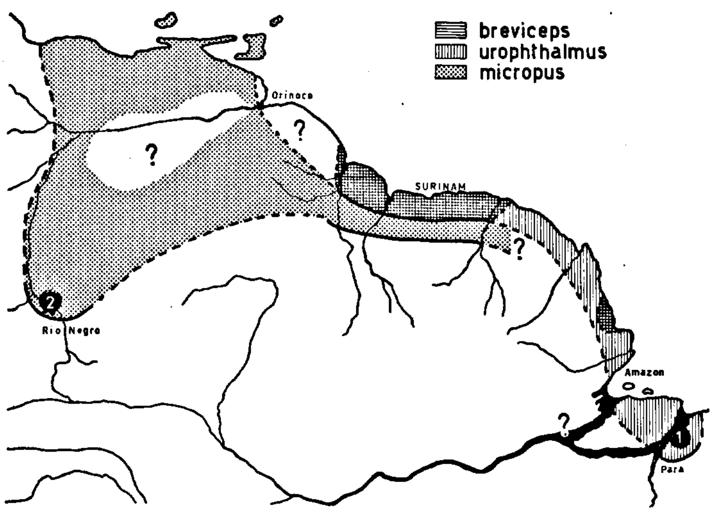

Fig. 35. Map showing the extralimital distribution of the Suriname *Rivulus* forms. The *urophthalmus* series (type locality of *urophthalmus* s.s. = 1. Pará, Brasil) apparently ranges from the eastern coast to the Guyana lowlands, and is not yet known to occur farther west than the outflows of the Essequibo in British Guiana. The *breviceps* complex almost has the same range, and may occur in the region between Carsevenne (French Guiana) and the Maroni system (boundary between Dutch and French Guiana). Both complexes are confined to the lowland regions, *urophthalmus* being apparently more salt tolerant than *breviceps*. The *micropus* complex includes forms that seem to be restricted to the hillstreams. No specimens have yet been secured in the lowlands below an elevation of about 150 m, and even in the islands they are confined to the hillregions. The sample of *micropus* studied came from Maroa on the Rio Negro, = 2.

The range of the important morphological characters for each group has already bee tabulated under 'Morphology' (p. 57 to 63), from which it can be seen that the *breviceps* complex has 30 to 35 lateral scales, and 19 to 24 predorsal scales. In both other complexes there are 35 to 49 lateral, and 27 to 37 predorsal scales. The fin ray indexes for both the *breviceps* and the *urophthalmus* complexes are about 200, against about 265 for the *micropus* complex (*holmiae*).

In conjunction with the results of the present study, including the data from the samples of *harti*, to be discussed hereafter, and pertinent data from literature, the map (fig. 35) may give a preliminary picture of the extralimital distribution of the Suriname species (complexes) of *Rivulus*.

Vertical distribution of *Rivulus*

In studying the distribution of this genus and the dispersal of the evolutionary lines, it appears to be rather important to have some indications as to the vertical distribution and the variations apparently caused by it. Table 1 gives a survey of the species names, and of the distribution of the species, and in some cases it is possible to trace the approximate elevation at which they occur. Reference to data gathered from the present material enables us to arrive at the general assumption that there is indeed a correlation between the elevation of the localities and the ratios of certain morphological characters. For instance, *holmiae* is confined to the hill streams, but the various localities are found to be situated at different elevations above sea level. And in the Suriname samples (see graphs, figs. 34–37) it appears that the number of dorsal and anal rays in *holmiae* tends to increase with a higher elevation of the localities.

If the whole genus *Rivulus* is considered as a unit, the same increase in number of the rays of the vertical fins from lowland-coastal waters towards the hill streams is found in all species. Both the *urophthalmus* and *breviceps* complexes have rather low numbers of dorsal and anal rays (6 to 9 and 10 to 13 respectively).

The species names in table 1 have been arranged in groups representing presumed

TABLE 7

Correlation between elevation of localities and their distance from the coast, and ratios of morphological characters.

Number of specimens in samples of fig. 31	dorsal rays			anal rays			distance from coast in kilometres	elevation above sea-level in metres
	variation	mean	standard deviation	variation	mean	standard deviation		
a (16)	9–10	9.95	0.002	15–17	16.00	0.040	100	100
b (11)	9–11	10.10	0.135	15–17	16.09	0.060	130	150
c (12)	9–11	10.50	0.151	16–18	16.78	0.049	130	550
d (19) [1]	10–12	10.80	0.120	15–18	16.41	0.116	250	1000

[1] The last sample, d, is the presumed *waimacui*.

complexes, based on the complexes established to accommodate the different species in the material studied. These complexes have also been indicated in the alphabetical list (p. 52–53). As regards the vertical distribution of the species included in each complex, it is found that, roughly speaking, the *breviceps* complex is confined to the borders of the Guyana plateau, i.e. the lowlands, although some forms not studied have been included. The *marmoratus* complex (cf. HOEDEMAN, 1958a) is confined to the coastal lowlands of some of the Antillean islands, Yucatan and the State of Rio de Janeiro. The *cylindraceus* record from Florida (FOWLER, 1928) no doubt relates to *marmoratus*. The *isthmensis* complex and the *urophthalmus* complex are also lowland forms, in spite of *volcanus* being found at a great elevation in an isolated volcanic lake (apparently a relic species). The three other complexes of the *cylindraceus* series, the *cylindraceus*, *elegans*, and *micropus* complexes, are confined to the hill streams. There are obviously three lines of evolution and three routes of dispersal within the genus *Rivulus*, as I shall discuss on a later page.

Horizontal distribution of *Rivulus*

The three complexes of forms found in Suriname have been named *breviceps*, *urophthalmus*, and *micropus* complex, respectively (cf. map, fig. 35). The extralimital distribution of each is indicated, in so far as it could be traced.

The *breviceps* complex should probably also include a number of species from various localities in the Amazon system. The records of *urophthalmus* and allied forms found outside the range given on map (fig. 35) are more or less doubtful. The range of the *micropus* series is apparently as indicated, though no records of it are known from the Orinoco basin proper. The records from near the coast of Venezuela and the islands of Margarita, Trinidad, and Tobago do not concern lowland populations, but populations strictly confined to hill streams. The *micropus* complex is most closely related to the *cylindraceus* series from Cuba, and the two complexes are obviously linked by the *elegans* series, ranging from Mexico to the Magdalena basin in Colombia.

The forms of this genus, the species names as listed on p. 52 and grouped together in complexes in table 1, represent three evolutionary lines, as I have said. Since I did not have at my disposal material of the other forms mentioned in table 1, the present survey and grouping should be considered preliminary, and further studies of material from outside Suriname will have to show whether or not this account requires amendment. The forms included in each group have only been placed there on the basis of the original descriptions. Future studies on relationship will need to confirm or challenge the supposed arrangement, and will also have to substantiate or contradict my conclusions regarding sympatry and hybridization in Suriname forms.

The three groups are the same as in Suriname, i.e. the *breviceps*, *urophthalmus*, and *micropus* series. However, each of the last two series has been divided into three complexes, and each of these complexes will no doubt turn out to be a geographical unit.

The *urophthalmus* series consists of the *marmoratus*, *isthmensis* and *urophthalmus* complexes. It ranges from the periphery of the total range of the genus, with the *marmoratus* complex (cf. HOEDEMAN, 1958a); the *isthmensis* complex, ranging from Central America to Peru, obviously links the *marmoratus* complex with the *urophthalmus* complex of the Guyanas and Amazonas (cf. HOEDEMAN, 1958b).

The *micropus* series comprises the *cylindraceus* complex from the hill streams of Cuba (including, for present, the form *zygonectes* from the Brazilian plateau); the *elegans* complex from Mexico to the Orinoco drainage area; and the *micropus* complex from eastern Venezuela and the islands to the Guyanas.

12. The *breviceps* Complex

The present complex is based in the first instance on the forms *breviceps*, *frenatus*, and *agilae*, material of which was available for study. The French Guiana form *geayi* is very closely related to both *breviceps* and *agilae* (cf. Boeseman, 1952, 1954).

All three Surinam forms are typified as follows:

a. caudal ocellus absent in both sexes, not even present in juveniles;
b. fishes of rather small size, not exceeding about 50 mm total length;
c. coarse-scaled forms, low scale counts;
d. a series of vertical, more or less oblique dark bars or stripes on the caudal (especially in juveniles; not always conspicuous in adults);
e. longitudinal markings or a broad lateral band often present in adults;
f. usually a rather striking difference in coloration between the sexes, most obvious in the markings of the caudal fin.

There seems to be, as yet, no reason why this complex should not be regarded as a superspecies. It is a series of morphologically defined forms (morphospecies) which are completely separated geographically, except perhaps for a slight overlap of *frenatus* and *breviceps* in the Maroni district (Nassau mountains). The latter two forms can only be differentiated by their coloration and markings; the present samples consist of but a few specimens (most of them in very bad condition), and no meristical feature is obviously distinct.

a. Material of forms included in the *breviceps* complex, Surinam samples

Identified as *Rivulus breviceps* by Boeseman:

Wia Wia, Geijskes & Creutzberg, 27.XI.1948, 1 ♂ (RML 27–11–48). Gold Placer, W. C. van Heurn, X.1911, 4 ♂♂, 3 ♀♀ (RML 18461). Maroni district, Stol, 21.XI.1951, 1 ♂ (RML 19305). Nassau mountains, Geijskes & Creutzberg, 25.II.1949, 2 ex. of which 1 half decayed (RML 19562); 1 ♀ (RML 25–2–49).

Identified as *Rivulus frenatus* by BOESEMAN:

BUSH CREEK, Geijskes, 4.XI.1942, 1 ex. (RML 18424). NASSAU MOUNTAINS, Geijskes & Creutzberg, 21.II.1949, 2 ex. (RML 19310). MARONI DISTRICT, ?, leg. Stol, 21.XI.1951, 1 ex. (RML 19311).

Identified as and referable to *Rivulus agilae:*

PARAMARIBO, surroundings, Blijdorp exp., IV.1953, 187 ex. of which only 8 were in condition for taking counts and measurements (RML 1–4–53). AGILA, rivulet between Agila and Berlijn, Suriname river, Blijdorp exp., III.1952, 2 ♂♂ (ZMA 100448); 6 ♂♂, 2 ♀♀, 18 juvs., most of the juvs. in very bad condition (ZMA 100449). ZANDERIJ, about 42 km S of Paramaribo, P. Wagenaar Hummelinck, 3.VIII.1948; 1 ♂, 1 ♀, 3 juvs. (ZMA 101058).

TABLE 8

Proportion rates in 1000ths of the standard length, and counts of the samples referred to the *breviceps* complex. – The figures in parentheses before the localities refer to the map of Suriname, fig. 24. The figures in the last column refer to the illustrations.

Localities and samples	mm st.l.	sex	D	A	prdl	pral	head	dpth	dcp	snt	eye	iob	scales			Plate
													lat/tr	prd	cpcf	
(1) Wia Wia																
RML 27-11-48	22.4	♂	9	10	724	612	277	176	125	42	71	94	32+3/10	22	16	IIIa
(2) Gold Placer																
RML 18461	29.7	♀	9	10	719	604	248	193	121	47	71	115	30+4/9	21	15	IIIb
	26.7	♂	9	12	725	617	270	218	135	49	86	112	32+4/9	22	15	–
	25.4	♂	9	12	710	613	251	–	–	47	78	–	31+?/10	21	16	–
	22.2	♂	9	11	740	622	251	225	140	36	81	140	32+3/9	21	14	–
	21.9	♂	8	12	708	609	274	228	143	51	86	145	31+4/9	23	16	–
	17.8	♀	8	11	715	614	248	–	–	39	78	118	30+3/9	22	15	–
	16.5	♀	9	11	730	625	271	–	–	42	85	–	31+2/9	23	16	–
(3) Maroni district																
RML 19305	24.7	♂	8	11	732	621	264	215	150	50	81	–	34+?/9	20	16	–
RML 19311	22.5	?	7	10	723	616	243	–	–	44	64	113	32+3/8	23	13	IIIc
(4) Nassau mountains																
RML 25-2-49	24.2	♀	8	11	737	622	266	–	–	–	–	–	30+3/9	23	14	–
RML 19310	20.2	?	7	10	730	607	272	–	–	46	74	128	32+4/9	22	13	–
	18.4	?	7	10	718	605	260	–	–	49	60	114	31+4/9	21	12	–
RML 19562	21.1	?	8	12	740	619	274	–	–	–	–	–	30+2/9	23	14	–
(6) Bush Creek																
RML 18424	18.4	?	7	10	726	608	245	–	–	36	72	110	31+2/8	24	13	–
(⊙) Agila																
ZMA 100448 (type)	28.8	♂	8	12	701	607	268	198	125	52	65	125	32+3/9	21	14	IVa,f
	29.5	♂	9	12	696	590	272	183	118	57	68	125	33+3/9	22	14	–
ZMA 100449	24.7	♀	8	11	712	604	274	194	132	50	73	119	33+2/9	21	14	IVd
	24.2	♀	9	12	713	603	267	201	119	42	65	121	32+3/9	21	14	IVb
	23.6	♂	9	12	706	598	264	168	124	63	78	128	31+2/9	23	14	–
	23.4	♂	9	12	698	601	271	173	126	51	76	107	32+3/9	21	14	IVe
	20.2	♀	8	11	702	607	258	195	120	54	78	124	35+3/9	22	14	–
	20.0	♂	9	12	708	600	261	181	130	48	69	119	32+3/9	23	15	–
	19.8	♂	9	12	708	607	267	176	127	53	57	126	33+2/9	21	14	IVc
	18.6	♂	9	12	706	603	270	169	115	50	72	123	33+3/9	22	14	–
	18.2	juv.	8	11	710	609	259	153	140	47	78	118	32+3/9	21	15	–
(10) Paramaribo																
RML 1-4-53	25.8	♀	8	11	703	–	248	–	–	49	78	125	32+2/9	19	14	IIId
	25.7	♂	8?	12	698	601	282	–	–	–	–	–	29+2/10	21	15	–
	25.0	♂	9	12	702	–	262	–	–	–	–	–	32+?/9	20	14	–
	24.9	♀	8	11	712	612	259	180	–	54	81	–	31+3/9	22	14	–
	24.5	♂	8?	12	–	–	–	–	–	–	–	–	32+2/9	20	15	–
	24.5	♂	9	12	706	602	262	–	–	61	–	–	31+?/10	20	14	–
	23.8	♀	8	11	711	612	–	–	–	–	–	–	– –	–	–	
	20.8	♂	9	12	708	601	259	165	–	–	–	–	32+2/9	20	14	–

b. Discussion of the *breviceps* samples

The samples previously enumerated, of which proportion and counts are given in table 6, are all most closely related, and are morphologically hardly distinguishable in the three forms to which they have been referred. Those referred to *breviceps* seem to be of that species, though they do not quite fit in the original description of the typical population from Shrimp Creek, British Guiana (EIGENMANN, 1909). I am in doubt about one specimen (RML 27-11-48, Wia Wia), which shows a caudal fin quite unlike that in *breviceps* proper but very much like that in *Rivulus urophthalmus lanceolatus* (cf. pl. IIIa). This may point in the direction of some affinity with the coastal *urophthalmus* populations (hybridization), but since the specimen in question bears no other resemblance to that species, I am leaving it under *breviceps*, for the time being.

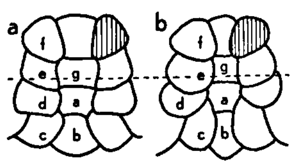

Fig. 36. Frontal patterns in Suriname forms of the *breviceps* group. a = *breviceps*, b = *agilae* and *frenatus*. See also plate IIIb, c, and d.

The frontal scalation of the *breviceps* specimens is as illustrated in fig. 36a. The scales of the frontal pattern shown are not much larger than the other scales on the back to the dorsal base, however, they are more rectangular in shape instead of gently rounded, as in *agilae* and *frenatus* (fig. 36b) and most other forms studied. The exposed scale pair *ff'* is only small. The samples referred to *Rivulus frenatus* comprise only 4 specimens in all; those referred to *Rivulus breviceps* comprise 11 specimens. The remaining specimens are referred to *Rivulus agilae*, a total of 198 specimens.

The question arises as to whether or not three forms so closely related, inhabiting a restricted area, can be distinct species. The samples are, however, unfortunately too small to enable this to be decided, and only the frontal pattern indicates that they are indeed probably distinct forms. The general markings and coloration, and the meristicals of table 8, have some value in enabling these forms to be distinguished. Percentage frequencies of the primary characters are shown in the graphs at figs. 38 to 41, under (e) 'Relationship'.

c. *Rivulus agilae* Hoedeman, 1954

The following description is based on the holotype (♂, 28.8 mm st.l., ZMA 100448), and the extremes from 18 paratypes (ZMA 100448, 100449, and RML 1-4-53, cf. table 6) are added in parentheses.

Dorsal rays 8 (8–9), anal rays 12 (11–12); both fins normally have 2 unbranched rays in males and females; pectorals usually have 13 (12–14) rays, and ventrals 7–7 (7–7) rays, including 1 unbranched ray in each; scales from upper edge of opercle to the end of the hypural 32, plus 3 more on the base of the caudal fin (29–34 + 2–3); scales from base of first dorsal ray obliquely downward and forward to base of anal

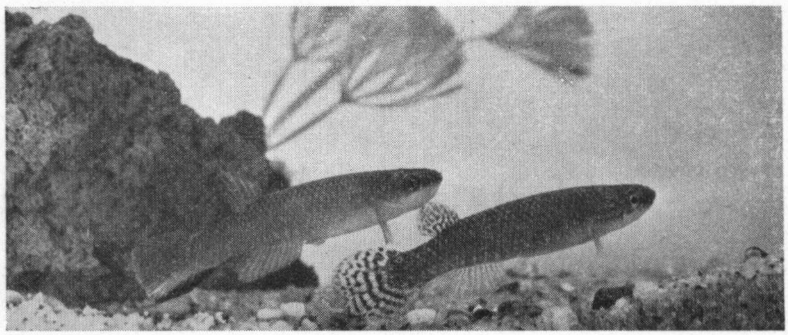

Fig. 37. Adult pair of *Rivulus agilae*, photographed in the home aquarium by G. J. M. TIMMERMAN.

fin 9 (8–10) mostly 9; predorsal scales 21 (19–23); scales in zigzag row around caudal peduncle at least depth 14 (14–15).

Body cylindrical, head only slightly depressed, caudal slightly compressed posteriorly; greatest depth of body (all proportion rates in thousandths of the standard length) 198 (153–201), length of head 268 (248–282); margin of eye not free, eye 65 (57–81), snout 52 (42–63), interorbital width 125 (107–128), predorsal length 701 (696–713), preanal length 607 (590–612). A tiny species, about 40 mm in total length in both sexes.

In alcohol the colour of the holotype (♂) consists of a rather dark brownish base, with a dark apical margin to each scale. There is no trace of longitudinal or trans-

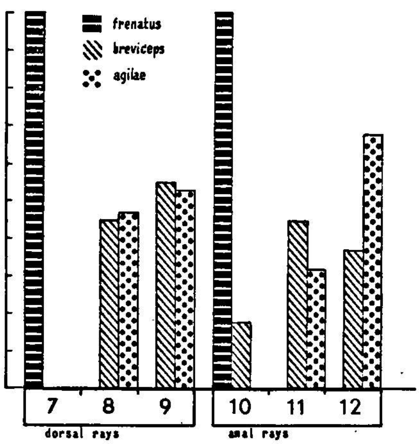

Fig. 38. Percentage frequencies of the number of dorsal and anal rays in the forms referred to the *breviceps* complex, based on 4 specimens of *frenatus*, 11 of *breviceps*, and 19 of *agilae*.

verse striation; belly and underside of head light brownish; upper three quarters of caudal fin brownish with faint lighter spots, bordered below by a pale light-yellow streak, and margined with black. The black extends forward as a delicate line underneath the tail to the last anal ray (cf. fig. 37 and pl. IVf); dorsal fin dusky with three irregular rows of darker spots or dots, anal dusky without markings; the other fins pale, translucent. The other males (paratypes) are mostly smaller in size (younger specimens); some of them still show faint longitudinal stripes between the scale rows. The females are very similar, except that their general colour is more light brownish, and the caudal fin has four or five bands of dark dots and blotches on a practically transparent base (cf. fig. 37 and pl. IVd); dorsal fin like the caudal, with bars of darker blotches, anal fin plain; there is often a dark, differently shaped fleck on the upper half of the tail root; this blackish mark is not a real caudal ocellus (cf. fig. 37 and pl. IVd) at least, there is no pale ring round it.

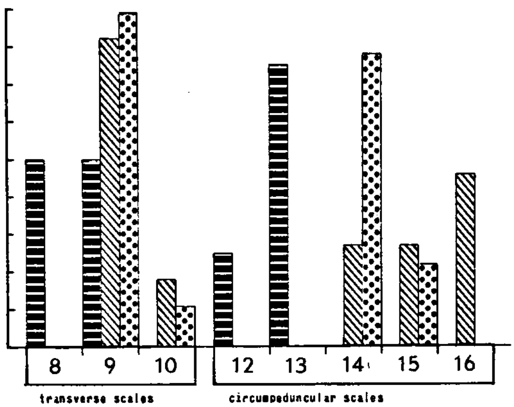

Fig. 39. Percentage frequencies of the number of transverse and circumpeduncular scales in the forms referred to the *breviceps* complex. Same as in fig. 38.

In life this is one of the most attractively coloured of the South American Rivulids hitherto imported alive, a serious competitor of its beautiful African relatives of the genus *Aphyosemion*. A colour photograph of the male holotype has been published in the 'Aquariumvissen Encyclopaedie' (Hoedeman, 1954, 1956, 1959) and is reproduced here in black and white (pl. IVf).

The male is brownish on the sides, the brown being mixed with violet towards the back; the belly and throat are light brown to yellowish, with series of crimson dots towards the sides; the lower part of the caudal peduncle has bars of deep crimson and light blue. Most typical is the caudal fin, the upper three quarters of which is coloured like the caudal peduncle, evenly accentuated with series of crimson flecks, bordered below by a pure orange-red to yellow band, and margined with a deep black seam, continuous underneath the caudal to the anal fin. Dorsal, anal, and ventral fins are orange-yellow, with blue spots near the base of the fins; light green-blue translucent pectorals.

The females are much duller, being light brownish with darker puncticulations; the dorsal and caudal striation is most attractive, the lower part of the latter being lighter and more finely marked than the upper part (cf. pl. IVd). The colouration of the caudal fin in young males is the same as in the females, but with age the upper markings become fainter and the lower pale and black streaks increase in intensity (cf. pl. IVa – c).

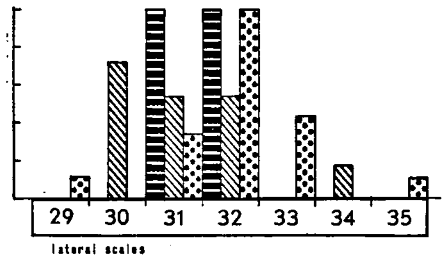

Fig. 40. Percentage frequencies of the number of lateral scales in the forms referred to the *breviceps* complex. Same as in fig. 38.

d. Ecological note

The specimens of *Rivulus agilae* collected by HUMMELINCK (sta. 409) at Zanderij, in 1948, comprise 1 ♂, 16.8 mm, 1 ♀, 16.3 mm, and 3 juveniles of 10.2, 8.6, and 5.0 mm st.l. The sampling place may be described as a pool at the source of a swampy rivulet, 8 × 3 × 1 m, permanent and practically stagnant. The bottom consists of quartz sand, mud, and plant decay from swamp forest; there is dense growth of *Utricularia* and algae; the water is clear, slightly brownish, containing only 17 mg/l Cl′, 60 mg/l HCO_3′, total hardness 3 German °.

e. Relationship

The close relationship of *Rivulus agilae* with Surinam *breviceps* and *frenatus* is obvious, when they are at all distinct. Though the specimens referred to *breviceps* and *frenatus* respectively answer the description of British Guiana *breviceps* and *frenatus* rather well, larger samples will have to be studied in order to decide on the perfect identity of the Suriname forms with the latter. *Agilae*, *breviceps* and *frenatus* have been compared with type material of *Rivulus geayi* from French Guiana by BOESEMAN, who finds them to be related but distinct. All four can be included in the *breviceps* complex, and are probably geographical representatives of one species.

The Surinam forms can be distinguished by a number of characters, of which general coloration is certainly not the least important.

	agilae ♂	*breviceps* ♂	*frenatus* ♂
Caudal fin:	three-coloured;	two-coloured;	two-coloured.
Caudal half:	faint oblique markings;	5 dark cross-bars;	longitudinal markings.
Body:	longitudinal stripes in young, none in adults;	broad lateral band from eye to midcaudal;	longitudinal markings, no broad lateral band.

The graphs in figs. 38 to 41 give the percentage frequencies of a number of morphological primary characters, and show that *frenatus* normally has only 7 dorsal rays and 10 anal rays. However, these data are based on 4 specimens only. In *agilae* and *breviceps* the number of dorsal rays is the same (in 18 specimens of *agilae*, and 11 of *breviceps*), but the number of anal rays is more frequently 12 in *agilae* and

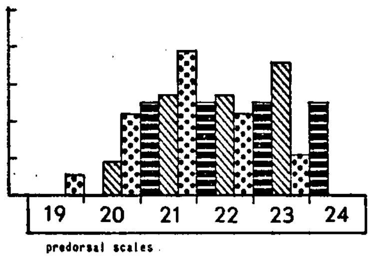

Fig. 41. Percentage frequencies of the number of predorsal scales in the forms referred to the *breviceps* complex. Same as in fig. 38.

11 in *breviceps*. The transverse scale rows are equally 8 and 9 in *frenatus*, and generally 9 in both *agilae* and *breviceps*. In the circumpeduncular count *frenatus* differs considerably in having a lower number of scales (12 to 13) than either of the other forms; of these *breviceps*, again, seems to have a higher number (mostly 16) than *agilae* (mostly 14). The number of lateral scales follows a perfectly regular curve in *agilae*, ranging from 29 to 35 (mostly 32), although this character does not differentiate the three forms (cf. graph fig. 40). The three are not (yet) known to occur together, and so may only represent local races of one species, as I remarked above. It seems advisable, however, to await further material. If they turn out to be sibling species the complex will be named after the oldest name to be included, as a superspecies. Though Suriname *breviceps* is not perfectly identical with British Guiana specimens, there can hardly be doubt that both belong to one natural assemblage. Besides the three Suriname forms *agilae*, *breviceps*, and *frenatus* (of which the two last-named also occur in British Guiana), *geayi* from French Guiana is to be placed here, and apparently the bulk of the species names in table 1, first section, which all agree with the general diagnosis for the complex. They are quite different from all other members of the genus in their rather small size and coarse scales, the absence of a caudal ocellus in both sexes, a series of vertical or oblique bars or stripes on the caudal, especially in juveniles, and longitudinal markings or one broad lateral band. Sexual dimorphism is usually prominent in coloration and markings, most obviously in the caudal fin.

Nothing is yet known about the variation limits of the non-Guyana forms, and since none of them is known to occur in the same vicinities or the same habitat as one of the others in this complex, they may all represent geographical races. They seem to be more or less completely isolated froms each other geographically.

13. The *micropus* Complex

The forms included in the *micropus* complex, viz. *micropus*, *bondi*, *harti*, *holmiae*, and the hybrid *waimacui* are, apparently, geographically isolated populations, each replacing the other. In Suriname this complex is represented by *holmiae*, which ranges from western British Guiana to eastern Suriname (and will probably also be found in French Guiana). To the west *holmiae* is represented by *harti* and *bondi* in Venezuela, and by *harti* on the islands of Margarita, Trinidad and Tobago (cf. HOEDEMAN, 1958a). Inland the form *micropus* is known from the Rio Negro (and middle Amazon).

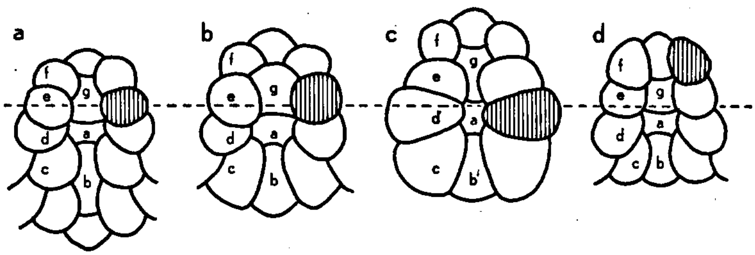

Fig. 42. Outline drawings of the principal scales of the frontal scalation pattern in Suriname *Rivulus*, to compare the characteristic features. The horizontal dotted line indicates the hind margin of the orbits. a = *urophthalmus*, b = *waimacui*, c = *holmiae*, and d = *breviceps* forms.

Only a single specimen of *micropus* was available for study (ZMA 100381, ♂, 71.8 mm st.l., Rio Negro, Maroa, leg. Steindachner, 1880). The frontal pattern of this specimen is illustrated in pl. Va, next to the pattern of an ordinary *harti* ♂ from Margarita. From the photographs it is evident that the two forms are quite similar, and this is confirmed by most other characters. Our single *micropus* specimen differs from typical *harti* merely in possessing a greater number of scales (43 + 5/11, predorsal 33, as against about 38 + 3/11, predorsal 26 in *harti*). Larger samples will probably show them all to be one variable species, thus including *holmiae* and *bondi*. With regard to the pattern, *micropus* occupies a position between *cylindraceus* and *harti/holmiae* (cf. HOEDEMAN, 1958a). Just as in *cylindraceus*, the exposed portions of scale pairs *ee'* and *cc'* meet in the middle, while pair *dd'* is not in contact with the exposed portion of central scale *a*, as is the case in (most) specimens of *harti*, and in all specimens of *holmiae* examined. The end of the *micropus* series is no doubt *holmiae*, with its fine and regular rosette-shaped pattern. Plates Vc and d illustrate two patterns of *harti* specimens, aberrant in structure. The first (pl. Vc) is regular *harti*, except for the lateral pair *dd'*, which is not in contact with *a*. The second is an example which probably indicates hybridization, in that the right lateral scales *d* and *e*, after a struggle for supremacy, receive each other in a notch (pl. Vd).

Despite their great similarity in most characters, populations and single specimens of *harti* and *holmiae*, and probably also of *micropus*, can easily be distinguished by their frontal scalation pattern. The Venezuelan samples of *Rivulus*, including those from the islands, can only be referred to *harti* s.s., as I pointed out, and this species therefore ranges from western Venezuela and the islands of Margarita, Trinidad and Tobago to eastern Venezuela, and is replaced by *holmiae* in the Guyanas. SCHULTZ, (1949, p. 89–90) is mistaken in stating that there are but 6 branched rays in the dorsal fin of *harti*. The 10 types from Trinidad have 7 and 8 branched rays in 3 and 7 specimens respectively (cf. HOEDEMAN, 1958a). The last two rays are not counted as one by BOULENGER, REGAN, TREWAVAS, or me, as SCHULTZ may have done. *Rivulus harti* from Margarita, as referred to that species name by MYERS (Copeia, 1924, p. 96) and by DE BEAUFORT (1940, p. 110), certainly belong to that species and not to *holmiae* (cf. SCHULTZ, l.c., p. 90). The specimens described and discussed by SCHULTZ originate from the Rio del Valle (= Rio Porlamar), Margarita, and therefore belong to the same population as the specimens recorded in my 1958a paper. *Rivulus harti* and *holmiae* are at once distinguishable by the shape of the exposed portion of scale *g* of the frontal pattern, which is more or less milkbottle-shaped in *harti* (anteriorly covered by lateral pair *ff'*), and mushroom-shaped in *holmiae* (anteriorly overlying pair *ff'*). In this respect *holmiae* seems to be more like *micropus*.

14. DISTRIBUTION AND DISPERSAL OF THE SURINAME *Rivulus* COMPLEXES

In the Suriname ichthyofauna the genus *Rivulus* is apparently represented by three evolutionary lines, i.e. the *breviceps*, *urophthalmus*, and *micropus* complexes. The known extralimital range of each has been discussed and is illustrated on the map at fig. 35.

These three complexes are representatives of the three main evolutionary lines which can be recognized within the limits of the genus (cf. table 1), i.e.:

The *breviceps* group, a series of forms which inhabit the lowlands of the Guyanas and Amazonas, and have one relic species on Saona island (Haïti);

The *urophthalmus*, *marmoratus* and *isthmensis* complexes form the second group, the *marmoratus* series. The *marmoratus* complex has been discussed in my 1958a paper. This group is chiefly confined to coastal drainage systems.

The third group, the *cylindraceus* series, is divided into three complexes, all more or less restricted to elevated river systems and hill stream regions. The *cylindraceus* complex from Cuba (and the Tocantins river) is replaced by the *elegans* complex from Mexico to the Orinoco system, and to the east again by the *micropus* complex.

These three groups can be preliminarily recognized as:

(1) rather small species with low scale counts, typified by a more or less complete series of vertical stripes, bars or streaks on the caudal, which fade with age and change into longitudinal markings; no real caudal ocellus in either sex. . *breviceps* series

(2) larger species, finely scaled, often with a marbling effect in the markings; caudal ocellus in young and females, and sometimes also in mature males, ... *marmoratus* series

(3) more or less robust forms, coarsely scaled, lateral band or longitudinal markings on or between the scale rows; caudal ocellus in young and females only . . . . . *cylindraceus* series

The supposed three main evolutionary lines, and a preliminary arrangement of the species names to be included, are given in table 1.

15. Summary and Conclusions

Material of the genus *Rivulus* from the Guyana province (including eastern Venezuela, the islands of Margarita, Trinidad and Tobago, and British, Dutch and French Guiana) has been studied with reference to morphology, ecology and ethology.

This study resulted in my paper on the Antillean Rivulids (Hoedeman, 1958a), and in the present article, with the conclusions that in Suriname it is possible to recognize three groups of forms or species complexes (superspecies), each representing an evolutionary line within the genus. All other forms, no material of which was available for study, can apparently be referred to one of these three groups. An attempt at a preliminary arrangement, based on literature and our own material is ventured in table 1.

In the material studied, the specific morphological character which has proved to be the most convenient one, and seemingly the most important, for recognition of the three types is the frontal scalation pattern, viz. the arrangement and position of the scales covering the surface of the head between the eyes. The three types are characterized by full exposure of three different scale pairs of this pattern, which I have named *ff'*, *ee'*, and *dd'* respectively.

From sympatry in two instances, and hybridization in various samples, evaluation of other morphological characters resulted, and it has been shown that hybridization is only determinable from deviations (and irregularities) in the frontal pattern and sometimes in general colouration. No perfect intermediate hybrids have been found.

The distribution of the complexes in Suriname shows a preference on the part of both the *breviceps* and the *urophthalmus* complexes for the lowland region, whereas the forms of the *micropus* complex inhabit the more elevated region of the watersheds and hill streams. In Suriname the range of the *breviceps* complex completely coincides with that of *urophthalmus*, and they must be regarded as sympatric species complexes. Any hybrids occuring can only be accidental, as the mating behaviour of these two forms (and probably the time and place of pairing) are quite different. Hybridization of both *breviceps* and *urophthalmus* with *holmiae* takes place in Suriname, though the nature of the hybrids indicates allopatry of the parental species.

From the vertical distribution it can be seen that there is a noticeable increase in the number of fin rays in dorsal and anal fins (and a corresponding decrease in predorsal and preanal lengths), with increasing elevation of the habitats. Moreover, it is obvious that the first groups of table 1, the *breviceps* series, and the *marmoratus* complex, are chiefly confined to the lowlands, whereas the *cylindraceus* series is confined to the hill streams.

From the horizontal distribution it can be assumed that the genus originated somewhere in tropical America and that dispersal took place by two routes, an eastern via the Greater and Lesser Antilles (*marmoratus* on Cuba, St. Martin, Barbuda, and on Los Roques, Bonaire, and Curaçao), and a western via Yucatan and the Middle American provinces (*cylindraceus-elegans-micropus* series).

Finally, I should like to remark that it would be better to look upon the complexes indicated as species (or superspecies), but that for practical reasons, I do not intend to alter any nomenclatural indication yet. For I am not quite certain which species names should be included in each complex, and the complex should bear the oldest available name as a species or superspecies name.

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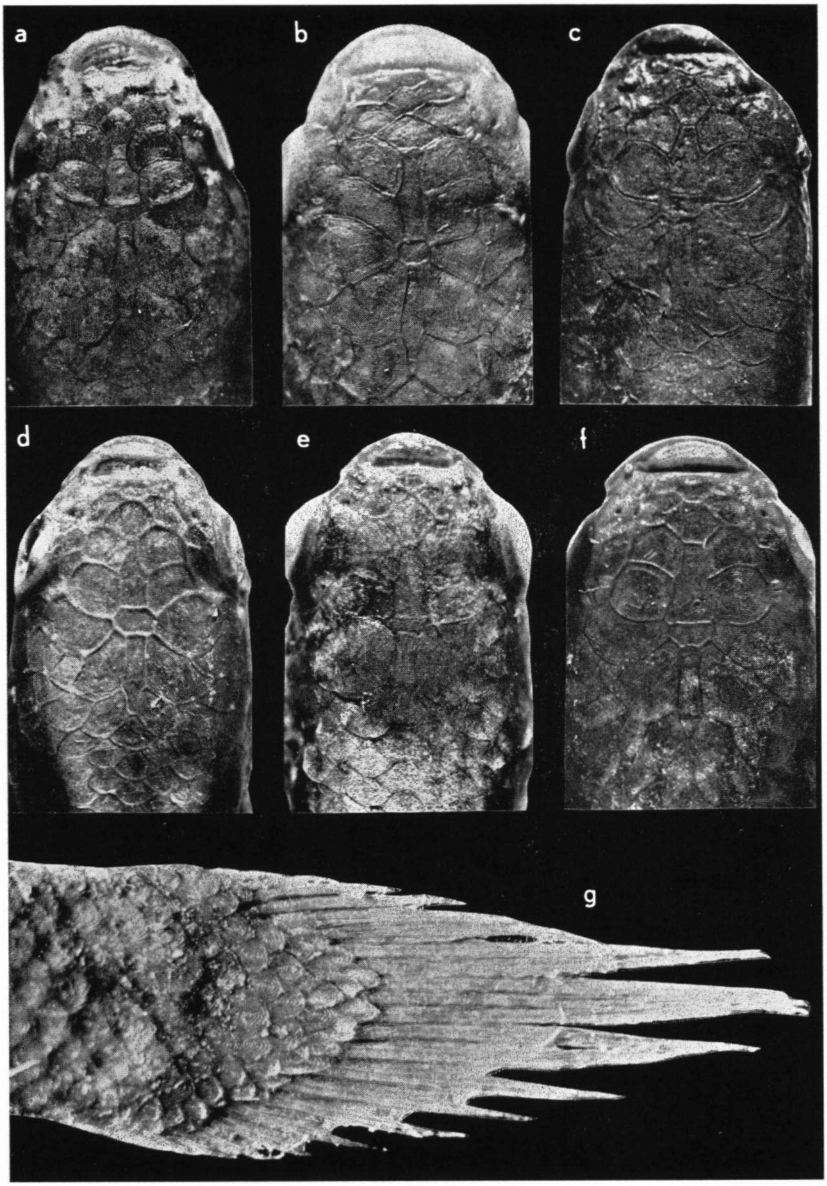
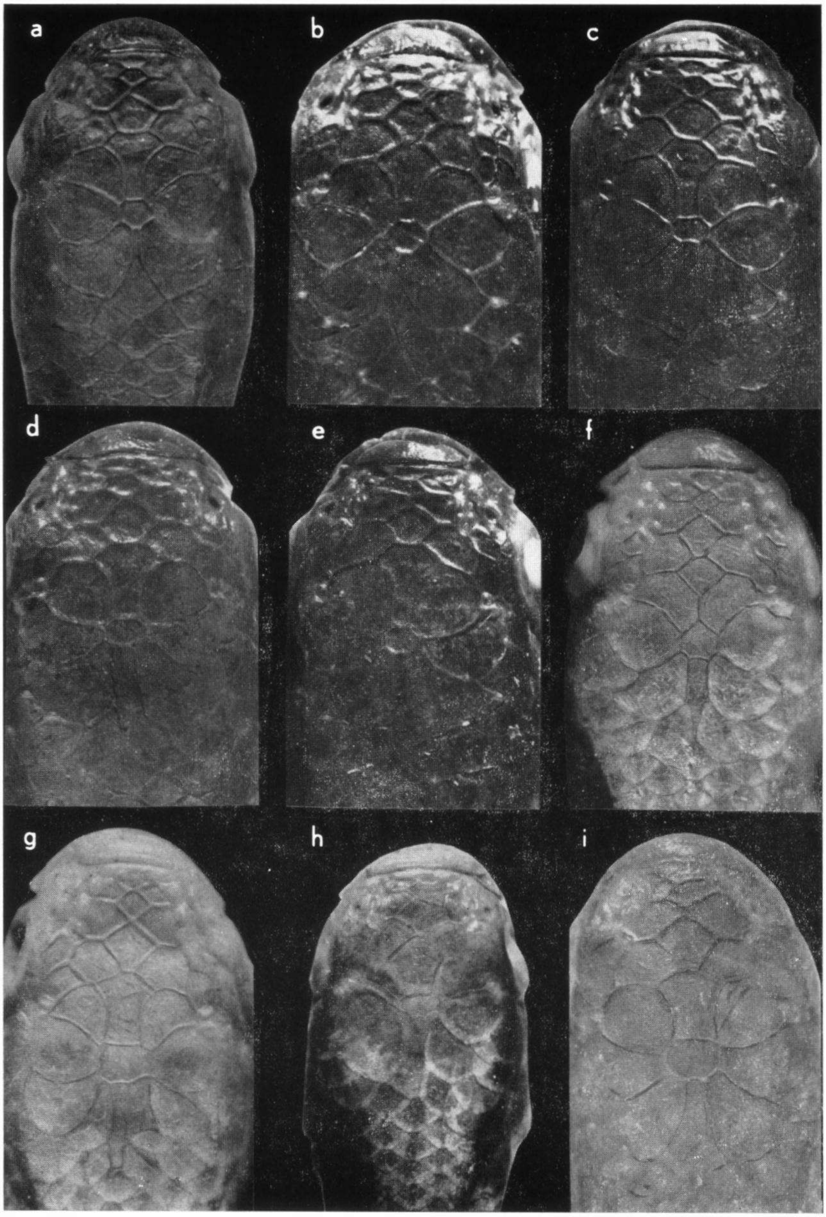
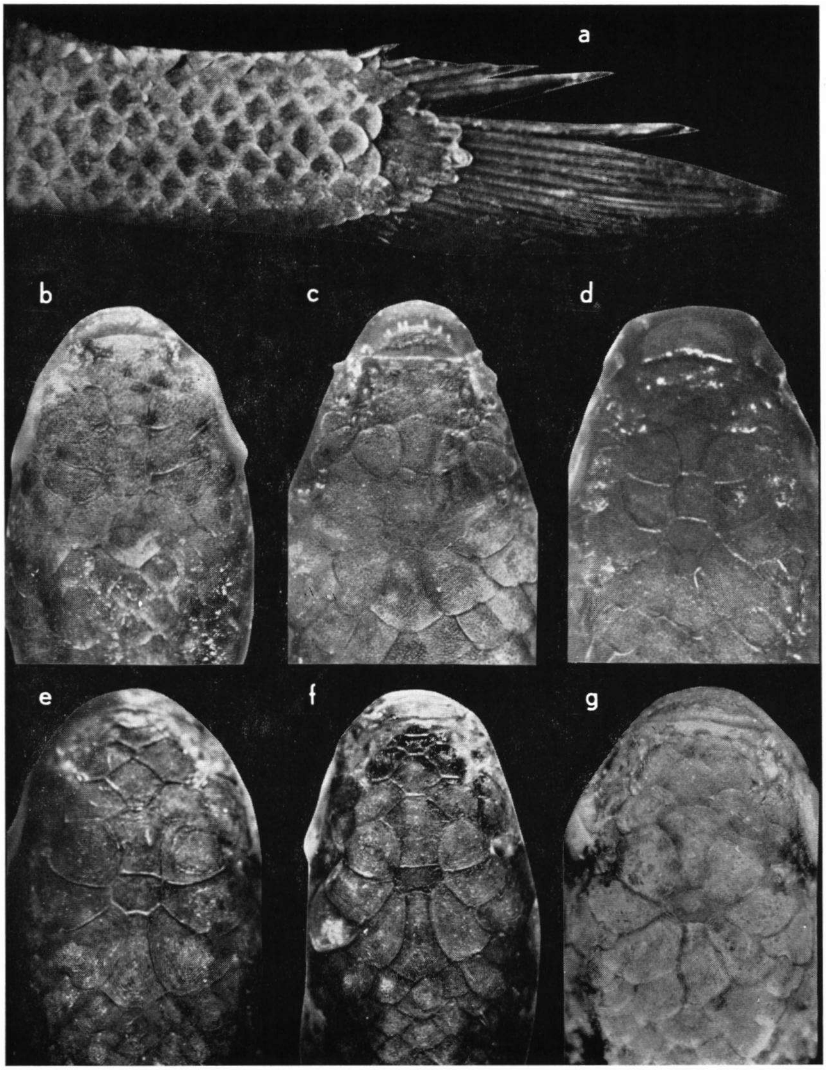


Frontal scalation patterns in Suriname *Rivulus urophthalmus*. a = typical regular pattern, female 54.0 mm standard length, ZMA 100438, b = male 39.4 mm st.l., ZMA 100447, c = male 34.6 mm st.l., RML 18463, d = female 31.7 mm st.l., RML 18425, e = female 36.8 mm st.l., RML 18426, f = female 25.9 mm st.l., RML 18465, and g = caudal of female 25.8 mm st.l., RML 18319, showing basal scalation and shape of fin. See for full meristicals table 3.

PLATE II.

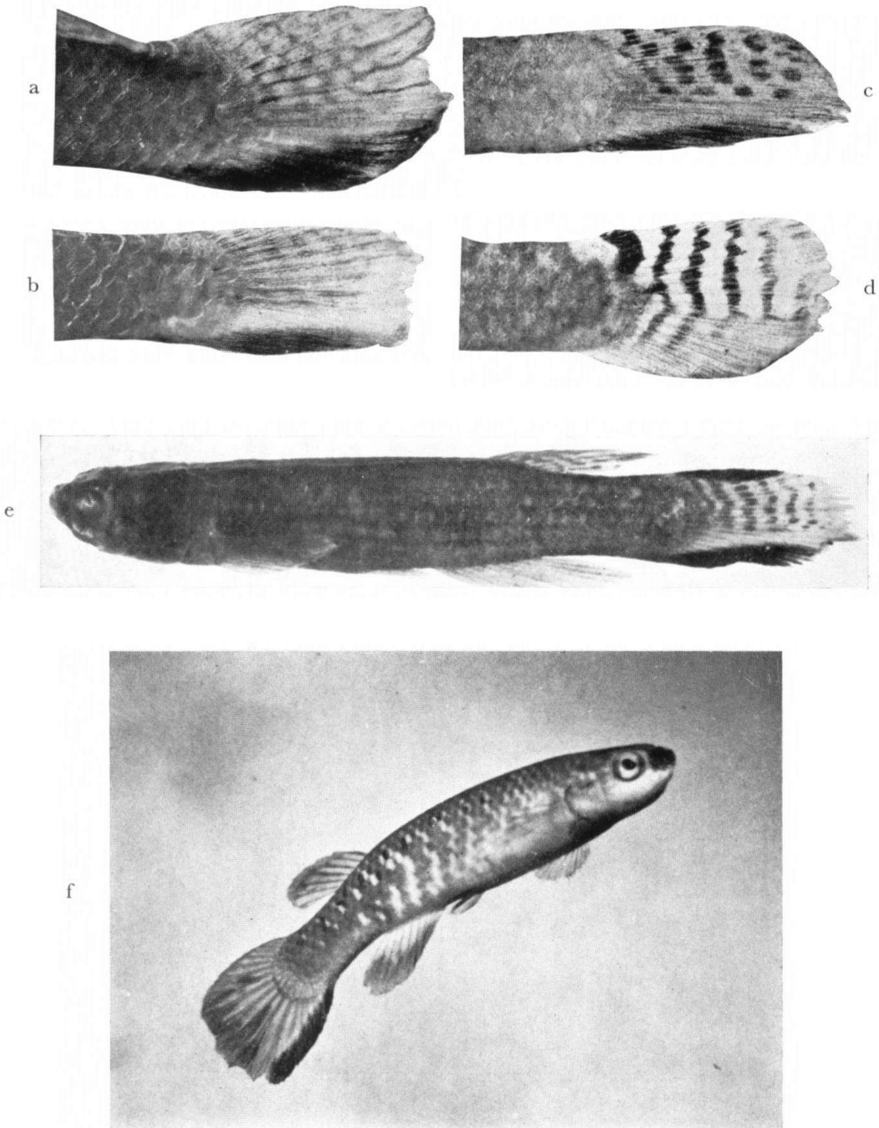


Frontal scalation patterns in Suriname *Rivulus holmiae*. a = typical regular pattern, male 39.7 mm st.l., b = male 50.3 mm st.l., c = male 45.3 mm st.l., d = male 44.6 mm st.l., e = male 46.9 mm st.l., all RML 18255–57; f = female 47.4 mm st.l., g = female 34.2 mm st.l., both RML 19499; h = male 45.4 mm st.l., RML 19436, i = male 51.0 mm st.l., RML 19516. See also table 4.

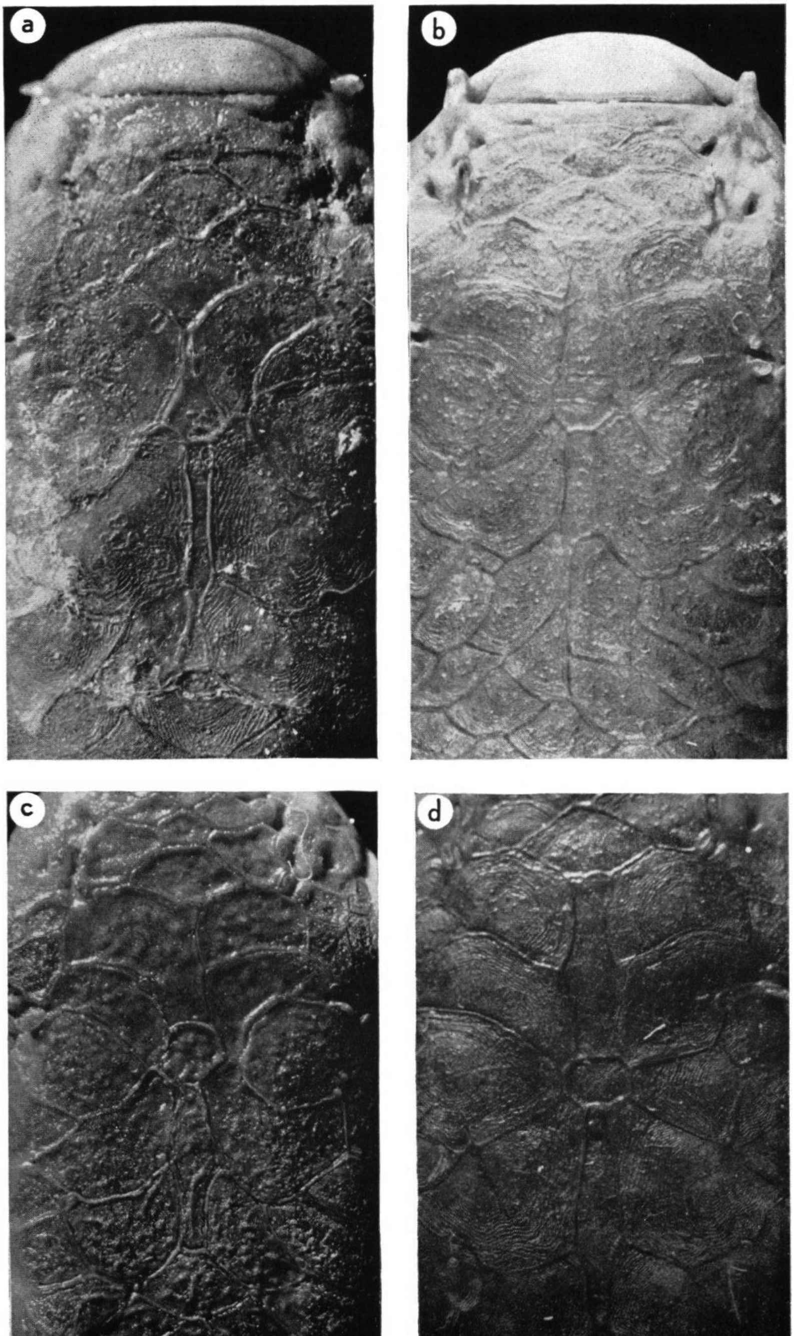


a = Lanceolate caudal of *Rivulus breviceps*, male 22.4 mm st.l., RML 27–11–48, and frontal patterns of *Rivulus breviceps*, b = male 21.9 mm st.l., RML 18461, *Rivulus frenatus*, c = ? sex, 22.5 mm st.l., RML 19311, and *Rivulus agilae*, d = female 25.8 mm st.l., RML 1–4–53; Suriname *Rivulus waimacui*, e = female 40.0 mm st.l., f = male 36.0 mm st.l., both RML 18427, and g = female 53.2 mm st.l., RML 18255–57. See also tables 5 and 8.

PLATE IV.



Rivulus agilae, caudals of a = holotype male 28.8 mm st.l., ZMA 100448, b = male 24.2 mm st.l., c = male 19.8 mm st.l., and d = female 24.7 mm st.l., all three ZMA 100449. The photographs show that the marking in the caudal fin of the female is more prominent in the upper half. The fleck in the tail root is conspicuous but not an ocellus. In the males the markings in the upper half of the fin fade with age and the pale and black margin gets more and more prominent. e = marking of caudal fin with both upper and lower margin black, in male 23.4 mm st.l., ZMA 100449; f = photograph of living holotype, male, in its typical resting attitude. See also table 8.



Frontal patterns of a = *Rivulus micropus* (ZMA 100381, male 71.8 mm st.l., Rio Negro, Maroa, leg. Steindachner, 1880); b = *Rivulus harti* (ZMA 100378, male 64.0 mm st.l., Rio Asunción, Margarita island, coll. Wagenaar Hummelinck, 1936); c and d = aberrant *Rivulus harti* patterns, c = fully exposed pair *dd'* not in contact with *a*, and scales *fg* are fused in the left half; d = scales *d'* and *e'* receive each other in a notch owing to struggle for supremacy.