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ARK - Arizona Rivulin Keepers

The Scheel Letters, No. 53; Part 4

Crossings Part 4: Rivulinae Myers in Cyprinodontidae

78) SJO/COG 1958

This cross between a huge male of the Callopanchax and the much smaller Aphyosemion Aphyosemion female was a great risk. This particular female however had been trained in crossings and she accepted any sort of male and also at once acted on the stimuli of the SJO male. 57 eggs were spawned in one spawning. The next day only very few of these eggs were alive. The next day I had only a single egg left. This egg lived for more than sixty days. At that time I did not control eggs for the development of a blastula. I was able to trace a certain "body" at the surface of the yolk, probably a development that comes after the gastrulation and before the development of the corda. The egg did not change through these sixty days. The crescent shaped "body" remained at its place. No pigments developed on the yolk. At that early time I had no clear understanding of the very bad results usually obtained in between members of these two subgenera.

(79) SJO/SJO 1964-65

During his three expeditions to Sierra Leone (1962-65) E. Roloff from Karlsruhe in Germany collected live individuals of SJO-like individuals of three demes in that country. These localities cover the extreme western, the extreme eastern and the central parts of that country. Roloff kindly sent me individuals of the central and the eastern demes. The eastern individuals originated from Blama near Kenema. This area belongs to the main Liberian rainforest area. The central deme lives near Magbenta and (more or less) could be considered as belonging to the Freetown forest area.

The individuals of these two demes were rather similar, at least compared with the individuals of the western deme for which I have seen color slides, and fresh material preserved in alcohol.

I produced a MA/BL hybrid strain containing more than a hundred individuals. These individuals were very viable and strong fish, probably more viable under aquarium conditions than individuals of the pure strains. Often SJO is a difficult fish to keep and to breed.

SJO is the sole real "annual Rivulin" of West Africa. In reproduction, such a form as SPU comes close, but in other West African species all eggs need a certain length of time ("resting eggs" of "stadium 1b") before the embryo development after the gastrulation takes place. For one large batch of eggs (426 eggs, 1959-60, published on previous pages of Killie Letters) I found the "induction period" for SJO to be

about 50 days. Not a single egg developed a corda during this length of time. Here are the findings of egg development of this large brood: 10% eggs developed after 58 days 20% eggs developed after 62 days 30% eggs developed after 67 days 40% eggs developed after 70 days 50% eggs developed after 71 days 60% eggs developed after 73 days 70% eggs developed after 75 days 80% eggs developed after 78 days 90% eggs developed after 83 days 100% eggs developed after 100 days

Eggs of other -less "annual"- West African Rivulins will develop a corda without much delay if the eggs are placed in clean water in open containers. At least most of the eggs will develop under these conditions. For counting I have preserved fifteen males and sixteen females of the hybrid strain in order to show that in this species males develop more dorsal and anal fin rays than females do.

D= 17 18 19 29 21 Dm males 0 0 2 6 7 20.2 females 1 2 8 5 0 19.1

A= 17 18 19 Am males 0 2 13 18.9 females 1 12 3 18.1

Sp-long= 32 33 34 35 Sqm males 0 4 16 10 34.2 females 2 6 14 10 34.0

Our preserved material of SJO is limited, but may give an idea of the variation in this species:

SJO-blue 0 2 2 0 0 0 SJO-MA 0 2 4 4 1 0 SJO-BL 0 0 2 2 3 0

AQ = old aquarium strain MA = Magbenta, Sierra Leone BL = Blama, Sierra Leone

One female of SJO-AQ had 21 dorsal fin rays.

Although SJO resembles the species in the group of Fundulopanchax SJO does not develop ctenoid spines in males. Instead Stenholt Clausen found a particular type of ctenoidy that might be called "wrinkled scales". These scales are found normally just behind the gill covers and often they are developed best in the mid rows of scales up to the root of the caudal fin. The "proof" that these scales are real "ctenoid scales" is found in the development of long and filamentous "sensory papillae" on anal fin rays (normally there are a few only). Shorter sensory papillae are found on the upper ray of the pectoral fin, like in Fundulopanchax. The development of wrinkled scales and sensory papillae in males is very variable and these developments might be absent in some full size males of SJO. These developments (no anal papillae!!) also occur in GUI and in LIB and some more forms in the ROL-LIB group of smaller species. I found also a few sensory papillae on dorsal fin rays in some large males of SJO. Some types of wrinkled scales also occur in some individuals of Epiplatys and Aplocheilus, but I do not know if these scales belong to the same type as found in SJO and other Callopanchax. Species in Cynopoecilus develop wrinkled scales in males and (if the scales near the root of the pectorals are "wrinkled") also pectoral papillae. In these species the wrinkling of scales no doubt is of the same type as found in Callopanchax.

(80) SJO/GUI 1965

This and the reciprocal crossing (GUI/SJO) have just started and the first about twenty eggs probably are not viable although blastulas have been discovered in some eggs. GUI was described from High Guinee and apparently there is no particular holotype. Stenholt Clausen had the synotypes from Dabola (no 60475), from Banian (no 60476) and from Banamanan, Cercle de Kissidougou (no 35226-227, first identified as CAM by Pellegrin, see Bull. Soc. Zool. Fran. vol. 60, 1935, page 466) from the Paris Museum and also individuals (also identified as CAM by Norman, see Ann. Mag. Nat. Hist. nr. 10, 1932, page 185) from "headwaters of River Bagbwe" and Sandaru in NE Sierra Leone from the British Museum. We also had many individuals from Keimaduya, situated on the NW slope of the Loma Mts. in Sierra Leone (coll. Schiotz in 1963) and individuals caught by E. Roloff north of Kenema. Individuals from the collection last mentioned are used for this particular cross.

GUI is a remarkable species as in this species the rare E scale pattern occurs. No other species of West African Rivulins develops this particular pattern of scales that is found among the Pachypanchax and in BLO in Aplocheilus. The E scale pattern in my opinion is a more ancient pattern than the common G pattern found in other Old World Rivulins. Species that live among plants and other obstacles need a scale pattern that gives the highest degree of scale protection and this indeed is the common G pattern. In the E pattern the E scales are situated upon the posterior edge of the G scale and also on the anterior edges of the D scales. The anterior edges of the E scales for this reason are not protected and scales might

easily be lost. According to Daget, GUI was found in biotopes where BIF and SEN were absent and in waters that had a stony or rocky bottom. GUI resembles SJO in many traits, but in GUI the anterior-most dorsal fin ray is not in advance of the anterior-most anal fin ray as in SJO (D/A = -2 to -5, as in ARN and FIL), but situated behind the anterior-most anal fin ray (/A = +5 to +7 anal rays). The color pattern of GUI is rather "primitive". A thin red reticulation (red scale edges) and a much reduced "wound" behind the root of the pectorals. As other species in Callopanchax also GUI does not develop any red throat pattern and as other male Callopanchax the whole area of the lower part of the head becomes deep black during display. The brilliance of the male is low, a violet blue shine only. The lack of bright colors is compensated by the milky white lower edge of (the anal and) the caudal fin. The male is easily seen in a dark aquarium against a dark background.

Females of GUI develop the "marking of Callopanchax females", a dark area in the center of the anterior part of the throat. No dark lateral band (as in SJO and a few of the smaller forms) has been seen so far.

The male SJO (and the male GUI) was not very interested in spawning with the GUI female (the SJO female). When together with their own females the males are indeed very active males.

Many of the preserved individuals were not suited for counts. Here is the sum of the counts. I found no important differences to exist between the individuals from the different demes. Schiotz' individuals from the Loma Mts. did differ somewhat.

D= 11 12 13 14 15 Dm GUI 1 5 25 5 3 13.1

A= 14 15 16 17 18 Am GUI 1 9 23 5 1 15.9

Sq-long= 29 30 31 32 33 34 Sqm GUI 3 6 8 23 16 1 31.8

D 12-14, A 14-17 and Sq-long 30-34 according to the description.

The results of the SJO/GUI and probably also of the GUI/SJO will be reported in a future issue of Killie Letters.

(81) SL4/NIG 1963

The code "SL4" or "Sierra Leone Aphyosemion no 4" is one of Roloff's many ROL like forms from Sierra Leone. The SL4 originated from the Kenema area, situated in the extreme east of that country. This form comes close to ROL and LIB, but it differs constantly in minor traits in the color pattern and in the genetics.

I used a female of the NIG-PH/Ak strain (for fertility of this strain in NIG see NIG/NIG). I had twenty eggs in one spawning. Six eggs only developed. After three days I found no trace of any development in the six eggs. On the fourth day I noticed the gastrulation on the yolk ball. On the fifth day masses of undifferentiated cells were visible at the animale pole. The cells formed "corda like" broken rows in some

eggs. After fifteen days no further development of the embryo was visible. Black pigment cells were seen here and there on the yolk. Next day all eggs were carefully inspected under the microscope. In some of the eggs a small embryo was detected. The gill arches and the end of the tail were visible. The "body" of the embryo was very short and blunt. In between the "head" and the tail a diffuse mass of cells was seen. Shapeless. As I did not expect further development all eggs were preserved in Bouin.

(82) SL4/ROL 1964

Roloff considered the SL4 form as representing a distinct species and different from his different strains of ROL like forms from the Freetown area. As we were not able to base an isolation of the SL4 form on differences in morphology I prepared for a crossing. For this cross I used a female from the strain in ROL that in nature lives closest to the population from which Roloff, in the late thirties, had the types for ROL. In morphology and in color patterns this strain was very close to the pre-war strain in ROL.

I had forty eggs in three spawnings. Thirty eggs developed normally and the hybrids apparently were no more feeble than fry of the two parent species. The first viable fry hatched after seventeen days. During my holidays however 23 of the hybrids were lost. Fry of these Sierra Leone forms sometimes are rather difficult to raise, so this may be the reason for the losses of so many hybrids. The remaining hybrids matured as two males and five females. After the maturing these individuals were not feeble. Both males were used several times in spawnings with their sisters and many eggs were harvested. Not a single egg developed (even a blastula), so apparently these two males were sterile. The females were spawned with ROL males (no matured SL4 males were had at that time). Their eggs were not normal and many eggs were not viable. Other eggs were normal and were able to develop. From these backcrossings I had 53 developing eggs and very many abnormal eggs from unknown reasons, no thrombus was discovered.

The F2 backcross individuals (SL4.ROL/ROL) were very feeble and in spite of good care I lost most individuals before maturing. In 1964 Pr. Kosswig took over the remaining SL4/ROL and SL4.ROL/ROL individuals except for two F1 females.

I had difficulties in keeping my old males of SL4 and ROL in fertile conditions as males often develop struma. This disease also sometimes is a problem in CIN males. Females of these three species that develop black color on male's throat during display do not develop struma. Males that suffer from struma are sterile. Individuals of AUS, another species developing black throats in males, also sometimes develop struma. I have not been able to cure this disease.

On my preserved individuals of SL4 and ROL (different strains) I prepared these counts:

D= 11 12 13 14 Dm ROL 1 9 16 5 12.8 SL4/ROL 0 0 2 0 13.0 SL4 0 6 17 9 13.1

A= 15 16 17 18 Am ROL 5 20 5 1 16.1 SL4/ROL 1 0 1 0 16.0 SL4 1 16 15 0 16.4

Sq-long= 29 30 31 32 33 Sqm ROL 6 13 12 5 0 30.4 SL4/ROL 0 2 2 0 0 30.5 SL4 2 7 30 10 3 31.1

These differences in the average figures for D, A and Sq counts do not support any separation of these two species from morphological characters. Also I found no sufficient differences when the orthodox characters were calculated and compared.

The color patterns differ but, in my opinion, only the pattern of the anal fin shows constant differences. In the ROL group of forms the anal fin has a dark red edge, whereas in SL4 and other forms in this group the fin has a dark red separation band that is close to the lower edge. This band was even more marked and separated from the lower edge in the two hybrid males. Apparently the SL4 species does not develop any yellow color at the upper and lower edge of the caudal fin as do most (but not all?) males of the ROL and LIB forms. Roloff sent me live individuals of a certain form (SL6) from a locality near Taylor Town in the Freetown area. This form I considered as a derivate of ROL (or a sibling species). In this form males may or may not develop yellow fin edges in the caudal fin. No Callopanchax develops any yellow color at the free edges of dorsal and anal fins.

As the SL4/ROL cross produced males which apparently were 100% sterile and females which were "semi sterile" the SL4 and ROL forms probably are not able to exchange genes directly. As no populations of any of these (or related) forms are found inside the broad savanna wedge which separates the Freetown forest from the main Liberian forest (which extends a little west of Kenema) I think that we also may consider the two forms as full species as there are no intermediates (geographically and genetically) to transport genes from the Freetown area to the Kenema area.

In Roloff's opinion the SL4 form also occurs in the Freetown area, but from what I have seen of preserved and live individuals from that area I hold some doubt. Roloff however caught a ROL like form in the Kenema area, close to the locality for SL4. This form may or may not fall out as a derivate (or similar to) of LIB = CAB.

At the present time the climatic conditions in Sierra Leone do not allow an unbroken rainforest to exist between the Freetown and the Kenema area. Rather small differences in the mean rainfall may change this situation and a small increase may permit the forest groups to unite. From geological and meteorological research in West Africa we know that the climatic conditions have changed much during the last million years. These changes in climate are linked to the glacial periods and interglacial periods in Europe and North America and probably a glacial period will produce a less moist climate along the Upper Guinean Coast. On the other hand interglacial periods may produce more humid climate in this part of Africa. These changes are made by the moving the climatic belts north and south of their current location in Africa north of the Equator. I give references in literature for these problems in the last issue of the Killie Letter (spring 1964). This means that during glacial periods the main Upper Guinean Rainforest from Cameroon to Lower Guinee will fall into fragments, and in these relict forest groups the forest-bound Rivulins and other organisms will survive the dry times. Probably sufficiently large relict forest groups will maintain most animals and plants that were found in these areas before the fragmentation. As the climate in the forest itself probably does not change (much) the milieu or biotope remains rather unchanged, even during severe fragmentation. If the different groups of organisms are maintained in not too small of a population size, a genetical "revolution" (in the sense of E. Mayr) probably will not take place. This means that the (visible traits of) a phenotype may remain rather unchanged because the selection pressure will not change. Other changes may occur in the chromosome arrangements and other "internal" matters that produce differences in the "reproduction".

In other words "if it was a good thing to look as ROL individuals do before the fragmentation, why should this change during the fragmentation if the ecological conditions remain unchanged"? If this is true then there is no "need" that ROL and SL4 should show large differences in morphology after the end of the fragmentation, whereas these two forms indeed may have developed "isolating mechanisms" during the separation.

As I now have both the SL4 and the ROL like forms from the Kenema area in my tanks, crossings will be arranged in order to see if also these two forms are genetically isolated. Beside differences in genetics disclosed from the SL4/ROL cross, differences in behavior exist.

The LIB-SL4-ROL group of apparently similar forms has more representatives that are about to be studied. One representative from the Upper Guinee area probably is identical with MAE (Aphyosemion maeseni Poll). We have not had live individuals of this form but we have about a thousand of preserved individuals. As the phenotype for this form was found to be very variable, I prepared counts (dorsal fin rays only) on about 500 individuals:

D= 08 09 10 11 12 13 14 Dm NZE 1 2 177 210 42 37 7 10.9

This variation in dorsal rays is high for individuals from a single micropopulation. I found nothing to support a division into two different species. In this form as in SJO (but not in GUI) the male develops more dorsal fin rays than does the female. This fact is responsible for some part of the variation, but not for all.

(83) SPU/NIG 1964-65 (not finished)

Two different crossings were prepared. In both a SPU male from Arnoult's strain was used. The females I used differed, as one came from the NIG-AK (Akure) and the other from the NIG-OW (Owo) strain.

Mr. Ib from Dragor prepared the cross mentioned first for me. He raised fourteen hybrids. All developed into females. Most of these (except for two) have been preserved now and they never gave eggs in spawnings. I also doubt that the two remaining large females ever will be able to produce eggs.

I crossed the SPU male to one of my OW females. I had 43 eggs. 25 of these developed. After eighteen days most hybrids hatched. They were very viable and not difficult to raise. In this combination I had males and females. Here are the counts for 30 NIG-AK, 18 NIG-OW and 10 SPU together with 2 (males)

NIG-OW/SPU, 12 SPU/NIG-AK and 18 SPU/NIG-OW:

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D= 12 13 14 15 16 17 Dm
NIG-AK 0 17 9 4 0 0 13.6
NIG-OW 2 15 1 0 0 0 13.0
NIG-OW/SPU 0 0 0 1 1 0 15.5
SPU/NIG-OW 0 0 0 6 11 1 15.7
SPU/NIG-AK 0 0 4 3 5 0 15.1
SPU 0 0 1 6 3 0 15.2
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A= 15 16 17 18 Am NIG-AK 3 22 5 0 16.1 NIG-OW 6 9 3 0 15.8 NIG-OW/SPU 0 0 1 1 17.5 SPU/NIG-OW 0 1 11 6 17.3 SPU/NIG-AK 0 6 5 1 16.6 SPU 0 2 8 0 16.8

Sq-long= 29 30 31 32 33 34 Sqm NIG-AK 0 3 14 12 6 0 31.5 NIG-OW 0 2 18 13 2 0 31.4 NIG-OW/SPU 0 1 3 0 0 0 30.8 SPU/NIG-OW 0 5 12 14 3 0 28.5 SPU/NIG-AK 0 2 6 9 6 1 32.0 SPU 2 8 8 2 0 0 30.5

A small but marked increase in the average figures for fin ray counts occurs in hybrids produced from the NIG-OW strain.

Males of NIG-OW/SPU did not differ in any visible detail (naked eye, live fish) from males of the SPU/NIG-OW strain. The red dots of the red pattern on the body sides were not as rounded as in NIG, but more like crescent shaped red markings, as in SPU. All males that matured completely developed very bright yellow-orange fin edges. The yellow color was well separated from the green blue color of the inner part of the fins by a very thin and not very conspicuous red line (SPU has no such separation line, NIG has a broad line). See NIG/SPU.

I found no development of H scales among the SPU/NIG-AK individuals (only females developed). Two of eleven SPU/NIG-AK individuals had one H scale each. These scales were situated on the anterior edge of the large G scale. Most larger males developed sensory papillae on the upper ray (rays) of pectorals, but no such papillae on anal fin rays. The ctenoidy in scales was concentrated to the mid rows of scales between the (over the) root of the ventrals and the middle of the caudal peduncle. In front of the ventrals there were a few spines. In the development of ctenoidy the hybrids were as SPU. In most males the branchiostegal membrane had many black pigments (as in SPU) and on the anterior part of the membrane (posterior part of the throat) a diffuse and weak dark area was visible, as in SPU, but less marked.

The hybrid males did not produce developing eggs in backcrossings and the hybrid females have not yet given any eggs at all. Two NIG-OW/SPU, two SPU/NIG-AK and one SPU/NIG-OW female are still kept in order to see if they later will be able to produce eggs.

(84) THI/ARN 1962

The status of the Rivulin here identified as Fundulosoma thierryi (AHL) is not quite clear. This aquarium fish was imported to Germany in 1959/60 from Ghana. In DATZ 1960, page 33, Meinken pictured (not very informative) and informed about the arrival of this small fish. Kluge who caught the fish said that it originated from SW Ghana, but I hold some doubt that this is correct. As a professional collector of aquarium fish Kluge in his good sight mislead us. In 1962 Stenholt Clausen caught a few individuals of a quite similar form in a swamp on the sediments east of Sogakofe in SE Ghana. This locality is indeed more "natural" for this particular species. Meinken did not identify the fish that was named "kleine Aphyosemion aus Ghana". In 1954 in his "Les Poissons du Niger Superieur" Daget identified a similar form as Aphyosemion aus Ghana" soon (I am responsible indeed) was known among aquarists as Aphyosemion or Nothobranchius walkeri (Boulenger). Daget's material originated from Diafarabe in the Upper Niger area in the dry savannah. Daget also reported Pellegrin's ten individuals from Fada N'Gourma to belong to this A. walkeri. Pellegrin (see Archiv fuer Hydrobiologie vol. XXVI, 1934 or Poiss. Afr. occd. 1927, page 226) identified his individuals as Fundulus walkeri Boulenger.

Fundulus walkeri originated from "Bokitsa Mine, Wasa, Gold Coast". We have not seen the types (badly preserved individuals, probably females), but we have seen a sample of "Epiplatys sexfasciatus" that was taken together with the types at that locality. Indeed this sample of E. chaperi contains also an individual belonging to A. petersi, thus indicating that the type locality is situated in the rainforest. The type locality is not found on any map today, but Stenholt Clausen recently disclosed where the Bokits Mine is situated. As we suggested this locality is found deep in the forest and far away from any savannah. This strongly indicates that WAL = SPU (or SPU = WAL, as the latter has priority). For this reason the "kleine Aphyosemion aus Ghana" cannot be identified as WAL. Only one species now remains: THI.

THI was described from "Mangu Gebiet, von Breite Kadjamba bis Bogu Moba, nach Panpamba bis Nacjaba noerdlich, Togo". This area is a savannah biotope containing many swamps. It belongs (more or less) to the Volta drainage from where Pellegrin's and Stenholt Clausen's individuals also originated. Individuals of "der kleine Aphyosemion aus Ghana" correspond Ahl's types to be identified as this form.

THI is the type for Ahl's genus Fundulosoma that has been based on the teeth only. This diagnosis probably will not prove to be sufficient for the maintenance of that genus. The egg of THI belongs clearly to the "Nothobranchius-type" as it is eliptic and has many rather stiff "hairs" evenly distributed all over the surface. In this it corresponds to the egg of ARN. The egg of THI has no trace of any reticulated membrane pattern and in this it differs markedly from the egg of ARN and has to be placed in the Nothobranchius egg group. The egg of THI however has a few long non-adhering filaments at the animale pole. Such filaments are found on eggs of ARN, not (in my opinion) on eggs of any Nothobranchius.

THI has rather perfectly rounded red dots on the body sides of the males. Species in Nothobranchius have no rounded red dots, not even crescent shaped red dots are found (normally) on the sides. In this THI comes very close to the species in Aphyosemion and also the weakly developed "lyra caudal fin" and the red pattern of that fin place THI in Aphyosemion, rather than in Nothobranchius.

Species in Aphyosemion and Nothobranchius differ rather much in their development of scale patterns on the forehead. THI develops a scale pattern that comes closest to Aphyosemion. This means that THI represents a "link" between the genus Nothobranchius and that of Aphyosemion (Fundulopanchax). As these two genera, in my opinion, are sufficiently separated, at least by their eggs and scale patterns, THI may stay where Ahl placed his new species, this is in the genus Fundulosoma.

Like species in Nothobranchius (plus ARN and FIL), THI has eggs that do not adhere mud particles. As THI in all matters is closest to ARN I prepared the THI/ARN cross. I had seven eggs. Four of these developed a blastula. After seven days a corda was visible in all eggs. The corda was small and not very distinct. After fourteen days there was no change in the development of the embryo. The corda still was small and indistinct. The yolk started decomposition in the usual "Nothobranchius way", small transparent oil drops were produced. Eggs of ARN and FIL (?) decompose in the way normal for Nothobranchius, but not for other Aphyosemion. After 20 days I had only one live egg left unchanged. Preserved.

After this result I crossed the THI male to one FIL female. Many eggs were harvested, but no egg developed. Probably these two individuals were not able to coordinate their movements during the spawning.

The result of the THI/ARN cross indicates that the resemblance of these two forms is not an indication of very close relationship.

I have only been able to prepare counts on three individuals from THI (Stenholt Clausen's individuals):

D= 12 13 14 15 16 17 Dm ARN 0 0 0 2 4 6 16.3 THI 1 2 0 0 0 0 12.6

A= 15 16 17 18 Am ARN 1 6 3 1 16.4 THI 1 1 1 0 16.0

Sq-long= 24 25 26 27 28 29 Sqm ARN 1 6 6 6 9 1 26.0 THI 1 1 4 0 0 0 25.5

Indeed the figures for dorsal fin rays differ much, but the important low figures for scale counts correspond.

For his many individuals in 1954 Daget said: D 12-16, A 14-19, Sq-long 27-29. For the statistics in the

first selection of this issue of the Killie Letters I have used Daget's identification of THI? as WAL.

These were the results of about ten years of crossing Old World Rivulins (not the Nothobranchius crossings and the Aphyosemion/Nothobranchius crossings which gave no development of eggs). These many crossings were not possible without the help of friends who kindly offered me live individuals of different nature caught strains of Rivulins. I wish to thank all these friends and in particular Herrn E. Roloff, Ulf Hannerz and H. Stenholt Clausen for their kind help which has been invaluable for my research in crossings. I also wish to thank Dr. Sick and Mr. Gyldenholm of the Genetisk Institut for their analysis of hemoglobine patterns that did clear up certain difficult problems. I think that it will be quite impossible for the amateur zoologist and biologist to "dive" into the zoological problems that adhere to the research of crossings without the help of a trained zoologist. Stenholt Clausen p.t. in the University of Kumasi, Ghana, has used much time through many years to teach me zoology and as you will realize from my comments on different crossings these are the results of our discussions through countless hours by day and night. In such close cooperation one does not develop ones own opinion on things. The ideas come mostly from the serious talks on the problems that arise from the research. Indeed Stenholt Clausen is not in full agreement with all the different opinions and ideas that I have given in this issue of the Killie Letters, but in most I think. I type the stencils myself (I do not need to inform you on that) and Senior Sergeant J. Nissen and Staff Sergeant E. Thomsen prepare the mailings. They did a nice work and I owe them many thanks for that.

Crossings under preparation: (85) ANN/ANN 1965 population cross

ANN belongs to the genus Epiplatys and it has the characters of that genus. It differs from other Epiplatys in several characters. The patterns of lateral organs and scales on the head are different from other Rivulins.

In May 1965 Stenholt Clausen caught a few individuals of ANN-MO near Monrovia in Liberia in the coastal "savannah" together with DAG-MO, LIB-MO and two more Rivulins. A month later E. Roloff kindly sent me individuals of his ANN strain from Kasewe in Sierra Leone (ANN-KA). Dr. W. Foersch in Munich has a third strain in ANN that originated from Conakry in Guinee. I expect individuals of this strain also for the population crossings in ANN.

So far eight ANN-KA/MO hybrids have been produced and the oldest are about to mature. ANN-MO differs from ANN-KA males only. In the MO strain the male probably is somewhat larger and it has a conspicuous orang- red marking in the posterior part of the anal fin and a very deep orange-red color at the lower edge of his very long pectoral fins. The ANN-KA male does not develop the orange marking in the anal fin, instead there is a similar marking in the dorsal fin. The pectorals are pale yellow, not orange-red. It is indeed easy to tell these two types of males apart.

ANN was described from Matca, an unidentified locality in Sierra Leone. This species has been reported from Conakry by Lambert and from Robertsport in Liberia by Fowler (Notulae Naturae 225/1950). Apparently ANN is a rare fish in Sierra Leone. Both Roloff and Schiotz were searching for this particular species in many places all over the interior of Sierra Leone and both (independently!!) found individuals at Kasewe only. There may however be further demes in the swamps along the coast.

The grouping of species according to certain non-orthodox characters

Grouping according to the characters of the egg For taxonomic research and for identification of individuals that have been preserved, the study of egg types probably is of no importance because the eggs are not so easily had. It would however not be too difficult to remove ripe eggs from ripe females if such females are in the sample.

I started this study of egg characters many years ago. Not for systematic purposes, but because I soon learned that that different species produced different eggs and often it was possible to say from which species a certain egg -found during the washing out of mud- originated.

The Rivulin egg is characterized by these characters:

- a) the size of the egg -the shape of the egg
- b) the development of filaments or "hairs"
- c) the distribution of these filaments
- d) the pattern of the egg membrane
- e) the color of the egg

I measured these sizes (under the microscope) and found these membrane patterns within: R = full reticulation, S = broken reticulation, D = further reduction (dots), P = complete reduction (plain)

Old World Rivulins: Size in millimeters: Pattern: ANN 0.9-1.0 P

ARN 1.0 R AUS 1.2 S BIF 1.2-1.3 P BIV 1.2-1.3 D **BLO 1.5 P** CAB 1.1-1.2 R CAL 1.3-1.4 S CHA 1.2-1.3 R/S CHR 1.2 R/S CIN 1.5 R COE 1.4-1.5 R/S COG 1.4-1.5 D DAG 1.0-1.1 R/P DAY 1.6 R/S DUB 1.1 D FAS 1.3-1.5 R/S FIL 1.3 R GRA 1.0 D GUI 1.6 R GUL 1.5-1.7 R/S LAB 1.6-1.8 D

LIN 1.6-1.9 R/P LON 1.4 D LUJ 1.3-1.4 P MAC 1.1 P NDI 1.3 R NIA 1.6 S/D NIG 1.0-1.5 R/S PAN 1.6-1.8 R PET 1.2-1.3 P ROL 1.1-1.2 R SEN 1.1-1.3 R/S SEX 1.4-1.5 D SHE 1.2-1.3 R/S SJO 1.4-1.5 R SL4 1.1 R SPU 1.4-1.5 R/S THI 1.0 P

The size of the egg is a rather constant character in a brood from one female at all ages, also for different females of one deme or strain, also for different demes of a single species and often for closely related species. These rules have been true for all species except for a strain in BEL (Cynolebias bellotti) from a certain pool about 250 km from Montevideo that D. Guevara of that city kindly sent me. In this strain, two rather different sizes of eggs occurred.

The large variation of egg size given for NIG is caused by the study of the egg size in the hybrids (PH/AK) that developed eggs up to 1.5 mm. The variation in FAS probably is caused by the differences also found in other characters within this very variable species. This probably also is true for LIN.

Within certain groups of apparently closely related forms rather large differences in egg sizes are seen: ARN-FIL, FAS-SEN and also NIG and FAS strains.

Large variations in egg sizes occur in eggs of certain hybrids and also in inter-population crossings (NIG).

The patterns of the egg membrane probably are a more important character. Indeed the differences in patterns do not split up the whole group into distinct units as there are many intergrades between different types of patterns, not only when species are compared, but also among eggs of a single female.

The reticulation of Rivulin eggs is a hexagonal reticulation. According to Peters (see previous pages) this pattern represents a reinforcement of the egg membrane. I think that Peters is right in this. Probably there are different ways in which an egg of an annual Rivulin can be reinforced. Within Cynolebias and Pterolebias, which belong to a group of species in which the "annual characters" are maximum, the eggs do not develop any reticulation at all. These eggs are probably reinforced by only the increased depth of the membrane.

In Callopanchax (SJO) and Fundulopanchax some species may reproduce in the "annual way" and their eggs have to survive in rather dry mud for many months. Most species of these two groups develop a full reticulation of the egg membrane. A more or less reduced reticulation also exists on eggs of species that are not at all considered as annuals. LIN and PAN in Aplocheilus are examples. As the reticulation probably is not a "pre-adaption" for annual life this character might be considered as an ancient character that has become less important for some species during their evolution. If this idea is true then most (if not all) Old World Rivulins originated from "an annual Cyprinodont".

In my opinion the different patterns of filaments on egg membranes found in Nothobranchius and in Fundulosoma represent another way of protecting the egg during "annual life". The many evenly distributed short "hairs" seen on the surface of such eggs may keep away from the egg membrane hard and longer particles (sand) and in this way supply the egg membrane with some sort of a protective layer of fine particles or even air (after the drying up of the mud). Such eggs do not need also the protecting reticulation. Here the eggs from the South American Rivulin, the Cynopoecilus, attract attention. In this genus (I have kept two species: MEL and LAD = C. melanotaenia and C. ladigesi) we will find many traits which point towards a closer relationship to Old World Rivulins than found among other South American Rivulins. First these Cynopecilus develop rather similar scale patterns of the forehead (as also Cynolebias do), but different patterns of lateral line organs. Next these species develop "wrinkled scales" in males and sensory papillae on pectoral fin rays (which WHI among Cynolebias also do). Next the eggs of Cynopoecilus do not adhere mud (all other South American Rivulins known to me produce eggs which adhere mud). Next the Cynopoecilus egg has a certain development of filaments on the membrane. These filaments (in my opinion) assemble six and six to form a short and very stiff protuberance on the egg surface. At the top of this formation the "loose ends" split up thus producing a small plate that may keep away sand etc. from the egg membrane. The six filaments that produce such "palm" originated from the corners of a hexagonal reticulation of the membrane just like the reticulation seen among Old World Rivulins. No further South American Rivulins develop a hexagonal reticulation of the egg membrane.

All these resembling characters found when Cynopoecilus species and Old World Rivulins are considered could not be convergence, but should reflect true relationship. Also MEL develops a premating dark lateral band, not in females (as in the Old World), but in males. It is indeed a good thing that also differences are found.

The complicated "egg protection" found in eggs of the Cynopoecilus species contain both types of protection found among Old World Rivulins: evenly distributed short and stiff hairs and reticulation of the membrane. It could be so that in Nothobranchius the reticulation was lost whereas in Callopanchax and Fundulopanchax the short stiff hairs and the non-adhesive properties were lost (except for FIL and even less reduced for ARN).

In Oryzias, another subfamily in Cyprinodontidae, eggs have the pattern found in Fundulosoma, but I do not remember if these eggs adhere mud. Probably they do. The color of the egg (the yolk) depends more or less on the food, but generally eggs of species in Epiplatys develop less yolk color than do eggs of Aphyosemion.

The study of egg structures -at least- gave a distinct grouping like this: a) "Notho type": Nothobranchius and Fundulosoma

b) ARN

c) FIL

d) All remaining Old World Rivulins (subdivision possible)

Grouping according to scale arrangement on the head From 1957 to 1960 I supplied Dr. J.J. Hoedeman with preserved material of Cyprinodonts and I learned to use his system of frontal scalation patterns for the identification of Cyprinodonts (South American species). Since that time all individuals belonging to Cyprinodonts which were at my disposal were studied according to this particular character also and photographed. Probably more than a thousand such photos are now in my collection.

See also: Hoedeman, J.J. "The frontal scalation pattern in some groups of tooth carps" in Bull. Aqua. Biol. vol. 1, 1958, pages 23-28 and "Notizen _ber die Gattung Aphyosemion" in Aquarien und Terrarien, vol. 4, 1957, pages 294-296 and Whitehead, P.J.P. "The Pantodontinae..." in Bull. Brit. Mus. (N.H.) Zool., ser. vol. 9, 1962, pages 105-136 As a marked connection exists between development of scale patterns and patterns for lateral line organs "the sensory canals of the head in some Cyprinodont fishes..." by Gosline, W.A. in Occ. Pap. Mus. Zool. Univ. Michigan, 519/1942 also might be considered.

The frontal scalation pattern found within Old Word Rivulins is a very stable pattern if the pattern (patterns) developed by this group of Rivulins is compared with the complicated patterns found among South American Rivulins, Procatopodins, Cyprinodontids, Aphanids and Fundulins. The reason for the few and small variations which develop in the frontal scalation patterns within Old World Rivulins may be considered as an indication of close relationship. In my opinion this marked uniformity is based on the "fact" that in this group of Cyprinodonts the frontal scalation has reached the final solution of the scalation problem in Cyprinodonts. Probably these Rivulins were forced (more than other Rivulins and Cyprinodonts) to develop the "idealized scale pattern" because these small fishes live in small bodies of water which often contain very many obstacles (plants, roots, branches etc.) which may tear off the frontal scales if the unprotected edge of these scales is directed forward. Procatopodins that also occur in the West African freshwaters generally develop less or much less "idealized" scale patterns but also these fish are generally found in the open waters where serious damages of the frontal scales from obstacles are less likely to occur. This may be the reason why in this group of Cyprinodonts almost all possible types of scale patterns develop, from the most ancient or primitive pattern found in Lamprichthys (A pattern) to the advanced H or I patterns developed in other Procatopodins.

In my opinion the original scale pattern in Cyprinodontidae is the A pattern that develops in Lamprichthys, in some Orestias, in some Fundulus and in Aphanius. According to Hoedeman, Austrofundulus (may) also develop this particular pattern. The A pattern is a very vulnerable pattern for fishes that live in waters where obstacles occur. The non-protected A scale soon will be lost.

The first (?) modification of this pattern may be the pattern developed in Rivulus, Pterolebias and Rachovia. In these patterns the A scale is situated not upon (as in the A pattern) but beneath all the scales in the ring around the pineal organ - the B-C-D-E-G series of scales. Because of that "replacement" of the central scale (the A scale) one pair (or single scale) of scales of the ring now is fully exposed. This

transformation of the ancient scalation will not however solve the problem of scale protection, but possibly the pineal organ obtains more protection. If an ideal scalation is needed, all scales of the head should be placed in such a way that their free and unprotected edges are directed (more or less) backwards.

In the Rivulus-Pterolebias-Rachovia pattern, the so-called B scale is situated on the A scale and for this reason the anterior edge of that scale is not protected. As only a small part of that scale edge is free, this exposing of the anterior edge of the B scale probably is not a serious matter. In the scale pattern (patterns) found among Old World Rivulins the anterior edge of the B scale is always below the anterior edge of the A scale. This is a step towards a more idealized scale pattern. Just that pattern is also found in Cynolebias and in Cynopoecilus. Hoedeman said: "This appears to be of primary importance, representing a situation bridging over the gap between the South American and the African members of the tribe Rivulini" (Hoedeman 1958, page 25). As we have seen from the egg characters this "bridging" also exists when Old World Rivulins and Cynopoecilus are compared. The development of "wrinkled scales" represents one more "bridge" and so on. Probably I had many more individuals of these South American Rivulins than Hoedeman had. My individuals belonged to Cynolebias bellotti, C. nigripinnis, C. whitei, C. adloffi and Cynopoecilus melanotaenia and C. ladigesi. This means that in Old World Rivulins, the row produced by the A and B scale is a normal row corresponding to all other scale rows on the body of the fish.

This indeed represents the first important step towards an idealized scale pattern (for species that live in water containing obstacles). C scales rest on the B scale and D scales rest on C scales. In most Old World Rivulins the edges of the D scales cover the right and left edges of the A scale. This is the ideal condition from a "protective point of view". In ANN and often among Procatopodins the inner edges of the D scales are however beneath the A scale. Sometimes within these forms only one of the D scales takes in this position. This fact indicates that these forms are a little behind other Old World Rivulins in their development of the idealized pattern.

From the ring of scales surrounding the pineal organ rows of scales extend over the body and the head of the fish. The B and C rows produce some of the scale rows on the body sides and as these two scale types are situated they will produce scale rows in which the free edge of the scale is directed -more or less- to backwards. The D rows (originating from the D scales of the ring) extend downwards and produce (some of ?) the scale rows of the posterior sides of the head and of the cheek. Below the eyes these (this) row/s of scales turns into a forward direction an in front of the eyes, the row of scales may turn in an upward direction if there is sufficient space for scales on the preorbital region. This is the "ancient" or primitive development of scales on the cheek. We will find this scale pattern in Cyprinodon (C. variegatus Lacepede). In this species the scale rows on the cheek are situated in a way that the anterior edges of the scales are directed forward below the eye and upwards on the preorbital region. It does not make this vulnerable scalation less "idealized" that strong ctenoidy develops on exposed scale edges in males. Also the ctenoid spines are at a right angle to the surface of the scale. Indeed such scalation is not suited for a life among plants or algae.

The primitive scalation of the cheek that develops in Cyprinodon variegatus might be improved in one of two ways. The first attempt of an improvement is found among species in Fundulus. In some species in Fundulus the base (roots) of the scale situated below the eyes are turned more or less away from the line

arrangement found in Cyprinodon. This means that the direction of growth for these scales is changed from a forward direction into a more or less marked downward direction. Now the scales might be arranged in two ways: the anterior edge of a certain scale on the cheek may be situated below the scale which is just in front of it or the anterior edge may be situated on the scale just mentioned. Indeed, in Aphanius, (which also develop this type of transformation of the scales on the cheek) both types of scale arrangement may be found. One type on is one side of the head and the other type of scalation is on the other side of the head. This means that in that particular individual of Aphanius, the scales on the cheek have their "free" edges directed forward on one side of the head whereas on the other side of the head they are directed backwards. In some species in Fundulus the "turning of scale bases" is almost complete and the exposed scale edges are directed backwards and downwards.

There is still one more possibility for a "reversal of scales of the cheek". This system is found -more or less- in Jordanella. In this Cyprinodontid, the preorbital region is wide and may give room for even more than a single row of scales. Just below and behind the eyes the scales are situated as in Cyprinodon variegatus. The scales on the preorbital region (not in all individuals) however are placed in a way that their exposed edges are directed downwards and not upwards as in C. variegatus. In my opinion the scale rows found on the preorbital area in Jordanella do not belong to the D series, but originated from one of the scale rows situated on the anterior part of the head. A close study of the scalation in Jordanella soon disclosed that the "reversed scales" of the preorbital region belonged to one of the scale rows on the anterior part of the forehead. These scale rows meet with the D series of scales in a line about 45 degrees (through the center of the eye) in a forward-downward direction. This line also represents the direction of the series of very small and numerous pit organs (of the lateral line system) that descends along the median part of the preorbital region and then turn upward-backward and produce the line of pit organs just below the eye. In Jordanella, one of the scale rows of the anterior part of the forehead probably once turned outwards-downwards and produced the scale rows on the preorbital region thus "forcing back" to a position below the eye the scales of the D series. If this forcing back of the D scale rows was more advanced in Jordanella also the scales below the eyes would indeed "reverse".

In Rivulinae (Old World species and South American species) all species develop a pattern of scales on the cheek in which the exposed edges of the scales are directed backwards in a most ideal way. In Procatopodinae also this scale pattern develops in all species that I have studied (most nominal species). In this group of Cyprinodontidae the preorbital region is wide and may indeed support scales. This fact is important for the study of scale development or scale evolution in Rivulinae (Old World only) and in Procatopodinae. Again Lamprichthys is a most interesting species. In this form the preorbital region is very wide and supports several rows of scales. From the upper part of the forehead scale rows (three normally) descend and cover the preorbital region. When they have covered this area they turn backwards and also cover the area below the eyes. Just behind the eye the D scale series still descend as in Cyprinodon and all other Cyprinodonts. These two systems of scales meet each other in a line that -in most species- runs through the center of the eye at an angle of 45 degrees backwards-downwards. In this way the idealized scale pattern of the cheek is produced in Rivulinae and Procatopodinae. These are very clever fishes indeed, more clever than those in Fundulinae and Cyprinodontidae. Indeed Jordanella developed the "idea" but was not able to finish the reversal of these scales.

Well, there are still more scales in the "ancient Cyprinodont" which need a "reversal" if that fish should

occupy water in which obstacles occur. We still have to "reverse" the scales of the forehead in front of the A scale. In the "ancient system" -very markedly developed in Lamprichthys- all scale rows of the forehead in front of the A scale have their exposed scale edges directed forward. Indeed this system was needed to "develop" the reversed scales of the cheek. After this reversal (they did the job) we also may reverse these scales. This could be done if in the "Cyprinodont system" the preorbital scale rows forced their scales up on the top of the head and forced back to the line through the A scale, all these E-F-G-H etc. scales rows which need a reversal. Such reversal of the frontal scales indeed would leave the scales of the cheek "unreversed". Apparently this type of evolution of scale systems has not been used in this group of fish. For the present it is not possible to explain in which way the reversal of the frontal scale in front of the A scale in front of the A scale took place. Some elements of this reversal of scales however may be explained.

Hoedeman probably is right when he assumes that fusion of scales did play an important role. This is quite clear when the so-called H scale, found in COE, GUL and NIG, are studied.

In most Old World Rivulins the anterior-most scale on the forehead is the large G scale. The root of this scale is situated at the anterior edge of that scale and the exposed edge is directed sidewards and backwards. The anterior edge of the scale is almost linear and the anterior part of the scale for this reason is almost quadrangular. If H scales occur the anterior corners of the G scale are lost and replaced by H scales which are situated below the anterior edge of the G scale in COE and GUL and below or upon the G scale in NIG. This is a strong indication that the anterior part of the G scale is produced by fusion of small scales. For this reason the G scale in Old World Rivulins probably is not a true G scale that is a scale that originated in the ring of scales around the pineal organ. The fact that the H scales in COE and GUL are situated below the anterior part of the G scale again indicates that, in these forms, the complete reversal of scales has not yet taken place. The situation we find in NIG however indicates that in this species a complete reversal of frontal scales is almost complete.

In Pachypanchax, in GUI and in some strains of BLO the reversal of frontal scales is still less complete because, in these forms, the E scales are situated on the G scale. In these species the anterior edges of the E scales are exposed and vulnerable. This may be the reason why GUI lives in mountain brooks and does not descent to the lowlands. This also indicates that, in scale pattern, GUI is less advanced than are almost all other species among Old World Rivulins.

GUI has no H scales in the many indivduals that I studied. My few individuals of PLA (Pachypanchax playfairi) also had no H scales. The anterior edge of the G scale is rather quadrangular in these forms. In HOM (Pachypanchax homalonotus) several H scales occur and the scale pattern of this species (I have four individuals only, but in all the scale pattern is undisturbed) resembles various species in Procatopodinae. This means that among the many species in Old World Rivulins HOM has the least developed frontal scale pattern.

There is however still one more way in which the frontal scales might be protected. This system is well marked in Nothobranchius and in Cynolebias (not in Cynopoecilus). In these species the size of the frontal scales is much reduced (or has not increased!) and the scale system has also withdrawn from the anterior part of the forehead, leaving (well marked in Nothobranchius) a thick layer of spongy skin. A rather similar covering produced by a spongy skin exists in SJO (less in the female) but in this species the

usual G pattern produced by large frontal scales is seen. Normally, in Nothobranchius, there are no scales in front of a line through the centers of the eyes. At least there are no exposed scales. A few very small scales might be hidden in the skin. The small scales produced on the forehead in Nothobranchius and in Cynolebias often do not overlap much or do not overlap at all. This makes a study of the scale pattern very difficult. In Nothobranchius one may speak of formal H or I patterns.

In some individuals the scales in the central row overlap the scales in the side rows, in other individuals the reverse system is found (approaching the Rivulus system). Generally Hoedeman nomenclature for scale patterns cannot be used on individuals belonging to these genera and Hoedeman also did not deal with Nothobranchius. The important thing probably is the anterior edge of the A scale. This scale, in all individuals that I have studied, has the posterior edge resting upon the B scale. This is the non-Rivulus pattern. I have studied the scale patterns of Nothobranchius cf. guntheri, N. cf. palmquisti, N. neumanni, N. orthonotus and N. rachovi. All individuals of these forms developed the "Nothobranchius pattern". There is no more difference between individuals of this genus and those of Aphyosemion (Epiplatys, Pachypanchax, Aplocheilus).

In BAT the scale system also -to some extend- recedes from the anterior part of the forehead, but not to such an extent as in Nothobranchius and also in BAT the normal G pattern produced by large scales (G and E) develops. BAT has no spongy skin in front of the G scale. Instead there are numerous papillae of the type that develops on the anterior part of the throat in most forms.

In ANN the area on the forehead that might contain scales is very narrow. The scales in the "mid row" do not double and the scale system is difficult to classify. Formal A or G or H or even I scale patterns develop. Also a single individual may develop the A type together with the I type as both scales are fully exposed. Hoedeman's system is not useful for this species. These were the scales belonging to the central row (rows) of the forehead. There are other scales on the head situated on the top of that part of the fish.

For his study of Rivulus and relatives of this group of killies, Hoedeman also used the name "F pattern". This type of pattern does not occur among Old World Rivulins. The formal F scales are always situated below the E scales and they produce a bridge (the "eye bridge") corresponding to the 4a-4b interruption of canals after the Gosline system for canals (lateral line organs). From the formal F scale a row of scales may extend forwards near the upper rim of the eye-lid. This row of scales often contains two scales only. If the individual develops the G scale pattern, the anterior-most scale of the F rows is fully exposed. This means that in these scale rows the full reversal of scales has taken place. However within species that develop a constant G pattern a few individuals may develop an "unreversed scale pattern" in the F rows.

In Fundulinae, Procatopodinae, Cyprinodontinae, etc., the F scale series branches above the eye. Two rows of scales are produced - one in a forward direction, another in a backward direction. The latter series of scales does not develop in Old World Rivulins and only HOM develops one scale in this series. This is one more indication of the incomplete evolution of scales in this particular species.

There is one more bridge of scales in some Procatopodinae, this bridge corresponds to the interruption 2a-2b in Gosline's system. This bridge belongs to the row of scales that descends from the top of the head into the preorbital region. The H scales in GUL-COE do not belong to this type of scalation, whereas the

H scales in HOM may belong to such a bridge, although no bridging of the lateral line groove takes place.

In Nothobranchius (most, if not all) individuals develop no scale bridge across the groove for lateral line pit organs (the "eye bridge") and also there are no F scales above the eyes. In this the species in Nothobranchius differ from all other Old World Rivulns (except for some individuals in ANN). As there is no "eye bridge", there is no interruption of the "4a-4b" type and the groove (corresponding to the canal in Gosline's system) is unbroken over the eyes in Nothobranchius and in ANN.

For the group of Old World Rivulins considered here we had this major grouping:

E-type: no H scales: BLO, GUI, PLA (not always in BLO) with H scales: HOM and ANN (ANN is variable)

G-type: no H scales: all forms not mentioned in other groups with H scales: COE and GUL and sometimes also NIG, GAR, SPU

This grouping probably does not reflect certain taxonomic grouping but might be of some importance in the phylogeny of these forms.

Grouping according to the development of ctenoidy in scales Stenholt Clausen is concentrating on this character and I learned much from his study. Ctenoid spines in scales is a male characteristic. This character is linked to the development of sensory papillae on fin rays. If the segments of the fin rays are studied under the microscope you will find that at the end of the segment certain spines develop, supporting the long and often filamentous papillae. The spine stands at a right angle to the ray segment as do the spines on the surface of the scale. Also many spines on the scales on the body sides develop such filamentous sensory "papillae".

If the ctenoidy is concentrated to the mid rows of scales, there are no anal fin papillae, whereas such papillae may develop on the rays of the pectoral fin. These papillae may be more easily seen than the spines on scales that may be lost in formalin.

The most marked ctenoidy occurs in Nothobranchius and in these males not only the anal fin normally has numerous papillae of the "filamentous type", but also on the dorsal fin rays such (reduced) papillae may develop. Also, in Fundulopanchax, the ctenoidy is well developed in ARN, FIL, COE, GUL and SPU and some strains of NIG. Probably all species now considered to belong to this group develop ctenoidy. BIV and LAB, and like forms, do not belong to this group.

In Callopanchax, no ctenoid spines develop on scales. Instead some males develop "wrinkled scales" and also sensory papillae.

Groupings:

- a) Nothobranchius and Fundulopanchax
- b) Callopanchax
- c) other species belonging to Old World Rivulins

Ctenoid spines do not occur in South American Rivulins, whereas "wrinkled scales" occur in Cynopoecilus and sensory papillae in Cynolebias whitei, but in no other species of that genus.

Ctenoid spines occur in males in Procatopodinae, Fundulinae, Cyprinodontinae, Aphanius and Orestias. So this character is widespread in Cyprinodontidae.

Grouping according to hemoglobine patterns Dr. Sick and Mr. Gyldenholm, both of the Genetisk Institut, prepared these analyses for us. The technique, for the present, is improved to such extent that individuals of ANN and DUB are analysed.

Apparently the "Rivulus-Aphyosemion" pattern is the dominating hemoglobine pattern in Rivulinae. Among Old World Rivulins this particular "four-line pattern" is found in all species of Aphyosemion (Callopanchax, Fundulopanchax and Aphyosemion s.s.) and in the FAS-SEN group and the DAG-GRA-MAC group in nominal epiplatys. In these patterns not only are four-lines are produced, but also these lines -one by one- correspond in all patterns. Three species of Rivulus (we had these three species only) developed this particular pattern, whereas Cynolebias developed a different pattern and so did Jordanella.

The Aplocheilus forms develop three different types of hemoglobine patterns. Those however of LIN and PAN are rather similar. They only differ in the concentration of hemoglobine in the two lines that develop in this simple pattern. BLO and DAY develop rather complicated patterns that correspond in some way to the CHA-LON-SEX pattern in Epiplatys, but the patterns developed by the two Aplocheilus species are not similar to the six-line Epiplatys pattern.

In Epiplatys, at least three different patterns occur. As mentioned above, two groups in Epiplatys (FAS group and DAG group) develop the Rivulus-Aphyosemion pattern. BIF develops a pattern different from all other species of this genus and CHE-SHE-CHA-SEX-LON-DUB represent the six-line pattern.

Some of these groupings probably are taxonomic groups, whereas other groups (six-line patterns) probably should not be considered as a group of closely related forms.

Grouping according to patterns of lateral line organs of the head Stenholt Clausen has worked out this system, but apparently he has not yet published his results. Generally this system is based on the position of the lateral line pit organs situated in front of the frontal scales in the median part of the forehead.

One will get an idea of the differences that develop in this pattern if an individual belonging to the Fundulopanchax is compared with an individual of Callopanchax. In the former the two pit organs are well separated and the corresponding system of fleshy lobes produced by the skin also are well separated. In the latter the two pit organs are close, one to the other, and in front of the pit organs an undivided fleshy lobe is seen. I have studied very many individuals belonging to these two groups of nominal Aphyosemion ("eastern Aphyosemion" and "western Aphyosemion") and I found (as Stenholt Clausen did) that these two patterns are very stable and that one will never hesitate in placing an individual in its own group. In a certain species of Callopanchax (from Upper Guinee, probably MAE) some individuals vary and in some of these a somewhat "intermediate" pattern develops. One will not however hesitate to place even the most "intermediate individuals" in Callopanchax.

In their lateral line pattern the species in the subgenus Aphyosemion correspond exactly to the species in Fundulopanchax. Species in Nothobranchius and Fundulosoma develop patterns that are similar to the Fundulopanchax pattern. In Epiplatys, the "formal" Callopanchax and Fundulopanchax patterns also develop. Most species develop the true Callopanchax, whereas the few species in the SEX-LON group develop a pattern that is similar or related to the Fundulopanchax pattern. To be sure, I did not indicate that the SEX-LON group is a derivate of the Fundulopanchax group. The SEX-LON pattern probably developed independently from the Fundulopanchax pattern.

In Pachypanchax, I only have a few individuals. Two individuals of PLA (Pachypanchax playfairi Guenther 1866), both individuals develop the typical "Fundulopanchax pattern" or SEX-LON pattern. In HOM (P. homalonotus Dumeril 1861) I have four individuals, all females, all sisters. These individuals came in "as eggs" from J. Scheidnass in 1958. Two individuals developed the typical Callopanchax pattern, whereas two more individuals developed the Fundulopanchax or SEX-LON pattern. This is an indication that in this "ancient species" the two types of patterns have not yet stabilized or are not selected in evolution. After this discovery, I am able to understand in a better way why the SEX-LON group developed the "Fundulopanchax pattern".

In Aplocheilus PAN has a very stable pattern of the "Fundulopanchax type", whereas most individuals of LIN also develop this pattern, but apparently it is not as stabilized as in PAN. In their patterns these species differ somewhat from the African species in minor details only.

Individuals of DAY also show some variation, but in this species the pattern belongs to the Callopanchax type. Also most individuals of BLO develop this pattern. It is not very stable and not very marked, as the pit organs and their lobes often are very indistinct. This is also true for most small forms as ANN, DUB and FLA in which the pit organs often are very difficult to trace.

If only the lateral lines on the head are considered we have these groupings:

a) Callopanchax and Epiplatys (without SEX and LON) and Aplocheilus (without LIN and PAN) b) Fundulopanchax and Aphyosemion s.s. and Nothobranchius and Fundulosoma and Pachypanchax (without HOM) and Aplocheilus (without DAY and BLO) and SEX and LON c) HOM that develops both patterns even in a single brood

Grouping according to throat patterns

Within Old World Rivulins many species belonging to different genera develop conspicuous color patterns on the throat. Such patterns do not occur in Procatopodinae, nor (generally) among South American Rivulins. These patterns probably are used by the fish for identification and for this reason they may be of a certain importance in the systematics of these species.

Generally, these patterns are used by the fish for the identification of the sex of an individual that is approaching head first. These patterns might be permanent or temporary. They are composed of red and black pigments.

In Nothobranchius the individuals do not develop any particular throat pattern. Preserved males of some species (in formole) have much more dark pigment on their lower part of the head than females have. In

life I did not notice that these males (which I raised myself in my aquarium) developed any dark color on their throats during display. In RAC (N. rachovi) the adult male develops an intense orange-red throat color not seen in females. This indeed is a primitive throat signal.

In Fundulosoma (THI) no particular throat pattern develops in individuals. In GAM the gill covers are orange and as the branchiostegal membrane is brown a throat pattern might be present in the male. As in GUL, SPU and certain males in NIG.

In nominal Aphyosemion two rather different types of throat patterns occur. In Callopanchax (plus CIN, AUS and apparently also to some extent COG) the male develops a very dark color (often with a clear blue shine) on the whole surface of the lower part of the head. This dark color is not permanent in most males and when the male is not spawning or fighting its throat does not differ (much) from that of the female. In SJO the blacking of the throat is almost nil in the adult male. Instead SJO develops an intense blue color on the lower part of the head. How this color (guanine?) is produced is still a problem for me, as one day one male had a red throat without blue color, the next day the throat was bright blue and the next day, again, the throat was red without a blue shine. These changes are only found in the male that is about to mature. When old, the male has a permanent blue color all over the lower part of the head.

In Fundulopanchax and in Aphyosemion sensu stricto no dark throat color develops in males (except for CIN, AUS and COG?). In this group of nominal Aphyosemion the male develops a (often complicated) pattern in red color. No species now considered to belong to Callopanchax develops any red pattern below the black color. In some males traces of such red patterns are seen in the line formed by the small pit organs behind the lower lip and at the corners of the mouth.

Some species in the group of "eastern Aphyosemion" develop a rather reduced red pattern in males (SPU and COE and some males in NIG). For the present it is impossible to split up the group of "red patterns of the throat" into subgroups. Such subgroups however probably exist. BIV males develop a particular black-and-red pattern related to the common "eastern Aphyosemion" pattern. All females belonging to Callopanchax and also females of CAL (which belongs to the "eastern Aphyosemion") develop a certain rounded dark spot on the throat during pre-mating display.

In Epiplatys several distinct types of throat patterns develop in different groups. The common "Epiplatys pattern" is closely related to the Callopanchax pattern, but in Epiplatys the pattern is more complicated. Usually there are two dark crossbars on the throat - one in or behind the lower lip and a second one between the corners of the mouth. These dark lines develop in both sexes and often the dark areas contain much red pigmentation that probably is "used" in identification. Often the red pigments are arranged in a way that these pigments would produce the normal pattern seen in Aphyosemion (eastern group) males if the black pigments were lost or reduced. During display the "common Epiplatys pattern" is changed in a very conspicuous way. In males the whole lower part of the head develops an intense black color, whereas in females the dark pigments in front of the "line between the corners of the mouth" often produce a uniform black area which reaches the lower lip. In other females only the two original dark bars are seen, more saturated as usual. This blacking of the anterior part of the throat in females of many Epiplatys may (or may not) correspond to the "dark spot" seen in females in Callopanchax.

The common Epiplatys pattern develops in FAS, SEN, CHA, SHE and less marked (normally) in BIF, CHE, SEX and LON. The blacking of the throat in males is nil or much reduced in the group last mentioned. Preserved males of this group also have more black pigments behind the line between the corners of the mouth than females in DUB have, no particular throat pattern develops, but also in this species the male has more dark pigments on the lower part of the head than after preservation females have.

In DAG a very distinct throat pattern system develops. See DAG/DAG.

In MUF the common Epiplatys pattern develops. In this species individuals may develop traces of a third black bar on the throat. This bar develops in a line below the centers of the eyes. In this species and also in some strains of SEX and LON the male develops many more red pigments in the dark bars than females do. If the concentration of dark pigments would decrease these males indeed would develop the common Aphyosemion (eastern group) pattern and females would develop no pattern (as also in that group of Aphyosemion).

In BIF also the third dark "crossbar" on the throat is present in a very reduced way that however is very constant and well suited for identification of BIF.

In GRA and MAC the males apparently do not develop any distinct black throat pattern, instead a red pattern composed by two crossbars corresponding to those of the common Epiplatys pattern may develop, more or less reduced posteriorly (in the line between the corners of the mouth). Females who are at ease may show no dark pattern at all. During display they may develop male's pattern in black. No red color normally develops on the throat of these females. This means that in this small group of species the throat patterns of both sexes are close to the common Aphyosemion type.

In Pachypanchax no individual develops any throat pattern. The male has only slightly more black pigments on the lower part of the head as females have.

In Aplocheilus no individual develops any throat pattern, except for DAY. In this species the throat pattern belongs to the temporary type of pattern and contains black pigments only. I have not a full understanding of the DAY pattern because it is rarely seen. It contains however most elements of the common Epiplatys pattern, but apparently also the two longitudinal dark lines seen in DAG.

Only about two years have passed since I became aware of the importance of the study of these signals or throat pattern in Old World Rivulins. More time, and more species, is needed before any distinct grouping of species according to this character is possible. The study of throat patterns takes much time because the temporary pattern only occurs during display and sometimes not even during display. Probably this character has some importance in the systematics of these Rivulins.

Grouping according to a pre-mating lateral band in females The pre-spawning dark lateral band normally is situated on the middle of the sides in between the gill covers and the root of the caudal fin. This pattern is the pattern of fear and as such it develops in individuals of both sexes if they are frightened. As I have already mentioned in connection with various crossings, this signal is not compulsory for many species that are able to develop this signal. Apparently all species belonging to Epiplatys are able to produce this

band. This is also true for DUB and ANN. In ANN the band is very rudimentary and probably plays no role in the pre-mating display because in this species the broad dark bands around the body cover the lateral band and only part of the band is seen in the light area on the hindmost part of the body in females in pre-mating display.

This band has developed permanent characters in BIF and BIV (or has developed temporary characters in other species).

In Aplocheilus this signal develops on the spawning female in DAY, but in this species the band is incomplete and apparently also may occur in males during spawning - in young males at least.

The lateral band does not develop in LIN, PAN and BLO during normal display, but as we have seen in the SEX/LIN cross LIN is able to produce the band.

This band does not occur in Pachypanchax, Nothobranchius and eastern Aphyosemion (except for BIV). In Callopanchax SJO uses this band as Epiplatys does, whereas in some species (or subspecies) belonging to the ROL-LIB group this band has become permanent or almost permanent in females.

Grouping according to black crossbars

Dark crossbars do not develop in species belonging to Nothobranchius, Fundulosoma, Pachypanchax and in the eastern group of Aphyosemion.

At the present it is difficult to make out if there are one or more types of black crossbars. Apparently there are at least two types. One type is seen on individuals in SEX and DAG. These bars are broad, vertical and normally arranged in accordance to a certain system (P, V, A). A second type is seen on females in PET (a species in Callopanchax) and also (more or less) in FAS, SEN and perhaps also DAY and LIN. Here the bars are more narrow and often rather oblique and rarely arranged according to a fixed system. In species in which dark crossbars develop in juveniles and females, old males may loose their crossbars more or less completely, but normally the bars will reappear during fight.

Some species belonging to nominal Epiplatys apparently do not develop any dark crossbars: DUB, BIF and MAC are examples. This is probably true for DUB, no trace of any crossbar is seen at any time. In very young BIF the dark lateral central band is not complete, but broken up into segments which are rather high and which resemble true dark crossbars. Such "bars" have been pictured for NDE. In MAC my sole female never developed even traces of dark crossbars. However during photographing I discovered that when this female was afraid all red dots situated in places where dark crossbars are found in GRA developed an intense black color, whereas other red dots remained red.

In Aplocheilus LIN and DAY develop dark crossbars in both sexes. In DAY the male soon loose its bars. In BLO juveniles may develop a dark pattern that resembles broad very indistinct crossbars.

PET is not the only species in Callopanchax that develops dark crossbars. Certain males of one of Roloff's ROL-like forms from Sierra Leone (SL7) developed a very regular system of broad, dark red crossbars on one side of the body in one male. On the other side of that male the regular system was broken into zig-zag red lines. Also females belonging to the small species in Callopanchax may develop

very irregular dark crossbars. If a juvenile of SJO is disturbed the fish may develop a dark lateral band as described for juveniles of BIF. The band is broken into segments which "look like" short crossbars.

Individuals of ANN develop their dark "crossbars" in quite a different way than other species in Epiplatys. In the very small juvenile of ANN there are three thin dark lines on the body sides. One line high on the back, one in the middle of the side and one in the keel and low on the belly. Later on these three lines are broken into segments corresponding to the three black bands around the body. The black pigments spread upwards and downwards from the remaining parts of the three black lines thus producing the broad bands. After this discovery I studied live fry from DAG, FAS, SEX and CHA in order to discover the black lines. No trace of these lines was found. These three black lines correspond to the black lines which develop on the sides of juvenile Procatopodins and which are seen in the keel and along the midline in adult individuals of this subfamily. Also FLA develops two of these black lines (the upper line is not present). Adult individuals of ANN loose the dark lines (segments of these lines) except for spawning females that develop a dark lateral band in the posterior light band. Adult individuals of FLA do not loose their dark lines. After maturing individuals of ANN may decrease the saturation of dark pigments in their broad dark bands. The anterior and the posterior edges of these bands remain very black however. A pattern (not very distinct) of six thin "crossbars" develops, not unlike (in arrangement) those found in DAG and SEX.

Grouping in accordance to the red pattern on male's body sides In Cyprinodontiformes, females often develop a marked brown reticulation on the body sides (Lebistes reticulatus etc.). This regular reticulation is linked to the scales. In the male the black color of this reticulation may be lost and a regular red pattern develops. This red reticulation stands in high contrast to the brilliant blue or green color of the body sides. In my opinion this is the "ancient red pattern" for this group of Rivulins. This simple pattern is found in all species belonging to the genus Nothobranchius and in some species in Epiplatys. As I have mentioned in connection with the DAG/GRA cross the next "step" in the evolution of the red pattern may be found in a certain concentration of the red pigments towards the joints of the reticulation. Thus the crescent shaped dots are produced. These dots may be present (few) on males of Nothobranchius and Fundulopanchax, but more pronounced in Epiplatys. In these species there may be a perfect reticulation on the back, a pattern of crescent shaped dots high on the sides and rounded red dots in the middle of the sides and below the middle. Also the red pattern tends to develop a red reticulation on the hindmost part of the body and rounded red dots on the anterior part of the body. This is also true for Aphyosemion. The western strain in SJO (blue SJO) has a perfect reticulation on the back, but on the sides the red pattern is lost.

The red reticulation is a simple pattern and is not able to produce much variation in a way that related species become different. The transformation of the red pattern into crescent shaped red dots or even rounded red dots in the joints of the reticulation does not improve this situation. If however the number of red dots (rounded or crescen-shaped) is much reduced certain possibilities occur which make it possible to produce several red patterns that are different. Red dots may confluent and produce lateral red lines or vertical red lines. Now related species may develop very different patterns on the body sides in males.

In Fundulosoma the male (THI and GAM) develops a much reduced number of red dots on the sides of the body. In this these species differ markedly from the species in Nothobranchius.

No species in nominal Aphyosemion develops a perfect red reticulation except SJO (and GUI?). Not even on the back this pattern is visible.

In Callopanchax the males develop rounded red dots which may produce zig-zag patterns. The dots are not perfectly rounded as in the subgenus Aphyosemion, nor are they of the crescent-shaped type. In the aquarium strain of SJO the red pigments do not concentrate in a particular pattern, but are rather evenly distributed all over the sides.

In Fundulopanchax most males tend to develop crescent-shaped red dots, in particular on the back and on the hindmost part of the body. In CIN the red dots are lost and in NIG and NDI the dots are more rounded than in other species.

In Aphyosemion s.s. no crescent-shaped dots normally occur, the dots are perfectly rounded. The red pattern of these species probably represents the last step in the evolution of the red pattern in Old World Rivulins.

All nominal Aphyosemion develop the "wound" in males. This marking is situated just behind the root of the pectorals. It is composed of a number of rounded red dots that heap into the wound. When at ease the "wound" of the Aphyosemion male often is not at all conspicuous, but this will change during fight. Now the wound is very conspicuous. Even in the strains of GUI where the red pattern of the body sides is almost nil the wound is present. Also CIN that has no further red pattern on body sides develops a "wound".

The "wound" is an Aphyosemion character as it develops in all males of this genus and because it does not develop in males of other genera. Pterolebias longipinnis develop a wound in males. In this species and in PET the "wound-like marking" indeed resembles a wound because the males are very dark and the brilliant red, confluenting dark edged dots produce an impression that the fish has been wounded.

In Epiplatys all types of red patterns occur. In BIF, FAS, SEN and DAG an almost complete red reticulation occurs. In CHA, SEX and LON the male may have a red reticulation on the back, crescent shaped red dots on the upper part of the sides and rounded red dots below and anteriorly on the side. In GRA, MAC and DUB the red pattern contains perfectly rounded red dots only. In ANN no red pattern develops on the body sides.

In Aplocheilus all four species may develop more or less rounded red dots on body sides. Most strains of PAN and BLO do not develop any red pattern on the sides, but in other strains of these two forms rounded (and numerous) red dots are found.

Grouping according to the red patterns in fins Only in the genus Aphyosemion the red bands that I have called "separation bands" occur. These bands are situated in the interior of the fin and separate (normally) the bright yellow color of the distal part of the fin from the green or blue basal part of the fin. These bands produce the marked contrast of the lyre pattern in the caudal fin. These separation bands are less developed in the dorsal and anal fin in Callopanchax, however in SJO and in SL4 such a band is present in the anal fin. Probably these bands do not develop in this subgenus because in these species the male

does not develop yellow color in dorsal and anal fin. The lyre pattern however develops in males of ROL and LIB (and SL4), more incomplete in SJO and less in GUI.

In FAS and DUB males (may) develop a thin separation band near the distal edge in the anal fin and in the lower part of the caudal fin. Males of ANN develop a pattern in the caudal fin that might be classified as a "lyre". Two dark violet separation bands occur in this fin.

Grouping according to the shape of the caudal fin All individuals belonging to the genera Epiplatys (except for DUB) and Aplocheilus develop a short and very distinct lobe in the central part of the fin. This lobe is produced by prolongation of the two central rays.

Individuals belonging to Fundulopanchax develop a like shape of this fin, in particular in females and juveniles. In very small juveniles (of some of these species?) the two central rays produce much and resemble the lobe in Epiplatys-Aplocheilus. Produced rays at the upper and lower corner of this fin occur in Aphyosemion and Fundulosoma only. Produced rays at the lower corner of this fin may occur in Epiplatys also (DAG, CHE, SEX).

Grouping according to "annual characters" Many aquarists and also some zoologists (Hoedeman) have tried to divide the species in Old World Rivulins into "plant spawning species" and "bottom spawning species". Indeed some species prefer to place their eggs close to the surface of the water (Aplocheilus and certain Epiplatys) whereas other species prefer to place the eggs near the bottom or into the bottom layer (Callopanchax [not all species], Fundulopanchax [more or less] and Nothobranchius. These species however are not very consistent in their choice and many so-called "bottom spawning species" may place their eggs even into the Riccia on the surface. No distinct grouping according to these "characters" is possible for the present.

Geographical grouping

The species in Nothobranchius occur in East Africa and on certain islands in the Indian Ocean. These species range from the Republic of South Africa to Somalia and Sudan in the north. From here, the group of species probably turns into a westward direction through the lowlands and reach the Lake Chad (RUR).

The Pachypanchax occur in Madagascar and on Zanzibar and probably also at some coastal places in East Africa. The genus contains four nominal species, but probably only two are good species (HOM and PLA).

The Fundulosoma species replace Nothobranchius in the savanna of West Africa west of the Chad drainage. They range to Gambia (GAM).

The Fundulopanchax occur isolated (SPU) in the humid forests of SW Ghana and SE Ivory Coast. The main lot of species is found from southern Nigeria (they reach the border to Dahomey at Meko) to Cameroon. In the coastal areas of this country they probably reach the border to Spanish Guinea, whereas in the highlands in the north they enter into the Dja-Sangha drainages (BAT).

The subgenus Aphyosemion apparently is not represented west of the dry Dahomey gap. The

westernmost species probably is CAL that lives near Lagos in SW Nigeria. From here the numerous nominal species extend westwards and southwards into the Ogooue and the Congo drainages.

In West Africa species belonging to Epiplatys are found in all places occupied by species of the previously mentioned genera. With BIF and SEN they extend their range into the Nile drainage.

The species in Callopanchax are found from Lower Guinea to Ghana.

The evolution of Old World Rivulins

The known species in Old World Rivulinae form a natural systematic group in Cyprinodontidae. All these forms probably originated from a single ancestor. These Cyprinodonts share several characters with the species in South American Rivulinae and apparently these two groups of nominal Rivulins grade into each other through the species in Cynopoecilus and more distantly in Cynolebias.

This is true, if scale patterns, egg types, annual characters and development of ctenoidy (wrinkled type) and sensory papillae are considered. If, however, the hemoglobin patterns and, in particular, the development of lateral line organs on the head are considered, marked differences exist between these two groups of Rivulins. In these two characters the species in Pterolebias (hemoglobin pattern not known for the present) and in Rivulus are much closer to Old World Rivulins than the species of the Cynopoecilus-Cynolebias group. Indeed a certain "bridging" is seen between these two groups of Cyprinodonts, but still this "bridge" has a wide gap.

Old World Rivulins also share several characters with the many species in Procatopodinae. However their scale arrangements and lateral line development are much more variable than are Old World Rivulins. Apparently Procatopodinae and Old World Rivulins are well separated one from the other in morphology and in biology, but a closer study of such forms as ANN and FLA may indeed reduce the differences between these two subfamilies to some extend, but still a wide gap will be left.

I am aware that Pr. G.S. Myers in 1955 considered the Rivulins as the most primitive forms in Cyprinodontidae, and also the species in Aplocheilus as the most primitive forms among Rivulins. In this Myers probably did not indicate that the species in Aplocheilus (the Aplocheilus phenotype) represent the ancient form from which all Rivulins developed through time.

I have developed a certain (not very distinct) idea on the ancient form in Cyprinodontidae from which Old World Rivulins originated. I believe that this form was an annual fish that developed the "annual egg characters" during some long period of dry climates when Africa and South America still were a single continent. Annual characters in eggs is a very rare character among fish and these characters are highly effective among Rivulins of the Old and the New World. Also the study of the egg type (membrane pattern etc.) supports this idea that the annual characters were existent when the two continents separated back in time (about 150,000,000 years ago). I do not believe that these fish which generally are restricted to freshwaters of low salinity were able to "cross the sea", not even over much smaller distances than the present distance between the two continents. In this ancient annual Cyprinodont the egg type probably contained a hexagonal reticulation as well as evenly distributed filaments or hairs.

This supposed ancient annual Cyprinodont probably was not too different from such forms as the species

in Nothobranchius or Cynolebias. A large rounded dorsal fin standing almost exactly over the root of the anal fin. Ctenoidy well developed in males and sensory papillae in the dorsal and the anal fin to hold the female during spawnings. This prototype for the Rivulins probably originated from some group in Cyprinodontidae. I suspect the Cyprinodontinae of having had something to do with this question. In particular such forms as C. variegatus Lacepede or some even more primitive Cyprinodontid might be responsible. In this particular species the patterns of lateral line organs (canals) and frontal scales probably are very ancient and primitive. Also in this form we find the shape of the body and the fins and the ctenoidy that we were looking for.

Rivulins might be considered as primitive in several morphological characters. Their habituation to the life as an annual fish, their almost perfect pattern of frontal scales, their (at least in Aphyosemion) complicated color patterns and maybe also their lateral line system are not primitive characters compared with other Cyprinodonts. If Old World Rivulins developed from an ancient Cyprinodon-like annual Cyprinodont then such forms as the species in Nothobranchius, Fundulopanchax and Callopanchax (SJO and GUI) have changed less than have the species in Aplocheilus and Epiplatys. The fact that in most species which develop a small and short dorsal fin the males are (still) trying to hold the female by its dorsal fin is a strong indication that these forms developed from forms which had larger and longer dorsal fins and not the reverse direction of evolution. "Clipping movements" occur even among species in Epiplatys during display. These movements probably have been linked to "lyre-like" color patterns as in NIG, ROL etc.

On these ideas I have based the diagram for phylogeny of Old World Rivulins. This diagram is tentative and this diagram is far from being thought to be the final solution of the phylogeny for this difficult group. I think that the evolution of Nothobranchius, Fundulosoma, Fundulopanchax and Aphyosemion sensu stricto is not too far from the truth.

The Callopanchax represent a difficult problem. In this group of nominal Aphyosemion we will find all the forms that developed in the large group first mentioned. The SJO species represents a true annual fish and also this species has been placed in Nothobranchius back in time. GUI represents a form that resembles the species in Fundulopanchax, whereas such forms as LIB and ROL represent the group of Aphyosemion sensu stricto. The Callopanchax even produced an Epiplatys-like form, the PET species. If also FAS and SEN are linked to the Callopanchax as I think they should be, this taxonomic unit has developed many very different forms. This group also probably is closer to the South American Rivulins. The wrinkled scales in males resemble the scales in Cynopoecilus. The Callopanchax (ROL-LIB group) also in their shape, color pattern (in females) and in behavior are close to the Rivulus phenotype. Also the Callopanchax live rather isolated in the far west of West Africa. For this reason I do not link these forms directly to the evolution line which probably produced the Fundulopanchax-Aphyosemion phenotype. Perhaps when more is known, Callopanchax should be placed somewhat closer to Fundulopanchax.

The East Africa-Asia forms of Pachypanchax and Aplocheilus represent a second problem. These two genera resemble each other. In all species individuals develop a small black dot on the basal part of the dorsal fin. Indeed such a marking is not a "large character", but, as the marking does not occur in other Old World Rivulins, it can be taken as an indication of relationship. Also there are scales over large areas of the caudal fin in some individuals of Aplocheilus. Both genera probably represent rather ancient forms.

The very primitive scale pattern in HOM is one indication. Also the few species in each of these genera show much variation if details are studied.

I had an idea that these two forms should be linked in some way to the Callopanchax group, but for the present I have not very much to support such an idea. For this reason I have considered these two genera to represent a third line of evolution out from the ancient annual form.

The many very different species in nominal Epiplatys represent the largest problem. Some forms probably might be linked to the Callopanchax group, as I have done for FAS and SEN. Maybe all nominal Epiplatys should be linked to this group. This, however, is to go too far for the present. There is a small possibility that some species in Epiplatys developed from some group in nominal Aphyosemion s.s. or vice versa. Another possibility is represented by the Aplocheilus that appear to be just as close to (some) Epiplatys as they are to the Pachypanchax. For these reasons I did not come to any final solution of the Epiplatys problem.

I am afraid that this "letter" grew too long. Someone probably will become tired before he reaches the end. I believe however that this letter contains information that may produce a better understanding of Rivulins and in particular of those of the Old World. I have been trying to inform you on all facts that I considered as important for such understanding and as I said before this information are not (all of them) my "property" as they originated from my cooperation with Stenholt Clausen and other people interested in killies with whom I correspond and exchange points of view.

The "Killie Letters" are not an official publication and people are not able to subscribe to these letters. For this reason it would not be quite correct to refer to these letters in official publications. "Personal information from J.J. Scheel" or "Briefliche Mitteilungen von..."

Typing closed on 20 July 1965.