A study of *Aphyosemion schmitti* (Romand, 1979) and a survey of the *Aphyosemion* of Liberia (Pisces, Cyprinodontidae)

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Aphyosemion schmitti can be separated from neighbouring species on the basis of colour pattern, crossing experiments, cytogenetics, genetics and zoogeographical distribution. Three groups of Aphyosemion can be distinguished, based on morphological and meristic characters, colour patterns and geographical distribution; i.e. the liberiense group, the guineense group and the occidentalis group. A differentiation of the Liberian Aphyosemion is proposed, and its possible phylogenetic relationships are discussed.

KEY WORDS:—Aphyosemion schmitti - Liberian Aphyosemion - systematics - colour pattern - zoogeography.

CONTENTS

Introduction										. 2	16
Study of Aphyosemion schmitti (Romand, 19											16
Morphometry and meristic character	rs.									. 2	16
Frontal scale pattern and lateral line	organ									. 2	17
Description of colour patterns										. 2	18
Crossing experiments										. 2	18
Cytogenetics										. 2	18
Genetic study											19
Habitat										. 2	21
Geographical distribution										. 2	22
Study of Liberian Aphyosemion											22
A. liberiense (Boulenger, 1908)										. 2	22
A. maeseni Poll, 1941											22
A. jeanpoli (Berkenkamp & Etzel, 197	79)									. 2	22
A. monroviae (Ladiges & Roloff, 1972) .										24
A. viridis (Ladiges & Roloff, 1973).										. 2	25
A. brueningi (Roloff, 1971)										. 2	26
A. occidentalis Clausen, 1966										. 2	27
A. bertholdi Roloff, 1965											27
Differentiation of Liberian Aphyosemion .										. 2	27
Liberiense group											28
Guineense group										. 2	28
Occidentalis group											31
Use of colour patterns in Aphyosemion spec	ies									. 2	31
Phylogenetic relationships between the Li	iberian	Aphyo	semion	and	other	Aphy	osemi	on sp	oecie	s. 2	32
Acknowledgements								. •			33
References										. 2	33

INTRODUCTION

The genus Aphyosemion includes some very beautifully coloured fish which are of particular interest because variations in colour patterns may be very large in a small geographical area. These variations may be related to cytogenetic polymorphism (Scheel, 1972a). Unfortunately, the real significance of such variations as a specific criterion is not fully understood at present. This is also true for most African Cyprinodontidae, except for the Aphyosemion elegans group (Scheel, 1972a). In some cases, differences in the colour patterns are so striking that one can clearly differentiate between some related species, but for most Cyprinodontidae populations this criterion cannot be applied alone. This is particularly true for the genus Aphyosemion which is endemic in W Africa. As the real significance of colour pattern in speciation is not yet known, and meristic characters are of limited use, the diagnosis of a new species only on the basis on these criteria is extremely difficult. In the case of a new species of Aphyosemion recently discovered in Liberia (Romand, 1979), although there were some marked colour variations between this and related species, cytogenetic experiments, crossing experiments and genetic analysis were carried out to determine the possible separation between neighbouring populations of Aphyosemion.

This new species of *Aphyosemion* was found in E Liberia in 1977 by G. Schmitt and the author. The population was named in a preliminary report (Romand, 1979) in honour of G. Schmitt who contributed significantly to the specific knowledge of this fish.

I shall first review the morphometric and meristic characters of A. schmitti, give a description of the colour pattern, and then examine its genetic differentiation from other related populations. I shall also consider the habitat and the distribution of this fish in Liberia and finally review all other Aphyosemion from Liberia and give guidelines for the determination of Aphyosemion species based mainly on colour patterns and morphometry. Phylogenetic relationships with other Aphyosemion will also be presented.

STUDY OF APHYOSEMION SCHMITTI (ROMAND, 1979)

Morphometry and meristic characters

Data are based on the holotype, the allotype, five paratypes, plus five additional specimens kept by the author from the type locality, Tchien in E Liberia (Fig. 1). Morphometric measurements are expressed in percentages of the standard length or the head length. The two extreme measurements, the mean and the standard deviation are given.

Measurements related to standard length

Total length (%), 118.2–133.3, 124.6 \pm 3.8; height of the body at origin of the anal fin, 16.2–23.8, 18.8 \pm 1.9; depth of the caudal peduncle, 11.2–14.4, 12.8 \pm 0.9; length of head, 21.1–26.1, 23.5 \pm 1.3; distance from the tip of snout to insertion of pectoral fins, 24.2–28.3, 25.7 \pm 1.4; tip of snout to insertion of pelvic fins, 43.8–51.9, 47.3 \pm 2.5; snout to origin of anal fin, 55.3–64.2, 59.6 \pm 2.6; snout to insertion of dorsal fin, 62.0–71.4, 67.2 \pm 2.8.

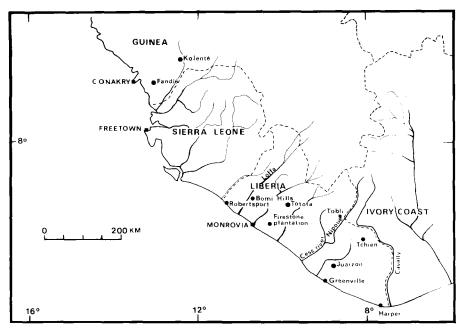


Figure 1. Map showing the various locations reported in the text.

Measurements related to the head length

Interorbital length (%), 41.6–50.5, 44.8 \pm 2.7; distance from tip of snout to preopercular, 63.1–75.0, 68.0 \pm 3.7; eye diameter, 24.7–32.2, 29 \pm 1.9.

Meristic values

The following meristic counts were made: caudal rays, 26-28, 26.6 ± 0.7 ; dorsal rays, 11-13; 12.2 ± 0.6 ; anal rays, 17-18; 17 ± 0.5 . Juxtaposition of the dorsal and anal fin, given by the number of anal rays anterior to the first dorsal fin ray, 6-9; 7.5 ± 0.8 . Number of scales from the upper edge of gill opening to caudal peduncle, 33-36; 34.5 ± 0.8 . The number of scales around the body at the origin of the anal fin is very stable and totals 17.

Frontal scale pattern and lateral line organ

In Cyprinodontidae the pattern of cephalic squamation and lateral line may have systematic value (Hoedeman, 1958; Whitehead, 1962; Clausen, 1967). Basically, for the *Aphyosemion* one can distinguish three head canals: the frontal anterior canal situated on the most anterior part of the head with two neuromasts; two supra-orbital canals along the eyes and two other post-orbital canals behind each eye. The supra-orbital and post-orbital canals possess three neuromasts each (Fig. 2). Every scale of the head or each row of scales is given a letter. The pattern of head squamation between the canals is characterized by the particular scale which overlies all the other. In *A. schmitti*, the scale pattern is of type G without H scales. The two frontal neuromasts of the anterior canal are separated by one unique frontal lobe. The supra-orbital and post-orbital are composed respectively of three neuromasts (Fig. 2).

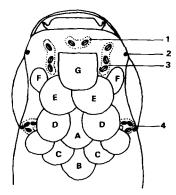


Figure 2. Lateral line organ and frontal scale pattern in Aphyosemion schmitti. 1, Frontal anterior canal with two neuromasts. 2, Pore of the orbital canal. 3, Supra-orbital canal with three neuromasts. 4, Post-orbital canal with three neuromasts. The G scale overlies the E scales; note the absence of H scales, which when present lie in front of the G scale.

Description of colour patterns

Colour pattern of live male

The sides present a bluish tint of varying intensity. The first third of the body from the head approximately to the pelvic fins is pale yellow. This coloration, which is characteristic of this species, varies distinctly depending on the health and behaviour of the fish. The coloration is present in all wild specimens but also in fish raised in tanks for several generations. The sides are irregularly spotted with red marks, which are larger and more numerous on the anterior part of the body (Fig. 3A).

The yellowish pectoral fins are edged with a yellow stripe. Pelvic, dorsal and anal fins are blue with red dots and edged by a red submarginal stripe. The blue caudal fin has red dots in the centre. The upper and lower edges of the latter fin have a red submarginal stripe and a yellow marginal stripe (Fig. 4A).

Colour pattern of live female

The body is less coloured than that of the male. The sides have a pale bluish colour that is more or less hidden by an incomplete red-brown reticulation. The uneven fins are blue, with dark red dots.

Crossing experiments

Crossing trials between males of A. schmitti and females of A. liberiense (from Monrovia) did not produce offspring, nor did crossing females of A. schmitti with males of A. liberiense. Typical reproductive behaviour was observed between males and females of both species, suggesting that the isolation is not of behavioural origin.

Cytogenetics

Simple cytogenetic observation after chromosome preparation according to Scheel (1966) from somatic cells in the fin epithelium shows a difference in the chromosome number. A. liberiense displays metaphases with 2n



Figure 3. A, A. schmitti from Juarzon Liberia. B, A. liberiense from Monrovia Liberia. C, A. maeseni from Léma Ivory Coast. D, A. jeanpoli from Voinjama Liberia. E, A. moroviae from Monrovia Liberia. F, A. bertholdi from Serabu Sierra Leone.

chromosomes = 42 with 44 arms, while A. schmitti displays only 2n = 40 with 54 arms.

Genetic study

A study was made of genetic differentiation between populations of the *Aphyosemion* genus using enzymatic electrophoresis. These populations belonged to three different species: two population of *A. geryi* from Guinea, three

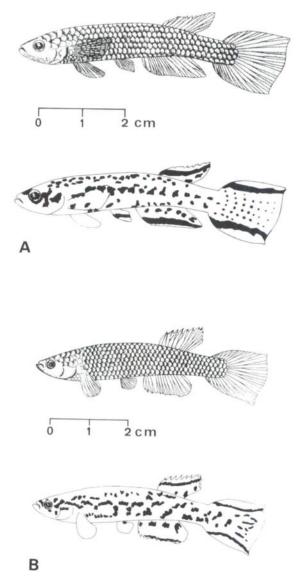


Figure 4. Males of Aphyosemion schmitti (A) and Aphyosemion liberiense (B) with their corresponding red colour patterns.

populations of A. liberiense and one population of A. schmitti (see Table 1 and Fig. 1). Twenty-one loci encoding nine categories of enzymes or other proteins were investigated on starch gel electrophoresis (Douchement, Romand & Pasteur, 1984): esterase (Es), glucose-6-phosphate dehydrogenase (G6pd), aspartate amino-transferase (Aat), phosphoglucose isomerase (Pgi), phosphoglucomutase (Pgm), glycerophosphate dehydrogenase (Gpd), lactate dehydrogenase (Ldh), malate dehydrogenase (Mdh) and five unspecific proteins.

The genetic differentiation was estimated by two indices: Nei's genetic distance (Nei, 1972) and the percentage of diagnostic loci. The latter index

Table 1. Nei's genetic distance (D, upper right-hand corner) and percentage of diagnostic loci (lower left-hand corner) based on a comparison of the polymorphism of 21 loci

	1	2	3	4	5	6
1		0.01	0.17	0.11	0.14	0.15
2	0	_	0.17	0.10	0.12	0.15
3	14	14	-	0.03	0.05	0.33
4	5	5	0		0.03	0.28
5	9	9	0	0		0.32
6	9	9	14	9	9	

^{1 =} A. geryi from Kolenté (Guinea).

gives a minimal estimate of the proportion of the genome that may be different between the populations studied.

The genetic distance between two populations of A. geryi from Kolenté and from Fandié in Guinea is very small (D=0.01) showing the low polymorphism between these two populations. This clearly indicates the small genetic distance between two populations of the same species. Similarly, the genetic distance between the three populations of A. liberiense is very small (D=0.03). Moreover, there are no diagnostic loci between the two populations of A. geryi and the three populations of A. liberiense.

The genetic distance between A. schmitti and A. geryi is smaller (D=0.15) than the distance between A. schmitti and A. liberiense (D=0.28-0.33) (Table 1). Comparing these three species, it would appear that A. geryi is genetically more close to A. schmitti than to A. liberiense, as shown by the diagnostic loci, despite the fact that A. liberiense is geographically closer to A. schmitti than to A. geryi. This result may be related to cytogenetics: A. schmitti has 2n=40 chromosomes (Romand, 1979) as does A. geryi, whereas A. liberiense has 2n=42 (Scheel, 1968; Grimm, 1972).

Although the comparison of Nei's genetic distance between populations does not give values that allow us to conclude that this is a new species, it does, however, give a measure of the genetic separation between related populations.

Habitat

Aphyosemion schmitti was found for the first time in a water hole 5–10 cm deep in a dry brook situated under forest cover where little light was able to reach the ground. The fish was found to be sympatric in two other biotopes with a much larger cyprinodontid, Epiplatys olbrechtsi. Two water analyses at an interval of one year showed reasonable stability of chemical and physical parameters. For instance, water temperature was between 23 and 24°C, pH between 6.0-6.5 and hardness was 17.8 ppm. It can be said that A. schmitti is usually found in the shallow water of small brooks or rivers. It stays on the bottom and likes standing water close to the bank.

^{2 =} A. geryi from Fandié (Guinea).

^{3 =} A. liberiense from Monrovia (Liberia).

^{4 =} A. liberiense from Firestone Plantation (Liberia).

^{5 =} A. liberiense from Totota (Liberia).

^{6 =} A. schmitti from Juarzon (Liberia).

Geographical distribution

According to observations to date, this fish is restricted to the eastern part of Liberia. The area forms a triangle with its apex around Tobli. Its eastern edge is the Cavally river which is the border between Liberia and the Ivory Coast. Its western edge is delimited by the Nipoué river drainage and the Cess river drainage. The base of the triangle is the coastal area between Harper and Greenville (Fig. 5A).

STUDY OF LIBERIAN APHYOSEMION

A. liberiense (Boulenger, 1908)

Distribution: Western coastal area of Liberia, and south of Bomi Hills, extending to SE Sierra Leone; also present around Totota (Fig. 5B).

Colour pattern: Male: sides bluish-green with large red markings. The uneven fins are blue with red dots, edged by two stripes, a red one and a more marginal one whose coloration may be either yellow or blue. The uneven fins are light blue with a blue marginal stripe (Figs 3B, 4B). Female: body brownish with darker dots which are arranged in a more or less lengthwise band from the gill covers to the base of the caudal fin.

Synonyms: A. calabaricus (Ahl, 1936); A. melantereon (Fowler, 1950); A. fredrodi (Vandersmissen, Etzel & Berkenkamp, 1980).

A. maeseni Poll, 1941

Distribution: NE Liberia, SE Guinea and the eastern part of the Ivory Coast (Fig. 5C).

Colour pattern: Male: the sides and fins are bluish-green: the body is spotted with light green dots and displays a red reticulation. The dorsal part of the body is brownish. Anal, caudal and dorsal fins are edged with a blue stripe. Dark red lines are also present on the dorsal and the caudal fins, between the fin rays, and there is also a typical dark spot behind the pectoral (Figs 3C, 6A). Female: body brownish with dark crossbars that are occasionally visible. Fins are light blue.

Synonym: None.

A. jeanpoli (Berkenkamp & Etzel, 1979)

Distribution: W Liberia, from the Bomi Hills to the north of the Loffa basin (Fig. 5D).

Colour pattern: Male: body varying from brownish to blue. Few red dots are arranged longitudinally. Depending on the fish behaviour, some dark red transverse marks are present on the side. The belly is orange-yellow. Red dark marks are present on the odd fins. A black stripe and a bluish marginal stripe line the dorsal, anal and caudal fins (Figs 3D, 6B). Female: the sides vary from brownish to light green-blue, with small red-brownish dots, fins are almost colourless.

Synonym: None (some populations have been referred to A. melantereon).

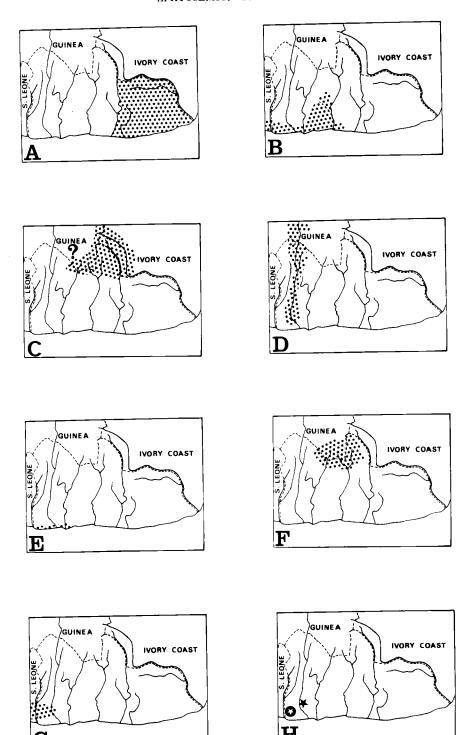


Figure 5. Geographical distribution of the various species of Aphyosemion from Liberia. A, A. schmitti; B, A. liberiense; C, A. maeseni; D, A. jeanpoli; E, A. monroviae; F, A. viridis; G, A. brueningi; H, locations of A. occidentalis () and A. bertholdi () where found in Liberia.

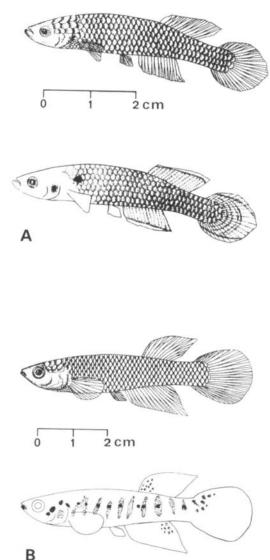


Figure 6. Males of Aphyosemion maeseni (A) and Aphyosemion jeanpoli (B) with their corresponding red colour patterns. The dotted area present in A. maeseni is not really red, it varies with behaviour from dark-red to purple.

A. monroviae (Ladiges & Roloff, 1972)

Distribution: Known in the coastal area from Monrovia to Robertsport (Fig. 5E).

Colour pattern: Male: sides green-blue with numerous marks and red dots arranged longitudinally on the anterior part of the body, becoming transverse on the posterior half of the body. On the head, a red stripe runs from the chin underneath the eye to the underpart of the gill cover. There are two other red stripes on the gill cover. The even fins are blue with large red crossbars. The first two or three fin rays of the dorsal are normally black. The caudal fin is blue with red and blue marginal stripes. Some different colour morphs may be

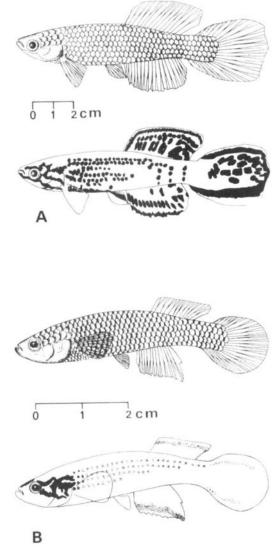


Figure 7. Males of Aphyosemion monroviae (A) and Aphyosemion viridis (B) with their corresponding red colour patterns. The dotted areas in A. viridis vary from dark-red to brownish coloration.

observed, but the main colour pattern is conserved (Figs 3E, 7A). Female: sides brownish-red with some red dots arranged in longitudinal rows. Synonym: None.

A. viridis (Ladiges & Roloff, 1973)

Distribution: NW Liberia, may also be present in SE Guinea (Fig. 5F).

Colour pattern: Male: sides greenish with a brownish back. Small red dots are arranged in more or less well defined rows running lengthwise. Dorsal, anal and caudal fins are greenish. Only the dorsal and caudal fins have light green marginal stripes (Fig. 7B). Female: sides brownish with fins almost without

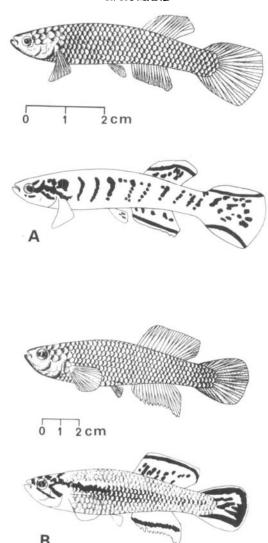


Figure 8. Males of Aphyosemion brueningi (A) and Aphyosemion occidentalis (B) with their corresponding red colour patterns. The dotted areas in A. occidentalis may change from vivid red to brownish colour depending on the fish behaviour.

colour. A. viridis is very close to A. maeseni, although it is a separate species. They have been found to be sympatric in some biotopes in Liberia.

Synonym: None.

A. brueningi (Roloff, 1971)

Distribution: Western part of Liberia, in the Bomi Hills, mainly present in E Sierra Leone (Fig. 5G).

Colour pattern: Male: sides bluish-green, with transversal red bars. The uneven fins are blue with red markings and a red margin. The upper and the lower parts of the caudal fin and the anal fin are edged by a yellow stripe (Fig. 8A).

Female: sides brownish with dark dots. Fins are not coloured, except for the anal and dorsal fins where some dark dots are present.

Synonym: None.

Radda (1976) considers A. brueningi to be a synonym of A. liberiense. This is possible, because these two species are very close in terms of morphology, colour pattern and ecology. However, Roloff (1971) in his original description pointed out that crossing experiments show a genetic separation between A. brueningi and A. liberiense.

The two following species are mainly endemic in Sierra Leone; they have been observed only occasionally in SW Liberia as reported by Berkenkamp & Etzel (1979).

A. occidentalis (Clausen, 1966)

Distribution: Southwestern part of Sierra Leone and possibly in SW Liberia as reported by Berkenkamp & Etzel (1979) (Fig. 5H).

Colour pattern: Male: sides brownish, with scales surrounded by a red margin. Longitudinal red markings are visible on the head, between the eye and the gill opening, over a dark blue colour that covers the sides of the head and the throat. The anal and dorsal fins are brown-red on the first half and bluish on the other half. There is a red stripe at the lower part of the anal fin, and the upper part of the dorsal fine. Red dots are present on the dorsal fin. Anal, dorsal and caudal fins are edged by a blue stripe (Fig. 8B). Female: sides light brown, darker on the back. Fins without pigmentation.

Synonym: Aphyosemion sjoestedti none (Lönnberg, 1895).

A. bertholdi (Roloff, 1965)

Distribution: Mainly restricted to Sierra Leone. This species has been reported to be present in the Bomi Hills in SW Liberia by Berkenkamp & Etzel (1979) (Fig. 5H).

Colour pattern: Male: sides bluish-green with red dots that are scattered on the head and the caudal fin. The red dots tend to merge, forming two or three red lines between the eye and the gill opening. The underside is pink. All the fins have the same background coloration as the sides of the body, except the pectoral fin. The lower part of the anal fin, the upper part of the dorsal fin, and the lower and upper sides of the caudal fin are edged by a red stripe and there is a blue margin at the uppermost extremity of these fins (Figs 4F, 9A). Female: sides brown, with several scattered red dots.

Synonym: None.

DIFFERENTIATION OF LIBERIAN APHYOSEMION

This determination is based on morphology, colour pattern of live specimens and zoogeography. Only the males are considered since they exhibit the most characteristic aspects of the species. Comparison of colour pattern is made on neutral behaviour, i.e. without specific significance.

Three groups can be separated on the basis of morphology and colour pattern as already reported by Radda (1976) for the Cyprinodontidae of Sierra Leone.

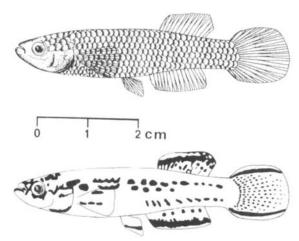


Figure 9. Males of Aphyosemion bertholdi with its corresponding red colour pattern.

Meristic data are of little value except for the differentiation of the occidentalis group (Table 3).

Liberiense group

This group includes A. liberiense, A. schmitti, A. bertholdi and A. brueningi. I include the representative of A. roloffi and A. geryi in the liberiense group. This group corresponds to all the small colourful Aphyosemion, that exhibit marked red pigmentation and very often yellow stripes on the uneven fins.

Both A. liberiense and A. schmitti have a more elongated body and a caudal fin with a lyre tail pattern in the adult, compared with the other species of this group, A. bertholdi, A. brueningi and A. geryi. A. liberiense is restricted to SW Liberia around Monrovia, Robertsport and Totota, whereas A. schmitti is endemic to E Liberia between the Nipoué and Cess rivers, and the Cavally river. The latter species can be distinguished from A. liberiense and the other Aphyosemion from Liberia by the yellow pigmentation on the first third of the anterior part of the body. A. schmitti can be differentiated from A. liberiense by the more anterior position of the anal fin, A. schmitti shows D/A = 6-9; and A. liberiense D/A = 4-5 (Table 3).

A. bertholdi and A. brueningi are present in the Bomi Hills area, but not on the coast. Criteria based on colour pattern, such as the constant absence of yellow stripes, can separate A. bertholdi from the other species. However, this criterion has to be applied by comparing populations, because some individuals of A. liberiense may lack yellow stripes. Moreover, A. bertholdi has a distinctive blue stripe on the extremity of the pectoral fins. A. brueningi can be separated from A. bertholdi by the irregular red transversal bars on its sides, and the presence of yellow stripes on the anal and caudal fins.

Guineense group

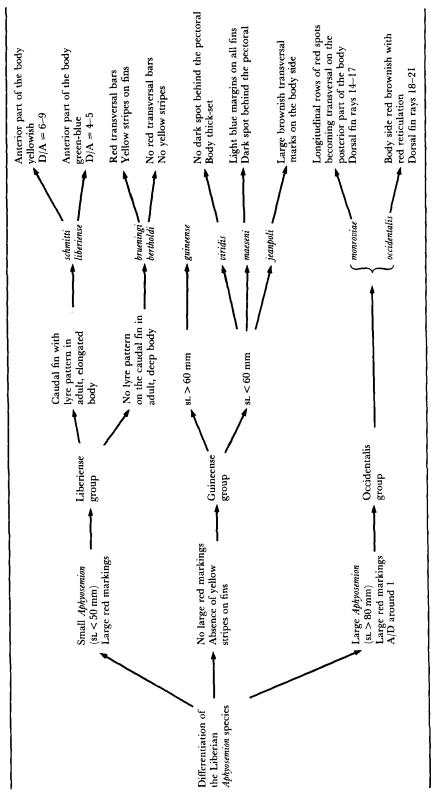
This group has three representatives presently known in Liberia, although A. guineense might be present, and can be distinguished by its larger size (over

Table 2. Morphometric and meristic characters of the Liberian Aphyosemion species

	A. schmitti	A. liberiense	A. maeseni	A. jeanpoli	A. monroviae	A. viridis	A. brueningi	A. occidentalis	A. bertholdi
Standard length	40-50	40-50	37-40	40-50	75–90	35-40	45-52	80-100	40-45
Dorsal fin rays	11-13	10 - 12	11-13	9-12	14-17	9-13	11-12	18-21	13 - 14
Anal fin rays	17-18	15–16	14-16	14-16	17–19	13-15	15–16	16-20	16-17
D/A*	6-9	4-5	2-6	2-8	1–3	2-6	3-5	1-3+	4-5
₽dL†	33–36	31 - 33	30 - 33	31–34	32-35	29–32	32–33	33–37	31–32

*Juxtaposition of the dorsal (D) and anal (A) fin, given by the number of anal rays anterior to the first dorsal fin ray. †Number of scales from the upper edge of gill opening to caudal peduncle. †The anal rays are posterior to the first dorsal fin ray.

Table 3. Separation of the three groups of Aphyosemion



80 mm sL) compared with the three other species, A. maeseni, A. viridis and A. jeanpoli. The most distinctive feature that differentiates this group from the liberiense group is the absence of large red markings on the sides and on the fins, along with a constant absence of yellow pigmentation. It is very difficult for a non-specialist to differentiate the two smaller species of this group, i.e. A. maeseni and A. viridis, localized in N and NE Liberia. However, one can put forward the following criteria that may help to separate these two species.

- (1) Dark spot behind the pectoral fin present in A. maeseni, absent in A. viridis.
- (2) Well defined light blue margin on all fins in A. maeseni, but restricted to the caudal and the dorsal fins in A. viridis.
 - (3) Small dark red lines restricted to the unpaired fins in A. maeseni.
 - (4) Body more thick-set in A. viridis.

The third species, A. jeanpoli, is present in the NW part of Liberia and possibly in the Bomi Hills. It can be recognized by the dark red transverse bars on its sides, that may become brownish, depending on behaviour.

Occidentalis group

This group is characterized by the large size of its representatives, reaching over 80 mm sl. Moreover, the larger number of rays on the anal and caudal fins, the very characteristic colour pattern in which red pigmentation predominates, the ratio A/D close to 1 or the dorsal in front of the anal (in the other groups this ratio is over 4) separate this group from the two others.

A. monroviae can be separated from A. occidentalis by the characteristic two or three black rays on the anterior part of the dorsal fin, and by some several longitudinal rows of red spots on the anterior half on the sides that become transversal on the posterior half. A. occidentalis has a larger number of dorsal fin rays (18–20), with sides displaying a red-brownish pigmentation with a red reticulation. The first dorsal fin ray occurs before the first anal fin ray.

USE OF COLOUR PATTERNS IN APHYOSEMION SPECIES

The value of vivid colour patterns as found in several Aphyosemion of Liberia (Fig. 3) and in other Aphyosemion species, is not yet well understood. Does it provide a means of recognition between males and females of the same species as is true of the cichlid Hemichromis bimaculatus (Noblet & Curtis, 1939), where females select the redder of two males? Does it help the female to choose a specific mate? The repertoire of colour patterns in Aphyosemion is, however, very limited and static compared to that of many cichlids (Voss, 1977) or even other Cyprinodontidae such as Epiplatys (Romand, 1978). Moreover, observations have shown that most Aphyosemion in Liberia are not sympatric, which indicates that colour patterns may not be very important, at least in extraspecific recognition. In other parts of Africa (Nigeria, Cameroon, Gaboon, Zaïre and Congo) many species of Aphyosemion have been found to be sympatric, and display more variations in colour patterns than Liberian species. It is thus possible that colour patterns are used as a sign of specific recognition as is the case among cichlids (Baerends & Baerends-Van Roon, 1950).

PHYLOGENETIC RELATIONSHIPS BETWEEN THE LIBERIAN APHYOSEMION AND OTHER APHYOSEMION SPECIES

The method of phylogenetic systematics, or cladism (put forward by Hennig, 1966) has been used with some success by Parenti (1981) on the Cyprinodontidae sensu Myers. By applying a similar cladistic methodology to Aphyosemion of Liberia, it is possible to propose a cladogram of hierarchic representation (Fig. 10) based on colour pattern, cytogenetics and genetics.

Red colour pattern with considerable variations is present in the three groups of Aphyosemion in Liberia. It is believed that the red colour patterns on the sides, with large red and yellow margins on the uneven fin, may be primitive characters, evolving towards a reduction of red pigmentation and the disappearance of yellow pigmentation and reaching a climax in the guineense group, which shows, during certain forms of behaviour, dark crossbars on its sides. The liberiense group may be situated between the two, with its yellow derived from the the occidentalis group.

The study of fish karyotypes, which is useful in phylogenetic analysis, shows a general trend towards a reduction in chromosomes (Ohno, 1970; Scheel, 1972b). The primitive karyotype is characterized by a large number of small chromosomes. This trend is observed in Liberian *Aphyosemion*. In the occidentalis group all species display n = 23 small chromosomes, whereas the liberiense group has n = 20-21 and the guineense group n = 19-21 chromosomes, including large metacentric ones (Scheel, 1972b; Grimm, 1972; Douchement, 1983).

Similarly, the study of biochemical differentiation between several species of Aphyosemion in W Africa (Douchement et al., 1984) shows that the liberiense group is not closely related to the occidentalis group, but more closely related to the Mesaphyosemion subgenera of equatorial Africa. Liberian Aphyosemion fall into two different subgenera, as proposed by Radda (1976), and correspond quite well to our hierarchic representation (Fig. 10). The primitive group was referred to as Callopanchax Myers, 1933 (genus Roloffia of Clausen, 1966). Unfortunately, Parenti (1981) placed this group with others in a separate genus,

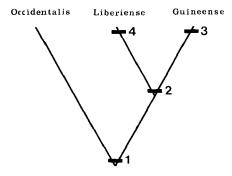


Figure 10. Possible cladogram of relationships of Aphyosemion of Liberia based on colour patterns, cytogenetics, genetics, behaviour and biology (see text). Node 1: dorsal origin in front of anal origin, large red pigmentation, large number of chromosomes, very aggressive, annual. Node 2: dorsal origin posterior to anal origin, less red pigmentation, caryotype with n=19-21 chromosomes, less aggressive, non-annual. Node 3: dark crossbars often present on the body sides, no yellow pigmentation on fins, few red pigments. Node 4: no dark crossbars, red pigments well represented, yellow pigmentation often present on fins.

Fundulopanchax, not recognizing the originality of this group among other subgenera.

Considering the colour pattern, cytogenetics (Scheel, 1972b), behaviour (Ewing, 1975; Douchement, 1983) and biology (annualism) of representatives of Callopanchax, we suggest that this subgenus may be one of the most primitive groups of the genus Aphyosemion (sensu Myers, 1924) from which most other Aphyosemion in W Africa may have derived. Even if most other Aphyosemion were derived from the occidentalis group, it is nevertheless true that the genus Aphyosemion has not been considered to be a monophyletic group (Parenti, 1981). Genetic investigations are currently underway to define the phylogenetic relationship between various groups of this genus and other African Cyprinodontidae genera.

The derived group, i.e. the liberiense and guineense groups, are included in the subgenera Archiophyosemion Radda, 1977 (a very unfortunate name), that corresponds to most Aphyosemion west of the Benin Gap. These fish are characterized by a reduction in red pigmentation, especially in the guineense group, a lower number of chromosomes, marked genetic differentiation and difference in behaviour and biology.

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