

A New Species Of Cyprinodont Fish, *Aphyosemion tirbaki* n. sp. (Cyprinodontiformes: Aplocheilidae) From Gabon, With Further Evidence Of The Frontier Species Concept

By Dr. Jean H. Huber

Abstract: *Aphyosemion tirbaki* n. sp. is described from two adjacent localities in the primary rainforest of southeastern Gabon. A member of the *Aphyosemion ogoense* superspecies complex, it is distinguished from other members of this complex by a combination of morphometric and meristic features, as well as male color pattern. Males bear a striking resemblance in color to *Aphyosemion coeleste*, a vicariant species belonging to a different species group. These species provide an example of the "frontier species" concept, which is defined as a cryptic species of one group occurring in a restricted area near the periphery of the geographical range of the group, and living in close geographic proximity to a congener belonging to a different species group, possibly with a color convergence of both species.

The genus *Aphyosemion*, Myers 1924, is a group of tropical fishes characteristic of small, quiet brooks in the primary rainforests of western Africa. Species are found living either singly or, more often, sympatrically in groups of up to five congeners, although in cases of sympatry, the respective ecological niches are not obvious (Huber, 1978). The often spectacular colors of the males have resulted in a high degree of popularity among aquarists specializing in Cyprinodonts (oviparous Cyprinodontiformes). This, in turn, has led to a number of taxonomic and karyological studies, as well as increased field investigations in Gabon and adjacent areas of western Africa inhabited by these fishes.

The history of collections in southeastern Gabon well illustrates the situation.

For many years, the genus *Aphyosemion* was known from that area only from a single species, which was first collected from the vicinity of Franceville during the late 1920's by the French civil administrator, Msr. Baudon, and which was described by

Pellegrin (1930) as *Haplochilus lujae* var. *ogoensis*.

No further ichthyological investigations of this area occurred until 1976, at which time a specialized expedition comprised of Radda, from Vienna University, Austria, and the author made collections that resulted in descriptions of the following four new species of *Aphyosemion*: *A. lamberti* Radda and Huber, 1977; *A. rectogoense* Radda and Huber, 1977; *A. coeleste* Huber and Radda, 1977; and *A. punctatum* Radda and Pürzl, 1977. Since then, more than a dozen expeditions to that region have resulted in the discovery of additional populations of the above taxa, as well as three additional species that were first described from the adjacent Republic of the Congo (formerly French Congo): *A. schluppi* Radda and Huber, 1978; *A. pyrophore* Huber and Radda, 1979; and *A. buytaerti* Radda and Huber, 1978.

The small area where the above species were collected, which encompasses only about 1500 square kilometers, is part of a homogeneous plateau known as the Massif Du-Chaillu, in central and southern Gabon and neighboring parts of Congo. There occurs a remarkable diversity of Cyprinodonts, including over twenty species of *Aphyosemion*, one of the genus *Epiplatys*, one of the genus *Procatopus*, and two of the genus *Hypsopanchax*. Although fish have so far been collected at over a hundred sites (Huber, 1996), these have been limited to the southern half of the region, which is the only area accessible by road. Considering the high diversity of killifishes therein, it is likely that additional species remain to be discovered in the still-unexplored northern areas.

The new nonannual species of *Aphyosemion* alluded to above, *A. tirbaki*, is described on the basis of material collected in 1996 from Gabon. It belongs to the subgenus *Mesoaphyosemion*, which comprises 51 species and is the largest of the 12

subgenera of *Aphyosemion* listed by Huber (1996). *A. tirbaki* is a member of the *A. ogoense* species group (i.e., superspecies), which is considered to contain nine species. As is true of other superspecies, the *ogoense* group is characterized by similarities in pigmentation pattern, life colors, and morphometric and meristic features, with the included forms differing in details of male pigmentation and color, as well as karyology. These are discussed and illustrated in the present paper. The species groups of *Aphyosemion* found in that part of the Massif Du-Chaillu Plateau are also discussed in this paper. *Aphyosemion tirbaki* bears a striking resemblance to *A. coeleste*, a vicariant species belonging to a different species group within the subgenus *Mesoaphyosemion*. Although superficially similar, *A. tirbaki* and *A. coeleste* differ in a number of meristic and morphometric features, which are compared later in this paper. They are examples of "frontier species" which are defined as cryptic species of a group occurring near the geographical periphery of that group. Such a species, in turn, characteristically lives in close geographic proximity to a congener belonging to a different species group, possibly with color convergence between the two species (Huber, 1977). The "frontier species" concept is discussed in the present paper.

Methods: Counts and measurements were made according to the methods originally described by Hubbs and Lagler (1958) and modified by Huber (1992), for the related neotropical Cyprinodont genus *Rivulus*. Measurements were made with dial calipers, read to the nearest 0.1mm and the percentages, in standard length (S.L.), were rounded, except for the computation of the mean values and the standard deviations. Radiographs were made of a small sample (eight specimens) in order to verify fin-ray counting procedure and, especially, to verify previous estimates made (using a binocular microscope) of the relative

TABLE 1:

Comparison of selected morphometric and meristic characters between specimens of *Aphyosemion tirbaki* and *Aphyosemion coeleste* (range, then between parenthesis, mean and standard deviation; measurements, expressed in hundredths of standard length).

	<i>A. tirbaki</i>	<i>A. coeleste</i>
No. of specimens	8	7
Standard length (mm)	29.5-38.5	20.3-30.4
Total length (%)	121-125 (123.25; 1.35)	117-125 (121.50; 2.57)
Predorsal length (%)	62-67 (64.50; 1.58)	62-67 (64.29; 1.91)
Body depth at anal origin (%)	20-22 (21.10; 0.62)	18-20 (19.36; 0.58)
Depth at peduncle level (%)	12-13 (12.50; 0.48)	10-11 (10.57; 0.47)
Head length (%)	24-30 (27.14; 1.73)	23-27 (24.80; 1.38)
Dorsal-fin rays	14-15 (14.50; 0.50)	10-12 (10.9; 0.6)
Anal-fin rays	16-17 (16.25; 0.43)	14-15 (14.6; 0.5)
D/A deviation ratio	+3 to +4 (3.5; 0.5)	+7 to +9 (8.1; 0.6)
Lateral line scales	26-28 (27.4; 0.7)	29-31 (30.1; 0.6)
Transversal body scales	8-9 (8.1; 0.3)	7-8 (7.7; 0.5)

positions of the dorsal and anal fins (termed the D/A ratio). A D/A value of +4 indicates that the dorsal-fin origin is situated above the fourth anal ray, a +5 value signifies a position above the fifth ray, etc. The frontal squamation (scalation) pattern follows Hoedeman (1958) and the cephalic neuromast pattern follows Clausen (1967). Both methods are also detailed in Huber (1978). Institutional abbreviations are as listed in Leviton *et al.* (1985).

Genus *Aphyosemion* Myers, 1924

Myers (1924) described the genus *Aphyosemion* with the following characters, diagnostic and opposite to those of the Indo-Asian and African genus *Panchax* Valenciennes (= *Aplocheilus* Mac Clelland, including *Epiplatys* Gill, in their present definition). They still stand firm (Huber, 1978): a less flat dorsal profile of head; a snout, shorter than eye diameter; a lyre-shaped caudal fin. In the same paper, he also described *Fundulopanchax*, as a subgenus of *Aphyosemion*, distinguished by "the dorsal fin being inserted forward, above or very slightly behind the anal origin, and the subequality of these two fins."

Parenti (1981: 476-479) added several osteological characters to the definition of both *Aphyosemion* and *Fundulopanchax* and upgraded the

latter to the genus level. The former was diagnosed by "being nonannual, having a dorsal fin count of 7 to 14 rays, which is situated no farther anteriorly than opposite the first quarter of the anal fin origin, and possessing a swimbladder extending posteriorly to the first one or two haemal arches." The latter, in contrast, is an annual, with over 14 rays and dorsal and anal fins near to opposite, with a nonextending swimbladder. However, her view was not followed by several subsequent authors (e.g., Wildekamp, Romand & Scheel, 1986; Romand, 1992; Huber, 1996), with the following arguments: first, the distinction between the annual and nonannual conditions is not clear cut, with a continuum of states and semi-annual species as intermediates; second, some nonannual subgenera (e.g., *Archiaphyosemion* Radda, 1977, then available and *Scriptaphyosemion* Radda and Pürzl, described later, in 1987) were thought to be phylogenetically related to an annual subgenus *Callopanchax* Myers, 1933, because all share a common micromorphological character (a closed pattern of the first frontal pair of neuromasts, as per Clausen, 1967); third, strictly nonannual subgenera, like *Chromaphyosemion* Radda, 1971 and *Diapteron*, Huber & Seegers, 1977,

placed by Parenti in *Aphyosemion* s.s. show opposite and subequal dorsal and anal fins (but, with less than 14 rays at dorsal); last, annual or semi-annual subgenera, like respectively *Paludopanchax* Radda, 1977 and *Paraphyosemion* Kottelat, 1976, placed by Parenti in *Fundulopanchax*, show less than 14 dorsal fin rays in some species.

Preliminary recent studies, though, which are based on mitochondrial genes (Murphy & Collier, 1997) or on otholiths (Zee & Wildekamp, 1995), suggest that *Aphyosemion* sensu Myers is paraphyletic. It may be further subdivided in the future, but not according to Parenti's delineation and diagnosis.

The new species, *tirbaki*, falls anyhow more in *Aphyosemion* than in *Fundulopanchax*, sensu Parenti: it is a strict nonannual, the dorsal and the anal fins are not subequal and not opposite, the swimbladder is extended. However, the dorsal fin count is at the upper limit (14-15) and the D/A ratio is unusually low (+3 or +4, near to the first quarter of the anal fin).

Subgenus *Mesoaphyosemion* Radda, 1977

Radda (1977) described four new subgenera of *Aphyosemion* on the basis of meristics, of biological conditions (annualism or not), of karyological data, on key characteristics of color pattern, and on distribution. For example, *Mesoaphyosemion* was described with 9 to 13 dorsal fin rays, 13 to 17 anal fin rays, 28 to 34 scales in lateral line, a D/A deviation of +5 to +10, and by encompassing nonannual species. The distribution is restricted to the central West African forest. No comparative diagnosis was provided for these subgenera and the other seven already described subgenera and overlapping characters were part of the definitions. A twelfth subgenus, *Scriptaphyosemion*, was subsequently described by him, together with Pürzl in 1987, with the same approach and limitations.

However, Radda assigned each so far known species to a subgenus. The new species, *A. tirbaki*, falls readily in the subgenus *Mesoaphyosemion*, because its closest relatives, the members of the *ogoense* superspecies (see further, the superspecies concept) are all listed in *Mesoaphyosemion*, because of its distribution and because of its meristics. The meristics do not fit, though, entirely, with Radda's

description.

This is not the scope of this study to present a review of these twelve subgenera (Parenti simply listed them, either in *Aphyosemion* or in *Fundulopanchax*), or to determine if *Mesoaphyosemion* is a valid subgenus, all the more that several other researchers are in the process of doing so, separately (e.g., Costa, Collier, Zee; pers. comm.). And the subgenus status will not be discussed further in this paper.

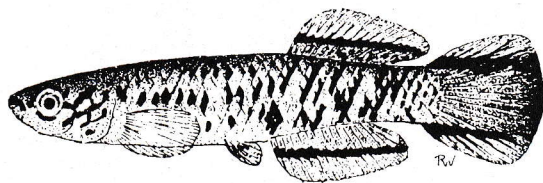
The Superspecies Concept

The genus *Aphyosemion* may be divided into a number of species groups, which are characterized by identical, or at least very similar, meristic and morphometric characters

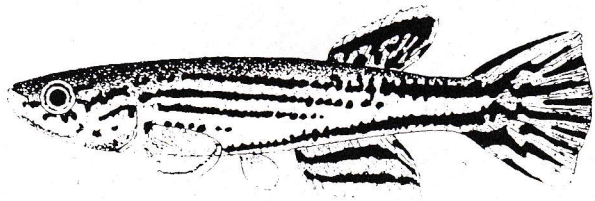
(isomorphism), and often are distinguished with certainty only by differences in male color pattern and by karyological differences. Scheel (1968) was the first to analyze these species groups, and his results were later expanded and elaborated upon by me (Huber, 1978).

Superspecies are known (Huber, 1992) for the related neotropical genus *Rivulus*, which ranges from southern North America south into South America, including the West Indies. Validity of these superspecies has been confirmed by the study of Murphy and Collier (1996), who expanded previously-held concepts by providing evidence that these monophyletic groups may also include certain aberrant nonisomorphic species.

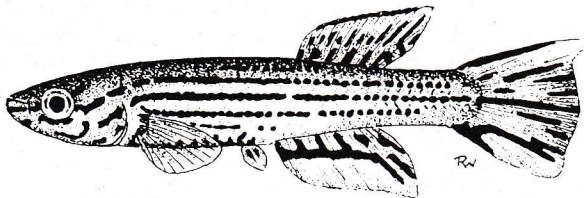
The *Aphyosemion* species dwelling the region of the biogeographically homogeneous Massif Du-Chaillu Plateau, where *tirbaki* is collected, can be grouped into five superspecies, based on key external characters. First, the *ogoense* superspecies is characterized by a medium size (total maximum length in aquarium: 50-70 mm), by a higher number of dorsal fin rays ($D = 11-14$, rarely 15), a lower D/A deviation ratio ($D/A = +3$ to $+6$), and by a lack of streamers in the unpaired fins. In the region, species include: *ogoense*, *pyrophore*. Second, the *coeleste* superspecies, also with rounded fins, is distinguished by a smaller size (T.L.: 40-50 mm), a slightly less deep body than the *ogoense* superspecies (19-20% versus



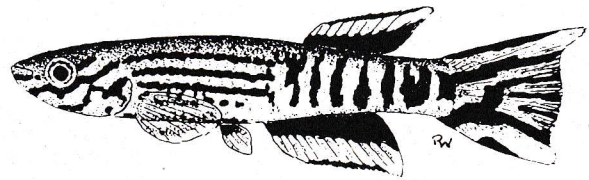
A. tirbaki from Tsozandzala, southeastern Gabon.



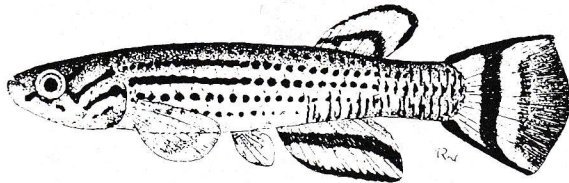
A. ogoense from Banbama, southern Congo.



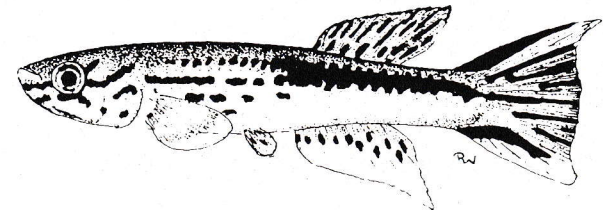
A. ottogartneri from Lutété, southern Congo.



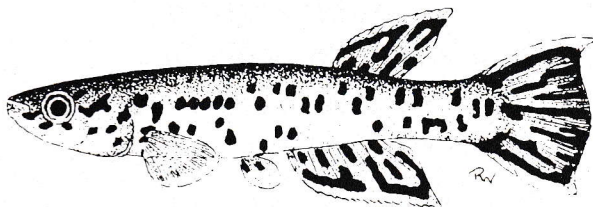
A. pyrophore from Mpoukou, southern Congo.



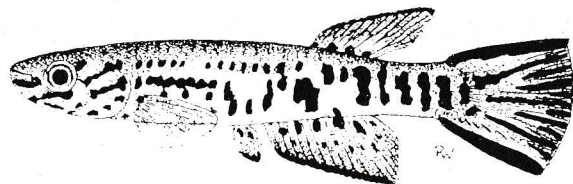
A. caudofasciatum from Ogowé, southern Congo.



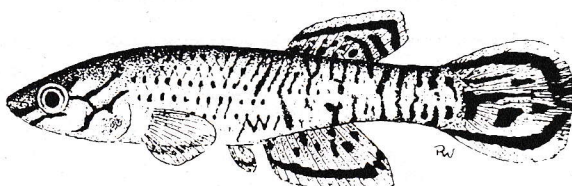
A. louessense from Lékoli Magogo, southwestern Congo.



A. zygaima from Mindouli, southern Congo.



A. labarrei from the Madimba area, southern Zaïre.



A. joergenscheeli from Mbigou, southwestern Gabon.

FIGURE 1:
Idealized sketches of males of the *ogoense* superspecies. R.H. Wildekamp.

21-22% in S.L.), by a lower number of dorsal rays ($D = 10-11$), by a complementary higher D/A deviation ($D/A = +6$ to $+8$), and by a post-opercular golden-pink contrasting zone with or without red markings. In this region, species include: *coeleste*, *passaroi*. Third, the *wildekampi* superspecies is only distinguished from the *coeleste* superspecies by the spade shape of the caudal fin, the pointed dorsal fin, and the lack of the post-opercular characteristic zone. In this region, species include: *punctatum*, *aureum*. Fourth, the *elegans* superspecies is distinguished from the three above superspecies by a slenderer body (depth = 17-18% in S.L.), by a short remote dorsal fin ($D = 7-9$; $D/A = +8$ to $+11$), and by the presence of medium sized streamers on unpaired fins of the male. Its size is similar (T.L. = 40-50 mm) to the *coeleste* and *wildekampi* superspecies. In this region, species include: *lamberti*, *rectogoense*. Fifth, the *batesii* superspecies is distinguished from all the above by the larger size (T.L., more than 80 mm, up to 150 mm), by the higher scale counts (LL = 32-35 versus 27-31 for the four above superspecies), by the higher and subequal counts of unpaired fins rays ($D = 15-17$; $A = 15-17$), by long streamers on male unpaired fins, and by its annual condition. In this region, species include: *splendidum*.

The *ogoense* superspecies is the most widespread and the most species rich in the Massif Du-Chaillu. It encompasses eight member species which are the following, with the corresponding respective meristics on average of limited material (Huber, 1996): *A. ogoense* ($D = 11$; $A = 14$; $D/A = +5$; LL = 30), *A. ottogartneri* (11, 15, +6, 30), *A. pyrophore* (12, 15, +6, 30), *A. caudofasciatum* (11, 14, +5, 30), *A. louessense* (13, 15, +5, 31), *A. zygaima* (12, 15, +6, 31), *A. labarrei* (13, 15, +6, 31), *A. joergenscheeli* (12, 15, +4, 29).

Based on its morphological characters, we infer that the new species *A. tirbaki* is a component of the *ogoense* superspecies (maximum T.L.: 70 mm; rounded unpaired fins; $D = 14-15$; $D/A = +3$). However, as stated in the introduction, the Cyprinodont fauna of the northern Du-Chaillu Plateau is unprospected and this hypothesis may be reappraised following future collections. *A. tirbaki*, as a component of the *ogoense* superspecies, is best separated from the other components by the male color

pattern, made of a series of broad irregular red markings on the sides and of a symmetrical organization of external bands on the caudal fin, comprising a yellow margin and a red submargin, whereas the other components are differently colored (Figure 1). The *ogoense* s.s. male shows a series of red longitudinal spots on the sides, including a broad basal red line from the anal insertion to the lower caudal, and an asymmetrical organization of external bands on the caudal fin (red margin and yellow/blue submargin on the upper part; the reverse on the lower part), plus a flamed pattern in the center of the fin. The *ottogartneri* male is similar to *ogoense*, but without the typical basal line on the sides. The *pyrophore* male is similar to *ottogartneri*, but the red longitudinal lines on the sides are replaced by thin red bars, posteriorly. The *caudofasciatum* male is similar to *pyrophore*, but with a red fasciated, instead of a flamed caudal fin. The *louessense* male is similar to *ogoense*, but the series of longitudinal spots are replaced by variable irregular blotches and a single broad mid-line on the sides. The *zygaima* male is similar to *louessense*, without the mid-line, but the caudal organization of external bands is symmetrical. The *labarrei* male is similar to *zygaima*, but the irregular spots are replaced by vertical

blotches and the caudal fin is lacking the yellow submargins and the margins are black, not red. The *joergenscheeli* male is vaguely similar to *ottogartneri*, but the series of side spots are arranged rather vertically and the caudal pattern is unique with a red circumcaudal submargin on a plain deep blue background.

All taxa for which the karyotype has been studied are determined by separate fundamental numbers and breed true to their characteristics, which discards the possibility of simple color variations or natural hybridization.

The inclusion of *tirbaki* with its symmetrical caudal pattern like *caudofasciatum*, *zygaima*, *labarrei*, and *joergenscheeli* allows us to notice that all symmetrically patterned species are distributed with a small range at the periphery of the superspecies (see further, distribution). All nine taxa represent a monophyletic line of distinctive cryptic biospecies, replacing each other vicariantly, the central phenotype, largely distributed, named *louessense*, displaying the most variable and generalized pattern (Huber, 1980), like in many *Aphyosemion* superspecies (e.g., the *cameronense* or *gardneri* superspecies).

***Aphyosemion tirbaki*, New Species**
Holotype: MNHN 1997-186, a

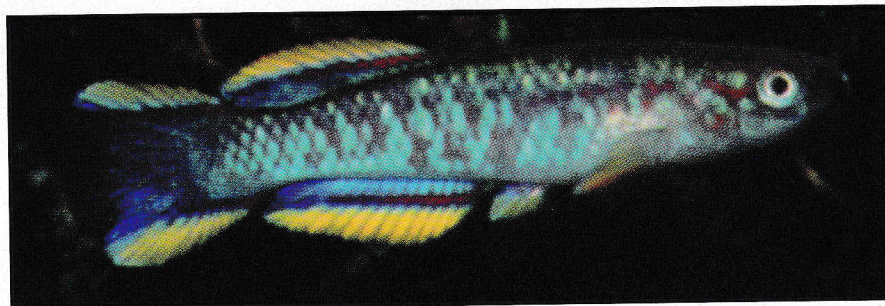


FIGURE 2
 Adult male, *A. tirbaki* topotype, not preserved. R. Lütje.



FIGURE 3:
 Adult male, *A. coeleste* from Malinga, southern Gabon (for comparison). M. Chauche.

male, 38.5 mm S.L., and 46.85 mm T.L., from a forest "marigot" near Tsoandzala, a village on the road from Lastourville to Moanda, 82.7 km from Lastourville, or about 38 km from Moanda, Joumini River, a part of Youmidié, then of Lékoudi basin (geographical coordinates in degrees and hundredths of degree: 1.28S; 13.03E); locality code: EBT 96/7; altitude: about 700 meters. W. Eberl, T. Blum and P. Tirbak, Coll. March 3, 1996.

Paratypes: MNHN 1997-187, 18 males; MNHN 1997-188, 26 females; NMW-93301, two males and two females; CAS 96952, four males and four females; BMNH-1997.8.28.7-14, four males and four females; MRAC-97-44-P-7-10, four males and 97-44-P-11-14, four females; UFRJ 3730, four males and four females; NRM 37494, four males and four females; ANSP 176179, four males and four females; all paratypes have been collected by the same collectors, at the same time and place as the holotype (paratopotypes).

Diagnosis: *A. tirbaki* is distinguished from all species of *Aphyosemion* sensu Myers by the combination of the following six characters. First, the relative position of the dorsal fin insertion, not far, vertically, from that of the anal (D/A = +3 or +4, i.e., 3 or 4 rays behind the anal fin insertion): this is a small deviation in *Aphyosemion* and the smallest one among the nonannual *Aphyosemion* species from the Southern Gabon and Congo Plateau. Second, the high number of dorsal fin rays (D = 14-15): this is the highest record in the genus if the annual species are excluded. Dorsal counts of nonannual species vary on average from D = 8 to D = 13 (Huber, 1996). Third, the somewhat deeper body at the anal fin level (depth: 21% in S.L.) and at the peduncle level (resp. 12-13%). These measurements are lower in the other nonannual *Aphyosemion* species of the region, except for the *ogoense* superspecies: the same proportions vary respectively from 17% to 20% and from 9% to 11% for them, on preserved field specimens (not aquarium-bred specimens which get fatter). Fourth, the male color pattern, made of a broad yellow margin and a red submargin on vertical fins and irregular red vertical markings on sides, without any post-opercular contrasting zone. Fifth, the rounded vertical fins, without extended rays. Sixth, the nonannual ecological

conditions, which implies a shorter incubation period of the eggs in water: annual species habitats completely suffer from desiccation during the dry season and the eggs undergo compulsory diapauses.

Among the over-120 presumably valid species of the genus (Huber, 1996), none is exhibiting those combined characters: only one species, *A. gardneri* s.l. from the coastal lowlands and corresponding foothills of Nigeria and northwestern Cameroun is coming close to this combination; however, it differs from the new species by its annual or semi-annual condition, by the presence of short streamers on the male caudal fin, by an even deeper body (depth at anal level: 22%-25% of S.L., according to Scheel, 1968). We infer that those shared characteristics of these two distantly related species are just the result of hazard, the total number of combinations being in essence limited.

Description: The key morphomeristical characters of eight types are the following (the holotype, first; average and standard deviation, last).

Sex: male, male, male, male, female, female, female. Standard length (in mm): 38.5; 36.8; 36.6; 37.9; 34.0; 30.5; 29.5; 32.3. Total length (in % of S.L.): 122%, 124%, 125%, 122%, 121%, 123%, 125%, 124% (mean: 123.25%; S.D.: 1.35%). Predorsal length (in % of S.L.): 62%, 64%, 65%, 63%, 64%, 65%, 67%, 65% (mean: 64.50%; S.D.: 1.58%). Preanal length (in % of S.L.): 60%, 61%, 61%, 58%, 60%, 63%, 63%, 60% (mean: 60.71%; S.D.: 1.72%). Preventral length (in % of S.L.): 47%, 53%, 50%, 48%, 49%, 51%, 49%, 48% (mean: 49.54%; S.D.: 1.84%). Depth at Anal level (in % of S.L.): 21%, 20%, 22%, 21%, 21%, 21%, 22%, 21% (mean: 21.10%; S.D.: 0.62%). Depth at Peduncle level (in % of S.L.): 12%, 13%, 13%, 13%, 13%, 12%, 13%, 13% (mean: 12.50%; S.D.: 0.48%). Head length (in % of S.L.): 26%, 30%, 27%, 28%, 27%, 29%, 27%, 24% (mean: 27.14%; S.D.: 1.73%). Interorbital (in % of S.L.): 16%, 13%, 13%, 12%, 13%, 14%, 13%, 12% (mean: 13.18%; S.D.: 1.23%). Eye diameter (in % of S.L.): 8%, 8%, 8%, 7%, 7%, 9%, 8%, 7% (mean: 7.52%; S.D.: 0.56%). Snout (in % of S.L.): 7%, 8%, 7%, 6%, 7%, 8%, 7%, 7% (mean: 7.16%; S.D.: 0.56%). Vertebrae (abdominal+caudal): 12+16, 12+15, 13+15, 12+16, 11+16, 12+16, 12+15, 11+16 (mean: 27.5; S.D.: 0.5).

Dorsal fin rays: 15, 15, 15, 15, 14, 14, 14, 14 (mean: 14.5; S.D.: 0.5). Anal fin rays: 17, 17, 16, 16, 16, 16, 16, 16 (mean: 16.25; S.D.: 0.43). D/A deviation: +4, +4, +3, +4, +3, +3, +4, +3 (mean: +3.5; S.D.: 0.5). LL (lateral scales + scales on caudal peduncle): 28+3, 27+3, 26+4, 28+3, 28+3, 27+3, 28+2, 27+2 (mean: 27.4; S.D.: 0.7). pDor (predorsal scales): 16, 16, 17, 15, 15, 16, 15, 16 (mean: 15.8; S.D.: 0.7). TRAV. (transversal scales): 9, 8, 8, 8, 8, 8, 8, 8 (mean: 8.1; S.D.: 0.3). CIR (circumpeduncular scales in a transversal zig-zag row): 16, 16, 15, 14, 16, 15, 16, 15 (mean: 15.4; S.D.: 0.7).

The frontal scalation of *tirbaki* is of the G-type and the cephalic neuromasts of the first frontal pair are of the open type, like all *Aphyosemion* from Gabon; no evidence of a significant sexual body dimorphism, except for fin length which is longer in male, can be disclosed, like in all *Aphyosemion* species (Scheel, 1968).

Because it is of utmost importance for the diagnosis of *tirbaki* and of *coeleste* (see further: systematic relationships), the specific count of the D/A deviation has been done, by the author with the microscope only, on larger samples: D/A = + 3.4 on average of 31 specimens of both sexes; standard deviation: 0.4: this value has never been found in *coeleste*, even the highest one, +5 in rare specimens. Moreover, in Table 1, a comparison of some characteristics with their range, mean and standard deviation, is given for the above eight types of *tirbaki* and for seven specimens of *coeleste* collected in 1979, in the Congo, and studied then by the author. On that small sample, *tirbaki* and *coeleste* appear to be distinct by the dorsal fin ray count, by the D/A ratio, by the depth of body and peduncle, maybe also by the lateral scale count and the anal fin count.

Life Colors: Male, red vertical irregular markings on the sides on a deep blue background; the yellow margins and red submargins of the caudal are also present in the dorsal, anal, and ventral fins. Female, strongly subdued as usual in the genus: overall brown with a few red irregular markings, rather in lines and in the median part of sides; the caudal fin is hyaline, whereas the dorsal and anal fins are irregularly flamed with red.

Colors In Preservative: Male, with the same markings as in life, except the blue background which has disappeared after alcoholic

maintenance; yellow colors are replaced by white in margins of the caudal, dorsal, and anal fins; in addition, the upper sides are darkly reticulated from the opercle level up to the peduncle and the caudal fin is innerly flamed with black (i.e., lines along rays); female shows also the dark upper sides, but only until the dorsal insertion level; some red spots, arranged in discontinuous lines, can be seen on sides, irregularly depending on specimens; dorsal and anal fins with a flamed pattern along rays, basally red then black distally; the anal fin margin is thinly bordered with black.

Systematic Relationships: As stated above (the superspecies concept), *A. tirbaki* is diagnosed by its color pattern only, from a series of eight isomorphic vicariant species, the members of the *ogoense* superspecies. Among them, it presents a somewhat higher number of unpaired fin rays ($D = 14-15$; $A = 16$), a lower D/A deviation ($D/A = +3$ or $+4$), and a lower longitudinal scales count ($LL = 27-28$), but knowing the overlapping variability observed with these fishes, from population to population, and, from species to species (Huber, 1978), this should be confirmed on larger samples from several localities.

On the other hand, *A. tirbaki* is morphologically separated from the components of the *coeleste* superspecies which lives also in southern Gabon and Congo, sometimes sympatrically with the *ogoense* superspecies and both are then assumed to be nonrelated; by color pattern, surprisingly, the *tirbaki* male is little separated from *coeleste*: the pattern of the sides is made of many red bars instead of a few red spots behind the opercle, the rest being identical (see Figures 2 and 3, for comparison, and further, the discussion on color convergence).

Ecology: The type locality is a forest stream containing crystal clear, slow-moving water and a gravel bottom. At the time of collection, the stream was 2.5 to 3.5 m wide and 30-60 cm deep, and was partially shaded by overhanging terrestrial plants and semi-aquatic plants along the edges. *A. tirbaki* was very abundant at the time of collection. Although it was the only Cyprinodont fish collected at this locality, it is likely that *Procatopus (Plataplochilus) terveri* Huber, 1981 is present in nearby areas. Other species collected were *Barbus* sp. (these are presently under

study), *Ctenopoma kingsleyae* Günther, 1896, and an undetermined characoid. Other animals included freshwater shrimps and tadpoles. The water was neutral to slightly acidic and relatively soft: pH = 6.2-6.4 and hardness less than 1dGH (P. Tirbak, pers. comm.).

Based on aquarium observations, *A. tirbaki* lays eggs among plants located close to the surface. Incubation time is about three weeks in water temperatures of 21°C. The maximum size is 70 mm (P. Tirbak and W. Eberl, pers. comm.).

Distribution: *Aphyosemion tirbaki* is thus far known only from two localities, the type locality and a second locality about 20 kms to the northwest (Blum locality BSWG 97/9 of August 1997), where the species was found sympatrically with one congener, *A. lamberti*. Both localities lie along the only passable road, which runs in a north-south direction. The closest known location for the superficially similar *A. coeleste* is the village of Mounana, about 20 km south of the type locality. It is doubtful if the range of the new species is very extensive, since not far to the north one finds a distinctively different fauna, with three different species of *Aphyosemion*: *A. lamberti* (member of the *elegans* superspecies), *A. punctatum*

(*wildekampii* superspecies), and *A. splendidum (batesii)* superspecies). The comparative distribution of the *ogoense* and *coeleste* superspecies is given in Figure 4 (based on the collecting localities, listed in Huber, 1996).

Companion Frontier Species:

A. tirbaki superficially bears a close resemblance to *A. coeleste*. Although both species are members of the subgenus *Mesoaphyosemion*, they belong to different superspecies and are not intimately related.

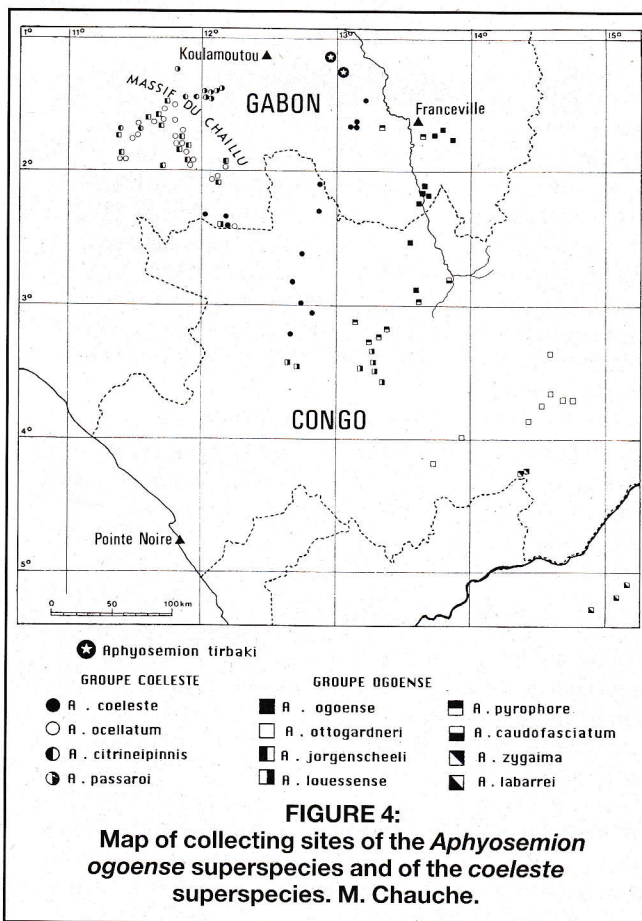
Etymology: The species is named in honor of one of its discoverers, Peter J. Tirbak, a renowned U.S. killi-hobbyist from Palo Alto, California.

The Frontier Species Concept

It has been observed in cyprinodontiform fishes that congeneric species within the same species group (i.e., superspecies) very rarely occur sympatrically (in a restricted sense; also termed syntopically, by some authors). They replace each other allopatrically, with neighboring distributions. Therefore, the distribution of a superspecies is the aggregation of the distribution of the individual members. Inversely, sympatry is common among congeners belonging to different superspecies

(Huber, 1977). These instances of sympatry may involve as many as five species (Huber, 1978; 1992), structured in independent tribes scattered all over the marigot. Brosset (1982) demonstrated that, during times of spawning, females are responsible for mate selection among sympatric congeners, and this is based, at least in part, by recognition of subtle differences in color pattern of the unpaired fins and posterior sides of the body.

In West Africa, especially in the area from eastern Nigeria to the Congo, one notices an abrupt change in species composition between the coastal plain and



the interior plateau. The superspecies are restricted to either upland or lowland areas, especially when the transition between the coastal plain (0-250m) and the plateau (350-700m) is sharp and rapid. On the narrow coastal plain, superspecies are distributed in straits parallel to the coast line, whereas on the plateau, a distribution in patches is observed (Huber, unpublished). Within areas of geographical transition, upland and lowland species may occur sympatrically, although there appears to be no significant reciprocal geographic penetration. And, apart from the barrier plain-plateau, no other barrier (e.g., river drainages, soil composition, change in forest coverage, etc.) has been established to explain the limits of distribution of an individual species or of a given superspecies (Huber, unpublished): the individual sympatric species or the resulting sympatric superspecies do not show, respectively, superimposed distributions. Nonetheless, the distributional structure of a superspecies appears to be made of two types, both in the plateau and in the plain. First, usually one or two species are largely distributed, usually near the center and with a variable, generalized color pattern (e.g., *lougessense* in the *ogoense* superspecies). Second, several species are restricted in some areas of the periphery, with much less variable and more typified color patterns (e.g., *caudofasciatum*, *zygaima*, *ogoense*, etc., in the *ogoense* superspecies). Each of these latter phenotypes is in direct conflict of expansion with a component of another allopatric superspecies. Both reject each other, mutually. No case of a species with a restricted range and a typified color pattern is known from the middle of the distribution of a given superspecies.

This was termed by me (Huber, 1980, 1981) the "frontier species" concept. Since then, lots of examples have been forwarded to strengthen the concept in *Aphyosemion* and also in other Cyprinodont genera, and also in South America. Frontier species occurring at the periphery of the overall distribution of the superspecies possess distinctive pigmentation which, in turn, may be very similar to that found, vicariously, in a peripherally distributed species belonging to another superspecies. Males belonging to different allopatric superspecies may be superficially very similar in appearance in such cases: a color convergence

Continued on page 116

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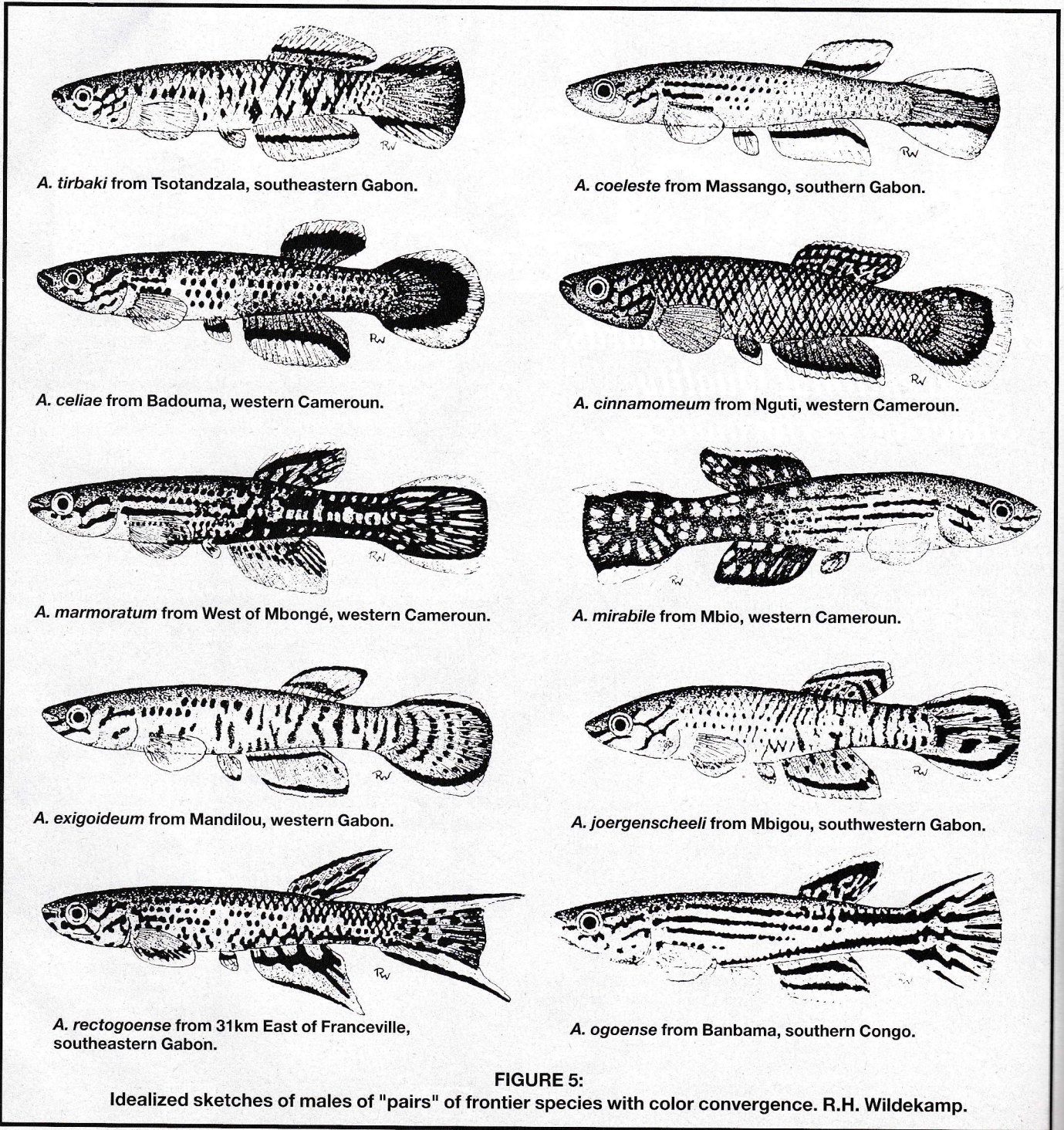
results. No such a case of a color convergence is known among sympatric congeners (which belong to distinctive superspecies separated by morphological characteristics) over the overall distribution of the genus.

In the genus *Aphyosemion*, the following examples can be reported (Figure 5). *A. celiae* is the frontier species of the *calliurum* superspecies in the Cameroun coastal plain, facing *A. cinnamomeum*, the frontier species of the *gardneri* superspecies in the plateau, both with a unique shared

color pattern of the caudal fin: a crescent shape organization of colors. *A. marmoratum* is the frontier species of the *scheeli* superspecies in the Nigeria/Cameroun coastal plain, facing *A. mirabile*, another frontier species of the *gardneri* superspecies in the plateau foothills, both with a marbled pattern of posterior sides and vertical fins. *A. exigoideum* is the frontier species of the *striatum* superspecies in the Gabon coastal plain, facing *A. joergenscheeli*, the component of the *ogoense* superspecies in the plateau, both with a circumcaudal red line on a blue-green background. *A. rectogoense* is the

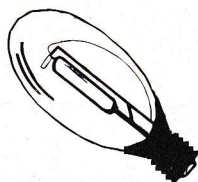
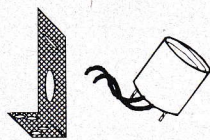
frontier species of the *elegans* superspecies in the Gabon/Congo savannah plateau, facing *A. ogoense*, the frontier species of the *ogoense* superspecies in the same but forested plateau, both with a basal red line on lower sides and a flamed caudal pattern.

Facing frontier species may share close similarities in color and color pattern, but display distinct differences in body size, body and fin shape, fin-ray counts, and especially D/A ratio. *A. tirbaki* and *A. coeleste* seem to provide another example of frontier species with color similarity. They



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differ in a number of meristic and morphological characters (Table 1), but are similarly colored, except for red vertical markings on the side of the body in *tirbaki* and the postopercular golden and red region in *coeleste*. Karyotypes of the two species have been studied by G. Collier, who states (pers. comm.), "the karyotype of *A. sp. EBT96/7* is superficially similar to that of *A. coeleste*; however, comparison of DNA sequences of portions of mitochondrial Cytochrome b and 12S RNA genes do not support a close relation between the two species."

Much remains to be learned about the taxonomy, distribution, and ecology of the killifishes inhabiting coastal regions of tropical West Africa. The inaccessibility of much of this area precludes detailed knowledge of population dynamics in areas near the peripheries (i.e., the "frontiers") of the ranges of different species. It may be observed that the primary role of the female in mate recognition of sympatric species rules out the possibility of the sympatric occurrence of similarly colored congeners. The theoretical consequence of this is that a hypothetical past occurrence of a mutational speciation accompanied of a color convergence with a sympatric congener would have induced a strong mutual geographic rejection. With or without color convergence, the concept of frontier species in tropical Cyprinodonts is hypothesized to be linked, for these fishes bound to reclusive biotopes, to the drastic climatic and ecological variations of

the early Holocene (Huber, Paris, March 1997). These ideas are conjectural, however, and, at present, no definitive answers are available to explain the "frontier species" phenomenon. Experimental work involving both behavior and genetic compatibility are required in order to resolve these problems, together with intensive field prospection.

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