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A systematic revision of the large-scaled *Marcusenius* with description of a new species from Cameroon (Teleostei; Osteoglossomorpha; Mormyridae)

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Nine out of 37 recognized species in the genus *Marcusenius* have eight large circumpeduncular scales rather than 12 or 16, which is more typical of the genus. They are: *M. dundoensis*, *M. fuscus*, *M. ghesquierei*, *M. intermedius*, *M. kutuensis*, *M. lambouri*, *M. moorii*, *M. paucisquamatus* and *M. schilthuisiae*. All nine are restricted to West-Central and Central Africa. A detailed morphometric analysis could not distinguish differences between *M. moorii*, *M. paucisquamatus* and *M. lambouri*. Therefore they are considered as synonyms with *M. moorii* as the senior synonym. The systematic status of *M. intermedius* is uncertain owing to the existence of only three specimens. Within this species complex a new species, *Marcusenius sanagaensis*, is described from the Sanaga River basin in Cameroon. It differs from all the others in the number of scales on the lateral line and in the extent of the broad dark band between the anterior base of the dorsal fin and the anterior base of the anal fin. All valid *Marcusenius* species with eight circumpeduncular scales are redescribed and a key to these species is given.

KEYWORDS: Systematics, morphometrics, Mormyridae, *Marcusenius*, Central Africa.

Introduction

The mormyrid electric fishes, endemic to subSaharan Africa, have received considerable attention recently because of their remarkable abilities to send and receive electric signals for purposes of communication and object-location. The electric organs of these fishes, located in the caudal peduncle, generate a discharge which is often species-specific (Bennett, 1971a; Hopkins, 1981, 1986; Crawford and Hopkins, 1989). The electroreceptors, three distinct classes of which are known (Bennett, 1971b; Bullock and Heiligenberg, 1986; Bell *et al.*, 1989), have been studied intensively as a model system for vertebrate sensory function. In spite of all the interest in electric signalling, however, the systematics of many mormyrids are still incompletely known.

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Gosse (1984) listed 18 mormyrid genera, including 189 species (erroneously reported as 198 in CLOFFA). An additional seven new species have been described since Gosse's list (Lévêque and Bigorne, 1985; Taverne and Thys van den Audenaerde, 1985; Roberts, 1989; Bigorne and Paugy, 1990, 1991). The most recent revision of the genera was based on osteological characteristics documented in detail by Taverne (1968, 1971, 1972). Since Taverne's work there have been a number of changes in generic placement of species.

Taverne's diagnosis (1971) of the genus *Marcusenius* Gill, 1862 included the following characters: an elongate body; a less well-developed snout, usually shorter than the postorbital segment; a rounded sub-mental swelling; a lower jaw slightly longer than the upper jaw; nostrils midway between the tip of the snout and the anterior margin of the eye; depth of caudal peduncle two to five times into its length; 19 to 36 dorsal-fin rays; 25 to 43 anal-fin rays; dorsal fin about the same length as the anal fin; 10–12 pectoral-fin rays; distance between pectoral and pelvic fins shorter than the distance between pelvic and anal fins; 36–46 caudal-fin rays; 38–98 lateral-line scales; 8–26/12–28 transversal scales on the body; 7–21/7–21 transversal scales between dorsal and anal fins; 8–18 caudal-peduncle scales; 3–8/3–10 conical or bicuspid teeth on the jaws; absence of a basisphenoid; lateral ethmoid present, median ethmoid reduced; caudal skeleton with a parhypural and four hypurals (five hypurals according to Taverne's nomenclature); and five circumorbitals.

Gosse (1984) recognized 37 valid species in the genus *Marcusenius*. Nine of these are characterized by having eight large circumpeduncular scales instead of the more typical counts of 12, 16 or more. They are: *M. dundoensis* (Poll, 1967), *M. fuscus* (Pellegrin, 1901), *M. ghesquierei* (Poll, 1945), *M. intermedius* Pellegrin, 1924, *M. kutuensis* (Boulenger, 1899), *M. lambouri* (Pellegrin, 1904), *M. moorii* (Günther, 1867), *M. paucisquamatus* Taverne, Thys van den Audenaerde and Heymer, 1976 and *M. schilthuisiae* (Boulenger, 1899). The distribution of these nine species is limited to West-Central and Central Africa, and in particular to the Lower Guinea and the Zairian ichthyofaunal provinces as defined by Roberts (1975). Overall, the genus *Marcusenius* has a much wider distribution from the Nilo-Sudan to South Africa.

The Lower Guinea ichthyofaunal province includes the coastal basins of Cameroon, Equatorial Guinea, Gabon, and Congo. The most important basins from north to south are: Sanaga, Nyong, Ntem (Cameroon), Ogowe (Gabon) and Kouilou (Congo). A complete list is given in Teugels and Guégan (1994). Some of these basins have been explored in detail only recently (review in Teugels and Guégan, 1994). Daget and Depierre (1980) and Daget (1984) provided a list of fishes from the coastal rivers of Cameroon, in particular the Sanaga and the Nyong rivers. The Lower Kouilou has been studied by Teugels *et al.* (1991), while part of the Central Kouilou was examined by Mamonekene and Teugels (1993). The fish fauna of the Ogowe river has been known since Pellegrin (1930). *Marcusenius moorii* Günther (1867) is the only species in this eight-scaled group from the coastal rivers in Cameroon, Gabon and Congo. Although it was originally described from specimens from the Ogowe River, the holotype, originally housed in the Liverpool Museum, is apparently lost. Taverne *et al.* (1976) described a second similar species, *Marcusenius paucisquamatus* from the rivers Nyong, Ntem and Ogowe in Lower Guinea and from the Dja (Zaire System).

The Zairian province covers the Zaire River Basin. Our knowledge of the distribution of fishes in this basin is very poor. The parts of the Zaire basin examined so far are Stanley-Pool (Poll, 1939; 1959), Yangambi (Poll and Gosse, 1963), Lac Tumba (Matthes, 1964), Dundo (Poll, 1967), Lualaba (Banister and Bailey, 1979), the Lower Zaire (Roberts and Stewart, 1976) and Sangha (Pellegrin, 1928). Nine species of *Marcusenius* with eight circumpeduncular scales are reported from this region: *M. dundoensis*, *M. fuscus*, *M. ghesquierei*, *M. intermedius*, *M. kutuensis*, *M. lambouri*, *M. moorii*, *M. schilthuisiae* and *M. paucisquamatus*.

Because identification of these species is difficult, we undertook a systematic revision of available material, including all available type-specimens, museum specimens, and newly collected fishes; and because of the recent interest in electric discharges in mormyrids, we used this opportunity to study the morphology of the electric organs of these fishes. Alves-Gomes and Hopkins (1997) have summarized the literature on electric organ morphology for mormyrids and found two morphotypes represented in the genus *Marcusenius*: those with electrocytes with penetrating stalks innervated on the anterior side (type Pa), and those with cells with non-penetrating stalks innervated on the posterior side (type NPp).

Material and methods

We examined 464 specimens in this study. They are housed in various Natural History Museums. Institutional abbreviations are listed as in Leviton *et al.* (1985) (see material examined).

Twenty-seven point-to-point measurements were taken on each fish using 'landmarks' shown in Fig. 1. Abbreviations and definitions for these measurements are given in Table 1. Eleven meristic counts were taken on each specimen, including the number of dorsal-fin rays (DFR), anal-fin rays (AFR), pelvic-fin rays (PLFR), pectoral-fin rays (PCFR), including both branched and unbranched rays. The number of scales on the lateral line (SLL) included only the pierced scales. The number of scales around the caudal peduncle (SCP) was verified to be eight in each case. Three additional scale counts were: the number of rows of scales between the anterior base of the dorsal fin and the anterior base of the anal fin (SDA), the number of scale rows between the anterior base of the dorsal fin and the lateral line (SDL) not including the pierced scale row of the lateral line, and the number of scale rows between the anterior base of the pelvic fin up to, but not including, the lateral line (SPL). We also measured the number of teeth in upper (TUJ) and lower jaws (TLJ).

To characterize the colour patterns on these fish we counted the number of scales on the lateral line included in the dark vertical band (SDB) running between dorsal and anal fins.

For some individuals, including the types, radiographs were made. The following counts were made: anterior vertebrae (AntV), defined here as the number of vertebrae anterior to the first abdominal vertebra; abdominal vertebrae (AV), defined as having closed haemal arches and carrying ribs; caudal vertebrae (CV) defined by a closed haemal arch; and the total number of vertebrae (TV) being the sum of AntV, AV and CV.

The electric organs of 14 specimens have been examined in histological sections using light microscopy. A piece of the electric organ from the caudal peduncle was removed after removing scales by cutting through to the spinal column and Gemminger's bones with a sharp razor blade. The tissue was dehydrated in 95% ethanol, infiltrated and embedded in JB4 plastic (Polysciences, Inc.) and sectioned in the sagittal plane with a tungsten carbide knife at 7 μm. The sections were stained with Toluidine blue (2%).

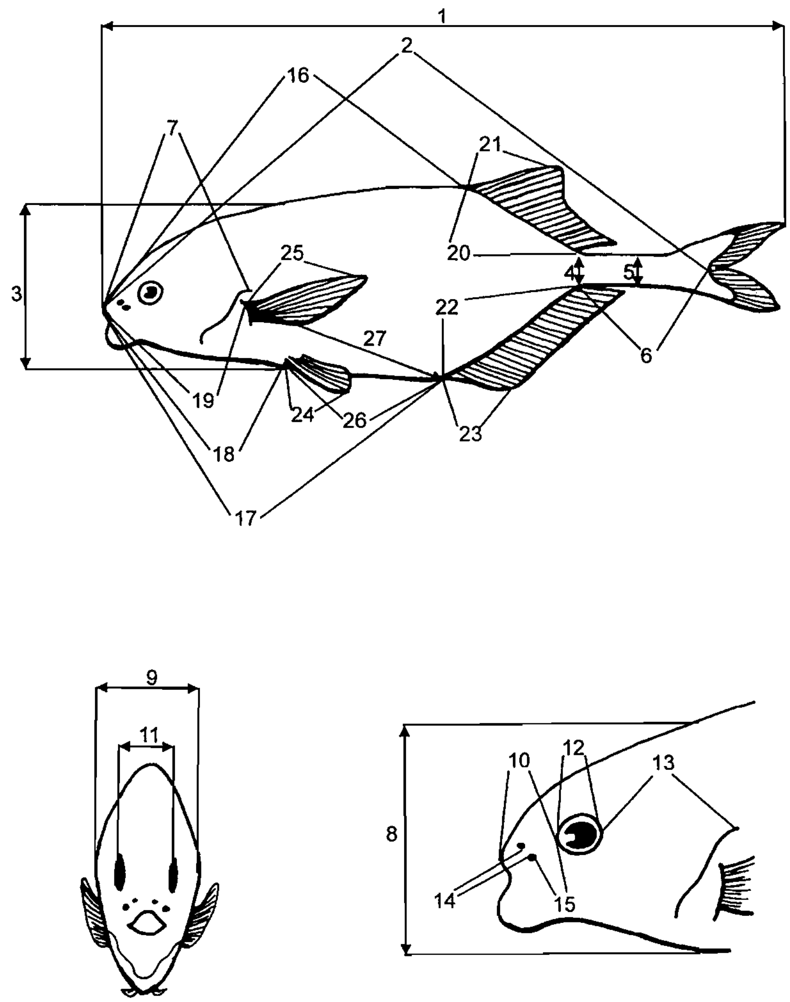


FIG. 1. Schematic illustration of measurements taken on *Marcusenius* specimen. Table 1 represents the explanation of the different numbers. All measurements are taken point to point.

Non-dimensional species analysis was used in this study (Mayr, 1970). We first made a comparison of a series of specimens from a given geographical region, sorting them into natural subgroups according to morphological characters. Subgroups from neighbouring regions were then compared in order to find identical or different groups in adjacent geographical areas. We then included the type-material in its own geographical context. This procedure led to the naming of the species groups and to the indication of synonyms. Finally we compared all these species and established a key to their identification.

The data obtained were submitted to factor analysis using a principal component analysis (PCA) program from Statistica (StatSoft Inc.) (versions 3.1 and 4.5). Measurements were log-transformed before the PCA was run on the covariance matrix. An independent PCA was run on the correlation matrix from the untransformed count data. We included 27 different measures in the morphometric analysis and nine counts in the metric analysis, including DFR, AFR, SLL, SDA, SDL, SPL, TUJ, TLJ and SDB. After examing the factor scores from these PCA's, we sometimes combined meristic and morphometric results into a single graph. All specimens were also examined qualitatively for additional characters that might be used for identification and classification.

Results

Morphometrics and meristics

We begin our analysis with specimens from the Lower Guinea Ichthyofaunal province and then continue with fishes from Zaïre.

Lower Guinea Ichthyofaunal Province. We examined 219 specimens originating from river systems from the Sanaga River to the Kouilou River, including the type specimens of all nominal species of *Marcusenius* from this area. Of the type-material, only *Marcusenius moorii*, which is probably lost, is missing from our data set. A PCA using the covariance matrix for 27 measurements results in a single group which was impossible to divide logically into subgroups (not shown). By contrast, a PCA on the correlation matrix for nine meristic characters revealed the presence of two groups with no overlap (Fig. 2). The first group located on the right, has first factor scores $>5{\cdot}0$, while the second located to the left, has first factor scores $<5{\cdot}0$. Factor loadings, shown in Table 2, show that the first component is dominated by various scale counts, while the second is dominated by the numbers of fin rays. The dominant character separating these two groups is the number of lateral-line scales, which is 49–56 in the first group and only 37–45 in the second. The first group also has more transverse scales between the dorsal- and anal-fin origins (22–28 *vs* 14–20) and more lateral-line scales on the dark band between the anterior end of the dorsal fin and the anterior end of the anal fin (3–4 *vs* 2–3 in the second group).

The first group occurs only in the Sanaga River while the second is present in all rivers of the Lower Guinea Province, including the Sanaga. This larger group contains all the existing type specimens of the nominal species known from this province, including parts of the type series of *M. paucisquamatus*. It also includes specimens from the Ogowe River, the type locality of *M. moorii*. We have examined the composition of the second group very carefully, but we are unable to distinguish any clear subgroups within these populations. We have re-run both principal component analyses mentioned above, after removing all of the cases recognized in the first group, to see if the larger group would divide into clusters when it was not dominated by the lateral-line scale counts of the first group. No differences could be found to distinguish subgroups, even after examining the different basins separately. Therefore, it is most likely that all specimens of the second group belong to a single species with widespread distribution throughout the Lower Guinea province.

Zairian Ichthyofaunal Province. We next examined 245 specimens originating from the Zairian Province. Included here were all type specimens found in this province, except for the holotype of *Marcusenius dundoensis*, which is supposedly housed in the Museo do Dundo, Angola, but could not be obtained for this study although the paratypes of this species were available to us. All specimens examined originate from the Lower or the Central Zaire basin.

A preliminary analysis of these 245 specimens enabled us to recognize immediately two groups based on the position of the dorsal fin. In the first group the dorsal-fin origin is anterior to the anterior margin of the anal fin, while in the second

Table 1. List with abbreviations and definitions of the measurements corresponding with the numbers in Fig. 1.

No. in Fig. 1	Abbreviation	Full name	Definition
1	TL	Total Length	Horizontal distance from tip of snout (upper jaw) to end of caudal fin
2	SL	Standard Length	Point-to-point distance from tip of snout (upper jaw) to base of caudal fin
3	BD	Body Depth	Vertical depth of body taken from the anterior base of the pelvic fin
4	CPD	Caudal Peduncle Depth	Vertical depth of the caudal peduncle taken from the posterior end of the anal fin base
5	MCPD	Middle Caudal Peduncle Depth	Depth of caudal peduncle taken in the middle of its length
6	CPL	Caudal Peduncle Length	Point to point distance from posterior end of anal fin base to end of vertebral column
7	HL	Head Length	Point to point distance from anterior tip of snout (upper jaw) to posterior end of opercular opening
8	HD	Head Depth	Vertical height measured at the anterior end of gill-opening
9	HW	Head Width	Distance between the posterior ends of the opercula
10	SNL	Snout Length	Distance from anterior tip of snout (upper jaw) to anterior border of eye
11	IOW	Interorbital Width	Width between the two eyes
12	ED	Eye diameter	Eye diameter
13	POL	Postorbital Length	Distance from posterior border of eye to posterior end of operculum
14	DNN	Distance between Nostrils	Smallest distance between anterior and posterior nostril
15	DNE	Distance between Nostril and Eye	Smallest distance between posterior nostril and eye
16	PDD	Predorsal Distance	Point to point distance from anterior tip of snout to anterior base of dorsal fin
17	PAD	Preanal Distance	Point to point distance from anterior tip of snout to anterior base of anal fin

18	PPLD	Prepelvic Distance	Point to point distance from anterior tip of snout to anterior base of pelvic fin
19	PPCD	Prepectoral Distance	Point to point distance from anterior tip of snout to anterior base of pectoral fin
20	DFL	Dorsal-fin Length	Distance from anterior to posterior dorsal-fin base
21	DFH	Dorsal-fin Height	Longest dorsal-fin ray length
22	AFL	Anal-fin Length	Distance from anterior to posterior anal-fin base
23	AFH	Anal-fin Height	Longest anal-fin ray length
24	PLFL	Pelvic-fin Length	Distance from anterior to posterior end of the fin
25	PCFL	Pectoral-fin Length	Distance from anterior to posterior end of the fin
26	DPLAF	Distance between Pelvic and Anal Fin	Distance between anterior base of pelvic fin to anterior base of anal fin
27	DPCAF	Distance between Pectoral and Anal Fin	Distance between anterior base of pectoral fin to anterior base of anal fin

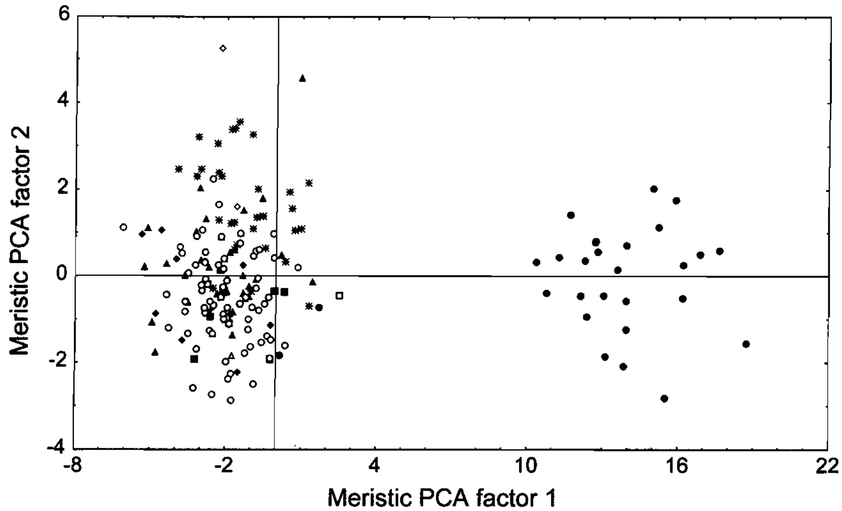


FIG. 2. Plot of the second principal component (factor 2) versus the first principal component (factor 1) taken from a principal component analysis of meristic counts, for 219 specimens known from the Lower Guinea Ichthyofaunal Province (◇ = syntypes of *Mormyrus lepturus*, □ = holotype of *Mormyrus grandisquamis*, △ = holotype of *Marcusenius paucisquamatus*, ○ = paratypes of *Marcusenius paucisquamatus*, ● = Sanaga river, ■ = Nyong river, ◆ = Ntem river, ▲ = Ogowe river and ✱ = Kouilou river).

Table 2. First and second factor score coefficients for the meristic PCA using nine counts for 219 specimens of the Lower Guinea Ichthyofaunal Province. For abbreviations see Material and Methods. The results of the PCA are shown in Fig. 2.

	Factor 1	Factor 2
SLL	4·12	−0·20
SDA	2·78	0·45
SDL	1·57	0·24
SPL	1·23	0·20
DFR	0·65	−0·69
AFR	0·57	−1·01

group, it is behind. Normally this should be reflected in the ratio of predorsal distance and preanal distance but because these measurements are dependent on the position of the snout which is sometimes turned upward or down, we found it to be less reliable for distinguishing these two groups. The first group does have dorsal fins which are slightly longer than their anal fins; and they have a high number of dorsal-fin rays. These two characters are plotted in Fig. 3. The first group also has a more pronounced falciform shape to the dorsal fin and the sub-mental swelling is small and round and does not extend beyond the anterior margin of the eye. The type material for two nominal species, *Marcusenius kutuensis* and *M. ghesquierei*, is present in the first group, while the types of all other nominal species are in the second. The first group shown in Fig. 3 seems to be composed of two subgroups. More detailed analysis confirmed this: the first has 27–31 dorsal-fin rays and the ratio dorsal-fin length/anal-fin length is $<1{\cdot}25$; the second has 32–34 dorsal-fin rays

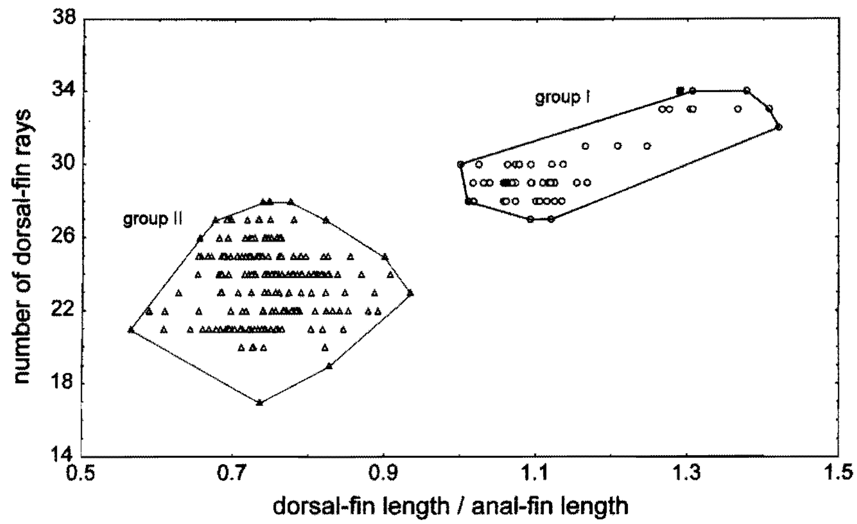


FIG. 3. Scatterplot showing the number of dorsal-fin rays in function of the ratio between the dorsal-fin length and the anal-fin length for two groups of the Zairian Ichthyofaunal Province (■ = holotype of *Marcusenius kutuensis*, ● = holotype of *Marcusenius ghesquierei*, ○ = group with dorsal-fin origin anterior to the anal-fin origin, △ = group with dorsal-fin origin posterior to or in line with the anal-fin origin).

and the ratio dorsal-fin length/anal-fin length is >1·25. The results of a PCA for the meristic counts of the specimens of this group (Fig. 4) clearly indicated the two subgroups, the first one contains the holotype of *M. kutuensis*, the second one contains the holotype of *M. ghesquierei*. We therefore conclude that both species are valid. The type of electrocytes is the same in the two species (see discussion later).

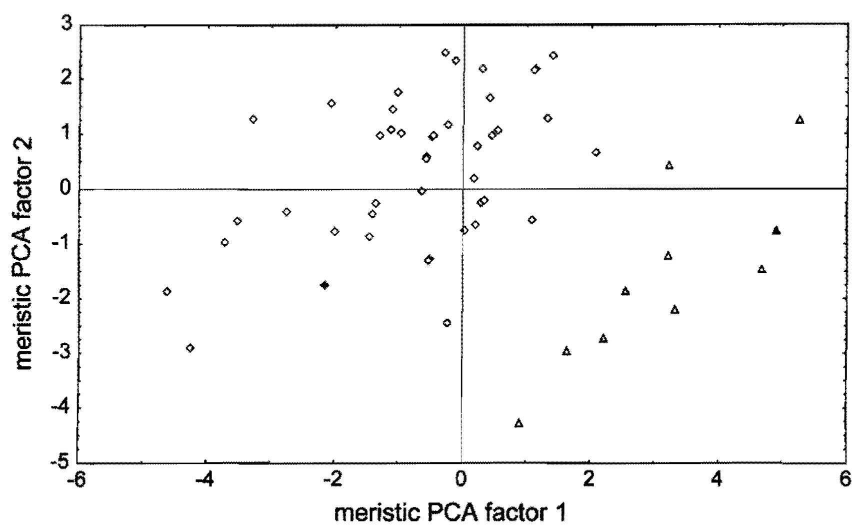


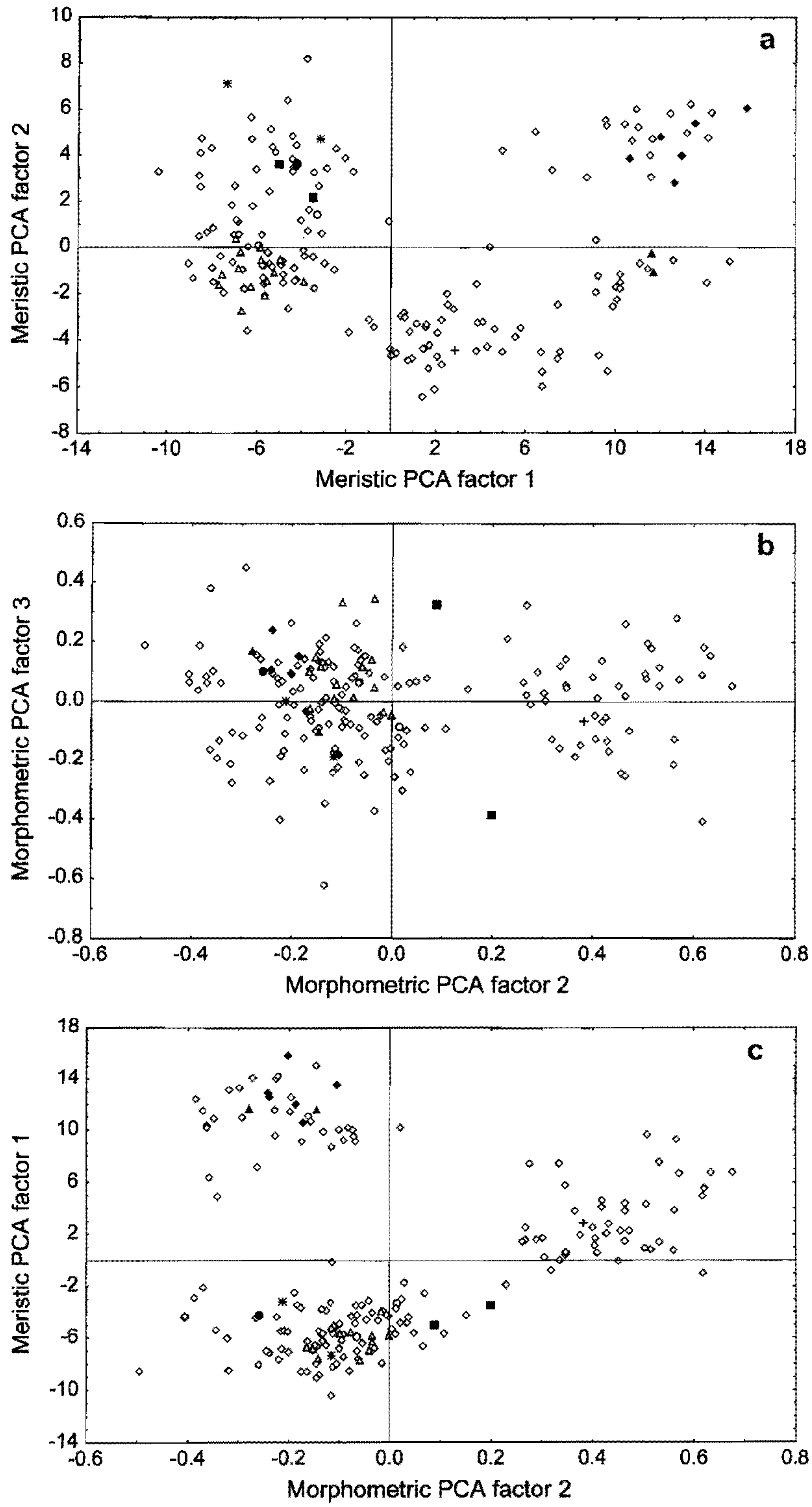
FIG. 4. Plot of the first principal component (factor 1) versus the second principal component (factor 2) taken from a principal component analysis of meristic counts, for 54 specimens belonging to group I in Fig. 3 (△ = *Marcusenius ghesquierei*; ◇ = *Marcusenius kutuensis*; full symbols refer to holotype).

For all specimens of the second group we did two PCAs, one using the covariance matrix for 27 morphometric characters, and one using a correlation matrix with 9 meristic counts. The results for the meristic PCA are given in Fig. 5a. In the upper right quadrat we can find a group of 25 specimens including the type-specimens of *Marcusenius dundoensis*. We conclude that this is a homogeneous group represented by this single species. For other specimens it is more difficult to identify species groups. Figure 5b shows a plot of the second and third factors for the morphometric PCA for the same set of specimens. The first factor was omitted from this analysis since it is dominated by standard length. We see here two overlapping groups, one on the left side of the horizontal axis (PCA factor $2<0{\cdot}2$) and one on the right side (PCA Factor $2>0{\cdot}2$). The holotype of *M. schilthuisiae* belongs to the second group. The cluster of points surrounding the holotype of *M. schilthuisiae* in Fig. 5a is difficult to separate from the group with type-material of *M. fuscus* but it is clearly separated using morphometrics.

Figure 5c combines the second factor scores for the measurements PCA with the first factor scores for the meristic PCA. Here type-material of *M. fuscus* and *M. schilthuisiae* are clearly separated from each other. Now one group, located in the upper left quadrat, contains the type material of both *Marcusenius dundoensis* and *M. fuscus*, while the second group located in the upper right quadrat of Fig. 5c, includes the type-specimen of *M. schilthuisiae*. Factor score coefficients for these analyses are given in Table 3. The dominant characters for the second principal component for the morphometric characters are distance between the two nostrils, anal-fin lengths and eye diameters; while for the first principal component of the meristic counts, scale counts are most important. The second principal component of the meristic counts is heavily influenced by the number of dorsal- and anal-fin rays.

The group in the upper left quadrat of Fig. 5c, clustering around the type-material of *M. dundoensis* and *M. fuscus* was then isolated for further analysis. Both are characterized by a high number of lateral-line scales and a low anal-fin length. In Fig. 5a we can distinguish both species due to the second principal component of the meristic counts. This is confirmed by an additional meristic PCA involving nine meristic characters. The results show two distinct sub-populations corresponding to the type-specimens of the two species, *M. dundoensis* and *M. fuscus*. We conclude that these two species are valid species for the Zaïre basin. The most important character to distinguish them is the number of anal-fin rays (26–30 in *M. dundoensis* and 31–34 in *M. fuscus*). Also the dorsal fin is obviously concave in

FIG. 5. (a) Plot of the second principal component (factor 2) versus the first principal component (factor 1) taken from a principal component analysis of meristic counts, for a group of specimens known from the Zairian Ichthyofaunal Province; (b) Plot of the second principal component (factor 2) versus the first principal component (factor 1) taken from a principal component analysis of log-transformed metric variables, for a group of specimens known from the Zairian Ichthyofaunal Province; (c) Plot of the second principal component taken from a principal component analysis of log-transformed metric variables (factor 2) versus the first principal component taken from a principal component analysis of meristic counts (factor 1), for a group of specimens known from the Zairian Ichthyofaunal Province (◆ = paratypes of *Marcusenius dundoensis*, ▲ = syntypes of *Marcusenius fuscus*, ● = holotype of *Marcusenius intermedius*, ■ = types of *Marcusenius lambouri*, ∗ = types of *Marcusenius moorii longulus*, △ = paratypes of *Marcusenius paucisquamatus*, + = holotype of *Marcusenius schilthuisiae*, ○ = Lower Zaïre, ◇ = Central Zaïre).


a
Meristic PCA factor 2
Meristic PCA factor 1
-14
-10
-6
-2
2
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18
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0
-2
-4
-6
-8
b
Morphometric PCA factor 3
Morphometric PCA factor 2
-0.6
-0.4
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c
Meristic PCA factor 1
Morphometric PCA factor 2
18
14
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2
-2
-6
-10
-14
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8

Table 3. Factor score coefficients for the PCA using 27 log-transformed morphometric variables, not standardized, (factor 2 and factor 3) and for the PCA using nine meristic counts (factor 1 and factor 2), both for the specimens of the Zairian Ichthyofaunal Province mentioned in Fig. 4. For abbreviations see Table 1 and Material and Methods.

	morphometric variables			Meristic variables	
	Factor 2	Factor 3		Factor 1	Factor 2
log DNN	−0·14	0·09	SLL	6·35	0·64
log AFL	0·11	0·02	SDA	2·52	−0·67
log ED	0·10	0·07	SPL	1·25	−0·21
log DFL	0·10	0·01	SDL	1·23	−0·38
log CPD	−0·08	−0·01	AFR	0·55	−2·61
log MCPD	−0·07	−0·02	SDB	0·51	0·43
log DNE	−0·01	−0·10	DFR	0·23	−1·77

M. dundoensis, while it has only a very slight concave rounding in *M. fuscus*. The dorsal-fin height is about the same as its length in *M. dundoensis*, but it is shorter in *M. fuscus. Marcusenius fuscus* also has a higher number of vertebrae (see also Table 7) than *M. dundoensis* or any other species of *Marcusenius* in this complex. *Marcusenius dundoensis* does not overlap geographically with *M. fuscus. Marcusenius dundoensis* is found only near Dundo, Angola, while *M. fuscus* occurs widely in the Zaire basin between Stanley-Pool and the Ruki river.

We now turn to the remaining specimens located in the lower left quadrat of Fig. 5c. Another group of three specimens including the type-specimen of *M. intermedius* can be separated quite easily, by a distinctive subinferior rather than terminal mouth (Fig. 6). This is the most obvious important factor for recognizing this species. These individuals also have a low number of lateral-line scales, a low number of scales between dorsal- and anal-fin origins and a low number of dorsal-fin rays. The dorsal fin is slightly concave and the snout is slightly elongated with the upper jaw being longer than the lower jaw. All three specimens originate from different localities in the Central Zaire basin. We tentatively conclude that they are all *M. intermedius*, but because the specimens are old and in poor condition, and since the sub-mental swelling may have become flattened in storage, thereby influencing the shape of the mouth, the systematic status of this species is questionable and more research is necessary.

After eliminating all specimens of *M. dundoensis*, *M. fuscus* and *M. intermedius* recognized in the previous PCA, we made another PCA on meristic data and a second PCA on log-transformed morphometric data for the remaining specimens. The results are combined in a single plot in Fig. 7. Two groups are recognized. The first group (upper right quadrat) includes the holotype of *M. schilthuisiae*; the second group (lower left quadrat) includes the types of *M. lambouri* and *M. moorii longulus* and the Zairian specimens in the paratypes of *M. paucisquamatus*. Factor score coefficients are shown in Table 4. Most important are the anal-fin length, the distance between the nostrils, the eye diameter, the number of lateral-line scales (42–54 versus 37–45 in the second group), the number of scales between the dorsal- and anal-fin origins (21–25 versus 15–20) and the number of anal-fin rays. With a combination of these characters, we were able to separate *M. schilthuisiae* from the other species. Some of these characters are included in the diagnostic key below.

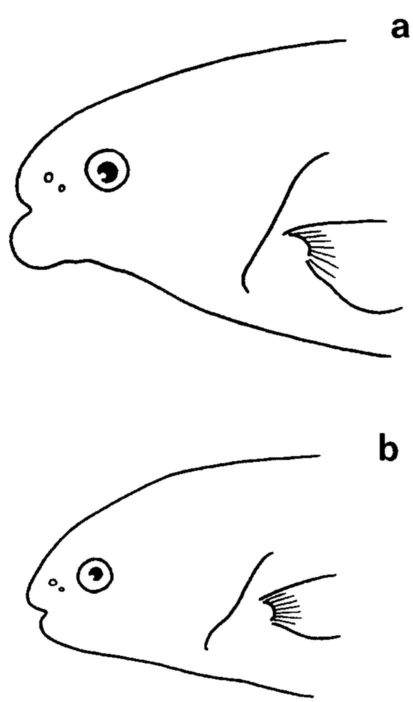

FIG. 6. Schematic illustration of the head region of two *Marcusenius* species: (a) *M. moorii*, (b) holotype of *M. intermedius*.

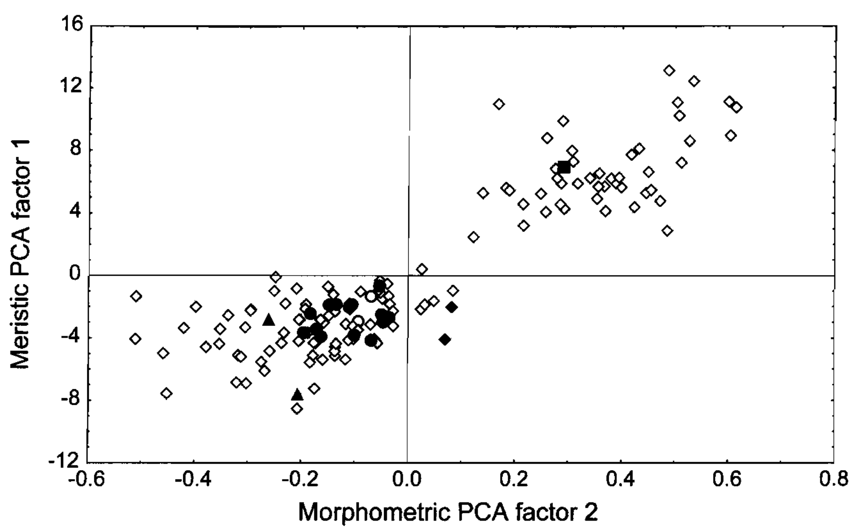

FIG. 7. Plot of the second principal component taken from a principal component analysis of log-transformed metric variables (factor 2) versus the first principal component taken from a principal component analysis of meristic counts (factor 1), for a group of specimens known from the Zairian Ichthyofaunal Province (◆ = types of *Marcusenius lambouri*, ▲ = types of *Marcusenius moorii longulus*, ● = paratypes of *Marcusenius paucisquamatus*, ■ = holotype of *Marcusenius schilthuisiae*, ○ = Lower Zaïre, ◇ = Central Zaïre).

Table 4. Factor score coefficients for the principal component analysis using 27 log-transformed morphometric variables (factor 2) and for the principal component analysis using nine meristic counts (factor 1), both for the specimens of the Zairian Ichthyofaunal Province mentioned in Fig. 6. For abbreviations see Table 1 and Material and methods.

	Factor 2		Factor 1
log AFL	0·12	SLL	3·39
log DNN	−0·12	SDA	2·29
log ED	0·12	AFR	2·11
log DFL	0·10	DFR	1·48
log CPD	−0·09	SDL	1·20
log MCPD	−0·08	SPL	1·02

Finally, for the Zaire specimens, we examined in detail the group containing the type-specimens of *Marcusenius lambouri* and *M. moorii longulus* and part of the type material of *M. paucisquamatus*. The type specimens of *M. lambouri* and *M. moorii longulus* are nearly identical. Poll (1948) has already considered *M. moorii longulus* as a junior synonym of *M. lambouri* and this is confirmed in our study (Table 8). The included type-specimens of *M. paucisquamatus* originate from the Dja river, part of the Central Zaire basin which extends into Cameroon. The type-specimens of the other species are also originating from the Central Zaire basin. All three nominal species are so close to each other with no clear differences that we conclude that they belong to the same species, *M. moorii* (*cfr. infra*).

Lower Guinea and Zairian Ichthyofaunal Provinces combined. We now combine the specimens of the Lower Guinea and Zairian Ichthyofaunal provinces into a single group and analyze morphometric and meristic characters in two PCA's as before. Figure 8 shows a plot of combined PCA scores including factor 1 from the meristic analysis and factor 2 from the morphometric analysis. As expected, the group of specimens of *M. moorii* from the Lower Guinea area (group 2 in Fig. 2), including the types of *M. paucisquamatus* and additional specimens from the Ogowe, overlaps perfectly with the specimens of *M. moorii* from the Zaire River basin including the types of *M. lambouri*, *M. moorii longulus*, and the remaining types of *M. paucisquamatus*. We suggest that all this material is conspecific. As only one *Marcusenius* species with eight circumpeduncular scales has been reported from the Ogowe river, we consider this group as *M. moorii*.

Two nominal species were previously synonymized with *M. moorii*: *Mormyrus lepturus* and *Mormyrus grandisquamis*, both by Boulenger (1898). This synonymy is confirmed here (Fig. 2). The characteristics of these two junior synonyms correspond precisely to the type-material of *M. paucisquamatus*, *M. lambouri* and *M. moorii longulus*. This is another argument favourable to our view that *M. paucisquamatus*, *M. lambouri* and *M. moorii longulus* should be considered as junior synonyms of *M. moorii*.

The distinct population of fishes found in the Sanaga River basin (Fig. 2) of the Lower Guinea Province is sufficiently distinct that we consider this population as a new species which we describe below. Three specimens identified as *M. moorii* by Daget and Depierre (1980) belong to this new species.

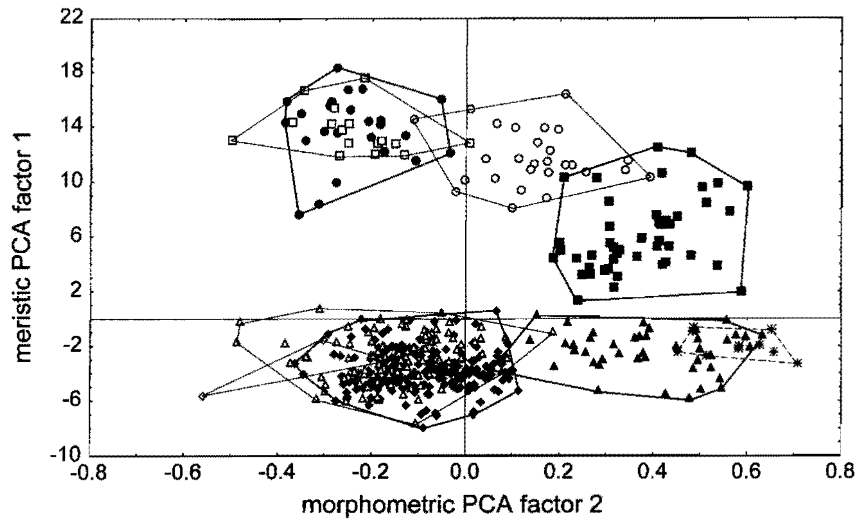

FIG. 8. Plot of the second principal component taken from a principal component analysis of log-transformed metric variables (factor 2) versus the first principal component taken from a principal component analysis of meristic counts (factor 1), for all *Marcusenius*-species known from the Lower Guinea Ichthyofaunal Province and the Zairian Ichthyofaunal Province (● = *M. dundoensis*, □ = *M. fuscus*, ◇ = *M. intermedius*, ▲ = *M. kutuensis*, ○ = first group of Lower Guinea Ichthyofaunal Province (= *M. sanagaensis* n. sp.), ■ = *M. schilthuisiae*, ✳ = *M. ghesquierei*, ◆ = second group of Lower Guinea Ichthyofaunal Province (= *M. moorii*), ◇ = last group of Zairian Ichthyological Province (= *M. moorii*)).

Morphology of the electric organ

We examined the electric organs of 14 specimens belonging to the seven species listed in Table 5. We found two types of electric organs in these samples, those with electrocytes with Non-Penetrating stalks with posterior innervation (type Npp) and those with electrocytes with Penetrating stalks with anterior innervation (type Pa). Schematic outlines of these two types of electrocytes are shown in Fig. 9. The morphology has been described for other species by Bennett (1971a), Bass (1986a) and Bass (1986b). In our sample all individuals of a given species had the same type of electric organ: three species had type NPp and four species had type Pa. Type NPp is typical of all specimens from the Lower Guinea Ichthyofaunal Province and for *M. dundoensis*. Type Pa electric organs are typical of *M. schilthuisiae*, *M. kutuensis*, *M. ghesquierei* and *M. fuscus*. Owing to lack of sufficient material, we were unable to examine *M. intermedius*.

We measured the distance between anterior and posterior faces of typical electrocytes for each specimen. All of these individuals had electrocytes of 5–12 micrometers thickness. Thin electrocytes like these are typical for fish with short (i.e. < 1 ms) duration electric organ discharges (EODs) (Bass, 1986b). Those with longer duration EODs (> 1 ms) generally have thicker electrocytes.

We noted that the penetrations in the electrocytes of type Pa tended to be both few and small. Bennett (1971b) already showed a relationship between the density and size of stalk penetrations and the magnitude of the initial head-negativity of the EOD in species with Pa electrocytes. It is likely therefore that the three species with Pa electrocytes have EODs with small initial head negative phases. We expect that

Table 5. Electric organ types of different specimens examined in this study. NPp = non penetrating stalk innervated on the posterior side; Pa = penetrating stalk innervated on the anterior side.

Specimen number	Species name	Basin	E.O. type
MRAC 87-07-P-57-73 nr. 1	*Marcusenius moorii*	Ogowe River, Gabon	NPp
MRAC 87-07-P-57-73 nr. 2	*Marcusenius moorii*	Ogowe River, Gabon	NPp
MRAC 87-07-P-57-73 nr. 3	*Marcusenius moorii*	Ogowe River, Gabon	NPp
MRAC 73-29-P-35	*Marcusenius moorii*	Nyong River, Cameroon	NPp
MRAC 75-24-P-288	*Marcusenius moorii*	Ogowe River, Gabon	NPp
MRAC 93-52-P-01	*Marcusenius sanagaensis*	Sanaga River, Cameroon	NPp
MRAC 94-74-P-38-40 1 ex.	*Marcusenius sanagaensis*	Sanaga River, Cameroon	NPp
MRAC 158547-549 nr. 1	*Marcusenius dundoensis*	Zaire River, Angola	NPp
MRAC 158547-549 nr. 2	*Marcusenius dundoensis*	Zaire River, Angola	NPp
MRAC 104560-566 1 ex.	*Marcusenius kutuensis*	Zaire River, Zaire	Pa
MRAC 73-23-P-790-791 1 ex.	*Marcusenius ghesquierei*	Zaire River, Zaire	Pa
MRAC 116499	*Marcusenius schilthuisiae*	Zaire River, Zaire	Pa
MRAC 116500	*Marcusenius schilthuisiae*	Zaire River, Zaire	Pa
MRAC 83-31-P-855-860 1 ex.	*Marcusenius fuscus*	Zaire River, Zaire	Pa

all three fish species with NPp electrocytes will have biphasic EODs with an initial head positivity as already shown by Bennett (1971b).

In an earlier study, Alves-Gomes and Hopkins (1997) demonstrated the presence of both NPp and Pa electrocytes within a single genus, *Brienomyrus*, that parallels that seen here for *Marcusenius*. In that study, which used molecular sequence data to arrange the species phylogenetically, type NPp electrocytes were seen as the primitive condition within the family Mormyridae while type Pa electrocytes were more derived. However, within *Brienomyrus*, type NPp electrocytes re-appeared in several species as a reversion to a more primitive condition. In a similar way we may conclude that type NPp electrocytes in these *Marcusenius* probably represent a reversion to a primitive condition.

Practical key for *Marcusenius* species with eight circumpeduncular scales

1 Fewer than 29 dorsal-fin rays, dorsal-fin origin posterior to or in line with the anal-fin origin and dorsal-fin length shorter than anal-fin length 2
– More than 26 dorsal-fin rays, dorsal-fin origin anterior to the anal-fin origin and dorsal-fin length equal to or greater than anal-fin length 7

2 21 or more transverse scale rows between dorsal- and anal-fin origins and more than 42 lateral-line scales 3
– 20 or fewer transverse scale rows between dorsal- and anal-fin origins and fewer than 45 lateral-line scales 6

3 Dorsal fin slightly concave with rounded anterior margin, dorsal-fin rays 22–26, anal-fin rays 31–34, 54–61 lateral-line scales and total vertebrae 48–49 . *Marcusenius fuscus*
– Dorsal fin deeply concave with pointed anterior margin; not with all these characters 4

4 Two rows of scales on transverse dark band between dorsal- and anal-fin origins, sub-mental swelling small, 42–54 lateral-line scales and 32–35 anal-fin rays . . . . *Marcusenius schilthuisiae*
– Three or more rows of scales on a transverse dark band between dorsal- and anal-fin origin, sub-mental swelling well developed, 49–61 lateral-line scales and 26–33 anal-fin rays 5

5 20–23 dorsal-fin rays; 26–30 anal-fin rays and dorsal-fin height about same as its length which is approximately 25% of the predorsal distance . *Marcusenius dundoensis*
– 24–28 dorsal-fin rays; 29–33 anal-fin rays and dorsal-fin height less than its length which is approximately 35% of the predorsal distance . *Marcusenius sanagaensis* n. sp.

6 Mouth subinferior; three scale rows on transverse dark band between dorsal- and anal-fin origin . . . . *Marcusenius intermedius*
– Mouth terminal; two, sometimes three, scale rows on transverse dark band between dorsal- and anal-fin origin . . . . *Marcusenius moorii*

7 27–31 dorsal-fin rays; ratio dorsal-fin length/anal-fin length $<1{\cdot}25$ *Marcusenius kutuensis*
– 32–34 dorsal-fin rays; ratio dorsal-fin length/anal-fin length $>1{\cdot}25$ . . . . *Marcusenius ghesquierei*

Marcusenius sanagaensis n. sp.

(Fig. 10)

Marcusenius moorii: Daget and Depierre, 1980

Material. Holotype: MRAC 93-072-P-0001. Bankim, river Mbam (Cameroon), 6°05′N–11°30′E. Coll. E. Van den Bergh, 1993. Paratypes: MRAC 73-29-P-618-620. Nachtigal, river Sanaga (Cameroon) 4°21′N–11°38′E. Coll. D. Thys van den Audenaerde, 1970; MRAC 73-29-P-621. Nachtigal, river Sanaga (Cameroon),

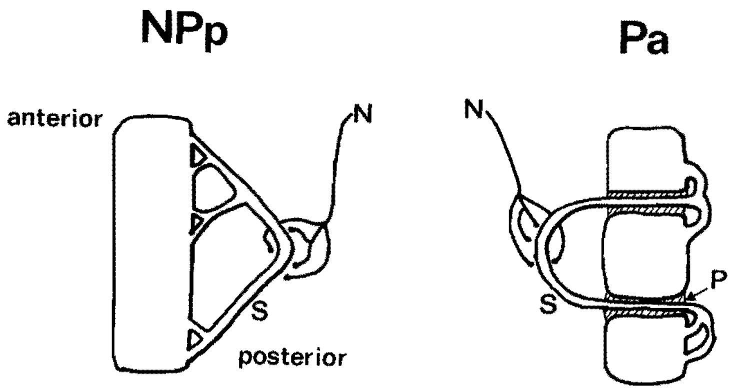

FIG. 9. Morphological diversity of electrocytes among the *Marcusenius* species with eight circumpeduncular scales, illustrated by two categories: (a) type NPp electrocytes has a non-penetrating stalk and is innervated on the posterior side, (b) type Pa electrocytes has a penetrating stalk with anterior innervation. N = nerve; S = stalk; P = penetration.

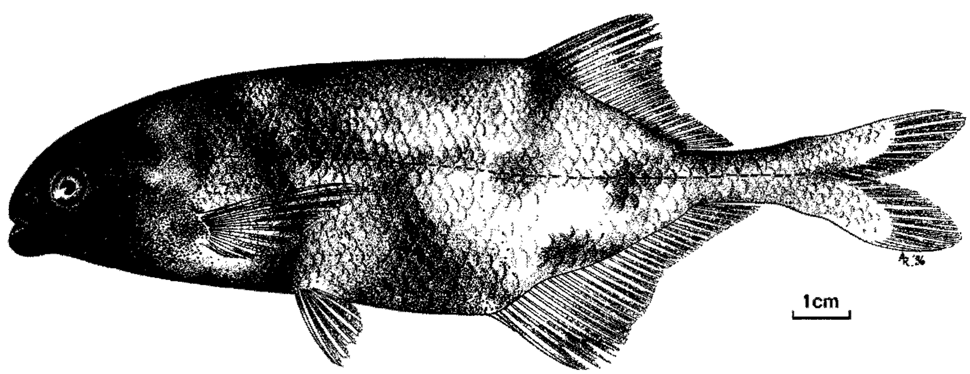

FIG. 10. *Marcusenius sanagaensis*, holotype, MRAC 93-072-P-0001, 137·2 mm SL.

4°21'N–11°38'E. Coll. D. Thys van den Audenaerde, 1970; MRAC 93-015-P-0003. Masaroum, river Mbam (Cameroon), 5°55'N–11°14'E. Coll. J. Breine and E. Van den Bergh, 1992; MRAC 93-052-P-0001. Mantoum, river Nchi (Cameroon), 5°36'N–11°09'E. Coll. M. Parrent and E. Van den Bergh, 1993; MRAC 93-052-P-0002. Mantoum, river Mbam (Cameroon), 5°36'N–11°09'E. Coll. M. Parrent and E. Van den Bergh, 1993; MRAC 93-072-P-0002. Bankim, river Mbam (Cameroon), 6°05'N–11°30'E. Coll. E. Van den Bergh, 1993; MRAC 94-022-P-0001. Ngambe, river Kim (Cameroon), 5°46'N–11°30'E. Coll. G. Teugels and E. Van den Bergh, 1994; MRAC 94-022-P-0002-0008. River Ndjim (Cameroon), 4°49'N–11°30'E. Coll. G. Teugels and E. Van den Bergh, 1994; MRAC 94-049-P-0016. Manki II, river Mvi (Cameroon), 5°51'N–11°06'E. Coll. E. Van den Bergh, 1994; MRAC 94-074-P-0038-0040. Foumbot, river Noun (Cameroon), 5°29'N–10°31'E. Coll. E. Van den Bergh, I. Forbin and A. Kamdem Toham, 1994; MRAC 94-074-P-0041-0043. Foumbot, river Noun (Cameroon), 5°29'–10°31'E. Coll. E. Van den Bergh, I. Forbin and A. Kamdem Toham, 1994; MNHN 1978-397. River Sanaga, Nanga-Eboko (Cameroon), 4°41'N–12°22'E. Coll. D. Depierre; MNHN 1978-398. River Sanaga, Nanga-Eboko (Cameroon), 4°41'N–12°22'E. Coll.

D. Depierre; MNHN 1978-399. River Sanaga, Nanga-Eboko (Cameroon), 4°41'N–12°22'E. Coll. D. Depierre.

Diagnosis. Dorsal-fin origin behind or in line with the anal-fin origin. The posterior base of the dorsal fin ends before the posterior base of the anal fin. Dorsal-fin margin is pointed and concave, its height shorter than its length. Lateral-line scales number 49–56; four, rarely three, scale rows on dark coloured transverse band. Scales between dorsal- and anal-fin origins number 22–28. Dorsal-fin rays are 24–28 while anal-fin rays are 29–33.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, five in upper jaw, six in lower jaw. Sub-mental swelling very rounded and projecting slightly forwards, its posterior margin located under anterior border of the eye. Snout rounded and blunt. Anterior nostril midway between tip of snout and eye; posterior nostril at about 0·25 the distance from eye to anterior end of the snout. Eye diameter 47–75% of snout length.

Preanal distance shorter or about the same length as predorsal distance. Dorsal fin shorter than anal fin. Height of both fins smaller than their lengths. Pectoral fin twice as long as pelvic fin, reaching halfway to the pelvic fin. Distance between pectoral- and pelvic-fin bases a little $>0{\cdot}33$ of the distance between pectoral-fin base and anal-fin origin. Posterior end of pelvic fin at about 0·4 of the distance between pelvic-fin base and anal-fin origin.

Number of dorsal-fin rays (24–28) less than anal-fin rays (29–33). Lateral-line scales numbers 49–56. Dark transverse band between dorsal- and anal-fin origin covered by 4, rarely 3, lateral-line scale rows. Scales between the dorsal- and anal-fin origins numbers 22–28. There are 43–45 vertebrae.

The electric organ electrocytes with non-penetrating stalks which are innervated on the posterior side (type NPp).

Coloration in life. Colour of the body grey, with head a little darker. Two dark vertical bands between the dorsal fin and the anal fin, the first situated between the anterior ends of the two fins, the second between the posterior ends. The latter is not always clearly visible.

Distribution and habitat (Fig. 11). At present, this species is only known from the Sanaga River basin in Cameroon. It has been recorded from the main river in the neighbourhood of Nanga-Eboko (Daget and Depierre, 1980), Nachtigal and from the Mbam and its tributaries Noun, Nchi, Ndjim and Kim.

Marcusenius sanagaensis is typically found in the raceways with sandy bottoms of larger rivers (50–200 m), in the tree savannah and the more or less degraded semi-tropical forest. At all collecting sites there was an important gallery forest on the riverbanks but with little or no live vegetation in the water, only dead wood and leaves. The water current ($0{\cdot}2\,\mathrm{m\,s^{-1}}$ to $1\,\mathrm{m\,s^{-1}}$), the water temperature at noon (21°–27·2°C), transparency (10 cm–1 m) and the depth of the water vary greatly, depending on the season. The water colour is greenish with great transparency during dry season.

Generally conductivity was rather low ($35{\cdot}5\,\mu\mathrm{s\,cm^{-1}}$ to $47\,\mu\mathrm{s\,cm^{-1}}$), dissolved oxygen rather high ($5{\cdot}5\,\mathrm{mg\,l^{-1}}$ to $7{\cdot}4\,\mathrm{mg\,l^{-1}}$), pH neutral or slightly alkaline (6·8–7·8) and hardness low: total hardness between 1 and 2°dH ($17{\cdot}8\,\mathrm{mg\,l^{-1}}$ to $36{\cdot}6\,\mathrm{mg\,l^{-1}}$) and carbonate hardness 1°dH ($17{\cdot}8\,\mathrm{mg\,l^{-1}}$). Silica varies between three and nine ppm and calcium between 0 and 6 ppm. Ammonium, nitrites and phosphates were not detected.

Other species found at the type localities are *Marcusenius mento*, *M. moorii*, *Mormyrops anguilloides*, *Mormyrus tapirus*, *Petrocephalus simus* (Mormyridae),

Table 6. Measurements of the different *Marcusenius* species with eight circumpeduncular scales. Abbreviations are mentioned in Table 1 or text, except: DPCPLF = Distance between base of pectoral fin and base of pelvic fin; stdev = standard deviation.

	M. dundoensis $n=24$ mean ± st.dev.	*M. fuscus* $n=16$ mean ± st.dev.	*M. ghesquierei* $n=10$ mean ± st.dev.	*M. intermedius* $n=3$ mean ± st.dev.	*M. kutuensis* $n=44$ mean ± st.dev.	*M. moorii* $n=293$ mean ± st.dev.	*M. sanagaensis* $n=27$ mean ± st.dev.	*M. schilthuisiae* $n=47$ mean ± st.dev.
%SL-TL	83·97 ± 1·68	86·22 ± 1·12	81·99 ± 0·81	85·18 ± 0·25	82·56 ± 1·03	83·52 ± 1·50	83·85 ± 1·11	84·31 ± 1·19
%BD-SL	24·95 ± 1·21	24·29 ± 1·45	32·72 ± 2·07	26·30 ± 2·34	29·73 ± 3·09	27·16 ± 2·47	27·53 ± 1·37	27·51 ± 2·50
%CPL-SL	15·97 ± 0·79	17·43 ± 1·32	19·73 ± 1·00	15·17 ± 1·04	19·55 ± 1·09	17·36 ± 1·53	17·65 ± 1·14	16·77 ± 0·97
%HL-SL	27·90 ± 1·90	24·40 ± 0·84	25·71 ± 0·37	24·54 ± 1·06	25·42 ± 1·37	26·03 ± 1·95	23·02 ± 1·03	24·16 ± 1·64
%PDD-SL	69·46 ± 1·29	64·00 ± 1·53	60·27 ± 1·23	70·06 ± 3·12	61·09 ± 1·96	65·22 ± 2·05	63·88 ± 1·56	62·62 ± 1·60
%PAD-SL	63·91 ± 1·97	58·97 ± 1·50	61·12 ± 1·80	64·12 ± 1·15	61·04 ± 1·43	62·21 ± 1·64	59·82 ± 2·08	58·18 ± 1·66
%PPLD-SL	42·04 ± 1·96	36·35 ± 0·74	38·99 ± 0·83	40·42 ± 2·00	38·23 ± 1·20	39·73 ± 1·51	36·90 ± 1·35	36·63 ± 1·45
%PPCD-SL	26·58 ± 0·35	22·72 ± 0·64	24·89 ± 0·55	24·56 ± 1·59	24·28 ± 1·02	24·58 ± 1·65	22·40 ± 0·95	23·12 ± 1·31
%DFL-SL	17·22 ± 1·18	19·94 ± 1·21	30·86 ± 1·30	17·82 ± 1·57	26·64 ± 1·24	19·45 ± 1·35	23·25 ± 1·26	21·95 ± 1·32
%AFL-SL	23·23 ± 1·13	27·70 ± 0·86	23·19 ± 0·91	24·01 ± 0·30	24·47 ± 0·92	24·76 ± 1·62	27·48 ± 1·43	30·49 ± 1·42
%PLFL-SL	10·38 ± 0·51	9·64 ± 0·42	10·59 ± 1·02	10·30 ± 0·20	10·88 ± 0·55	10·27 ± 0·86	10·50 ± 0·46	9·66 ± 0·55
%PCFL-SL	19·67 ± 1·02	17·56 ± 0·68	24·02 ± 1·62	18·89 ± 0·84	22·67 ± 1·26	20·61 ± 1·42	20·22 ± 0·78	20·25 ± 1·01
%CPD-CPL	38·61 ± 2·72	37·00 ± 3·84	28·56 ± 1·57	45·84 ± 1·20	29·44 ± 2·62	37·16 ± 5·61	34·24 ± 2·96	29·59 ± 2·57
%HD-HL	79·26 ± 3·99	80·59 ± 3·63	86·36 ± 3·83	79·96 ± 4·11	85·40 ± 6·42	82·76 ± 6·03	89·98 ± 5·14	86·13 ± 5·47
%HW-HL	32·75 ± 2·80	37·13 ± 3·81	33·07 ± 4·74	36·95 ± 4·95	33·66 ± 4·97	35·76 ± 6·67	43·39 ± 3·53	34·79 ± 4·35
%SNTL-HL	27·60 ± 1·51	27·86 ± 1·57	24·51 ± 1·11	29·58 ± 1·39	26·41 ± 1·99	26·57 ± 2·03	28·06 ± 1·20	24·98 ± 1·78
%ED-HL	15·03 ± 1·65	13·43 ± 1·13	21·27 ± 1·07	13·97 ± 1·20	17·14 ± 1·67	14·27 ± 1·32	18·07 ± 1·81	18·52 ± 1·80
%POL-HL	61·47 ± 1·72	62·35 ± 2·51	58·14 ± 1·56	57·27 ± 1·86	60·12 ± 2·35	62·42 ± 2·96	56·40 ± 2·18	60·35 ± 2·89
%DNN-HL	4·40 ± 0·51	4·88 ± 0·58	3·25 ± 0·46	4·96 ± 0·94	3·27 ± 0·41	4·19 ± 0·62	4·16 ± 1·05	3·45 ± 0·46
%DNE-HL	4·74 ± 1·49	7·63 ± 1·22	5·42 ± 1·13	6·05 ± 0·73	6·94 ± 1·39	5·89 ± 1·51	7·13 ± 1·21	6·02 ± 1·16
%DFL-PDD	24·81 ± 1·95	31·16 ± 1·97	51·21 ± 1·88	25·54 ± 3·41	43·66 ± 2·54	29·85 ± 2·19	36·42 ± 2·27	35·09 ± 2·50
%AFL-PAD	36·40 ± 2·52	47·01 ± 1·89	37·94 ± 1·06	37·45 ± 1·02	40·11 ± 1·92	39·82 ± 2·62	46·01 ± 3·26	52·47 ± 3·34
%PAD-PDD	92·04 ± 3·00	92·19 ± 3·30	101·41 ± 2·47	91·68 ± 5·57	100·01 ± 3·65	95·45 ± 2·92	93·67 ± 3·34	92·92 ± 1·89
%PPLD-PDD	60·53 ± 2·70	56·83 ± 1·88	64·71 ± 1·09	57·84 ± 5·36	62·63 ± 2·43	60·98 ± 3·22	57·78 ± 2·03	58·49 ± 1·92
%PPCD-PDD	38·26 ± 2·32	35·51 ± 1·42	41·32 ± 1·31	35·04 ± 0·83	39·77 ± 1·63	37·75 ± 3·11	35·07 ± 1·39	36·92 ± 1·96
%DFH-DFL	110·54 ± 11·64	74·53 ± 3·98	60·35 ± 5·75	95·76 ± 5·56	69·80 ± 4·28	93·42 ± 7·46	76·29 ± 7·18	76·63 ± 0·94
%AFH-AFL	79·80 ± 6·76	56·77 ± 4·39	79·44 ± 3·91	70·16 ± 1·64	73·96 ± 5·45	70·73 ± 5·94	62·77 ± 4·93	53·19 ± 4·77
%DFL-AFL	74·21 ± 4·79	71·98 ± 4·15	133·18 ± 5·59	74·31 ± 7·37	108·96 ± 5·07	78·76 ± 5·76	84·74 ± 5·07	72·03 ± 3·75

Table 7. Meristic counts of the different *Marcusenius* species with eight circumpeduncular scales. Abbreviations are mentioned in text.

	M. dundoensis $n=24$ median (range)	*M. fuscus* $n=16$ median (range)	*M. ghesquierei* $n=10$ median (range)	*M. intermedius* $n=3$ median (range)	*M. kutuensis* $n=44$ median (range)	*M. moorii* $n=293$ median (range)	*M. sanagaensis* $n=27$ median (range)	*M. schilthuisiae* $n=47$ median (range)
DFR	21 (20–23)	25 (22–26)	33 (32–34)	21 (21–22)	29 (27–31)	24 (17–26)	25 (24–28)	26 (23–28)
AFR	27 (26–30)	33 (31–34)	28 (27–29)	28	28·5 (27–30)	30 (24–33)	31 (29–33)	33 ((27)32–35)
SLL	56 (51–61)	55·5 (54–61)	39 (37–42)	41 (38–43)	39 (36–42)	41 (37–45)	52 (49–56)	47 (42–54)
SDA	23 (21–25)	23 (22–25)	21·5 (19–24)	17 (17–18)	21 (17–23)	17 (14–20)	25 (22–28)	22 (21–25)
SDL	11 (10–12)	11 (10–12)	10·5 (9–12)	8 (8–9)	10 (8–11)	8 (7–10)	12 (11–14)	11 (10–12)
SPL	13 (11–15)	13 (11–14)	12 (11–13)	10 (10–11)	11 (9–13)	10 (8–11)	13 (12–14)	12 (10–14)
TUJ	5 (4–5)	5 (3–5)	5 (4–5)	5	5 (1–5)	5 (2–6)	5 (3–6)	5 (2–6)
TLJ	6 (3–6)	5·5 (3–6)	6 (5–6)	6	6 (3–6)	6 (3–8)	6 (5–6)	6 (2–7)
TV	45 (44–46)	48 (48–49)	43	43 (42–43)	43 (42–44)	44 (43–47)	44 (43–45)	44·5 (43–46)

Table 8. Measurements and meristic counts for the different type-specimens with eight circumpeduncular scales. Paratypes are not mentioned.

	Gnathonemus fuscus syntype 1 mnhn 90-8	*Gnathonemus fuscus* syntype 2 mnhn 90-9	*Gnathonemus ghesquierei* holotype mrac 46288	*Marcusenius intermedius* holotype mrac 15164	*Gnathonemus kutuensis* holotype mrac 664	*Gnathonemus moorii longulus* holotype mrac 31710	*Gnathonemus lambouri* lectotype mnhn 86-319	*Mormyrus lepturus* syntype 1 bmnh 1872-1-27-4-5	*Mormyrus lepturus* syntype 2 bmnh 1872-1-27-4-5	*Mormyrus grandisquamis* holotype zmb 9331	*Marcusenius sanagaensis* holotype mrac 93-72-P-0001	*Marcusenius paucisquamatus* holotype mrac 73-18-P-11	*Gnathonemus schilthuisiae* holotype mrac 663
TL	—	212	132	118	111	—	—	78	75	198	162	182	95
SL	195	180	109	100	92	108	127	64	61	167	136	152	81
BD	42	40	36	24	22	26	27	17	17	40	36	44	19
CPD	13	12	6	7	5	7	6	5	4	11	8	10	4
MCPD	13	13	6	6	4	7	6	4	4	11	8	10	4
CPL	29	27	20	15	19	15	21	12	11	30	24	25	13
HL	45	41	27	25	20	27	27	18	16	36	31	38	20
HD	36	31	24	19	15	20	20	15	14	29	29	35	15
HW	16	16	11	8	7	9	9	5	5	13	13	17	6
SNTL	13	12	7	7	5	7	7	4	4	10	8	11	5
IOW	16	14	9	8	7	8	9	6	5	11	11	12	6
ED	6	5	6	4	4	4	4	3	3	6	6	6	4
POL	29	25	16	14	12	17	16	12	10	22	17	23	12
DNN	3	2	1	1	1	1	1	1	1	1	1	2	1
DNE	3	4	2	1	1	2	1	1	1	3	2	3	1
PDD	127	118	67	72	52	76	83	44	41	104	88	100	50
PAD	116	111	67	65	56	72	80	38	38	100	82	101	48
PPLD	71	67	44	39	35	44	47	24	23	60	49	60	30
PPCD	41	40	27	25	22	25	26	15	14	37	29	35	19
DFL	42	36	33	18	25	21	26	11	11	36	30	31	18
DFH	27	27		16	18	18	23	11	11	30	24	28	14
AFL	53	49	26	24	24	25	31	14	14	44	40	42	23
AFH	30	29	19	17	17	18	20	11	11	27	24	26	13
PLFL	18	17	11	10	11	11	13	6	6	16	14	18	8
PCFL	34	31	28	19	21	21	22	12	12	30	28	30	15
DPLAF	46	46	26	24	22	28	32	14	14	40	33	42	17
DPCAF	76	72	43	38	34	46	53	25	24	60	51	65	29
DFR	25	25	34	21	29	21	23	20	22	25	25	24	27
AFR	32	31	29	28	28	26	27	25	27	30	31	32	33
PLFR	6	6	6	6	6	6	6	6	6	6	6	6	6
PCFR	10	10	10	10	10	10	10	10	10	10	10	10	10
SLL	57	57	38	43	42	44	43	41	43	44	51	40	47
SDA	23	23	23	17	19	18	16	17	15	19	28	17	23
SDL	11	11	11	8	9	9	7	8	7	9	14	8	11
SPL	13	13	13	10	11	10	9	10	10	11	14	10	12
TUJ	5	5	5	5	5	4	3	5	4	5	5	5	5
TLJ	4	6	5	6	6	6	5	6	6	6	6	6	6
PV	4	4	4	4	4	4	4	4	4	—	4	4	4
AV	17	16	14	15	13	16	16	15	15	—	14	14	14
CV	28	28	25	24	25	24	25	25	25	—	26	26	25
TV	49	48	43	43	42	44	45	44	44	—	44	44	43
SDB	0	0	2	3	2	0	2	2	2	0	4	2	2

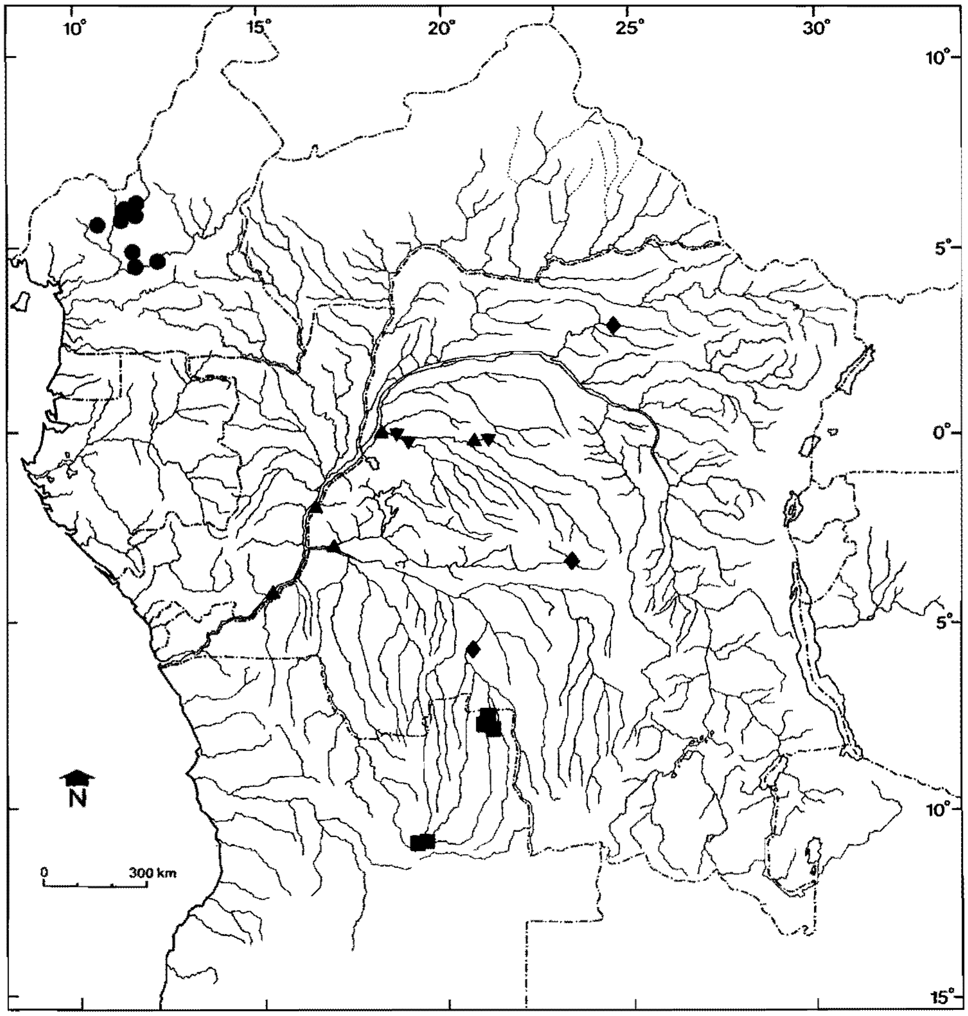

FIG. 11. Geographical distribution of *Marcusenius sanagaensis* (●), *M. dundoensis* (■), *M. fuscus* (▲), *M. intermedius* (◆) and *M. ghesquierei* (▼).

Alestes macrophthalmus, Brycinus kingsleyae, B. macrolepidotus, Hydrocynus forskalii (Characidae), *Distichodus kolleri* (Distichodontidae), *Barbus brevispinis, B. guirali, B. habereri, B. mbami, B. progenys, Raiamas senegalensis* (Cyprinidae), *Bagrus bajad* (Bagridae), *Chrysichthys longidorsalis, Parauchenoglanis ballayi* (Claroteidae), *Schilbe djeremi, S. mystus* (Schilbeidae), *Clarias gariepinus* (Clariidae), *Synodontis rebeli* (Mochokidae), *Hemichromis fasciatus, Oreochromis niloticus, Sarotherodon galilaeus sanagaensis* and *Tilapia camerunensis* (Cichlidae).

Etymology. Named *sanagaensis* after the Sanaga River basin, a coastal basin in Cameroon, where the type material was collected.

Maximum size. SL 168 mm.

Affinities. This species is one of the three *Marcusenius* species present in the Sanaga. *Marcusenius mento* can easily be distinguished because it has twelve scales around the caudal peduncle. Of the three, *Marcusenius moorii* has eight scales around the caudal peduncle, but it has fewer scales on the lateral line (37–45 versus 49–56 in *M. sanagaensis*).

Marcusenius dundoensis (Poll, 1967)
(Fig. 12a)

Gnathonemus dundoensis Poll, 1967

Material. HOLOTYPE: MD 1040 (not seen). River Sanga, tributary on the right side of river Luachimo, in the neighbourhood of Dundo (Angola), 7°24′S–20°52′E.

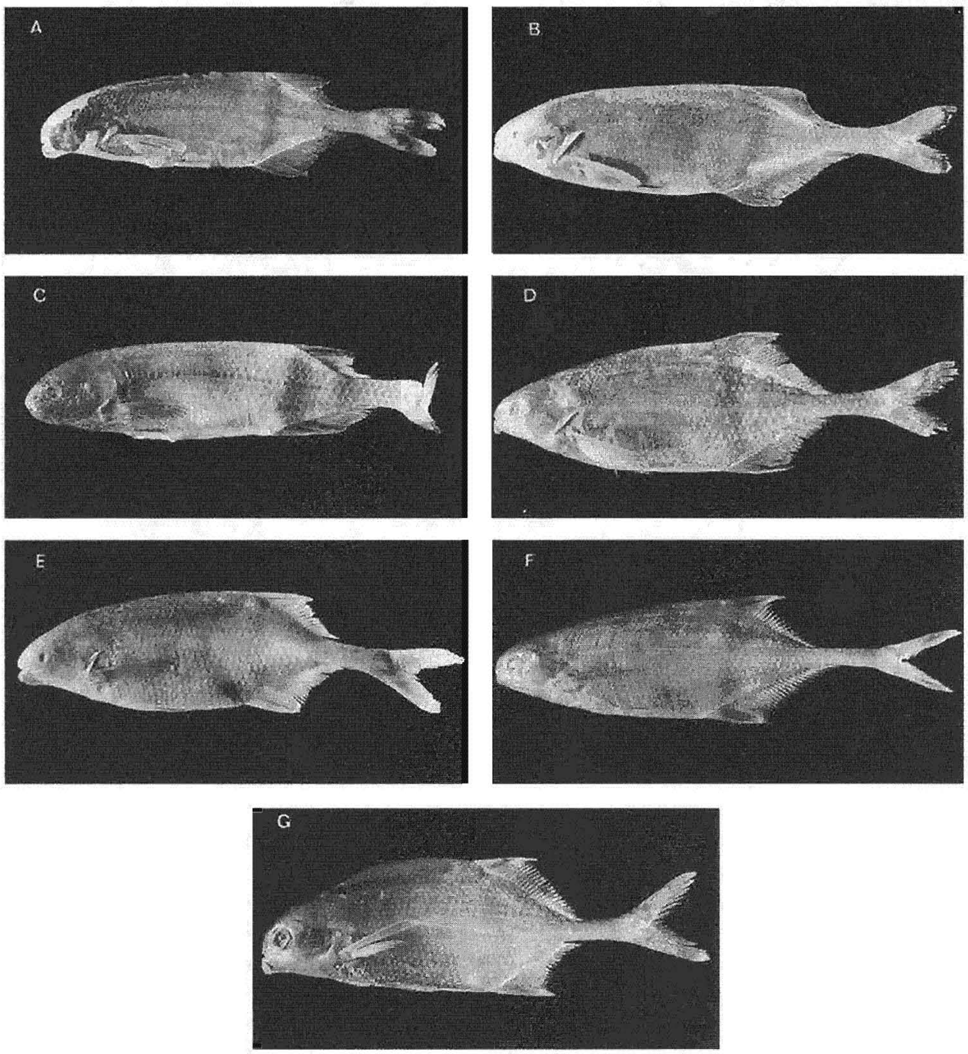

FIG. 12. (a) *Marcusenius dundoensis*, paratype, MRAC 158533, 106·6 mm SL; (b) *Marcusenius fuscus*, MRAC 73-23-P-852, 163·9 mm SL; (c) *Marcusenius intermedius*, holotype, MRAC 15164, 100·3 mm SL; (d) *Marcusenius kutuensis*, MRAC 68893, 130·6 mm SL; (e) *Marcusenius moorii*, neotype, MRAC 87685, 135·0 mm SL; (f) *Marcusenius schilthuisiae*, MRAC 94386–94390, 112·2 mm SL; (g) *Marcusenius ghesquierei*, MRAC 73-23-P-790-791, 99·1 mm SL.

PARATYPES: MRAC 158528-530. River Sanga, tributary on the right side of river Luachimo, in the neighbourhood of Dundo (Angola), 7°24'S–20°52'E; MRAC 158531. River Kazulu, tributary on the left side of river Luachimo, about 50 km south of Dundo (Angola), 7°38'S–20°49'E; MRAC 158532. River Tchitatu (Angola), 7°17'S–20°49'E; MRAC 158533. River Mololo, tributary of river Chiumbe (Angola), 7°49'S–21°05'E.

Diagnosis. Dorsal-fin origin located behind anal-fin origin, dorsal-fin base terminating before anal-fin base. Dorsal-fin margin concave and pointed, its height the same as the length of its base. Dark band between dorsal and anal fin generally clearly visible. Lateral-line scales number 51–61, four or five, rarely three, lateral-line scales on the dark coloured transversal band. Dorsal fin short, with 20–23 rays. Anal fin longer with 26–30 rays.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, five in upper jaw, six in lower jaw. Sub-mental swelling large and rounded, its beginning at its posterior end at a point below the anterior margin of the eye. Snout rounded and blunt. Anterior nostril in the middle between the tip of the snout and the anterior border of the eye. Posterior nostril at 0·25–0·33 distance from the eye. Eye diameter 38–66% of snout length.

Preanal distance shorter than predorsal distance. Anal-fin base longer than dorsal. Dorsal-fin height about the same as its base. Anal-fin height less than its base. Pectoral fin twice as long as pelvic fin and reaching the pelvic-fin base. Distance between pectoral and pelvic fins as long as pelvic-fin length or a little shorter. Pelvic-fin base midway between pectoral-fin base and anal-fin origin or closer to the pectoral. Length of pelvic fin half the distance between pelvic-fin base and anal-fin origin.

Compared to other species in this group, *M. dundoensis* has a low number of dorsal- (20–23) and anal- (26–30) fin rays, a high number of lateral-line scales (51–61) and there are 21–25 scales between dorsal- and anal-fin origins. Dark band between origin of dorsal and anal fins covered with four or five (rarely three) lateral-line scales. Caudal peduncle and head darker than the rest of the body except for the dark transverse band between dorsal and anal fins.

The electric organ is composed of electrocytes with non-penetrating stalks innervated on the posterior side (NPp).

Distribution (Fig. 11). *M. dundoensis* is found in the Central Zaire basin in the Dundo area (Angola). It is the only part of the Zaire basin from which it is known.

Maximum size. SL 123 mm.

Material examined. Twenty-five specimens. MRAC 158528-530. River Sanga, tributary on the right side of river Luachimo, in the neighbourhood of Dundo (Angola), 7°24'S–20°52'E; paratype. MRAC 158531. River Kazulu, tributary on the left side of river Luachimo, about 50 km south of Dundo (Angola), 7°38'S–20°49'E; paratype. MRAC 158532. River Tchitatu (Angola), 7°17'S–20°49'E; paratype. MRAC 158533. River Mololo, tributary of river Chiumbe (Angola), 7°49'S–21°05'E; paratype. MRAC 158356–158357. Mwaoka (Angola), 7°39'S–20°51'E. MRAC 158472. Alto Chicapa, near the sources of the river Cuilo (Angola), 10°52'S–19°24'E. MRAC 158534–546. River Tchitatu (Angola), 7°17'S–20°49'E. MRAC 158547–549. Alto Chicapa, swamp of river Coca, tributary of river Cutele (Angola), 10°56'S–19°05'E.

Marcusenius fuscus (Pellegrin, 1901)
(Fig. 12b)

Gnathonemus fuscus Pellegrin, 1901

Material. LECTOTYPE: MNHN 90-9. Congo; 180 mm SL; designated in this paper. PARALECTOTYPE: MNHN 90-8. Congo; 195 mm SL; designated in this paper.

Diagnosis. Dorsal-fin origin is behind the anal-fin origin. Dorsal-fin base ends anterior to the end of the anal fin. Dorsal-fin margin rounded anteriorally and slightly concave, sometimes nearly straight. Dorsal- and anal-fin heights shorter than the lengths of their bases. Lateral-line scales 54–61; generally three lateral-line scales on the dark coloured transversal band. Dorsal-fin rays 22–26. Anal-fin rays 31–34. Number of vertebrae higher than in other species (48–49).

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, five in upper jaw, six in lower jaw. Sub-mental swelling less rounded, beginning well before the anterior margin of the eye. Snout more or less rounded, not blunt. Anterior nostril midway between the tip of snout and the anterior eye-border. Posterior nostril 0·25–0·33 the distance between snout and anterior eye-border. Eye-diameter 33–60% of snout length.

Preanal distance shorter than predorsal distance. Dorsal-fin base less than anal. Dorsal-fin height 0·66–0·75 of the length of its base. Anal-fin height also shorter than its base. Pectoral fin nearly twice as long as pelvic fin, extending to, and sometimes beyond the pelvic-fin base. Base of pelvic fin about 0·33 the distance between pectoral-fin base and anal-fin origin. Length of pelvic fin half the distance between pelvic-fin base and anal-fin origin.

Low number of dorsal-fin rays (22–26), high number of anal-fin rays (31–34). High number of lateral-line scales (54–61). Twenty-two to 25 scales between dorsal- and anal-fin origins. Three, sometimes four, lateral-line scales cover the dark band between dorsal and anal-fin origins. Dark band not always clearly visible. Head and caudal peduncle darker than the rest of the body.

The electrocytes have penetrating stalks innervated on the anterior side (Pa).

Distribution (Fig. 11). *Marcusenius fuscus* inhabits the Central Zaire basin where it is found in the Zaire and some affluents (Tshuapa, Kasaï) between Kinshasa and the Equator.

Maximum size. SL 199 mm.

Material examined. 16 specimens. MNHN 90-9. Congo; lectotype. MNHN 90-8. Congo; paralectotype. MRAC 15119. Ikengo (Zaire), 0°08′S–18°09′E. MRAC 56593. Kunungu, village N'Dva (Zaire), 2°06′S–16°26′E. MRAC 67218. Region of Mushie, river Kasaï (Zaire), 3°02′S–16°55′E. MRAC 68781. Mushie (Zaire), 3°02′S–16°55′E. MRAC 68795–68798. Mushie (Zaire), 3°02′S–16°55′E. MRAC 73-23-P-852. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 83-31-P-255-260. Kinshasa (Zaire), 4°18′S–15°18′E. 5 specimens.

Marcusenius intermedius Pellegrin, 1924
(Fig. 12c)

Material. HOLOTYPE: MRAC 15164. Kabambaie (Zaire), 5°45′S–20°49′E.

Diagnosis. Mouth subinferior rather than terminal as in the other species. Dorsal-fin origin behind anal-fin origin. Dorsal-fin base ends before anal fin. Dorsal-fin margin rounded anteriorally and slightly concave, its height about the same length as its base. Dark transverse band between dorsal and anal fin, not always clearly visible, covered with three lateral-line scales. Lateral-line scales 38–43. Short dorsal and anal fin, with 21–22 and 28 rays respectively.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth subinferior. Teeth bicuspid, five in upper jaw, six in lower jaw. Sub-mental swelling small and hardly visible, probably damaged in the three available specimens, with posterior end terminating well under the middle of the eye. Snout pointed slightly. Anterior nostril a little closer to the eye than to the anterior tip of the snout. Posterior nostril at 0·2–0·25 distance between snout and anterior eye border. Eye diameter 45–49% of snout length.

Preanal distance a little shorter than predorsal distance. Dorsal fin shorter than anal fin. Dorsal-fin height about the same as its base, but anal-fin height shorter than its base. Pectoral fin twice as long as pelvic fin and reaching the pelvic-fin base. Pelvic-fin base at about 0·4 of the distance between pectoral-fin base and anal-fin origin. Its length is a little shorter than half the distance between its basis and the anal-fin origin.

Low number of dorsal- (21–22) and anal- (28) fin rays. Lateral-line scales 38–43. Transversal dark band between origin of dorsal and anal fins covered with three lateral-line scales. Seventeen to 18 transversal scales between dorsal and anal fins. Caudal peduncle height is about half its length. Caudal peduncle, head, and transversal dark band are darker than the rest of the body. Low number of vertebrae (42–43).

Distribution. (Fig. 11). This species is distributed in the Central Zaire basin, where it is found in three different localities far from each other.

Comment. As already mentioned above, the systematic status of this species is questionable. Moreover, only three specimens are presently available for study. More material is necessary to obtain a correct idea on the status of this species. Meanwhile we continue to consider it as a valid taxon.

Maximum size. SL 136 mm.

Material examined. Three specimens. MRAC 15164. Kabambaie (Zaire), 5°45′S–20°49′E; holotype. MRAC 23198. Koteli (Zaire), 2°51′N–24°34′E. MRAC 29260. Komi, Lodja (Zaire), 3°30′S–23°23′E.

Marcusenius kutuensis (Boulenger, 1900)
(Fig. 12d)

Gnathonemus kutuensis Boulenger, 1900

Material. HOLOTYPE: MRAC 664. Kutu (Zaire), 2°44′S–18°08′E.

Diagnosis. Dorsal-fin origin situated before anal-fin origin. Both fins end at the same level. The ratio dorsal-fin length/anal-fin length is $<1{\cdot}25$. Dorsal-fin margin pointed and deeply concave (falciform). Anal fin slightly concave. Lateral-line scales 36–42, generally two scales on dark coloured transversal band. Dorsal fin long, with 27–31 rays, and 27–30 anal-fin rays.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, 5 in upper jaw, 6 in lower jaw. Sub-mental swelling rounded and very small, its posterior end not reaching the anterior margin of the eye. Snout rounded. Anterior nostril in the middle between anterior tip of snout and eye, or at 0·33 distance from the eye. Posterior nostril at 1/5 to 1/6 distance from the eye. Eye-diameter 44–82% of snout length.

Preanal distance longer than predorsal distance. Anal fin always shorter than dorsal fin. Their heights never reaching the length of their bases. Pectoral fin twice as long as pelvic fin and its posterior end close to posterior end of pelvic fin. Distance between pectoral and pelvic fins about 0·66 of pectoral-fin length. Base of pelvic fin 0·33 closer to pectoral fin than to anal-fin origin. Pelvic-fin length half the distance from pelvic-fin base to anal-fin origin.

High number of dorsal- (27–31) and anal- (27–30) fin rays. Low number of scales on the lateral line (36–42). Scales between dorsal- and anal-fin origins are 17–23. Two scales, sometimes three, on the lateral line cover the dark coloured transverse band between dorsal- and anal-fin origins. Head and transversal band somewhat darker than rest of the body. Body not elongated, but with a high back.

The electrocytes have penetrating stalks innervated on the anterior side (Pa).

Distribution (Fig. 13). *M. kutuensis* is located in the Central Zaire basin. We examined specimens from the river Ruki, the Mushie area, lake Tumba and lake Leopold II. A few specimens were found from Bumba.

Maximum size. SL 195 mm.

Material examined. Forty-four specimens. MRAC 664. Kutu (Zaire), 2°44′S–18°08′E; Holotype. MRAC 15146. Mongende (Zaire), 2°06′S–16°20′E. MRAC 15147. Mongende (Zaire), 2°06′S–16°20′E. MRAC 31709. Bumba (Zaire), 2°11′N–22°32′E. MRAC 31745 Bumba (Zaire), 2°11′N–22°32′E. MRAC 42846. Flandria (Zaire), 0°20′S–19°05′E. MRAC 42889. Bokuma (Zaire), 0°06′S–18°41′E. MRAC 66900. Neighbourhood of Mushie, river Kasai and Fimi (Zaire), 3°02′S–16°55′E. MRAC 67103. Region of Mushie, river Kasai (Zaire), 3°02′S–16°55′E. MRAC 68893. Mushie (Zaire), 3°02′S–16°55′E. MRAC 78546. Nkombo (Zaire), 0°06′S–18°41′E. MRAC 94399–94406. Village Bantoi, river Ruki (Zaire), 0°04′S–18°19′E. MRAC 99675. River Momboyo (Zaire), 0°20′S–19°05′E. MRAC 99679–99680. Flandria, river Momboyo (Zaire), 0°20′S–19°05′E. MRAC 99688. Flandria, river Momboyo (Zaire), 0°20′S–19°05′E. MRAC 99951–100009. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. Five specimens. MRAC 101394. Bokuma (Zaire), 0°06′S–18°41′E. MRAC 101398. Bokuma (Zaire), 0°06′S–18°41′E. MRAC 104550. River Momboyo (Zaire), 0°20′S–19°05′E. MRAC 104560–104566. River Ruki (Zaire), 0°16′S–18°17′E. MRAC 131231–131233. Lake Tumba, Bay I.R.S.A.C., Mabali (Zaire), 0°53′S–18°04′E. MRAC 73-23-P-792. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 73-23-P-853. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 73-23-P-911. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E.

Marcusenius moorii (Günther, 1867)
(Fig. 12e)

Mormyrus moorii Günther, 1867
Synonyms. Mormyrus lepturus Günther, 1871 (see Boulenger, 1898)
Mormyrus grandisquamis Peters, 1877 (see Boulenger, 1898)
Gnathonemus lambouri Pellegrin, 1904 (new synonymy)
Gnathonemus moorii longulus David and Poll, 1936 (new synonymy)
Marcusenius paucisquamatus Taverne, Thys van den Audenaerde and Heymer, 1976 (new synonymy)

Material. HOLOTYPE: presumed to be lost. Neotype: MRAC 87685. Talagouga, Ogowe (Gabon), Coll. Miss Kingsley; 135 mm SL; designated in this paper.

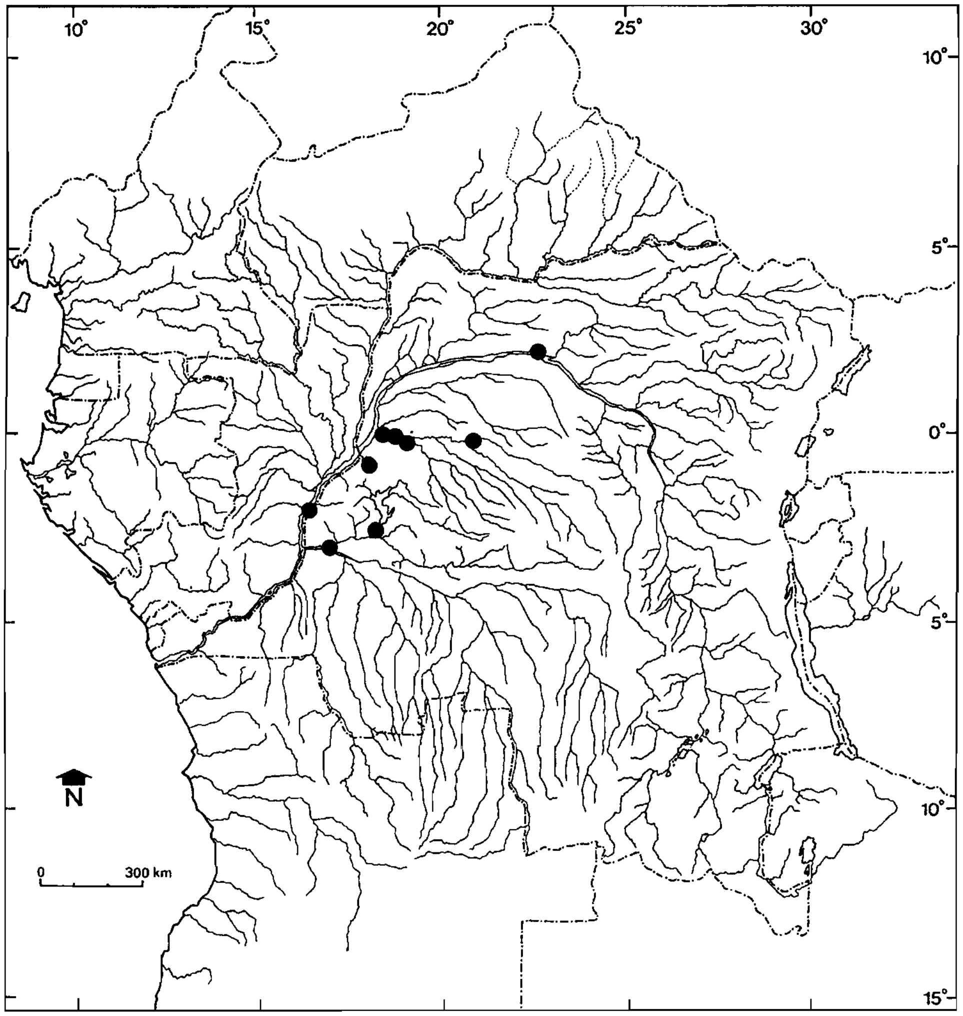

FIG. 13. Geographical distribution of *Marcusenius kutuensis*.

Diagnosis. Dorsal-fin origin situated behind anal-fin origin. Dorsal fin ends before anal fin. Dorsal fin pointed and clearly concave. Its height shorter than its length. Dorsal-fin rays are 17–26 and 24–33 anal-fin rays. Lateral-line scales 37–45. If the dark transversal band between dorsal and anal fin is visible, it is covered by only two lateral-line scales. Scales between dorsal-fin origin and anal-fin origin are 14–20.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, 5 in upper jaw, 6 in lower jaw. Submental swelling rounded, not reaching the eye margin. Snout rounded and slightly blunt. Anterior nostril in the middle between anterior tip of snout and eye, or a little closer to the eye. Posterior nostril 0·25 the distance from the eye. Eye diameter 36–74% of snout length.

Preanal distance generally shorter than predorsal distance. Anal-fin base longer than dorsal. Dorsal-fin height about the same as its base. Anal-fin height shorter than its length. Pectoral fin twice as long as pelvic fin and reaching a little further than pelvic-fin base. Pelvic-fin base 0·33 closer to pectoral-fin base than to anal-fin origin. Posterior end of pelvic fin at 0·33–0·5 the distance between pelvic-fin base and anal-fin origin.

Low number of dorsal-fin rays (17–26). Large variability in anal-fin rays (24–33). Lateral-line scales 37–45. Fourteen to 20 scales between dorsal- and anal-fin origins. Dark band between dorsal- and anal-fin origins, when present, extending over two lateral-line scales. Head, transversal band and a spot on the caudal-fin base dark coloured compared to rest of the body. Sometimes a second dark transversal band between the posterior ends of dorsal and anal fins. Body elongated.

The electric organ has electrocytes with non penetrating stalks innervated on the posterior surface (NPp).

Note on the synonyms. Boulenger (1898) has already synonymized *Mormyrus lepturus* and *Mormyrus grandisquamis* with *Marcusenius moorii*. These synonyms are confirmed here. *Marcusenius lambouri* is described by Pellegrin (1904) on the basis of a more slender body and shorter pectoral fins. Later, Poll (1948) has synonymized *Marcusenius moorii longulus* with this species. Taverne *et al.* (1976) described *Marcusenius paucisquamatus* characterized by a low number of lateral-line scales in comparison to other *Marcusenius* species, but no comparison is made with *M. moorii*. The description of *M. paucisquamatus* fits into that of *M. moorii*. Our study of the type-specimens of all these nominal species (Table 8; Fig. 2, 7 and 8) did not reveal any differences between all these species and therefore they should be considered as synonyms.

Distribution (see Fig. 14). This species has a wide distribution. In the Lower Guinea Ichthyofaunal Province, it is present in all the important rivers. In the Zairian Ichthyofaunal Province it is restricted to the Lower and the Central Zaire basin. It is the most widespread species in this group.

Maximum size. SL 214 mm.

Material examined. Two hundred and ninety-three specimens. (Holotype lost). BMNH 1872.1.27.4–5. Gabon; syntypes of *Mormyrus lepturus*. ZMB 9331. River Ogowe (Gabon); holotype of *Mormyrus grandisquamis*. MNHN 86-319. River Alima, Diélé (Congo Brazzaville); lectotype of *Gnathonemus lambouri*, designated by Eschmeyer and Bauchot, 1995. MNHN 86-324. River Alima, Lékéti (Congo Brazzaville); paralectotype of *Gnathonemus lambouri*, designated by Eschmeyer and Bauchot, 1995. MRAC 1509–1510. Mayumbi, Nayili (Zaire), 5°06′S–12°28′E. MRAC 1818. Kelé, Dungu (Zaire), 3°37′N–28°33′E. MRAC 20041-20042. Haut Ogôoué, Liboumbi (Gabon), 1°34′S–13°24′E. MRAC 20043. Franceville Passa (Gabon), 1°36′S–13°31′E. MRAC 21170–21174. Kunungu (Zaire), 2°06′S–16°26′E. MRAC 21571. Kunungu (Zaire), 2°06′S–16°26′E; paratype of *Gnathonemus moorii longulus*. MRAC 30553–30557. Kunungu (Zaire), 2°06′S–16°26′E. MRAC 30799. Buta (Zaire), 2°47′N–24°50′E. MRAC 31710. Bumba (Zaire), 2°11′N–22°32′E; holotype of *Gnathonemus moorii longulus*. MRAC 38631. Kunungu (Zaire), 2°06′S–16°26′E. MRAC 44901. River Luie, region of Djuma, Kwango (Zaire), 4°13′S–18°20′E. MRAC 46751. Karawa (Zaire), 3°17′N–20°16′E. MRAC 56594. Village Ndva, Kunungu (Zaire), 2°06′S–16°26′E. MRAC 57247. Village Ndva, Kunungu (Zaire), 2°06′S–16°26′E. MRAC 57351–57355. Village Ndva, Kunungu (Zaire), 2°06′S–16°26′E. MRAC 80788–80789. Bamania (Zaire), 0°00′S–18°20′E. MRAC 87685. Talagouga, Ogowe river (Gabon), 0°10′S–10°43′E; neotype. MRAC 99684. Flandria, river Momboyo (Zaire), 0°20′S–19°05′E. MRAC 104309–104310.

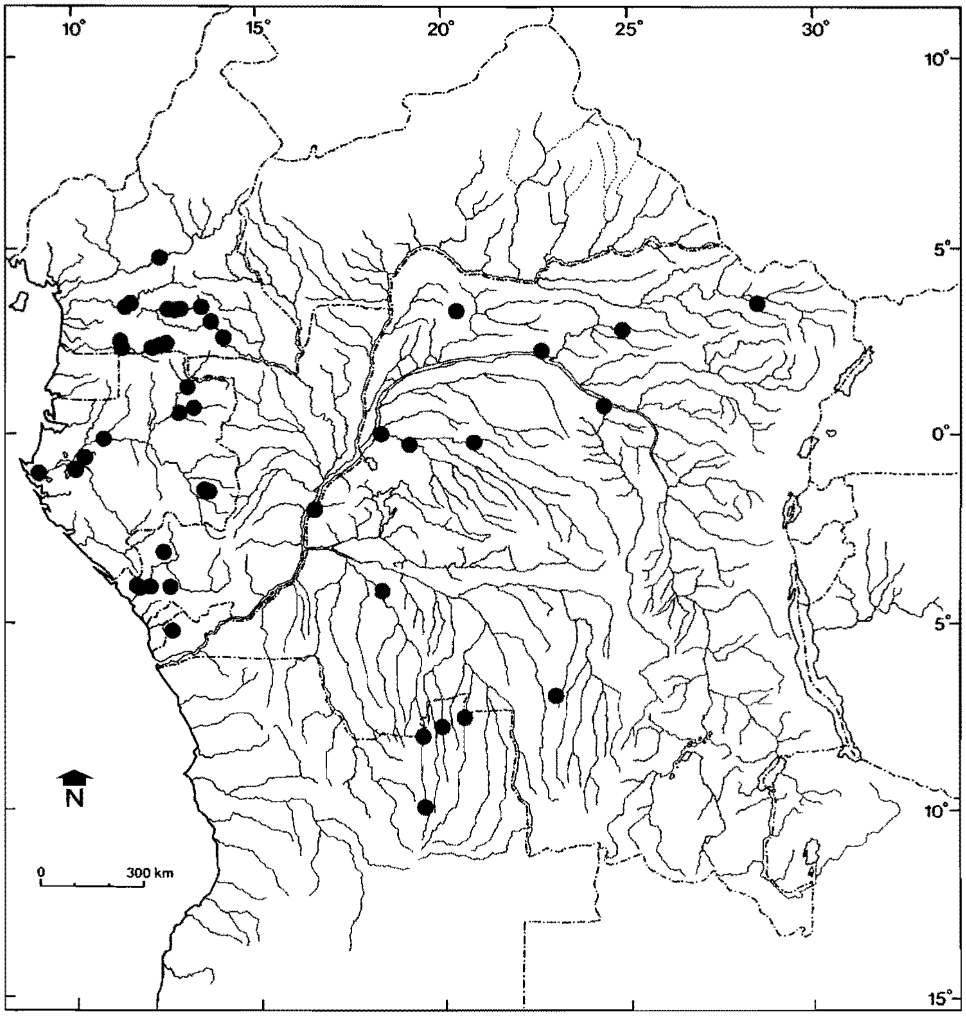

FIG. 14. Geographical distribution of *Marcusenius moorii*.

River Lubi, au Sud du 7° (Zaire), 7°00'S–22°55'E. MRAC 104567–104569. River Ruki (Zaire), 0°16'S–18°17'E. MRAC 131497. Yangole, river Lilanda (Zaire), 0°48'N–24°17'E. MRAC 137968. Yangole, river Lilanda (Zaire), 0°48'N–24°17'E. MRAC 158293–158297. River Lucoge (Angola), 7°33'S–20°27'E. One specimen. MRAC 158358. Swamps on right side, downstream of Lake Carumbo (Angola), 7°52'S–19°55'E. MRAC 158471. Alto Cuilo, river Cavuemba (Angola), 10°00'S–19°30'E. MRAC 158473. Station of Cuilo, Xa-Ua, river Luita (Angola), 8°02'S–19°25'E. MRAC 179207–179208. River Nyong, upstream of Mbalmago near Ekombitye (Cameroon), 3°33'N–11°40'E. MRAC 73-2-P-15. Soasi-Ebogo, river Nyong (Cameroon), 3°23'N–11°28'E. MRAC 73-2-P-31-32—Lambarene, river Ogowe (Gabon), 0°42'S–10°13'E. MRAC 73-2-P-33—Andoumi, swampy area near dam of Allam, Evonha (Gabon), 1°00'S–9°00'E. MRAC 73-18-P-11. Ebogo, river Nyong (Cameroon), 3°23'N–11°28'E; holotype of *Marcusenius paucisquamatus*. MRAC 73-18-P-12. Ebogo, river Nyong (Cameroon), 3°23'N–11°28'E; paratype of *Marcusenius paucisquamatus*. MRAC 73-18-P-13-18. Aboulou, river Ntem (Cameroon), 2°17′N–12°03′E; paratypes of *Marcusenius paucisquamatus*. MRAC 73-18-P-19-25. Aboulou, river Ntem (Cameroon), 2°17′N–12°03′E; paratypes of *Marcusenius paucisquamatus*. MRAC 73-18-P-76-77. Mvam, 5 km south of Oveng, river Yété (Cameroon), 2°22′N–12°14′E; paratypes of *Marcusenius paucisquamatus*. MRAC 73-18-P-441-446. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E. MRAC 73-23-P-855-861. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 73-29-P-865-885. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 73-29-P-31-32. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E; paratypes of *Marcusenius paucisquamatus*. MRAC 73-29-P-33. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E; paratype of *Marcusenius paucisquamatus*. MRAC 73-29-P-34. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E; paratype of *Marcusenius paucisquamatus*. MRAC 73-29-P-35. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E; paratype of *Marcusenius paucisquamatus*. MRAC 73-29-P-36. Village Ngoazik, river Ntem (Cameroon), 2°18′N–11°18′E; paratype of *Marcusenius paucisquamatus*. MRAC 73-29-P-622. Ebogo, river Nyong (Cameroon), 3°23′N–11°28′E. MRAC 75-24-P-276. River Ivindo, near M'Passa, Makokou (Gabon), 0°34′N–12°52′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-24-P-285-287. River Ivindo, near M'Passa, Makokou (Gabon), 0°34′N–12°52′E; paratypes of *Marcusenius paucisquamatus*. MRAC 75-24-P-288. Swampy area of Bialé near M'Passa, Makokou (Gabon), 0°34′N–12°52′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-24-P-289. River Ivindo, near M'Passa, Makokou (Gabon), 0°34′N–12°52′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-24-P-396. Swampy area of Bialé near M'Passa, Makokou (Gabon), 0°34′N–12°52′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-24-P-401. Km 18 from Makokou on 'Route Fang', swampy area of Nabarre (Gabon), 0°34′N–12°52′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-24-P-587-646. Swampy area of M'Passa (Gabon), 0°34′N–12°52′E. 58 specimens; paratypes of *Marcusenius paucisquamatus*. MRAC 75-56-P-978. Djaposten, river Dja (Cameroon), 3°25′N–13°32′E; paratype of *Marcusenius paucisquamatus*. MRAC 75-56-P-1030-042. Djaposten, river Dja (Cameroon), 3°25′N–13°32′E; paratypes of *Marcusenius paucisquamatus*. MRAC 76-27-P-1. Lake Onangué (Gabon), 0°57′S–10°04′E. MRAC 87-07-P-57-73. St. 13 High Ivindo, mouth of the Nounah (Gabon), 1°12′N–13°08′E. MRAC 87-07-P-74-90. St. 13 High Ivindo, mouth of the Nounah (Gabon), 1°12′N–13°08′E. MRAC 87-07-P-91. Makokou, river Ivindo (Gabon), 0°34′N–12°52′E. MRAC 87-07-P-97. St. 9 swampy tributary of the Liboumba near Zoolende, PK72 road Makokou-Mekambo (Gabon), 0°46′N–13°16′E. MRAC 90-57-P-2561. River Midounvo, tributary on left side of Nanga, near M'Boukou-Massi (Congo Brazzaville), 4°16′S–11°50′E. MRAC 90-57-P-2562-569. Mouth of the Nanga in the Kouilou (Congo Brazzaville), 4°19′S–11°52′E. 6 specimens. MRAC 90-57-P-2575. Lake Kobambi (Congo Brazzaville), 4°08′S–11°45′E. MRAC 90-57-P-2581. River Ngoumbi, tributary Dola, tributary Lake Dinga (Congo Brazzaville), 4°07′S–11°54′E. MRAC 90-57-P-2592-599. River Nanga, between M'Boukou-Massi and his mouth in the Kouilou (Congo Brazzaville), 4°18′S–11°51′E. MRAC 90-57-P-2624-627. River Louvoumou, near Bena I, road to Kayes-Bena I, 3 km before Loundji (Congo Brazzaville), 4°02′S–11°48′E. MRAC 90-57-P-2668-670. River Kouilou at Kakamoeka (Congo Brazzaville), 4°08′S–12°04′E. MRAC 90-57-P-2671-674. Confluence of rivers Kissafou and Kouilou, at 5 km of Kakamoeka, towards Sounda (Congo Brazzaville), 4°07′S–12°05′E. MRAC 90-57-P-2675-676. River Kouilou at

Kakamoeka (Congo Brazzaville), 4°08′S–12°04′E. MRAC 91-68-P-66. River Loubomo at 4 km of Moukondo towards Makongo (Congo Brazzaville), 4°09′S–12°35′E. MRAC 91-79-P-88. River Loukénini, on the road of Loukomo-Gabon, Kouilou-Niari-basin (Congo Brazzaville), 3°14′S–12°12′E. MRAC 93-085-P-0031. River Dasseu, Ntem, tributary Mboro, between Akonekyé and Ngom Adjap (Cameroon), 2°29′N–11°11′E. MRAC 93-108-P-0016. River Mvoé, after Ngbwassa, near Oveng (Cameroon), 2°24′N–12°32′E. MRAC 93-108-P-0024-0032. Aboulou, river Kom (Cameroon), 2°18′N–12°03′E. MRAC 95-06-P-0051. Ngoyla, river Mie (Cameroon), 2°37′N–14°02′E. MRAC 95-06-P-0054-0055. Maleng I, river Mien (Cameroon), 3°21′N–12°55′E. MRAC 95-06-P-0056-0063. Maleoleu, river Fom (Cameroon), 3°21′N–12°58′E. 1 specimen. MRAC 95-06-P-0064-0065. Nemeyong, river Mien (Cameroon), 3°20′N–12°55′E. MRAC 95-06-P-0066. Kanyol, river Djul (Cameroon), 3°20′N–12°50′E. MRAC 95-06-P-0088-0091. Ngala, river Dja (Cameroon), 3°21′N–12°29′E. MRAC 95-06-P-0092-0095. Djeula, river Dja (Cameroon), 3°21′N–12°57′E. MRAC 95-06-P-0096-0099. Nemeyong, river Edjie (Cameroon), 3°07′N–13°50′E. MRAC 95-17-P-01-02. River Tede at Enga, basin of the Sanaga (Cameroon). MNHN 1982-1042. River Sanaga (Cameroon).

Marcusenius schilthuisiae (Boulenger, 1900)

(Fig. 12f)

Gnathonemus schilthuisiae Boulenger, 1900

Materials. HOLOTYPE: MRAC 663, Kutu (Zaire), 2°44′S–18°08′E.

Diagnosis. Dorsal-fin origin situated behind anal-fin origin. Dorsal-fin base ends well before anal fin. Dorsal-fin margin pointed and concave, its height not as long as its length. Dark band between dorsal and anal fin generally visible. Lateral-line scales 42–54; two lateral-line scales on dark coloured transversal band. Twenty-one to 25 scales between dorsal-fin origin and anal-fin origin. Dorsal-fin rays are 23–28. High number of anal-fin rays (32–35).

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, 5 in upper jaw, 6 in lower jaw. Submental swelling rounded and small, extending slightly beyond the mouth. Snout rounded, not blunt. Anterior nostril in the middle between anterior tip of snout and eye, posterior nostril at 0·25 distance from the eye. Eye diameter 60–96% of snout length.

Preanal distance shorter than predorsal distance. Anal fin markedly longer than dorsal fin. Dorsal- and anal-fin heights shorter than their length. Pectoral fin twice as long as pelvic fin; its posterior end sometimes reaches posterior end of pelvic fin. Distance between pectoral and pelvic fins 0·66 of pectoral-fin length. Pelvic-fin base at about 0·33 of the distance between pectoral-fin base and anal-fin origin. Its length reaching half the distance between its base and the anal-fin origin.

High number of anal-fin rays (32–35) compared to other species in this group. One specimen has only 27 rays. Dorsal-fin rays are 23–28. Lateral-line scales 42–54 and 21–25 scales between dorsal- and anal-fin origins. A transversal dark band between origins of dorsal and anal fin, covered with two lateral-line scales. Head, caudal peduncle and transversal band darker than rest of the body.

The electric organ has penetrating stalks innervated on the anterior side (Pa).

Distribution (Fig. 15). This species can be found in the Central Zaire basin, from Stanley-Pool to Kisangani. It is not only inhabiting the mainstream, but also some important affluents like the Ruki river and the environment of Kutu.

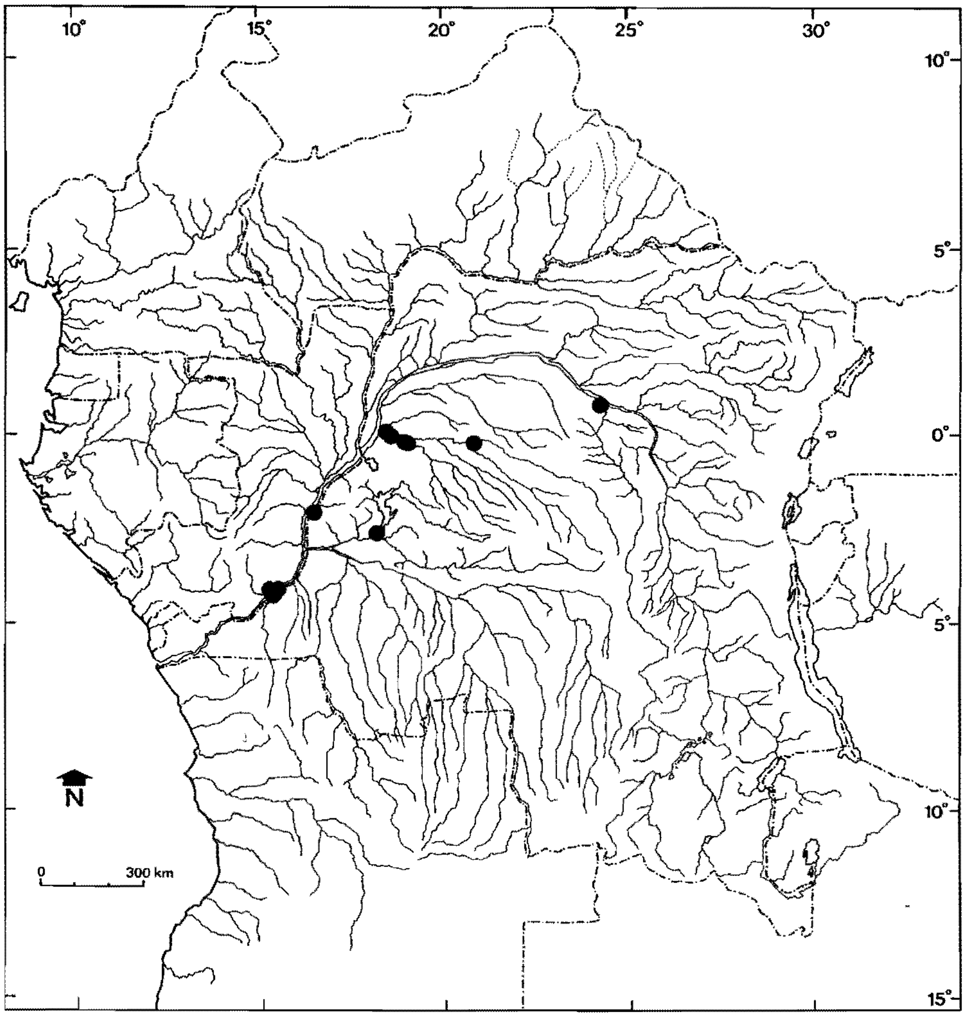

FIG. 15. Geographical distribution of *Marcusenius schilthuisiae*.

Maximum size. SL 148 mm.

Material examined. Forty-seven specimens. MRAC 663. Kutu (Zaire), 2°44'S–18°08'E; holotype. MRAC 39606–39608. Leopoldville (Zaire), 4°15'S–15°20'E. MRAC 55312. Leopoldville (Zaire), 4°15'S–15°20'E. MRAC 57245–57246. Village Ndva, Kunungu (Zaire), 2°06'S–16°26'E. MRAC 78543. Nkombo (Zaire), 0°06'S–18°41'E. MRAC 80130. Leopoldville (Zaire), 4°15'S–15°20'E. MRAC 93839–93840. Leopoldville (Zaire), 4°15'S–15°20'E. MRAC 94385. Village Bantoi, river Ruki (Zaire), 0°04'N–18°19'E. MRAC 94386–94390. Village Bantoi, river Ruki (Zaire), 0°04'N–18°19'E. MRAC 95535. Bokuma (Zaire), 0°06'S–18°41'E. MRAC 99681. Flandria, river Momboyo (Zaire), 0°20'S–19°05'E. MRAC 104570–104577. River Ruki (Zaire), 0°16'S–19°01'E. MRAC 104578. River Ruki (Zaire), 0°16'S–19°01'E. MRAC 104878–104891. Boende, river Tshuapa (Zaire) 0°14'S–20°50'E. Seven specimens. MRAC 116476. Stat. 2 Stanley-Pool, archipelago N'Djili, pass of Yankau (Zaire), 4°20'S–15°24'E. MRAC 116483–116484. Stat. 33

Stanley-Pool, channel before Maluku (Zaire), 4°04′S–15°33′E. MRAC 116485. Stanley-Pool, mouth of the N'Sele (Zaire), 4°15′S–15°33′E. MRAC 116498. Stanley-Pool (Zaire), 4°06′S–15°15′E. MRAC 116499. Stat. 2 Stanley-Pool, archipelago N'Djili, pass of Yankau (Zaire), 4°20′S–15°24′E. MRAC 116500. Stanley-Pool, swamp of Kinkole (Zaire), 4°18′S–15°32′E. MRAC 118789. Stanley-Pool (Zaire), 4°06′S–15°15′E. MRAC 131498. Yangole, river Lilanda (Zaire), 0°48′N–24°17′E. MRAC 73-23-P-854. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 83-31-P-261-262. Kinshasa (Zaire), 4°18′S–15°18′E. One specimen.

Marcusenius ghesquierei (Poll, 1945)
(Fig. 12g)

Gnathonemus ghesquierei Poll, 1945

Material. HOLOTYPE: MRAC 46288, river Busira (Zaire), 0°15′S–18°59′E.

Diagnosis. Dorsal-fin origin situated before anal-fin origin. Both fins end at the same level. The ratio dorsal-fin length/anal-fin length is $>1{\cdot}25$. Dorsal-fin margin pointed and deeply concave (falciform). Anal fin slightly concave. Lateral-line scales 37–42, generally two scales on dark coloured transversal band. Dorsal fin long, with 32–34 rays, and 27–29 anal-fin rays.

Description. Measurements and meristic counts are given in Table 6, Table 7 and Table 8. Mouth terminal. Teeth bicuspid, five in upper jaw, six in lower jaw. Sub-mental swelling rounded and very small, its posterior end not reaching the anterior margin of the eye. Snout rounded. Anterior nostril in the middle between anterior tip of snout and eye, or at 0·33 distance from the eye. Posterior nostril at 0·2 to 0·16 distance from the eye. Eye diameter 79–95% of snout length.

Preanal distance longer than predorsal distance. Anal fin always shorter than dorsal fin. Their heights never reaching the length of their bases. Pectoral fin twice as long as pelvic fin and its posterior end close to posterior end of pelvic fin. Distance between pectoral and pelvic fins about 0·66 of pectoral-fin length. Base of pelvic fin 0·33 closer to pectoral fin than to anal-fin origin. Pelvic-fin length half the distance from pelvic-fin base to anal-fin origin.

High number of dorsal- (32–34) and anal- (27–29) fin rays. Low number of scales on the lateral line (37–42). Scales between dorsal- and anal-fin origins are 19–24. Two scales, sometimes three, on the lateral line cover the dark coloured transverse band between dorsal- and anal-fin origins. Head and transversal band somewhat darker than rest of the body. Body not elongated, but with a high back.

The electrocytes have penetrating stalks innervated on the anterior side (Pa).

Distribution (Fig. 11). *Marcusenius ghesquierei* is known from the Central Zaire basin, especially from the rivers Tshuapa and Ruki.

Maximum size. SL 108·8 mm.

Material examined. Ten specimens. MRAC 46288. River Busira (Zaire), 0°15′S–18°59′E; HOLOTYPE. MRAC 94382–94384. Village Bantoi, river Ruki (Zaire), 0°04′S–18°19′E. MRAC 94407. Village Bantoi, river Ruki (Zaire), 0°04′S–18°19′E. MRAC 101392. Bokuma (Zaire), 0°06′S–18°41′E. MRAC 73-23-P-790-791. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E. MRAC 73-23-P-793-794. Boende, river Tshuapa (Zaire), 0°14′S–20°50′E.

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References

ALVES-GOMES, J. and HOPKINS, C. D., 1997, Molecular insights into the phylogeny of mormyriform fishes and the evolution of their electric organs, *Brain, Behavior and Evolution*, (in press).

BANISTER, K. E. and BAILEY, R. G., 1979, Fishes collected by the Zaire River Expedition, 1974–1975, *Zoological Journal of the Linnean Society*, **66**, 205–249.

BASS, A. H., 1986a, Electric organs revisited: Evolution of a vertebrate communication and orientation organ, in T. H. Bullock and W. Heiligenberg (eds), *Electroreception* (New York: John Wiley), pp. 13–70.

BASS, A. H., 1986b, Species differences in electric organs of mormyrids: substrates for species-typical electric organ discharge waveforms, *Journal of Comparative Neurology*, **244**, 313–330.

BELL, C. C., ZAKON, H. and FINGER, T. E., 1989, Mormyromast electroreceptor organs and their afferent fibers in mormyrid fish. I. Morphology, *Journal of Comparative Neurology*, **286**(3), 391–407.

BENNETT, M. V. L., 1971a, Electric organs, in W. Hoar and D. J. Randall (eds), *Fish Physiology*, Vol. 5 (New York: Academic Press), pp. 347–491.

BENNETT, M. V. L., 1971b, Electroreception, in W. Hoar and D. J. Randall (eds), *Fish Physiology*, Vol. 5 (New York: Academic Press), pp. 493–574.

BIGORNE, R. and PAUGY, D., 1990, Description de *Marcusenius meronai*, espèce nouvelle de Mormyridae (Teleostei) de Sierra Leone, *Ichthyological Exploration of Freshwaters*, **1**(1), 33–38.

BIGORNE, R. and PAUGY, D., 1991, Note sur la systématique des *Petrocephalus* (Teleostei; Mormyridae) d'Afrique de l'Ouest, *Ichthyological Exploration of Freshwaters*, **2**(1), 1–30.

BOULENGER, G. A., 1898, A revision of the genera and species of fishes of the family Mormyridae, *Proceedings of the Zoological Society of London*, pp. 775–821.

BULLOCK, T. H. and HEILIGENBERG, W. (eds), 1986, *Electroreception* (New York: John Wiley), 722 pp.

CRAWFORD, J. D. and HOPKINS, C. D., 1989, Detection of a previously unrecognized mormyrid fish (*Mormyrus subundulatus*) by electric discharge characters, *Cybium*, **13**(4), 319–326.

DAGET, J., 1984, Contribution à la faune du Cameroun. Poissons des fleuves côtiers, *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **4**(6), 177–202.

DAGET, J. and DEPIERRE, D., 1980, Contribution à la faune de la République Unie du Cameroun. Poissons du Sanaga moyen et supérieur, *Cybium*, **3**(8), 53–65.

GOSSE, J. P., 1984, Mormyridae, in J. Daget, J. P. Gosse and D. F. E. Thys van den Audenaerde (eds), *Check-list of the freshwater fishes of Africa*, CLOFFA I (MRAC/Tervuren and ORSTOM/Paris), pp. 63–122.

GÜNTHER, A., 1867, New fishes from the Gaboon and Gold Coast, *Annals and Magazine of Natural History*, **20**(3), 110–117.

HOPKINS, C. D., 1981, On the diversity of electric signals in a community of mormyrid electric fish in West Africa, *American Zoologist*, **21**, 211–222.

HOPKINS, C. D., 1986, Temporal structure of non-propagated electric communication signals, *Brain, Behavior and Evolution*, **28**, 43–59.

LÉVÊQUE, C. and BIGORNE, R., 1985, Le genre *Hippopotamyrus* (Pisces, Mormyridae) en Afrique de l'Ouest, avec la description d'*Hippopotamyrus paugyi* n. sp., *Cybium*, **9**(2), 175–192.

LEVITON, A. E., GIBBS, JR, H. R., HEAL, E. and DAWSON, C. E., 1985, Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology, *Copeia*, **1985**(3), 802–832.

MAMONEKENE, V. and TEUGELS, G. G., 1993, Faune des poissons d'eaux douces de la Réserve de la biosphère de Dimonika (Mayombe, Congo), *Annales du Musée Royal de l'Afrique Centrale*, MRAC-UNESCO, **272**, 1–126.

MATTHES, H., 1964, Les poissons du Lac Tumba et de la région d'Ikela, *Annales du Musée Royal de l'Afrique Centrale*, série in-8°, Sciences Zoologiques, no 126, 206 pp.

MAYR, E. (ed.), 1970, *Populations, species, and evolution: an abridgment of animal species and evolution* (Cambridge, MA.: The Belknap Press of Harvard University Press), 453 pp.

PELLEGRIN, J., 1901, Poissons nouveaux ou rares du Congo français, *Bulletin du Muséum National de l'Histoire Naturelle, Paris*, **7**, 328–332.

PELLEGRIN, J., 1904, Mormyridés nouveaux de la collection du Muséum, *Bulletin du Muséum National de l'Histoire Naturelle, Paris*, **10**, 438–442.

PELLEGRIN, J., 1928, Poissons du Chiloango et du Congo récueillis par l'expedition du Dr. Schouteden (1920–1922), *Annales du Musée du Congo Belge*, zoologie série 1, tome III, fascicule 1, pp. 1–50.

PELLEGRIN, J., 1930, Poissons de l'Ogôoué, du Kouilou, de l'Alima et de la Sangha recueillis par M. A. Baudon. Description de cinq espèces et cinq variétés nouvelles, *Bulletin de la Société zoologique de France*, **1930**, 196–210.

POLL, M., 1939, Les poissons du Stanley-Pool, *Annales du Musée de Congo Belge*, zoologie série 1, tome IV, fascicule 1, 60 pp.

POLL, M., 1948, Note sur une série de types de Mormyridae, de Characidae et de Citharinidae du Muséum de Paris, *Bulletin du Muséum National de l'Histoire Naturelle*, 2ᵉ série, tome XX, n° 1, pp. 75–81.

POLL, M., 1959, Recherches ecologiques sur la faune ichthyologique du Stanley-Pool, *Annales de la Société Royale Zoologique de Belgique*, **89**(1), 183–201.

POLL, M., 1967, *Contribution à la faune ichthyologique de l'Angola* (Lisboa: Museo do Dundo), 381 pp.

POLL, M., and GOSSE, J. P., 1963, Contribution à l'étude systématique de la faune ichthyologique du Congo central, *Annales du Musée Royal de l'Afrique Centrale*, série in-8°, Sciences Zoologiques, n° 116, pp. 45–110.

ROBERTS, T. R., 1975, Geographical distribution of African freshwater fishes, *Zoological Journal of the Linnean Society*, **57**(4), 249–319.

ROBERTS, T. R., 1989, *Mormyrus subundulatus*, a new species of mormyrid fish with a tubular snout from West Africa, *Cybium*, **13**(1), 51–54.

ROBERTS, T. R., and STEWART, D. J., 1976, An ecological and systematic survey of fishes in the rapids of the Lower Zaire or Congo river, *Bulletin of the Museum of Comparative Zoology*, **147**(6), 239–317.

TAVERNE, L., 1968, Ostéologie du genre *Gnathonemus* Gill *sensu stricto* [*Gnathonemus petersii* (Gthr) et espèces voisines] (Pisces Mormyriformes), *Annales du Musée Royal de l'Afrique Centrale*, série in-8°, Sciences Zoologiques, n° 170, 91 pp.

TAVERNE, L., 1971, Ostéologie des genres *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers, *Pollimyrus* Taverne et *Brienomyrus* Taverne (Pisces Mormyriformes), *Annales du Musée Royal de l'Afrique Centrale*, série in-8°, Sciences Zoologiques, no 188, 144 pp.

TAVERNE, L., 1972, Ostéologie des genres *Mormyrus* Linné, *Mormyrops* Müller, *Hyperopisus* Gill, *Isichthys* Gill, *Myomyrus* Boulenger, *Stomatorhinus* Boulenger et *Gymnarchus* Cuvier. Considérations générales sur la systématique des poissons de l'ordre des Mormyriformes, *Annales du Musée Royal de l'Afrique Centrale*, série in-8°, Sciences Zoologiques, n° 200, 194 pp.

TAVERNE, L. and THYS VAN DEN AUDENAERDE, D. F. E., 1985, *Brienomyrus hopkinsi* nov. sp. du nord du Gabon (Pisces Teleostei, Mormyridae), *African Journal of Zoology*, **99**(1), 49–52.

TAVERNE, L., THYS VAN DEN AUDENAERDE, D. F. E. and HEYMER, A., 1976, *Marcusenius paucisquamatus et Marcusenius conicephalus*, deux espèces nouvelles du sud du Cameroun et du nord du Gabon (Pisces, Mormyridae), *Revue de zoologie africaine*, **90**(4), 872–882.

Teugels, G. G. and Guégan, J.-F., 1994, Diversité biologique des poissons d'eaux douces de la Basse-Guinée et de l'Afrique Centrale, in G. G. Teugels, J.-F. Guégan and J.-J. Albaret (eds), *Diversité biologique des poissons des eaux douces et saumâtres d'Afrique*, Vol. 275 of *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques*, pp. 67–85.

Teugels, G. G., Snoeks, J., De Vos, L. and Diakanou-Matongo, J. C., 1991, Les poissons du bassin inférieur du Kouilou (Congo), *Tauraco Research Report*, **4**, 109–139.