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A systematic revision of the African catfish genus *Heterobranchus* Geoffroy-Saint-Hilaire, 1809 (Pisces: Clariidae)

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The economically important African catfish genus *Heterobranchus* has been revised using biometrical and osteological features. From the 11 nominal species assigned to this genus, four are recognized as valid: *H. bidorsalis*, *H. isopterus*, *H. longifilis* and *H. boulengeri*. A key to the species together with species descriptions and data on the distribution of each species are given, as is a discussion of their phylogeny.

KEY WORDS:—Taxonomy – phylogeny – fish – Africa.

CONTENTS

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INTRODUCTION

The catfish family Clariidae contains at present some 13 valid genera, all of which are restricted to the African continent except for *Clarias* Scopoli, 1777 which also occurs throughout south-east Asia and *Encheloclarias* Herre & Myers, 1937 which is only known from Banka and Borneo. This paper deals with an alpha-level revision of the genus *Heterobranchus* Geoffroy-Saint-Hilaire, 1809. Twelve nominal species have been assigned to this genus; all but one, *Heterobranchus tapeinopterus* Bleeker, 1863, originate from Africa. The latter was subsequently transferred to a new, monospecific genus *Encheloclarias* by Herre & Myers (1937) and is endemic to a restricted area in south-east Asia. Its relationships within the Clariidae are in need of revision. From the remaining 11 nominal species, four are currently recognized as valid (Teugels, 1986a). Two of them, *Heterobranchus longifilis* Valenciennes, 1840 and *H. isopterus* Bleeker, 1863 are extremely closely related and impossible to separate with existing identification keys. Another species, *H. boulengeri* Pellegrin, 1922 displays striking differences in several characters compared with its congeners and its position within the genus seems questionable. In order to redefine the genus and its valid species, we examined both external and internal features in a large number of specimens housed in the collections of various natural history museums.

MATERIAL AND METHODS

The *Heterobranchus* collections housed in the British Museum (Natural History) (BMNH), London (England), the Muséum National d'Histoire Naturelle (MNHN), Paris (France) and the Musée Royal de l'Afrique Centrale (MRAC), Tervuren (Belgium) have been studied. Type material registered in the American Museum of Natural History (AMNH), New York (U.S.A.), the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden (The Netherlands) and the Zoologisches Museum der Humboldt-Universität zu Berlin (ZMB), Berlin (German Democratic Republic) was examined. A detailed list of the specimens examined is given in the appendix.

Measurements and meristic counts were made according to Teugels (1986b), except for the adipose fin features (see Fig. 1). Results obtained were submitted to overall among-groups principle component analysis, following the SYSTAT package. The correlation matrix was factored. Osteology was examined using radiographs and cleared and stained specimens.

RESULTS

Genus *Heterobranchus* Geoffroy-Saint-Hilaire, 1809

Type species. Heterobranchus bidorsalis Geoffroy-Saint-Hilaire, 1809 by subsequent designation of Bleeker (1863).

Diagnosis. Synapomorphies uniting species of *Heterobranchus*: (1) increased length (between 20.0 and 33.0% standard length (SL)) and depth (equal or nearly equal to dorsal fin depth) of adipose fin, and in relation shortened dorsal fin (26.0–44.0% SL) with fewer dorsal fin rays (26–45); (2) presence of 21 to 27 extended neural spines entering and supporting adipose fin.

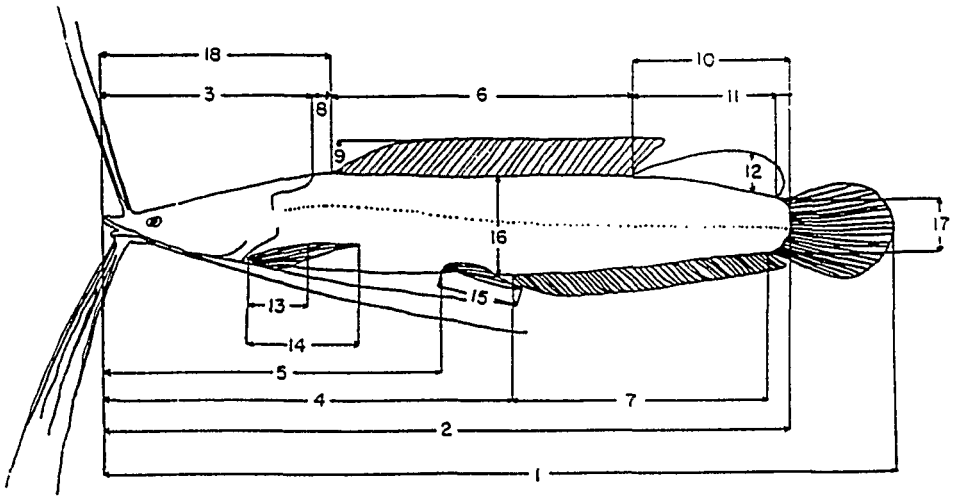

Figure 1. Important body measurements of *Heterobranchus* specimens: 1, total length (TL); 2, standard length (SL); 3, head length (HL); 4, preanal distance; 5, prepelvic distance; 6, dorsal fin length; 7, anal fin length; 8, distance between occipital process and dorsal fin origin; 9, dorsal fin depth; 10, distance between dorsal and caudal fin; 11, adipose fin length; 12, adipose fin depth; 13, pectoral spine length; 14, pectoral fin length; 15, pelvic fin length; 16, body depth at anus; 17, caudal peduncle depth; 18, predorsal distance.

In our opinion these characters are derived for the *Heterobranchus* species compared to other clariid genera and in particular to the genus *Clarias*. The subgenera of *Clarias* (*Dinotopteroides* and *Clarias* as defined by Teugels, 1986b) seem closely related on the basis of such morphological and osteological features as the structure of the cranium and the body proportions (see Discussion for further details).

Within the genus *Heterobranchus*, two subunits are recognized by a combination of characters involving the head and the branchial cavity.

The first subunit is characterized by a long (mean between 30.3 and 32.5% SL) and deep head; the mouth is terminal, with the upper jaw always extending beyond the lower jaw; the gill arches show normal proportions and the highest number of gill rakers on the first arch was 29 in a fish of 520 mm SL. The barbels are long or very long with the maxillary barbel always longer than the head. The results of morphometric analyses of the specimens conforming to the diagnosis of the first subunit, were submitted to various principal component analyses. Figure 2 illustrates the results of the analysis for six measurements (premaxillary toothplate width, vomerine toothplate width, head length, dorsal fin length, adipose fin length and interorbital distance). Three distinct groups are recognized; one is entirely situated in the negative sector of the second axis (*Heterobranchus bidorsalis*), another is situated in the negative sector of the first axis and partially in the negative sector of the second axis (*H. isopterus*) and the third is for the larger part located on the positive sector of the first axis (*H. longifilis*). The factor score coefficients for this analysis are given in Table 1: the premaxillary and vomerine toothplate widths and the head length are the most important features for distinguishing groups on the first axis, while the dorsal fin length and the adipose fin length showed to be most discriminating on the second axis.

TABLE 1. Factor score coefficients for the principal component analysis using six variables taken on specimens of the first subunit

Variables	PC 1	PC 2
Premaxillary width	0.40	0.06
Vomerine width	0.36	0.01
Head length	0.41	0.26
Interorbital distance	0.13	−0.22
Dorsal fin length	−0.26	−0.62
Adipose fin length	0.09	−0.44
Variance explained by rotated loadings	2.44	1.92

The second subunit is characterized by a longer (mean, 35.6% SL) and shallower head. The lower jaw extends beyond the upper jaw. The gill arches are extended anteriorly and the number of gill rakers on the first branchial arch is very high (54 to 84, 84 in a specimen of 555 mm SL). The barbels are extremely short, always shorter than the head length. The second subunit contains only *H. boulengeri.*

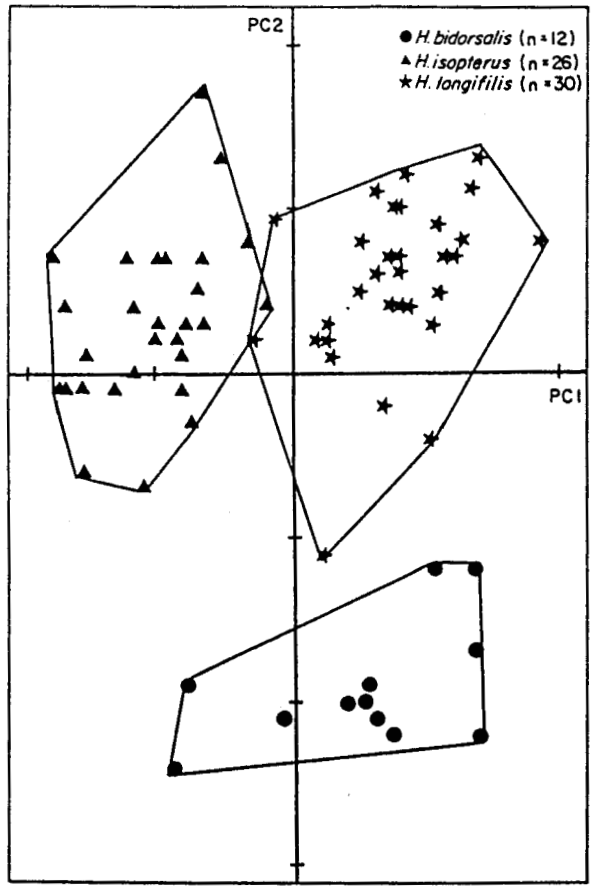

Figure 2. Results of principal component analysis, using six variables, on the specimens of *Heterobranchus* from the first subunit (see text for details).

Key to the species

1 Lower jaw extending beyond upper jaw; numerous 54–84 gill rakers (84 in specimen of 555 mm SL) on first branchial arch; barbels never exceeding head length. . *Heterobranchus boulengeri*

1′ Upper jaw extending beyond lower jaw; relatively few (17–29) gill rakers (29 in specimen of 520 mm SL) on first branchial arch; barbels long, maxillary barbel always longer than head . 2

2 Pectoral spine not serrated; dorsal fin length (37.2–42.5% SL) distinctly longer than adipose fin length (21.6–26.8% SL); 40–46 dorsal fin rays. . . *Heterobranchus bidorsalis*

2′ Pectoral spine serrated on anterior side; dorsal fin length (26.9–36.0% SL) just longer than adipose fin length (24.3–33.5% SL); 26–35 dorsal fin rays 3

3 Premaxillary toothplate width 29.5–36.9% head length (HL); vomerine toothplate width 25.0–32.2% HL; posterior part of adipose fin generally blackish; caudal fin generally with clearly marked light transversal band . . . *Heterobranchus longifilis*

3′ Premaxillary toothplate width 25.2–30.9% HL; vomerine toothplate width 20.8–25.0% HL; no black spot on posterior part of adipose fin; caudal fin uniform darkish . *Heterobranchus isopterus*

Heterobranchus bidorsalis Geoffroy-Saint-Hilaire, 1809
(Fig. 3)

Heterobranchus geoffroyi Valenciennes, 1840
?*Heterobranchus senegalensis* Valenciennes, 1840
Heterobranchus intermedius Günther, 1864

Iconotype. Geoffroy-Saint-Hilaire (1809): pl. 16.

Diagnosis. Distinguished from congeners by long dorsal fin (37.2–42.5% SL), always longer than adipose fin, by 40–46 dorsal fin rays and by smooth pectoral spine.

Description. Based on 29 specimens. Most important measurements and meristic counts given in Table 2. Largest specimen 800 mm, total length.

Head oval-shaped to rectangular in dorsal outline (Fig. 3). Snout broadly rounded. Eyes rather laterally positioned and interorbital distance about half of head length. Frontal fontanelle long and narrow: in small specimens anterior tip reaching line connecting anterior eye borders; in larger specimens, fontanelle with more posterior position, anterior tip reaching line connecting posterior eye borders. Occipital fontanelle relatively long and oval-shaped: in small specimens partially situated on supraoccipital process, but early in ontogenic development occupying more anterior position in front of occipital process. Latter pointed in juveniles and becoming more rounded in adults. Toothplates broad, with premaxillary plate broader than vomerine plate. Premaxillary teeth all conical; vomerine and mandibular teeth subgranular to granular. Skull fully ossified early in ontogenetic development with the 'postorbital' bones completely united. Suprabranchial cavity completely filled with well-developed dendritic suprabranchial organ.

TABLE 2. Measurements and meristic counts for specimens of *Heterobranchus bidorsalis*, *H. longifilis* and *H. isopterus*

	H. bidorsalis				*H. longifilis*				*H. isopterus*			
Characters	Min–Max	n	m̄	SD	Min–Max	n	m̄	SD	Min–Max	n	m̄	SD
Standard length (SL) (mm)	72.0–705.0	29	—	—	53.5–520.0	61	—	—	94.0–414.0	86	—	—
Head length (HL) (%SL)	30.1–33.5	29	32.5	0.8	28.4–35.9	58	32.4	2.0	27.7–32.8	83	30.3	1.2
Interorbital dist. (%HL)	45.5–53.7	29	49.2	2.3	42.5–51.5	58	46.2	1.7	41.9–47.4	84	44.5	1.4
Premaxillary width (%HL)	29.6–36.8	29	33.7	2.1	29.5–36.9	58	32.0	1.6	25.2–30.9	84	27.5	1.6
Vomerine width (%HL)	25.3–30.8	29	28.9	1.5	25.0–32.2	58	27.2	1.4	20.8–25.0	84	23.0	1.0
Dorsal fin length (%SL)	37.2–42.5	29	41.1	1.6	26.9–34.1	58	31.4	1.8	27.6–36.0	84	32.6	1.9
Adipose fin length (%SL)	21.6–26.8	29	23.7	1.4	24.3–32.8	58	28.2	1.5	25.2–33.5	84	29.2	1.9
Occ. proc. to dors. (%SL)	3.1–5.4	29	4.3	0.7	4.0–11.0	58	7.3	1.6	4.3–12.8	84	9.8	1.3
Gill rakers on 1st arch	17–27	29			16–29	58			14–26	84		
Dorsal fin rays	40–46	28			26–35	57			28–35	67		
Anal fin rays	49–58	18			42–52	41			40–51	40		
Vertebrae	62–63	5			55–61	20			53–60	18		

Dorsal fin origin close to supraoccipital process, distance between both being smallest found in *Heterobranchus* (about 4% SL). Adipose fin originating just after last dorsal fin ray and extending to near caudal fin origin, shortest found in *Heterobranchus* (21.6–26.8% SL). Relation between dorsal fin length and adipose fin length for three species in this subunit illustrated in Fig. 4. Pectoral fins extending from operculum to origin of first dorsal fin rays. Pectoral spine not serrated, readily distinguishing this species from congeners. Pelvic fins inserted at about same distance from tip of snout as from caudal fin base; reaching first anal fin rays. Anal fin origin situated below posterior third of dorsal fin.

Lateral line appearing as small whitish line running from posterior end of head to middle of caudal fin base. Openings of secondary sensory canals, though often hardly visible, with regular geometric pattern.

Coloration. Both alcohol-preserved and living specimens show a uniform yellowish-brown coloration, with blackish brown on their dorsal side and on the flanks as well as on the upper side of the paired fins and with light brown on the belly and on the lower side of the paired fins. The body and the fins occasionally may

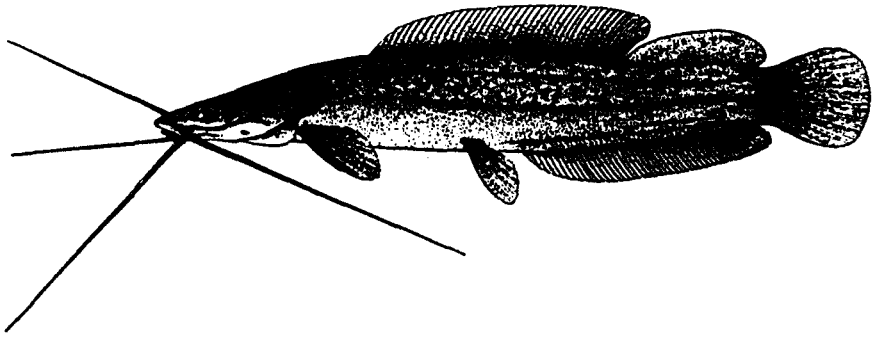

Figure 3. Lateral view of a specimen of *Heterobranchus bidorsalis*, 235 mm TL, from the Oti river (Volta basin) at Passere, Togo (MRAC 73-13-P-257-258).

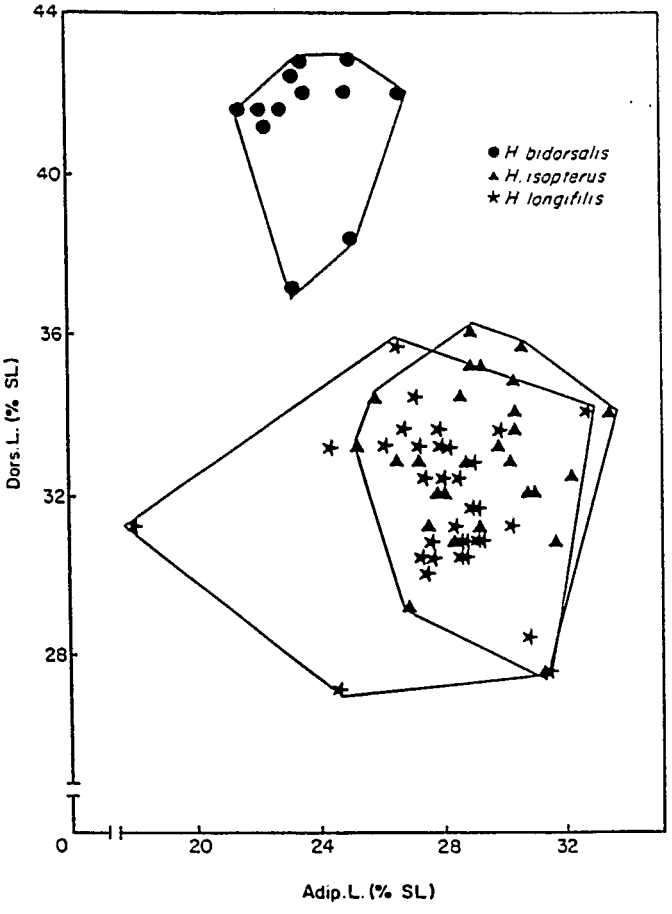

Figure 4. Dorsal fin length in relation to adipose fin length for *Heterobranchus* specimens of the first subunit.

show small, irregularly placed black spots. In living specimens, the unpaired fins are reddish, especially near the edges.

Distribution. (Fig. 5). The localities of the specimens examined together with literature records of specimens whose identity could be checked, served to produce a distribution map for this species. It occurs in the Nile, the Chad basin, the Niger basin including the Benoue and the Volta, the Senegal and the Gambia river systems. It therefore seems to be a typical Nilo-Sudanic species *sensu* Roberts (1975).

Notes on the synonymy. Valenciennes (1840) proposed the replacement of *Heterobranchus bidorsalis* by *H. geoffroyi* to honour the first describer of this species. Due to nomenclatorial priorities, the *nomen novum H. geoffroyi* has to be considered as an objective synonym of *H. bidorsalis*. Günther (1864) already listed this nominal species as a synonym of the latter.

In the same work, Valenciennes (1840) described *Heterobranchus senegalensis* after a skull from the Senegal river. According to the author, the rugosity of the cranial bones together with the longer teeth distinguish this nominal species from *H. bidorsalis*. In 1907, Boulenger synonymized this species with *H. bidorsalis*. The

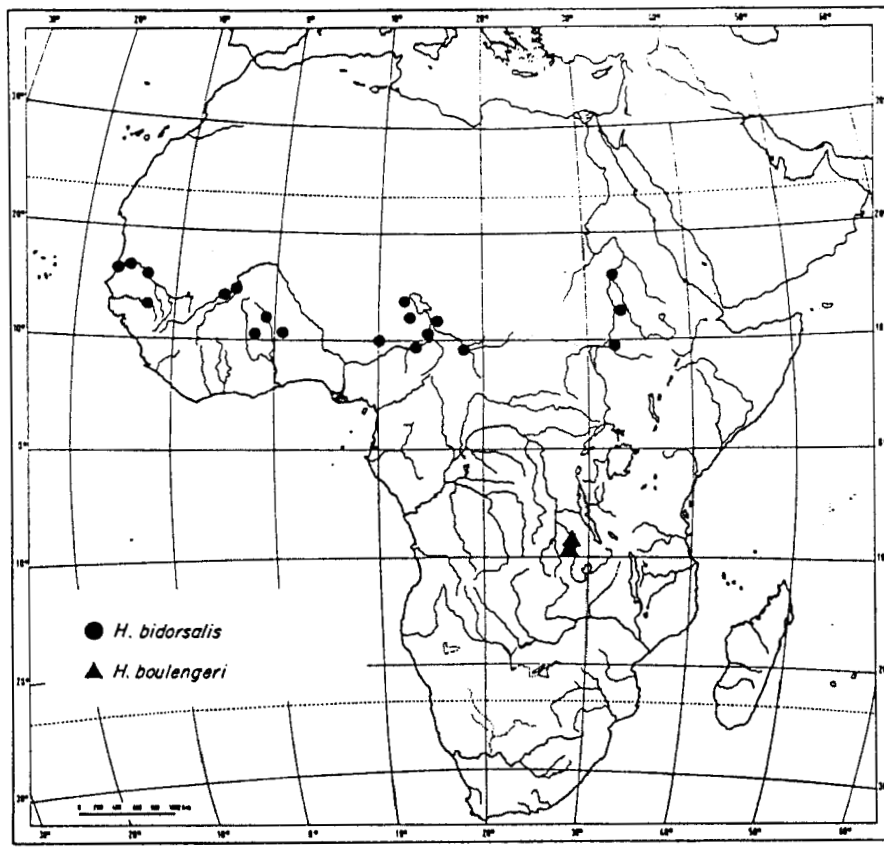

Figure 5. Geographical distribution of the specimens examined of *Heterobranchus bidorsalis* and *H. boulengeri*.

skull examined by Valenciennes (1840) is lost. As already pointed out by Greenwood (1972), however, it is very difficult if not impossible to make a reliable generic identification between a *Heterobranchus* and a large-headed *Clarias* (*C. gariepinus* and *C. anguillaris*) on the basis of the skull. As the *Clarias* species mentioned do occur in the Senegal river, it might well be that the skull examined by Valenciennes belonged to one of them. On the other hand, *Heterobranchus bidorsalis* is at present the only *Heterobranchus* species reported from the Senegal river. In conclusion, we prefer to consider this species as a *nomen dubium*.

Günther (1864) described *Heterobranchus intermedius* after two specimens from the Nile at Khartoum but in 1869 synonymized his new species with *H. bidorsalis*, a synonymy subseqently repeated by Boulenger (1907). During our revision we examined the two syntypes of *H. intermedius* (BMNH 1862.1.17.54 & 1863.10.6.1). Our specific characters of *H. bidorsalis* (dorsal fin length 39.1–41.4% SL; adipose fin length 25.1–25.8% SL; smooth pectoral spine) were found to be present and thus support Günther's synonymy.

Finally it should be noted that Steindachner (1870) when reporting on Valenciennes' *Heterobranchus senegalensis*, erroneously mentioned the name *H. biserialis* for *H. bidorsalis*. The former has to be considered as a *nomen nudum*.

Little is known on the ecology and the biology of this species. Daget (1954) mentioned that reproduction takes place at the end of the dry season.

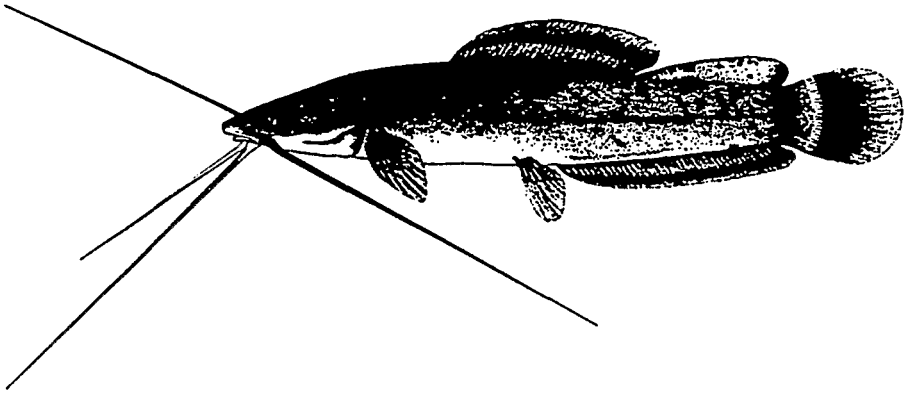

Figure 6. Lateral view of a specimen of *Heterobranchus longifilis*, 201 mm TL, from the Lualaba river at Kindu, Zaire (MRAC 70096).

Specimens of *Heterobranchus bidorsalis* attain a large and edible size. Sydenham (1970) reported a specimen of 1520 mm in total length, weight 27 kg.

Heterobranchus longifilis Valenciennes, 1840
(Fig.6)

Heterobranchus laticeps Peters, 1852
Clarias loangwensis Worthington, 1933
Heterobranchus platycephalus Nichols & La Monte, 1934

Holotype. MNHN no. B.273 from the Nile in Egypt, collected by de Joannis.

Diagnosis. Distinguished from other *Heterobranchus* species by larger premaxillary (29.5–36.9% HL) and vomerine (25.0–32.2% HL) toothplate width, blackish posterior part of adipose fin and barred caudal fin coloration.

Description. Based on holotype and 60 specimens. Most important measurements and meristic counts given in Table 2. Largest specimen 610 mm, total length (520 mm SL).

Long and broad head, somewhat rectangular in dorsal outline (Fig. 6). Snout broadly rounded. Eyes with supero-lateral position, interorbital distance generally less than half of head length. Frontal fontanelle long and narrow: in

TABLE 3. Measurements and meristic counts for specimens of *Heterobranchus boulengeri*

Character	Min–Max	n	m̄
Standard length (SL) (mm)	382.0–550.0	4	—
Head length (HL) (%SL)	33.0–37.0	3	35.6
Interorbital distance (%HL)	30.5–31.2	3	30.8
Premaxillary width (%HL)	24.1–27.2	4	25.8
Vomerine width (%HL)	19.3–20.9	4	20.3
Dorsal fin length (%SL)	34.6–36.6	2	35.6
Adipose fin length (%SL)	23.2–25.1	3	24.5
Occ. proc. to dors. fin (%SL)	5.1–5.6	3	5.3
Gill rakers on 1st arch	54–84	4	
Dorsal fin rays	31–39	4	
Anal fin rays	46–50	4	

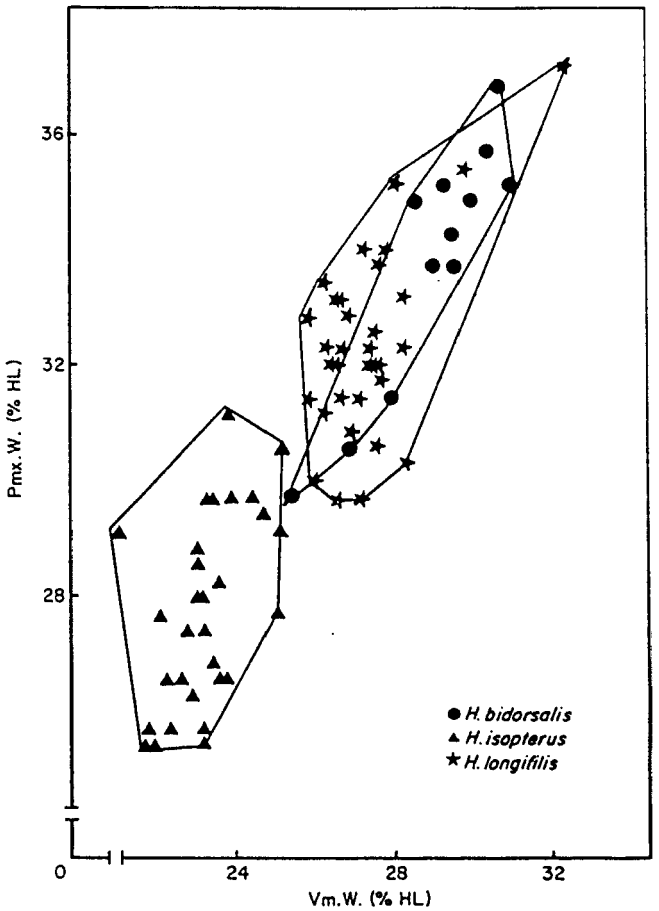

Figure 7. Premaxillary width in relation to vomerine width for *Heterobranchus* specimens of the first subunit.

small specimens anterior tip reaching line connecting anterior eye borders; in larger specimens, fontanelle with more posterior position, anterior tip reaching line connecting posterior eye borders. Occipital fontanelle oval-shaped and, in small specimens, partially situated on occipital process. In larger specimens (> 120 mm SL), more anteriorly positioned. Occipital process pointed in juveniles becoming more rounded with age. Toothplates width, related to head width, very large and thus differing from closely related *Heterobranchus isopterus* (Fig. 7). Premaxillary teeth conical; vomerine and mandibular teeth subgranular to granular. As in other *Heterobranchus* species, skull entirely covered with bone. Juvenile (<80–90 mm SL) postorbital margin not yet completely ossified and 'postorbital' bones separated by distinct gap. Suprabranchial cavity completely filled with well-developed dendritic accessory air-breathing organ. Distance between dorsal fin origin and supraoccipital process about 7% SL. Adipose fin originating immediately after last dorsal fin ray and extending to caudal fin base; length equal to or slightly shorter than dorsal fin length. Pectoral fin extending from behind operculum to origin of first dorsal fin rays. Pectoral spine strongly serrated on anterior side; posterior side smooth or occasionally with few minute serrations. Pelvic origin closer to tip of snout than to caudal fin base.

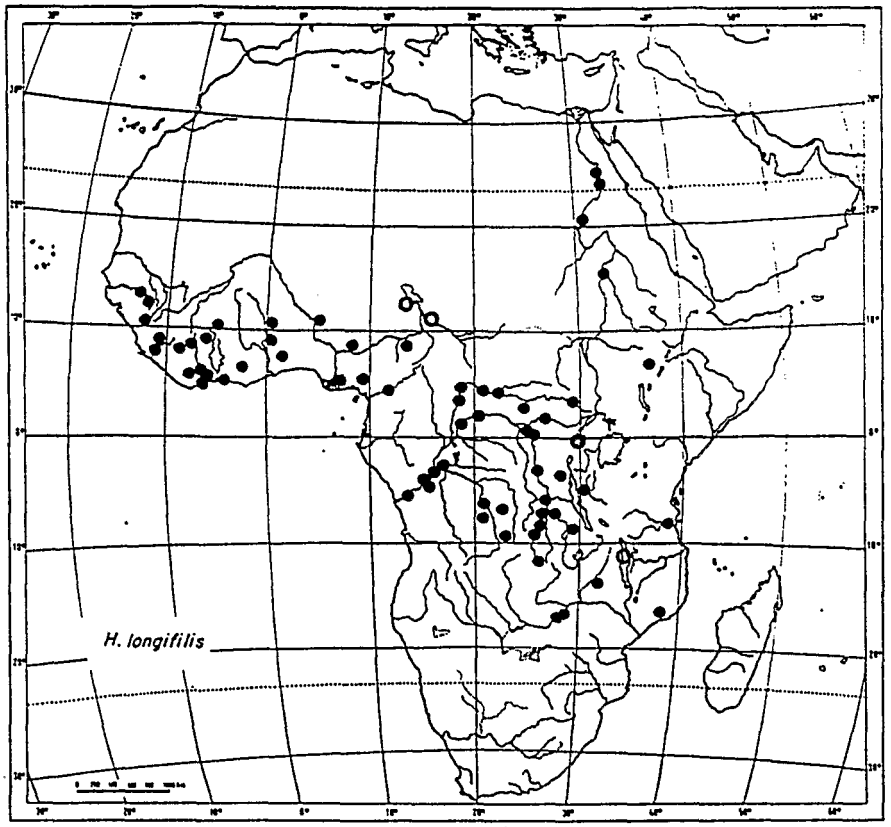

Figure 8. Geographical distribution of the specimens examined of *Heterobranchus longifilis*; open circles refer to literature data.

Pelvic fins reaching first anal fin rays. Anal fin origin situated below posterior half of dorsal fin.

Lateral line appearing as thin white line extending from posterior end of head to middle of caudal fin base. Openings of secondary sensory canals hardly visible but displaying regular pattern.

Coloration. Both alcohol-preserved and living specimens are generally grey-brown or grey to dark-grey, with the belly and the lower surface of the paired fins whitish to light-brown. The body and the flanks show irregular dark spots in specimens up to about 300 mm SL (juvenile condition). Generally, the posterior part of the adipose fin is darkly coloured, a character that enables a fast identification. The caudal fin usually has a dark basal band followed by a small, clearly marked, light band, then by a thin, black line and then a less dark area extending over the remainder of the fin. It is important to notice that this particular coloration is typical for the juvenile stage and tends to disappear with age. In fish kept under rearing conditions, the dark spots on the flanks disappear at about 350 mm TL. The dark colour of the adipose fin and the light band on the caudal fin last longer but diminish progressively and become indistinct in specimens of about 700 mm TL. Occasionally a marbled coloration is found on the flanks, probably relating to stress conditions.

Distribution (Fig. 8). The specimens examined and those mentioned in literature whose identification could be checked, have a wide distribution: they were found in the Nile, the Chad basin including the Benoue and the Chari, the Niger, the Volta, The Gambia and several smaller coastal basins in West Africa from Guinea to the Sanaga (Cameroon), the Zaire basin (lower, central and upper), lakes Edward and Tanganyika, the lower and middle Zambezi river, lakes Kariba and Malawi, the Shire river and the Pungwe and Buzi rivers.

Notes on the synonymy. Peters (1852) described *Heterobranchus laticeps* based on two specimens from Mozambique. According to this author, the species is closely related to *H. longifilis*, but differs in the skull shape and in a larger distance between dorsal and adipose fin. Boulenger (1907) synonymized these species. We examined the two syntypes of *H. laticeps* (ZMB 3072) and found the differences mentioned by Peters (1852) to be irrelevant. Moreover, the specimens have a dorsal fin length of 31.4–32.2% SL, the pectoral spine is, in both, serrated on the anterior side, the premaxillary width ranges between 34.5–36.3% HL and the vomerine width varies between 29.3–29.9% HL; therefore we support the synonymy introduced by Boulenger.

Worthington (1933) described *Clarias loangwensis* based on a single specimen from a tributary of the Zambezi river in Southern Rhodesia (Zimbabwe). According to this author the dorsal fin is damaged in the type specimen so that it presents the appearance of a divided dorsal fin. Ricardo-Bertram (1943) considered this specimen as an aberrant *Heterobranchus longifilis*, with the caudal fin damaged and partly regenerated. Jackson (1961) examined the type specimen and confirmed this synonymy. We studied the holotype (BMNH 1932.12.16.501), a specimen of 296 mm SL. It showed all specific features of *H. longifilis* and we too agree with the synonymy as introduced by Ricardo-Bertram.

Nichols & La Monte (1934) described *Heterobranchus platycephalus* based on a single specimen from the Zaire river. David (1935) synonymized this species with *H. longifilis*. We examined the holotype (AMNH 12356). Its dorsal fin length (32.4% SL), adipose fin length (30.0% SL), premaxillary width (32.6% HL), vomerine width (26.3% HL), and the presence of serrations on the anterior side of the pectoral spine, clearly indicate that the specimen belongs to *H. longifilis*.

Ecology and biology. Heterobranchus longifilis is the only *Heterobranchus* species for which general biological data have been published. The species seems to prefer quiet water with deep pools and stretches, not necessarily associated with vegetation, and is found in larger waterways and main river channels. It is an omnivorous scavenger and will eat anything small enough to fit into its massive jaws including aquatic invertebrates and vertebrates, plants, mud, etc. Reproductive biology has not been studied in detail, but juveniles have been found in tributary rivers and floodplains during the rainy season, indicating that migration from the normal dry season habitat take place before spawning (Bell-Cross, 1976; Gosse, 1963; Planquette & Lemasson, 1975).

The species has recently been introduced in experimental fish culture in the Ivory Coast. The results obtained so far are most promising (Legendre, 1983; 1986), comparable to commercially produced *Clarias gariepinus* (Burchell, 1822). Like the latter species, *H. longifilis* attains an edible size and is highly prized by local inhabitants. The largest known specimen, 1170 mm SL, was caught in Lake Kariba (Frank, 1974).

Heterobranchus isopterus Bleeker, 1863
(Fig. 9)

Heterobranchus macronema Bleeker, 1863

Holotype. RMNH no. 2977 from "Rio Boutry, Guinea" collected by H. S. Pel. As pointed out by Holthuis (1968), Pel's collections were made mainly at Butri and the neighbouring Dabo Krom in Ghana.

Diagnosis. Distinguished from other *Heterobranchus* species by relatively small premaxillary (25.2–30.9% HL) and vomerine (20.8–25.0% HL) widths correlated with narrower head (compared to other species).

Description (Fig. 9). Based on holotype and on 85 specimens. Most important measurements and meristic counts given in Table 2. Largest specimen 510 mm total length.

Head shortest of all *Heterobranchus* species and somewhat between rectangular and oval-shaped in dorsal outline. Interorbital distance relatively small (less than half of head length) and eyes with a supero-lateral position. Frontal fontanelle long and narrow; anterior tip nearly reaching line connecting anterior eye borders in small specimens; more posterior in larger specimens. Oval-shaped occipital fontanelle, in juveniles, partially situated on occipital process. In adults more anterior in position. Occipital process pointed in juveniles, becoming more rounded with age. Because of relatively narrow head width, toothplates in *Heterobranchus isopterus* have smallest width of all *Heterobranchus* species (see Fig. 7). Premaxillary teeth conical; vomerine and mandibular teeth subgranular to granular. Head completely covered with bone. Only in juvenile specimens (<90 mm SL) 'postorbital' bones separated by distinct gap. Suprabranchial cavity completely filled with well-developed dendritic suprabranchial organ.

Distance between occipital process and dorsal fin origin largest found in *Heterobranchus* species (about 10% SL). Dorsal fin close to adipose fin, latter extending to caudal fin base. Pectoral fins hardly reaching first dorsal fin rays. Pectoral spine distinctly serrated on anterior side while posterior side occasionally with few minute serrations. Pelvic fins situated halfway between tip of snout and caudal fin origin, reaching first anal fin rays. Anal fin origin situated below posterior half of dorsal fin base.

Lateral line present as thin white line extending between posterior end of head and caudal fin origin. Openings of secondary sensory canals hardly visible but displaying regular pattern.

Coloration. Both alcohol preserved and living specimens are greenish-brown or dark brown on the dorsal side and on the flanks as well as on upper side of the paired fins. The belly and the lower side of the paired fins are generally yellowish. Occasionally, irregular blackish spots are found on the body. The caudal fin never has a light coloured transverse band as in *H. longifilis*; it is uniformly coloured. Occasionally, a marbled colour pattern is present on the flanks.

Distribution (Fig. 10). The specimens examined were found in coastal basins in West Africa, from the Konkoure (Guinea) to the Ohumbe (Cameroon). The species is present in the upper Senegal (Bafing). A locality in Northern Nigeria seems doubtful; an erroneous labelling is possible.

Note on the synonymy. Together with the description of *Heterobranchus isopterus*, Bleeker (1863) described another new species *H. macronema* based on three

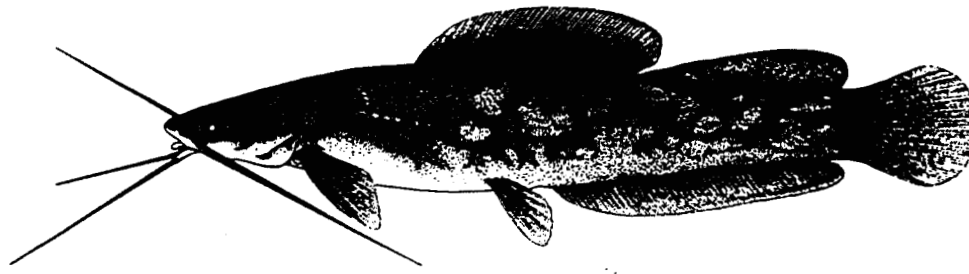

Figure 9. Lateral view of a specimen of *Heterobranchus isopterus*, 214 mm TL, from Abokouamekro, Ivory Coast (MRAC 73-5-P-3006).

specimens from "Dabo Krom, Guinea". As mentioned above, this locality is not situated in Guinea but in Ghana. Günther (1864) synonymized this species with *H. isopterus*, a synonymy subsequently confirmed by Boulenger (1907). During this study we examined the three syntypes of *H. macronema* (RMNH 2978) and uphold Boulenger's synonymy: the specimens conform with the description of *H. isopterus* and the minor differences between both as mentioned by Bleeker (1863; barbel length; dorsal and anal fin ray counts) are obviously related to allometry and individual variation respectively.

Daget & Iltis (1965) reported a specimen of about 900 mm in total length from the Ivory Coast.

Heterobranchus boulengeri Pellegrin, 1922
(Fig. 11)

Syntypes. MRAC no. 14763–14764(2) from Lake Mweru at Lukonzolwa.

Diagnosis. Distinguished from *Heterobranchus* species by lower jaw extending beyond upper jaw, numerous gill rakers on first branchial arch and short barbels.

Description (Fig. 11). Based on two syntypes and two additional specimens.

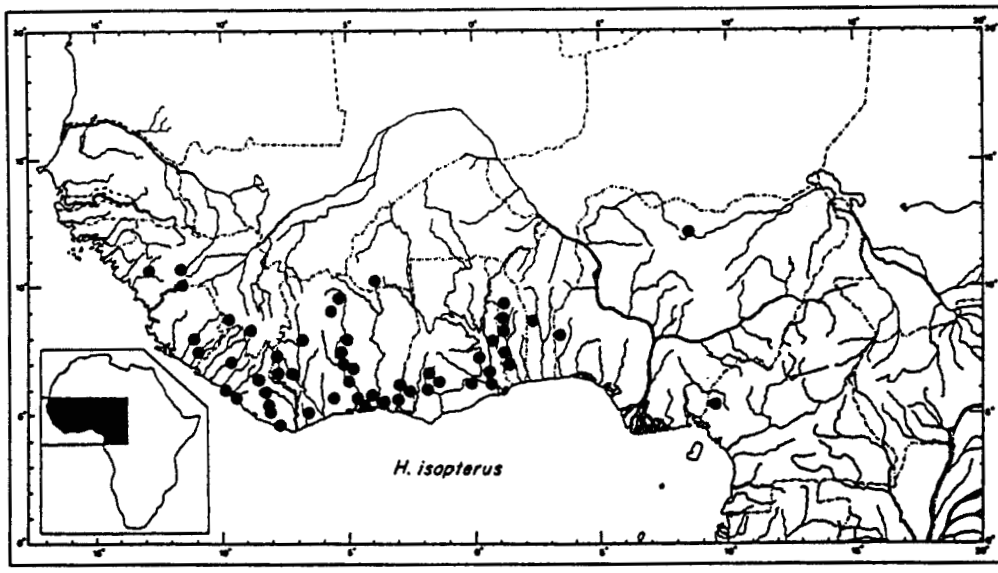

Figure 10. Geographical distribution of the specimens examined of *Heterobranchus isopterus*.

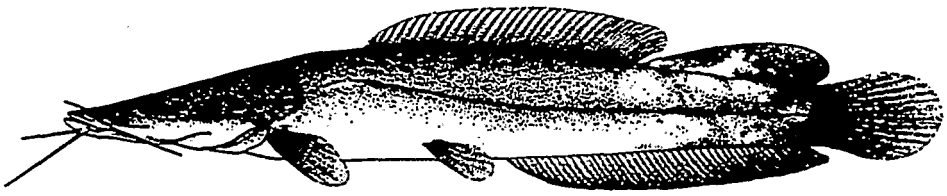

Figure 11. Lateral view of a specimen of *Heterobranchus boulengeri*, 640 mm TL, from Lake Mweru at Lukonzolwa (MRAC 14764).

Most important measurements and meristic counts given in Table 3. Largest specimen 640 mm, total length.

Head generally longer and much more flattened than in other *Heterobranchus* species. In dorsal outline, spatulate. Snout rectangular and lower jaw extending beyond upper. Interorbital distance relatively narrow (m=30.8% HL) compared to other species, and eyes in more dorsal position. As only four large-sized specimens available for study, no data given on shape of frontal and occipital fontanelle in young specimens. In specimens examined, tip of frontal fontanelle not reaching line connecting posterior eye borders and relatively short (12.7–14.0% HL). Small occipital fontanelle situated in front of occipital process. Latter relatively long and pointed in specimens examined. Relatively small toothplates compared to congeners; premaxillary plate broader than vomerine plate. Premaxillary teeth conical; vomerine and mandibular teeth subgranular or granular. Barbels short, none of them exceeding half head length. Branchial cavity considerably larger than in other species. Gill arches extended anteriorly, containing numerous gill rakers (up to 84 on first gill arch of specimen of 555 mm SL). Suprabranchial cavity nearly filled with dendritic suprabranchial organ. Skull completely ossified and fourth infraorbital (postorbital of authors) greatly enlarged.

Dorsal fin origin rather close to occipital process (about 5% SL). Adipose fin originating just after last dorsal fin ray, extending to near caudal fin origin. Pectoral fins extending from operculum to near origin of first dorsal fin rays. Pectoral spine serrated on base of outer side. Pelvic fins inserted at about same distance from tip of snout as from caudal fin base; reaching first anal fin rays. Anal fin origin situated below posterior half of dorsal fin.

Lateral line appearing as thin whitish line running from posterior end of head to middle of caudal fin base. Openings of secondary sensory canals show regular geometric pattern.

Coloration. Alcohol-preserved specimens are dark-brown dorsally, on the flanks and on the upper side of the paired fins, and light-brown to greyish on the belly and the lower side of the paired fins. In two of the four specimens examined, irregular dark blotches were found on the flanks. In living specimens, the colour is dark chocolate brown with the under parts of the head bright yellow (Jackson, 1961).

Distribution (Fig. 5). Only four specimens of this species are known. Apart from the type locality, Lake Mweru at Lukonzolwa, where it occurs sympatrically with *H. longifilis* (see list of specimens examined), this species has been collected in the same lake at Kilwa and in the Luapula river at N'Kole. Jackson (1959) reports this species as very common in Lake Mweru (where it is of commercial

importance) and the Kalungwishi and Lower Luapula rivers, but mentioned that it has never been recorded from the rest of the Rhodesian Congo system above the Johnston Falls on the Luapula.

DISCUSSION

The presence of an adipose fin is not a unique character within the Clariidae. The genus *Dinotopterus* Boulenger, 1906, with its supposed junior synonym *Bathyclarias* Jackson, 1959 (see Greenwood, 1961) as well as two species of the genus *Clarias* (see Teugels, 1983a), all have this feature. However, the adipose fin length in these taxa is much smaller than in *Heterobranchus* and the hyperdevelopment of the fin is unique to this genus. The presence of extended neural spines to support the adipose fin also appears unique to these clariid taxa (Teugels, 1983b); therefore, it seems that on the bases of these derived features, the taxa form a monophyletic assemblage within the Clariidae.

Heterobranchus species possess the most truncated dorsal fin as well as the lowest dorsal fin ray count of all Clariidae.

Within *Heterobranchus*, two subunits are recognized. In the first, *H. bidorsalis* appears to be the most primitive species: it has the smallest adipose fin, with the fewest extended neural spines; the other two species, *Heterobranchus longifilis* and *H. isopterus*, form a monophyletic lineage recognized by the adipose fin length, exceeding 25% SL; pectoral fin spines are smooth in both *H. bidorsalis* and *H. boulengeri*, but in *H. isopterus* and *H. longifilis* they are serrated along the outer surface. Serrated pectoral spines are commonly distributed in siluroids and it might appear that loss of serrations is a derived feature. Assuming this, the condition in *H. isopterus* and *H. longifilis* must either be considered as a retention of the primitive condition or secondarily derived. On the basis of the distribution of the synapomorphies the most economic explanation is that serrations have been secondarily regained. Both *H. isopterus* and *H. longifilis* show an increased number of neural spines with a correlated enlargement of the adipose fin and reduction of the dorsal fin. *Heterobranchus isopterus* is distinguished from its congeners by small toothplates. The width of toothplates is variable amongst clariids, but nonetheless can be used to distinguish subgroups (Teugels, 1986) and it seems that within these subgroups a reduced condition is indicative of derived species. *Heterobranchus longifilis* possesses a unique colour pattern.

The second subunit is monospecific, containing only *Heterobranchus boulengeri* which is characterized by its extended lower jaw, the extended fourth infraorbital bone, the numerous gill rakers and the short barbels. We believe that this species might well be related to the *Dinotopterus-Bathyclarias* complex: several characters are shared, especially those related to cranial morphology but as yet, the polarity of these characters have not been assessed. Since *H. boulengeri* possesses the synapomorphies defining *Heterobranchus*, its position within this genus seems presently correct, but we are aware that a discovered relationship with *Dinotopterus* would lead to a taxonomic reassessment of the genus.

A cladogram showing the most parsimonious hypothesis of relationships within *Heterobranchus* is given in Fig. 12. This hypothesis also signifies a basal dichotomy between Nilo-Sudanic and Zairean areas for the two subunits. The Nilo-Sudanian distribution of *H. bidorsalis* corresponds with the plesiomorphic condition as found in other groups (Vari, 1979; Howes, 1984).

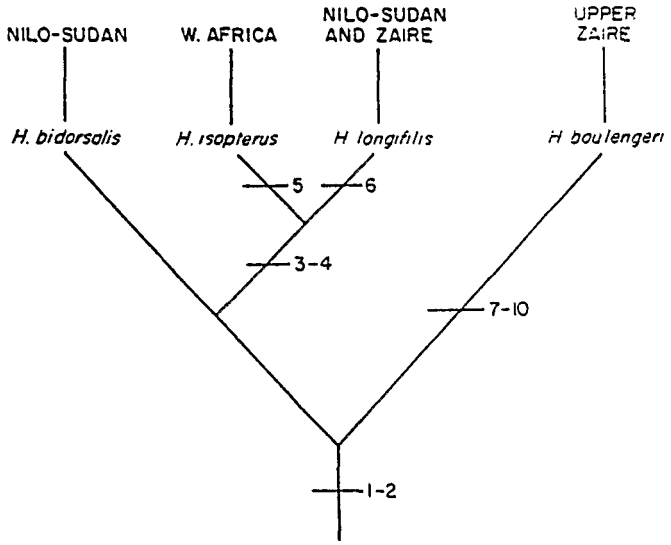

Figure 12. Cladogram showing the most parsimonious hypothesis of relationships within the genus *Heterobranchus*. 1, Increased length and depth of adipose fin, with correlated shortening of dorsal fin and reduced number of dorsal fin rays; 2, presence of 21 to 27 extended neural spines entering and supporting the adipose fin; 3, ?pectoral spine serrations; 4, increased number of neural spines with correlated lengthening of adipose fin and further reduction of dorsal fin length and dorsal fin ray number; 5, small toothplates; 6, unique colour pattern; 7, extended lower jaw; 8, extended 4th infraorbital; 9, numerous gill rakers on first arch; 10, short barbels.

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APPENDIX: LIST OF SPECIMENS EXAMINED

Heterobranchus bidorsalis

MRAC 144235 Volta Blanche 60 km E. of Ouagadougou, Upper Volta, coll. Roman, 2.xi.1964; MRAC 144236 R. Massili, tributary of Volta Blanche, Upper Volta, coll. Roman, 5.xii.1964; MRAC 153923 Bahr-Sara, mouth of R. Mandoul, Chad, coll. Sutter, iii.1965; MRAC 73-5-P-2958 Ross Bethio, R. Lampsar, delta R. Senegal, Senegal, coll. Thys van den Audenaerde, 10.iii.1966; MRAC 73-5-P-2959 Richard Toll,

R. Taoué, tributary R. Senegal, Senegal, coll. Thys van den Audenaerde, 15.iii.1966; MRAC Dagana, R. Senegal, Senegal, coll. Thys van den Audenaerde, 16.iii.1966; MRAC 73-12-P-383-384 Mopti Nord, Mali, coll. Matthes, 3.ix.1969; MRAC 73-13-P-257-258 Passere, R. Oti, Togo, coll. De Vree-Vanderstraeten, 12.xii.1969; MRAC 77-43-P-76-79 Ngalenka, Senegal, coll. Reizer, viii.1974; MRAC 80-56-P-31 Niokolo Koba, R. Gambie, Senegal, coll. Lévêque & Paugy, iv.1980; MNHN 1900-362-363 L. Chad, Komadougou at Turban Guida, Niger, coll. Tilho; MNHN 1959-438 & 1959-506 L. Chad, Logone Gamsaye, Chad, coll. Blache; MNHN 1961-512 Diafarabé, Niger, Mali; coll. Daget; MNHN 1961-513 Ouana, coll. Daget; MNHN 1962-503 Benue at Kinada, Niger basin, Cameroon; coll. Stauch; BMNH 1862.1.17.54 Khartoum, Sudan, coll. Petherick, syntype of *Heterobranchus intermedius*; BMNH 1863.10.6.1 Khartoum, Sudan, coll. Petherick, syntype of *Heterobranchus intermedius*; BMNH 1884.6.9.25-26 R. Niger, coll. Forbes; BMNH 1900.6.28.127-129 Kaëdi, Senegal, coll. Delhez; BMNH 466 Goz Shebesha, White Nile, coll. Loat; BMNH 1905.3.15.19 R. Shari, Wasu at Maidugari, coll. Gosling; BMNH 1907.12.2.1740 Goz abu Gumah, White Nile, coll. Loat; BMNH 1907.12.2.1741 Fashoda, White Nile; BMNH 1928.7.3.63 R. Kiyawa, near Katagum, Nigeria, coll. Lloyd; BMNH 1928.7.4.59 R. Shari, below junction of R. Logone, L. Chad bassin, coll. Markham; BMNH 1981.2.17.1032 Black Volta, Mombelu near Lawra, coll. Hopson.

Heterobranchus longifilis

MRAC 1150 Banzyville, Belgian Congo, coll. Royaux, 1901; MRAC 1894 Stanley-Falls, Belgian Congo, coll. Christy, 21.vi.1912; MRAC 2069 Stanley Falls, Belgian Congo, coll. Christy, 20.vi.1912; MRAC 2783 Kwamouth (Leopoldville) Belgian Congo, coll. Maes, 1913; MRAC 14737 L. Moero at Lukonzolwa, Belgian Congo, coll. Stappers, 18.xi.1910; MRAC 15654 Stanleyville, Belgian Congo, coll. Lang & Chapin; MRAC 17408 Tshikapa, Belgian Congo, coll. Schouteden; MRAC 19099 Luebo, Belgian Congo, coll Schouteden (squelette); MRAC 19966-970 Nyonga, Belgian Congo, coll. de Witte, 8-12.v.1925; MRAC 35645 Kiambi, R. Luvua, Belgian Congo, coll. de Witte, 4-20.v.1931; MRAC 20856 Nyonga, Belgian Congo, coll. de Witte, 8-12.v.1925; MRAC 19606 Luluabourg, Belgian Congo, coll. Callewaert; MRAC 22191, 22724 & 29534 Koteli, Belgian Congo, coll. Schouteden, 1-23.i.1925; MRAC 22744 & 29485 Panga, Belgian Congo, coll. Schouteden, 12.ix.1925; MRAC 39481 Kapanga, Belgian Congo, coll. Overlaet, 1933; MRAC 41991 Sandoa, Belgian Congo, coll. Overlaet, 1934; MRAC 47550 Lower Congo, Belgian Congo, coll. Schwetz, 1936; MRAC 48599 & 48608 Mombangi Region, R. Ley Yole, Mo, Méba (Lisala), Belgian Congo, coll. Ghenne, 1937; MRAC Bukama, Belgian Congo, coll. Brien, vii. 1937; MRAC Kikondja (L. Kisale), Belgian Congo, coll. Brien, viii.1937; MRAC Yakoma (Ubangi) Belgian Congo, coll. Rosy, 1938; MRAC 67215-216 Mushie Region, R. Kasai, Belgian Congo, coll. Vleeschouwers, vi.1945; MRAC 68678 Yangambi, islands, Belgian Congo, coll. Hulot, 28.i.1952; MRAC 69850 Kabumbula, Belgian Congo, coll. Poll, 22.vi.1947; MRAC 69914 & 69943 Kabalo, R. Lualaba, Belgian Congo, coll. Poll, 6.vii.1947; MRAC 70096 Kindu R. Lualaba, Belgian Congo, coll. Poll, 19-22.vii.1947; MRAC 87397 R. Lulua, Belgian Congo, coll. Jobaert, 1953; MRAC 83388 pools of Manono, Belgian Congo, coll. Miss Pisc. Kat., 22.iii.1947; MRAC 90313 Delta of Malagarasi, Belgian Congo, coll. Poll, 21.v.1947; MRAC 123725-738 Léopoldville, R. Michakuchaku, Belgian Congo, coll. Hulot, x.1948; MRAC 130032 Kitutu, R. Kukuluzi, Belgian Congo, coll. Leleup, iv.1958; MRAC 135433 Yaekela, Belgian Congo, coll. Gosse, 8.ii.1955; MRAC 138149-159 Yaekama, R. Ikonga, Belgian Congo, coll. Hulot, 28.i.1952; MRAC 141741 R. Kou, tributary of Volta Blanche, Upper Volta, coll. Roman, 4.ii.1960; MRAC 155070 Khartoum, Sudan, coll. Abu Gideiri, 1967; MRAC 161878 Dundo, tributary R. Luachimo, Angola, coll. Museu do Dundo, vi.1949; MRAC 161879-884 Mwaoka, tributaries of R. Luachimo, Angola, coll. Museu do Dundo, vi.1964; MRAC 167309-310 Molenga-Boma, R. Ubangi, Belgian Congo, coll. Cremer & Neumann, xii.1947; MRAC 182364 Gangala na Bodio, R. Dungu, Belgian Congo, coll. Cornet d'Elzius, 1954-1955; MRAC 187089 R. Lufua, estuary, Rhodesia, coll. Matthes, 23.xi.1965; MRAC 187090 L. Kariba, Redcliffe Island, Rhodesia, coll. Matthes, 25.ii.1965; MRAC 187091-092 R. Mlolo, Rhodesia, coll. Matthes, 1964; MRAC 187093 Sanyati Gorge, Rhodesia, coll. Matthes, 24.xii.1964; MRAC 181474-475 Gangala na Bodia, R. Dundu, Belgian Congo, coll. Poll, xi.1956; MRAC 73-5-P-2954-955 Korrékopé, R. Mono, Togo, coll. Thys van den Audenaerde, 6-7.x.1966; MRAC 73-5-P-2956-957 Dotékopé, R. Mono, Togo, coll. Thys van den Audenaerde, 7.x.1966; MRAC 73-14-P-279 Kolékopé, R. Mono, Togo, coll. Thys van den Audenaerde, 12-14.iii.1970; MRAC 73-14-P-74 Poli, Cameroon, coll. De Vree, Hulselmans & Geraert, 15.viii.1972; MRAC 73-22-P-3086-087 Stanley Pool, between Iseba and Nsele, Belgian Congo, coll. Mandeville, 28.x.1957; MRAC 73-22-P-3088-089 Stanley Pool, R. Nsele, coll. Mandeville, 29.x.1957; MRAC 73-22-P-3090 Stanley Pool, along the shores of M'Bamu archipelago, Belgian Congo, coll. Mandeville, 30.x.1947; MRAC 73-29-P-2115-2117 Mamfe, R. Cross, Cameroon, coll. Thys van den Audenaerde, 22.iv.1970; MRAC 73-29-P-2118 Nachtigal, Cameroon, coll. Thys van den Audenaerde, 12.v.1970; MRAC 75-21-P-8-9 Bangui, R. Ubangi, Central African Republic, coll. Voss, xii.1972; MRAC 76-32-P-2545 R. Malendo, Nigeria, coll. Clausen, 27.vii.1962; 76-32-P-2574 Troebro Syd for Keffi, Nigeria, coll. Clausen, 13.vii.1959; MRAC 79-1-P-4413 Lufira, Belgian Congo, coll. de Witte, 10-14.x.1947; MRAC 79-1-P-4414-4423 Mabwe, R. W. of L. Upemba, Belgian Congo, coll. de Witte, 19-1-1949; MRAC 79-2-P-276-277 Ba Foula Be, R. Gambie, Senegal, coll. K. U. L. exp., 2.i.1979; MRAC 79-36-P-17-19 Layo, Ebrié lagoon, Ivory Coast, coll. Thys van den Audenaerde, 20.x.1979; MRAC 80-19-P-199 Soubré, R. Sassandra close to bridge, Ivory Coast, coll. Teugels & Risch, 24-25.iv.1980; MRAC 80-56-P-29-30 Mako, R. Gambie, Senegal, coll. Lévêque & Paugy, iv.1980; MRAC 80-56-P-32 Koulountou, R. Koulountou,

Senegal, coll. Lévêque & Paugy, iv.1980; MRAC 82-13-P-632 Landja, R. Oubangui, Central African Republic, coll. De Vos & Kempeneers, 13.i.1982; MRAC 83-30-P-97 Elephantine island, Nile at Aswan, Egypt, coll. Van Neer & Lauwers, ix.1983; MRAC 83-30-P-98 Lake Nasser, Egypt coll. Van Neer & Lauwers, ix.1983; MRAC 85-29-P-506 Bac Sémien, R. Sassandra, Ivory Coast, coll. Teugels, iv.1985; MRAC 85-39-P-187-188 Tortiya, R. Bou, tributary of Bandama, Ivory Coast, coll. Teugels, 6-7.ix.1985; MRAC 85-39-P-189-191 R. Bandama, on the route between Niakaramandougou and Tortiya, Ivory Coast, coll. Teugels, 6-ix.1985; MRAC 85-55-P-309 R. Férédougouba (Bagbé) Ngolodougou on the way from Touba to Borotou, Ivory Coast, coll. Teugels, xii.1985; MRAC 86-10-P-73 Omoku market. R. Orashi, Nigeria, coll. Akiri, 13.xi.1985; MRAC 86-18-P-1265 Tai, Cavally, Ivory Coast, coll. Traore, 17.v.1986; MRAC 86-21-P-128 Inga, R. Zaire, Zaire, coll. Mutambwe Shango, xii.1985; MRAC 86-36-P-203 route between Niakaramandougou and Tortiya, R. Bandama, Ivory Coast, coll. Teugels, 27-28.viii.1986; MRAC 87-18-P-4225 R. Léraba, tributary Comoé at Le Léraba, border bridge at Burkina Faso, Ivory Coast, coll. Teugels, 29.1.1987; MRAC 87-18-P-4226 R. Maraoué, about 15 km from Mankono, on the track between Mankono and Séguela, Ivory Coast, coll. Teugels, 5.ii.1987; MRAC 87-18-P-5746 R. Bandama, on the track between Niakaramandougou and Tortiya, Ivory Coast, coll. Teugels, 28.i.1987; MNHN 1986-412 R. Oti at Sabari, Ghana, coll. Benech; MNHN 1986-674 R. Kolenté at Kolenté, Guinea, coll. Lévêque, 1986; MNHN 1986-675 R. Kaba at Kouloundala, Little Scarcies basin, Guinea, coll. Lévêque, 1986; MNHN 1986-676 R. Mafou, Niger basin, Guinea, coll. Lévêque, 1986; MNHN 1986-677 Boussoulé, R. Milo, Niger basin, Guinea, coll. Lévêque, 1986; MNHN 1987-692 San Pedro road to Sassandra, R. Méné, Ivory Coast, coll. Teugels, 1986; MNHN 1987-693 San Pedro, R. San Pedro, Ivory Coast, coll. Teugels, 1986; MNHN 1987-1141 Tai, R. Cavally, Ivory Coast, coll. Traore, 1986; MNHN unregistered R. Tinkisso (Niger basin) close to Dabola, Guinea, coll. Teugels, v.1987; BMNH 1899.6.28.27 Kasai district, Congo, coll. De Meuse; BMNH 1901.12.21.40 Monsembe, Upper Congo, coll. Weeks; BMNH 1901.12.21.64 Monsembe, Upper Congo, coll. Weeks; BMNH 1902.11.10.120-125 Agberi, Southern Nigeria, coll. Ansorge; BMNH 1907.12.2.1743 Luxor, Egypt, coll. Loat; BMNH 1907.12.2.1744-47 between Luxor and Aswan, Egypt, coll. Loat; BMNH 1907.12.2.1750 Aswan, Egypt, coll. Loat; BMNH 1907.12.2.1751-52 Kosheh, Nubia, coll. Loat; BMNH 1908.1.20.189 R. Ergino, Omo, coll. Zaphiro; BMNH 19007.26.7 R. Orah, Lagos, Nigeria, coll. Bruce; BMNH 1909.9.10.246 Stanley Falls, coll. Christy; BMNH 1921.9.6.52 Nyassa, coll. Wood; BMNH 1922.4.18.20 Mpanganye, R. Rufigi, Tanganyika Terr.; coll. Loveridge; BMNH 1923.3.2.33-34 R. Bandama, Ivory Coast, coll. Lowe; BMNH 1935.9.2.99 Goazo, Gold Coast, coll. Lowe; BMNH 1935.9.2.107-109 R. Appam, Gold Coast, coll. Lowe; BMNH 1971.6.23.14 Kigoma district, R. Luicke, Tanganyika, coll. Lockley, 1949; BMNH 1976.3.30.26 Ibara Market, Abeokuta, R. Ogun, Western Nigeria, coll. Sydenham, 1974; BMNH 1932.12.16.501 R. Loangwa, Zambezi system, coll. Pitman, holotype of *Clarias loanguensis*; ZMB 3072 Zambeze, Tette Boror, Mozambique, syntypes of *Heterobranchus laticeps*; AMNH 12356 Luluabourg, Kasai district, Belgian Congo, holotype of *Heterbranchus platycephalus*.

Heterobranchus isopterus

MRAC 141978 R. Comoé, Upper Volta, coll. Roman, 1963; MRAC 73-5-P-2961-962 Bouaké, R. Kan dam, Ivory Coast, coll. Thys van den Audenaerde, 8-9.vii.1966; MRAC 73-5-P-2963-964 Flampleu, R. Cavally, Ivory Coast, coll. Thys van den Audenaerde, 20-24.vii.1966; MRAC 73-5-P-2965 Sahibli, R. Cavally, Ivory Coast, coll. Thys van den Audenaerde, 29-30.vii.1966; MRAC 73-5-P-2966-3005 Toyebli, R. Nipoué, Ivory Coast, coll. Thys van den Audenaerde, 29.vii-3.vii.1966; MRAC 73.5.P-3006 Abokouamekro, Ivory Coast, coll. Thys van den Audenaerde, 18.vii.1966; MRAC 73-5-P-3007-3008 around Toulepleu, Ivory Coast, coll. Thys van den Audenaerde, vii.1966; MRAC 73-5-P-3009-013 Bakanou, forest brook at Bandama, Ivory Coast, coll. Thys van den Audenaerde, 3.ix.1966; MRAC 73-5-P-3014-17 & 3020 Dunkwa, R. Ofin, Ghana, coll. Thys van den Audenaerde, 21-22.ix.1966; MRAC 73-5-P-3018-3019 Abono, L. Bosumtwi, Ghana, coll. Thys van den Audenaerde, 13-19.ix.1966; MRAC 73-5-P-3023 Dotékopé, R. Mono, Togo, coll. Thys van den Audenaerde, x.1966; MRAC 73-8-P-124-125 Lamto, marigots, Ivory Coast, coll Van Mol. vii.1968; MRAC 73-8-P-126 R. Kan, near Dimbokro, Ivory Coast, coll. Van Mol, vii.1968; MRAC 73-9-P-61 Nuatja, Togo, coll. Verheyen, De Vree & De Roo, vii.1968; MRAC 73-10-P-4020-022 Guiglo, R. Nzo, near bridge, Ivory Coast, coll. Thys van den Audenaerde, x.1966; MRAC 73-10-P-4023 Sahibli, R. Cavally, Ivory Coast, coll. Thys van den Audenaerde, iii.1969; MRAC 73-10-P-4024 Toyebli, R. Cess, Ivory Coast, coll. Thys van den Audenaerde, iii.1969; MRAC 73-10-P-4025-029 Zoguiné, marigots of Cavally basin, Ivory Coast, coll. Thys van den Audenaerde, iii.1969; MRAC 73-10-P-4032-033 Majihun, bogs and marigots of tributary brook of R. Moa, Sierra Leone, coll. Thys van den Audenaerde, iv.1969; MRAC 73-10-P-4034 Bombo junction, bogs and marigots 16 km W. of Mano on Mano-Bomi-Hills route, Liberia, coll. Thys van den Audenaerde v.1969; MRAC 73-10-P-4035 Hartford, R. St. John, downstream of bridge and in first rapids, Liberia, coll. Thys van den Audenaerde, v.1969; MRAC 73-10-P-4036 Suakoko, Liberia, coll. Thys van den Audenaerde, v.1969; MRAC 73-11-P-729-731 & 734 Misahohe, Togo, coll. Verheyen, Hulselmans & Puylaert, vii.1969; MRAC 73-11-P-732 Fazao, Togo, coll. Verheyen, Hulselmans & Puylaert, viii.1969; MRAC 73-11-P-733 Alejo, Togo, coll. Verheyen, Hulselmans & Puylaert, iii.1969; MRAC 73-11-P-733 Alejo, Togo, coll. Verheyen, Hulselmans & Puylaert, iii.1969; MRAC 73-40-P-602 R. Ohumbe at Nguti, Cameroun, coll. Grimshaw, xi.1970; MRAC 76-32-P-2512-534 Lige S. for Anyaboni ved Volta, N. of Oterkpolu, Ghana, coll. Clausen, x.1965; MRAC 76-32-7-2537-540 Asin Sibiksu's sydlige indkorsel, Ghana, coll. Clausen, x.1965; MRAC 76-32-P-2541 Ca 10

miles fra Ho, Ghana, coll. Clausen, x.1965; MRAC 76-32-P-2542 4–5 miles from Tsito towards Asikuma, Ghana, coll. Clausen, x.1965; MRAC 76-32-P-2543 Sydlige indkorsel sit Atakpame, Togo, coll. Clausen; MRAC 76-32-P-2544 Andet Lille vandlob vest for Wegbe mod Ahenkro, Ghana, coll. Clausen, x.1965; MRAC 76-32-P-2599-601 between Kano and Jos plateau, Nigeria, coll. Clausen, 1960; MRAC 76-32-P-2535-536 Mellem Ichlio og I Werre, Nigeria, coll. Clausen; MRAC 79-36-P-15-16 Layo, Ebrie Lagoon, Ivory Coast, coll. Thys van den Audenaerde, x.1979; MRAC 80-19-P-198 Aghien lagoon at Aghien, Ivory Coast, coll. Risch & Teugels, iv.1980; MRAC 80-36-P-2037-040 Duzei, Cestos bekken, Liberia, coll. Louette & Rigaux; ii.1980; MRAC 80-36-P-2041-050 Cestos, S. of LTC, Liberia, coll. Louette & Rigaux, ii.1980; MRAC 80-36-P-2051 Senewehn, Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2052-054 & 2126 Cestos, S. of LTC, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2055 Sweke, Cavalla bekken Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2056-057 Tatuke, Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2058-060 & 2063-069 & 2098 Pahlwoken, Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2061-062 & 2099 Sweke, Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2079-097 Kleken, ?Cavalla bekken, Liberia, coll. Louette & Rigaux, iii. 1980; MRAC 80-36-P-2100-111 & 2112 Duo Town ?Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2113 Zleh Town, Cavalla bekken, Liberia, coll. Louette & Rigaux, iii.1980; MRAC 80-36-P-2114-119 Jusohn, Sangwin bekken, Liberia, coll. Louette & Rigaux, iv.1980; MRAC 80-36-P-2120-121 Dibli, Sangwin bekken, Liberia, coll. Louette & Rigaux, iv.1980; MRAC 80-36-P-2122 Jaudi, Sangwin bekken, Liberia, coll. Louette & Rigaux, iv.1980; MRAC 80-36-P-2123-125 Chesla, Sangwin bekken, Liberia, coll. Louette & Rigaux, iv.1980; MRAC 80-47-P-73 R. Bafing near Timbo, Guinea, coll. Lévêque & Paugy, v.1980; MRAC 80-56-P-26 near Macenta, R. Lofa, Guinea, coll. Lévêque & Paugy, v.1980; MRAC 80-56-P-27 Méné, R. Méné, Ivory Coast, coll. Paugy, xii.1979; MRAC 80-56-P-28 Djakoteti, R. Bouin, Ivory Coast, coll. Paugy, xii.1979; MRAC 81-19-P-22 near Mafere, tributary of Ehania, Ivory Coast, coll. De Bruyn & Couvreur, vii.1980; MRAC 85-29-P-507 Toyebli, R. Nipoué, Ivory Coast, coll. Teugels, iv.1985; MRAC 85-29-P-508 Babokon, R. Boubo, Ivory Coast, coll. Teugels, v.1985; MRAC 85-39-P-192-193 R. Bandama, on the route between Badikaha and Korhogo, Ivory Coast, coll. Teugels, viii.1985; MRAC 85-39-P-194-200 R. Bandama on the route between Niakaramandougou and Tortiya, Ivory Coast, coll. Teugels, vii.1985; MRAC 85-39-P-201 Bouaké, R. Kan, Bandama basin, Ivory Coast, coll. Teugels, ix.1985; MRAC 85-39-P-202-208 Tiebissou, R. Kan, Bandama Basin, Ivory Coast, coll. Teugels, ix.1985; MRAC 86-18-P-1260 Yakassé-Attobrou, R. Mé, Ivory Coast, coll. Traore, iv.1986; MRAC 86-18-P-1261-262 R. Mafou, tributary R. Mé at Yakassé Mé bridge, Ivory Coast, coll. Traore, iv.1986; MRAC 86-18-P-1263 Bianouan, R. Bia, Ivory Coast, coll. Traore, iv.1986; MRAC 86-18-P-1264 Koui, near Yaou, R. Bia, Ivory Coast, coll. Traore, iv.1986; MRAC 87-18-P-4227-231 R. Sassandra, near Bac Sémien, Ivory Coast, coll. Teugels, ii.1987; MRAC 87-18-P-4232 R. Kosua, tributary of R. Wawa near Dodi Papase, Ghana, coll. Teugels, ii.1987; MNHN 1982-944 R. Beffa à Vossa, Benin, coll. Paugy, 1981; MNHN 1985-187 R. Anié at Blitta, Togo, coll. Paugy, 1983; MNHN 1985-188 R. Aou at Aou-Losso, Togo, coll. Paugy, 1983; MNHN 1896-409 Amou-Oblo, Togo, coll. Benech, 1985; MNHN 1986-410 R. Na at Pouatao, Togo, coll. Benech, 1985; MNHN 1986-411 R. Wawa at Dodi Papase, Ghana, coll. Benech, 1985; MNHN 1986-348 R. Bafing at Dounet, Senegal basin, Guinea, coll. Lévêque & Paugy, 1980; MNHN 1986-672 R. Kakrima at Kasseri, Konkouré basin, Guinea, coll. Lévêque, 1986; MNHN 1986-673 R. Kaba at Kouloundala, Little Scarcies basin, Guinea, coll. Lévêque, 1986; MNHN 1987-1139 R. Bia at Koui, Ivory Coast, coll. Traore, 1986; MNHN 1987-1140, R. Nipoué at Gbinta, Ivory Coast, coll. Traore, 1986; MNHN unregistered R. Kaba at Kouloundala, Little Scarcies basin, Guinea, coll. Teugels, v.1987; MNHN unregistered Kolenté at Kolenté, Guinea, coll. Teugels, v.1987; MNHN unregistered Bafing at Sokotoro (Senegal basin), Guinea, coll. Teugels, v.1987; BMNH 1903.4.24.67 Infoan, R. Ofin, Ghana; BMNH 1908.4.24.68 Nyankoma, Gold Coast; BMNH 1912.2.15.20 R. Tano, Gold Coast, coll. Spurrell; BMNH 1912.9.26.3 west of Dunkwa, Gold Coast, coll. Spurrell; BMNH 1919.8.15.28 Gribingui, Shari, coll. Baudon; BMNH 1932.5.18.56-57 Tributary of R. Bagbwe, Sierra Leone, coll. Bates; BMNH 1934.8.31.129-132 Ashanti Forest, Wenchi, Gold Coast, coll. Lowe; BMNH 1935.9.2.110-111 Goazo, Gold Coast, coll. Lowe; BMNH 1936.11.24.41 R. Kaduna, Nigeria, coll. Welman; BMNH 1937.4.19.41-42 R. Kaduna, Nigeria, coll. Welman; BMNH 1947.11.19.1 R. Pra near Kumasi, Gold Coast; coll. Zool. Soc.; BMNH 1949.10.20.53 Senchi, Volta, Gold Coast, coll. Buxton; RMNH 2978 Dabokrom, Ghana; syntypes of *Heterobranchus macronema*.

Heterobranchus boulengeri

MRAC 72691 N'Kole, R. Luapula, Belgian Congo, coll. Miss. Pisc. Kat., 10.vii.1947; MRAC 83387 Kilwa, L. Mocro, Belgian Congo, coll. Miss. Pisc. Kat., 2.v.1947.