

Morphological and Osteological Evidence for the Generic Position of *Mormyrus kingsleyae* in the Genus *Brienomyrus* (Teleostei: Mormyridae)

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The Mormyridae have attracted widespread interest because they are capable of generating weak electric discharges for use in electrolocation and communication (Bullock and Heiligenberg, 1986). However, the systematics of this group are incompletely known, and the complexities are reflected in a high degree of taxonomic instability. *Pollimyrus kingsleyae* (Günther, 1896) is a historically important, valid species; but its identification, classification, and biogeography have been problematic. It was described from a single specimen collected by M. H. Kingsley from the locality "Old Calabar" (approximately 4°58'N, 8°19'E), currently known as the mouth of the Cross River basin in Nigeria. As part of a series of systematic and neuroethological studies of the Mormyridae, we have reexamined the generic placement of this species.

In a revision of the Mormyridae, Boulenger (1898) transferred this species from *Mormyrus*, where it was originally placed by Günther (1896) to *Marcusenius* Gill, 1862, without comment. Following his identification key, this placement was based upon the position of the mouth, which is terminal in *Mormyrus* and inferior or subinferior in *Marcusenius*.

In 1901, Pellegrin reported *P. kingsleyae* from the lower Ogowe River in the French Congo (present Gabon). Boulenger (1909), in the *Catalogue of the Fresh-Water Fishes of Africa*, presented a detailed description of the species based on the holotype and on additional specimens collected in the Kribi and Ja Rivers in Cameroon, the Benito River in Spanish Guinea (present Equatorial Guinea), and the marshes of Kop-Malafu in the Mayombe (Congo-Brazzaville).

Pollimyrus kingsleyae was mentioned subsequently by several authors, but its distribution range remained the same as that given by Boulenger (1909), namely from Old Calabar to the Mayombe. A reference by Holly (1928) reporting this species from the Chari River (Chad basin) was based on an erroneous identification. In 1970, Daget and De Rham reported an important range extension based on specimens from the Ivory Coast, but later Bigorne (1990a) defined a new subspecies, *P. kingsleyae eburneensis*, based on this population.

The genus *Pollimyrus* was established by Taverne (1971) on the basis of a detailed osteolog-

ical study of the Mormyridae. *Pollimyrus isidori* (Valenciennes, 1846) was taken as the type species, and *Marcusenius kingsleyae* (Günther, 1896) was transferred to *Pollimyrus*. Finally, Mamonekene and Teugels (1993) questioned the generic assignment of *P. kingsleyae* and suggested that it should be placed in *Brienomyrus* Taverne, 1971.

Recently, Alves-Gomes and Hopkins (1997) did a partial phylogenetic survey of the Mormyridae, using molecular sequence data derived from mitochondrial DNA, and reported on five undescribed species of *Brienomyrus* from Gabon, which form a monophyletic assemblage. These five species are very similar in external morphology to *P. kingsleyae*; they each have dorsal and anal fins of approximately equal length, an elongated body, a subterminal mouth, and a well-developed submental swelling. We shall refer to this group as the "*kingsleyae*" complex of *Brienomyrus*. We are tempted to reassign *P. kingsleyae* to *Brienomyrus* without further discussion; but because of the confusion surrounding the distinction between these two genera, we support our conclusions with specific morphological and osteological characters. Descriptions of these five new species are currently underway.

MATERIALS AND METHODS

We used radiographs to examine type material, cleared-and-double-stained material to examine skeletons (Taylor and Van Dyke, 1985), light microscopy to examine sectioned material from electric organs (Alves-Gomes and Hopkins, 1997), and digital electrical recording methods to study waveforms of electric organ discharges from live specimens (Hopkins, 1995; Alves-Gomes and Hopkins, 1997). The material examined is listed below. Institutional abbreviations are those listed in Leviton et al. (1985).

RESULTS AND DISCUSSION

Although the type locality of this species is listed as Old Calabar, no additional specimens have ever been found there since Kingsley's "temporary stay" from January until May 1895. This is in spite of extensive collections from the Cross River (Teugels et al., 1992) and the neigh-

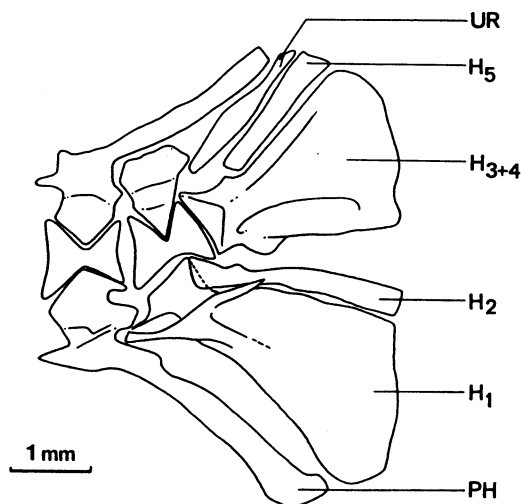


Fig. 1. Caudal skeleton in the holotype of *Mormyrus kingsleyae* Günther, 1896. PH, parhypural; H, hypural; UR epural.

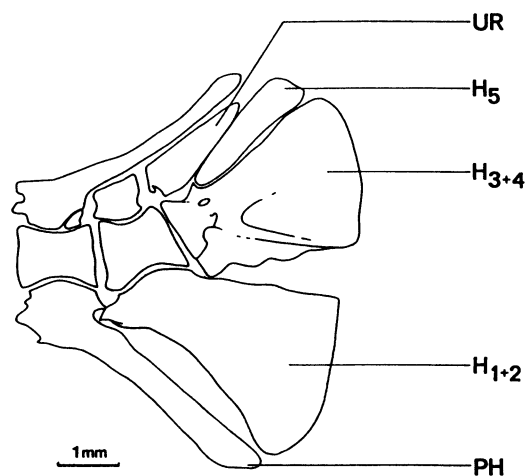


Fig. 2. Caudal skeleton in a specimen of *Pollimyrus isidori* (MRAC 92-72-P-164). PH, parhypural; H, hypural; UR epural.

boring Niger Delta (G. G. Teugels and C. B. Powell, unpubl.). Interestingly, Kingsley traveled to Gabon after her stay in Old Calabar (Kingsley, 1897) and, while in Gabon, made extensive collections in the Ogowe River, where specimens from the above-mentioned *kingsleyae* complex of species are abundant (Alves-Gomes and Hopkins, 1997). We suspect that the holotype of *P. kingsleyae* may have been collected from the Ogowe River rather than from Old Calabar.

A comparison of the generic description of *Brienomyrus* and *Pollimyrus* (Taverne, 1971) reveals two major osteological differences. In *Brienomyrus*, hypurals 1 and 2 are unfused, and the skull lacks a lateral ethmoid bone; whereas in *Pollimyrus*, hypurals 1 and 2 are fused, and the lateral ethmoid is present, although often reduced. Taverne (1971, fig. 68) illustrated the caudal skeleton in *Brienomyrus* for specimens of *B. brachyistius* (Gill, 1862), the type species for the genus. We describe the caudal skeleton as having one parhypural plus four hypurals [P, H1, H2, H3 + H4 (fused), and H5]. Taverne (1971) erroneously counted the parhypural as the first hypural; thus, his counts are invariably one greater than ours. For the caudal skeleton in *Pollimyrus*, Taverne (1971, fig. 78) described the condition seen in *P. tumifrons* (Boulenger, 1902) as having four distinct bones: one, that we again identify as the parhypural, a fused H1 + H2, a fused H3 + H4, and H5.

We have studied radiographs of the holotype of *P. kingsleyae*. Shown in Figure 1, H1 and H2 are separated (not fused); thus, there are four distinct hypural bones present in addition to

the parhypural. This corresponds to the (emended) condition for *Brienomyrus*. We find the same condition in the five undescribed species of *Brienomyrus* in the *kingsleyae* complex, referred to in Alves-Gomes and Hopkins (1997) as *Brienomyrus* sp. 1, 2, 3, 4, and 5. We also studied, using radiographs, the caudal skeleton of type specimens of the following nominal *Brienomyrus* species and also find H1 and H2 to be unfused in the following specimens: the holotypes of *B. curvifrons* Taverne et al., 1977; *B. hopkinsi* Taverne et al., 1985; *B. longicaudatus* Taverne et al., 1977; *Mormyrus microcephalus* Günther, 1867 (synonymous with *B. brachyistius* according to Boulenger, 1898), *B. sphecodes* (Sauvage, 1879); two syntypes of *Marcusenius cabrae* Boulenger, 1900 (synonymous with *Mormyrus kingsleyae* according to Boulenger, 1912); and one of the two syntypes of *B. longianalis* (Boulenger, 1901). In the second syntype of *B. longianalis* and in the holotype of *B. niger* (Günther, 1866), H1 and H2 are partly fused at the distal end although they can still be recognized individually. Examination of additional nontype material confirms that in *Brienomyrus* the caudal skeleton is usually comprised of four distinct hypurals but that occasionally H1 and H2 are partly fused. The holotype of *B. brachyistius* is damaged, and the caudal bones are no longer present. By contrast, in all *Pollimyrus* specimens examined, hypurals H1 and H2 are always completely fused (Fig. 2), corresponding to the ancestral condition in mormyrids as seen in *Petrocephalus* Marcusen, 1854, the most primitive of the Mormyridae (Taverne, 1971).

In all *Brienomyrus* specimens examined in

cleared-and-double-stained material, the lateral ethmoid bone is lacking, as reported by Taverne (1971). This material includes *B. brachyistius*, *B. curvifrons*, *B. hopkinsi*, *B. longicaudatus*, *B. niger*, and the five undescribed species in the *kingsleyae* complex reported by Alves-Gomes and Hopkins (1997; see our list of material examined). Because of its type status, the condition of this character in the holotype of *P. kingsleyae* could not be verified. In all *Pollimyrus* specimens we studied, including *P. isidori*, *P. marchei*, *P. adspersus*, and *P. petricolus*, a small lateral ethmoid is present, corresponding to the condition illustrated by Taverne (1971, figs. 70–71). The presence of a lateral ethmoid in mormyrids is also considered as the ancestral condition and is present in *Petrocephalus* (Taverne, 1971).

Electric organs and electric organ discharges (EODs) have proven useful in systematic work with mormyrids, both for the recognition of new species (Crawford and Hopkins, 1989) and for studies of phylogeny (Bass, 1986; Alves-Gomes and Hopkins, 1997). However, we could not directly examine the morphology of the electric organ of the holotype of *M. kingsleyae* without damaging the specimen, and we have been unable to obtain any additional specimens from the type locality. At the present time, we are obliged to use indirect evidence when using EODs and electric organs for generic classification of this species, in particular that coming from the five undescribed species in the *kingsleyae* complex, referred to by Alves-Gomes and Hopkins (1997).

First, we compared the electric organs and EODs of four species of *Pollimyrus* to define some of the variation in morphology for this genus. Three species have electric organs with electrocytes with double penetrating and nonpenetrating stalks [Type DPNP in Bass (1986) and in Hopkins (1995), see Fig. 3A1]. These include *P. isidori* (Valenciennes, 1846), the type species, *P. adspersus* (Günther, 1866), and *P. petricolus* (Daget, 1954). One species, *P. marchei* (Sauvage, 1879), has electrocytes with nonpenetrating stalks [Type NPP in Hopkins (1995), see Fig. 3B1].

The EOD waveforms of these four species of *Pollimyrus*, although species typical, showed considerable variation within this genus. *Pollimyrus marchei* has a simple biphasic EOD with an initial head positive phase followed by a larger head negative phase (Fig. 3B2). *Pollimyrus isidori* has a similar biphasic waveform, which is preceded by an early head-positive prepulse (Fig. 3A2). *Pollimyrus adspersus*, erroneously identified as *P. isidori* in earlier papers by Crawford (1992) and Kramer (1990), has a bi- or triphasic EOD

depending on the sex (not shown; see Kramer, 1990; Crawford, 1992) and *P. petricolus* has a four-phase waveform with an initial head negativity (Fig. 3A3).

Second, we examined the electric organs of 10 species of *Brienomyrus* to describe the variation within this genus. Four species had electrocytes with nonpenetrating stalks innervated on the posterior side (Type Npp, Fig. 3B1). These include *B. longicaudatus*, *B. curvifrons*, *B. hopkinsi* (see Bass, 1986) and *Brienomyrus* sp. 4 (see Alves-Gomes and Hopkins, 1997). The EODs of these species were all biphasic discharges with initial head positivity as shown in Figure 3B3 (see Bass, 1986; Alves-Gomes and Hopkins, 1997).

Two *Brienomyrus* species had electrocytes with double-penetrating stalks with posterior innervation (Type DPP; Fig. 3C1). This morphology was first described by Alves-Gomes and Hopkins (1997). It is very similar to a morphology where the stalks are penetrating with anterior innervation (Type Pa); but with DPP electrocytes, the enlarged innervated end of the stalk system lies on the posterior side of the electrocyte rather than on the anterior side. This morphology is found in *B. brachyistius* and in *B. niger* (Günther, 1866). The EODs of these two species are triphasic, with an initial head-negative peak followed by a large head-positive peak, followed by a final head-negative peak (Fig. 3C2–3).

Finally, from the five undescribed *Brienomyrus* species in the *kingsleyae* complex, four species possess electrocytes with penetrating stalks with anterior innervation (Type Pa, Fig. 3D1–2). All four have discharges with three phases beginning with a head negative phase (which may be visible only at high gain, as shown in the expanded trace in Fig. 3D2).

Thus, we find three different types of electric organs among the *Brienomyrus* so far examined, NPP, Pa, and DPP, whereas we find two types of electric organs among the *Pollimyrus*, DPNP and NPP. In spite of the diversity of electrocyte morphology, the character is inconclusive and does not resolve the generic placement of *P. kingsleyae*. It is possible that *P. kingsleyae* could have NPP electrocytes, and unfortunately this would be consistent with its classification in either of the two genera.

Günther (1896) does not mention the presence of a submental swelling in the holotype of *P. kingsleyae*, and Taverne (1971) repeats Günther's description. Upon examination of the holotype, however, we noticed that the fleshy submental protuberance is present but damaged probably because of poor preservation. The submental swelling is reduced or lacking in all species of *Pollimyrus*, except for *P. petricolus*. By

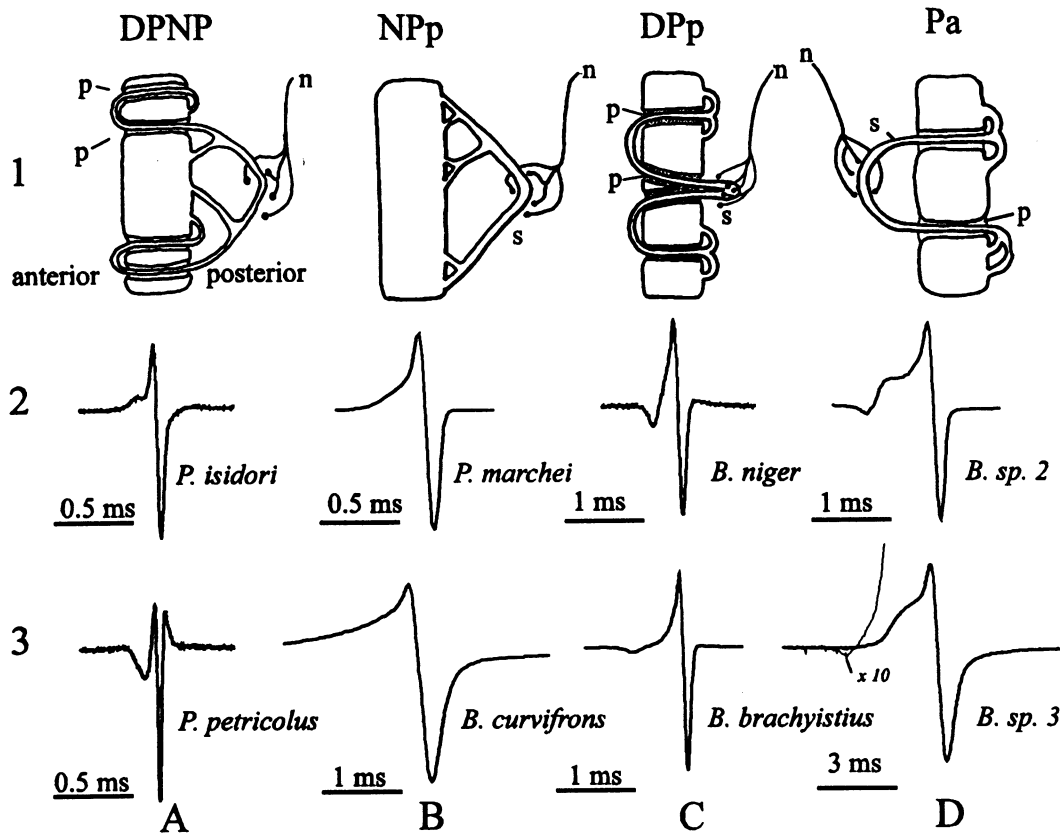


Fig. 3. Row 1: Diagrammatic sagittal cross-section of single electrocytes from electric organs of several mormyrids where the anterior surface (ant.) is always to the left and the posterior surface (post.) is to the right. The nerve, n, stalks system, s, and penetrations, p, are shown with labels. Type DPNP have doubly penetrating stalks and nonpenetrating stalks. Type NPp have nonpenetrating stalks with posterior innervation. Type DPp have doubly penetrating stalks with posterior innervation. Type Pa have penetrating stalks with anterior innervation. Rows 2 and 3: Electric organ discharge (EOD) waveforms from selected species illustrating the anatomical subtype listed in row 1. The EOD for *Brienomyrus* sp. 3 (D3) is shown both at normal and expanded ($\times 10$) gains. Time base in milliseconds. Head positivity is upward in all traces.

contrast, all the specimens of 10 species of *Brienomyrus* examined have a well-developed submental swelling. It is likely that the absence of a submental swelling represents the primitive condition in mormyrids, typical of *Petrocephalus* (see Taverne, 1971).

All the species of *Pollimyrus* are deep bodied. For *P. isidori*, *P. adspersus*, and *P. marchei*, the ratio of standard length/body depth ranges from 2.7–4.2. In 10 species of *Brienomyrus* that we examined, this ratio ranged from 4.4–6.8. Only *B. niger* had a lower ratio (2.9–4.3; holotype 3.7), and for this reason, *B. niger* is placed in a separate subgenus (Taverne, 1971). The holotype of *P. kingsleyae* has a ratio of 4.7, representing an elongate body form, typical of *Brienomyrus*. The primitive condition for this character in mormyrids (Taverne, 1971) is a low value as is

found in *Petrocephalus* (2.6–4.0 after Bigorne, 1990b).

To summarize, we have examined the generic placement of *P. kingsleyae* using five characters (hypurals 1 and 2 unfused, absence of a lateral ethmoid, presence of Pa type electrocytes, presence of submental swelling and elongate body). On the basis of four of them, we conclude that *P. kingsleyae* should be reassigned to the genus *Brienomyrus*.

MATERIAL EXAMINED

Brienomyrus brachyistius: USNM 4098; holotype, probably from Liberia (89.7 mm Standard Length). BMNH 1867.5.22.6; holotype of *Mormyrus microcephalus*, Ogowe River (Gabon), R. B. N. Walker (161 mm SL). MRAC 90-57-P-2846:

cleared-and-stained specimen, Ngoumbi River, tributary of Kouilou River (Congo-Brazzaville), L. De Vos, J. Snoeks, and G. G. Teugels (83.8 mm SL). CU 77303, cleared-and-stained specimen, aquarium trade specimen presumed from Nigeria (114 mm SL). *Brienomyrus curvifrons*: MRAC 75-24-P-132; holotype, Ivindo River near M'Passa, Makokou (Gabon), A. Heymer (106.6 mm SL). CU 77300 (89 mm SL), CU 77301 (124 mm SL), cleared-and-stained specimens, Gabon, Ivindo River, near Makokou (Gabon), C. D. Hopkins. *Brienomyrus hopkinsi*: MRAC 84-34-P-10; holotype, Makokou, Ivindo River (Gabon), C. D. Hopkins (66.5 mm SL). *Brienomyrus kingsleyae*: BMNH 1896.5.5.10; holotype, Old Calabar (Nigeria), M. H. Kingsley (92.9 mm SL). MRAC 274-275; syntypes of *Marcusenius cabrae*, Marshes of Kop-Malafu, Mayombe (Congo-Brazzaville), Cabra (87-117.7 mm SL). *Brienomyrus longianalis*: BMNH 1901.1.28.5-6; syntypes, Sabelle Station, at the junction of the Ethiops and Jamieson Rivers (Nigeria), W. J. Ansorge (126.5-136.9 mm SL). *Brienomyrus longicaudatus*: MRAC 75-24-P-290; holotype, Ivindo River near M'Passa, Makokou (Gabon), A. Heymer (111.8 mm SL). CU 77302 (106 mm SL) and CU 77303 (117 mm SL), cleared-and-stained specimens, Ivindo River near Makokou (Gabon), C. D. Hopkins and J. D. Crawford. *Brienomyrus niger*: BMNH 1862.5.20.5; holotype, Gambia, J. T. Dalton (166.5 mm SL). CU 77310; cleared-and-stained specimen, aquarium trade specimen presumed from Nigeria (tail missing). *Brienomyrus sphaecodes*: MNHN A.893; holotype, Doume, Ogowe River (Gabon), P. De Brazza (113.9 mm SL). *Brienomyrus* species 1: CU 77319 (100 mm SL, field no. 85-252), Ivindo River near Makokou (Gabon), C. D. Hopkins and J. D. Crawford. *Brienomyrus* species 2: CU 77305 (75 mm SL), CU 77306 (64 mm SL), CU 77307 (83 mm SL); cleared-and-stained specimens, Ivindo drainage, Balé Creek near Makokou (Gabon), C. D. Hopkins. *Brienomyrus* species 3: CU 77308 (76.8 mm SL), CU 77309 (88.7 mm SL); cleared-and-stained specimens, Ivindo River drainage, Balé Creek near Makokou (Gabon), C. D. Hopkins. *Brienomyrus* species 4: CU 77308 (76.8 mm SL, field no. 1073), CU 77309 (88.7 mm SL, field no. 1076), Leoui Creek, Ogooué River drainage, near Oyou village, Gabon, C. D. Hopkins, and M. A. Friedman. *Brienomyrus* sp. 5: CU 77317 (58.9 mm SL, field no. 1106a), CU 77318 (63.9 mm SL, field no. 1106b) Ogooué River drainage near Franceville; C. D. Hopkins and M. A. Friedman. Additional unidentified *Brienomyrus*: MRAC 91-68-P-24; cleared-and-stained specimen, Voulou River, tributary of Loukoula River (Congo), V. Ma-

monekene and G. G. Teugels (65.4 mm SL). MRAC 90-57-P-2833; cleared-and-stained specimen, Ngoumbi River, tributary of Kouilou River (Congo-Brazzaville), L. De Vos, J. Snoeks, and G. G. Teugels (mm SL). MRAC 94-50-P-70-72; cleared-and-stained specimens, Ivindo drainage, IRET (Gabon), C. D. Hopkins and J. D. Crawford. *Pollimyrus isidori*: MRAC 92-72-P-164; cleared-and-stained specimens, Powei Creek, Niger delta (Nigeria), C. B. Powell (60.8 mm SL). CU 77297 (53.9 and 58.2 mm SL), Lac de Guiers, Senegal, C. D. Hopkins. *Pollimyrus petricolus*, CU 77298, (66 mm SL, field no. 1305), Niger River near Batamani, C. D. Hopkins, P. Jacob, V. Bénech, R. Bigorne. *Pollimyrus adspersus*, CU 77296 (74 mm SL and 77 mm SL) from the aquarium trade and presumed to come from Nigeria, C. D. Hopkins. *Pollimyrus marchei*, CU 77294 (94 mm SL, field no. 85-155), Loa Loa Rapids, Ivindo River near Makokou, Gabon, C. D. Hopkins, and J. D. Crawford.

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