

First Report on the Karyotype of the Freshwater Weakly Electric Fish; *Marcusenius brucii* (Osteoglossiformes: Mormyridae) in Asejire Reservoir, Osun River Basin, Nigeria

Jegede, O. I

Department of Fisheries and Aquaculture, Adamawa State University, Mubi, Nigeria

*E-mail of the corresponding author: jegede264@adsu.edu.ng

Abstract

The weakly electric fishes of the family Mormyridae are one of the dominant fish groups in Africa; they are represented in all the major freshwater bodies in the tropical regions of the continent, except the Southernmost Cape Provinces, the Sahara and the Northernmost Maghreb. The Mormyridae boasts 225 species in 22 genera, making it the most speciose Osteoglossiformes family. Such great diversity requires many systematics approaches for good comprehension; to this end, cytogenetics provides valuable data for a better definition of this diversity. However, cytogenetics data on mormyrids are still scarce, thus limiting its usefulness in the biodiversity study of the group. In this study, the chromosome composition of a mormyrid species, *Marcusenius brucii*, was investigated to reveal its chromosome number and standard karyotype for the first time; to enhance the understanding of the karyotype organization of the group. The fish was sourced from a local fisherman in Asejire Reservoir, Osun River Basin, Nigeria. Metaphase chromosomes were prepared from the fish kidney after *in vivo* injection with 0.05% colchicine solution. Slide preparation and karyotyping followed conventional cytogenetics techniques. The study showed that *M. brucii* karyotype consists of a diploid number of $2n = 50$ dominated by two-armed chromosomes. While the chromosome number is in harmony with the general chromosome number in the order Osteoglossiformes and the hypothetical diploid number for the family Mormyridae, it differed mainly in its possession of bi-armed elements. The phylogeny of *Marcusenius* is yet to be resolved; this, coupled with the limited karyotyped individuals in the genus, makes the karyotype evolution of the genus difficult to infer. This scenario will improve as the cytogenetics knowledge of the genus increases.

Keywords: Cytogenetics, chromosomes elephantfishes, karyotype, mormyrids, Osteoglossiformes

DOI: 10.7176/JNSR/13-18-03

Publication date: October 31st 2022

Introduction

Mormyrids, also known as elephantfishes, is a large and highly diverse group of fish endemic to the tropical African freshwaters; they are absent only in the Cape Provinces, the Sahara, and the Northernmost Maghreb (Roberts, 1975). The family Mormyridae consists of about 225 species distributed in 22 genera, making it the most speciose Osteoglossiformes family (Froese & Pauly, 2022; Fricke *et al.*, 2022). Mormyrids provide a means of livelihood and cheap, high-quality animal protein for many African Riverine dwellers; some others, such as *Gnathonemus*, harbour species of global interest due to their value in the international aquarium trade (Kuřiková, 2015). Mormyrids and their relative; *Gymnarchus niloticus*, are also well-known for possessing electrical organs that generate weak electrical discharges and perceive similar electrical signals from other fishes (Lissmann & Machin, 1958; Hopkins *et al.*, 2007; Lavoué *et al.*, 2012). Most mormyrids are nocturnally active, reside in dark, turbid waters, and possess small eyes; they rely on the electric organs to locate food and prey, recognize mates, communicate among conspecifics, and for social interaction (Arnegard & Carlson, 2005; Hopkins *et al.*, 2007; Sullivan *et al.*, 2016). In addition, the electric organ discharge system is species and sex-specific and plays a vital role in discovering cryptic species, species identification, evolution, phylogeny, and classification of the group (Hopkins *et al.*, 2007; von der Emde *et al.*, 2008; Kramer & Wink 2013; Sullivan *et al.*, 2016; Lamanna *et al.*, 2016).

The genus *Marcusenius* is characterized by an elongate and laterally flattened body with a poorly developed snout. Its superior mouth bears a few teeth and a slightly projected lower jaw to which a short cylindrical-like fleshy appendix is attached (Bigorne, 2003). The genus exhibits a high variation in body size; some species, such as *M. greshoffii*, *M. cuangoanus*, and *M. angolensis*, are less than 15 cm, while *M. devosi* reaches a length of about 120 cm (Froese & Pauly, 2022). Boden *et al.* (1997) documented more diagnostic features of the genus. *Marcusenius* and *Petrocephalus* are the largest Mormyridae genera, each constituting 46 species, with probably more species yet to be discovered (Kramer & Wink 2013). In addition to their great diversity, *Pollimyrus*, *Brienomyrus*, and *Marcusenius* have been recovered as polyphyletic (Lavoué *et al.*, 2000; Hilton & Lavoué, 2018); this necessitates a robust approach to their systematics. To this end, morphological, osteological, and analysis of their electric organ discharge system have played significant roles in the redefinition of the phylogeny of the genera using improved morphological and other systematic procedures (Hopkins *et al.*, 2007;

Hilton, 2003; Sullivan *et al.*, 2016; Hilton & Lavoué, 2018). Karyotype analysis provides an additional systematic tool for discovering biodiversity, species characterization, and taxonomy. (reviewed in Cioffi *et al.*, 2018; Paula *et al.*, 2022)

The application of molecular cytogenetics techniques to the study of biodiversity is receiving considerable attention and has enhanced the understanding of the phylogeny and evolution of many biological entities (Krysanov & Demidova, 2018; Kretschmer *et al.*, 2021; de Souza *et al.*, 2022; Machado *et al.*, 2022). However, compared to its enormous diversity, cytogenetics information on Mormyridae is still scarce and available on less than 10% of the 225 valid species (Simanovsky *et al.*, 2021a). Furthermore, in the genera for which karyotype data have been documented, few species have been studied, thus limiting intra-genetic comparison. For example, out of the 46 *Marcusenius* species, karyotype data have been provided for only two species: *M. moorii* and *M. cyprinoides* (Ozouf-Costaz *et al.*, 2015; Simanovsky *et al.*, 2020).

In Nigeria, *Marcusenius* is represented by five species: *M. abadii*, *M. brucii*, *M. cyprinoides*, *M. kanji*, and *M. senegalensis* (Bigorne, 2003; Froese & Pauly, 2022). *M. brucii* is meristically similar to *M. senegalensis*, but the two species differ morphologically and in their distribution area. While *M. brucii* is restricted to the forest region and occurs in River Mono in Togo and Ogun and Osun Rivers in Nigeria; *M. senegalensis*, on the other hand, is not found in the forest zones; but is distributed in the Gambia, Senegal, Niger, Chad, Sassandra, Volta basins and in the basins of all large Sudanian and North-Guinean zones (Roberts, 1975; Bigorne, 2003; Froese & Pauly, 2022). This study provides the first report on the cytogenetics of *M. brucii* to increase the understanding of Mormyridae chromosome organization.

Materials and methods

Sample Collection and Metaphase Chromosomes Preparation

Ten samples of *Marcusenius brucii* (Figure 1) were purchased from a fisherman in Asejire Reservoir, Osun River Basin; the Osun River is about 270 km long and flows through the forest belt of western Nigeria to the Lagos Lagoon complex (Anifowose *et al.*, 2019). After collection, the fish was transported in an aerated plastic container to a private facility for acclimatization; but the laboratory procedure was done at the Department of Zoology, Obafemi Awolowo, University, Ile-Ife. At the expiration of the acclimatization period, the fish was injected *in vivo* with a yeast suspension to stimulate mitosis (Bertolo *et al.*, 2015); this was followed by another *in vivo* injection with 0.05% colchicine solution at the rate of 0.01 mg⁻¹ fish mass. Then, the fish was, euthanized 24 hrs. later, the kidney was removed, teased out in a petri dish containing 5ml of 0.56% KCl solution, and kept for about 30 minutes at an ambient temperature of about 35^o C. Potassium chloride solution is hypotonic and causes cells to be turgid thus enhancing chromosome dispersal. Afterwards, the kidney tissue remnants were discarded, and the suspension was homogenized and centrifuged to obtain cell precipitates. The precipitates were washed thrice in 3: 1 methanol: acetic acid fixative; after the last centrifugation, the precipitated cells were re-suspended in 1 ml of the fixative.

Slide Preparation and Karyotyping

Slide preparation followed Bertollo *et al.* (2015). One or two drops of the chromosome preparation were placed on different parts of a pre-cleaned slide and dried on a slide warmer. Giemsa staining was in 6% Giemsa solution for 20 minutes; excess stains were washed under a running tap and air-dried. The slides were examined under a microscope to detect metaphases. Good ones were further examined at a magnification of 100 X under immersion oil, and the images of metaphase chromosomes were captured with a GALEN™ professional photomicroscope, Model BA 120. The chromosomes were arranged into metacentrics, submetacentrics, and acrocentrics (Terminal point [T], Terminal region [t], and subterminal region [st] as acrocentrics [a]). Position of the centromere, chromosome classification, and nomenclature was, according to Levan *et al.* (1964). Within each group, homologous chromosomes were paired according to the size and position of the centromere.



Figure 1. *Marcusenius brucii* from Asejire Reservoir, Osun River Basin, Nigeria

Results

Metaphases were obtained from three specimens of *M. brucii*. The modal chromosome number from 29 metaphases was $2n = 50$ (Figure 2). Chromosomes 1 to 13 were metacentrics showing slight gradation in size. The largest chromosomes (14 to 16) were submetacentrics, while the acrocentrics were represented by chromosomes 17 to 25, of which chromosomes 17 to 19 were large, 20 to 23, and 24 and 25 were medium and small chromosomes, respectively (Figure 3). Details of chromosome arm measurements and chromosome nomenclature are presented in Table 1

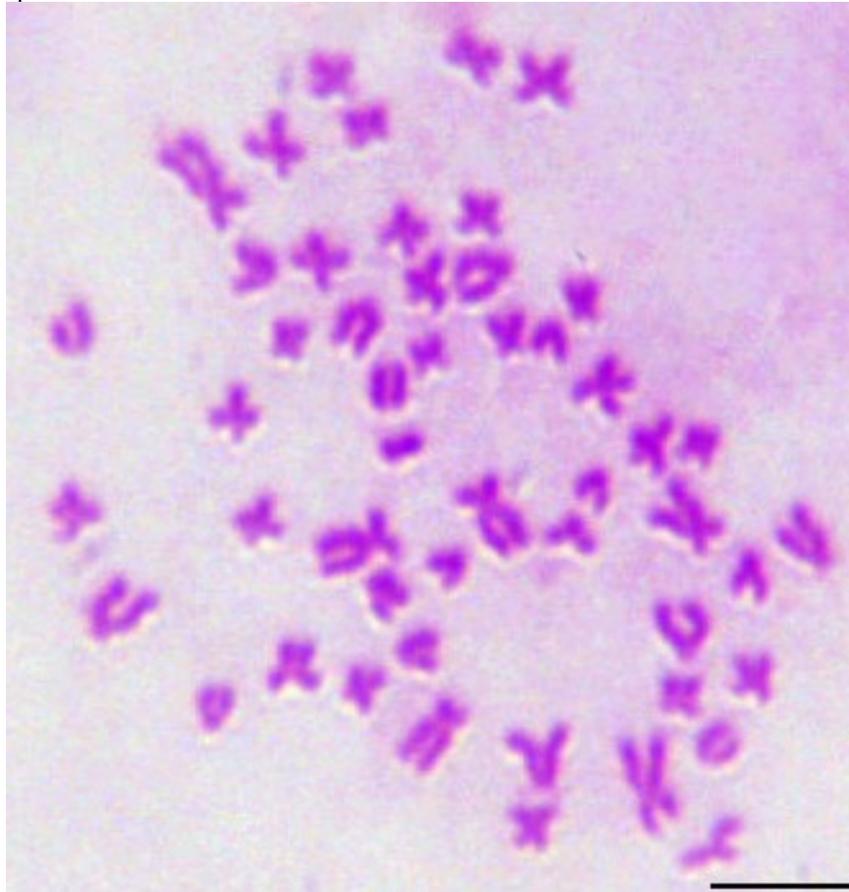


Figure 2. Metaphase Chromosome of *Marcusenius brucii* in Asejire Rsevoir, Osun River Basin, Nigeria. $2n = 50$, Bar = 5μ

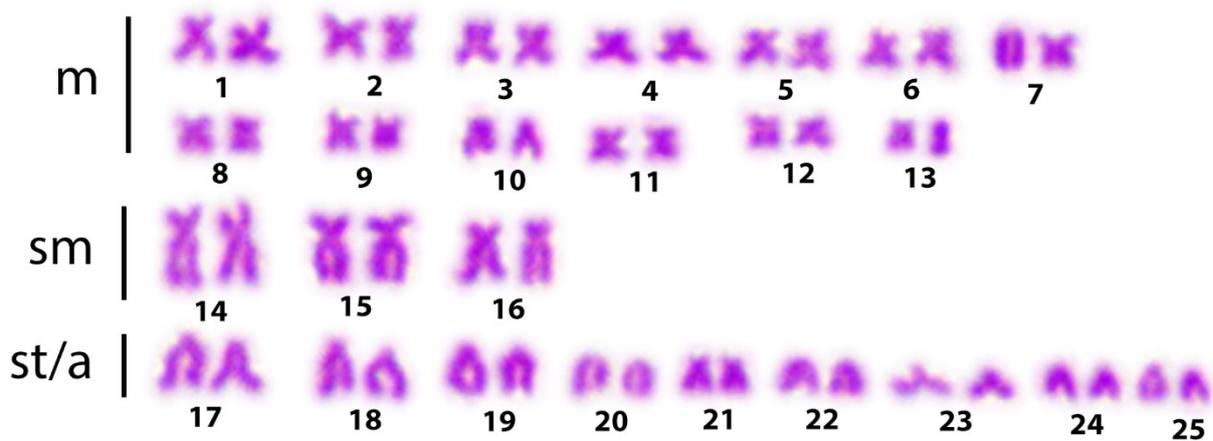


Figure 3. Karyogram of *Marcusenius brucii* in Asejire Reservoir, Osun River Basin, Nigeria. Karyotype formula = $2n = 50$ ($26m+6sm+18st/a$), FN = 82. Bar = 5μ

Table 1. Chromosome arm measurements, centromeric positions, and chromosome nomenclature of *Marcuseinius brucii* from Asejire Reservoir, Osun River Basin, Nigeria.

Sn.	p(px)	q (px)	cl	r	d	ci	tcp	cn
1	13.25	14.46	27.71	1.09	0.44	47.82	2.30	m
2	12.06	14.62	26.68	1.21	0.96	45.20	2.21	m
3	12.01	12.58	24.59	1.05	0.23	48.84	2.04	m
4	10.35	12.79	23.14	1.24	1.05	44.73	1.92	m
5	9.49	13.53	23.02	1.43	1.75	41.23	1.91	m
6	10.28	12.50	22.78	1.22	0.97	45.13	1.89	m
7	10.53	11.35	21.88	1.08	0.37	48.13	1.81	m
8	9.89	11.44	21.33	1.16	0.73	46.37	1.77	m
9	9.41	11.82	21.23	1.26	1.14	44.32	1.76	m
10	9.99	10.94	20.93	1.10	0.45	47.73	1.73	m
11	9.59	11.19	20.78	1.17	0.77	46.15	1.72	m
12	8.84	11.20	20.04	1.27	1.18	44.11	1.66	m
13	9.56	10.04	19.60	1.05	0.24	48.78	1.63	m
14	14.26	26.84	41.10	1.88	3.06	34.70	3.41	sm
15	13.82	24.93	38.75	1.80	2.87	35.66	3.22	sm
16	11.08	23.11	34.19	2.09	3.52	32.41	2.83	sm
17	5.03	23.35	28.38	4.64	6.46	17.72	2.35	a
18	3.56	24.43	27.99	6.86	7.46	12.72	2.32	a
19	3.39	23.11	26.50	6.82	7.44	12.79	2.20	a
20	4.72	15.63	20.35	3.31	5.36	23.19	1.68	a
21	0.00	20.25	20.25	∞	10.00	0.00	1.68	a
22	4.43	15.35	19.78	3.47	5.52	22.40	1.64	a
23	1.96	17.76	19.72	9.06	8.01	9.94	1.64	a
24	0.83	16.76	17.59	20.19	9.06	4.72	1.46	a
25	1.67	15.41	17.08	9.23	8.04	9.78	1.42	a

*p = short arm length, q = long arm length, cl = p + q, $d = \left(\frac{q}{cl} - \frac{p}{cl}\right) 10$, $r = \frac{q}{p}$, $ci = (p/cl)100$, tcp = total chromosome percent (cl/778.92)100, cn = centromeric nomenclature, m = metacentric, sm = submetacentric, a = acrocentric, px = pixels.

Discussion

The diploid chromosome number of *M. brucii* is $2n = 50$; the number is in harmony with $2n = 48-50$, postulated as the ancestral chromosome number for the order Osteoglossiformes; being recorded in its largest three families: Osteoglossidae, Notopteridae and Mormyridae (Canitz *et al.*, 2017; Barby *et al.*, 2018; Cioffi *et al.*, 2019). The mormyrids, in particular, are dominated by a $2n = 50$ chromosomes; this scenario is shown in 9 genera and 21 species out of the 15 genera, and 21 species for which karyotypes record is available (Simanovsky *et al.*, 2021a; Table 2). Although most mormyrids exhibit a conserved diploid number of $2n = 48-50$ chromosomes (except, *Pollimyrus*, *Hyperopisus* [40] and *Mormyrops* [52] species), there is a high variation in the distribution of their one and two-armed constituents; this variation is reflected in their fundamental number; FN = 42-84 (Simanovsky *et al.*, 2021a; Table 2).

Compared to the genus *Mormyrus* which touts FN = 84 for all the four species karyotyped till now, *Marcuseinius* show a high variation in their fundamental chromosome number (FN = 54-82; Table 2). The phylogenetic studies of Lavoué *et al.* (2000) recovered three Mormyridae genera: *Pollimyrus*, *Brienomyrus* and *Marcuseinius*; as polyphyletic, the non-monophyly of *Marcuseinius* may be adduced for the high karyotype variation in the genus. Simanovsky *et al.* (2020) hypothesized a $2n = 50$ composed entirely of acrocentrics as the basal karyotype condition of the Mormyridae, but the karyotype of *M. brucii* did not support this position by possessing majorly bi-armed chromosomes. However, the karyotype of *Petrocephalus microphthalmus* and *Stomatorhinus* species ($2n = 50$ [2sm+48a]; Table 2) is close to the proposed basal karyotype condition. Since the sister relationship of the genus, *Petrocephalus* (subfamily Petrocephalinae) and all other mormyrids (subfamily Mormyrinae) are well-supported phylogenetically; the basal chromosome number; $2n = 50$, all acrocentrics may be harboured within *Petrocephalus* or any of the basal mormyrids' genera.

The polyphyly, the limited number of karyotyped individuals and the lack of chromosome banding data for *Marcuseinius* species makes it difficult to infer the mechanisms of chromosomal re-arrangements involved in *M. brucii* karyotype organization. However, large metacentrics and submetacentric are usually products of centric fusion leading to a reduction in chromosome number without a corresponding reduction in FN; therefore, to derive the karyotype of *M. brucii*; $2n = 50$ (26m+6sm+18a), FN = 82 from that of *M. moorii*; $2n = 50$ (4sm+46a),

FN = 54 will also involve some fission events. Therefore, the wide variation in the FN observed was due to the non-monophyly of the genus or otherwise could not be ascertained.

Table 2: Available karyotypes of Mormyridae species that exhibit a diploid number of $2n = 50$

Genus/Species	Karyotype	FN	Place of collection	Reference
Mormyrus				
<i>M. rume</i>	24m+10sm+16a	84	Asejire Reservoir, Osun River basin, Nigeria	Jegade, 2022 (In press)
<i>M. caschive</i>	20m+14sm+16a	84	Alvero River, Nile basin, Ethiopia	Simanovsky <i>et al.</i> , 2021b
<i>M. hasselquistii</i>	20m+14sm+16a	84	Alvero River, Nile basin, Ethiopia	Simanovsky <i>et al.</i> , 2021b
<i>M. kannume</i>	20m+14sm+16a	84	Gibe River, Omo-Turkana basin, Ethiopia	Simanovsky <i>et al.</i> , 2021b
Marcusenius				
<i>M. moorii</i>	4sm+46a	54	Ntem River, Gabon.	Ozouf-Costaz <i>et al.</i> , 2015
<i>M. cyprinoides</i>	22m+4sm+24a	76	Alvero River, Nile basin, Ethiopia	Simanovsky <i>et al.</i> , 2020
<i>M. brucii</i>	26m+6sm+18	82	Asejire Reservoir, Osun River basin, Nigeria	Present study
Brienomyrus				
B. species	2m+6sm+42a	58	Woleu River, Gabon	Ozouf-Costaz <i>et al.</i> , 2015
Ivindomyrus				
<i>opdenboschi</i>	10m+2sm+38a	62	Ntem River, Gabon	Ozouf-Costaz <i>et al.</i> , 2015
Stomatorhinus				
<i>S. walker</i>	2sm+48a	52	Lambaréné, Ogooué Basin, Gabon	Ozouf-Costaz <i>et al.</i> , 2015
Petrocephalus				
<i>P. microphthalmus</i>	2sm+48a	52	Lambaréné, Ogooué, Basin, Gabon	Ozouf-Costaz <i>et al.</i> , 2015
Hippopotamyrus				
<i>H. pictus</i>	24m+4sm+22a	78	Alvero River, Nile basin, Ethiopia	Simanovsky <i>et al.</i> , 2020
Cyphomyrus				
<i>C. petherici</i>	18m+4sm+28a	72	Alvero River, Nile Basin, Ethiopia	Simanovsky <i>et al.</i> 2020
Brienomyrus				
B. species	2m+6sm+42a	58	Woleu River, Gabon	Ozouf-Costaz <i>et al.</i> 2015

Conclusion

This study presents the chromosome composition of *Marcusenius brucii* as $2n = 50$ (26m+6sm+18a), FN = 82, making it the third karyotyped species in the genus. However, more *Marcusenius* species karyotypes, including molecular cytogenetics and phylogenetic data, are needed to better understand karyotype evolution in the genus and the family Mormyridae.

References

- Anifowose & Oyeboade (2019). Studies on heavy metals contents of Osun River at the pre-urban settlement and across Osogbo City. *Nigerian Journal of Taibah University of Science*, 13(1), 318–323. <https://doi.org/10.1080/16583655.2019.1567899>
- Arnegard, M. E. & Carlson, B. A. (2005). Electric organ discharge patterns during group hunting by a mormyrid fish. *Proceedings of the Royal Society B* (2005), 272, 1305–1314 doi:10.1098/rspb.2005.3101
- Barby, F. F., Ráb, P., Lavoué, S., Ezaz, T., Bertollo, L. A. C. et al. (2018). From chromosomes to genome: insights into the evolutionary relationships and biogeography of Old World knife fishes (Notopteridae; Osteoglossiformes). *Genes*, 9, Article 306. <https://doi.org/10.3390/genes9060306>
- Bertollo, L. A. C., Cioffi, M. B. & Moreira-Filho, O. (2015). Direct chromosome preparation from freshwater teleost fishes. In: Ozouf-Costaz, C., Pisano, E., Foresti, F., Almeida Toledo, L. F. (Eds). *Fish Cytogenetic*

- Techniques (Chondrichthyans and Teleosts)* (Vol. 1, pp 21–26). CRC Press: Enfield USA.
- Bigorne, R. (2003). Mormyridae. In Paugy, D., Lévêque, C. & Teugels, G. G. (Eds). *The fresh and brackish water fishes of West Africa* (vol.1, pp 155 – 221). Institut de recherché pour le developpement Paris France. Musée royal de l’Afrique Centrale Tervuren, Belgique.
- Boden, G., Teugels, G. G. & Hopkins, C. D. (1997) A systematic revision of the large-scaled *Marcusenius* with description of a new species from Cameroon (Teleostei; Osteoglossomorpha; Mormyridae). *Journal of Natural History*, 31: 1645–1682. <http://dx.doi.org/10.1080/00222939700770881>
- Canitz, J., Kirschbaun, F. & Tiedermann, R. (2017). Karyotype description of the African weakly electric fish, *Campylomormyrus compressirostris* in the context of chromosome evolution in Osteoglossiformes. *Journal of Physiology Paris*, 110 (3), 273 – 280. <https://doi:10.1016/j.physparis.2017.01.002>.
- Cioffi, M. B., Moreira-Filho, O., Ráb, P. Sember, A., Molina, W. F. et al. (2018). Conventional cytogenetic approaches—useful and indispensable tools in discovering fish biodiversity. *Current Genetic Medicine Reports*, 6, 176– 186. <https://doi.org/10.1007/s40142-018-0148-7>
- Cioffi, M. B., Ráb P., Ezaz, T., Bertollo, L. A. C., Lavoué, S. et al. (2019). Deciphering the evolutionary history of arowana fishes (Teleostei, Osteoglossiformes, Osteoglossidae): Insight from comparative cytogenomics. *International Journal of Molecular Science*, 20, Article 4296. <https://doi.org/10.3390/ijms20174296>
- von der Emde, G., Amey, M., Engelmann, J., Fetz, S., Folde, C., et al. (2008). Active electrolocation in *Gnathonemus petersii*: Behaviour, sensory performance, and receptor systems. *Journal of Physiology-Paris*, 102(4-6), 279–290. <https://doi.org/10.1016/J.JPHYS-PARIS.2008.10.017>
- Fricke, R., Eschmeyer, W. N., & Fong, J. D. (2022). Species by family/subfamily [Online] Available <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>. (May 29, 2022)
- Froese, R. & Pauly, D. (2022). FishBase. World Wide Web Electronic Publication. [Online] Available www.fishbase.org (May 29, 2022)
- Hilton, E. J. (2003). Comparative osteology and phylogenetic systematics of fossil and living bony-tongue fishes (Actinopterygii, Teleostei, Osteoglossomorpha) *Zoological Journal of the Linnean Society*, 137, 1 – 100. <https://doi.org/10.1046/j.1096-3642.2003.00032.x>
- Hilton, E. J. & Lavoué, S. (2018). A review of the systematic biology of fossil and living bony-tongue fishes, Osteoglossomorpha (Actinopterygii: Teleostei). *Neotropical Ichthyology*, 16(3), 1-35. <https://doi.org/10.1093/biolinnean/bly098>
- Hopkins, C. D., Lavoué, S. & Sullivan, J. P. (2007). Mormyridae. In: Stiassny, M. L J., Teugels, G. G., & Hopkins, C. D. (Eds). *The fresh and brackish water fishes of Lower Guinea, West-Central Africa* (Vol. 1, pp 219–334). Collection faune et flore tropicales 42, IRD-MNHN-MRAC, Paris and Tervuren,
- Jegade, O. I. (2022) Chromosomal analysis of the freshwater fish *Mormyrus Rume* (Mormyridae) from Asejire Reservoir, Oyo State, Nigeria. *Nigeria Journal of Fisheries*, 19(1) (In Press)
- Kramer, B. & Wink, M. (2013). East-west differentiation in the *Marcusenius macrolepidotus* species complex in Southern Africa: the description of a new species for the lower Cunene River, Namibia (Teleostei: Mormyridae) *Journal of Natural History*, 47 (35–36), 2327–2362. <http://dx.doi.org/10.1080/00222933.2013.798699>
- Kretschmer, R.; Franz, I.; de Souza, M. S.; Garneró, A. D. V.; Gunski, R. J. et al. (2021). Cytogenetic Evidence Clarifies the Phylogeny of the Family Rhynchocyclidae (Aves: Passeriformes). *Cells*, 2021, 10, 2650. <https://doi.org/10.3390/cells10102650>
- Krysanov, E. & Demidova, T. (2018). Extensive karyotype variability of African fish genus *Nothobranchius* (Cyprinodontiformes). *Comparative Cytogenetics*, 12(3), 387-402. <https://doi.org/10.3897/CompCytogen.v12i3.25092>
- Kuřiková, P., Patoka, J., & Kalous, Z. (2015). The estimation of import quantity of elephantnose fish *Gnathonemus petersii* (Günther, 1862). to the Czech Republic. In pp 33-38 Kubík, Š. and Barták, M. (eds.) 7th Workshop on Biodiversity, Jevany. December 2015. <https://doi:10.13140/RG.2.1.4026.2166>
- Lamanna, F., Kirschbaum, F., Ernst, A. R. R., Feulner, P. G. D., Mamonekene, V. et al. (2016). Species delimitation and phylogenetic relationships in a genus of African weakly-electric fishes (Osteoglossiformes, Mormyridae, *Campylomormyrus*). *Molecular Phylogenetics and Evolution*, 101, 8-18
- Lavoué, S., Bigorne, R., Lecointre, G. & Agnese, J. (2000). Phylogenetic relationship of mormyrid electric fishes (Mormyridae; Teleostei) inferred from cytochrome b sequences. *Molecular Phylogenetics and Evolution*, 14(1), 1 – 10. <https://doi.org/10.1006/mpev.1999.0687>
- Lavoué, S., Miya, M., Arnegard, M. E., Sullivan, J. P., Hopkins, C. D. et al. (2012). Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. *Public Library of Science ONE*, 7(5), Article e36287
- Levan, A., Fredgaa, K. & Sandberg, A. A. (1964). Nomenclature for centromeric position on chromosomes. *Hereditas*, 52, 201-220. <https://doi.org/10.1111/j.1601-5223.1964.tb01953.x>
- Lissmann, H. W. & Machin, K. E. (1958). The mechanism of object location in *Gymnarchus niloticus* and

- similar fish. *Journal of Experimental Biology*, 35, 451–486.
- Machado, M. A., da Silva, M., Feldberg, E., O'Brien, P. C. M., Ferguson-Smith, M. A. *et al.* (2022) Chromosome Painting in *Gymnotus carapo* “Catalão” (Gymnotiformes, Teleostei): Dynamics of Chromosomal Rearrangements in Cryptic Species. *Frontiers in Genetics*, 13:832495. doi: 10.3389/fgene.2022.832495.
- Ozouf-Costaz, C., Coutanceau, J., Bonillo, C., Belkadi, L., Fermon, Y. *et al.* (2015). First insights into karyotype evolution within the family Mormyridae. *Cybium*, 39(3), 227-236. <https://doi.org/10.26028/cybium/2015-393-006>
- Paula, G. B. N., Gavazzoni, M., Zawadzki, C. H., Fernandes, C. A., Portela-Castro, A. L. B. *et al.* (2022). Identification of cryptic species in allopatric populations of *Hypostomus tietensis* (Siluriformes: Loricariidae) through cytogenetics analyses. *Neotropical Ichthyology*, 20(2), Article e210158. <https://doi.org/10.1590/1982-0224-2021-0158>
- Roberts, T. R. (1975). Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society*, 57, 249-319. <https://doi.org/10.1111/j.1096-3642.1975.tb01893.x>
- Simanovsky, S., Medvedev, D., Tefera, F. & Golubtsov, A. (2020). First cytogenetic information for five Nilotic elephantfishes and a problem of ancestral karyotype of the family Mormyridae (Osteoglossiformes). *Comparative Cytogenetics*, 14(3), 387–397. <https://doi.org/10.3897/CompCytogen.v14i3.52727>
- Simanovsky, S., Medvedev, D., Tefera, F. & Golubtsov, A. (2021a). Derived karyotypes in two elephantfish genera (*Hyperopisus* and *Pollimyrus*): lowest chromosome number in the family Mormyridae (Osteoglossiformes). *Comparative Cytogenetics*, 15(4), 345-354. <https://doi.org/10.3897/compcytogen.v15.i4.67681>
- Simanovsky, S., Medvedev, D., Tefera, F. & Golubtsov, A. (2021b). Similarity of karyotype structure in three *Mormyrus* species (Mormyridae) from the White Nile and Omo River tributaries (Ethiopia). *Journal of Ichthyology*, 61(2), 323-326. <https://doi.org/10.1134/S003294522102017X>
- de Souza, F. H. S., Sassi, F. M. C., Ferreira, P. H. N., Bertollo, L. A. C., Ezaz, T. *et al.* (2022). Integrating cytogenetics and population genomics: allopatry and neo-sex chromosomes may have shaped the genetic divergence in the *Erythrinus erythrinus* species complex (Teleostei, Characiformes). *Biology*, 11, Article 315. <https://doi.org/10.3390/biology11020315>
- Sullivan, J. P., Lavoué, S. & Hopkins, C. D. (2000). Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *Journal of Experimental Biology*, 203, 665 – 683. <https://doi.org/10.1242/jeb.203.4.665>
- Sullivan, J. P., Sébastien, L. & Hopkins, C. D. (2016). *Cryptomyrus*: a new genus of Mormyridae (Teleostei, Osteoglossomorpha) with two new species from Gabon, West-Central Africa. *ZooKeys*, 561, 117–150. <https://doi.org/10.3897/zookeys.561.7137>