Derived karyotypes in two elephantfish genera (Hyperopisus and Pollimyrus): lowest chromosome number in the family Mormyridae (Osteoglossiformes)

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Academic editor: Patrícia Parise-Maltempi | Received 21 April 2021 | Accepted 25 August 2021 | Published 8 October 2021

Citation: Simanovsky S, Medvedev D, Tefera F, Golubtsov A (2021) Derived karyotypes in two elephantfish genera (Hyperopisus and Pollimyrus): lowest chromosome number in the family Mormyridae (Osteoglossiformes). CompCytogen 15(4): 345–354. https://doi.org/10.3897/compcytogen.v15.i4.67681

Abstract
The African weakly electric elephantfish family Mormyridae comprises 22 genera and almost 230 species. Up-to-date cytogenetic information was available for 17 species representing 14 genera. Here we report chromosome number and morphology in Hyperopisus bebe (Lacepède, 1803) and Pollimyrus isidori (Valenciennes, 1847) collected from the White Nile system in southwestern Ethiopia. Both taxa displayed the diploid chromosome number 2n = 40, but they differed in fundamental numbers: FN = 66 in H. bebe and FN = 72 in P. isidori; previously the same diploid chromosome number 2n = 40 was reported in an undescribed species of Pollimyrus Taverne, 1971 (FN = 42) from the same region. Our results demonstrate that not only pericentric inversions, but fusions also played a substantial role in the evolution of the mormyrid karyotype structure. If the hypothesis that the karyotype structure with 2n = 50–52 and prevalence of the uni-armed chromosomes close to the ancestral condition for the family Mormyridae is correct, the most derived karyotype structures are found in the Mormyrus Linnaeus, 1758 species with 2n = 50 and the highest number of bi-armed elements in their compliments compared to all other mormyrids and in Pollimyrus isidori with the highest number of bi-armed elements among the mormyrids with 2n = 40.

Keywords
Africa, chromosomes, karyotype evolution, chromosome fusions, Hyperopisus, Pollimyrus
Introduction

The African weakly electric elephantfishes comprise the family Mormyridae including 22 genera and almost 230 species (Eschmeyer et al. 2021; Froese and Pauly 2021). To date, the representatives of 14 mormyrid genera have been studied cytogenetically (Uyeno 1973; Krysanov and Golubtsov 2014; Ozouf-Costaz et al. 2015; Canitz et al. 2016; Simanovsky et al. 2020, 2021). The diploid chromosome numbers in most elephantfishes vary between 48 and 52 with the mode 50 (Simanovsky et al. 2020). While a single studied species of the genus *Pollimyrus* Taverne, 1971 exhibited 2n = 40 (Krysanov and Golubtsov 2014).

A problem of the ancestral karyotype for the family Mormyridae was discussed by Canitz et al. (2016) and Simanovsky et al. (2020). In the first study, the most likely ancestral chromosome number for the family was identified as n = 24 or n = 25. In the latter study, three most parsimonious scenarios of the early karyotype evolution within the family were considered and the karyotype structure with 2n = 50–52 and prevalence of the uni-armed elements was suggested for a hypothetical ancestor. This suggestion was based on the following points. First, the family Mormyridae belongs to one of the most primitive groups of teleostean fishes, the cohort Osteoglossomorpha (Nelson et al. 2016), while the recent genomic data give evidence for the ancestral Euteleostomi karyotype of 50 chromosomes with domination by acrocentric elements (Nakatani et al. 2007; Sacerdot et al. 2018; de Oliveira et al. 2019). Second, for the family Notopteridae, the osteoglossomorph group closely related to mormyrids (Lavoué and Sullivan 2004, Nelson et al. 2016), the ancestral karyotype structure with 2n = 50 composed exclusively of uni-armed elements was suggested (Barby at al. 2018). Third, the karyotype structure with 2n = 50–52 and prevalence of the uni-armed elements is rather infrequent among mormyrids but appears in the genera displaying primitive morphology (mainly, dentition and electrocyte structure) and mainly basal phylogenetic positions (Taverne 1972; Alves-Gomes and Hopkins 1997; Sullivan et al. 2000).

Indeed, such karyotype structure is found in the two genera (*Petrocephalus* Marcusen, 1854 and *Mormyrops* Müller, 1843) appearing among the basal groups in molecular phylogenies of the family Mormyridae (Alves-Gomes and Hopkins 1997; Sullivan et al. 2000; Lavoué et al. 2003). The third basal genus (*Myomyrus* Boulenger, 1898) is not yet studied cytogenetically, while one more group with the seemingly primitive karyotype – *Stomatorhinus walkeri* (Günther, 1867) (2n = 50, FN = 52) – does not display a basal position in the phylogenetic trees but its stemming is varying and poorly supported (Lavoué et al. 2003; Sullivan et al. 2016; Levin and Golubtsov 2018).

The karyotype structure with chromosome number unusually low for mormyrids was reported by Krysanov and Golubtsov (2014) for a representative of the genus *Pollimyrus*. This genus is among the most species-rich of mormyrid genera, and includes 19 species widely distributed throughout sub-Saharan Africa (Eschmeyer et al. 2021; Froese and Pauly 2021). Variation of the karyotype structure among the different *Pollimyrus* species has not been studied. The genus *Hyperopisus* Gill, 1862 not yet studied cytogenetically includes the only species *H. bebe* distributed in the Sahelo-
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Sudanese river basins (Eschmeyer et al. 2021; Froese and Pauly 2021). Both Pollimyrus and Hyperopisus never appeared among basal groups in the mormyrid molecular based phylogenies (Alves-Gomes and Hopkins 1997; Sullivan et al. 2000; Lavoué et al. 2003). Moreover, both genera exhibit some apparently derived morphological features related to the peculiarities of electrogeneration in Pollimyrus (Sullivan et al. 2000) and molluscivory in Hyperopisus (Taverne 1972; Bailey 1994).

In the present study, we address the uniqueness of the low chromosome numbers in mormyrids; H. bebe and the second species of the genus Pollimyrus were cytogenetically analyzed (for chromosome number and morphology). Based on the obtained and previous results, the two types of karyotype structure most derived from a hypothetical ancestral condition within the family Mormyridae were defined.

Material and methods

Fishes were collected in Ethiopia within the framework of the Joint Ethiopian-Russian Biological Expedition (JERBE) with permission from the National Fishery and Aquatic Life Research Center under the Ethiopian Institute of Agricultural Research and the Ethiopian Ministry of Innovation and Technology. The experiments were carried out in accordance with the rules of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences.

Three individuals (two females and a male) of each of the two species – Hyperopisus bebe (Lacepède, 1803) (standard length, SL 131–356 mm) and Pollimyrus isidori (Valenciennes, 1847) (SL 54–60 mm) – were karyotyped; total numbers of complete metaphase plates studied for each species were 30 and 33, respectively. Fish were sampled in the Gambela Peoples’ Region, a regional state in western Ethiopia at two sites in November of 2017: P. isidori from the Baro River downstream of the City of Itang (8°10’47”N, 34°15’2”E) and H. bebe from the Alvero River downstream of the Abobo Dam (7°52’23”N, 34°29’48”E). Both rivers belong to the Sobat River drainage discharging into the White Nile in South Sudan. Fish were caught with gill (H. bebe) and cast (P. isidori) nets, delivered in 80-l plastic containers into the field laboratory, where they were kept in permanently aerated water for several hours before treatment.

Before preparation fish were treated intraperitoneally with 0.1% colchicine for 3–4 hours. Then fish were euthanized with an overdose of tricaine methanesulfonate (MS-222), identified based on morphological key characters, measured to an accuracy of 1 mm, dissected for gonad examination and tissue sampling, and preserved in 10% formaldehyde. Vouchers are deposited at the Severtsov Institute of Ecology and Evolution (Moscow) under provisional labels of JERBE.

Chromosome preparations were obtained from anterior kidney according to Kligerman and Bloom (1977), procedures were described by Simanovsky and coauthors (2020, 2021). Giemsa-stained chromosome spreads were analysed under an “Axioplan 2 Imaging” microscope (Carl Zeiss, Germany) equipped with a “CV-M4+CL” camera (JAI, Japan) and “Ikaros” software (MetaSystems, Germany). Karyotypes were established according to
the centromere position following the nomenclature of Levan et al. (1964). Chromosomes were classified as metacentric (m), submetacentric (sm) and acrocentric (a), including subtelocentric and telocentric chromosomes, and grouped according to their morphology in order of decreasing size. To determine the fundamental number (FN), metacentrics and submetacentrics were considered bi-armed and acrocentrics as uni-armed.

**Results and discussion**

*Hyperopisus bebe* has karyotype with $2n = 40$ (Fig. 1) consisting of 24 metacentrics, 2 submetacentrics and 14 acrocentrics, the fundamental number $FN = 66$. *Pollimyrus isidori* has karyotype with $2n = 40$ consisting of 26 metacentrics, 6 submetacentrics and

![Figure 1](image-url). Karyotypes of *Hyperopisus bebe* and *Pollimyrus isidori* after conventional Giemsa staining. Scale bars: 10 μm.
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8 acrocentrics, FN = 72. In agreement with the lack of reports on sex chromosomes in other mormyrids, no distinguishable sex chromosomes were observed in complements of the two species.

For comparative purposes, all the currently available data on the karyotype structure in mormyrids are given in Table 1. Usage of the name *Pollimyrus prope nigricans* (Boulenger, 1906) has been substantited by Krysanov and Golubtsov (2014). Division of the family Mormyridae into two subfamilies Petrocephalinae (including the single genus *Petrocephalus*) and Mormyrinae (including all other mormyrid genera), as well as usage of the names *Brienomyrus brachyistius* (Gill, 1862), *Campylomormyrus rhynchophorus* (Boulenger, 1898) and *Paramormyrops* sp.7, have been discussed by Simanovsky et al. (2020). The karyotypes most similar to a hypothetical ancestral condition within the family based on arguments considered above are highlighted with bold in the Table 1.

The chromosome set of the undescribed species reported by Krysanov and Golubtsov (2014) as *Pollimyrus prope nigricans* possessing 2n = 40 includes 2 small metacentric and 38 acrocentric chromosomes (FN = 42). Thus, despite the same diploid number of chromosomes (2n = 40), three taxa – *H. bebe* and two *Pollimyrus* species studied –

### Table 1. Cytogenetically studied elephantfishes of the family Mormyridae arranged in accordance with increasing (1) diploid chromosome number – 2n and (2) fundamental number – FN; karyotypic formulas most close to that in a hypothetic ancestor of the family are highlighted with bold.

| Taxon                          | 2n  | Karyotypic formula | FN  | Origin                                      | References            |
|-------------------------------|-----|-------------------|-----|---------------------------------------------|-----------------------|
|                               | 2n  |                   |     |                                             |                       |
| *Pollimyrus prope nigricans*  | 40  | 2m + 38a          | 42  | White Nile and Omo-Turkana Basins, Ethiopia | Krysanov and Golubtsov 2014 |
| *Hyperopisus bebe*            | 40  | 24m + 2sm + 14a   | 66  | White Nile Basin, Ethiopia                  | This study            |
| *Pollimyrus isidori*          | 40  | 26m + 6sm + 8a    | 74  | White Nile Basin, Ethiopia                  | This study            |
|                               | 2n  |                   |     |                                             |                       |
| *Brienomyrus brachyistius*    | 48  | 1m + 4sm + 2st + 41a | 53  | Unknown (fish store)                        | Uyeno 1973            |
| *Brevimyrus niger*            | 48  | 4m + 2sm + 42a    | 54  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2020 |
| *Gnathonemus petersii*        | 48  | 10m + 6sm + 32a   | 64  | Unknown (fish store)                        | Uyeno 1973            |
| *Campylomormyrus rhynchophorus* | 48  | 26m + 4sm + 18a   | 78  | Unknown (laboratory stock)                  | Canitz et al. 2016    |
|                               | 2n  |                   |     |                                             |                       |
| *Petrocephalus microphthalmus* | 50  | 2sm + 48a         | 52  | Ogooué Basin, Gabon                         | Ozouf-Costaz et al. 2015 |
| *Stomatotherinus walkeri*     | 50  | 2sm + 48a         | 52  | Ogooué Basin, Gabon                         | Ozouf-Costaz et al. 2015 |
| *Marccwsicus moorii*          | 50  | 4sm + 46a         | 54  | Ntem River, Gabon                           | Ozouf-Costaz et al. 2015 |
| *Paramormyrops* sp.7          | 50  | 2m + 6sm + 42a    | 58  | Woleu River, Gabon                          | Ozouf-Costaz et al. 2015 |
| *Eivndomyrus opdenboschi*      | 50  | 10m + 2sm + 38a   | 62  | Ntem River, Gabon                           | Ozouf-Costaz et al. 2015 |
|                               | 2n  |                   |     |                                             |                       |
| *Cyphomyrus petherici*        | 50  | 18m + 4sm + 28a   | 72  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2020 |
| *Marccwsicus cyanoclados*     | 50  | 22m + 4sm + 24a   | 76  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2020 |
| *Hippopotamyrus pictus*       | 50  | 24m + 4sm + 22a   | 78  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2020 |
| *Mormyrus cachive* Linnaeus, 1758 | 50  | 20m + 14sm + 16a  | 84  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2021 |
| *Mormyrus hasselquistii*      | 50  | 20m + 14sm + 16a  | 84  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2021 |
| *Mormyrus kannume* Fabricius, 1775 | 50  | 20m + 14sm + 16a  | 84  | Omo-Turkana Basin, Ethiopia                 | Simanovsky et al. 2021 |
|                               | 2n  |                   |     |                                             |                       |
| *Mormyrus anguilloides* Linnaeus, 1758 | 52  | 52a               | 52  | White Nile Basin, Ethiopia                  | Simanovsky et al. 2020 |
display the substantially diverged structure of their karyotypes. Interestingly, two *Pollimyrus* species differ from each other in karyotype structure – mostly in the number of uni-armed elements – more than both from *H. bebe*. Judging from the molecular phylogenies (Lavoué et al. 2003; Sullivan et al. 2016; Levin and Golubtsov 2018), there is a possibility of independent reduction of the chromosome numbers in *Hyperopisus* and *Pollimyrus*. Eight studied species of the latter genus form a well supported monophyletic clade within the mormyrid tree, while the two *Pollimyrus* species analyzed cytogenetically are closely related (Levin and Golubtsov 2018). *Stomatorhinus* in some analyses appears as a sister group to the *Pollimyrus* clade, but the clade *Pollimyrus + Stomatorhinus* is poorly supported (Lavoué et al. 2003; Sullivan et al. 2016; Levin and Golubtsov 2018). The phylogenetic position of *Hyperopisus* is not resolved in any molecular phylogenetic studies. The unusually low number of chromosomes for mormyrids in this genus makes the question of its phylogenetic position even more intriguing.

*Pollimyrus* appears the third mormyrid genus for which the data on intrageneric variation of the karyotype structure are available (Table 1). In this genus the pronounced divergence between species is similar to the situation in *Marcusenius* Gill, 1862, where two species studied have the same diploid chromosome number, but different karyotypic formula – *M. moorii* ( Günther, 1867) has 4sm + 46a, *M. cyprinoides* (Linnaeus, 1758) has 22m + 4sm + 24a (2n = 50 for both) (Ozouf-Costaz et al. 2015; Simanovsky et al. 2020). On the contrary, among three species of the genus *Mormyrus* Linnaeus, 1758 no difference in their karyotype structure was found (Simanovsky et al. 2021). Thus, a search for interspecific differences in the non-monotypic mormyrid genera looks quite informative.

Pericentric inversions are considered as the main type of chromosomal rearrangements in mormyrid karyotype evolution by Ozouf-Costaz et al. (2015). Finding of the three species with substantially reduced chromosome numbers (Table 1) indicates that fusions also played a substantial role in the evolution of the mormyrid karyotype structure. Along with the family Mormyridae, a substantial reduction of chromosome numbers seems to occur in the related lineages of the cohort Osteoglossomorpha. Very interesting data on *Gymnarchus niloticus* Cuvier, 1829, the only representative of the family Gymnarchidae and a sister group of the Mormyridae, reveal unexpectedly different karyotype structures – 2n = 34 (26m + 8sm) and 2n = 54 (26m + 14sm + 14sta) – in the two Nigerian populations separated by a distance of less than 200 km (Hatanaka et al. 2018; Jegede et al. 2018). Notopteridae is a sister group of Mormyridae + Gymnarchidae (Lavoué, Sullivan 2004; Nelson et al. 2016). Concerning the only notopterid *Papyrocranus afer* (Günther, 1868) exhibiting karyotype with 2n = 50 (2m + 2sm + 46a), it was suggested that its diploid number remains unchanged compared to a hypothetical common ancestor of notopterids but the karyotype structure in *P. afer* is formed by intrachromosomal rearrangement of two chromosome pairs, resulting in bi-armed elements (Barby et al. 2018). The other notopterids possess exclusively uni-armed elements in their karyotype with 2n ranging from 38 to 46. For this group of taxa Barby et al. (2018) suggest the reduction of 2n via tandem fusions.
One may suggest that just tandem fusions played an important role in reduction of chromosome number to 2n = 40 at least in *Pollimyrus* prope *nigricans* with FN = 42 (Table 1). Based on hypotheses about the dominating role of pericentric inversions in karyotype evolution in most other mormyrids (Ozouf-Costaz et al. 2015) and the ancestral karyotype structure with 2n = 50–52 and prevalence of the uni-armed chromosomes (Simanovsky et al. 2020), it is possible to consider the most parsimonious scenarios of an emergence of the karyotype diversity in the family. It is noteworthy that the karyotypes of all species with 2n = 50 could evolve from the ancestral karyotype with 2n = 50 and FN = 50 via pericentric inversions exclusively: from rearrangement of a single chromosome pair in *Petrocephalus* and *Stomatorhinus* to rearrangements of 17 chromosome pairs in *Mormyrus* Linnaeus, 1758 (Table 1). In our view, the karyotypes characterized by the lowest numbers of uni-armed elements may be considered as the most derived condition of the karyotype structure within the family. Particularly, based on the most parsimonious scenarios, the *Mormyrus* karyotype may be recognized as most derived among the mormyrids with 2n = 48–52, while the karyotype of *Pollimyrus isidori* seems to be most derived among the mormyrids with 2n = 40. Further studies with the use of more advanced cytogenetic techniques could verify the presented suggestions on the karyotype evolution within the family Mormyridae.

**Acknowledgements**

We gratefully acknowledge the JERBE coordinator Andrey Darkov (IEE RAS, Moscow) for logistic support, Sergey Cherenkov (IEE) for sharing field operations and assistance in collecting material, Eugeny Krysanov (IEE) for precious help at different stages of our work. This work is financially supported by the Russian Foundation for Basic Research Project no. 18-34-00638 for SS and benefits also (at the stage of manuscript preparation) from the Russian Science Foundation Project no. 19-14-00218 for AG.

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