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REVIEW

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A review of the reproductive biology of mormyroid fishes: An emerging model for biomedical research

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Abstract

Mormyroidea is a superfamily of weakly electric African fishes with great potential as a model in a variety of biomedical research areas including systems neuroscience, muscle cell and craniofacial development, ion channel biophysics, and flagellar/ciliary biology. However, they are currently difficult to breed in the laboratory setting, which is essential for any tractable model organism. As such, there is a need to better understand the reproductive biology of mormyroids to breed them more reliably in the laboratory to effectively use them as a biomedical research model. This review seeks to (1) briefly highlight the biomedically relevant phenotypes of mormyroids and (2) compile information about mormyroid reproduction including sex differences, breeding season, sexual maturity, gonads, gametes, and courtship/spawning behaviors. We also highlight areas of mormyroid reproductive biology that are currently unexplored and/or have the potential for further investigation that may provide insights into more successful mormyroid laboratory breeding methods.

KEYWORDS

biomedicine, electric fish, mormyrid, reproduction, teleost

1 | INTRODUCTION

The ability to produce electric fields has independently evolved among fishes several times, famously noted by Darwin when considering electric organs (EOs) as a "special difficulty" to reconcile with his theory of natural selection (Darwin, 1859). A particularly difficult issue to resolve for Darwin was the existence of organs in some lineages that resembled the EOs of the strongly electric *Electrophorus* and *Torpedo*, but did not appear to produce electricity. Nearly 100 years later, Lissmann demonstrated that species used these organs to produce weak electric fields to sense surroundings and communicate (Lissmann, 1951, 1958). Strongly electric fish have served as a model system in biology, including biomedicine, since the times of Volta and von Humboldt (Finger & Piccolino, 2011), providing deep insight into the nature of bioelectrogenesis and the molecular structure of the synapse (Godfrey et al., 1984; Nitkin et al., 1987; Noda et al., 1982; Unwin, 1993). Since their "discovery," weakly electric fish have also shaped biomedical science, particularly as an important model system for understanding neuronal circuitry underlying complex vertebrate behaviors (e.g., Heiligenberg, 1991). More recently, a growing community of researchers has steadily progressed toward deeper understanding of the general biology of weakly electric fish, which has uncovered a wealth of phenotypes with great biomedical "potential."

Weakly electric fish generate electric fields by discharging a specialized organ in the tail, called the electric organ (EO). These electric organ discharges (EODs) result from the simultaneous action potentials of a thousand or more electrocytes which determine EOD waveform characteristics (Bass, 1986). Weakly electric fish detect self-generated and conspecific EODs using an array of electroreceptors on the skin (electroreception). The fish analyze distortions of their self-generated electric field caused by nearby objects in the water to create high-resolution electrical images of their surroundings (von der Emde, 1999) using dedicated electroreceptors and sensory processing circuits (von der Emde & Bell, 2003). In parallel, weakly electric fish use a second electroreceptor system to sense conspecific EOD waveforms, allowing them to use electricity as a social communication signal analogous to birdsong or frog vocalizations (Curtis & Stoddard, 2003; Hagedorn & Zelick, 1989). Perhaps most impressive about electric fish is the highly convergent nature of these abilities: two clades of weakly electric fishes, the Gymnotiformes of South America and the Mormyroidea of Africa, have independently evolved *both* EOs *and* two distinct sensory systems for the analysis of self-generated and conspecific electric fields (Gallant & O'Connell, 2020). The value of this to both evolutionary biology and biomedical science cannot be overstated: weakly electric fish provide an unparalleled opportunity whereby phenotypes at multiple levels of biological analysis can be studied in independent systems to make important discoveries.

This review focuses on one lineage of weakly electric fishes, the Mormyroidea, which have been extensively studied as a weakly electric fish model since Lissmann's famous experiments in the 1950s (Lissmann, 1951; Lissmann, 1958). Mormyroidea (mormyroids) is a superfamily of 232 Osteoglossiform fish species that consists of the monospecific family Gymnarchidae (*Gymnarchus niloticus*) and the species-rich family Mormyridae (mormyrids) (Peterson, Sullivan, Hopkins, et al., 2022). Mormyroids live in lacustrine and riverine habitats throughout the African continent and are culturally (Ouzman, 1995) and commercially (Okedi, 1965) significant in their native regions. With a strong history as model system for neurobiology and evolution, and more recently as a genetic model with the availability of genomic resources (e.g., Cheng et al., 2023; Gallant et al., 2017; Peterson, Sullivan, & Pirro, 2022) and gene-manipulation protocols (Constantinou et al., 2019), several unusual phenotypic properties of mormyroids represent fertile grounds for the investigation of biomedically relevant questions. Despite their great potential as a biomedical model system, mormyroid researchers face a significant hurdle: mormyroids are notoriously difficult to breed reliably within the laboratory setting. For several biomedically relevant questions, understanding the developmental mechanisms that result in phenotypes of interest is crucial. Hence, there is a need for access to embryological material to support this work. Therefore, to utilize the potential of mormyroids as a model in biomedical research and support comparative work with other electric fish lineages, a comprehensive understanding of mormyroid reproductive biology is needed. The purpose of this review is (1) to briefly illustrate the numerous biomedically relevant phenotypes afforded by the mormyroid system, (2) to provide an extensive review of the current state of knowledge of mormyroid reproductive biology, and (3) outline the challenges facing mormyroid breeding that prevent the much-needed developmental data to enable this model system to make great strides in the future.

2 | BIOMEDICALLY RELEVANT PHENOTYPES IN MORMYROIDS

2.1 | Large brains and high metabolic costs: A model for extreme encephalization

Given that mormyroid fishes have evolved the ability to exploit a sensory modality unavailable to most other fishes, they are first and foremost an exciting system to ask questions about the evolution of sensory systems and how sensory information is integrated across sensory modalities (e.g., Skeels et al., 2023). An important key to understanding the sensory lives of mormyroid electric fishes is the fact that mormyroid brains are strikingly large (Figure 1a) in proportion to their body size, comparable to the brain-body proportion of humans (Kaufman et al., 2003). The mormyroid species *Gnathonemus petersii* has a brain that is 3.1% of its body mass and, critically, uses 60% of its total oxygen consumption. This proportional amount of oxygen consumption is higher than any other known vertebrate (Nilsson, 1996). A recent study comparing brain sizes among mormyroid genera reveals there have been multiple independent origins of large brains within mormyroids (Sukhum, 2018), making them a powerful system for the study of the mechanisms and consequences of extreme encephalization in vertebrates in a framework with multiple independent evolutionary events.

Much of the increased size in mormyroid brains is accounted for by the enlargement of regions involved in electroreception (Schumacher & Carlson, 2022). This, coupled with the ability of mormyroids to produce metabolically costly electric signals (Clarke et al., 2020), suggests that there is likely strong selective pressure on mormyroids to economize on metabolically costly biological functions, including redundant sensory processing.

Presently, there is some evidence of sensory trade-offs in weakly electric fish in cone opsin gene loss and brain region size evolution. Both gymnotiformes and mormyroids have lost the cone opsin gene *SWS*$_1$ indicating a link between loss of this gene and the evolution of electroreception (Liu et al., 2017, 2019). Studies on brain region size in mormyroids also indicate trade-offs in sensory system processing: regions associated with non-electrosensory sensory systems, including the optic (Lázár et al., 1984; Stevens et al., 2013) and olfactory systems (Moller, 1995; Schumacher & Carlson, 2022), are reduced. Further investigation in the nonelectrosensory sensory systems of mormyroids is likely to yield important clues into how mormyroids manage to support their metabolically costly brains. A mechanistic basis for understanding how total and regional brain size evolves is still poorly understood across vertebrates, but the considerable variation in brain size within mormyroids sets up mormyroids as a powerful experimental model for investigating these questions with a key caveat: poor availability of embryonic materials to study brain development.

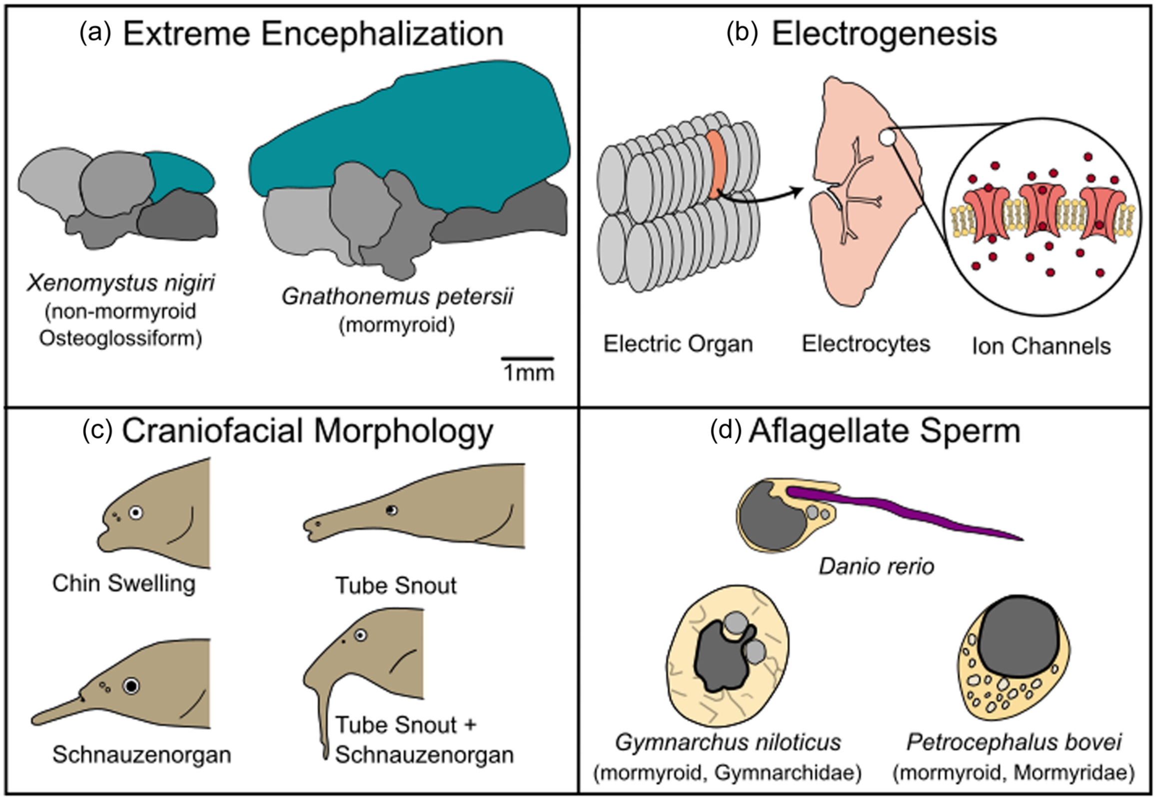

FIGURE 1 Biomedically relevant phenotypes in mormyroids. (a) Mormyroid brains (represented by *Gnathonemus petersii*) exhibit extreme encephalization with significant enlargement of the cerebellum (blue) compared to other Osteoglossiforms (represented by *Xenomystus nigiri*) (brain illustrations modified from Sukhum, 2018). (b) Mormyroids are capable of electrogenesis using an electric organ located in the caudal peduncle. This organ is composed of specialized cells, electrocytes (pink), and discharges of the electric organ are the result of action potentials facilitated by the ion channels of individual electrocytes (Bass, 1986). (c) Mormyroid craniofacial morphology is diverse and includes several unique mouth/jaw morphologies including chin swellings (*Marcusenius moorii*), tube snouts (*Mormyrops zanclirostris*), Schnauzenorgans (*Gnathonemus petersii*), and a combination of tube snouts and Schnauzenorgans (*Campylomormyrus mirus*) (Ford et al., 2022; Peterson, Sullivan, Hopkins, et al., 2022). (d) The sperm of most teleosts is flagellated, but mormyroid sperm is uniquely aflagellate. The "typical" teleost sperm, represented by *Danio rerio* (modified from Zhang et al., 2014), has a flagellum (purple), a condensed nucleus (dark gray), and some varying number of mitochondria (light gray). Gymnarchidae sperm (modified from Mattei et al., 1967), represented by the only species *Gymnarchus niloticus*, has no flagella, an uncondensed nucleus, few mitochondria, and a network of submembrane microtubules which provides it ameboid-like motility. Mormyridae sperm (modified from Mattei et al., 1972), represented by *Petrocephalus bovei*, has no flagella and abundant mitochondria.

2.2 | Cerebellar-like circuits and the corollary discharge

It is commonly understood in modern neuroscience that many sensorimotor systems have a mechanism to cancel predictable reafferent input, a concept referred to as the *corollary discharge* or *efference copy* (Crapse & Sommer, 2008). Dysfunction in corollary discharge is associated with several disease phenotypes including aberrant limb movements (as in cases of bradykinesia and anarchic hand syndrome), Alzheimer's disease, autism, and schizophrenia (Parlikar et al., 2019). Therefore, understanding the mechanisms of corollary discharge including what factors may lead to its dysfunction is crucial for understanding these diseases.

Teleost model systems have been key to understanding the anatomical and physiological basis of corollary discharges, particularly mormyrids (Bell et al., 2008; Fukutomi & Carlson, 2020; Sawtell et al., 2005). Mormyrids produce a corollary discharge alongside the EOD motor command, which provides information to the electrosensory system to modulate sensory processing (Bell, 1989) of electroreceptors dedicated to communication and electrolocation discussed above. Mormyrids have become a premier system for the study of corollary discharges because of how simple it is to record from and manipulate reafferent stimuli: the command signal for EOD production can be noninvasively recorded far away from the brain, and the reafferent input to electroreceptors is a simple pulse of electricity which can be easily manipulated (Fukutomi & Carlson, 2020).

Corollary discharges are found across a wide variety of sensory modalities and species; however, very little is known about their evolution and development. Comparative studies in mormyroids may be an excellent opportunity to study both: the monotypic Gymnarchidae, which produce quasisinusoidal EOD discharges lack a corollary discharge (Kawasaki, 1994); however, all members of the Mormyridae, which produce intermittent, variable rate EODs, possess a corollary discharge (Vélez & Carlson, 2016). Remarkably, EOD duration is highly variable among mormyrids (0.1–10 ms), and long-duration EODs have evolved several times within mormyrids (Gallant & O'Connell, 2020). Recent evidence suggests that corollary discharge function in mormyrids with long-duration EODs time-shift their corollary discharge to optimally block electrosensory responses to the fish's own EOD suggesting that corollary discharge mechanisms may evolve among species to match communication system evolution (Fukutomi & Carlson, 2020). The mechanisms by which the evolutionary changes in corollary discharge timing take place are presently unknown but remain an important area in understanding this common phenomenon found in sensory systems and mormyroids are well poised for such future studies, by virtue of their numerous experimental advantages.

2.3 | Electric organs and the evolution and development of muscle regulation

Several studies have begun to elucidate the genetic and developmental processes underlying major novel vertebrate traits including fins (Davis et al., 2007), limbs (Schneider et al., 2011), feathers (Harris et al., 2002), and teeth (McCollum & Sharpe, 2001); however, few of these structures have evolved repeatedly, particularly in extant lineages where molecular and developmental studies are possible, preventing the analysis of molecular and developmental processes underlying novel vertebrate traits in a comparative framework. EOs have evolved multiple times in vertebrates, and derive during development either from skeletal muscle precursors or directly from fully differentiated muscle through a process called transdifferentiation (Gallant, 2019). Mormyroid EOs (Figure 1b) very strongly resemble differentiated muscle fibers both anatomically (including the retention of sarcomeric structures, Bass et al., 1986; Denizot et al., 1978), and transcriptionally (Gallant et al., 2012, 2014). A recent study demonstrates that despite the considerable diversity of fishes that have evolved EOs, EO gene expression appears to be convergent in key genes across several lineages, including mormyroids (Gallant et al., 2014).

A major outstanding question concerning EO development is how the transformation from skeletal muscle to EO takes place: several key transcription factors (e.g., *myogenin*, *MyoD*, *Six2a*, and *Hey1*) have been identified in multiple lineages to exhibit unusual patterns of expression which may alter muscle development networks (Gallant et al., 2014), though these hypotheses have yet to be examined. Perhaps the most obvious and fundamental reasons behind this gap is the paucity of embryological materials available for developmental work. Therefore, to resolve this issue and exploit the potential of work on EO development, reliable breeding of electric fishes, including mormyroids, is crucial.

Aside from the impact on understanding how muscle development is altered to produce EOs, characterizing EO development may 1 day have broad impacts for fields such as developmental biology, regenerative medicine, and even biological engineering. The ability to produce "biological batteries" from stem cells may 1 day inspire new classes of artificial biological devices with their own power supplies (Ozbolat & Hospodiuk, 2016).

2.4 | Convergent evolution of craniofacial morphology

Craniofacial diseases are one of the most common types of congenital diseases in humans and can cause medical as well as social consequences (Naqvi et al., 2022). Therefore, understanding the underlying genetic and developmental mechanisms that lead to variation in facial morphology is pertinent. Historically, animal models for craniofacial biology were mostly limited to mammals due to their relatedness and similarity in facial muscle development to humans (Siegel & Mooney, 1990). However, due to the high level of conservation in developmental mechanisms across animals, model organisms within other taxa including birds (*Gallus gallus*, chicken), amphibians (*Xenopus laevis/tropicalis*, frogs), and fish (*Danio rerio*, zebrafish) have become common models in craniofacial research as well (Van Otterloo et al., 2016). Outside of these common model organisms, East African cichlids have also famously been used as an important model for craniofacial disease and development due to their extraordinary diversity in craniofacial morphologies which represent morphologies that are not present within other models including facial asymmetry (Albertson et al., 2008).

Mormyroids also possess unique craniofacial morphologies, particularly in the mouth and jaw, exhibiting blunt-nose snouts, tube snouts, chin-swellings, and Schnauzenorgans (Figure 1c) (Peterson, Sullivan, Hopkins, et al., 2022). Recent work by Peterson et al. (2023) demonstrates that some of these morphologies have convergently evolved within different mormyroid lineages at the macroscopic and histological scales. Remarkably, these unusual craniofacial morphologies have also convergently evolved between mormyrids and gymnotiforms (Ford et al., 2022). To date, there have been no developmental or genetic studies to examine potential genetic underpinnings of these unusual adaptations. Given the multiple scales of convergence in mormyroid craniofacial morphologies, identification of the responsible developmental mechanisms is of interest. Are these mechanisms the same among lineages and might they also play a role in craniofacial development in humans? To perform the developmental studies needed to answer these questions, reliable access to mormyroid embryos is necessary.

2.5 | Ion channel biophysics

Ion channels are crucially important molecules responsible for the regulation of action potentials in excitable tissues. In humans, mutations in ion channel genes can cause channelopathies, diseases characterized by aberrant ion channel function, such as epilepsy, cystic fibrosis, and some cases of sudden infant death syndrome (Kim, 2014; Köhling & Wolfart, 2016). Because of the vitally important role of ion channels in maintaining homeostasis, they are subject to intense purifying selection, and ion channel sequences are highly conserved among vertebrates, and to some extent among metazoans. This general lack of variation presents a problem for those wishing to study the relationship between ion channel gene sequence and physiology through comparative means.

Weakly electric fish have managed to escape the constraints of purifying selection on the ion channels used in the generation of their electric discharges (Figure 1b) and serve as a natural "laboratory" to explore the biophysical consequences of sequence variation in key regions of sodium and potassium channels. A genome duplication at the origin of teleosts generated duplicate copies of all vertebrate genes (Glasauer & Neuhauss, 2014). All teleost fish muscle expresses two paralogous voltage-gated Na+ channel genes (*scn4aa*, *scn4ab*). In both mormyroids and gymnotiformes one gene (*scn4aa*) is compartmentalized in the EO where it evolves rapidly, presumably under selection pressures associated with electrical signaling and sensing, and the other (*scn4ab*) retains its expression in muscle where it is functionally constrained and evolves slowly (Arnegard et al., 2010; Zakon et al., 2006). Recently, comparison of genomic sequences among weakly electric fish species uncovered a previously unknown conserved noncoding element (CNE), present in all vertebrates that drives *scn4a* expression in all vertebrate tissues. This small CNE is absent in the *scn4aa* genes found in South American weakly electric fish, where the mechanism of *scn4aa* loss in mormyrids is unknown (LaPotin et al., 2022).

Remarkably, a paralogous voltage-gated potassium channel gene (*kcna7a*, *kcna7b*) has followed a similar trajectory; however, most teleosts have lost the paralogous *kcna7b* while mormyrids have retained it. At the origin of the Mormyridae, *kcna7a* underwent rapid evolution, presumably under selective pressure associated with electric signaling where kcna7b retains its ancestral function (Swapna et al., 2018). Study of these ion channels in systems where they are released from their typical purifying selection pressures in nervous systems and muscles has been enormously fruitful for understanding the biophysics of voltage-gated ion channels (Swapna et al., 2018; Zakon et al., 2006). In mormyrids, a recent study found that the amino acid substitutions in the S3–S4 linker of the potassium channel lead to a shortening of the action potentials, uncovering a previously unknown role of "voltage tuning" in this protein region (Swapna et al., 2018). Outside of protein sequence, mutations in regulatory elements that affect gene expression are another factor that might have driven changes in mormyroid ion channel function. However, identification of these elements, through assay for transposase-accesible chormatin sequencing methods, has not yet been feasible since it would require embryological material.

2.6 | Flagellar loss and ciliary function

Finally, mormyroid sperm lacks flagella (Figure 1d) (Mattei et al., 1967, 1972). Aflagellate sperm has evolved several times within invertebrate lineages, but mormyroids are the only known case of aflagellate sperm evolving within vertebrates (Morrow, 2004). In many taxa, sperm flagella are essential to the ability of sperm to swim to and subsequently fertilize eggs. Therefore, aberrant or absent sperm flagella can have immense consequences for fertilization success. For example, asthenospermia is a condition that causes the production of sperm with decreased motility due to a variety of possible issues in sperm flagella structure (Chemes et al., 1998). Asthenospermia is a common cause of male infertility and although the cause of asthenospermia at a gamete morphology level can be determined using microscopy, the underlying mechanism for why these morphological abnormalities occur is more difficult to assess (Chemes et al., 1998). Mormyroids are a vertebrate lineage in which aflagellate sperm are viable and, as such, provide the unique opportunity to understand the development of vertebrate aflagellate sperm. This line of research may provide insights into gene mutations and processes involved in the formation of aberrant/absent sperm flagella, but also has potential on a pleiotropic scale. Flagella and cilia are very similar in terms of development, structure, and function (Witman, 1990). Cilia are essential to numerous body processes including normal development during the embryonic stage across several taxa (Drummond, 2012). Mormyroids lack sperm flagella, but the state of cilia across other body tissues is unknown. Does the mechanism that results in mormyroid aflagellate sperm have pleiotropic consequences that affect cilia in other tissues? To tackle these questions surrounding sperm flagella and possible pleiotropic consequences, access to breeding populations in the laboratory to obtain sperm and embryos is necessary.

3 | MORMYROID REPRODUCTIVE BIOLOGY

3.1 | Sex differences

The ability to differentiate between sexes is important from both the perspective of the fish attempting to mate and researchers that need to determine the sex of individuals for mating or other purposes. In some mormyroids, sexual dimorphism in external anatomy can easily allow for sex identification, but in others, the sexes are externally indistinguishable. Another method for the identification of sex in some species is sexual dimorphism in electric signal structure and signaling behaviors.

3.1.1 | Anal fin notch

The major anatomical sexual dimorphism in Mormyroidea is the male anal fin notch (Figure 2). The earliest report of this anatomical feature is likely by Svensson (1933) in *Mormyrops delicious* and *Gnathonemus gambiensis*. It has since been described in several other species: *Brevimyrus niger* (Stell & Moller, 2017a, 2017b), *Brienomyrus brachyistius* (Brown et al., 1996), *Gnathonemus cyprinoides* (Nawar, 1959a), *Gnathonemus petersii* (Pezzanite & Moller, 1998), *Hyperopisus*

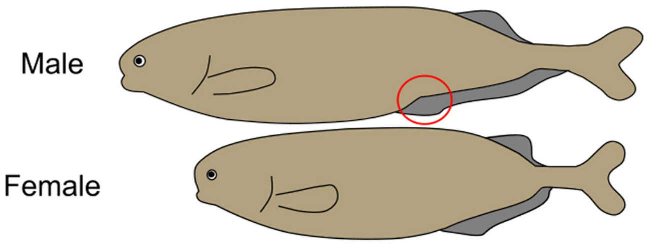

FIGURE 2 Illustrations of the major anatomical sexual dimorphism in mormyroids: the male anal fin notch. Male mormyroids (top) have a characteristic notch (red circle) in the ventral body wall along the anal fin whereas females (bottom) have a relatively linear body wall along the anal fin.

bebe bebe (Nawar, 1959a), *Ivindomyrus marchei* and *Ivindomyrus opdenboschi* (Lavoué et al., 2008), *Mormyrops anguilloides* (Nawar, 1959a), *Mormyrus cashive* (Nawar, 1959a), *Mormyrus kannume* (Iles, 1960; Nawar, 1959a), *Paramormyrops kingsleyae* (Brown et al., 1996), *Petrocephalus bane* (Nawar, 1959a), and *Pollimyrus adspersus* (Kirschbaum, 1987).

With the onset of sexual maturity in males, the fin ray bases in the anal fin expand to create a characteristic notch shape along the ventral edge of the body (Stell & Moller, 2017a). Stell and Moller (2017a) measured the angle of the anal fin notch in *Brevimyrus niger* and found the angle was significantly different in mature males, immature males, and females. However, there is no defined minimum angle for this feature to be considered the anal fin notch and likely there cannot be given the immense diversity in morphology among mormyroids. Nawar (1959a) described it as "an S-shaped wave at the anterior region of [the] anal fin." Once formed, this feature is permanent in some species (Okedi, 1969) but seems to seasonally regress in others (Iles, 1960; Moller et al., 2004). Formation of the indentation is likely under androgen control. In female *Brevimyrus niger*, the formation of the anal fin notch can be induced by exposure to amortizable 17α-methyltestosterone (Stell & Moller, 2017b). In juvenile and female *Gnathonemus petersii* anal fin notch formation can be induced by exposure to testosterone or dihydrotestosterone (Landsman & Moller, 1988; Landsman et al., 1990). Females and immature males of some species may naturally show a slight indentation in the body wall, but generally, this feature is noticeably more prominent in mature males. However, in some mature male individuals, the notch may be nonobvious and requires careful examination to observe as in some *Pollimyrus adspersus* (Kirschbaum, 1987), *Mormyrus cashive*, *Mormyrus kannume*, *Petrocephalus bane*, and *Mormyrops anguilloides* (Nawar, 1959a).

In response to tactile stimulation, both males and females of several species will concavely flex the anal fin (Brown et al., 1996; Kirschbaum, 1987). This behavior has been termed the anal fin reflex and in males is hypothesized to function in forming a fertilization pocket during spawning (Iles, 1960). This pocket would be created by the male curving his anal fin around the female's genital opening during spawning and then eggs and sperm would be released into this closed-off space. Pezzanite and Moller (1998) hypothesize that the fin ray expansion may increase the surface area for muscle attachment and facilitate the anal fin reflex behavior. Nguyen et al. (2017) hypothesized that the formation of the fertilization pocket is an adaptation to compensate for sperm aflagellism and that coordinated formation of the fertilization pocket may increase fertilization rates. However, more research is needed to confirm these hypotheses.

Although the anal fin notch has been observed in several mormyroid species, it is notably absent from some, including *Gymnarchus niloticus* (Agbugui et al., 2021; Oladosu, 1997), and presence or absence is unknown in many species. Therefore, it should not be assumed that the anal fin notch can be used for sex identification in all mormyroids. In cases where this sexual dimorphism is not present, sex can be determined by inspecting internal anatomy for either an ovary or testis (Agbugui et al., 2021) or by inspecting fluid extracted by hand stripping for spermatozoa (Oladosu, 1997). However, in some cases, sex can also be determined by examination of the electric signal structure or behavior.

3.1.2 | Electric signal structure and signaling behavior

Sexual dimorphism with respect to EOD structure and electric signaling behavior is also present among species of Mormyroidea and the manifestation of this dimorphism varies. In *Ivindomyrus marchei* and *I. opdenboschi*, males produce EODs with longer duration waveforms and lower peak frequencies than females (Lavoué et al., 2008). In *Marcusenius macrolepidotus*, EOD duration is shortest in immature individuals (416.4 ms), longer in mature females (519 ms), and nearly 11.5 times longer in mature males than immature individuals (4779 ms) (Kramer, 1997). Longer duration waveforms in males compared to females are also seen in *Stomatorhinus corneti* (Hopkins, 1981) and *Paramormyrops magnostipes* (Arnegard et al., 2005). However, in *Petrocephalus catostoma*, males produce shorter duration EODs than females: 395 ms for males and 419 ms for females (Kramer, 1997).

In several species, sexual dimorphism in EOD structure is under hormonal control and related to differences in electrocyte structure. Females and juveniles treated with androgen hormones produce male-like EODs and in species where males produce longer duration EODs male electrocytes are thicker and have more surface invaginations along the anterior face (Bass & Hopkins, 1985; Bass et al., 1986). In addition to EOD structure, differences in electric signaling behavior may also be used for sex identification. Male and female *Pollimyrus adspersus* can be distinguished from one another by their responses to an artificial EOD stimulus (Bratton & Kramer, 1989). Males produce a preferred latency response (PLR)/echo response characterized by alternating bursts with respect to the stimulus (Hopkins, 1986). Females will produce a preferred latency avoidance (PLA) characterized by bursts in synchrony with the stimulus. However, it is unknown if males and females of other mormyroid species also respond in this way to electrical stimuli.

Mormyroids may use these differences in EOD structure and signaling behavior in sex identification and these differences can also be used by researchers to determine the sexes of individuals in cases where such sexual dimorphisms are known for the species.

3.2 | Breeding season and sexual maturity

3.2.1 | Breeding season period

In wild populations of Mormyroidea, the breeding season coincides with the rainy season. Several species of Mormyroidea are anadromous and move to smaller bodies of water that form during the rainy season to spawn (Blake, 1977; Corbet, 1961; Crawford et al., 1997; Daget, 1957; Okedi, 1969). The breeding seasons of several species have been reported (Table 1); however, it is important to consider that variations in the timing of the rainy season can consequently change the timing of the breeding season. For example, the breeding season for several different populations of *Mormyrus kannume* has been reported and there is great variation. Okedi (1970) studied *M. kannume* in Lake Victoria and found two extended spawning seasons with no ripe gonads observed only during July and August. Scott (1974) studied two populations in Lake Victoria and considered one to be monoestrous with spawning season between November to January and the other to have a long spawning period from October to May/June. Ashour et al. (1990) and Zaher et al. (1991) studied fish in the River Nile at Beni Seuf, Egypt and reported a spawning season between May and August with peaks in June/July. Aly (1993) similarly observed peaks in spawning during June/July in Lake Nasser. Mekkawy and Hassan (2012) observed year-round spawning in *M. kannume* from the Nile in Assiut, Egypt. With such variance in the breeding season, it is important for researchers wanting to study wild populations during the breeding season to know when the rainy season where the population of interest occurs rather than plan field expeditions based on historical accounts of when a species is in breeding condition.

3.2.2 | Breeding season sex ratios

Several authors studying the reproductive biology of Mormyroidea populations have reported sex ratios during the breeding season. In some species, breeding season sex ratios are male-biased, including *Gymnarchus niloticus* (Agbugui et al., 2021; Odo et al., 2013; Opadokun & Ajani, 2015) and *Pollimyrus isidori* (Ikomi, 1996), which may indicate a reproductive strategy to ensure a small number of eggs have a very high chance of being fertilized. Interestingly, *Gymnarchus* and *Pollimyrus* are also the only two genera of mormyroids known to perform parental care (discussed below in Nest Building and Parental Care). In other species, the sex ratio is balanced including *Brienomyrus longianalis* (Ikomi, 1996) and *Hyperopisus bebe occidentalis* (Oniye & Onimisi, 2010). There have been no reports of female-biased sex ratios in mormyroids during the breeding season. Knowing the sex ratios of wild breeding populations for a species of interest may inform more successful laboratory breeding setups. For example, laboratory breeding success for *Hyperopisus bebe occidentalis* may be greatest in setups with an equal number of males and females, but breeding success for *Pollimyrus isidori* might be greatest with a male-biased sex ratio. Previous work in species of *Campylomormyrus* does demonstrate that species breeding success may depend on pair versus group mating setups (see Section 3.2.4), but it is currently unknown how differences in sex ratios among groups may change laboratory breeding success.

TABLE 1 The breeding seasons of several species of mormyroids.

Species	Breeding season months	Reference(s)
Gymnarchus niloticus	May to July and October/ November to January	Agbugui et al. (2021); Opadokun & Ajani (2015)
Brienomyrus longianalis	May to July	Ikomi (1996)
Gnathonemus cyprinoides	May to August	Nawar (1959a)
Hyperopisus bebe bebe	July to October	Nawar (1959a)
Hyperopisus bebe occidentalis	June to October	Oniye & Onimisi (2010)
Petrocephalus bane	May to August	Nawar (1959a)
Pollimyrus isidori	July to October	Crawford et al. (1997)
Mormyrops anguilloides	July to August	Nawar (1959a)
Mormyrus cashive	July to August	Nawar (1959a)
Mormyrus kannume	Varies greatly by population	Aly (1993); Ashour et al. (1990); Mekkawy & Hassan (2012); Okedi (1970); Scott (1974); Zaher et al. (1991)

3.2.3 | Gonadal recrudescence

Mormyroidea exhibit cyclic changes in gonadal state that coincide with the rainy and dry seasons. With the onset of the rainy season, gonadal recrudescence initiates and during the dry season the gonad regresses. Aly (1993) defined six maturity stages for the ovary in *Mormyrus kannume*: (1) immature, (2) resting stage, (3) maturation, (4) maturity, (5) reproduction, and (6) spent. Similar stages for testis recrudescence have not been defined. As an individual progresses through the reproductive cycle, gonadal somatic index (GSI) fluctuates. GSI has been measured in several mormyroid species including *Brienomyrus longianalis* (Ikomi, 1996), *Gymnarchus niloticus* (Opadokun & Ajani, 2015), *Hippopotamyrus ansorgii* (Odedeyi & Odedire, 2017), *Hyperopisus bebe occidentalis* (Oniye & Onimisi, 2010), *Marcusenius senegalensis* (Adjibade et al., 2020), *Mormyrus kannume* (Khallaf & Authman, 2012), *Mormyrus rume proboscirostris* (Kirschbaum et al., 2008; Schugardt & Kirschbaum, 2004), and *Pollimyrus isidori* (Crawford et al., 1997). However, many authors do not report the phase of the reproductive cycle during which measurements were made and therefore comparison of these measurements is confounded. Despite this, mormyroid GSI, similar to other Osteoglossiformes (Adite et al., 2006; Hussain et al., 2015), is generally considered low, especially male GSI. However, as Koenig and Gallant (2021) state, it is unclear how these low GSI values compare to other teleost species because, again, many authors do not report the phase of the reproductive cycle and, unlike many other teleosts, Osteoglossiformes have singular rather than paired gonads.

Additionally, body length at first sexual maturity has been reported for four species (Table 2). As many studied individuals come from wild populations that are not strictly monitored, it can be difficult to assess the age of a fish when it is caught. Therefore, body length often acts as a sort of proxy for age although there is not a defined age-length relationship as many factors can influence body size. In any case, body length at first sexual maturity can be a useful measure for researchers to determine whether or not an individual is likely to be able to breed. However, seeing as this measurement is only currently known for four species, it would be useful for future mormyroid researchers to report body length at first sexual maturity for other species.

TABLE 2 Length at first sexual maturity for four mormyroid species.

Species	Length at first sexual maturity (cm)	Reference
Hyperopisus bebe bebe		Nawar (1959a)
Females	30	
Males	28	
Marcusenius macrolepidotus		Kramer (1997)
Females	unknown	
Males	12.3–12.4	
Mormyrops anguilloides		Nawar (1959a)
Females	38	
Males	41	
Mormyrus kannume		Mekkawy & Hassan (2012)
Females	31.7–31.8	
Males	31.5–46.6	

Note: Length at first sexual maturity is unknown for other species.

3.2.4 | Laboratory-induced breeding

Induction of gonadal recrudescence, gamete production, and spawning behavior has been achieved in the laboratory for several species of mormyroids (Table 3). However, as acknowledged by Constantinou et al. (2019), obtaining fertilized embryos from weakly electric fish can be challenging and requires careful monitoring of husbandry conditions. Aforementioned, mormyroids breed during the rainy season when the environment undergoes a myriad of changes. This prompted researchers to investigate which environmental factors induce sexual maturation and spawning. In *Pollimyrus adspersus* Kirschbaum (1987) studied several possible factors (conductivity, water hardness, water level, simulated rain drops, water temperature, photoperiod, and pH) and determined that gonadal recrudescence in *P. adspersus* can be induced by decreasing water conductivity. However, there is no target low conductivity that must be reached. Rather, the relative drop in conductivity acts as the trigger. For example, Kirschbaum (1987) was able to induce gonadal recrudescence under several ranges of conductivity including 2300–1200, 800–450, and 350–160 μS cm^{-1}.

This method of decreasing water conductivity was used to induce reproductive condition in all species in Table 3. However, a couple of important considerations must be made with regard to using this method to induce breeding. First, this method seems to have varied success among species as well as among individuals of the same species. For example, Nguyen et al. (2017) attempted to induce reproduction in four species of *Campylomormyrus*: *C. compressirostris*, *C. rhynchophorus*, *C. tshokwe*, and *C. numenius*. *C. compressirostris* and *C. rhynchophorus* produced some fertilized eggs during spawning events, but many spawning events resulted in unfertilized eggs. *C. tshokwe* spawning events only resulted in unfertilized eggs, but Nguyen et al. were able to collect gametes to perform artificial reproduction. Finally, in *C. numenius* reproductive condition was achieved in males, but not in females. Second, although Table 3 clearly demonstrates that decreasing water conductivity to induce reproductive condition has worked for a number of species, there are still over 200 species on which this method has not been tested. As such, we cannot claim this method works for all mormyroids, but it does appear to be a good guiding principle for researchers wanting to breed mormyroids in the laboratory.

TABLE 3 Mormyroid species in which gonadal recrudescence and gamete production has been induced by decreasing water conductivity in laboratory housing.

Species	References(s)
Brienomyrus brachyistius	Carlson et al. (2000); Constantinou et al. (2019)
Campylomormyrus cassaicus	Kirschbaum & Schugardt (2002)
Campylomormyrus compressirostris	Nguyen et al. (2017)
Campylomormyrus phantasticus	Kirschbaum & Schugardt (2002)
Campylomormyrus rhynchophorus	Nguyen et al. (2017)
Campylomormyrus tamandua	Schugardt & Kirschbaum (1998)
Campylomormyrus tshokwe[a]	Nguyen et al. (2017)
Gnathonemus petersii	Kirschbaum et al. (2016)
Hippopotamyrus pictus	Kirschbaum & Schugardt (2002)
Marcusenius mento	Schugardt & Kirschbaum (2006)
Marcusenius macrolepidotus	Werneyer & Kramer (2005)
Mormyrus rume proboscirostris	Kirschbaum & Schugardt (1995); Kirschbaum & Schugardt (2002); Schugardt & Kirschbaum (1998); Schugardt & Kirschbaum (2004)
Mormyrus rume	Schugardt & Kirschbaum (2006)
Paramormyrops magnostipes	Nguyen (2011)
Petrocephalus soudanensis	Kirschbaum & Schugardt (2002); Kirschbaum (2006)
Pollimyrus adspersus	Bratton & Kramer (1989); Kirschbaum & Schugardt (2002); Kirschbaum (1987); Kramer & Postner (1997); Postner & Kramer (1995)
Pollimyrus isidori	Diedhiou et al. (2007)
Pollimyrus castelnaui	Baier & Kramer (2007)
Pollimyrus marianne	Baier & Kramer (2007)

[a] Successfully bred using artificial fertilization but did not naturally spawn due to male aggression towards the female.

Other factors to consider when breeding mormyroids are the number of individuals housed together, materials present in the tank, and the possibility of aggressive behavior. As demonstrated by Nguyen et al. (2017), *C. rhynchophorus* will spawn as a mating pair, but *C. compressirostris* only successfully spawn as a group of two males and two females. Some species require or prefer certain materials in the tank. For example, *Pollimyrus* species require material such as plants for males to build nests (Kirschbaum, 1987). Many mormyroids do not build nests and thus do not need such materials, yet they may still demonstrate a preference for certain spawning substrates. For example, *Campylomormyrus cassaicus* and *Mormyrus rume proboscirostris* demonstrate a preference for gravel substrate and running water during spawning and *Hippopotamyrus pictus* prefers substrate with holes (Kirschbaum & Schugardt, 2002). Finally, as in many animal species, male aggression is heightened when reproductive condition is achieved in many mormyroid species (Constantinou et al., 2019; Nguyen et al., 2017). This aggression can be intrasexual or intersexual and can even prevent breeding pairs from being able to spawn naturally, as seen in *C. tshokwe* (Nguyen et al., 2017).

3.3 | Gonads and gametes

3.3.1 | Ovary structure and oogenesis

Mormyroidea females have a single unpaired ovary located on the left side of the body. However, Nawar (1959a) reported two cases of a right ovary represented by a vestigial hind part of the gono-duct (in *Gnathonemus cyprinoides* and *Hyperopisus bebe bebe*) and two cases of fully formed paired ovaries have been reported in *Mormyrus kannume* (Golubtsov & Orlov, 2014; Okedi, 1970). Although unique in comparison to many teleosts, a singular ovary is characteristic of Osteoglossiformes (with the exception of *Pantodon buccholzi*; Nysten, 1962). Ovary structure and oogenesis has been studied in four species of mormyroids (*Brevimyrus niger*, *Gnathonemus petersii*, *Marcusenius cyprinoides*, and *Mormyrus rume*) and in all four species the ovary is cystovarian, the ovarian wall is formed by a multilayer epithelium, and the epithelium lining the lumen is squamous (Dymek et al., 2022). In wild populations, ovary recrudescence occurs with the onset of the rainy season and in the laboratory can be induced by decreasing water conductivity (Kirschbaum, 1987). One study has examined the effects of hormones in ovary recrudescence and found that exposure to amortizable 17α-methyltestosterone results in acceleration of ovary growth and induction of vitellogenesis in *Brevimyrus niger* (Stell & Moller, 2017b). Ovary maturity stages have been described in one species, *Mormyrus kannume*: (1) immature, (2) resting stage, (3) maturation, (4) maturity, (5) reproduction, and (6) spent (Aly, 1993).

3.3.2 | Eggs

Egg size in Mormyroidea varies from 0.69 mm for the smallest reported eggs in *Mormyrus kannume* (El-Etriby, 1985) to 7.9 mm for the largest reported eggs in *Gymnarchus niloticus* (Agbugui et al., 2021). Table 4 lists reports of average egg diameter by species. For *Gymnarchus*, two measurements are given because average egg diameter has been calculated in two separate populations. In one species, *Mormyrus kannume*, authors acknowledge that egg diameter varies with fish size and age, time of year, and population (Aly, 1993; Ashour et al., 1990; El-Etriby, 1985; Mekkawy & Hassan, 2012; Zaher et al., 1991). Therefore, it is possible that these factors also have an effect on egg size in other species. In other fish species, egg size is used as an indicator of egg quality as it can represent the maternal investment in gamete production (Lahnsteiner et al., 2008). Typically, fish egg size tends to decrease as the female's egg reserves gradually deplete over subsequent spawns (Lahnsteiner et al., 2008). The link between egg size and offspring viability in mormyroids is unknown, but may represent a fertile area of research. For example, if large egg size is positively correlated with offspring survival in mormyroids then measuring egg sizes of reproductively active females could be a method to assess females for reproductive potential.

Other mormyroid egg characteristics described include coloration, adhesiveness, and, in one species, accessory structure morphology. In *Gymnarchus niloticus*, egg color has been described as golden yellow or amber-like (Budgett, 1901; Oladosu, 1997). *Hyperopisus bebe bebe* eggs are yellow in color, semitransparent, and are slightly ovular in shape (Budgett, 1901). *Pollimyrus* eggs are nonadhesive (Diedhiou et al., 2007; Kirschbaum, 1987), but eggs of some species (*Campylomormyrus tamandua*, *C. phantasticus*, *Hippopotamyrus pictus*, and *Mormyrus rume proboscirostris*) have been described as slightly to strongly adhesive (Kirschbaum & Schugardt, 2002). Diedhiou et al. (2007) described the chorion of *Pollimyrus isidori* eggs as appearing smooth at low magnification, but at high magnifications using scanning electron microscopy a “curly microplicae net” can be seen covering the entire surface of the egg. The function of these accessory structures on the surface of *P. isidori* eggs is unknown. It is also unknown if these structures are widespread among the eggs of mormyroids or if they are unique to *P. isidori*.

TABLE 4 Average egg diameters for several Mormyroidea species.

Species	Average egg diameter (mm ± standard deviation)	Reference(s)
Gymnarchus niloticus	5.41 ± 1.29	Agbugui et al. (2021); Opadokun & Ajani (2015)
	4.72 ± 1.69	
Campylomormyrus cassaicus	2.0	Kirschbaum & Schugardt (2002)
Campylomormyrus phantasticus	3.0	Kirschbaum & Schugardt (2002)
Gnathonemus cyprinoides	1.35	Nawar (1959a)
Gnathonemus victoriae	1.63 ± 0.007	Okedi (1970)
Gnathonemus longibarbis	1.60 ± 0.012	Okedi (1970)
Hippopotamyrus pictus	3.0	Kirschbaum & Schugardt (2002)
Hyperopisus bebe bebe	1.72	Nawar (1959a)
Marcusenius grahami	1.52 ± 0.014	Okedi (1970)
Marcusenius nigricans	2.38 ± 0.025	Okedi (1970)
Mormyrus cashive	1.7	Nawar (1959a)
Mormyrus kannume	2.14 ± 0.014	Okedi (1970)
Mormyrus rume proboscirostris	2.5	Kirschbaum & Schugardt (2002)
Petrocephalus bane	1.45	Nawar (1959a)
Petrocephalus catostoma	1.57 ± 0.012	Okedi (1970)
Petrocephalus soudanensis	1.8	Kirschbaum & Schugardt (2002)
Pollimyrus adspersus	2.5	Kirschbaum & Schugardt (2002)

Note: Diameter is measured in millimeters. When available, standard deviation for the measurement is also given.

3.3.3 | Female fecundity

Measures of female fecundity have been conducted in several species; however, the measurement method varies. For example, fecundity can be measured as the total number of eggs within the ovary of a mature female (absolute fecundity) or the total number of eggs in the ovary with relation to weight (relative fecundity). Here, we will discuss absolute fecundity because it is the most common measurement method within the literature. However, readers should be hesitant to compare absolute fecundity among species since mormyroid species vary greatly in size and thus in possible capacity for eggs. Table 5 lists reported averages for absolute fecundity of mature females for several mormyroid species.

When measuring fecundity, it is important to consider the reproductive stage of the fish. For example, a fish with an immature or spent ovary will have fewer eggs than a fish with a fully mature ripe ovary. Fecundity can also vary with factors such as weight, length, age, and time of year. Authors have found a significant positive correlation between weight and fecundity in *Hyperopisus bebe bebe* (Nawar, 1959b), *Hyperopisus bebe occidentalis* (Oniye & Onimisi, 2010), *Gymnarchus niloticus* (Agbugui et al., 2021; Opadokun & Ajani, 2015), and *Mormyrus kannume* (Mekkawy & Hassan, 2012). Positive significant correlations between length and fecundity have been found in *Mormyrus kannume* (Mekkawy & Hassan, 2012), *Gymnarchus niloticus* (Agbugui et al., 2021; Opadokun & Ajani, 2015), and *Hyperopisus bebe bebe* (Nawar, 1959b). However, the correlation between length and fecundity was determined insignificant in *Hyperopisus bebe occidentalis* (Oniye & Onimisi, 2010). Mekkawy and Hassan (2012) found variation in fecundity based on age and time of year in *Mormyrus kannume*: fecundity increased with age (up to 6 years old) and average fecundity was highest during the month of December. Kankonda et al. (2016) also demonstrated variation in fecundity based on time of year in *Stomatorhinus cf polli* which has higher fecundity during rainy season periods and lower fecundity during other parts of the year. These variations in fecundity based on season are concordant with the breeding season occurring during the rainy season. Similar to egg size, female fecundity might be a useful indicator of mormyroid female reproductive potential. Therefore, it is significant to consider factors that may affect female fecundity when designing breeding setups.

3.3.4 | Testis and sperm

Mormyroidea males have a single unpaired testis located on the left side of the body. Testis structure has been studied in one species, *Pollimyrus isidori*, and was determined to be tubular (Lücker & Kramer, 1981). In wild populations, testis recrudescence occurs with the onset of the rainy season and in the laboratory can be induced by decreasing water conductivity (Kirschbaum, 1987). Stages of testis growth throughout sexual maturity and spawning have not been defined.

Mormyroidea sperm is unique because it is the only known case of aflagellate sperm in a vertebrate lineage (Morrow, 2004). This phenotype was first described in *Gymnarchus niloticus* by Mattei et al. (1967) and has subsequently been described in other species including *Gnathonemus senegalensis*, *Hyperopisus bebe bebe*, *Mormyrus rume*, *Petrocephalus bovei* (Mattei et al., 1972), and *Paramormyrops kingsleyae* (Figure 3). The sperm of Gymnarchidae and Mormyridae have notable differences. Gymnarchidae sperm lack the typical motility apparatus of sperm, the flagellum, but have secondarily evolved motility utilizing a submembrane network of microtubules (Mattei et al., 1967). This microtubule network allows them to move in an ameboid-like fashion and is similar to the evolutionary trajectory of sperm motility seen in some insect lineages (Dallai, 1979). According to Mattei (1991), Gymnarchidae sperm "no longer has the appearance of a spermatic cell" due to its uncondensed central nucleus, abundant cytoplasm, and the submembrane microtubule

TABLE 5 Absolute fecundity of several species of Mormyroidea.

Species	Average number of eggs within the mature ovary ± SD	Reference(s)
Gymnarchus niloticus	925.61 ± 106.90 957.69 ± 112.31	Agbugui et al. (2021); Opadokun & Ajani (2015)
Hippopotamyrus ansorgii	3231 (SD not reported)	Odedeyi & Odedire (2017)
Hyperopisus bebe occidentalis	2822.4 ± 781.43	Oniye & Onimisi (2010)
Marcusenius grahami	2177 ± 224	Okedi (1970)
Marcusenius nigricans	408 ± 18	Okedi (1970)
Mormyrus kannume	6869 ± 421	Okedi (1970)
Gnathonemus victoriae	6363 ± 421	Okedi (1970)
Gnathonemus longibarbis	4688 ± 507	Okedi (1970)
Petrocephalus catostoma	557 ± 25	Okedi (1970)

Abbreviation: SD, standard deviation.

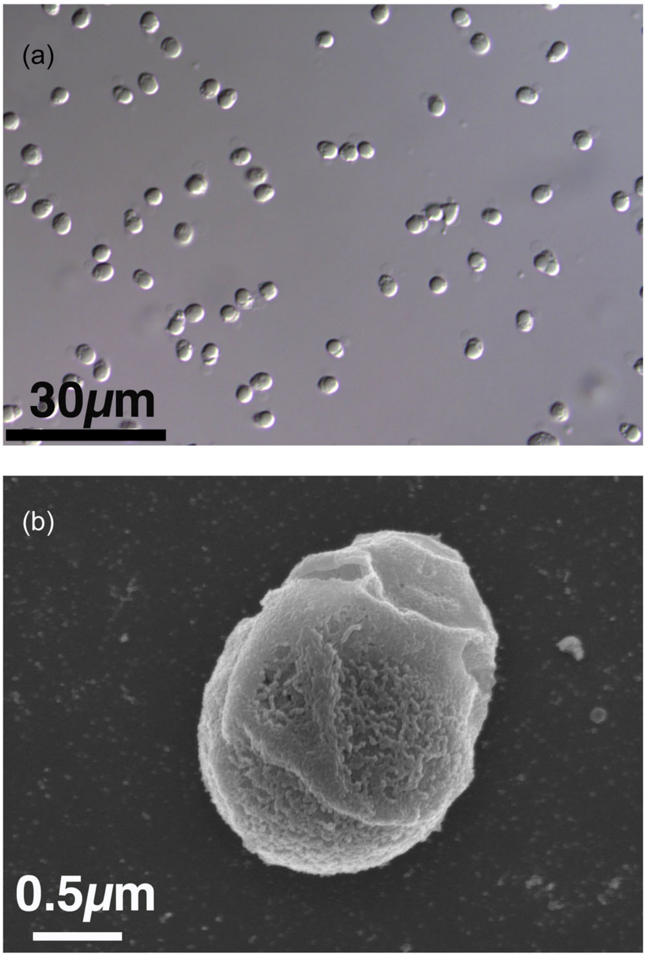

FIGURE 3 Light microscope (a) and scanning electron microscope (b) images of mormyroid sperm (species *Paramormyrops kingsleyae*). The sperm cells lack flagella, but retain the spherical head and distinct midpiece sections typical of simple teleost sperm.

network. On the other hand, Mormyridae sperm structure is more similar to that of other fishes with a round nucleus, two centrioles at the nucleus base, and mitochondria in vesicular cytoplasm (Figure 1d) (Mattei, 1991). The overall shape of Mormyridae sperm is ovoid with the diameter of the larger side being 5–6.5 µm and the smaller side being 3.5–4 µm (Mattei et al., 1972). The aflagellate sperm of mormyroids has great potential as a focus of research on the evolution of gametes and evolutionary pressures that act upon sex traits. The mechanisms by which mormyroid sperm travel to the egg and subsequent sperm-egg interactions are unknown in. A deeper understanding of these gamete-level interactions may prove to be a fruitful area of research in regard to the goal of mormyroid laboratory breeding.

3.4 | Courtship and spawning behavior

Understanding mormyroid courtship and spawning behavior is essential to the researcher wanting to breed mormyroids in the laboratory. For example, mormyroids are fractional spawners which means that fish cannot reach their full reproductive potential with just one night of laboratory spawning and as such need to be allowed to spawn for multiple days/weeks. Furthermore, for species with identifiable courtship and spawning behavior, careful observation of fish behavior can be indicative of reproductive condition and therefore if laboratory-induced sexual maturity and spawning were successful. Finally, some species, including the nest-building species of the genus *Pollimyrus*, require materials to build nests within the breeding aquaria, and without knowing this and providing them with such materials breeding may not be successful. The below sections describe fractional spawning and fertilization rates, nest building and parental care, and courtship and spawning behaviors in mormyroids.

3.4.1 | Fractional spawning and fertilization rate

Mormyroidea are external fertilizers and fractional spawners (Kirschbaum, 1987; Nguyen, 2011; Schugardt & Kirschbaum, 2004). Fish will mate on several different nights throughout the breeding season, but also have multiple bouts of spawning during a single night. For example, *Pollimyrus adspersus* females lay between 2 and 4 eggs per spawning bout and will lay between 50 and 92 eggs per spawning night after multiple bouts of spawning in the laboratory (Kirschbaum, 1987). Both the number of eggs produced during a spawning night and the spawning interval, time between subsequent spawning nights, vary among species (Table 6). Species differences in size, which can directly influence female fecundity (discussed in Section 3.3.3), may explain some of the variation among species in egg production per night. Furthermore, some species are known to engage in egg-eating, such as *Campylomormyrus compressirostris* (Nguyen et al., 2017) and *Marcusenius macrolepidotus* (Werneyer & Kramer, 2005), so actual number of eggs spawned may be higher in some cases. With regard to spawning interval, for some species, the spawning interval for a pair of fish is much longer after the first spawn and/or just before the last spawn and is shorter in between other spawning nights (Kirschbaum, 1987).

Fertilization rate has been assessed in a few species. Using artificial fertilization in *Mormyrus kannume*, Iles (1960) reports that 10%–25% of eggs were fertilized. During laboratory matings of *Campylomormyrus*, 7.3%–42.4% of *C. compressirostris* eggs were fertilized and 0%–67.1% of *C. rhynchophorus* eggs were fertilized (Nguyen et al., 2017). Nguyen et al. (2017) observed that fertilization rates for specific pairs of fish increased over successive spawning events and hypothesizes that this could be due to increased coordination of the fertilization pocket during spawning. Rates of fertilization using artificial fertilization or natural spawning within a laboratory setting have been shown to decrease fertilization rates in other fishes (Coward et al., 2002) and therefore these rates may not reflect fertilization rates in wild populations of mormyroids. Furthermore, fertilization rates in mormyroids are low relative to some other fishes, such as the zebrafish which has a fertilization rate of 86% (Mukhi & Patiño, 2007).

3.4.2 | Nest building and parental care

Nest building and parental care have been reported in two genera, *Gymnarchus* and *Pollimyrus*, and appears to be absent from others. With the onset of the rainy season, wild *G. niloticus* build elliptical floating nests of plant material. Budgett (1901) reported the exterior measurements of the nest to be two feet by one foot (60.96 × 30.48 cm) and interior measurements to be one foot by six inches (30.5 × 15.24 cm). In terms of nest structure, three sides project out of the water and the fourth lies approximately two inches (5.08 cm) below the surface. Spawning occurs within 10 days of nest building (Hopkins, 1986; Oladosu, 1997). Adults demonstrate parental care by guarding nests and offspring from potential threats including humans who have reported the fish have a "very formidable bite" (Agbugui et al., 2021; Budgett, 1901). In laboratory populations of *Pollimyrus adspersus*, males build 3 × 3 × 4 cm nests using plant materials within their territories days to weeks before spawning occurs (Bratton & Kramer, 1989; Kirschbaum, 1987). Males may build additional nests if subsequent spawning events occur less than 18 days apart. After spawning, males will collect the eggs in their mouth and deposit them into the nest. Males guard embryos and larvae for several weeks and occasionally fan the eggs using the caudal fin.

3.4.3 | Locomotor, acoustic, and electrical behavior

Courtship and spawning behavior have been studied in some mormyroid species including *Marcusenius macrolepidotus*, *Brienomyrus brachyistius*, and four species of *Pollimyrus*. These behaviors can consist of locomotor, acoustic, and electrical displays and may be simple or complex. For characterization of communication signals discussed below see Crawford et al. (1986) for acoustic signals and Bratton and Kramer (1989), Werneyer and Kramer (2005), and Wong and Hopkins (2007) for electrical signals.

Locomotor behavior: Locomotor behavior during courtship/spawning varies among species, but generally may consist of behaviors such as the female repeatedly entering/exiting the male's territory, initial male aggression towards the female (including lunging and chasing), decrease in male aggression, fish hovering near each other, head-to-tail circling, and coupling at the genital pore (Baier & Kramer, 2007; Bratton & Kramer, 1989; Kirschbaum, 1987; Werneyer & Kramer, 2005; Wong & Hopkins, 2007). Upon coupling, the male flexes his anal fin concavely around the female's genital pore to create a closed-off fertilization pocket into which eggs and sperm are released. In *Pollimyrus* courtship, fish may become coupled but not release gametes and instead will rotate vertically before separating (Bratton & Kramer, 1989; Kirschbaum, 1987). In terms of duration, courtship before spawning may last minutes, as in *M. macrolepidotus* (Werneyer & Kramer, 2005), or several hours, as in *Pollimyrus* (Bratton & Kramer, 1989; Kirschbaum, 1987). In *P. adspersus*, periods of courtship with no spawning event on the same night have been observed (Bratton & Kramer, 1989). Spawning duration also varies; *Pollimyrus* may spawn for 2–6 h (Bratton & Kramer, 1989) while the two described spawning events in *M. macrolepidotus* lasted 20 and 45 min each (Werneyer & Kramer, 2005). However, fish do not remain coupled during this entire duration. Rather, fish repeatedly couple, spawn, and separate over this period of time. After spawning, *Pollimyrus* males will return to the spawn site, collect eggs, and deposit them into a nest constructed of plant material where they will engage in parental care of eggs and larvae (Baier & Kramer, 2007; Bratton & Kramer, 1989; Kirschbaum, 1987). Other species do not exhibit parental care.

Acoustic behavior: Mormyroidea are well-known for electric communication, but they are also capable of acoustic communication. In the context of breeding, these acoustic signals have only been studied in *Pollimyrus*. During courtship/spawning *P. adspersus* males produce three types of vocalizations: grunts, moans, and growls. The male begins producing these vocalizations before nest building.

TABLE 6 Eggs produced per spawning night and spawning intervals for several mormyroid species.

Species	Eggs produced per spawning night	Spawning interval (days)	Reference(s)
Hippopotamyrus pictus	66–772	20–30	Kirschbaum & Schugardt (2002)
Marcusenius macrolepidotus	25–60 per bout, 27 bouts[a]	12	Werneyer & Kramer (2005)
Mormyrus rume proboscirostris	364	21	Schugardt & Kirschbaum (2004)
Petrocephalus soudanensis	180–283	34	Kirschbaum & Schugardt (2002)
Pollimyrus adspersus	50–192	5–20	Bratton & Kramer (1989); Kirschbaum (1987)
Campylomormyrus cassaicus	121–1662	15–80	Kirschbaum & Schugardt (2002)
Campylomormyrus compressirostris	132[a]	18	Nguyen et al. (2017)
Campylomormyrus phantasticus	250–400	14–43	Kirschbaum & Schugardt (2002)
Campylomormyrus rhynchophorus	645	6–66	Nguyen et al. (2017)
Campylomormyrus tshokwe	608	10–75	Nguyen et al. (2017)

Note: All measurements come from breeding in laboratory experiments.

[a] Known to engage in egg eating so actual counts may be higher.

Vocalization frequency increases as the spawning night approaches and is inversely correlated with aggression towards the female as she visits the male's territory. Vocalization frequency peaks during the hours before courtship but decreases significantly during courtship and spawning activity. In between spawning bouts, the male will resume vocalization but will cease vocalization when the female returns. Vocalizations produced by the female have not been reported. Crawford et al. (1986) concluded that these vocalizations are advertisement calls to inform the female of a potential mate and breeding site. Similar vocalizations have also been reported in *P. isidori* (Crawford et al., 1997) and *P. castelnaui* and *P. marianne* (Baier & Kramer, 2007).

Electrical behavior: Finally, electrical behaviors during courtship and spawning have been observed and vary among species. In *B. brachyistius*, fish engage in "electrical duetting" where a pair will produce an alternating sequence electrical communication signals. Males will produce rasps and females will produce bursts in response, or vice versa (Wong & Hopkins, 2007). Wong and Hopkins (2007) hypothesize that rasps and bursts may function as the male's advertisement signal or convey fitness information. In *M. macrolepidotus*, males will switch between periods of extremely short interdischarge intervals (IDIs) and longer IDIs during courtship; however, these electrical patterns were not correlated with any specific courtship behavior and have also been observed in agonistic interactions (Werneyer & Kramer, 2005).

Pollimyrus exhibit more complex electrical behavior during courtship/spawning than the other species. These electrical behaviors consist of different patterns of EOD pulses that can be described as either low and/or medium, depending on how quickly pulses are produced, and uniform or sporadic, depending on if pulses are produced at a regular interval or not. On nights when a spawning event occurs, *P. adspersus* females will produce a medium uniform rate before entering the males territory, but will become electrically silent when entering the territory. Once courtship is initiated, the female will produce a low-medium sporadic rate and after fish separate the female resumes a medium uniform rate. When the female enters his territory, the male switches from the typical territory patrol EOD pattern, a medium sporadic rate, to a medium uniform rate. The male continues to produce this medium uniform rate throughout courtship, but is electrically silent during coupling. After fish separate, the male resumes a medium uniform rate. In *P. castelnaui* and *P. marianne* electrical behavior is different (Baier & Kramer, 2007). The male is electrically silent when the female approaches the spawning site, but will produce double pulse patterns of alternating short and long IDIs during other steps of courtship and spawning. The female produces regular 50 ms IDIs during all steps of courtship and spawning.

3.5 | Artificial reproduction and hybridization

Attempts at artificial reproduction have only been reported in a few species of mormyroids: *Mormyrus kannume* (Iles, 1960), *Campylomormyrus tshokwe* (Nguyen et al., 2017), and *Brienomyrus brachyistius* (Constantinou et al., 2019). There have been no reports of cryopreservation of sperm for later use in artificial fertilization. Artificial reproduction has also been used to create Intragenus and intergenus mormyroid hybrids which is discussed below.

Successful hybrid matings of individuals from different species morphs and even different genera have occurred. The *Paramormyrops magnostipes* (previously *Brienomyrus magnostipes*) species complex is a group of three closely related species that are indistinguishable with regard to external morphology, but differ in EOD waveform (Arnegard et al., 2005). It is hypothesized that differences in waveform are used for species recognition during courtship, but successful hybridization between morphs has been observed in wild populations in Gabon. Similarly, there is evidence for hybridization between different electric signal morphs of *Paramormyrops kingsleyae* which also reside in Gabon (Gallant et al., 2011; Picq et al., 2020). Viable hybrids of mormyroids in wild populations can have great consequences for studies in which species is an important variable, including speciation work, and as such the possibility of hybridization should be considered by researchers.

Hybridization has also been achieved in the laboratory. Intragenus and intergenus *Campylomormyrus* hybrids have been created in the laboratory using artificial fertilization (Kirschbaum et al., 2016; Korniienko et al., 2022). Intragenus hybrids were created using pairs from the following species: *C. compressirostris*, *C. tamandua*, *C. tshokwe*, and *C. rhynchophorus*, and *C. numenius*. Hybrids from all pairs of species were viable, and *C. compressirostris* female × *C. tamandua* male hybrids were fertile. Attempted intergenus hybridizations include *Hippopotamyrus pictus* female × *C. numenius* male (embryos nonviable), *C. rhynchophorus* female × *Mormyrus rume proboscirostris* male (viable up to 40 days), and *C. rhynchophorus* female × *Gnathonemus petersii* male (viable to adulthood, fertile).

4 | CONCLUSIONS AND FUTURE DIRECTIONS

The Osteoglossiform superfamily Mormyroidea is a species-rich and diverse group of teleost fishes that possesses great potential in biomedical research (see Section 2). However, the inability to reliably breed these fishes in the laboratory setting has hindered widespread use of mormyroids as biomedical models. To facilitate progress toward the goal of reliable mormyroid laboratory breeding, we extensively examined the current landscape of mormyroid reproductive biology literature in this review. While mormyroids exhibit considerable variation across species, there are several common themes within the group including (1) sexual dimorphism in anal fin morphology and/or electric signal structure/signaling behavior in several species, (2) unpaired gonads that recrudesce during the rainy season in the wild or with decreasing water conductivity in the laboratory, (3) aflagellate sperm in all species examined thus far, and (4) fractional spawning and external fertilization in all species and courtship/parental care present in some species. We would also like to recognize several key points that the aspiring mormyroid breeder should be aware of. First, reproductive condition can be induced in the laboratory by exposing fish to a decrease in water conductivity. However, there is varied success among and within species using this method. Second, some species (such as *Pollimyrus sp*. and *Gymnarchus niloticus*) build nests and as such require additional materials to be present in the tank. Although other species do not build nests, they may show some preference for certain spawning substrates. Third, since mormyroids are fractional spawners, they cannot reach their full reproductive output with a single night of spawning. Therefore, fish should be set up for mating for several weeks and allowed to spawn for multiple nights. Finally, reported fertilization rates range from 0% to 67.1% and vary with species and fertilization method (natural spawning vs artificial fertilization). Despite the abundance of information pertaining to mormyroid reproductive biology that is available, there are several areas that are understudied or wholly unexplored, many of which may lead to insights about how to improve laboratory breeding success.

First, the information known about Mormyroidea reproductive biology comes from 42 species (considering the *Paramormyrops magnostipes* complex as a single species, the subspecies *M. rume rume* and *M. rume proboscirostris* as one species, and the subspecies *H. bebe bebe* and *H. bebe occidentalis* as one species) which represents approximately 18% of the 232 currently recognized species (Peterson, Sullivan, Hopkins, et al., 2022). Furthermore, there is disparity in the depth of information known about each species. For example, there has been only one study of the genus *Ivindomyrus* (Lavoué et al., 2008), whereas the genus *Pollimyrus* has been studied extensively with regard to anatomical and electrical sex differences (Bratton & Kramer, 1989; Kirschbaum, 1987), breeding season (Crawford et al., 1997), testis structure (Lücker & Kramer, 1981), triggers of gonadal recrudescence (Kirschbaum, 1987), egg size (Kirschbaum & Schugardt, 2002; Postner & Kramer, 1995), and detailed accounts of courtship and spawning behaviors (Baier & Kramer, 2007; Bratton & Kramer, 1989; Kirschbaum, 1987). Since Mormyroidea are so diverse, it would be imprudent to assume that the reproductive biology of any individual mormyroid species applies to the entire group. Our main message is to encourage future researchers to increase the taxonomic scope of mormyroid reproductive research, which may help answer questions relevant to laboratory breeding success. In particular, (1) How prevalent are the anal fin and electric signal sexual dimorphisms across the group? And are there any other notable sexual dimorphisms that may be used for sex identification purposes in some species? (2) Is decreased water conductivity a reliable trigger for gonadal recrudescence in all mormyroids, as it seems to have varied success? (3) What is the ideal laboratory mating setup for different species (sex ratios, pair/group mating dynamics, nesting materials, preferred spawning substrate)?

A second, poorly understood aspect of mormyroid reproduction are the physiological and anatomical changes induced by the onset of the rainy season or decrease in water conductivity. One study examined ovary structure in four mormyroid species (Dymek et al., 2022) which gives some insights into changes that occur within the ovary throughout oogenesis. However, the use of only 1–2 specimens per species in this study limits known information about oogenesis to a single point of the reproductive cycle for each species. An expansion upon this study to include (1) more species and (2) multiple points during the reproductive cycle for each species would be beneficial to understanding female gonadal recrudescence and gamete production. Similarly, a study such as this should be completed for males as well to understand spermatogenesis, particularly given the aflagellate morphology of mormyroid sperm. Furthermore, the mechanisms by which environmental triggers lead to reproductive condition in mormyroids are presently unknown, and may be a fruitful area of future study: elementary physics suggest that the electrosensory system of mormyroids is susceptible to changes in water conductivity, suggesting a potential mechanism for detecting seasonal change in conductivity, but the connection between these reliable environmental cues, hormonal state, and gonadal development needs much deeper exploration.

Finally, there are several outstanding questions regarding mormyroid sperm. First, mormyroid sperm is the only known case of aflagellate sperm evolving within a vertebrate lineage (Morrow, 2004). What evolutionary pressures resulted in the evolution of aflagellate sperm within only this vertebrate lineage? Second, in other animal taxa, absent or abnormal sperm flagella is a common cause of infertility and typically is linked to some genetic mutation (Chemes et al., 1998). What is the genomic basis of sperm aflagellism within mormyroids and might be it something to scan for in human males with asthenospermia? Finally, the fertilization dynamics of mormyroid sperm are wholly unknown. How does mormyroid sperm successfully travel to the egg and down the micropyle to initiate fertilization without the typical motility apparatus? There are several possible avenues to approach this question. In some teleost species, accessory structures on the egg surface function in guidance of sperm to the micropyle (Amanze & Iyengar, 1990; Riehl & Kokoscha, 1993) and similar structures even appear within species of Osteoglossiformes (Britz, 2004; Daget, 1957; Mookerjee & Mazumdar, 1946; Yanwirsal et al., 2017). Therefore, it is possible that such features exist within mormyroids that have yet to be discovered due to lack of studies on egg morphology (with the exception of Diedhiou et al. (2007) which provides only a brief description of the *Pollimyrus isidori* egg surface). Other areas that may be pertinent to explore regarding mormyroid fertilization dynamics may be ovarian fluid composition and presence of chemoattractants, both of which are important in fertilization in some teleosts (Alonzo et al., 2016; Kholodnyy et al., 2020; Myers et al., 2020) but are completely unexplored within mormyroids.

Mormyroids have great potential as a model system in several areas including extreme encephalization, the neural basis of behavior, muscle evolution and development, craniofacial evolution and development, ion channel function, and flagella/ciliary function. Despite this enormous potential, they are notoriously difficult to breed in the laboratory setting which currently hinders widespread use of mormyroids as biomedical model organisms. Here, we have comprehensively integrated available data on mormyrid breeding with the ultimate goal of breaking this present impasse, and have highlighted major questions and future directions for research that may 1 day promote the more widespread use of mormyroids as a biomedical research model.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data sets were generated or analyzed during the current study.

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