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REVIEW PAPER

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Sperm competition, sexual selection and the diverse reproductive biology of Osteoglossiformes

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Abstract

Osteoglossiformes are an order of “bony tongue” fish considered the most primitive living order of teleosts. This review seeks to consolidate known hypotheses and identify gaps in the literature regarding the adaptive significance of diverse reproductive traits and behaviour of osteoglossiforms within the context of sperm competition and the wider lens of sexual selection. Many of the unusual traits observed in osteoglossiforms indicate low levels of sperm competition; most species have unpaired gonads, and mormyroids are the only known vertebrate species with aflagellate sperm. Several osteoglossiform families have reproductive anatomy associated with internal fertilization but perform external fertilization, which may be representative of the evolutionary transition from external to internal fertilization and putative trade-offs between sperm competition and the environment. They also employ every type of parental care seen in vertebrates. Geographically widespread and basally situated within teleosts, osteoglossiforms present an effective study system for understanding how sperm competition and sexual selection have shaped the evolution of teleost reproductive behaviour, sperm and gonad morphology, fertilization strategies, courtship and paternal care, and sexual conflict. The authors suggest that the patterns seen in osteoglossiform reproduction are a microcosm of teleost reproductive diversity, potentially signifying the genetic plasticity that contributed to the adaptive radiation of teleost fishes.

KEYWORDS
adaptation, fish, natural selection, reproduction, sexual selection, sperm competition

1 | INTRODUCTION

The approximately 26,000 known species of teleost fish occupy a wide range of aquatic habitats (Froese & Pauly, 2019) and exhibit a remarkable array of reproductive strategies (Helfman *et al*., 2009). It is presently unclear which factors contribute to the evolution of such numerous reproductive strategies within teleosts (Smith & Wootton, 2016). The basally situated Osteoglossiformes (“bony tongue”) are a microcosm of teleost reproductive diversity. They exhibit variation in reproductive anatomy, gamete morphology and reproductive behaviour, all suggesting flexibility early in teleost evolution (Figure 1). Osteoglossiforms are distributed worldwide and are comprised of five families: Osteoglossidae (15 species in South America, Africa, Asia and Australia), Notopteridae (10 species in Africa and Southeast Asia), Pantodontidae (one species in Africa), and two families of weakly electric fish, Mormyridae (>200 species, Africa) and Gymnarchidae (one species, Africa). In accordance with osteoglossiforms' cosmopolitan distribution and their ancestral position within teleosts, insights into the evolution of their reproductive diversity may lead to a new understanding about the factors underlying the evolution of reproduction in teleosts (Figure 2).

Several reviews have considered osteoglossiform reproductive behaviour (Britz, 2004; Hopkins, 1986; Karino, 2009; Kolm, 2009; Yanwirsal, 2013) and sperm morphology (Jamieson, 1991;

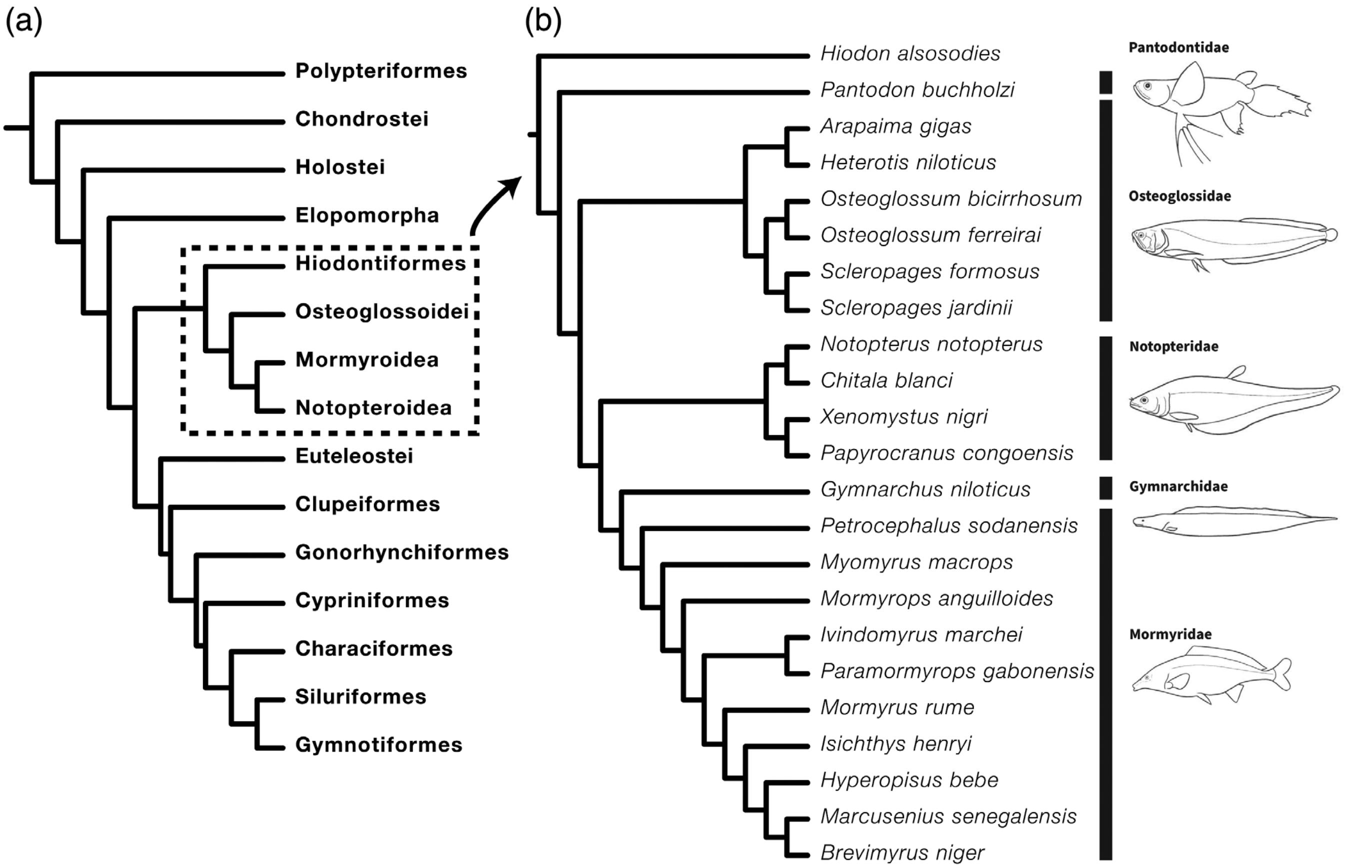
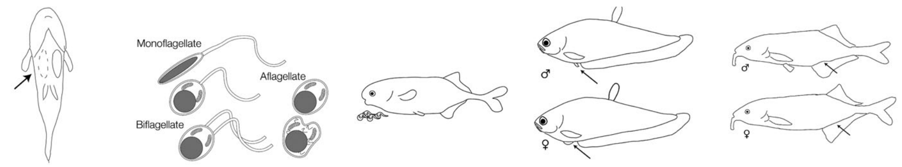


FIGURE 1 (a) Phylogeny of all major teleost clades (adapted from Nelson *et al*., 2016). (b) Detailed phylogeny of Osteoglossiformes, including selected names and illustrations of representative species from the families Pantodontidae, Osteoglossidae, Notopteridae, Gymnarchidae and Mormyridae. Representative images of each group are from Nelson *et al*. (2016), reproduced with permission from publisher



Family	Location	Singular Gonad	Sperm Type	Parental Care	Genital Papillae	Anal Fin Notch
Pantodontidae	Africa	N	Monoflagellate	N	Y	Y
Osteoglossidae	Africa, Asia, Australia	Y	Biflagellate	Y	N	N
Notopteridae	Africa, Asia	Y	Monoflagellate	Y	Y	N
Mormyridae	Africa	Y	Aflagellate	Y/N	N	Y
Gymnarchidae	Africa	Y	Aflagellate	Y	N	N

FIGURE 2 Summary of the geographic distribution and reproductive traits in various families of Osteoglossiformes. Y = yes, N = no, see text for supporting references. Images depict reproductive traits from representative species

Mattei, 1988, 1991; Mattei *et al*., 2018; Pitnick *et al*., 2009). The purpose of this review is to integrate and contextualize current understanding of reproductive anatomy, gametic morphology and reproductive behaviour in light of sperm competition and sexual selection, discussed in Section 2. Section 3 assesses the role of sperm competition and sexual selection in contributing to osteoglossiform reproductive anatomy with a focus on their unusual unpaired gonads and sexually dimorphic traits. Section 4 discusses how sperm competition may select for aflagellate, monoflagellate and biflagellate sperm in osteoglossiforms, and whether this gamete morphology imposes specific sperm–egg interactions. Section 5 considers how morphological traits, sperm competition and sexual selection interact and contribute to adaptive reproductive behaviour during courtship and parental care. Section 6 details the challenges of differentiating the effects of sperm competition and sexual selection from environmental constraints and includes suggestions for studies to fill current gaps in knowledge on these topics. This article concludes with recommendations for combining research on osteoglossiform reproduction with genomics for the benefit of understanding teleost diversity.

2 | SPERM COMPETITION

Sperm competition theorists largely agree that ejaculate expenditure is determined by sexual selection in accordance with economic principles (Parker & Pizzari, 2010). A major sperm competition theory models sperm competition as a raffle, in which each male has a probability of fertilization that is dependent on the number of sperm he has contributed, compared to his competitors (Parker, 1990). Under conditions in which there is less competition among males either pre-fertilization (*e.g*., internal fertilization or close proximity of a mating pair) or post-fertilization (*e.g*., females mate only once), a single male would be expected to provide sperm of lower quantity and quality. In situations where sperm competition risk is high, sperm competition has the potential to act as a type of quality control and favour high volumes of efficient, error-free sperm. This strategy has limitations, however; while producing sperm is not considered to be as energetically expensive as producing eggs, sperm and ejaculate fluid is not low cost (for a review see Pitnick *et al*., 2009). Thus, sperm competition suggests that males will not produce high-quality sperm unless the benefits exceed the costs of production.

Sperm competition and sexual selection are cyclically linked from the cellular to behavioural levels of biological organization (Parker, 2014). Females contribute more resources than males to gamete production and often invest further in offspring survival by providing parental care. Because their fitness is limited by their ability to produce gametes, females typically become the choosy sex. Male fitness is limited instead by the availability of the opposite sex. This leads to sexual selection, in which males compete with other males for mating opportunities with the opposite sex. When males experience strong sexual selection, sperm competition is expected to be high.

3 | ANATOMICAL TRAITS

The diversity of teleost body plans presents a challenge for identifying rules of selection on fish reproduction. The relationship between reproductive anatomy and overall body anatomy can be confounded by the effects of phylogeny, foraging mode and hydrodynamic and environmental concerns on body shape (Montgomerie & Fitzpatrick, 2009). Nonetheless, general patterns in osteoglossiform morphology, as a sub-set of teleosts, can serve as useful indicators of selective factors, such as sperm competition and sexual selection, that shape reproductive traits in fishes. This section focuses on two anatomical traits in osteoglossiforms, unpaired gonads and sexual dimorphism, and discusses the relationship of these features with parental care and divergent fertilization strategies.

3.1 | Singular gonads

Although most teleost fish have paired gonads, most osteoglossiforms have a single gonad. The one known exception is *Pantodon buccholzi*, in which females have both left and right developed ovaries (Nysten, 1962). A single gonad on the left side of the body has been observed in adult Osteoglossidae (Fontanele, 1948; Lake & Midgley, 1970; Lüling, 1964; Merrick & Schmida, 1984; Moreau, 1982), Notopteridae (Argumedo, 2009; Dalela *et al*., 1976; Nyonje, 2006; Yanwirsal *et al*., 2017), Mormyridae (Adjibade *et al*., 2020; Iles, 1960; Nawar, 1959; Schugardt & Kirschbaum, 2004; Scott, 1973) and Gymnarchidae (Opadokun & Ajani, 2015). Unpaired gonads are synapomorphic for the Osteoglossiformes, whereas paired ovaries are likely a plesiomorphic trait of Osteoglossomorpha (Britz, 2004; Yanwirsal *et al*., 2017).

Although singular gonads are relatively uncommon, identifying the selective pressures that led to their development in other species may be fruitful for understanding how they evolved in osteoglossiforms. In teleosts, the evolution of an unpaired testis appears to be a rare occurrence. Nonetheless, a single median ovary is observed in most viviparous teleosts, such as poecillids (Scrimshaw, 1945) and the marbled swamp eel (Synbranchiformes: Symbranchidae) (Ravaglia & Maggese, 2002), as well as both oviparous and viviparous goodeids (Uribe *et al*., 2012). Fertilization can take place in the ovarian cavity or follicles, with the ovary providing a nutritional role for internally gestating young (Aranzábal *et al*., 2009).

Ovarian asymmetry is also associated with viviparity in other ancestral groups of fishes. Coelacanths tend to have asymmetric ovaries in which the right ovary is functional and the left is sterile (Millot *et al*., 1978). Many sharks and rays also have asymmetric ovaries (Wourms, 1977). Nurse sharks (*Ginglymostoma cirratum)* develop only one ovary on the right side of the body (Castro, 2000). Amazonian freshwater stingrays (*Potamotrygon wallacei*) have two functional ovaries, but the left ovary is 55 times larger than the right ovary (da Silva *et al*., 2017). The presence of ovarian asymmetry in both Chondrichthyes and Osteichthyes suggests that this primitive trait may go as far back as the Gnathosomes.

Asymmetric gonads are found in other vertebrate species (Yu, 1998), including platypus, which have a functioning ovary only on the left side (Grützner *et al*., 2008), as well as contrasting directional asymmetry found in frogs (Liu *et al*., 2011; Zhou *et al*., 2011) and birds (Friedmann, 1927). Males in many avian species have a smaller right testis than the left (Lake, 1981). For example, the left testis of the male zebra finch is about 50% larger than the right testis (Birkhead *et al*., 1998). Females typically only develop a left ovary and oviduct, whereas the right ovary regresses and degenerates after hatching (Wakamatsu *et al*., 2000). This reversed pattern of asymmetry between males and females implies that the loss of a functional gonad is not homologous between the two sexes in birds (Ligon, 1997). It is hypothesized that the right ovary is vestigial in females and this loss is an adaptation to reduce weight for flight (Guraya, 2013; Zhang *et al*., 2014). Nonetheless, considering that ovarian asymmetry exists in non-flying platypus and ratite birds, it is also possible that coordination of egg production through a single oviduct provides protection for fragile eggs (Guioli *et al*., 2014). In birds, it takes time for the eggshell to develop between ovulation and when the egg is laid, and it has been suggested for raptors that multiple eggs in close proximity within the mother's abdomen could reduce their survival (Guioli *et al*., 2014; Walter, 1979). If a potential relationship exists between single gonads and egg protection, it is possible that this may be a practical cause of single gonads in other egg-producing species, including amphibians or fish.

The cause and mechanisms of directional asymmetry in most avian males are unknown, but male coucals (Cuculiformes: Centropodinae) exhibit atrophied or complete loss of the left testis (Rand, 1933). Several studies suggested that coucals may develop only one functional testis as the by-product of a physiological mechanism that decreases testosterone and promotes paternal care (Goymann *et al*., 2004b; Ligon, 1997). But, this idea was subsequently rejected due to male coucals exhibiting testosterone levels similar to those of socially monogamous male birds with two testes, as well as presenting high levels of androgens overall (Goymann *et al*., 2004a; Goymann *et al*., 2004b; Goymann & Wingfield, 2004; Voigt & Goymann, 2007).

3.2 | Sexual dimorphism

Sexual dimorphism in osteoglossiforms appears to be primarily functional for reproduction and, similar to many fishes, related to key differences that define internal from external fertilization strategies (Evans & Meisner, 2009; Meisner, 2005). A notched anal fin is attributed to the males of *Pantodon* (Hjerresen, 1937) and several mormyrid species (Brown *et al*., 1996; Iles, 1960; Kirschbaum, 1987; Nawar, 1959; Pezzanite & Moller, 1998; Svensson, 1933), and Notopteridae have sexually dimorphic genital papillae (Weitkamp, 2005; Yanwirsal, 2013; Yanwirsal *et al*., 2017). Interestingly, these species exhibit behaviours attributed to both external and internal fertilizers, even though sexually dimorphic anal fins, elongated genital papillae and elongated spermatozoa are all traits associated with internal insemination in species belonging to Characiformes, Siluriformes, Osmeriformes, Ophiidiformes, Atheriniformes, Beloniformes, Cryprinodontiformes, Scorpaeniformes and Perciformes (Burns *et al*., 1995; Evans & Meisner, 2009; Jamieson, 1989; Koya *et al*., 2002; Luo *et al*., 2011; Spadella *et al*., 2012).

P. buccholzi is the only osteoglossiform species with all three of these traits and also the only one hypothesized to perform internal fertilization; visual observations are still required for definitive confirmation. Males have paired orifices adjacent to the anal fin that lead to a pouch holding a complex copulatory organ (Lastein & Van Deurs, 1973). The cone-shaped organ is made of connective tissue that forms two folded structures situated in two pouches, each covered by a bony plate that protrudes during spawning and that appears to function to internally inseminate the female (Hjerresen, 1937; Lastein & Van Deurs, 1973). In combination with their unusual sperm phenotype (see Section 4.1), *P. buccholzi* is the only member of this order with anatomy wholly suited for insemination, exhibiting reproductive anatomy similar to that of several internally fertilizing species belonging to Galaxiidae (Pusey & Stewart, 1989), Aphyonidae (Nielsen, 1984) and Bythidae (Suarez, 1975), among others (Evans & Meisner, 2009). Among the nine teleost orders listed earlier that contain internally inseminating species with modified anal fins and/or elongated genital papillae (Evans & Meisner, 2009), those species which instead perform external fertilization often have modified reproductive features that do not form a true intromittent organ, but rather allow the male to direct sperm towards the female. These modifications can range from elongated and thickened anal fins with hooks or spines to anal fins whose rays have been fused to create a pseudopenis. There are, however, additional notable exceptions and gaps within whole family studies of teleosts in which one or more defining features of sexual dimorphism and internal fertilization are lacking (*e.g*., Grier *et al*., 1990). This makes it impossible, thus far, to link the presence of these traits to a specific reproductive strategy without evidence of the reproductive mode in question.

The notopterids *Notopterus notopterus*, *Chitala ornata* (Asia) and *Xenomystus nigri* (Africa) exhibit sexually dimorphic genital papillae which differ by species. *N. notopterus* and *C. ornata* males have a narrow, reddish genital papilla that is longer than the pelvic fin, whereas the *N. notopterus* females have a broader, whitish papilla that is shorter than the pelvic fin (Yanwirsal, 2013) and the *C. ornata* females have an elongated papilla that is wider than the anal opening (Castro *et al*., 2019). The female's papilla appears to grow and is larger during the courtship and spawning phases (Yanwirsal, 2013). In *X. nigri*, the female's genital papilla is surprisingly longer than the pelvic fin, whereas the male's genital papilla is shorter and located underneath the pelvic fin (Nyonje, 2006; Yanwirsal, 2013). These features are likely adaptive for egg deposition: tubular papillae, when swollen, can help fish propel eggs away from their body and contribute to precise positioning of the eggs on the substrate (Castro *et al*., 2019; Martin & Page, 2015).

Mormyrids represent an anomaly among osteoglossiforms in that they are known external fertilizers that share the anatomical and behavioural traits of species that reproduce *via* internal fertilization. Several species have a sexually dimorphic fin anal fin notch (Brown *et al*., 1996; Iles, 1960; Kirschbaum, 1987; Nawar, 1959; Pezzanite & Moller, 1998; Svensson, 1933) which, when accompanied by a behavioural sequence, may help males deliver immotile sperm (see Section 4) to the female. The specific function of the anal fin notch is unknown, but it could simply provide structural flexibility, allowing the males to bend their body at a typically rigid midpoint. In mormyrids, the male is thought to cup his fin around the female's genital opening, creating a confined fertilization space in which the female releases her eggs (Brown *et al.*, 1996; Iles, 1960; Pezzanite & Moller, 1998). Similar spawning behaviour has been observed in other distantly related fish species that have a modified anal fin (Britz & Bartsch, 1998). Although the cupping behaviour has never been directly observed during spawning, a reflexive anal fin cupping motion can be stimulated through tactile stimulation in *Pollimyrus isidori* (Kirschbaum, 1987), *Campylmormyrus compressirostris*, *Campylmormyrus rhynchophorus* and *Campylmormyrus tamandua* (Feulner *et al.*, 2009). The notch may assume its original form when the testes regress after the breeding period (Iles, 1960).

3.3 | Singular gonads and sexual dimorphism as they relate to sperm competition

Initially, osteoglossiforms' loss of a second gonad from an equally sized gonad pair appears to be a handicap to reproduction due to a potential loss in gamete production (Frey & Goymann, 2009). Nonetheless, it is not currently known whether a single gonad doubles gamete production as compensation for the loss of the pair. The absence of a paired gonad can also be viewed as a loss of a "back-up" organ. Redundancy within a general bilateral body plan affords continued reproductive success to any individual that damages or loses one gonad in a set.

Exceptions to the "paired gonad" pattern may demonstrate ways in which a single gonad may actually be adaptive, or at least neutral, for osteoglossiforms. Species that perform parental care typically have low sperm competition and are expected to have a smaller relative testis size (for review see Montgomerie & Fitzpatrick, 2009; Pitnick *et al.*, 2009), but not specifically the evolution of singular gonads. Osteoglossiforms demonstrate a positive association between parental care and single testis development from an anatomical perspective, indicating that there may be some relationship between these traits other than *via* a hormonal mechanism for the purpose of facilitating paternal care. This association could also be mediated differently in fish than it is in birds such as the coucals. Most osteoglossiforms have one gonad, and most species demonstrate parental care; *Pantodon*, which has paired gonads, lacks parental care. Nonetheless, parental care is also lacking in a majority, but not all mormyrid species (Budgett, 1901a; Crawford *et al.*, 1986; Diedhiou *et al.*, 2007; Heymer & Harder, 1975; Kirschbaum & Schugardt, 2002), even though all mormyrids have single gonads.

Many osteoglossiform males demonstrate a low gonadosomatic index (GSI) (Adite *et al.*, 2006; Adjibade *et al.*, 2020; Hussain *et al.*, 2015; Khallaf & Authman, 2012; Opadokun & Ajani, 2015). Nonetheless, it is unclear how these values compare to other teleosts, because not all GSI reports consider cyclical fluctuations in gonad size. GSI values could be due to osteoglossiforms' singular testis being of comparatively smaller size than either one or both gonads in other teleosts. Nevertheless, low GSIs are associated with conventional male strategies (Neff *et al.*, 2003) and decreased sperm competition in fish (Peterson & Warner, 1998), amphibians (Jennions & Passmore, 1993) and birds (Birkhead & Moller, 1992), suggesting that osteoglossiforms' GSI values provide further support for low competition in these species as well.

Sexual dimorphism is often associated with sperm competition in that competition between males for access to females leads to the evolution of male alternative reproductive tactics (MARTs) (Taborsky, 1998) and secondary sex characteristics such as body size, male armaments to outcompete other males or ornaments to impress choosy females (Darwin, 1871). MARTs have been associated with intra-male variation in sperm traits; sneaker males tend to have higher-performing sperm than conventional males (Kustra & Alonzo, 2020), such as in the more motile sperm of male sneaker *Heterololigo bleekeri* squids (Hirohashi *et al.*, 2016). Nonetheless, there is currently no evidence of intra-male variation in mating tactics or sperm traits within any osteoglossiform species. Variation in secondary sex characteristics, and the adaptative nature of their functionality for survival and reproduction, represents raw material during intraspecific choice contests which may select for more extreme sexual dimorphic traits (West-Eberhard, 1983). Yet, osteoglossiforms have no notable differences in male and female colours or ornamentation (Bian *et al.*, 2016; Moreau, 1982; Yanwirsal, 2013). Most osteoglossiforms, like many fishes, also have similarly sized males and females. Further evidence of other secondary sex characteristics mediated by sexual selection may not comprise human-visible cues (Karino, 2009), such as the sexually dimorphic signals produced by electric fish; these signals may also be responsible for their rapid radiation (Carlson & Arnegard, 2011; Hopkins, 1986; Rabosky *et al.*, 2013).

In conclusion, the reduction in gonad number and sexually dimorphic structures associated with functional value, rather than secondary sex traits, indicates that osteoglossiforms have reproductive adaptations consistent with internal fertilization, even though most of them employ external fertilization. Internal fertilization often creates a mating environment with low sperm competition. Subsequently, these traits and fertilization strategies together point to low sperm competition as a driving force behind their adaptive functionality, and suggest that osteoglossiforms may be positioned midway on the evolutionary path from external to internal fertilization.

4 | SPERM MORPHOLOGY

Sperm morphology is often a reliable indicator of sperm competition because the cell itself is under such strong selection for achieving fertilization. Sperm ultrastructure has been extensively studied since the 1960s and described in over 280 species of fish (Mattei, 1991). Among fish, there are more than 70 derived sperm character states relative to a shared vertebrate ancestor (Jamieson, 1991). The order Osteoglossiformes presents a unique system for examining the relationship between sperm competition and morphology because it claims monoflagellate, biflagellate and aflagellate sperm types.

4.1 | Monoflagellate sperm – Pantodontidae and Notopteridae

P. buccholzi sperm is exceptionally elongated with a notably developed midpiece and extensive, modified mitochondria; it is morphologically more similar to the sperm of reptiles, birds and snakes than other teleost fish (Van Deurs, 1975; Van Deurs & Lastein, 1973). Taken into consideration with the male copulatory organ, this sperm phenotype further suggests that this species reproduces by internal fertilization (Lastein & Van Deurs, 1973). The ultrastructure of a single species from Notopteridae has been identified: *Papyrocranus afer*, the only other notopterid species besides *X. nigri* found in Africa, has a simple, monoflagellate sperm that resembles the ancestral sperm of Neopterygii (Mattei, 1970).

4.2 | Biflagellate sperm – Osteoglossidae

The sperm ultrastructure of only one osteoglossid species, *Heterotis niloticus*, has been described, and it has biflagellate sperm (Mattei *et al*., 2018). Biflagellate sperm is relatively uncommon: it has been observed in flatworms (Bakhoum *et al*., 2017; Orido, 1988), polychaetes (Franzén, 1982), freshwater clams (Komaru & Konishi, 1996), acoelomorphs (Barneah *et al*., 2007), one amphibian family (Mainoya, 1981) and 31 fish species across seven orders (Montgomerie & Fitzpatrick, 2009). Most of these fish species perform external fertilization, but biflagellate sperm is found in at least one internally fertilizing species, the ocean pout (Perciformes: Zoarcidae) (Yao *et al*., 1995). These fishes are distantly related, and without a clear phylogenetic pattern underlying the evolution of biflagellate sperm, it appears that this sperm morphology independently evolved many times (Montgomerie & Fitzpatrick, 2009).

4.3 | Aflagellate sperm – Mormyridae and Gymnarchidae

All mormyroid (Gymnarchidae and Mormyridae) sperm studied thus far (*Gymnarchus niloticus*, *Hyperopisus bebe*, *Mormyrus rume*, *Gnathonemus senegalensis*, *Gnathonemus niger* and *Petrocephalus bovei*) have an aflagellate morphology (Mattei *et al*., 1972). This is the only known origin of aflagellate sperm in vertebrates (Mattei *et al*., 1972), although there are reports of aflagellate sperm in two deep-sea Myctophidae (order: Myctophiformes) that require further confirmation (Jamieson, 1991), especially considering that the internal structure of these species' sperm is more similar to monoflagellated sperm (Young *et al*., 1987). The internal architecture of mormyrid spermatozoa resembles other teleost sperm more closely than the sperm of *G. niloticus* (Mattei *et al*., 1967; Mattei *et al*., 1972). In addition to lacking an acrosome (absent in all teleosts, see Section 6), mormyrid sperm specifically lack flagella and submembrane microtubules. They possess a rounded nucleus with two centrioles at its base, and some mitochondria in an abundant vesicular cytoplasm (Mattei, 1991). Although this structure appears to negate the possibility of the sperm being motile, the immotility of live spermatozoa has yet to be confirmed.

In contrast, *G. niloticus* has an aflagellate spermatozoan that has the most anomalous phenotype of all osteoglossiforms (Mattei *et al*., 2018). Due to its resemblance to basic metazoan sperm, it appears likely that *G. niloticus* secondarily evolved motility after the loss of flagella (Mattei, 1988). The uncondensed nucleus is at the centre of the cell, there is a large amount of cytoplasm and the plasma membrane is lined internally with a network of microtubules which contribute to its mobility *via* amoeboid motion (Mattei *et al*., 1967). Mattei noted that the internal structure is so aberrant that it barely ascribes to the typical definition of spermatozoa (Mattei, 1988).

4.4 | Sperm morphology as it relates to sperm competition

Monoflagellate sperm are known as a “primitive” sperm type and observed in the majority of teleost fishes. These sperm are made of a small round, nucleus followed by two centrioles, a midpiece with several mitochondria and a flagella with a typical 9 + 2 axoneme pattern that provides movement and propulsion (Jamieson *et al*., 1999). The basic sperm model is typical of externally fertilizing species and tends to be shorter and less divergent than those found in internally fertilizing species (Franzén, 1956). Sperm modifications, such as the extended midpiece found in *Pantodon*, are often adaptive in response to sperm competition and functional demands of their environment, specifically the female reproductive tract in internally fertilizing species (Lüpold & Pitnick, 2018; Pitnick *et al*., 2009). Notopterids demonstrate similar breeding behaviour to species with low sperm competition, suggesting that they also experience low sperm competition (Montgomerie & Fitzpatrick, 2009). Although motile flagella are common to all living things, they come at an energetic cost (Pitnick, 1996). Males that experience higher levels of sperm competition may benefit from spending energy on motile sperm, but species without strong sperm competition may be at a greater advantage by adopting modified sperm without flagella (Morrow, 2004).

Aflagellate sperm is associated with low sperm competition (Morrow, 2004) and internal fertilization (for arthropods see Dallai *et al*., 1973). Nonetheless, mormyrids and Gymnarchidae reproduce by external fertilization, which is typically associated with high sperm competition. These fishes may use behavioural strategies to reduce the risk of sperm competition: mormyrid males may minimize the risk of multipaternity by facilitating contact between sperm and eggs through ventral coupling during courtship (see Section 3.2). *G. niloticus* and two mormyrid species are known to build and guard nests, which is potentially another way to reduce competition among males. Nonetheless, these behaviours are not shared by all aflagellate mormyrid species.

It is presently unclear if aflagellism is adaptive. In the laboratory, studies on *Mormyrus kannume* macerated testis material was combined with eggs to simulate fertilization (Iles, 1960), and reported low fertilization success rates of 10%–25%, though it is likely that simulated fertilization may not be an accurate representation of natural fertilization success. Alternatively, it is possible that mormyroids experience low sperm competition. In that case, sperm competition would not be high enough to drive selection for costly, motile sperm at the expense of other traits required for reproduction. Speculatively, the energetics of electrogenesis and electroreception may require metabolic trade-offs (Salazar *et al*., 2013), and the ability to reproduce without producing sperm flagella may confer a metabolic fitness advantage (Montgomerie & Fitzpatrick, 2009). Evidence for low sperm competition in mormyrids is consistent with low GSI of about 0.5%, in *M. kannume* (Iles, 1960; Khallaf & Authman, 2012). Nonetheless, it is important to consider other life-history traits, such as mating rate, that can conflate with GSI results (Parker & Pizzari, 2010). A cross-metazoan meta-analysis of flagellar motility demonstrated an overall relationship between sperm competition and the presence of aflagellate sperm, primarily in invertebrate taxa (Morrow, 2004). Considering that the monoflagellated notopterids are the mormyroids' nearest sister family, it is possible that relaxed selective pressure by sperm competition is common to both families and has led to directional selection in which the ancestral flagellated sperm type transitioned to immotile, aflagellate sperm (Montgomerie & Fitzpatrick, 2009).

It is unclear whether biflagellate sperm confer motility or fertility advantages (Pitnick *et al*., 2009), and there is an overall absence of information on sperm behaviour and fertilization dynamics in these systems (Montgomerie & Fitzpatrick, 2009). If biflagellate sperm are advantageous when sperm competition is high, it may be expected that additional flagella confer greater competitive abilities, potentially by enhancing motility, improving manoeuvrability or excluding other sperm from entering the micropyle (Montgomerie & Fitzpatrick, 2009). Males from various species of cardinal fish (Kurtiformes: Apogonidae), which experience low sperm competition, have ejaculate that contain 50%–80% biflagellate sperm among monoflagellated sperm (Fishelson *et al*., 2006; Lahnsteiner, 2003). Neither biflagellate nor monoflagellate sperm appear to be maladaptive for cardinal fish because both are produced within a single male, and biflagellate sperm may hold a competitive advantage by being more effective at vertical, undulatory motions that help it enter the egg micropyle of this species (Fishelson *et al*., 2006). Nonetheless, biflagellate sperm has also been found in species, such as the plainfin midshipman (Batrachoidiformes: Batrachoididae), that experience high sperm competition (Brantley & Bass, 1994). To summarize, although the adaptive value of specific types of sperm morphology remains unclear, sperm competition and the fertilization environment play a major role in selecting sperm form. The relationship between sperm competition and specific sperm morphology will continue to require examination on a case-by-case basis before enough life-history information is available to draw clade-wide conclusions, especially when considering rarer morphologies like biflagellate sperm.

5 | REPRODUCTIVE BEHAVIOUR AND PARENTAL CARE

This section discusses osteoglossiform courtship behaviour, parental care and the potential relationships between their reproductive behaviour, sperm competition and sexual selection. Current knowledge about osteoglossiform reproductive behaviour is extremely limited, with the exception of mormyrid electrical signalling. Courtship and fertilization events for osteoglossiforms have rarely been witnessed in the wild, infrequently in the lab and never with advanced imaging techniques. Observations of courtship and fertilization, combined with identifying operational sex ratios, would provide essential information for evaluating the degree of polyandry and competition among males. If sperm competition levels are measurable, then it may be possible to correlate them with the evolution of various morphological adaptations and fertilization strategies.

5.1 | Osteoglossidae

Within Osteoglossidae, *Scleropages leichardtii* form direct pairs, in which males and females stay together for several days leading up to the spawning event at night (Merrick & Green, 1982). *S. leichardtii* males are known to participate in at least two spawning events and pair with a new female within several weeks (Merrick & Green, 1982). In contrast, *Osteoglossum bicirrhosum* are serially monogamous and form pairs every breeding season (Queiroz, 2008), indicating low risk of multipaternity and sperm competition. Nonetheless, another osteoglossid species, *Arapaima gigas*, constructs nests (Lüling, 1964), a behaviour associated with low sperm competition, and also exhibits multipaternity (Verba *et al*., 2014), a feature associated with high sperm competition.

Females from the *Osteoglossum* and *Scleropages* genera produce large, yolky eggs. *S. leichardtii* was reported to produce 30–130 eggs 10 mm in diameter (Lake & Midgley, 1970), whereas *S. formosus* was described as producing 30–80 eggs 14–18 mm in diameter (Scott & Fuller, 1976). *O. bicirrhosum* produces 23–220 yellow or orange eggs 11–12 mm in diameter that are non-adhesive and sink to the substrate (Yanwirsal, 2013; Yanwirsal *et al*., 2017). Other osteoglossid eggs are much smaller, such as those of *H. niloticus*, whose eggs are about 2.5 mmm, adhere to each other when they sink to the bottom of the nest and have a grooved micropyle (Daget, 1957). Similarly, the greenish, ovoid eggs of *A. gigas* are around 3 mm wide and stick together to form an egg mass (Fontanele, 1948). Reports of *A. gigas* clutch sizes are ambiguous (Britz, 2004), but females may contribute about 1000 fry year (Núñez *et al*., 2011). Osteoglossids exhibit diverse parental care: males in multiple *Scleropages* species and both *Osteoglossum* species are mouthbrooders (Queiroz, 2008; Scott & Fuller, 1976). Only in *S. leichardtii* have females been identified as the mouthbrooding parent (Merrick & Green, 1982). *O. bicirrhosum* males also form aggregations called “hatcheries” during the parental care season; this may be tied to cooperative breeding, as suggested by some broods exhibiting multipaternity in this species and in *A. gigas*

(Verba *et al.*, 2014). As noted previously, large, shallow nests for protecting eggs are built by adult male *A. gigas* (Lüling, 1964; Val & de Salvo Souza, 1990) and *H. niloticus* (Adite *et al.*, 2006; Budgett, 1901b). It is unclear if there is a predominant guardian in *H. niloticus* (Daget, 1957; Moreau, 1974), but Adite *et al.* (2006) reported that both parents transported larvae in their mouths to another location when the original nest was disturbed.

5.2 | Pantodontidae

Pantodontids likely undergo internal fertilization, and their courtship behaviour involves males and females swimming close together. This behaviour is similar to that of externally fertilizing osteoglossiforms; only their internal anatomy indicates that their courtship does not terminate in external fertilization. Females are reported to produce a range of 33–153 buoyant eggs with a 2.3 mm diameter; each egg has a micropyle 10 μm in diameter located in the middle of an 80 μm wide, ridged, funnel-shaped micropylar pit (Britz, 2004). *P. buccholzi* does not perform parental care (Britz, 2004). By reproducing through internal fertilization, *P. buccholzi* males may experience such low levels of sperm competition that further male investment may add little benefit for ensuring reproductive success.

Pantadon's taxonomic position has been debated for decades (reviewed in Hilton & Lavoué, 2018) and its derived traits indicate that it may be better classified as a sister group to other osteoglossiforms (Lavoué, 2016). *Pantodon* shares an absence of paternal care with *Hiodon alosoides*, a basal, freshwater osteoglossomorph (Britz, 2004). The eggs of both species contain a large oil globule that allows them to be buoyant; semipelagic eggs like these are typically found in more ancestral marine species (Ahlstrom & Moser, 1980; Battle & Sprules, 1960). Together with its reproductive behaviour, *Pantodon*'s paired gonads and modified gametes suggest that it is more phylogenetically distant from other osteoglossiforms. Nonetheless, more morphological and molecular data are needed to resolve its position within Osteoglossomorpha (Hilton & Lavoué, 2018).

5.3 | Mormyroidea

Courtship behaviour has been documented for several species of mormyrids (Bratton & Kramer, 1989; Kirschbaum, 1987; Landsman, 1993; Machnik & Kramer, 2008; Werneyer & Kramer, 2006; Wong & Hopkins, 2007; Yanwirsal, 2013). Mormyrid species often demonstrate male choice, in which males recognize female electric organ discharges (EODs) (Arnegard *et al.*, 2006; Nagel *et al.*, 2018). In addition to recognizing EOD waveforms, males and females actively interact by modifying their EOD discharge rate to produce stereotyped electrical displays called sequences of pulse intervals (SPIs) (Bratton & Kramer, 1989; Wong & Hopkins, 2007). Several motor behaviours typically occur alongside electrical signalling during courtship, and some species, such as *Brienomyrus brachyistius*, exhibit sex-specific courting behaviours (Wong & Hopkins, 2007). Although males may often begin the courtship phase with antagonistic reactions to the female's approach, the male appears to tolerate the female's presence more than usual compared to times outside of courtship (Bratton & Kramer, 1989; Kirschbaum, 1987;Werneyer & Kramer, 2006; Wong & Hopkins, 2007). Observations of immediate spawning after pairing of *Marcusenius macrolepidotus* suggest that motor courtship behaviour may not be as necessary as electrical signals for inducing spawning in some species (Werneyer & Kramer, 2006; Wong & Hopkins, 2007).

Mormyrid species typically do not demonstrate parental care, with the exception of a few species known to build nests. Parental care has been recorded in *Stomatorhinus* (Heymer & Harder, 1975) and nestbuilding *P. isidori*, *Pollimyus adspersus* (Diedhiou *et al.*, 2007; Kirschbaum & Schugardt, 2002) and *H. bebe* (Budgett, 1901b). *P. isidori* males will build multiple nests made of algae or macrophytes within their territory (Crawford *et al.*, 1986). They will also continue to defend the nest for 1–2 weeks after spawning, even against the mother. *P. isidori* and *P. adspersus* are the only two species that produce non-adhesive eggs (Kirschbaum & Schugardt, 2002), a feature common to nestbuilding Osteoglossid species. Mormyrid eggs are much smaller than those of nestbuilding Osteoglossids, with the exception of *H. niloticus*, but mormyrid females are also smaller in body size. *P. isidori* females are described as producing 28–132 eggs that are 2 mm in diameter (Kirschbaum, 1987), whereas the quantity of eggs produced by *M. kannume* (Kirschbaum & Schugardt, 1995), *Camplyomormyrus cassaicus* (Schugardt & Kirschbaum, 1998) and *Hippopotamyrus pictus* (Kirschbaum & Schugardt, 2002) typically numbers in the hundreds and their size is about 2–3 mm in diameter. A substrate with holes for attaching eggs is preferred *by H. pictus*, and a rocky substrate is preferred by *M. kannume* (Kirschbaum & Schugardt, 2002). These substrate specializations may reflect differences in reproductive behaviour. Parental care was specifically determined to be nonexistent in *M. macrolepidoptus* (Werneyer & Kramer, 2006) and *M. rume* (Kirschbaum & Schugardt, 1995).

The monotypic Gymnarchidae also exhibit nestbuilding. After spawning during the rainy season, *G. niloticus* builds large floating elliptical nests about 1 m in diameter that contain about 1000 large, amber coloured eggs that are 10 mm in diameter, similar to the large-sized eggs of nestbuilding Osteoglossids (Budgett, 1901a; Budgett, 1901b; Svensson, 1933). The nest is built in shallow water and is made of dense vegetation that projects from the surface around the periphery. Adults actively patrol the nests (Hopkins, 1986), which can contain advanced stages of larvae over 3 weeks old (Budgett, 1901b). This behaviour similarly exemplifies an indication of high male parental investment that likely reduces levels of sperm competition.

5.4 | Notopteridae

Breeding behaviours for notopterids are similar to those of mormyrids: in the lab, *N. notopterus* fish appear to choose individual territories, and males create a spawning site by removing gravel and cleaning the area with their mouth (Yanwirsal *et al.*, 2017). During the courtship phase, the male approaches and swims alongside a potential female partner, which is followed by multiple interactions in which both fish swim towards and away from one another. This phase ends when the female approaches the male and the male leads the female to his spawning site, where the female lays the eggs and he fertilizes them on the substrate (Yanwirsal *et al*., 2017). Eggs are slightly larger than those of mormyrids, but smaller than most osteoglossids. *N. notopterus* females have been described as laying anywhere from 15 to 225 adhesive eggs per spawning events, and eggs are about 3.8–4 mm in diameter (Yanwirsal *et al*., 2017). *N. notoperus* eggs also appear to have a micropyle with a spiralling pattern of ridges on the egg's surface (Mookerjee & Mazumdar, 1946; Yanwirsal *et al*., 2017). Older reports of notopterid egg numbers describe *Chitala chitala* females as laying 300–500 adhesive eggs with a 5.2 mm diameter (Southwell & Prashad, 1919) and *C. ornata* as laying several thousand adhesive eggs with a 4 mm diameter (Smith, 1933).

Among notopterids, it is known that male *N. notopterus* (van Pinxteren, 1974; Yanwirsal, 2013) and males of both *Chitala* species (Smith, 1933) perform parental care and guard freshly spawned eggs. *X. nigri* was assumed to lack parental care (Siraad, 1999) and little information is available about *Papyrocranus* species reproduction. *N. notopterus* males guard and aggressively defend the eggs against the female and other males (Yanwirsal *et al*., 2017).

5.5 | Reproductive behaviour and parental care as it relates to sperm competition

Most osteoglossiforms are morphologically similar between the sexes, which may indicate that sexual selection has not had a large effect on the evolution of their morphology (see Section 3.2). Nonetheless, sexual selection likely plays a much larger role in their courtship displays, in which females appear to choose their mates based on courtship activity (*e.g*., Merrick & Green, 1982). Courtship may serve as a signal of males' ability to contribute to offspring survival and fitness through parental care or signify a male's specific physiological and genetic advantages. Rather than rely heavily on morphological cues, females may prefer to choose mates depending on courtship frequency, type and length of duration.

Like osteoglossids, mormyrids do not physically display showy secondary sexual features, but they have complicated courtship behaviour involving choosy males and diverse electrical signalling. In combination with their aflagellate sperm and modified anal fins (see Section 3.2), mormyrid behaviour further underscores the likelihood that they experience low levels of sperm competition. Females mate with more than one male in a breeding season, but they do so monogamously and sequentially (Iles, 1960; Morrow, 2004).

The diversity of teleost family structures, ranging from no care to paternal, maternal and biparental care, has led to fish, especially among the Cichlidae, serving as exemplary systems for investigating the evolutionary origins of parental care (Gonzalez-Voyer *et al*., 2008). Nonetheless, the pathway by which uniparental or biparental care evolved from the ancestral state of no care remains unresolved (Kolm, 2009). Osteoglossiforms demonstrate all parental care strategies within a single order, including evidence of cooperative breeding. Therefore, like cichlids, they may be helpful for examining evolutionary questions of parental care at a more compact phylogenetic scale. The greater geographic spread of osteoglossiforms may also allow them to be useful for comparative analysis with cichlid parental care.

Males provide most of the parental care in osteoglossiforms. As demonstrated empirically in other teleosts, their investment is shaped by the risk of multipaternity and sperm competition (Neff, 2003), as well as parental care serving as a sexual selection trait for female choice (Kolm, 2009). With the exception of most mormyrid species, osteoglossiforms appear to demonstrate a relationship between reduced sperm competition and parental care.

6 | FUTURE RESEARCH DIRECTIONS

Sperm form must adapt to the environment, and within the context of sperm competition, males need to balance selection for sperm traits against environmental variance (for review see Snook, 2005). Most empirical work on this topic is concerned with the female reproductive tract as an active environment that can induce sperm motility, namely in arthropods (Alberti, 2000; Dallai *et al*., 1973; Dallai *et al*., 1992). For internally fertilizing fish, increased sperm length is associated with an improved ability to navigate the viscosity of the female reproductive tract (Fitzpatrick *et al*., 2009). In externally fertilizing fish, some work has focused on the importance of appropriate environmental conditions conducive for external fertilization. For instance, increased sperm length has been associated with substrate-fertilizing species, potentially because the length provides benefits that allow sperm to overcome difficulties navigating the substrate to locate an egg (Balshine *et al*., 2001). Pipefish (Syngnathiformes: Syngnathidae) were found to have immotile sperm that earn motility upon contact with a combination of sea water and ovarian fluid (Ah-King *et al*., 2006). Seven teleost species demonstrated sperm motility that responded to changes in osmolality, whereas two other fishes exhibited sperm that became motile in response to ionic changes in the water (Morisawa & Suzuki, 1980). Experiments aimed at describing sperm motility and fertilization mechanisms must accurately replicate natural conditions at the risk of studying adaptive traits in an environment lacking the selective forces responsible for their existence (Lüpold & Pitnick, 2018).

Mimicking natural fertilization conditions will be especially important for future work that seeks to describe the fertilization mechanism of African weakly electric fish. *G. niloticus*, whose sperm displays amoeboid movement, may have regained motility by coopting "ancestral amoeboid movement" (Dallai *et al*., 1973). Nonetheless, *G. niloticus* also faces the difficulty of transferring amoeboid sperm as an external fertilizer; the mechanism by which amoeboid sperm achieve fertilization in fresh water without being dispersed by the current remains unknown. In mormyrids, it will first be necessary to determine whether the sperm are truly immotile before possible mechanisms by which they are transported in their environment are investigated. It is important to note, however, that although claims of absolute immotility may be a cause for suspicion, mormyrid sperm may simply lack the underlying structural features necessary for motility.

Replicating accurate environmental conditions will also be necessary for investigations of sperm–egg interactions and coevolution. There is presently no research into the presence of chemoattractants or sperm receptor proteins that could facilitate the union of sperm and egg in osteoglossiforms. Comparative studies of the egg structure would greatly improve the current understanding of coevolution between sexes of species, particularly in those species that reproduce with aflagellate sperm. Assessing ovarian and seminal fluid is also vital for understanding the complementary roles of post-copulatory sexual selection and sperm competition. Ovarian fluid was found to affect the outcome of sperm competition in ocellated wrasse (Labriformes: Labridae); the presence of female ovarian fluid favoured sperm velocity over sperm number, enabling increased fertilization by paternal males in spite of intense sperm competition with other male types (Alonzo *et al*., 2016). Similarly, increased concentrations of ovarian fluid are associated with increased sperm motility, speed and linearity of sperm movement in Arctic charr (Salmoniformes: Salmonidae) (Turner & Montgomerie, 2002). More research on cryptic choice in external fertilizers like osteoglossiforms will also provide insight into their fertilization mechanisms. Considering the diverse and unusual combinations of reproductive traits in osteoglossiforms, subsequent studies may elucidate novel methods by which cryptic choice or sexual conflict act to promote fertilization. Moreover, osteoglossiforms employ nearly all possible mating strategies, making them an ideal system for exploring the evolutionary basis and consequences of sexual conflict theory.

Sexual conflict may lead to coevolution in which females evolve to resist male mating attempts that may be harmful to the female (Parker, 1979). This can be examined at the gametic level by comparing adaptations between eggs and sperm. Initial research on sexual conflict in osteoglossiforms should investigate features often associated with sexual selection, such as biased sex ratios in the population and polyandrous mating strategies. A second aspect could be a more comprehensive study of egg morphology. Like all teleosts, the sperm of osteoglossiforms lack an acrosome (Jamieson, 1991; Mattei, 1970). This absence is associated with the presence of an egg micropyle, the only entrance within the egg which permits a single sperm to penetrate the oocyte and enables attachment of the sperm to the egg's plasma membrane. Once fertilization is achieved, the egg swells, causing the sperm-guiding ridgelines to disappear as a means to prevent additional incoming sperm from fertilizing the egg (Amanze & Iyengar, 1990). The eggs of notopterid *N. notopterus* have been described as having numerous external ridges around the micropyle (Mookerjee & Mazumdar, 1946; Yanwirsal *et al*., 2017), similar to eggs of the osteoglossids *H. niloticus* and Pantodontids (Britz, 2004; Daget, 1957). The chorion of mormyrid *P. isidori*, however, has been described as smooth (Diedhiou *et al*., 2007). The vastly different sperm morphology of these species indicates that further research is necessary for determining if there are any similarities in their sperm–egg interactions. Visualization and scanning electron microscopy studies of osteoglossiform eggs are strongly recommended to investigate for the presence of any structural features (*e.g*., the radial micropylar furrows of *Pantodon*, *H. nilotus*, and *N. notopterus* eggs) that may facilitate sperm entry (Britz, 2004).

Finally, the study of genetic basis and changes in genetic architecture that have led to extreme specializations among osteoglossiforms has yet to be explored. The teleost specific whole genome duplication event (TS-WGD), which occurred early in the teleost lineage, is a potential source of genetic plasticity, whereby gene function may have been reallocated to lead to the evolution of some successful reproductive strategies, such as the development of egg buoyancy required to survive in the open ocean (Finn & Kristoffersen, 2007). Nonetheless, whole genome duplication events do not always lead to radiation, and the TS-WGD does not satisfactorily explain why some teleost orders have exceptionally higher reproductive diversity than others (Glasauer & Neuhauss, 2014). The degree of interaction between genetic material and additional biological and environmental processes that shape teleost reproductive adaptability remains largely unknown (Desjardins & Fernald, 2009; Wootton & Smith, 2014). Given that genomes have now been sequenced for multiple osteoglossiform species (*Scleropages formosus*, Austin *et al*., 2015; Bian *et al*., 2016; *Paramormyrops kingsleyae*, Gallant *et al*., 2017; *Arapaima gigas*, Vialle *et al*., 2018; *Mormyrus lacerda*, NCBI Accession: JAABNX010000000; *Mormyrus iriodes*, NCBI Accession: JAAGVU000000000; *Brevimyrus niger*, NCBI Accession: JAABNY000000000; *Gymnarchus niloticus*, NCBI Accession: JAACJT010000000) these resources could be leveraged to understand the genetic basis of some of the traits observed in osteoglossiforms and enable comparative studies with other teleosts.

Situated at the base of Teleostei, osteoglossiforms have long been appreciated for understanding early evolution of teleosts (Hilton & Lavoué, 2018). The development of their diverse reproductive anatomy also highlights early plasticity integral for successive adaptations across the teleost group. An increasingly integrative examination of osteoglossiform reproduction is both feasible and has potential for uncovering a comprehensive understanding spanning genomics to behaviour. Morrow (2004) noted a research trend that remains relevant to date: “curiously, sperm morphology and ultrastructure is often the first (and sometimes the last) aspect of an organism's reproductive biology that is examined.” Relating this information to behavioural traits and observations about mating systems will help untangle the selective forces that drive and connect anatomical, physiological and behavioural adaptations. Other than examining sexually dimorphic electrical signalling in mormyrids, little research has examined osteoglossiform reproductive strategies for signposts of sexual selection. Yet, osteoglossiforms embody morphological traits with clear form and function relationships that are opportune for studies seeking to sort intrasexual from intersexual selection. In this manner, identifying general patterns in osteoglossiform morphology helps clarify the rules governing sperm competition, whereas applying an understanding of those rules to osteoglossiform reproductive behaviour and morphology may explain their diversity. Considering that osteoglossiforms are the most primitive living teleost order, evaluating their reproductive diversity may shed key insights into the role of reproductive adaptations in large-scale teleost speciation.

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L.A.K. conducted the literature review and outlined, drafted and finalized the manuscript. J.R.G. conceptualized the review, authored figures, edited and revised the manuscript.

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