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Paternal mouthbrooding in the chocolate gourami *Sphaerichthys osphromenoides* (Osphronemidae)

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Abstract We examined sexual dimorphism and parental care in the chocolate gourami (*Sphaerichthys osphromenoides*) by visual observations, video recording of spawning, and histological analysis of the gonads of individuals in which spawning and mouthbrooding was previously observed. *S. osphromenoides* is considered a rare exception among labyrinth fishes (Osphronemidae family) because of the presumed maternal parental care, which is not found in other species of this family. According to our observations of 32 spawning events, parental care in this species was always performed by the male. Our visual observations were confirmed by video and histological analysis. This suggests that the sex in this species has probably been misidentified so far. We argue that the putative "females" (previously defined by external features) were in fact males, and that there are probably no exceptions to male parental care in osphronemid fishes.

Keywords Sexual dimorphism · Male parental care · Male mouthbrooding · Gonadal development · Labyrinth fish

Introduction

Labyrinth fishes (Osphronemidae) are a family of tropical freshwater fishes with about 135 species (Fricke et al. 2023). All known labyrinth fishes exhibit parental care in one of two ways: bubble nesting or mouthbrooding (Rüber et al. 2006; Zworykin 2017). Despite the popularity of osphronemid fish in the aquarium hobby, the reproductive behaviour of many of them remains poorly studied. One such understudied species is the chocolate gourami *Sphaerichthys osphromenoides* Canestrini 1860. The earliest observations of this fish were made more than a century ago by Reichelt, who first brought them alive to Europe. After finding fairly large and well-coloured juveniles in an aquarium with adults, he assumed that *S. osphromenoides* was viviparous (Reichelt 1911). A few years later, Stansch proposed another explanation for Reichelt's observations, suggesting that this is a mouthbrooding fish (Stansch 1914).

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In the following decades, several articles appeared in aquarium magazines on the experience of breeding *S. osphromenoides*. Surprisingly, these descriptions were radically different. Some authors confirmed that chocolate gourami was indeed a mouthbrooder (van den Nieuwenhuizen 1956), while others insisted that the breeding of this fish is no different from other well-known Osphronemidae that build bubble nests (Bahr 1955). Several hypotheses have been proposed as possible explanations for this disagreement: the presence of similar species with different types of reproduction, reproductive behavioural alteration under unnatural aquarium conditions, flexibility of reproductive strategy depending on water flow rate (Weise 1950; Breder and Rosen 1966). Thanks to further observations, the debate over chocolate gourami reproduction had subsided, and almost all authors now believe that all four known *Sphaerichthys* species are mouthbrooders by the 1980s, although some researchers reported that this species sometimes allegedly builds rudimentary bubble nests (Pinter 1986; Vierke 1988).

The second crucial issue that remains controversial is the sex of the caring parent (Hallmann 2021). With few exceptions (presumably biparental *Belontia* spp.), all osphronemid fishes are paternal caregivers. Most authors consider *S. osphromenoides* and closely related *S. selatanensis* to be rare exceptions, in which these duties are assigned to females (Linke 1991; Britz et al. 1995; Rüber et al. 2006). However, there is still no general consensus, and several aquarium hobbyist reports have appeared in recent years suggesting that *S. osphromenoides* may also be a male mouthbrooder (see the list of video links in Supplement No. 1).

In this paper, we question the exceptional status of *S. osphromenoides* within the family of Osphronemidae and present two types of data which document paternal mouthbrooding in this species. The first type of evidence is a video recording of chocolate gourami spawning, showing the fertilised eggs being taken in the mouth by the male. Data of the second type represent the results of histological analyses of the gonads of two individuals: one of which was repeatedly observed keeping eggs in the mouth, and the other spawned several times but never incubated eggs (the respective mate always did).

Material and methods

Study species

One of the main distribution areas of *S. osphromenoides* is the island of Borneo (Parenti and Lim 2005; Thornton et al. 2018). It was also previously reported in Sumatra (Hui and Ng 2005) and Peninsular Malaysia (Ng et al. 1994; Zakaria et al. 1998), but more recent data indicate that many populations have severely reduced or extinct altogether due to destruction of riparian zone and overharvesting for the ornamental fish trade (Shah et al. 2006; Siow et al. 2014; Low 2019). Chocolate gourami mostly inhabit peat swamps and associated black water streams, with dark-coloured and highly acidic waters, so that it is often considered as a stenotopic blackwater species (Ng et al. 1994; Beamish et al. 2003). Clearwater populations are also reported but these findings could also result from individuals that were transferred from one location to another after heavy rain or flooding (Richter 1983). An important reason for the lack of information about the chocolate gourami is that, even though it was first imported before World War I, it is not a so-called hardy fish and reports about its natural behavior remained scarce for a long time (Pinter 1986; Linke 1991).

Study specimens

Four individuals used in our work were obtained from aquarium trade without reliable information about their exact origin but presumably wild-caught. The other fish were F1 or F2 progeny of these individuals and of other fish from the trade. Commercial breeding of this demanding fish is not carried out. Accordingly, all individuals used in our work were wild-caught or descendants of wild fish in few generations. No animals were killed for this study. The fish used for histological analysis died of natural causes shortly after each other at an undetermined age and probably of senility on December 12th and December 17th, 2022.

Aquarium observations

We conducted observations of spawning and parental care of *S. osphromenoides* under aquarium conditions in Leiden and Zutphen (NL) from October 2019 to

August 2021. Fish were maintained in groups of 4 to 13 individuals in 54, 70 and 120 L planted aquaria. The photoperiod was a 12:12 h light:dark cycle, and the water temperature was maintained at 25–27 °C. The pH fluctuated between 5.5 and 6.5, which was maintained by using rainwater and reverse osmosis water, and adding peat and alder cones. Fish were fed to satiation once a day with one day off per week with live food (planktonic crustaceans, Diptera larvae and Grindal worms), frozen food (Diptera larvae) and a variety of food pellets.

Video

Since these fish rely on tanks with dense plant cover, observing or filming is always challenging. The pair for which breeding could be filmed spawned together several times and were maintained in company with four other conspecifics. The video was recorded in November 2020, both individuals were 18 months old at the time (see Supplement No. 2). The video could only be recorded with a smartphone camera because the event occurred unexpected.

Histological sampling

The pair from which the gonad samples were taken spawned four times together (between 7 October 2019 and 14 January 2020), once in the presence of another pair, and three times in a separate 70-L aquarium with identical water parameters (see above). One of these individuals had a rounded anal fin, the base of which became reddish in colour during spawning. This individual never picked up eggs after spawning. We labelled this fish as No. 1. The second fish had a more elongated anal fin and a different colour pattern, in particular more contrasting white stripes on the body. This individual incubated eggs in the mouth after spawning in all cases. This fish was labelled as No. 2. A photograph of the fish fixed in 70% ethanol is provided in Fig. 1.

Sex identification and estimation of gonadal development were conducted by using blind histological analysis. The gonad samples were fixed in individual 30 mL tubes with 70% ethanol after fish dissection. The samples were dehydrated using Tissue Processing Center TPC-15 (Medite GmbH, Germany) in increasing ethanol concentrations and Isoprep solution (Biovitrum, Russia), cleared in xylene, impregnated in paraplast X-tra (Leica, Netherlands). We embedded gonad samples by Tissue Embedding Center TES 99 (Medite GmbH, Germany). Five µm thick sections were made by Meditome M530 (Medite GmbH, Germany). Sections were stained with Ehrlich's Hematoxylin and Eosin standard technique (Pearse 1980). The photographs of gonad sections were made on Biorevo BZ-9000 microscope (Keyence, Japan). The perimeter of oocyte sections was measured using Keyence BZ-II Analyzer v.1.42 software and their diameters were counted by the circle perimeter formula. The gonadal development was estimated according to Núñez and Duponchelle (2009).

Results

Aquarium observations

Reproductive behaviour of *S. osphromenoides* was observed several dozen times during the period, of which 32 spawning events were recorded in detail. Spawning always occurred in pairs. Two of the observed pairs were removed to a separate tank for breeding, while the others bred in a common aquarium. No behavioural differences between spawning in pairs, small and large groups could be observed. Presumably wild-caught individuals from the aquarium trade and the F1 and F2 generations also showed no differences in spawning behaviour. The duration of mouthbrooding was 12–16 days. Spawning behaviour and parental care were consistent with what is described in aquarium literature and no exceptions to mouthbrooding could be observed (Pinter 1986; Linke 1991; Hallmann 2021). However, contrary to the common belief, based on our observations of spawning of different pairs, we concluded that eggs were always collected by the individual that fertilised them and not by the one that laid them. No oral egg exchange between the parents could be observed afterwards. To verify this conclusion, we carried out a video recording and histological analysis of the gonads.

Video

The video clearly shows the female leaning sideways and releasing the eggs. The male then picks

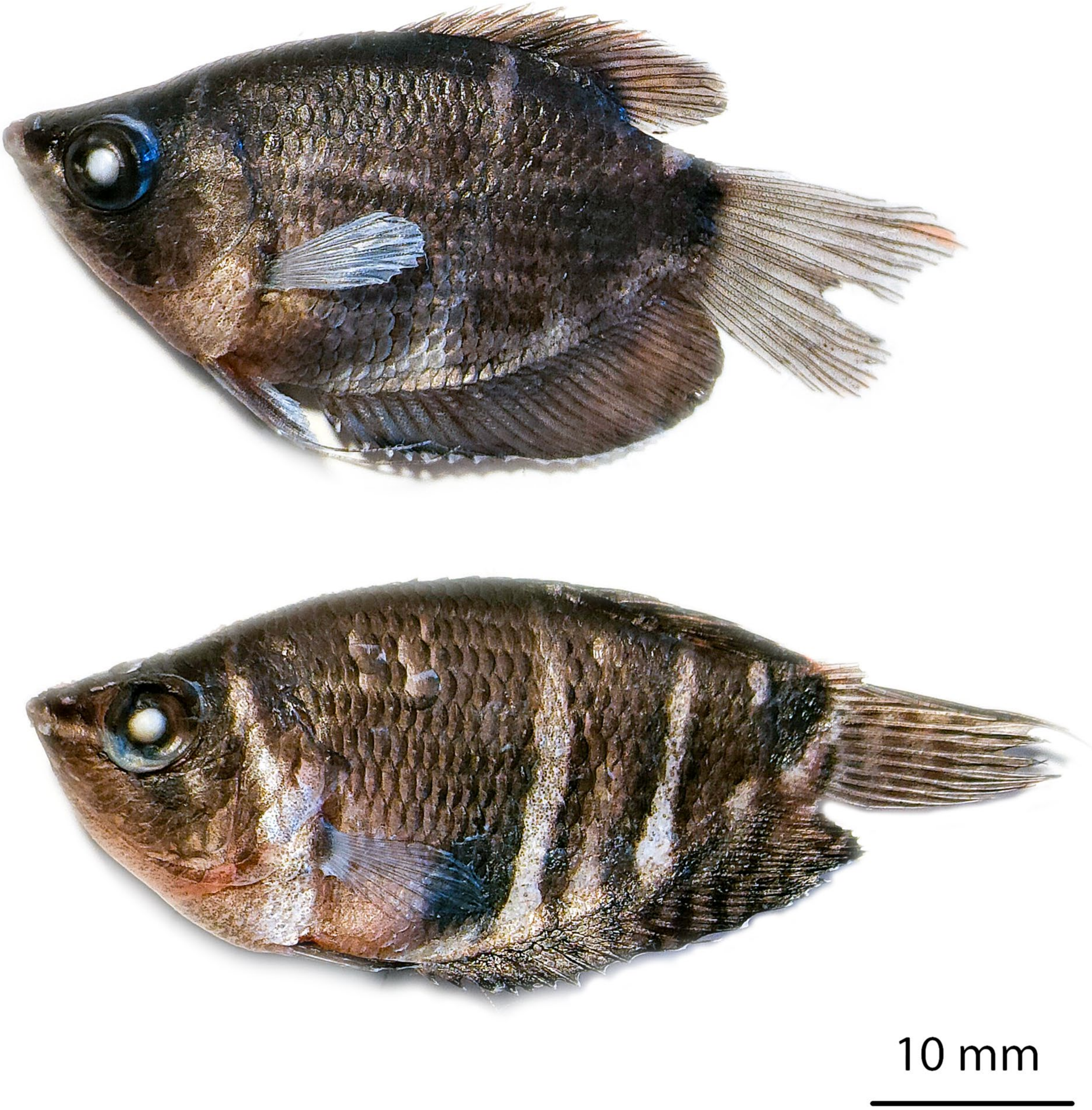

Fig. 1 The pair of *S. osphromenoides* from which the gonad samples were taken (fixed in 70% ethanol). Specimen No. 1 above, specimen No. 2 below. As the results of histological analysis revealed (see Results), specimen No. 1 is a female and specimen No. 2 is a male

up and keeps them in its mouth. The parents do not pass the eggs to each other, as is common in some mouthbrooding *Betta* species, where the female first collects the eggs and then passes them to the male (Linke 1991). This is consistent with all of our other observations of *S. osphromenoides* reproduction, as well as earlier records from one of the authors (H.G.) who has been breeding this fish since 1987. As already noted, spawning typically takes place under cover of plants or other shelter and is therefore difficult to observe. To our knowledge, this is one of the most clear and indisputable documentation of spawning in this species, which also clearly evidences that the eggs are collected by the male.

Gonadal development

Histological analysis showed that the first fish (No. 1, female) had ovaries and the second one (No. 2, male) had testes. Atresia of remnant material in ovaries indicated that female already spawned (Fig. 2a). Post-ovulatory follicles had thickened ovarian wall, large empty spaces within the ovarian lamellae and contained mass of extracellular material under atresia. Some of these materials included oocyte yolk and atretic follicles that usually formed after oocytes resorption. Ovaries contained new batches of developing oocytes: previtellogenic oocytes with diameter 91 ± 3.1 (37–165) µm ($n=79$) and more developed vitellogenic oocytes 266 ± 12.1 (205–352) µm ($n=17$) (Fig. 2a, b). Numerous previtellogenic oocytes characterized homogenous cytoplasm structure and central or sub-central 4–5 nucleoles located in the cell nucleus. Vitellogenic oocytes had cytoplasm which fully or partially filled with lipid droplets and yolk granules (Fig. 2b).

The testes had partially empty spermatic ducts with less numbers of indistinguishable cell types and hypertrophy of connective tissue in some zones (Fig. 2c). Spermatogonia had often been present in male gonads. This cytological structure of generative tissue characterized post-spawning maturity stage.

Discussion

The results of this study indicate that the sex of the caregiving parent in *S. osphromenoides* has not yet been correctly identified. According to our data, this species exhibits paternal mouthbrooding. Our findings do not only show that the current state of knowledge on parental care in chocolate gouramis needs revision but also suggest that there are probably no exceptions to the rule of paternal care in Osphronemidae.

What is the origin of the controversy and misinterpretations of observed *S. osphromenoides* spawning and parental care? As our survey of the existing literature on the topic suggests, the main reason may be the misidentification of sex in this species. All known descriptions of chocolate gourami sexing and breeding were published in aquarium literature or passed on by word of mouth. According to many amateur breeders' observations, the eggs were typically incubated by the less colourful individual of the spawning pair. Apparently, based on knowledge of general trends, the observers decided a priori that the caring sex was female (see e.g., Pinter 1986; Linke 1991). No evidence was provided to support these conclusions. In scientific publications, aquarium observations are often used without verification, because of which some erroneous judgments have been and are still being propagated. Some of these data need to be reassessed. In particular, Hallmann mentions the results of a gonad analysis carried out by H. Linke and J. Geck (Hallmann 2021). These results were briefly summarised in an aquarium magazine (Geck 2012). The authors assumed that the incubating *S. osphromenoides* was a female. However, J. Geck later informed us that the condition of the observed samples did not allow for an unambiguous assessment and that the analysis could have led to erroneous results, which seems likely. Histological analysis could not be performed (J. Geck, personal communication, 3 September 2023), whereas our behavioural observations of spawning were confirmed by histological data on the sex of the spawners.

Colouration, fin shape, body size and proportions are commonly used for sexing in chocolate gourami. Linke states that the identification of the sexes in this fish is not difficult, because the dorsal fin in males is pointed, and in females is smoothly rounded (Linke 1991: 123). Sandford suggests that this rule applies not only to the dorsal fin but also to the anal fin, and notes that females are more robust than males (Sandford 1987: 26). Vierke wrote that males are larger (Vierke 1988: 158). According to van den Nieuwenhuizen, males and females have different head shapes (Nieuwenhuizen 1956: 31). Richter considers as a reliable indicator of males the presence, in contrast to females, of white margins on fins (Richter 1983: 106). Riehl and Baensch point out yellow margins on the anal and caudal fins of males (Riehl and Baensch 1985: 644), and Vierke believes that females also have margins on the anal fin, but slightly weaker (Vierke 1988: 158).

Unfortunately, none of these characters appear to be universal or consistent. For example, Geisler notes that although the reddish colouration of the anal fin is considered to be a feature of males, along with the elongated upper and lower caudal fin rays, sexing by these features is unreliable because colouration is variable and females may also have slight elongations

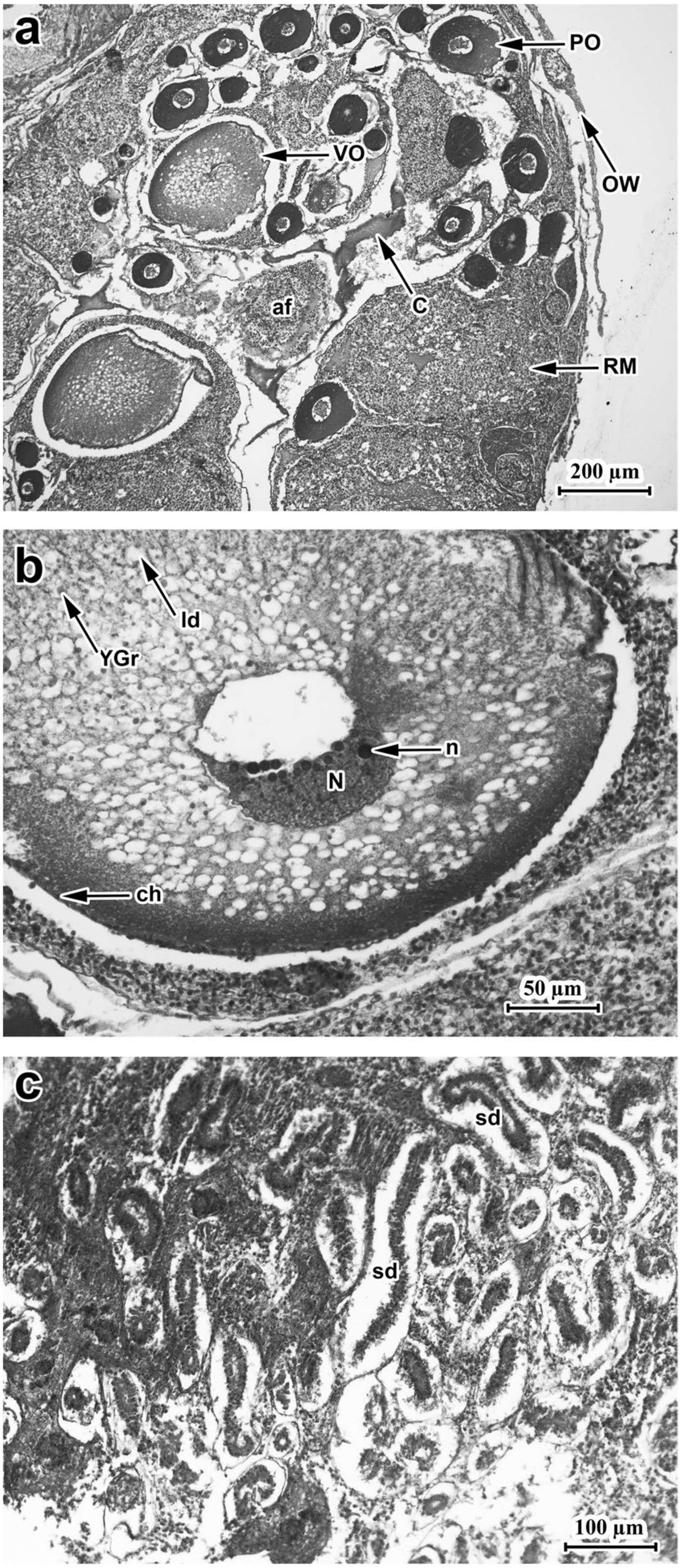

Fig. 2 Cytological structure of ovaries (**a**, **b**) and testes (**c**) of *S. osphromenoides*. OW – ovarian wall, ch – chorion, RM – remnant material, C – cytoplasm, af – atretic follicle, YGr – yolk granule, PO – previtellogenic oocyte, VO – vitellogenic oocyte, N – nucleus, n – nucleoli, ld – lipid droplet, sd – spermatic ducts

of the fin rays (Geisler 1954: 54). According to our observations, reddish base of anal fin is characteristic for females, but not for males (in contrast to Geisler 1954). At the same time, this feature is observed in fish of only some strains. The unreliability of colouration as a sexual trait is also reported by Richter (Richter 1983: 106) and Sandford (Sandford 1987: 26). In Richter's photographs, male and female chocolate gourami do not differ in their fin shape (Richter 1983: 76–77), and the author admits that this criterion can be used only when the fins are well spread (Richter 1983: 106).

Sexual dimorphism in fish is closely related to the mating system (Gonzalez-Voyer et al. 2008), sex of caregiver (Mank et al 2005) and some other traits of the reproductive strategy (Magurran and Garcia 2000). Despite numerous observations of spawning in Osphronemidae, many aspects of the reproductive tactics of most of these fishes remain unexplored. For example, surprisingly, almost nothing is known about the mating system of most of not only Osphronemidae, but of all Anabantoidei. Nearly the only two exceptions are the papers by Pollak et al. (1981) and Zworykin (2022) on *Trichopodus trichopterus* and *Anabas testudineus*, respectively. Meanwhile, intersexual differences in morphology and behaviour among Anabantoidei (including Osphronemidae) vary considerably from nearly monomorphic *Anabas testudineus* and *Belontia signata* to extremely polymorphic *Macropodus opercularis* and *Betta splendens*. In those Anabantoidei that, unlike the osphronemids, do not exhibit parental care, sexual differences are often not pronounced (Vierke 1988; Zworykin 2022). Sexual dimorphism is also weaker in mouthbrooding *Betta* species than in bubble nesters (Rüber et al. 2004). Remarkably, two other *Sphaerichthys*, namely *S. vaillanti* and *S. acrostoma*, in which the male was always correctly distinguished from the female, are species with well pronounced sexual dimorphism (Linke 1991; Priest 2011; Hallmann 2021).

The mating system in *S. osphromenoides* is not studied, but it can be assumed to be sequential monogamy. The weak expression of sexual dimorphism in this fish is most likely related to mouthbrooding. *S. osphromenoides* probably exhibits a case of the slightly pronounced reversed sexual dimorphism, various forms of which are known in fishes. Besides the closely related *S. vaillanti*, the reversed sex differences in size, colour and behaviour were found in cichlid *Archocentrus myrnae* (Tobler 2007) and *Nanochromis transvestitus* (Stewart and Roberts 1984), and in some poeciliids (Bisazza and Pilastro 1997), among others.

Many fishes demonstrate plasticity in parental care and reproductive strategy, and various forms of plasticity can be found in some bubble-nesting Osphronemidae, in which the male usually takes care of the offspring, but sometimes both parents share these duties. For example, this was observed in *Trichogaster lalius* (Forselius 1957), *Betta splendens* (Vierke 1991) and *B. smaragdina* (Schmidt 2020), but usually brooding males still do not tolerate females in close proximity to the nest. Female involvement in mouthbrooding osphronemid species has not been reported so far, even though many mouthbrooding *Betta* species, e.g., *B. pugnax* or *B. albimarginata*, engage in the so-called "ball game" where the female first catches the fertilized eggs and spits them back to the male which then picks them up (Linke 1991: 44). This exchange of the fertilized eggs can be sometimes several rounds but the brooding parent is always the male. Although it cannot be completely ruled out that the reproduction of the chocolate gourami is flexible and can vary according to conditions, we conclude that empirical evidence of female mouthbrooding in this species, as well as in the family Osphronemidae as a whole, is lacking.

Bony fishes (Teleostei) exhibit a diversity of parental care unrivalled among vertebrates (Mank et al 2005). Whereas maternal and biparental care are common in terrestrial organisms, male-only care dominates in aquatic species, including fish (Blumer 1982; Gross and Sargent 1985). Many attempts have been made to explain this intriguing phenomenon, but in most cases the explanations are themselves hypotheses in need of further substantiation (Dawkins and Carlisle 1976; Gross 2005; Benun Sutton and Wilson 2019; Goldberg et al 2020). The only significant exception to the rule is the family Cichlidae, in which approximately 58% of species exhibit maternal care (Balshine and Abate 2021). This exception, like the rule itself, is the subject of speculation and numerous hypotheses (Keenleyside 1991; Goodwin et al 1998; Mank et al 2005). As for other families of bony fishes, uniparental maternal care is extremely rare, especially if we consider only egg-layers and leave aside viviparous and ovoviviparous species, as constituting a special category. In some cases, maternal care, although assumed, needs to be confirmed. For many years, the family Osphronemidae was thought to represent all types of parental care in terms of sex involvement. However, while biparental care in *Belontia* spp. still needs to be verified, maternal care in *S. osphromenoides* and closely related *S. selatanensis* has not been confirmed, as evidenced by our results and observations of aquarium enthusiasts. It is very likely that all members of the family follow the general rule and show paternal care.

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Author contribution Idea generation: D.Z. and J.M.; aquarium observations: J.M. and H.G.; video: H.G.; histological analyses: E.P.; manuscript preparation: D.Z., J.M., and E.P.

Data availability Video of the spawning and photograph of alcohol-fixed fish are included as supplementary material. Additional histological data are available upon reasonable request.

Declarations

Ethics approval All studies were conducted on captive individuals. The species studied is not endangered or protected by wildlife law. No animals were killed for this study and the welfare of the experimental fish was not endangered and was not harmed. Thus, research ethics committee approval was not required to achieve the aims of this study.

Conflict of interest The authors declare no competing interests.

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