A new species of *Schindleria* (Teleostei: Gobiiformes: Gobiidae) from the Red Sea (Saudi Arabia) with a specialized caudal-fin complex

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Abstract

Species of the gobiid genus *Schindleria* are among the smallest and fastest reproducing vertebrates of the oceans. We describe a new species, *Schindleria qizma,* from the Red Sea, Saudi Arabia. It is an extreme example of progenesis, within the already paedomorphic genus, with morphological traits clearly differentiating it from its congeners. *Schindleria qizma* has a unique, unflexed notochord with a straight urostyle of which the tip is inserted into the hypural cartilage, rather than the typical flexed notochord with an upturned urostyle of the other species of *Schindleria*. *Schindleria qizma* belongs to the short dorsal-fin type of *Schindleria*. It is further characterized by an elongated but relatively deep body; a short dorsal fin originating just slightly anterior to the anal fin (predorsal-fin length 59.4% of SL vs. preanal-fin length 60.2% of SL); a head continuously increasing in depth posteriorly with a straight dorsal profile; a short snout (18.6% of head length); large eyes (34.4% of head length); a short pectoral-radial plate (6.3% of SL); 13 dorsal-fin rays; 11 anal-fin rays; 0–2 procurrent rays (where the last procurrent ray is short, if present); an anal fin with the first anal-fin ray situated opposite the second dorsal-fin ray; toothless oral jaws; females with few (10–11, total) but very large (4.6% of SL) eggs and with a conspicuous urogenital papilla characterized by a wide urogenital opening flanked by two long, bilobed projections; a dorsally pigmented swim-bladder; blackish, iridescent eyes, capped by a silvery layer with irregular rows of black dots or blotches; and no additional external pigmentation on its body, at least in preserved specimens.

Keywords

Introduction

Species of the gobiid genus *Schindleria* are among the "most extreme example of progenetic developmental truncation known among fishes" (Johnson and Brothers 1993). Some species already mature at a size of 10 mm total body length (TL) or less and are the smallest vertebrates of the oceans (Watson and Walker 2004). They are also among the fastest reproducing vertebrates in the world with an extremely short generation time (of up to

nine generations per year) reaching maturity at 23 to 60 days of age (Kon and Yoshino 2002). So far, very little research has been undertaken on the biology and ecology of this taxon (Robitzch et al. 2021, 2022), likely because species of *Schindleria* are tiny, translucent, and resemble larval stages for which they are easily mistaken (Bogorodsky and Randall 2019; Robitzch et al. 2021).

Progenetic, developmentally truncated fishes resemble the larval stages of their ancestors with the gonadal development distinctly exceeding the somatic development (Rüber et al. 2007; Britz and Conway 2009; Britz et al. 2014). Characteristic for the larvae of most teleost species are three stages in the development of the notochord (chorda dorsalis): the "preflexion" stage with a straight notochord, the "flexion" stage during which a dorsal flexion of the caudal-most part of the notochord starts, and the "postflexion" stage at which the caudal-most part of the notochord is fully bent dorsally (Kendall et al. 1984). During the preflexion stage, the hypurals, the skeletal elements that carry the principal caudal fin rays, start to develop on the ventral side of the caudal end of the notochord and are thus pointing ventrally in most teleost species. During the dorsal flexion of the caudal end of the notochord, the hypurals and finally also the caudal fin gradually moves into a final, horizontal position (e.g., Ott et al., 2012; Desvignes et al., 2018; Thieme et al., 2021). With the transformation of the notochord into the vertebral column, this gradual up-turning of the chorda dorsalis becomes less distinct, and once ossified as the urostyle (or terminal compound centrum) is barely recognizable (Schultze and Arratia, 1989; Thieme et al., 2021).

Generally, in Gobiidae, the urostyle is relatively small, of about half the size of a regular caudal centrum, and is fused with the upper half of the hypural plate (= hypural 3+4) (e.g., Murdy 1985; Scsepka et al. 1999; Kindermann et al. 2007; Ghanbarifardi et al. 2020). As a synapomorphy of the genus, the urostyle in *Schindleria* is exceptionally elongated and of about the same length as preural vertebrae 2–5 (Schindler 1932; Johnson and Brothers 1993). The two hypural plates are tightly fused to each other and form a roughly triangular cartilaginous plate (hypural 1–4; hypural 5 is missing in *Schindleria*) (Johnson and Brothers 1993). The upturned tip of the urostyle is hook-like and firmly attached to the edge of the upper half of this plate, dorsally. This arrangement of the caudal skeleton is typical for *Schindleria* (Johnson and Brothers 1993; Ahnelt and Sauberer 2018) and independent of the species and its size. It is present in large species such as *S. praematura* (22 mm TL) (Schindler 1930) or small species such as *S. brevipinguis* (8.6 mm TL) (Watson and Walker 2004).

Because species of *Schindleria* reach maturity within a few weeks and at an extremely early somatic developmental stage (Kon et al. 2007), the skeleton, but also the entire bauplan of adult *Schindleria* leaves the impression of overall morphological simplification. Such a simplification by undeveloped or incompletely developed characters in relation to close relatives make it challenging to separate *Schindleria* species at a morphological level (Kon et al. 2007; Ahnelt and Sauberer 2018; Ahnelt

2019). This is possibly the major reason why only nine species have been nominally described so far: *S. praematura* (Schindler, 1930), *S. pietschmanni* (Schindler, 1931), *S. brevipinguis* Watson & Walker, 2004, *S. nigropunctata* Fricke & Abu El-Regal, 2017, *S. elongata* Fricke & Abu El-Regal, 2017, *S. macrodentata* Ahnelt & Sauberer, 2018, *S. multidentata* Ahnelt, 2020, *S. parva* Abu El-Regal, El-Sherbiny, Gabr & Fricke, 2021, and *S. edentata* Ahnelt, Robitzch & Abu El-Regal, 2022. Nevertheless, it can be assumed that a number of undescribed species still remain unrecognized given the huge distributional range of this genus, which spans the entirety of the tropical and subtropical Indo-Pacific, from Central and South America in the East, to South Africa and the Red Sea in the West (Ahnelt and Sauberer 2020). So far, based on just two genetic studies in the Western Pacific, as many as 25 genetic species-level lineages have been identified (Kon et al. 2007, 2010). Because many of these lineages were restricted to single islands, generally a high level of endemism is expected in *Schindleria*. The Red Sea is known as a hotspot for marine endemism (e.g., DiBattista et al. 2015) and may also harbor high levels of endemism in *Schindleria*. Just from a single locality in the northern Red Sea, close to Hurghada, Egypt, four species have been documented, from which three have been new (Fricke and Abu El-Regal 2017a, 2017b; Abu El-Regal and Kon 2019; Ahnelt et al. 2022) (Fig. 1).
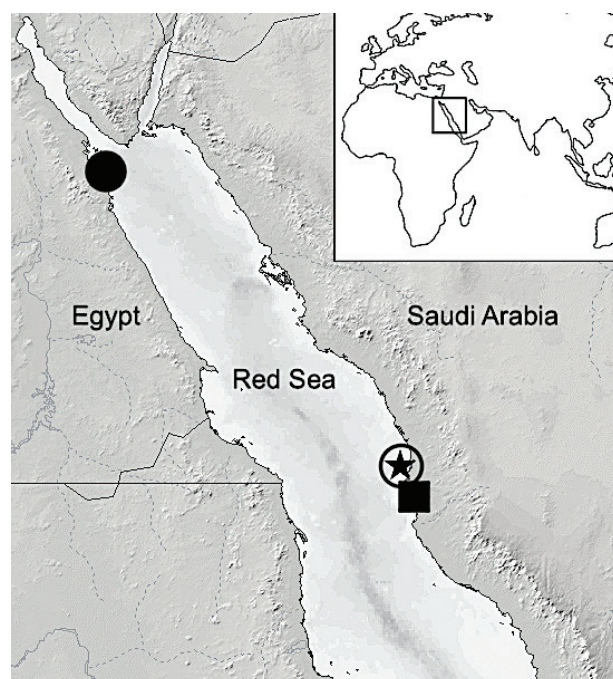
Figure 1. Published records of *Schindleria* in the Red Sea: star = *S. qizma* n. sp., in Thuwal; filled circle = *S. elongata*, *S. nigropunctata* (Fricke & Abu El-Regal, 2017a, b), *S. praematura* (Abu El-Regal and Kon, 2019), and *S. edentata* (Ahnelt et al., 2022), all in Hurghada; black square = *Schindleria* sp. (Al-Solami and Abu El-Regal, 2020) and *S. parva* (Abu El-Regal et al., 2021), both in Jeddah; empty circle = *Schindleria* sp., in Thuwal (Robitzch et al., 2021). The map is from https://www.landkartenindex.de/kostenlos/cliparts/cliparts_gruppe_1/saudiarabien.gif.

Herein, we describe a new species of *Schindleria*, based on three females from the Red Sea, Saudi Arabia, which is characterized by two peculiar characters: (1) a straight unflexed urostyle, which is not fused to but inserted into the hypural cartilage and (2) very few but very large eggs.

Material and methods

The three type specimens of *Schindleria qizma* are deposited in the Naturhistorisches Museum in Wien (NMW), Vienna, Austria and registered as NMW 99999 (holotype) and as NMW 100000 and NMW 100001 (paratypes).

The three adult (i.e., females with visibly developed eggs) specimens of *Schindleria qizma* were collected at the mid-shelf reef Al Fahal (Arabic for "the great/mighty", due to its large size) off of the coast of Thuwal, Red Sea, Saudi Arabia, using three Bellamare collapsible LED battery-powered light traps (of 500-micron mesh), set at ~ 2 m below the surface, fixed to moorings at the wave-protected, northern-end of the reef (22°18'24.54"N, 38°57'47.25"E), with a bottom depth of approx. 10 m to 12 m. LED lights are efficient in attracting fish larvae as well as *Schindleria* during the night time (see e.g., Robitzch et al. 2020, 2021). The light traps were deployed during the day around new moon for a period of ~ 24 h for collections to take place during the entire night. The specimens of *S. qizma* were collected on 19 and 22 of February 2015 and on 17 of June 2015. Sampling was in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST, Saudi Arabia) and permits for sampling were obtained from the relevant Saudi Arabian authorities. The collection did not involve endangered species.

We consider Schindleriidae a junior synonym of Gobiidae (Thacker 2009; Agorreta et al. 2013), a view adopted by Gill and Mooi (2010), Nelson et al. (2016), Betancur-R et al. (2017), and Parenti (2021).

We follow the distinction into species groups in *Schindleria* based on the two dorsal-fin types as defined by Ahnelt (2019).

Because the three females of our new species have their very large eggs arranged in a double row anteriorly, we provide the total number of eggs and compare these with the total number of eggs in other species. This is in contrast to previous counts of the number of eggs in female *Schindleria*, which has been given for one of the two ovaries only and counted in a single row (e.g., Fricke and Abu El-Regal 2017a; Ahnelt and Sauberer 2018; Ahnelt 2020; Abu El-Regal et al. 2021).

Pictures of the specimens preserved in 70% EtOH were taken with a Nikon DSRi-2 camera mounted on a Nikon SMZ25 stereo microscope using NIS-Elements Microscope Imaging Software (BR V.5.02) with a Real Time Extended Depth of Focus patch. The images were processed with Adobe Photoshop CS5 for the final figure plates.

Measurements were made with the aid of a stereo-microscope and a micrometer eyepiece to the nearest 0.1 mm by H.A.

Abbreviations of collections

AMS – Australian Museum, Sydney, Australia; **BMNH** – Natural History Museum, London; United Kingdom; **CAS** – California Academy of Sciences, San Francisco, USA; **NMW** – Naturhistorisches Museum Wien, Vienna, Austria; **SMF** – Senckenberg Museum Frankfurt, Frankfurt, Germany; **ZMUC** – Statens Naturhistoriske Museum, Zoologisk Museum København, Kopenhagen, Denmark.

Comparative material

Schindleria brevipinguis: paratype (AMS I 2632-003), 6.6 mm standard length (SL), Australia, Queensland, Carter Reef, 18 January 1982. Photographs of the holotype (AMS I 23552-006).

Schindleria edentata: holotype (BMNH 2007.5.20.1), 9.0 mm SL, Red Sea, Egypt, Hurghada, reef lagoon, 05 February 2005.

Schindleria elongata: photographs of holotype (SMF 35780) and paratype (SMF 35781).

Schindleria macrodentata: holotype (ZMUC 77624), 16.5 mm SL, female, Molucca Sea, Indonesia, between the islands of Sulawesi and Halmahera, March 1929. Paratype (ZMUC 77617), 18.7 mm SL, female, Sulu Sea, Philippines, northwest of the north tip of the Island Panaya, 27 June 1929.

Schindleria multidentata: holotype (ZMUC P771779), 20.0 m SL, female and paratype ZMUC P771800, Society Islands, Tahiti, harbor of Papeete, 10–15 October 1928.

Schindleria nigropunctata: holotype (SMF 35956), 15.9 mm SL, female, Red Sea, Egypt, Magawish Island, 23 April 2016. Paratype (SMF 35957), male, 13.9 mm SL, same data as holotype.

Schindleria parva: holotype (SMF 38020), 11 mm SL, female, Red Sea, Shaara Public Beach, Jeddah, Saudi Arabia. Paratype (SMF 38021), 9 mm SL, male, same data as holotype.

Schindleria pietschmanni: 42 syntypes (NMW 99182), 15.1–17.0 mm SL, North West Hawaiian Islands, French Frigate Shoal, May 1928.

Schindleria praematura: 49 syntypes (NMW 99183), 18.3–20.5 mm SL, North West Hawaiian Islands, French Frigate Shoal, May 1928.

Results

Schindleria qizma, sp. nov.

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Figures 2–7; Tables 1–3

Holotype. NMW 99999. Female, 10.6 mm SL, north Al Fahal reef, sheltered side, north-central Red Sea, Thuwal, Saudi Arabia, 19th February 2015, V. Robitzch.
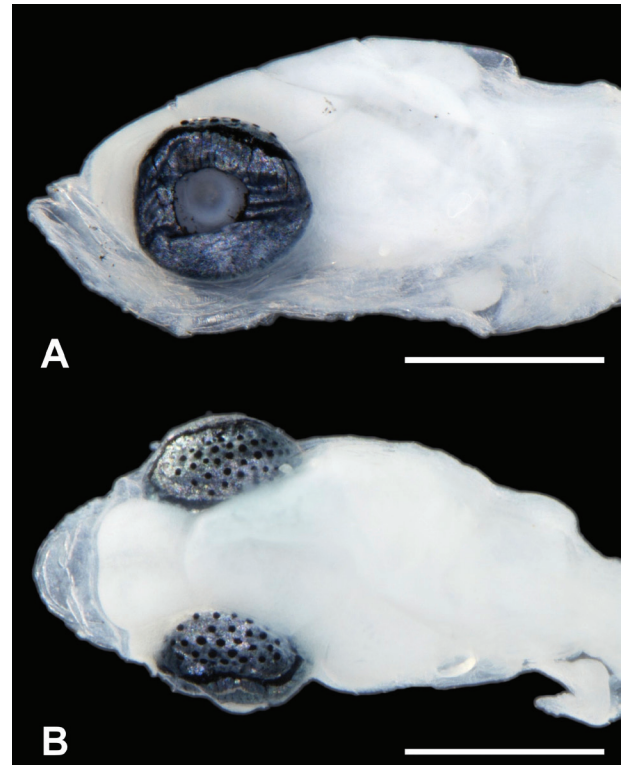
Figure 2. Holotype of *Schindleria qizma* (NMW 99999), female, 10.6 mm SL; Thuwal, Saudi Arabia. Same specimen shown in reflected (white) and transmitted light (dark). Arrows indicate position of swim bladder. Scale bar = 1 mm.

Paratypes. NMW 10000. Female, 10.7 mm SL, 22nd February 2015 and NMW 100001. Female, ~10.9 mm SL, 17th June 2015 2015. Otherwise, same data as the holotype.

Diagnosis. A member of the SDF group of *Schindleria*, which can be distinguished from all members of the LDF group by a combination of following characters: (i) the dorsal fin about the same or nearly the same length of the anal fin (vs. dorsal fin distinctly longer than anal fin), (ii) a relatively short (5.8 % of SL vs. 8.7% of SL) and deep (2.2% of SL vs. 1.5% of SL) caudal peduncle, (iii) a straight (vs. flexed) urostyle, fewer procurrent rays (0–2 vs. 5–8), and absence of teeth in both jaws (vs. both jaws with teeth).

From the four other species of the SDF group (i.e., *S. brevipinguis, S. edentata, S. parva* and *S. pietschmanni*), *S. qizma* can be distinguished as follows: (i) anal-fin rays (11 vs. 10 in *S. brevipinguis*, 13 in *S. edentata*, 9 in *S. parva* and 14–17 in *S. pietschmanni*), (ii) a shorter pre-anal-fin length (60.2% of SL vs. 71.4% in *S. brevipinguis*, 64.8% in *S. edentata*, 71.8% in *S. parva* and 65.6% in *S. pietschmanni*), (iii) a shorter head (12.4% of SL vs. 14.3% in *S. brevipinguis*, 14.9% in *S. edentata* and 19.1%

Figure 3. Paratype of *Schindleria qizma* (NMW 100000), female, 10.7 mm SL; Thuwal, Saudi Arabia. **A** head in lateral view. **B** head in dorsal view. Scale bar = 0.5 mm.
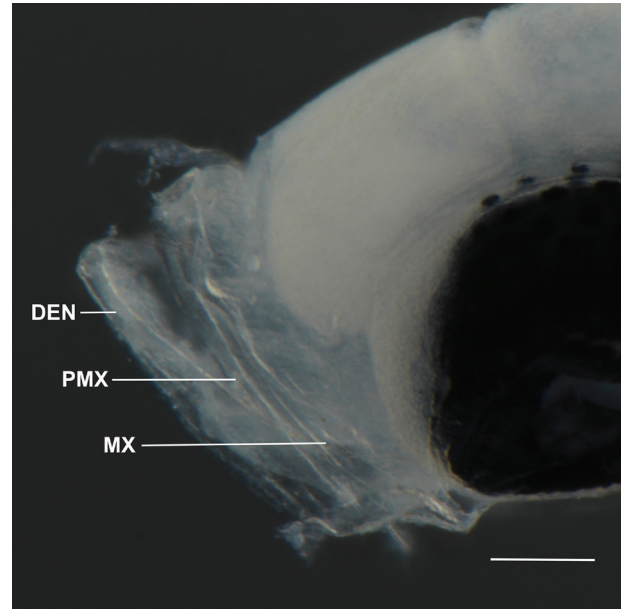
Figure 4. Head of *Schindleria qizma*, paratype (NMW 100000), 10.7 mm SL, lateral view. Note toothless jaws. DEN = dentary; MX = maxilla; PMX = premaxilla. Scale bar = 0.1 mm.

in *S. parva*), (iv) a shorter snout (18.6% of head length vs. 25.0% in *S. brevipinguis*, 23.1% in *S. edentata* and ~29% in *S. parva*), (v) a shorter tail (excluding caudal fin) (its length 32.6% in SL vs. 39.4% in *S. brevipinguis*, 36.2% in *S. edentata* and 39.4% – 49.2% in *S. pietschmanni*) (vi) a larger eye (35.3% of head length vs. 33.3% *S. brevipinguis*, 27.7% in *S. edentata* and ~23% in *S. parva*),

(vii) a straight, unflexed urostyle, dorsally enclosed by the hypural cartilage (vs. posterior tip flexed, hook-like, attached to the anterior, upper-edge of the hypural cartilage), (viii) head depth ± increasing continuously (vs. increasing steeply [except *S. pietschmanni*]) and (ix) an urogenital papilla with two long, flat, and bilobed projections in females (vs. an urogenital papilla without such projections).

Schindleria qizma can be further distinguished from *S. pietschmanni* by (i) number of dorsal fin rays (13 vs. 15–19), (ii) toothless jaws (vs. jaws with numerous tiny teeth), (iii) deeper body (body depth at anus 8.2%–9.6% SL vs. 5.5%), (iv) a deeper head (53.4% in head length vs. 34.3 %), (v) a short urostyle (3.6% of SL vs. 5.8% of SL), (vi) fewer procurrent rays (0–2 vs. 6–7), (vii) smaller adult size (<13mm TL vs. >17 mm TL) and (viii) females with few (11 vs. >40), very large (3.5 – 4.6% SL vs. 1.2% – 1.8% SL) eggs vs. more (in total) and smaller () eggs.

Schindleria qizma can be further distinguished from *S. parva* by (i) toothless jaws (vs. premaxillary with many tiny teeth), (ii) a shorter predorsal-fin length (59.4% of SL vs. 63.6% of SL), (iii) more dorsal-fin rays (13 vs. 9–10), (iv) more anal-fin rays (11 vs. 7–9), and (v) females with few eggs (11 vs. 60).

Schindleria qizma can be further distinguished from *S. brevipinguis* by (i) a shorter predorsal-fin length (59.4% SL vs. 64.3% SL), (ii) a shorter preanal length (54% SL vs. 61.2% SL), (iii) a shallower body (5.9% SL at pectoral-fin base vs. 9.3% SL, 7.6% SL at base of 4th anal-fin ray vs. 11.5% SL), (iv) a narrower (51.9% head length vs. 57%) and shallower head (53.4% head length vs. 59.6%), (v) mouth cleft oblique (vs. nearly vertical), (vi) a narrower interorbital width (25.4% head length vs. 35.2%), (vii) a shorter tail (32.6% SL vs. 39.4%), (viii) a deeper caudal peduncle (35.6% caudal peduncle length vs. 25%), and (ix) a shorter urostyle (3.6% SL vs. 6.3%).

Schindleria qizma can be further distinguished from *S. edentata* by (i) fewer dorsal-fin rays (13 vs. 15) and (ii) fewer anal-fin rays (11 vs. 13), (ii) a shorter tail (32.6% SL vs. 36.2%), (iii) the shape of the postabdominal region (continuously decreasing in depth vs. evenly deep in anterior half but rapidly decreasing in depth in posterior half), (iv) a shallower body at base of 4th anal-fin ray (7.6% SL vs. 10.9%), (v) a greater eye diameter (35.6% head length vs. 27.7%, 139.3% interorbital width vs. 111.1%), (vi) a narrower interorbital width (25.4% head length vs. 30.8%), (ii) larger maximum width of pectoral radial plate (76.8% pectoral radial plate length vs. 36.4%), (viii) a deeper caudal peduncle (35.6% of caudal peduncle length vs. 25.6%), and (ix) a shorter urostyle (3.6% SL vs. 5.8% SL).

Description. Morphometric (Table 1) and meristic information (Table 2) is given separately for the holotype and the paratypes. Body slender, elongate, somewhat compressed; body depth increases only very slightly from head to anus; head short and oval in lateral view, with head profile gradually rising posteriorly (Fig. 3A); snout short and rounded; jaws short and posteriorly just reach a vertical line through the anterior quarter of or-
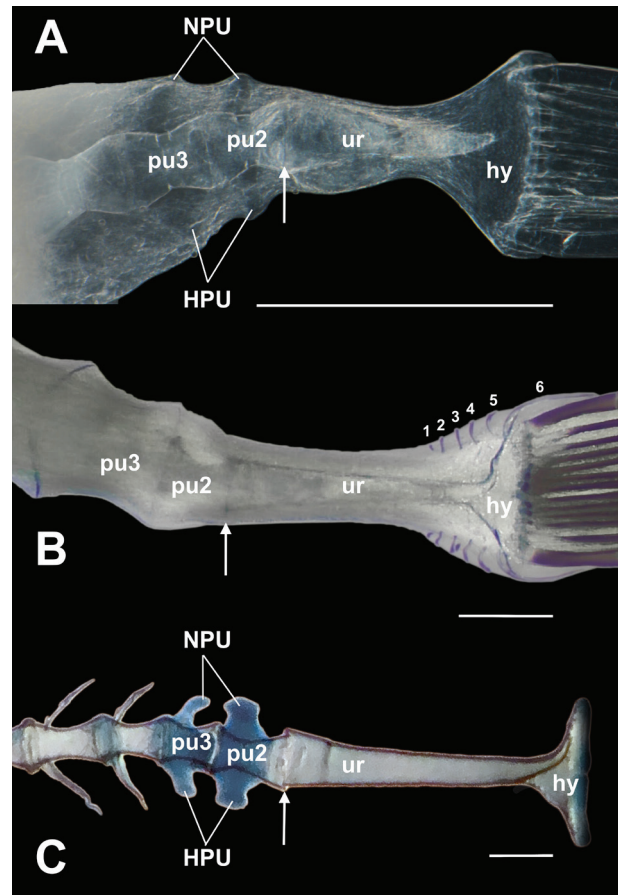
Figure 5. Comparison of caudal-fin skeleton in *Schindleria*. **A** *Schindleria qizma* (NMW 100000), paratype, 10.7 mm SL, preserved in ethanol, not stained: urostyle straight and ending inside hypural plate. **B** *Schindleria* sp. (uncatalogued), 16.9 mm SL, preserved in ethanol, stained with cephalopod ink. **C** *Schindleria* sp. (CAS 38797), 17.7 mm SL, cleared (muscles were digested) and stained with Alcian blue; procurrent rays not shown. **B**, **C** flexed urostyle, hook-like tip fused to hypural plate. HPU = haemal spines of preural vertebrae; hy = hypural plate; NPU = neural spines of preural vertebrae; pu2 and pu3 = second and third preural vertebra; ur = urostyle; 1–6 = procurrent rays, last ray elongated. Scale bar = 0.5 mm.

bit; lower jaw only slightly projecting; mouth somewhat superior; no teeth on premaxilla or on dentary (Fig. 4); premaxilla long, thin with shallow, indistinct post-maxillary process; maxilla also long, thin, anteriorly hook-like and only slightly widened distally; postabdominal region distinctly shorter than abdomen region, ends in an elongated, relatively short caudal peduncle (Fig. 2); urostyle conical, relatively short, just about length of last 2 1/2 caudal vertebrae; tip of urostyle not flexed but straight, ends in middle of cartilage of hypural plate (Figs 5, 6); hypural plate large, triangular; externally, the preserved body without pigmented except for black eyes; all three females have few (10–11) but very large (3.5% – 4.6% of SL) eggs (Fig. 2) in the abdominal cavity, arranged in two rows anteriorly, but just a single row posteriorly.

If different, values for paratypes are given in parentheses: first dorsal fin and pelvic fin absent; dorsal-fin
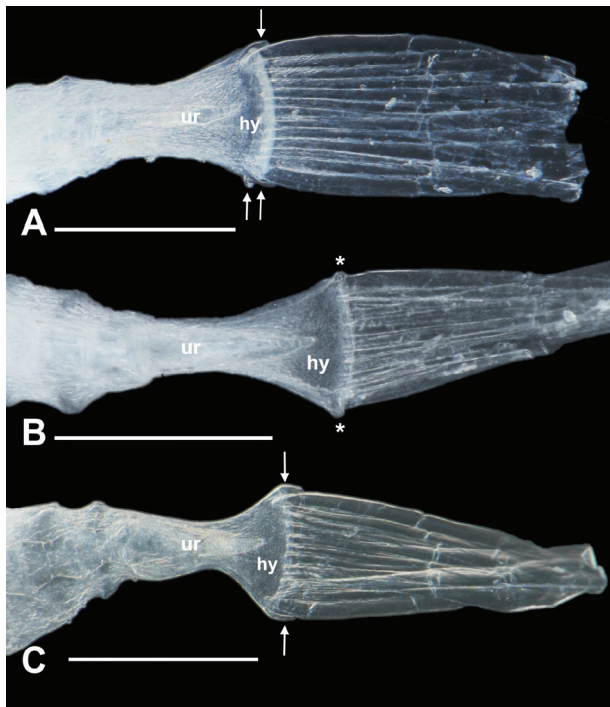
Figure 6. Caudal-fin skeleton in *Schindleria qizma*; **A** holotype (NMW 99999), 10.6 mm SL; **B** paratype (NMW 100001), ~10.9 mm SL; **C** paratype (NMW 100000), 10.7 mm SL. hy = hypural plate; ur = urostyle, straight and inserted into hypural plate. Each arrow indicates a procurrent ray; asterisk = no procurrent ray developed. Scale = 0.5 mm.

rays 13; anal-fin rays 11; principle caudal-fin rays 7+6=13, all segmented once, none branched; caudal fin truncated; procurrent rays 1 (0–1) dorsal and 2 (0–1) ventral, when present short, with no additional spine (Fig. 6); base of first dorsal-fin ray at myomere 21, that of last dorsal-fin ray at myomere 34; base of first anal-fin ray at myomere 22 and that of last at myomere 34; 37 myomeres total, 21 precaudal and 16 caudal; 38 total vertebrae (including urostyle), with 22 precaudal and 16 caudal; 5 branchiostegal rays; a relatively wide pectoral-radial plate, of paddle-like shape, distally only slightly wider than at its origin; gut straight; female urogenital papilla conspicuous, slightly bulbous with opening flanked by two long, flat, bilobed projections (Fig. 7); swim bladder small, oval-shaped, inconspicuous, pigmented dorsally, located at myomeres 14/15, in posterior half of abdomen (Fig. 2).

Coloration in life. Unknown.

Coloration preserved. The entire body, including the head, is uniformly whitish. The iris of the eye is black and capped dorsally with an iridescent silvery layer spotted with numerous melanophores (Fig. 3). The black pigment cap on the swim bladder is visible through the body wall (Fig. 2). The fins are translucent.
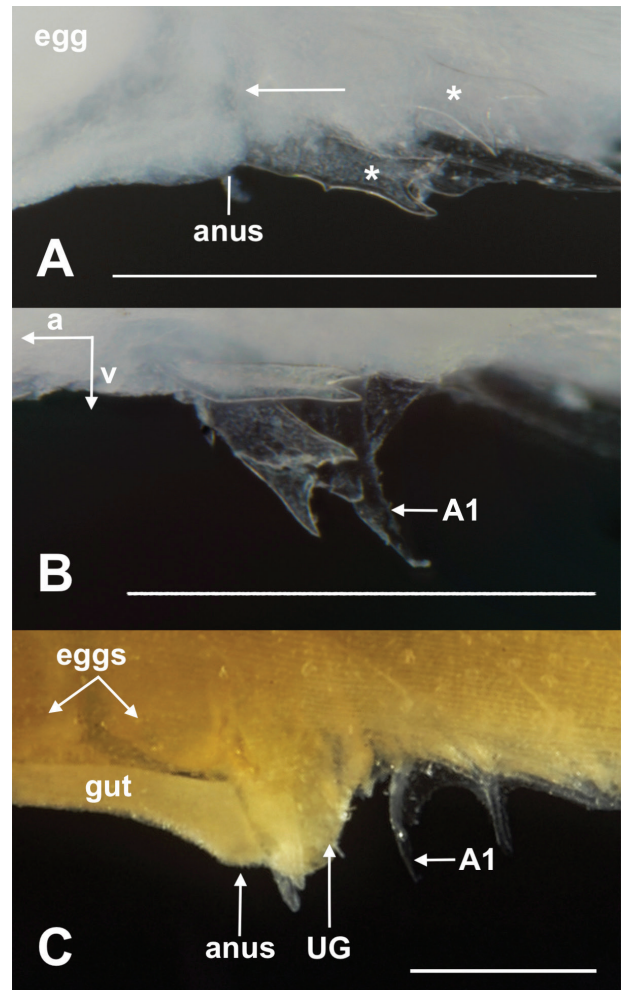
Figure 7. Comparison of urogenital region in *Schindleria* females. **A** *Schindleria qizma* (NMW 99999), holotype, 10.7 mm SL; asterisks indicate paired bilobed projections on left and right side of urogenital opening; arrow indicates urogenital opening covered by mucus. **B** *Schindleria qizma*, (NMW 100000), paratype, 10.7 mm SL. **C** *Schindleria praematura* (NMW 86241), 18.5 mm SL; urogenital papilla with two short, hornlike projections. A1 = first anal-fin ray; UG = urogenital papilla; a = anterior; v = ventral. Scale = 0.5 mm.

Distribution. *Schindleria qizma* is so far only known from Al Fahal reef in the north-central Red Sea, Thuwal, Saudi Arabia, 22°18'24.54"N, 38°57'47.25"E (Fig. 1).

Etymology. The name 'qizma' comes from the Arabic word 'qizm' (قزم), which means dwarf. It is a noun in apposition and refers to the very small size of the species.

Table 1. Body proportions in % of standard length of *Schindleria qizma* **sp. nov.**, holotype (NMW 99999), one paratype (NMW 100000), in comparison with the other three small (<14 mm TL) species of *Schindleria*: *S. brevipinguis* (AMS-I-26323-003, male and AMS-I-23552-006, female), *S. edentata* (BMNH 2007.5.20.1), and *S. parva* (SMF 38021). Data for *S. parva* were calculated from measurements of Abu El-Regal et al. (2021) (Table 1). Data for the holotype of *S. brevipinguis* were calculated from Walker and Watson (2004) (Table 2). * = Total length of the holotype of *S. edentata* from Abu El-Regal and Kon (2008). Differences are highlighted in grey. No measurements were taken from the second paratype (NMW 100001) due to its poor condition.

Species	*S. qizma*	*S. qizma*	*S. edentata*	*S. brevipinguis*	*S. parva*
Specimen	Holotype	Paratype	Holotype	Para-(Holotype)	Holotype
Sex	female	female	male	male (female)	female
Total length (TL) in mm	11.5	11.6	10.0*	7.3 (9.1)	12.1
Standard length (SL) in mm	10.6	10.8	9.0	6.6 (8.4)	11.0
% Standard length					
Predorsal-fin length	59.4	59.3	60.9	63.0 (65.5)	63.6
Preanal-fin length	60.1	60.2	64.8	66.7 (71.4)	71.8
Preanal length	53.4	54.6	56.1	61.2	–
Gut length	40.2	41.3	41.4	42.4	–
Length of dorsal-fin base	25.5	26.4	29.8	28.5	–
Length of anal-fin base	22.6	23.1	24.3	23.0	–
Tail length (excluding caudal fin)	32.1	33.0	36.2	39.4	–
Head length	12.3	12.4	14.9	18.4 (14.3)	19.1
Head width	6.2	6.4	11.6	10.6 (8.5)	–
Head depth	6.3	6.7	8.3	9.2	–
Caudal-fin length	8.5	8.3	damaged	10.6	10.0
Body depth at pectoral-fin base	6.3	5.6	7.3	10.3 (8.3)	5.5
Body depth at anus	8.6	7.7	9.6	13.3 (9.5)	–
Body depth at anal-fin origin	8.4	7.8	10.8	13.3	8.2
Body depth at base 4th anal-fin ray	7.8	7.4	10.9	11.5	–
Position of swim bladder	42.7	43.3	44.6	45.5	–
Caudal-peduncle length	5.4	6.1	8.2	11.5 (9.5)	–
Caudal-peduncle depth (min.)	2.0	2.4	2.1	2.8 (2.4)	–
Urostyle length	3.8	3.4	5.8	6.3	–
Pectoral-radial plate length	6.3	6.2	7.6	5.8 (6.0)	–
Pectoral-radial plate width (origin)	4.2	4.3	2.7	3.6	–
Pectoral-radial plate width (max.)	4.8	4.8	3.4	5.6 (4.8)	–
Snout length	2.8	2.3	3.4	4.3 (3.6)	–
Eye diameter horizontal	4.3	4.4	4.1	5.7 (4.8)	3.6
Eye diameter vertical	4.1	4.3	4.1	6.1 (4.8)	–
Postorbital length	5.9	5.5	6.9	8.5 (6.0)	–
Interorbital width	3.0	2.8	4.6	6.7	–
% Caudal-peduncle length					
Caudal-peduncle depth	36.5	39.8	25.6	25.0 (25.0)	–
% Head length					
Snout length	18.2	18.9	23.1	23.0 (25.0)	~29
Eye diameter horizontal	34.8	35.8	27.7	31.1 (33.3)	~23
Eye diameter vertical	34.4	36.7	27.7	32.8 (33.3)	~27
Postorbital length	47.1	46.3	46.2	45.9 (41.7)	~49
Interorbital width	24.5	26.3	30.8	35.2	–
Head width	50.9	53.0	35.9	55.7 (58.3)	–
Head depth	51.4	55.4	56.5	59.6	~54
% Eye diameter horizontal/vertical					
Interorbital width	144.0	134.6	111.1	112.0	–
% Pectoral-radial plate length					
Pectoral-radial plate width (origin)	66.7	69.4	36.4	53.7	–
Pectoral-radial plate width (max.)	76.1	77.4	45.5	97.9 (80.0)	–

Table 2. Meristic information for *Schindleria qizma* **sp. nov.**, NMW99999 (holotype) and NMW 100000 and NMW 100001 (paratypes). Paratype NMW 100001 in poor condition, thus missing information on several meristic characters.

Specimen	Holotype	Paratype	Paratype
Sex	female	female	female
Total length (TL) in mm	11.5	11.6	~11.7
Standard length (SL) in mm	10.6	10.8	~10.9
Dorsal-fin rays	13	13	– (13?)
Anal-fin rays	11	11	11
Pectoral-fin rays (left/right)	14/damaged	damaged	damaged
Caudal-fin rays (dorsal/ventral)	13 (7+6)	13 (7+6)	13 (7+6)
Procurrent rays (dorsal/ventral)	1/2	0/0	1/1
1st anal-fin ray ventral to dorsal-fin ray x	2	2	2
Gut ends ventral to dorsal fin ray x	1	1	1
Total number of myomeres	37	37	—
Number of abdominal myomeres	21	21	—
Number of caudal myomeres	16	16	—
Number of vertebrae (inclusive urostyle)	38	38	38
Number of abdominal vertebrae	22	22	—
Number of caudal vertebrae (incl. urostyle)	16	16	16
Position of swim-bladder at myomere x	14-15	14	—
Position of first dorsal-fin ray at myomere x	21	21	—
Position of last dorsal-fin ray at myomere x	34	34	—
Position of first anal-fin ray at myomere x	22	22	—
Position of last anal-fin ray at myomere x	34	34	—
Teeth on premaxillary	no	no	no
Teeth on dentary	no	no	no
Eggs in both ovaries	10	11	11
Pigmentation body preserved (except eyes)	no	no	no

Table 3. Meristic information for *Schindleria qizma* **sp. nov.**, NMW99999 (holotype), NMW 100000 and NMW 100001 (paratypes), and of the three other small (<14 mm TL) species: *S. brevipinguis*, holotype (AMS-I-123552-006), *S. edentata*, holotype (BMNH 2007.5.20.1) and *S. parva*, holotype (SMF 38020). * = Total length of the holotype of *S. edentata* from Abu El-Regal and Kon (2008). Data of *S. brevipinguis* from Watson and Walker (2004), of *S. edentata* from Ahnelt et al. (2004), and of *S. parva* from Abu El-Regal et al. (2021).

Species	*S. qizma*	*S. edentata*	*S. brevipinguis*	*S. parva*
Sex	female (n=3)	male (n=1)	female (n=1)	female (n=1)
Total length (TL) in mm	11.6	10.0*	9.1	12.1
Standard length (SL) in mm	10.8	9.0	8.4	11.0
Dorsal-fin rays	13	15	13	10
Anal-fin rays	11	13	10	9
Pectoral-fin rays (left/right)	d	14/d	–	13
Caudal-fin rays (dorsal/ventral)	13 (7+6)	13 (7+6)	13 (7+6)	13 (7+6)
Procurrent rays (dorsal/ventral)	1/2	4/4	5/5	—
1st anal-fin ray ventral to dorsal-fin ray x	2	3	4	4
Gut ends ventral to dorsal-fin ray x	1	1	—	—
Total number of myomeres	37	36	34	—
Number of abdominal myomeres	21	21	20	—
Number of caudal myomeres	16	15	14	—
Number of vertebrae (inclusive urostyle)	38	37	35	—
Number of abdominal vertebrae	22	—	20	—
Number of caudal vertebrae (incl. urostyle)	16	—	15	—
Position of swim-bladder at myomere x	14-15	13	—	—
Position of first dorsal-fin ray at myomere x	21	21	18	24
Position of last dorsal-fin ray at myomere x	34	35	28	36
Position of first anal-fin ray at myomere x	22	23	—	26
Position of last anal-fin ray at myomere x	34	35	—	—
Teeth on premaxillary	no	no	no	yes
Teeth on dentary	no	no	no	no
Eggs in both ovaries	11	—	~12	30
Pigmentation body preserved (except eyes)	no	no	no	no

Discussion

The new species *Schindleria qizma* is characterized by a unique caudal complex with a modified urostyle. The tip of the urostyle is not flexed, nor is it tightly attached to the anterior, upper margin of the hypural plate, as is characteristic for *Schindleria* (e.g., Johnson and Brothers 1993; Ahnelt and Sauberer 2018) but it is straight and deeply inserted into the cartilage of the hypural plate. Generally, the caudal complex of *Schindleria* is a unique propulsion system. It comprises modified preural vertebrae 2 and 3, an extremely elongate urostyle, a relatively large, triangular hypural plate, a system of modified muscles with an elongated pair on each side of the urostyle, and a caudal fin with segmented and partly branched principal caudal fin rays (Ahnelt and Sauberer 2018; Robitzch et al. 2022). Despite overall progenesis in this genus, the advanced developmental stage of the caudal complex in *S. qizma* is outstanding. Possibly the straight urostyle is the result of the reduction of notochord flexion and may represent a derived state and an apomorphy for *S. qizma* among the species of *Schindleria*.

In general, the dentition of the genus *Schindleria* is variable (Ahnelt 2020). Five different dentition patterns are known from just nine nominally described species (as the dentition of *S. elongata* is not known in detail): (i) no teeth on upper and lower jaws in *S. brevipinguis*, *S. edentata,* and *S. qizma* (Watson and Walker 2004; Ahnelt et al. 2022; this study); (ii) minute teeth on the upper jaw but no teeth on the lower jaw in *S. parva* (Abu El-Regal et al. 2022); (iii) minute and densely positioned teeth along the entire length of the premaxilla, but only anteriorly positioned teeth on the dentary close to the symphysis in *S. nigropunctata*, *S. pietschmanni,* and *S. praematura* (Johnson and Brothers, 1993; Fricke and Abu El-Regal 2017a; Ahnelt 2019); (iv) minute and densely positioned teeth along the entire length of the premaxilla and along the dentary up to its coronoid process in *S. multidentata* (Ahnelt 2021); and (v) few, very large, and widely spaced teeth on both jaws in *S. macrodentata* (Ahnelt and Sauberer 2018). It is yet unclear how and on what these tiny fishes are feeding and the functional relevance of the various dentition patterns of *Schindleria* remains unknown (Ahnelt 2020). Nevertheless, specimens of *Schindleria* are active feeders, as all investigated specimens have had guts full with amorphous, unidentifiable material (authors' personal observations during numerous collections), similar to the anguilliform leptocephalus larvae, which feed on "marine snow" or particulate organic matter (POM) (Tsukamoto and Miller, 2020, see Fig. 5c, d).

The mode of reproduction in *Schindleria* is also unknown. Some authors assume a demersal egg deposition (Watson and Leis 1974; Whittle 2003; Thacker and Grier 2005), but documentation of *Schindleria* among benthic and environmental studies is very rare (Robitzch et al. 2022) and evidence of such a spawning strategy is missing (Whittle 2003; Thacker and Grier 2005). Addi-

tionally, adult and juvenile specimens were collected far offshore, some between 200–360 km distance from the next shoreline (Ahnelt and Sauberer 2020). Nonetheless, data show that the total egg number and egg size differs distinctly among species of *Schindleria*, comprising ~200 eggs (0.4% of SL) in *S. macrodentata,* ~90 (1% – 1.1% of SL) in *S. multidentata*, ~50–60 (1.3% – 1.8% in SL) in *S. nigropunctata*, *S. parva*, *S. pietschmanni,* and *S. praematura,* and ~11 (2.5% – 5% of SL) in *S. brevipinguis* and *S. qizma*. These differences in egg numbers and sizes suggest differences in spawning strategies. Some species of *Schindleria* reproduce multiple times as more than one size class of eggs have been found in the ovaries of *S. pietschmanni* and *S. praematura* (Schindler 1930, 1931; Whittle 2003; Thacker and Grier 2005).

Generally, reproductive isolation is often accompanied by genital diversity (Langerhans et al. 2016). For males of *Schindleria* a high diversity in the shapes of the urogenital papillae hs been documented. Kon et al. (2007) describe 10 different morphotypes of such papillae. Seemingly less variable are the urogenital papillae of female *Schindleria* (e.g., Robitzch et al. 2021a). Just two general types have so far been reported: (i) a plain urogenital opening (Ahnelt and Sauberer 2018; Ahnelt 2020) and (ii) a roundish, bulbous papilla with two short horn-like projections lateral to the urogenital opening (e.g., Bruun 1940; Sardou 1974; Johnson and Borthers 1993; Ahnelt 2019) (Fig. 7C). A third and very conspicuous type of urogenital papilla is now described for *S. qizma*. here, the urogenital opening of females is flanked by two long, flat, and bifurcated projections (Fig. 7A, B).

Although some recent studies investigated sexual dimorphism (Robitzch et al. 2021a), lunar migration cycles (Robitzch et al. 2021b), and swimming mode (Robitzch et al. 2022) of *Schindleria*, the entire lifecycle, habitat, and basic biology and ecology of these enigmatic fishes are virtually unknown and still need detailed exploration. Nonetheless, the collection in which this new species was found may allow for the inference of a few more details on the habitat or distribution of *S. qizma*. The specimens come from a year-long study and a collection of over 2000 *Schindleria* specimens, collected monthly using the same method at three different reef sites along a cross-shelf gradient during the same time period (Robitzch et al. 2021a). The collection sites included a reef at the shelf-edge, one mid-shelf reef, and one inshore reef. However, *S. qizma* could be found only at the mid-shelf reef and in very low numbers. The rest of the collection is thought to mainly be comprised of one to three LDF species (unpublished data). This mid-shelf reef is known to be particularly large (about 10 km long) and has some of the regionally lowest average current speeds, wave action and visibility at its sheltered side, where *S. qizma* has been collected (Robitzch and Berumen 2020). Altogether, the uniqueness of *S. qizma* and the parameters of its habitat may hold evidence of an extreme example of endemism, with a relatively narrow distribution range and the specialization to a very specific habitat within the Red Sea.

Authors contributions

V.R. and H.A. conceived the idea. V.R. identified and sampled the material. H.A., V.R., and O.M. generated, analyzed, interpreted, and discussed the data, contributing significantly to the final version of the manuscript.

Competing interest's statement

The authors declare no competing interests.

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