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RESEARCH PAPER

Schindleria nana, a new extremely progenetic gobiid fish species (Teleostei: Gobiiformes: Gobiidae) from Lizard Island, Great Barrier Reef, Australia

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Abstract. Here, we describe a new species of Schindleria, *Schindleria nana*, from Lizard Island, Great Barrier Reef, Australia. The new species belongs to the long dorsal-fin type (LDF) of *Schindleria* and is the first very small ('dwarf') LDF species (< 13 mm TL) to be described. It is characterized by an elongate and narrow body; a dorsal fin longer than the anal fin (predorsal-fin length 63.3% of SL: preanal-fin length 72.1% of SL); a long, relatively narrow head (head width 46.2% of head length) with a straight profile; small and round eyes (24.9% of head length); a large postorbital distance (52% of head length); a narrow, slender pectoral radial plate (width at origin 46.4%, maximum width 57.0% of pectoral radial plate length); 16 dorsal-fin rays; 11-12 anal-fin rays; first anal-fin ray ventral to the sixth dorsal-fin ray; six procurrent rays gradually increasing in length, last ray elongated, twice the length of the penultimate ray; premaxilla with tiny, conical, densely set teeth; dentary with zero teeth in the holotype and with two teeth on the left dentary and five teeth on the right dentary in the adult paratype; females with few (approx. 4-7) but very large eggs (3.4-3.9% of SL); urogenital papilla inconspicuous, *de facto* just an urogenital opening; swim bladder not pigmented; black eyes; no other external pigmentation on the body.

Key words: coral reefs, Indo-Pacific, miniaturization, new species, progenesis, taxonomy

Introduction

During the last years, a series of studies on the ecology, faunistic, morphology, and taxonomy of *Schindleria* (infantfishes) have increased our current knowledge on this enigmatic gobiid genus (e.g. Ahnelt & Sauberer 2018, Robitzch et al. 2021a, b, Ahnelt et al. 2022). These tiny (10-23 mm TL) and extremely rapidly reproducing fishes (with up to nine generations per year; Kon et al. 2007) inhabit the entire tropical and sub-tropical Indo-Pacific, from Central and South America to East Africa and the Red Sea (Fig. 1). At its discovery, the first two described species, *Schindleria praematura* (Schindler, 1930) and *S. pietschmanni* (Schindler, 1931), were morphologically distinguished by a very conspicuous character in their

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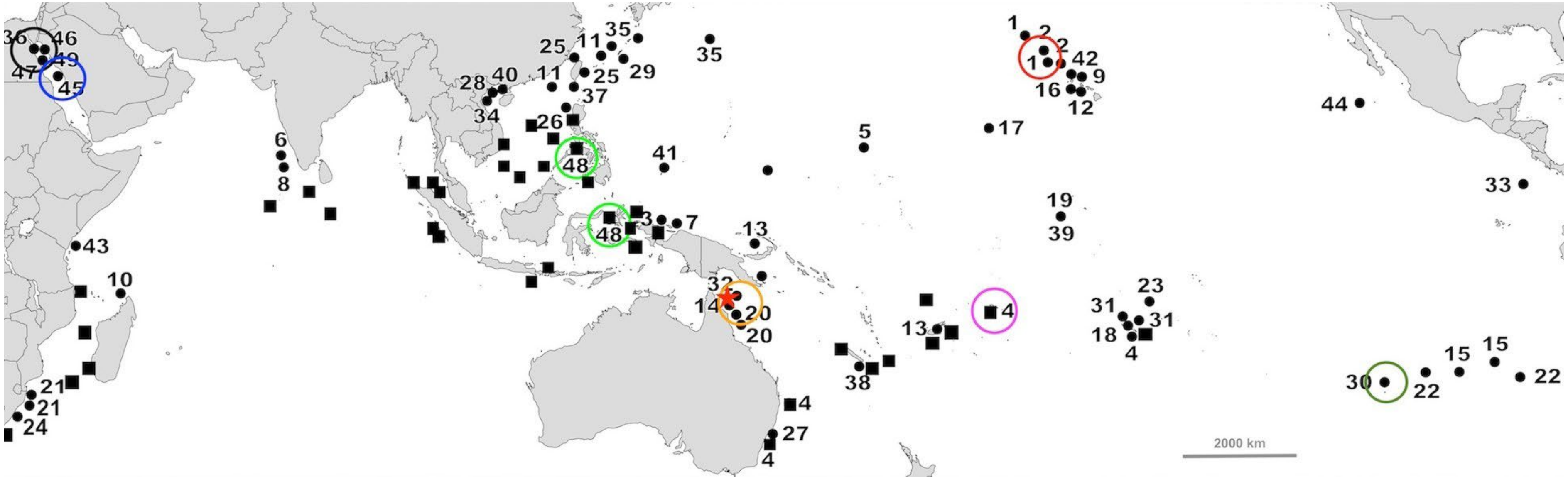

Fig. 1. Published records of *Schindleria* from 49 publications (black dots with numbers 1-49) and from the Dana Expedition 1928-1930 (black squares); for references and a detailed description of the Dana Expedition samples, see Ahnelt & Sauberer (2020). Type localities of all formally described species of *Schindleria* are encircled. These represent from west to east: *S. edentata*, *S. elongata*, and *S. nigropunctata* (black circle); *S. parva* and *S. qizma* (blue circle); *S. macrodentata* (light green circles); *S. brevipinguis* and *S. nana* sp. nov. (orange circle and red star for the latter); *S. multidentata* (pink circle); *S. pietschmanni* and *S. praematura* (red circle); and *S. squirei* (dark green circle). Map from Ahnelt & Sauberer (2020), modified.

dorsal and anal fins, where *S. praematura* featured a notably longer dorsal fin compared to its anal fin, while *S. pietschmanni's* dorsal and anal fins were approximately equal in length (Schindler 1930, 1931, 1932). Thus, subsequent studies started grouping new species of *Schindleria* in two species groups based on this character: the long dorsal fin type (LDF) as in *S. praematura* and the short dorsal fin type (SDF) as in *S. pietschmanni* (Ahnelt 2019). Virtually all reports of *Schindleria* across their Indo-Pacific distribution range resemble morphologically one of these two types (summarized in Ahnelt & Sauberer 2020). Nevertheless, the evolutionary history of this morphological trait is not known, nor whether these two fin types might have evolved convergently in allopatry multiple times.

More than 70 years after the first descriptions of the two Hawai'ian species of *Schindleria*, a third species, *S. brevipinguis*, was described from the Great Barrier Reef (Australia) close to Lizard Island. This species was morphologically clearly distinguishable from the two other species by a deeper body, toothless jaws, larger eyes, lower number of dorsal and anal fin rays, a non-pigmented swim bladder, and especially its much smaller size at maturity (< 10 mm TL) (Watson & Walker 2004). A further intriguing and distinctive character in the description of *S. brevipinguis* was the few but extremely large eggs of females. Among all described *Schindleria* species, females of the larger species *S. nigropunctata*, *S. pietschmanni*, *S. praematura*, and *S. squirei* have relatively numerous (in total 50-60) eggs of a size from 1.3-1.8% in SL, while the two smaller sized (< 11 mm SL) species, *S. brevipinguis* and *S. qizma*, have only a few (approx. 10) and distinctly large (2.5-5% of SL) eggs (Ahnelt et al. 2023).

Herein, we describe a new species of *Schindleria* of the LDF species group, two adult females and one juvenile, from Lizard Island (Queensland, Australia). This species is characterized by very small size, few and very large eggs, oral jaws with no or few teeth on the lower jaw, an inconspicuous urogenital papilla, *de facto* just a urogenital opening, and an unpigmented swim bladder.

Material and Methods

The three specimens of *S. nana* sp. nov. are deposited in the Australian Museum Sydney (AMS), Sydney, Australia, and are registered as AMS.I.23115-004 (holotype) and as AMS.I.23115-040 (paratypes). The sample was collected by J.M. Leis with a plankton tow at 6-10 m depth off of Lizard Island (Queensland, Australia), in the lagoon 'Lizard Island Reef', 14°41' S, 145°27' E (Fig. 2). The specimens were deposited at the Australian Museum, Sydney.

Based on three genetic studies in which *Schindleria* clustered within Gobiidae (Thacker 2009, Agorreta et al. 2013, Tornabene et al. 2018), we consider Schindleriidae a junior synonym of Gobiidae. We separate the species of *Schindleria* into two species groups, a long dorsal-fin type group (LDF) and a short dorsal-fin type group (SDF), as defined by Ahnelt (2019). The 12 formally described species of these two species groups are listed in Table 1.

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

Abbreviations of collections: AMS – Australian Museum, Sydney, Australia; BMNH – Natural History Museum, London, UK; 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 materials

Schindleria brevipinguis: Paratype (AMS.I.2632-003), 6.6 mm standard length (SL), Australia, Queensland, Carter Reef. 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.

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

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

Schindleria multidentata: Holotype (ZMUC P77177), 20.0 mm SL, female and paratype (ZMUC P771800), Society Islands, Tahiti, harbour of Papeete.

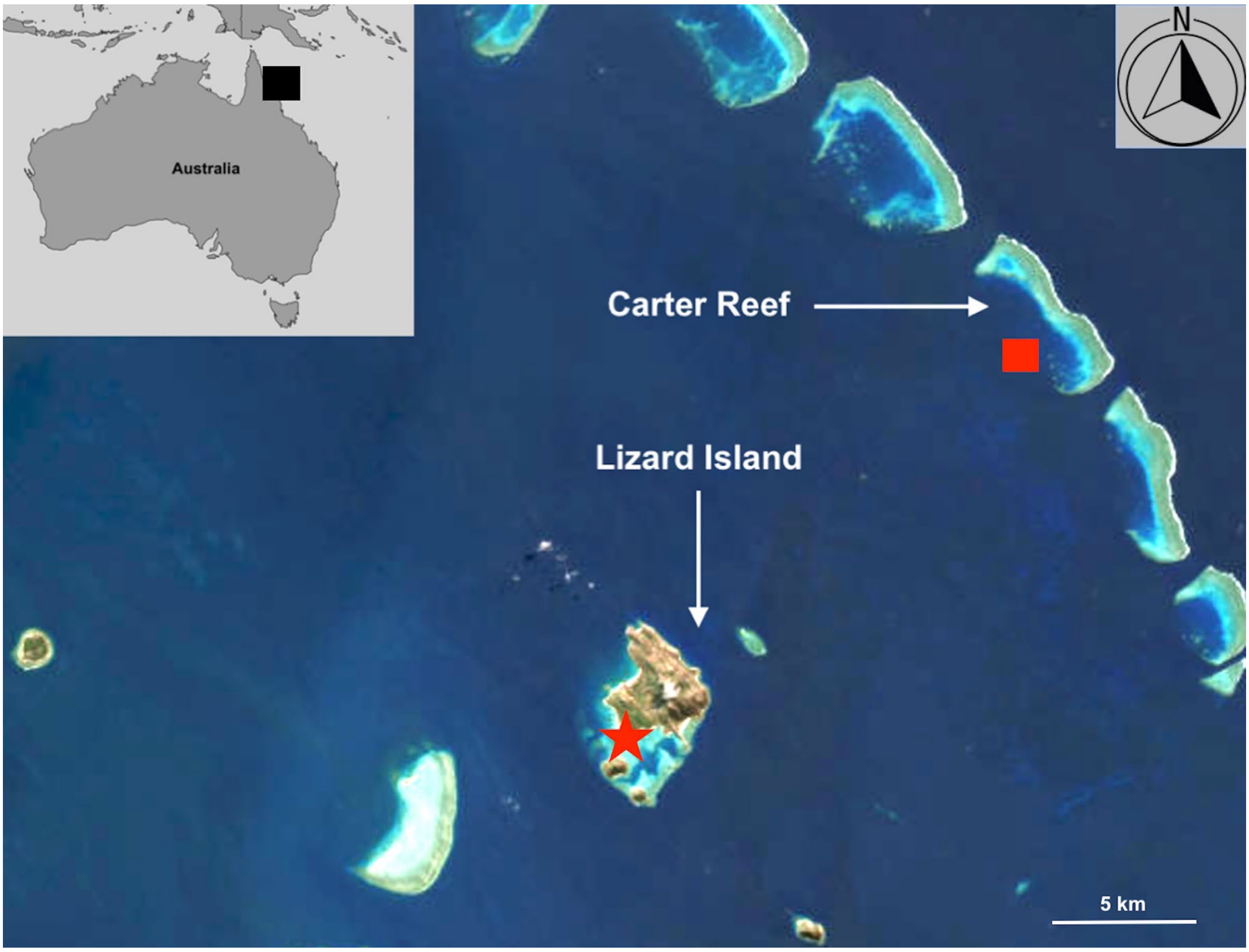

Fig. 2. The sampling sites of *Schindleria nana* (red star) and *Schindleria brevipinguis* (red square), the two smallest *Schindleria* species of the Pacific Ocean. The sampling location, Lizard Island (black square), is off the north-eastern Australian coast. Available at https://apps.gov.au/reef-monitoring/reefs.

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

Schindleria parva: Photograph of the 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.

Schindleria praematura: 49 syntypes (NMW 99183), 18.3-20.5 mm SL, North West Hawai'ian Islands, French Frigate Shoal.

Schindleria qizma: Holotype (NMW 99999), 10.6 mm SL, female, north Al Fahal reef, sheltered side, north-central Red Sea, Thuwal, Saudi Arabia. Paratypes (NMW 10000), 10.7 mm SL, female and NMW 100001, approx. 10.9 mm SL, female. Otherwise, the same data as the holotype.

Schindleria squirei: Holotype (NMW 100576), female, 19.2 mm SL, female, 20.7 mm SL, Southeast Pacific, Chile, Rapa Nui (Easter Island), Hanga Roa. Paratypes (NMW 100577); 19.2 mm SL, female, and 20.9 mm SL; one male, 17.2 mm SL. Otherwise, the same data as the holotype.

Results

Genus *Schindleria* Giltay, 1934
Schindleria nana (Figs. 3-6, Tables 2-3)

Type series: Holotype: Female, 9.0 mm SL; Australia, Queensland, Great Barrier Reef, Lizard Island in the lagoon 'Lizard Island Reef', 14°41' S, 145°27' E; January 20, 1980, 19:54-21:00; Australian Museum register number AMS.I.23115-004 (Fig. 3).

Table 1. Ratio of the depth of the hypural plate (HYP) to the length of the urostyle (UL) of adult *Schindleria* species of the 'long dorsal fin type' (n = 7) and of *Schindleria* species of the 'short dorsal fin type' (n = 3); latter are shaded in grey. Values for two species, *S. elongata* and *S. parva*, were not available.

Species	n	HYP %UL
S. praematura (Schindler, 1930)	9	47.2
S. squirei (Robitzch, Landaeta & Ahnelt, 2023)	2	48.1
S. pietschmanni (Schindler, 1931)	8	48.5
S. macrodentata (Ahnelt & Sauberer, 2018)	1	50.0
S. nigropunctata (Fricke & Abu El-Regal, 2017)	1	52.9
S. multidentata (Ahnelt, 2020)	2	53.3
S. nana sp. nov. (present study)	3	66.9
S. edentata (Ahnelt, Robitzch & Abu El Regal, 2022)	1	79.6
S. brevipinguis (Watson & Walker, 2004)	2	80.3
S. qizma (Ahnelt, Macek & Robitzch, 2023)	2	89.1
S. elongata (Fricke & Abu El-Regal, 2017)	-	-
S. parva (Abu El-Regal, El-Sherbiny, Gabr & Fricke, 2021)	-	-

Paratypes: Two specimens, same data as for holotype: female, 8.5 mm SL; juvenile, 6.8 mm SL; AMS.I.23115-040 (Fig. 4).

Diagnosis: The new species *S. nana* stands out from its congeners because it is the first small-sized species (< 10 mm SL) in the LDF species group and the first LDF *Schindleria* with only a few (4-7) and very large eggs (3.1-3.6% of SL) (Figs. 3, 4A). It differs from its congeners in the combination of the following characters: body elongated, slender, and not pigmented in preserved specimens; tail (postabdominal region) distinctly shorter than abdomen; origin of the dorsal fin distinctly anterior to origin of the anal fin (LDF type); predorsal-fin length 63.1-63.5% of SL; preanal-fin length 71.2-73.0% of SL; body depth at the origin of the

Fig. 3. Holotype of *Schindleria nana*, AMS.I.23115-004, female, 9.0 mm SL; Australia, Queensland, Lizard Island. an – anus, ug – urogenital opening. Black asterisk – position of first anal-fin ray, white asterisk – position of first dorsal-fin ray. Scale bar: 1 mm.

Fig. 4. Paratypes of *Schindleria nana*, AMS.I.23115-040; A – female, 8.5 mm SL; B – juvenile, 6.8 mm SL; Australia, Queensland, Lizard Island. Scale bar: 1 mm.

anal-fin 5.9-6.6% of SL; head length 14.4-15.6% of SL; head depth 7.8-8.1% of SL; eye diameter 3.3-3.6% of SL and 23.1-26.1% of the head length; pectoral radial plate length 5.6-5.8% of SL; maximum width of the pectoral radial plate 3.2-3.3% of SL and 56.9-57.1% of pectoral radial plate length; depth of the hypural late 66.7% of the urostyle length; 16 dorsal-fin rays; 13 anal-fin rays, first anal-fin ray positioned below the 5-6th dorsal-fin ray; six procurrent rays; swim-bladder not pigmented; continuous row of small, conical teeth on premaxillary but zero teeth on the dentary of the holotype or five teeth (right) plus two isolated teeth (left) in the dentary of the paratype. See detailed comparisons below.

Comparisons: Schindleria nana, a member of the LDF species group, can be distinguished from all members of the SDF group by a combination of the following characters: i) length of dorsal fin (distinctly longer than the anal fin *vs.* dorsal and anal fin of about the same length), ii) longer preanal-fin length (72.2% *vs.* 60.1-71.8% of SL), iii) smaller eyes (24.6% *vs.* 27.4-35.6% of head length), iv) longer postorbital length (52% *vs.* 43.8-59% of head length), and v) a relatively narrow hypural plate (66.7% *vs.* 79.6-89.1% of urostyle length).

Schindleria nana can be distinguished from the other species of the LDF species group by its i) small adult body size (8.8 mm SL *vs.* > 15 mm SL), ii) the unique type of dentition (0-5 teeth on the dentary *vs.* at least 8-9 teeth on the dentary), and iii) the females' few (approx. 10 *vs.* 50-200) and large (3.4-3.9% of SL *vs.* 1-1.8% of SL) eggs (Table 4).

Schindleria nana can be further distinguished from *S. macrodentata* by i) the size, position, and number of teeth (many, tiny, conical, and densely set on the premaxillary and few or no on the dentary *vs.* few, large, and widely spaced on both jaws), ii) fewer dorsal-fin rays (16 *vs.* 19), iii) more anal-fin rays (13 *vs.* 10), iv) a longer head (15% *vs.* 11.1% of SL), v) a longer tail (30.4% *vs.* 22.1% of SL), vi) a distinctly wider pectoral radial plate (57% *vs.* 32.6% of pectoral radial plate length), vii) the shape of the last and longest procurrent ray (simple *vs.* with an additional spiny process at the base), and viii) females with few large eggs (total approx. 10) *vs.* with numerous small eggs (possibly up to 150-160).

Schindleria nana can be further distinguished from *S. multidentata* by i) the number and position of the teeth on the lower jaw/dentary (zero or up to five *vs.* approx. 30 divided by a diastema in two series, approx. 21 + 8), ii) fewer dorsal fin rays (16 *vs.* 19), iii) the position of the first anal-fin ray (below the dorsal-fin ray 5 or 6 *vs.* 10), iv) a deeper body (body depth at the pectoral-fin base 6.3% *vs.* 4.1% of SL and at the origin of the anal-fin 6.3% *vs.* 5.6% of SL), and v) a swim bladder unpigmented *vs.* dorsally pigmented.

Schindleria nana can be further distinguished from *S. nigropunctata* by i) more anal-fin rays (13 *vs.* 12), ii) the number and position of the teeth on the lower jaw/dentary (zero or up to five *vs.* approx. 8-9 teeth), iii) a longer predorsal-fin length (63.3% *vs.* 61.1% of SL), iv) a deeper body (body depth at the pectoral-fin base 6.3% *vs.* 4.8% of SL and at the origin of the

Table 2. Body proportions in % of standard length (SL) of *Schindleria nana* sp. n., holotype, AMS.I.23115-004, paratype, AMS.I.23115-040 in comparison with the other four small (< 11.5 mm SL, all SDF) species of *Schindleria*: *S. brevipinguis* (AMS.I.26323-003, male and AMS-I-23552-006, female), *S. edentata* (BMNH 2007.5.20.1), *S. parva* (SMF 38021), and *S. qizma* (NMW 100000, 100001). Data for *S. parva* were calculated from measurements by Abu El-Regal et al. (2021). Data for the holotype of *S. brevipinguis* were calculated from Watson & Walker (2004). Characters highlighted in light grey are different in *S. nana* sp. n. compared to all other species. Values highlighted in dark grey indicate additional differences between *S. nana* sp. n. and the sympatrically occurring *S. brevipinguis*.

Species	*S. nana*	*S. qizma*	*S. parva*	*S. brevipinguis*	*S. edentata*
Specimen	Holo- (Paratype)	Holo- (Paratype)	Holotype	Holo- (Paratype)	Holotype
Sex	females	females	female	female (male)	male
Total length (TL) in mm	9.8 (9.3)	11.5 (11.6)	12.1	9.1 (7.3)	10.0*
Standard length (SL) in mm	9.0 (8.5)	10.6 (10.8)	11.0	8.4 (6.6)	9.0
% Standard length					
Predorsal-fin length	63.1 (63.5)	59.4 (59.3)	63.6	65.5 (63.0)	60.9
Preanal-fin length	73.0 (71.2)	60.1 (60.2)	71.8	71.4 (66.7)	64.8
Preanus length	71.0 (69.4)	53.4 (54.6)	-	(61.2)	56.1
Gut length	52.2 (51.8)	40.2 (41.3)	-	(42.4)	41.4
Base of dorsal fin	28.9 (27.6)	25.5 (26.4)	-	(28.5)	29.8
Base of anal fin	18.9 (19.4)	22.6 (23.1)	-	(23.0)	24.3
Tail length (excluding caudal fin)	29.2 (31.5)	32.1 (33.0)	-	(39.4)	36.2
Head length	14.4 (15.6)	12.3 (12.4)	19.1	14.3 (18.4)	14.9
Head width	6.6 (8.2)	6.2 (6.4)	-	8.5 (10.6)	11.6
Head depth	7.8 (8.1)	6.3 (6.7)	-	(9.2)	8.3
Caudal-fin length	8.9 (9.3)	8.5 (8.3)	10.0	(10.6)	-
Body depth at pectoral-fin base	6.6 (5.9)	6.3 (5.6)	5.5	8.3 (10.3)	7.3
Body depth at anus	7.4 (7.1)	8.6 (7.7)	-	9.5 (13.3)	9.6
Body depth at origin of anal-fin	6.6 (5.9)	8.4 (7.8)	8.2	(13.3)	10.8
Body depth at base of 4th anal-fin ray	6.6 (5.9)	7.8 (7.4)	-	(11.5)	10.9
Position of swim bladder along body	42.7 (45.6)	42.7 (43.3)	-	(45.5)	44.6
Caudal peduncle length	8.9 (8.1)	5.4 (6.1)	-	9.5 (11.5)	8.2
Caudal peduncle depth (min.)	2.2 (2.2)	2.0 (2.4)	-	2.4 (2.8)	2.1
Urostyle length	4.5 (4.7)	3.8 (3.4)	-	(6.3)	5.8
Pectoral radial plate length	5.6 (5.8)	6.3 (6.2)	-	6.0 (5.8)	7.6
Pectoral radial plate width (at origin)	2.6 (2.6)	4.2 (4.3)	-	(3.6)	2.7
Pectoral radial plate width (max.)	3.2 (3.3)	4.8 (4.8)	-	4.8 (5.6)	3.4
Snout length	3.3 (3.8)	2.8 (2.3)	-	3.6 (4.3)	3.4
Eye diameter horizontal	3.3 (3.5)	4.3 (4.4)	3.6	4.8 (5.7)	4.1
Eye diameter vertical	3.3 (3.5)	4.1 (4.3)	-	4.8 (6.1)	4.1
Postorbital length	7.8 (8.3)	5.9 (5.5)	-	6.0 (8.5)	6.9
Interorbital distance	2.2 (2.3)	3.0 (2.8)	-	(6.7)	4.6
% Caudal peduncle length					
Caudal peduncle depth	25.0 (27.0)	36.5 (39.8)	–	25.0 (25.0)	25.6
% Head length					
Snout length	23.1 (26.7)	18.2 (18.9)	approx. 29	25.0 (23.0)	23.1
Eye diameter horizontal	23.1 (26.1)	34.8 (35.8)	approx. 23	33.3 (31.1)	27.7
Eye diameter vertical	23.1 (26.1)	34.4 (36.7)	approx. 27	33.3 (32.8)	27.7

Table 2. continued.

Species	*S. nana*	*S. qizma*	*S. parva*	*S. brevipinguis*	*S. edentata*
Specimen	Holo- (Paratype)	Holo- (Paratype)	Holotype	Holo- (Paratype)	Holotype
Sex	females	females	female	female (male)	male
Postorbital length	53.8 (50.2)	47.1 (46.3)	approx. 49	41.7 (45.9)	46.2
Interorbital distance	15.3 (19.2)	24.5 (26.3)	-	(35.2)	30.8
Head width	46.2 (46.6)	50.9 (53.0)	-	58.3 (55.7)	35.9
Head depth	51.2 (46.1)	51.4 (55.4)	approx. 54	(59.6)	56.5
% Eye diameter horizontal/vertical					
Interorbital distance	150.0	144.0 (134.6)	-	(112.0)	111.1
% Pectoral radial plate length					
Pectoral radial plate width (at origin)	46.4 (44.8)	66.7 (69.4)	-	(53.7)	36.4
Pectoral radial plate width (max.)	57.1 (56.9)	76.1 (77.4)	-	80.0 (97.9)	45.5

* Total length of the *S. edentata* holotype from Abu El-Regal & Kon (2008).

anal-fin 6.3% *vs.* 5.0%), v) a longer head (15% *vs.* 12.2% of SL), vi) a wider head (46.4% *vs.* 35.6% of the head length), vii) larger eyes (24.6% *vs.* 20.6% of the head length), viii) a longer pectoral radial plate (5.7% *vs.* 2.8% of SL), ix) a narrower pectoral radial plate (57% *vs.* 62.2% of the pectoral radial plate length), x) a longer snout (24.9% *vs.* 21.6% of the head length), xi) longer tail (30.4% *vs.* 26.7% of SL), xii) a more anterior positioned swim-bladder (44.2% *vs.* 53.5% of SL), and xiii) the swim bladder not pigmented *vs.* dorsally pigmented; females with inconspicuous urogenital papilla, *de facto* just the urogenital opening *vs.* conspicuous bulbous urogenital papilla with two horn-like projections.

Schindleria nana can be further distinguished from *S. praematura* by i) a lower number of dorsal-fin rays (16 *vs.* 18-20), ii) a first anal-fin ray placed more anteriorly (at dorsal-fin ray six *vs.* at dorsal-fin ray 8-9), the number and position of the teeth on the lower jaw/ dentary (zero or up to five *vs.* approx. 12 teeth), iii) a longer predorsal-fin length (63.3% *vs.* 58.5% of SL), iv) a shorter dorsal-fin base (28.3% *vs.* 33.5% of SL), v) a longer head (15% *vs.* 12.2% of SL), vi) a deeper body (body depth at the pectoral-fin base 6.3% *vs.* 4.0% of SL and at the origin of the anal-fin 6.3% *vs.* 46.5% of SL), vii) a deeper caudal peduncle (26.0% of caudal peduncle length *vs.* 15.9% of caudal peduncle length), viii) a narrower pectoral radial plate (57% *vs.* 79.3% of the pectoral radial plate length), ix) a shorter snout (24.9% *vs.* 31.3% of the head length), x) a longer postorbital length (52.0% *vs.* 45.1% of the head length), xi) a more anterior positioned swim-bladder (at 44.2% *vs.* at 54.2% of SL), and xii) the swim bladder not pigmented *vs.* dorsally pigmented; females with inconspicuous urogenital papilla, *de facto* just the urogenital opening *vs.* conspicuous bulbous with two distinct horn-like projections.

Schindleria nana can be further distinguished from *S. squirei* by i) a lower number of dorsal-fin rays (15-16 *vs.* 20-21), ii) a first anal-fin ray ventral to the dorsal-fin ray six *vs.* 9-10, iii) fewer teeth on the premaxillary (approx. 20 *vs.* approx. 40) and on the dentary (zero to five teeth *vs.* approx. 12-14), iv) a longer predorsal-fin length (63.3% *vs.* 57.6% of SL), v) a shorter dorsal fin (28.3% *vs.* 32.2% of SL), vi) a longer head (15% *vs.* 11.4% of SL), vii) a deeper body (7.4% *vs.* 4.5% of SL), viii) a longer (5.7% *vs.* 3.8% of SL) and wider (3.2% *vs.* 2.0% of SL) pectoral-radial plate, ix) a deeper caudal peduncle (26% *vs.* 12.7% of the caudal peduncle length), x) a wider interorbital distance (150% *vs.* 93.4% of the eye diameter), and xi) the swim bladder not pigmented *vs.* dorsally pigmented; females with inconspicuous urogenital papilla, *de facto* just the urogenital opening *vs.* conspicuous bulbous with two small horn-like projections.

Description: Morphometric (Table 2) and meristic (Table 3) information is given separately for the holotype and the paratypes. Body slender, elongate, and somewhat compressed; body depth increases slightly from head to anus; head long and elongate in the lateral view with a straight head profile; jaws reach a vertical, posteriorly through the origin of the orbit; lower jaw projecting the upper jaw, mouth superior; premaxilla with approx. 20 tiny, conical, and densely set teeth along the entire ventral margin; dentary with 0-5 tiny teeth on the anterior third: zero teeth on both dentaries (Fig. 5), in the holotype, and two plus five

Table 3. Meristic information for *Schindleria nana* sp. n., holotype, AMS.I.23115-004, paratypes, AMS.I.23115-040 in comparison with the other four small (< 11.5 mm SL, all SDF) species of *Schindleria*: *S. brevipinguis* (AMS-I-23552-006), *S. edentata* (BMNH 2007.5.20.1), *S. parva* (SMF 38021), and *S. qizma* (NMW 100000, 100001).

Species	*S. nana*	*S. nana*	*S. qizma*	*S. parva*	*S. brevipinguis*	*S. edentata*
Specimen	Holo- (Paratype)	Paratype	Holo- Paratypes	Holotype	Holotype	Holotype
Sex	females	juvenile	females	female	female	male
Standard length (SL) in mm	9.0 (8.5)	6.1	10.8	11.0	8.4	9.0
Dorsal fin rays	16 (16)	16	13	10	13	15
Anal fin rays	12 (11)	12	11	9	10	13
Pectoral fin rays (left/right)	(15/15)	-	D	13	-	14/-
Caudal fin rays (dorsal/ventral)	13 (13)	13	13	13	13	13
Procurrent rays (dorsal/ventral)	6/6 (5/6)	6/6	1-2	-	5/5	4/4
1st anal fin ray ventral to dorsal fin ray x	6/6	6	2	4	4	3
Gut ends ventral to dorsal fin ray x	5/5	5	1	-	-	1
Total number of myomeres	37 (36)	36	37	-	34	35
Number of precaudal myomeres	23 (23)	23	21	-	20	21
Number of caudal myomeres	14 (13)	13	16	-	14	15
Number of vertebrae (inclusive urostyle)	37 (36)	36	38	-	35	37
Number of precaudal vertebrae	23 (23)	23	22	-	20	-
Number of caudal vertebrae	14 (13)	13	16	-	15	-
Pos. of swim-bladder at myomere x	14 (14)	14	14-15	-	-	13
Pos. of first dorsal fin ray at myomere x	18 (18)	18	21	24	18	21
Pos. of last dorsal fin at myomere x	34 (33)	33	34	36	28	35
Pos. of first anal fin ray at myomere x	23 (22)	22	22	26	-	23
Pos. of last anal fin ray at myomere x	34 (33)	33	34	-	-	35
Teeth on premaxillary	approx. 20	-	no	yes	no	no
Teeth on dentary	0-5	-	no	no	no	no
Eggs (total)	7 (4)*	-	11	approx. 60	approx. 10	-

* Both specimens: likely some eggs were already released.

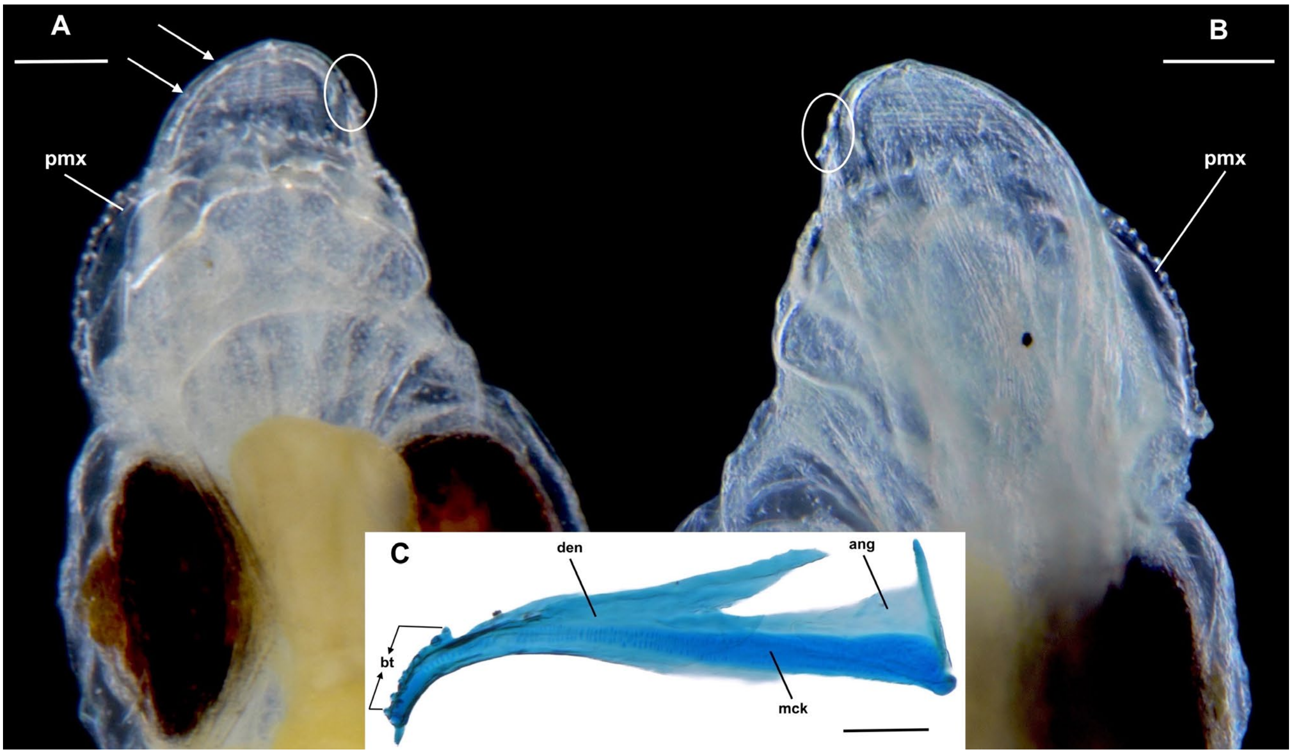

Fig. 5. A, B – Dentition of *Schindleria nana*, paratype (AMS.I.23115-040), 8.5 mm SL; C – right lower jaw of *Schindleria* sp. (*S. pietschmanni* or *S. praematura*), Hawai'i (CAS uncatalogued) in dorsomedial view; the teeth were lost during the staining process, only the bases for the teeth are visible. A – dorsal view of the head, B – ventral view of the head. Teeth on the right dentary are encircled; two isolated teeth on the left dentary are marked with arrows. Note continuous row of small, conical teeth along the entire ventral margin of the premaxilla. ang – anguloarticular, bt – bases for the teeth, den – dentary, mck – Meckel's cartilage, pmx – premaxilla. Scale bar: 0.2 mm.

teeth on the left and the right dentary, respectively, in the paratype (Figs. 5, 6); except for the posterior-most tooth on the right dentary, all other teeth (left and right) of the paratype are very small and seemingly not fully developed; premaxilla long, thin with indistinctive postmaxillary process; maxilla long and thin, slightly widening distally; postabdominal region distinctly shorter than abdominal region, ends in an elongated, relatively long caudal peduncle (Figs. 3, 4); urostyle elongated and flexed, its upturned tip attached to the antero-dorsal rim of the large, triangular hypural plate (depth of the hypural plate in urostyle length is 66.7%); externally, the preserved body without pigmentation except for the eyes; the two females have few (4-7) but very large eggs (3.4-3.9% of SL) in the abdominal cavity, arranged in a single row (Fig. 7, Table 4).

If different, values for paratypes are given in parentheses: first dorsal fin and pelvic fin absent; dorsal-fin rays 16, anal-fin rays 12 (11); principle caudal fin rays 13 (from dorsal to ventral 7 + 6), all segmented four times, none branched; caudal fin truncated; six (five) ventral and six dorsal procurrent, last elongated (approx. 17% of first principle caudal fin ray); base of the first dorsal-fin ray at myomere 18 and that of the last dorsal-fin ray at myomere 34 (33); base of the first anal-fin ray at myomere 23 (22) and that of the last at myomere 34 (33); 37 (36) myomeres in total, 23 precaudal and 14 (13) caudal; 37 (36) vertebrae (including urostyle), with 23 precaudal and 14 (13) caudal; 5 branchiostegal rays; pectoral radial plate of paddle like shape, distally wider than at its origin; gut straight; swim bladder slightly oval in shape, small, unpigmented, located in the posterior half of the abdomen (Fig. 4A); urogenital papilla of the female inconspicuous, barely more than an urogenital opening (Figs. 3, 7A) .

Colouration in life: Unknown.

Colouration preserved: The body is uniformly yellowish except for the ventral side of the abdomen and the head, which are translucent. The eyes are rubiginose to blackish (Figs. 3, 4). The fins are translucent.

Geographic range: Only known from Lizard Island, Queensland, Australia (Figs. 1, 2).

Etymology: The specific name '*nana*' (from the Latin 'nanus' – dwarf) refers to the small size of this species.

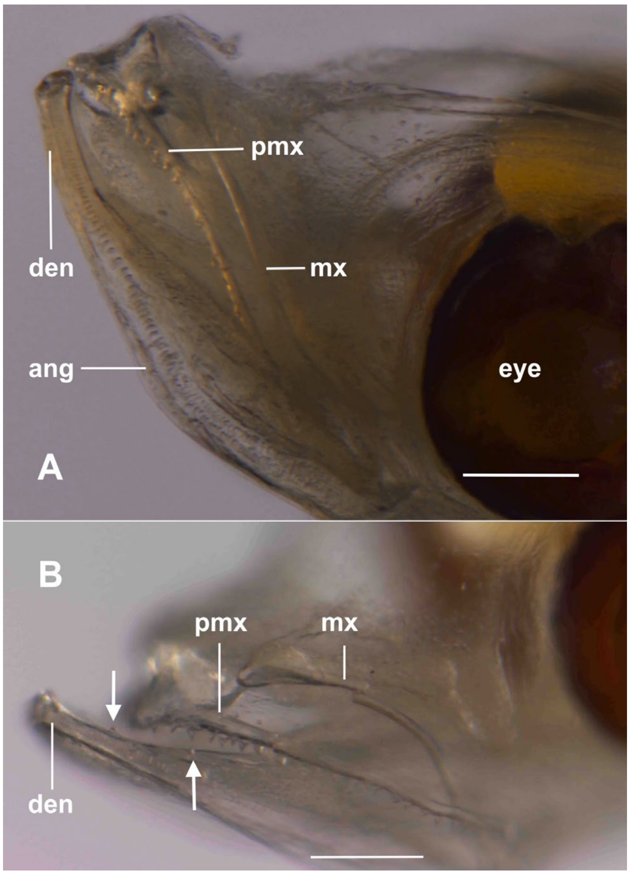

Fig. 6. Dentition of *Schindleria nana*, head, lateral view. A – Holotype (AMS.I.23115-004), 9.0 mm SL; B – Paratype (AMS.I.23115-040), 8.5 mm SL. A – no teeth on the dentary, tiny conical teeth on the premaxilla. B – two isolated teeth on dentary (arrows); maxillary out of position, broken, and distorted. Conical and densely set teeth along the entire ventral margin of the premaxilla. a – anterior, ang – anguloarticular, den – dentary, mx – maxillary, pmx – premaxillary. Scale bar: 0.5 mm.

Discussion

The relative position of the dorsal fin to the anal fin is a reliable character to group species of *Schindleria* and has resulted in two groupings: the SDF species group and the LDF species group (Ahnelt 2019). Although adult specimens can generally unambiguously be assigned to one of these two groups, the assignment is less evident in juvenile LDF species because juveniles have fewer dorsal fin rays than adults (see Fig. 177D in Watson 2000, Fig. 1 in Ozawa & Matsui 1979). This ontogenetic difference in fin ray number is characteristic of teleost fishes because the dorsal fin rays appear sequentially in a bidirectional pattern during larval development (e.g. Mabee et al. 2002, Ott et al. 2012, Figs. 2, 6 in Koch et al. 2022). This difference is also true among gobiid fishes (e.g. Daoulas et al. 1993, Figs. 2, 3 in Strydom & Neira 2006, González-Navarro et al. 2021), where late larvae have more fin rays developed than earlier larval stages of the same species. *Schindleria* species are extremely progenetic (Johnson & Brothers 1993) and do not develop beyond a larval stage (Kon & Yoshino 2002, Kon et al. 2007). Generally, the first anal fin ray is positioned below the dorsal fin ray eight to eleven in LDF species such as *S. macrodentata*, *S. multidentata*, *S. nigropunctata*, *S. praematura*, or *S. squirei* (Ahnelt & Sauberer 2018, Ahnelt 2019, 2020, Robitzch et al. 2024) and below the dorsal fin ray one to four in SDF species such as S. *brevipinguis*, *S. parva*, *S. pietschmanni*, or *S. qizma* (Schindler 1932, Watson & Walker 2004, Abu El-Regal et al. 2021). In the new species, *S. nana*, the

Table 4. The species of *Schindleria* grouped in typical 'large' species (> 15 mm SL), and very small ('dwarf') species (< 11 mm SL). Additionally, the number of ovaries (from *S. edentata*, no females are known), the size of the eggs and the origin of the type localities (for details, see Fig. 1) are given. The five 'dwarf' species are shaded in grey. No data concerning the ovaries and the size and number of the eggs are available from the twelfth species, *S. elongata* (Red Sea); therefore, this species is not considered in this Table.

Species	Size	Ovaries	Egg size %SL	Type localities in:
S. macrodentata	> 16 mm SL	paired	0.4	West Pacific
S. multidentata	> 17 mm SL	paired	1.0-1.1	Central Pacific
S. nigropunctata	> 15 mm SL	paired	1.3-1.8	Red Sea
S. pietschmanni	> 16 mm SL	paired	1.3-1.8	Central Pacific
S. praematura	> 16 mm SL	paired	1.3-1.8	Central Pacific
S. squire	> 17 mm SL	paired	1.3-1.8	East Pacific
S. brevipinguis	< 11 mm SL	single	2.5-5.0	West Pacific
S. nana sp. nov.	< 11 mm SL	single	3.4-3.9	West Pacific
S. qizma	< 11 mm SL	paired/single*	3.5-4.6	Red Sea
S. parva	< 11 mm SL	paired	1.0-1.8	Red Sea
S. edentata	< 11 mm SL	-	-	Red Sea

* *S. qizma*: the ovaries are paired anteriorly but end up as a single ovary.

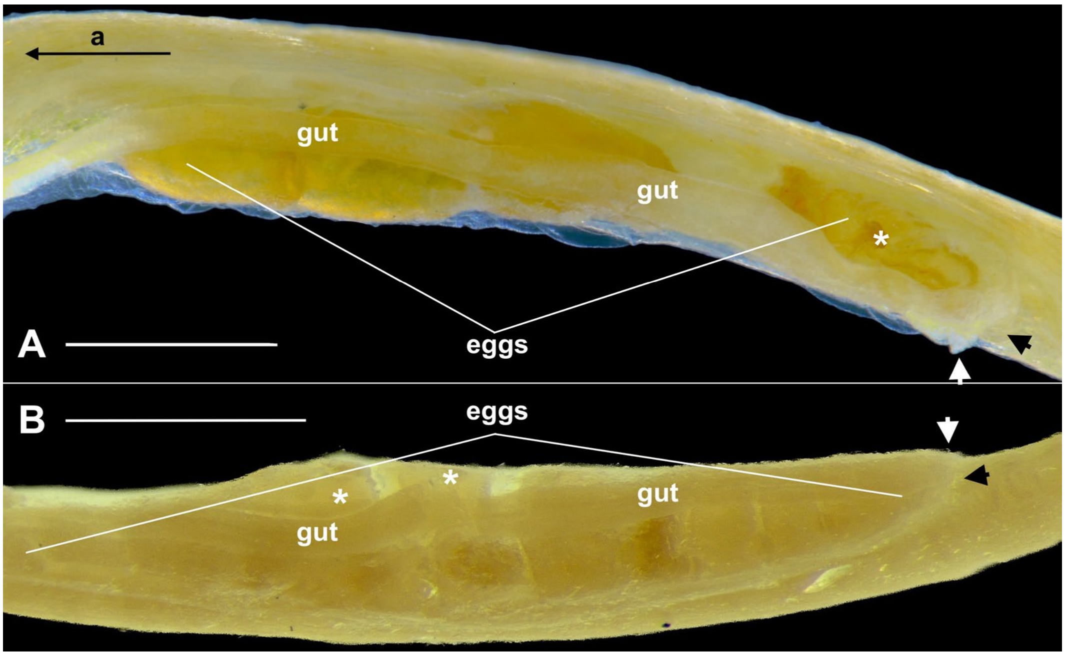

Fig. 7. A, B – ventral view of the abdomen of A) the holotype of *Schindleria nana*, AMS.I.23115-004, 9.0 mm SL, four eggs (photo Oliver Macek and Harald Ahnelt) and of B) the holotype of *Schindleria brevipinguis*, AMS.I.23552-006, 8.4 mm SL, 10 eggs (photo Anthony Miskiewicz, Australian Museum) to show the single rows of few and large eggs. a – anterior, asterisks – squeezed and/or distorted eggs, white arrowheads point to anus, black arrowheads point to urogenital opening. Scale bar: 0.5 mm.

only known small-sized (< 11 mm SL) LDF species, the first anal fin ray is positioned below the dorsal fin ray six. This is not as distinctly far anterior as in the larger (> 15 mm SL) adult LDF species and could be related to an even faster progenic development in *S. nana* sp. n., where specimens reach maturity at an earlier larval stage than larger LDF species.

Another character which allows the differentiation of *Schindleria* species is the dentition of the oral jaws, which is also hypothesized to be related to size (Ahnelt et al. 2022). In many gobiid fishes, teeth first appear in a larval stage of 4-9 mm TL (e.g. Kondo et al. 2012, Zanella et al. 2017, Hwang et al. 2018). Watson (2000) found teeth in *Schindleria* sp. larvae at a size of 4.2-4.5 mm SL, and Watson & Walker (2004) in *S. pietschmanni* larvae of 4.5-5 mm SL, with teeth first forming on the premaxilla and subsequently on the dentary. The large *Schindleria* species *S. macrodentata*, *S. multidentata*, *S. praematura*, *S. nigropunctata*,

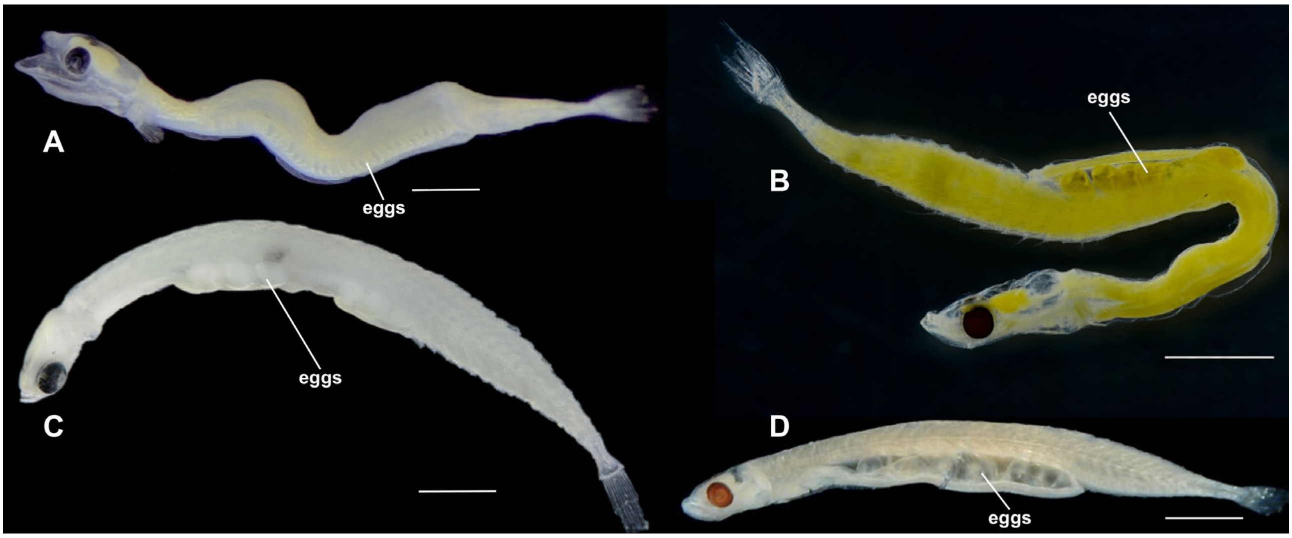

Fig. 8. The holotypes of the four small *Schindleria* species (< 11.1 mm SL). A – *S. parva*, SMF 38020, 11.0 mm SL; B – *S. nana*, AMS.I.23115-004, 9.0 mm SL; C – *S. qizma*, NMW 99999, 10.6 mm SL; D – *S. brevipinguis*, AMS.I.23552-006, 8.4 mm SL. Note the high total number of small eggs (approx. 60) of *S. parva* and the low total number of large eggs (approx. 4-12) of the other three species. Scale bar: 1 mm.

S. pietschmanni, and *S. squirei* have teeth on both oral jaws (Schindler 1930, Fricke & Abu El-Regal 2017, Ahnelt & Sauberer 2018, Ahnelt 2020, Robitzch et al. 2024). The smaller species (< 11 mm SL) *S. brevipinguis*, *S. edentata*, and *S. qizma* are characterized by the lack of teeth on the oral jaws (Watson & Walker 2004, Ahnelt et al. 2022, 2023) or by teeth only on the premaxilla and no teeth on the dentary as is the case for *S. parva* (Abu El-Regal et al. 2021). Ahnelt et al. (2022) discussed the possibility that the toothlessness of *S. brevipinguis*, *S. edentata*, and *S. qizma* and the lack of teeth on the dentary of *S. parva* could be the result of a more truncated development of these small species (< 11 mm SL) compared to the larger *Schindleria* species (> 15 mm SL). The few teeth on the lower jaw and their asymmetric position, or the overall lack of teeth in *S. nana* sp. n., a species of only 10 mm SL, supports this hypothesis. Seemingly, *S. nana* sp. n. reaches maturity during and prior to the full development of dentition, which is hence completed for the premaxilla but not for the dentary. This pattern also aligns with the observation by Watson & Walker (2004), where the formation of teeth (in *S. pietschmanni*) starts earlier in development on the premaxilla than on the dentary. This chronological appearance of the first teeth on the oral jaws is also known from other gobioids such as *Bathygobius soparator* Valenciennes, 1837 (Peters 1983) and *Tridentiger obscurus* Temminck & Schlegel, 1845 (Hwang et al. 2018), but it is reverse in some percomorphs such as *Porichthys notatus* Girard, 1854 (Vaz & Hilton 2022) or *Sander lucioperca* Linnaeus, 1758 (Löffler et al. 2008).

Another interesting morphological character of *Schindleria* is the relation between the depth of the hypural plate and the length of the urostyle. The urostyle is extremely elongated (Johnson & Brothers 1993) in *Schindleria* and plays a crucial role in swimming behaviour (Robitzch et al. 2022). Hence, we compared the relation of the depth of the hypural plate and the length of the urostyle of ten of the twelve described species and concluded that the hypural plate is distinctly less deep in the large species compared to the small species, regardless of whether they belonged to the LDF or the SDF species group (Table 1). Except for *S. nana* sp. n., the other three small species have less elongated but deeper bodies than the large species and deeper caudal peduncles (e.g. Ahnelt 2020, Ahnelt et al. 2022, 2023) (Fig. 8). This is also characteristic for *S. edentata*, the fifth small *Schindleria* species described, based on a single male. These characters are linked to the swimming abilities of fishes (Langerhans & Reznick 2010). Occurrence in different habitats often results in adaptive differences in fish species, particularly affecting locomotion (e.g. Walker 1997, McGuigan et al. 2003). Detailed habitat descriptions are missing for *S. brevipinguis*, *S. edentata*, *S. nana* sp. n., *S. parva*, and *S. qizma*, but seemingly all five small-sized species occur in calm waters of sheltered coastal lagoons (*S. edentata*, *S. nana* sp. n., *S. parva*) (Abu El-Regal et al. 2021, Ahnelt et al. 2022, present study) or in especially sheltered sites of a coral reef (*S. brevipinguis*, *S. qizma*) (Watson & Walker 2004, Ahnelt et al. 2023).

Yet an enigma, is the spawning strategy and the mode of reproduction in *Schindleria*. Although some authors assume a demersal egg deposition (Watson & Leis 1974, Whittle 2003, Thacker & Grier 2005), offshore records of up to 360 km distance to the next shore (Ahnelt & Sauberer 2020) may indicate that at least some species could be pelagic spawners. High diversity in the shape of urogenital papillae (Kon et al. 2007, Ahnelt et al. 2023) and in the size and number of eggs (Ahnelt & Sauberer 2018, Ahnelt et al. 2023) in *Schindleria* can be further indicative of differences in spawning strategies. Kon et al. (2007) described ten different types of male urogenital papillae. Among females, three morphotypes of urogenital papillae are known, i) two long, flat, and flexible bifurcated projections flanking the urogenital opening (Ahnelt et al. 2023), ii) a roundish and bulbous papilla with two short horn-like projections (e.g. Bruun 1940, Sardou 1974, Ahnelt 2019), and iii) a plain urogenital opening (Ahnelt & Sauberer 2018, Ahnelt 2020, this study). The most common urogenital papilla morphotype among female *Schindleria* across the Indo-Pacific is a bulbous-like opening with two horn-like projections (Bruun 1940, Sardou 1974, Ahnelt & Sauberer 2020). Furthermore, in the ovaries of some large species (i.e. *S. pietschmanni* and *S. praematura*), more than one size class of eggs have been found in the same specimen (Jones & Kumaran 1964, Whittle 2003, Thacker & Grier 2005), indicating that these species are capable of reproducing multiple times. On the other hand, in small-sized species with few but large eggs (*S. brevipinguis*, *S. nana* sp. n., and *S. qizma*), only one size class of eggs has been found (Ahnelt et al. 2023, this study), which may hint towards a shorter lifespan in these species, with only a single spawning event, and/or at least the production of only a single, very small egg clutch.

Like in most teleost fishes, the ovaries of female gobioid fishes are paired and of about equal size (Thacker & Grier 2005). However, a shift from paired ovaries to eggs in a single, unpaired ovary, as in some very small-sized *Schindleria* species, is not likely linked to their small size. Similar to the larger *Schindleria* species, the very small *S. parva* has paired ovaries and relatively small eggs (1.0-1.8% of SL). In contrast, the eggs of *S. nana* are about twice the size (3.4-3.9% of SL) of those found in *S. parva* and are arranged in a single, unpaired ovary (Table 4). Therefore, we conclude that the distinctly increased egg size likely induced the shift from paired-ovary eggs to a single-ovary egg row in *Schindleria*.

The high diversity in the shape of urogenital papillae and the size and number of eggs suggest reproductive isolation (Langerhans et al. 2016). Based on two genetic studies, Kon et al. (2007, 2011) identified 25 genetic species-level lineages from the Ryukyu and Ogasawara Islands (Japan) and Palau (Western Pacific). Many of these lineages were restricted to single islands, and because of the short lifespan and extremely short generation times of *Schindleria* (Kon & Yoshino 2002), high levels of endemism were proposed (Kon et al. 2011).

Diversity in egg size and the shape of urogenital papillae could result in reproductive isolation and favour a high level of endemism. Interestingly, nine of twelve to date known and formally described *Schindleria* species occur sympatrically at least with one other species: *S. praematura* and *S. pietschmanni* at Hawai'i, *S. elongata*, *S. nigropunctata* and *S. edentata* in the northern Red Sea, *S. parva* and *S. qizma* from the Central Red Sea near Jedda and *S. brevipinguis* and *S. nana* sp. n. from Lizard Island-Carter Reef from Queensland, Australia (Fig. 1); and the species-pairs are comprised of an LDF and SDF species. Considering the vast distribution range of *Schindleria*, there may be hundreds of undescribed species within this unique genus.

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Author Contributions

V. Robitzch and H. Ahnelt conceived the idea. O. Macek and H. Ahnelt made the photographs. H. Ahnelt wrote most of the manuscript. H. Ahnelt, O. Macek and V. Robitzch analysed, interpreted, and discussed the data. O. Macek and V. Robitzch contributed significantly to the final version of the manuscript.

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