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Reconsideration of the species assigned to *Faustula* Poche, 1926 (Digenea: Microphalloidea) with the proposal of five new genera in the Faustulidae Poche, 1926

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Abstract

The assignment of species to *Faustula* Poche, 1926 (Faustulidae Poche, 1926) is reconsidered with the proposal of *Gangafaustula* **n. gen.** to accommodate *Gangafaustula makundai* (Agarwal & Verma, 1981) **n. comb.**; *Gobifaustula* **n. gen.** to accommodate *Gobifaustula qikouensis* (Qui & Li, 1995) **n. comb.**; *Lingulitrema* **n. gen.** to accommodate *Lingulitrema hilsai* (Kumar & Agarwal, 1984) **n. comb.**; *Schellitrema* **n. gen.** to accommodate *Schellitrema gasterostei* (Schell, 1973) **n. comb.** and *Varanasifaustula* **n. gen.** to accommodate *Varanasifaustula indica* (Agarwal & Verma, 1981) **n. comb.** *Faustula hilsai* Kumar & Agarwal, 1984 is determined to be a species distinct from *Faustula hilsai* Rizvi, 1971 and *F. hilsai* Rizvi, 1971 is synonymized with *Faustula basiri* Hafeezullah & Siddiqi, 1970. *Faustula rahemii* Al-Daraji, 2004 also is synonymized with *F. basiri*. *Faustula pyriformis* Kumar & Agarwal, 1984 is transferred to *Pronoprymna* Poche, 1926 as *Pronoprymna pyriformis* (Kumar & Agarwal, 1984) **n. comb.** *Faustula sayori* (Yamaguti, 1942) Yamaguti, 1958, now synonymized with *Pronoprymna petrowi* (Layman, 1930) Bray & Gibson, 1980, is renamed *Pronoprymna sayori* (Yamaguti, 1942) **n. comb.** based on the presence of an entire (smooth) ovary in *P. petrowi* (Syn. *Monorcheides petrowi* Layman, 1930) as originally described, and *Faustula varanasiensis* (Agarwal & Kumar, 1977) is transferred to *Bacciger* Nicoll, 1914 as *Bacciger varanasiensis* (Agarwal & Kumar, 1977) **n. comb.** We currently propose the following 5 species be retained in *Faustula*: *F. basiri*; *Faustula brevichrus* (Srivastava, 1935) Yamaguti, 1958; *Faustula clupeae* (Srivastava, 1935) Yamaguti, 1958; *Faustula gangetica* (Srivastava, 1935) Yamaguti, 1958 and *Faustula keksooni* (MacCallum, 1918) Poche, 1926. A revised key to the species of *Faustula* and a key to the genera within the Faustulidae are provided.

Key words: Arabian Gulf; *Bacciger varanasiensis* **n. comb.**; Bo-Hai Sea; *Faustula*; *Faustula rahemii*; *Gangafaustula* **n. gen.**; *Gangafaustula makundai* **n. comb.**; Ganges River; *Gobifaustula* **n. gen.**; *Gobifaustula qikouensis* **n. comb.**; India; Japan; key to genera; key to species; *Lingulitrema* **n. gen**.; *Lingulitrema hilsai* **n. comb.**; new genera; *Pronoprymna pyriformis* **n. comb.**; *Pronoprymna sayori* **n. comb.**; Puget Sound; San Juan Islands; *Schellitrema* **n. gen.**; *Schellitrema gasterostei* **n. comb.**; Sindh River; Singapore; synonymies; Tutiura; Varanasi; *Varanasifaustula* **n. gen**.; *Varanasifaustula indica* **n. comb.**; Washington State; Yellow Sea

Introduction

Bray (2008) provided a conventional morphology/host-based identification key to the families currently considered to be assigned to the Microphalloidea Ward, 1901. However, because of the innate complexity within the superfamily and the "wide variety of morphologies" displayed by members of the various families in the Microphalloidea

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the author's ability to develop "an entirely reliable key" was limited. Given the morphological limitations in assigning families to the Microphalloidea, only 7 families (Anenterotrematidae Yamaguti, 1958; Diplangidae Yamaguti, 1971; Eumegacetidae Travassos, 1922; Exotidendriidae Mehra, 1935; Renschetrimatidae Yamaguti, 1971; Stomylotrematidae Poche, 1925 and Taiwantrematidae Fischthal & Kuntz, 1981) could be recognized as microphalloids based solely on morphology; many of the families listed in the superfamily by Bray (2008) had to be defined based largely on available molecular data (Tkach *et al*. 2000, 2001, 2003; Cribb *et al*. 2001; Olsen *et al*. 2003; Bray *et al*. 2005) and to some extent known host relationships (Tkach *et al*. 2003) (see pp. 447–448 of Bray 2008a for details). Amongst those morphologically problematic families that were recognized primarily using molecular evidence (see p. 447 of Bray 2008 for details) was the Faustulidae Poche, 1926, the subject of the current study.

MacCallum (1918, p. 85) established *Eurema keksooni* MacCallum, 1918 (Digenea: Faustulidae) based on a single damaged specimen reportedly dislodged from the gills of a "small unspotted ray" (Chondrichthyes) collected off Singapore. Poche (1926) replaced *Eurema* MacCallum, 1918 with *Faustula* Poche, 1926, based on the previous use of *Eurema* Hübner, 1818 (Insecta: Lepidoptera) and erected the Faustulidae to accommodate *Faustula keksooni* (MacCallum, 1918) Poche, 1926. Species of *Faustula* generally are intestinal parasites of marine and anadromous clupeids. The majority of species currently assigned to this genus have been described from the Hilsa shad, *Tenualosa ilisha* (Hamilton) (Syns. *Clupea ilisha* [Hamilton]; *Hilsa ilisha* [Hamilton]) (Clupeiformes: Clupeidae). *Tenualosa ilisha* is primarily a marine fish frequently found in the Indian Ocean and Arabian Gulf (Persian Gulf). Like most clupeids, it is known to be anadromous and/or a migrant, often entering rivers to breed. It is an important food-fish in the region and is used extensively in aquaculture (Froese & Pauly 2021). There have been recent declines in the natural population of this fish species that have been attributed to overfishing and the erection of dams along rivers which obstruct access of clupeid fishes to their breeding grounds (Freyhof 2014).

Some previously recognized species of *Faustula* have been reported from other localities and/or non-clupeid fish hosts. For example, in addition to the type species, *F. keksooni* described from off Singapore, *Faustula gasterostei* Schell, 1973 was described from the three-spined stickleback, *Gasterosteus aculeatus* Linnaeus (Gasterosteidae), from Puget Sound, Washington, USA (Schell 1973). *Faustula qikouensis* Qiu & Li, 1995 (in Shen & Qiu 1995) is known from the Asian freshwater goby, *Synechogobius ommaturus* (Richardson) (Perciformes: Gobiidae), from the Yellow Sea off China and *Faustula sayori* (Yamaguti, 1942) Yamaguti, 1958 (Syn. *Orientophorus sayori* Yamaguti, 1942) was described from the Japanese halfbeak, *Hyporhamphus sajori* (Temminck & Schlegel) (Beloniformes: Hemiramphidae), off Tutiura, Japan. Simha (1974) described *Faustula mandapamensis* Simha, 1974 from the silver pomfret, *Pampus argenteus* (Euphrasen) (Syn. *Stromateus cinereus* Bloch) (Perciformes: Stromateidae), off India; however, Hafeezullah & Dutta (1998) and the World Register of Marine Species (WoRMS 2021a) considered this species as a synonym of *Faustula gangetica* (Srivastava, 1935) Yamaguti, 1958. Based on Bray & Gibson (1980), WoRMS (2021a) now considers *F. sayori* as a synonym of *Pronoprymna petrowi* (Layman, 1930) Bray & Gibson, 1980. The original report of *F. keksooni* from the gills of a "small unspotted ray" either was an error or represented an accidental infection (Bray 2008). The ray likely would have been from the marine system because the only ray currently known from freshwater in Singapore is the South American freshwater stingray or ocellate river stingray, *Potamotrygon motoro* (Müller & Henle) (Myliobatiformes: Potamotrygonidae), which is an invasive species with definite spots that apparently was introduced from South America through aquarium trade.

Based on the ambiguities of existing descriptions ("important misinterpretations"), Price (1938; see p. 9) redescribed *F. keksooni* from the type specimen. Yamaguti (1958), Bray (2008) and currently WoRMS (2021b) have recognized the synonymy of *Orientophorus* Srivastava, 1935 with *Faustula*, and WoRMS (2021a) has accepted *Orientophorus brevichrus* Srivastava, 1935, *Orientophorus clupeae* Srivastava, 1935, *Orientophorus gangetica* Srivastava, 1935 and *Orientophorus ilishii* Srivastava, 1935 as species of *Faustula*. WoRMS (2021a) has accepted *Faustula chauhani* Gupta & Srivastava, 1960, described by Gupta & Srivastava (1960) in *T. ilishii* from Allahabad, India, as a synonym of *F. brevichrus* (Srivastava, 1935) Yamaguti, 1958. Garner *et al*. (2019) synonymized *Faustula ilishii* (Srivastava, 1935) Yamaguti, 1958 with *F. gangetica*. Hafeezullah & Siddiqi (1970) reported *F. gangetica* in the Toli shad, *Tenualosa toli* (Valenciennes) (Clupeiformes: Clupeidae) (Syn. *Hilsa sinensis* [Linnaeus]), collected off Mumbai (previously Bombay); however, *F. gangetica* was originally reported in the Hilsa shad, collected in freshwater from India. Although Hafeezullah & Siddiqi (1970) provided neither a detailed description nor measurements of their specimens, and although their fig. 2 appears to indicate a somewhat more elongate body form, Garner *et al*. (2019) had encountered similar body shapes in some of their specimens of *F. gangetica* and

considered fig. 2 of Srivastava (1935) to represent *F. gangetica*. WoRMS (2021a) also recognized *Faustula hilsai* Kumar & Agarwal, 1984 as a synonym of *Faustula hilsai* Rizvi, 1971 (both described from *T. ilisha*). WoRMS (2021a) currently recognizes 5 other species of *Faustula*: *Faustula basiri* Hafeezullah & Siddiqi, 1970 in *T. toli* collected off Veraval, southwestern India; and *Faustula indica* Agarwal & Verma, 1981, *Faustula makundai* Agarwal & Verma, 1981, *Faustula pyriformis* Kumar & Agarwal, 1984 and *Faustula varanasiensis* Agarwal & Kumar, 1977 all in *T. ilisha* from the Ganges River, Varanasi, India. A previously overlooked/unlisted species, *Faustula rahemii* Al-Daraji, 2004, was described from the intestine of the Hilsa shad, *T. ilisha* (Syn. *C. ilisha*), from the Khor Al-Zubair lagoons by Al-Daraji (2004).

The purpose of this study was to reevaluate the 13 species currently assigned to *Faustula* and develop updated keys to the genera within the Faustulidae and to the species of *Faustula*.

Materials and methods

The following specimens of species of *Faustula* were examined from the Parasite Collection, Department of Invertebrate Zoology, National Museum of Natural History, the Smithsonian Institution (USNM): *F. basiri* (holotype 1358919); *F. gangetica* (voucher 1358920); *F. gasterostei* (holotype 1368020); and *F. keksooni* (type 1337171). Additional specimens of *F. gangetica* used in this study were collected by 2 of us (MB and EM) from the Arabian Gulf in conjunction with the Species Diversity Program based at the Marine Science Center, University of Basrah, Iraq. Specimens were relaxed in saline, observed alive, heat fixed, preserved in formalin or AFA (alcohol-formalin-acetic acid), stored in 70% ETOH and sent to the Laboratory of Parasitology, Department of Ecology & Conservation Biology, Texas A&M University in College Station, Texas for further evaluation. Specimens were stained in Semichon's carmine, mounted in Canada balsam and examined using an Olympus BX 40 compound microscope. All measurements in descriptions are in micrometers (μm) and are given with the mean followed by the range in parentheses, and length is followed by width for two-dimensional structures, unless otherwise stated. Critical morphometric percentages based on measurements as a percentage of the body length and morphometric ratios are provided where necessary. Comparative characteristics of species in *Faustula* were taken from their original descriptions and/or museum specimens (Table 1). The redescription of *F. keksooni* by Price (1938) based on the original type specimen was used for species comparisons because of the limitations of the existing descriptions by MacCallum (1918) and Poche (1926). Measurements not provided or which were obviously in error in existing descriptions were calculated from the original figures where necessary as indicated in Table 1. Descriptions utilized characteristics commonly used in the descriptions of digeneans and were generally presented in the conventional order for members of the subclass. To promote ease of comparing descriptions we followed the older convention of providing the basic characteristics and the respective positions of structures in the body relative to characteristics and the positions of structures that previously had been defined as benchmarks in the descriptions. Fish classification and authorities follow FishBase (Froese & Pauly 2021). The following voucher specimens of *Faustula gangetica* were deposited in the USNM: Voucher specimens (14 specimens on 6 slides) USNM 1480557 (3); USNM 1480558 (2); USNM 1480559 (2); USNM 1480560 (1); USNM 1480561 (3); USNM 1480562 (3).

Results

Phylum Platyhelminthes Claus, 1887

Class Trematoda Rudolphi, 1808

Order Plagiorchiida La Rue, 1957

Family Faustulidae Poche, 1926

Faustula Poche, 1926 (*sensu stricto*)

(Syn. *Orientophorus* Srivastava, 1935)

Type species: *Faustula keksooni* (MacCallum, 1918) Poche, 1926
(Syn. *Eurema keksooni* MacCallum, 1918 *nec* Hübner, 1820)

Museum specimen: USNM 1337171.

Emended diagnosis: Body small, oval, elliptical (elongate-oval) to lingulate (see fig. 43 of McCallum 1918 and fig. 3 of Price 1938), spinose (type species *F. keksooni* originally described as aspinose, but apparently body spines were lost during fixation). Forebody occupies less than one-half of body length. Oral sucker subterminal, sometimes approaching terminal. Ventral sucker muscular, about same size to slightly larger than oral sucker, located some distance anterior to midlevel of body. Prepharynx short to absent. Pharynx small, muscular, oval to elliptical, somewhat globular. Esophagus relatively long. Intestinal bifurcation in forebody about one-half distance from anterior end and ventral sucker or slightly more posterior, well anterior to midlevel of body. Ceca relatively short, blind, terminate about midlevel of body. Testes 2, entire, symmetrical (opposite, side by side) or nearly so, largely intercecal, located about level of ventral sucker or slightly more posterior. Intertesticular space generally wide. Cirrus sac generally claviform (somewhat retort-shaped in *F. keksooni*, may be a product of the poor condition of the single specimen used to establish the species), encloses short invaginable cirrus (documented in some species); short ejaculatory duct with few prostatic glands that surround it posteriorly; short pars prostatica and long tubular seminal vesicle that spirals through posterior two-thirds of cirrus sac, at least partially embedded in numerous large glandular cells. Genital pore median to somewhat submedian, often posterior to intestinal bifurcation, sometimes bifurcal or prebifurcal. Genital atrium small, sometimes indistinct. Ovary multilobate (8 or more distinct lobes), usually slightly submedian, located short distance posterior to testes and ventral sucker, far removed from the posterior extremity, larger than either. Laurer's canal present, relatively long, opens dorsally close to posterior extremity where known. Canalicular seminal receptacle present, formed as dilation of proximal end of Laurer's canal where documented. Vitelline follicles distributed in 2 clusters, 1 on each side of body from about level of intestinal bifurcation or somewhat more anterior to about level of ovary or somewhat more posterior. Uterus occupies bulk of hindbody, extends from level of ovary posteriorly to near posterior extremity. Eggs numerous, relatively small, operculate. Excretory vesicle V-shaped, may approach Y-shaped with short stem; excretory arms reach anterior to about level of posterior margin of pharynx; excretory pore terminal to somewhat dorsal. Most commonly intestinal parasites of clupeid fishes in India (rivers) and northern Indian Ocean.

Remarks: Despite the damage apparent in the specimen representing the type species ("Specimen was mutilated, anterior end being torn off and the body partly crushed. The crushing apparently resulted from over flattening and was sufficient to rupture the intestinal ceca and force a part of the ingesta into the tissues, thereby causing outpocketings which were regarded by McCallum as openings of vaginae" [see pp. 9–10 of Price 1938;] and generally confirmed in examination of the type specimen by NOD in the present study), NOD also noted that the specimen had been rolled. However, despite the apparent fixation-induced variability of many specimens used to describe subsequent species, some species are easily assigned to *Faustula* based on morphology (e.g., *F. basiri* [see fig. 1 of Hafeezullah & Siddiqi 1970], *F. brevichrus* [see fig. 1 of Srivastava 1935], and *F. gangetica* [see fig. 2 of Srivastava 1935 and fig. 1 of Garner *et al*. 2019]). Of these 3 species, we consider *F. gangetica* to be the most fully documented species.

Species recognized within *Faustula* (*senso stricto*)

There are some relatively reliable characteristics (or combinations of these characteristics) we feel are useful in distinguishing genera within the Faustulidae and in many genera such as *Faustula* determining species: the shape of the body (e.g., oval, elongate oval, lingulate or conical); the placement of the oral sucker (e.g., terminal or subterminal); the level in the body where the ventral sucker is located and whether it is acetabulate or pad-like; the position of the genital pore; the placement, shape and contents of the cirrus sac (especially the presence or absence of large glandular cells and the type of seminal vesicle); the shape of the ovary (e.g., entire, irregular, and if lobed, the number of lobes); the placement of the ovary and testes relative to each other as well as their location in the body; and the distribution of the vitelline fields (see basic measurements and other morphological data in Table 1). We currently propose the following species be retained in *Faustula*: *F. basiri*, *F. brevichrus*, *F. clupeae*, *F. gangetica* and *F. keksooni*.

TABLE1. Comparative measurements, morphometric percentages and morphometric ratios of species of *Faustula* Poche, 1926 we recognize as valid from marine/freshwater fishes. *Faustula mankundi* has been moved to *Gangafaustula* **n. gen.**, *F. qikouenseis* to *Gobiofaustula* **n. gen.**, *F. hilsai* to *Lingulitrema* **n. gen.**, *F. gasterostei* to *Schellitrema* **n. gen.** and *F. indica* to *Varanasifaustula* **n. gen.** and also are included in the table. *Faustula pyriformis* Kumar & Agarwal, 1984 and *F. sayori* (Yamaguti, 1942) Yamaguti, 1958 are transferred to *Pronoprymna* Poche, 1926; *F. varanasiensis* (Agarwal & Kumar, 1977) is transferred to *Bacciger* Nicoll, 1914 and *F. rahemii* Al-Daraji, 2004 and *F. hilsai* Rizvi, 1971 are synonymized with *F. basiri* Hafeezullah & Siddiqi, 1970. Ranges are given in parentheses and morphometric percentages relative to body length are given in brackets.

Species/ characteristics	*F. basiri* Hafeezullah & Siddiqi, 1970 (Syn. *F. hilsai* Rizvi, 1971) n=5	*F. brevichrus* (Srivastava, 1935) Yamaguti, 1958 n= NG	*F. clupeae* (Srivastava, 1935) Yamaguti, 1958 n= NG	*F. gangetica* (Srivastava, 1935) Yamaguti, 1958 (Syn. *F. ilishii* [Srivastava, 1935] Yamaguti, 1958) n=NG	*F. keksooni* (MacCallum, 1918) Poche, 1926[1] n=1
Body length	(2,140–2,580)	(1,300–1,700)	(1,300–1,500)	(1,340–1,650)	2,800
Body width	(1,030–1,100)	(700–900)	(700–800)	(790–970)	1,200
Forebody length [% of body length]	(912–1,158) [42–49%]	415[3] [31%]	475[3] [36%]	410[3] [30%]	Oral sucker missing from forebody [30+%][3]
Oral sucker width	(200–243)	(150–190)	(130–150)	(170–180)	Missing from specimen
Pharynx width [% of body length]	(104–135) [4–6%]	(90–110) [6–7%]	90 [7%]	(80–120) [7–8%]	132 [5%]
Oral sucker/ pharynx width ratio	(1:1.8–1:2.0)	(1:1.6–1:1.8)	(1:1.4–1:1.6)	(1:1.5–1:2.2)	Specimen extensively damaged
Esophagus length [% of body length]	(240–456) [11–18%]	(120–200) [9–12%]	(80–100) [6–7%]	(160–180) [11–12%]	370 [13%]
Ventral sucker width [% of body length]	(195–245) [9–10%]	(140–250) [10–15%]	(160–170) [11–13%]	(170–200) [12–13%]	285 [10%]
Ventral sucker/oral sucker width ratio	(1:0.9–1:1.1)	(1:0.9–1:1.4)	(1:1.1–1:1.3)	(1:1.0–1:1.2)	1:0.1
Cirrus sac length [% of body length]	(408–528) [19–21%]	(310–360) [21–24%]	280 [19%]	(360–400) [24–27%]	640 [13%]
Ovary width	230	(190–310)	260	(240–260)	380
Number of ovarian lobes	(9–10)[3]	(9–10)[3]	(9–10)[3]	(9–10)[3]	(9–10)[3]
Mean testes width	150	120	140	160	255
Testes/ ovary width ratio	1:0.7	1:0.3[3]	1:0.5	1:0.6	1:0.7
Post-ovarian space length [% of body length]	660[3] [30%]	455[3] [34%]	475[3] [35%]	355[3] [26%]	1,000[3] [36%]
Egg length	(12–18)	(13–20)	15	(16–25)	(16–20)
Egg width	(9–12)	(10–12)	10	12	(9–11)

.....continued on the next page.

TABLE 1. (Continued)

Species/ characteristics	*G. makundai* (Agarwal & Verma, 1981) **n. comb.** (Syn. *F. makundai* Agarwal & Verma, 1981) n=2	*G. qikouensis* (Qiu & Li, 1995) **n. comb** (Syn. *F. qikouensis* Qiu & Li, 1995) n=NG	*L. hilsai* (Kumar & Agarwal, 1984) **n. comb.** (Syn. *F. hilsai* Kumar & Agarwal, 1984) n=5	*S. gasterostei* (Schell, 1973) **n. comb.** (Syn. *F. gasterostei* Schell, 1973) n=15	*V. indica* (Agarwal & Verma, 1981) **n. comb.** (Syn. *F. indica* Agarwal & Verma, 1981) n=2
Body length	1,200[2]	(731–799)	(1,300–1,500)	(702–919)	850
Body width	500	(391–459)	(470–500)	(187–202)	470
Forebody length [% of body length]	350[2] [43%]	215[3] [28%]	430[3] [29%]	390[3] [42%]	350 [41%]
Oral sucker width	110	(85–102)	(90–100)	(149–180)	100
Pharynx width [% of body length]	80[2] [7%]	68 [9%]	(80–90) [6–7%]	(30–35) [3–4%]	60 [7%]
Oral sucker/ pharynx width ratio	1:1.4	1:1.4[3]	(1:1.1–1:1.2)	(1:4.9–1:5.1)	1:1.7
Esophagus length [% of body length]	90 [8%]	66[3] [9%]	(120–140) [9–10%]	41[3] [5%]	70 [8%]
Ventral sucker width [% of body length]	(80–90)[2] [7–9%]	(102–135) [13–17%]	(160–180) [12–13%]	(111–135) [15%]	100 [12%]
Ventral sucker/oral sucker width ratio	(1:0.7–1:0.9)	(1:1.2–1:1.3)	(1:1.7–1:1.8)	1:0.8	1:1.0
Cirrus sac length [% of body length]	250 [23%]	(136–153) [18–19%]	(340–360) [24–27%]	175[3] [19%]	470 [55%]
Ovary width	140[2]	85[3]	(130–150)	(67–85)	120
Number of ovarian lobes	4	3	(5–6)	8[3]	6
Mean testes width	115	(68–85)	135	95	115
Testes/ ovary width ratio	1:0.8	1:0.9[3]	1:1.0	1:1.1	1:1.0
Post-ovarian space length [% of body length]	230[2] [28%]	NG	440[3] [32%]	320[3] [35%]	350[3] [36%]
Egg length	14	(15–18)	(30–50)	(28–32)	NG
Egg width	11	(9–12)	(20–30)	(14–16)	NG

n = Sample size. NG = Not given.

[1]Measurements are based on the redescription of the type specimen of *F. keksooni* (MacCallum, 1819) by Price (1938) because of the excessive damage to the type and the resulting incomplete descriptions and inadequate interpretations of morphology provided by earlier authors (e.g., MacCallum [1918]; Poche [1926]).

[2]Note that the calculated measurement for most structures from fig. 1 of *F. makundai* (original description) are different from those reported in the description (e.g., body length is shorter [830 *vs* 1,200]; the oral sucker is wider [130, 16% of body length *vs* 110, 9%], the pharynx is longer than wide rather than wider than long [86 × 60 *vs* 70 × 80]; the ventral sucker is wider [115, approx. 14% *vs* 80–90, approx. 7%]; and the ovary is narrower [117 *vs* 140]).

[3]Estimated from the original description and /or figures.

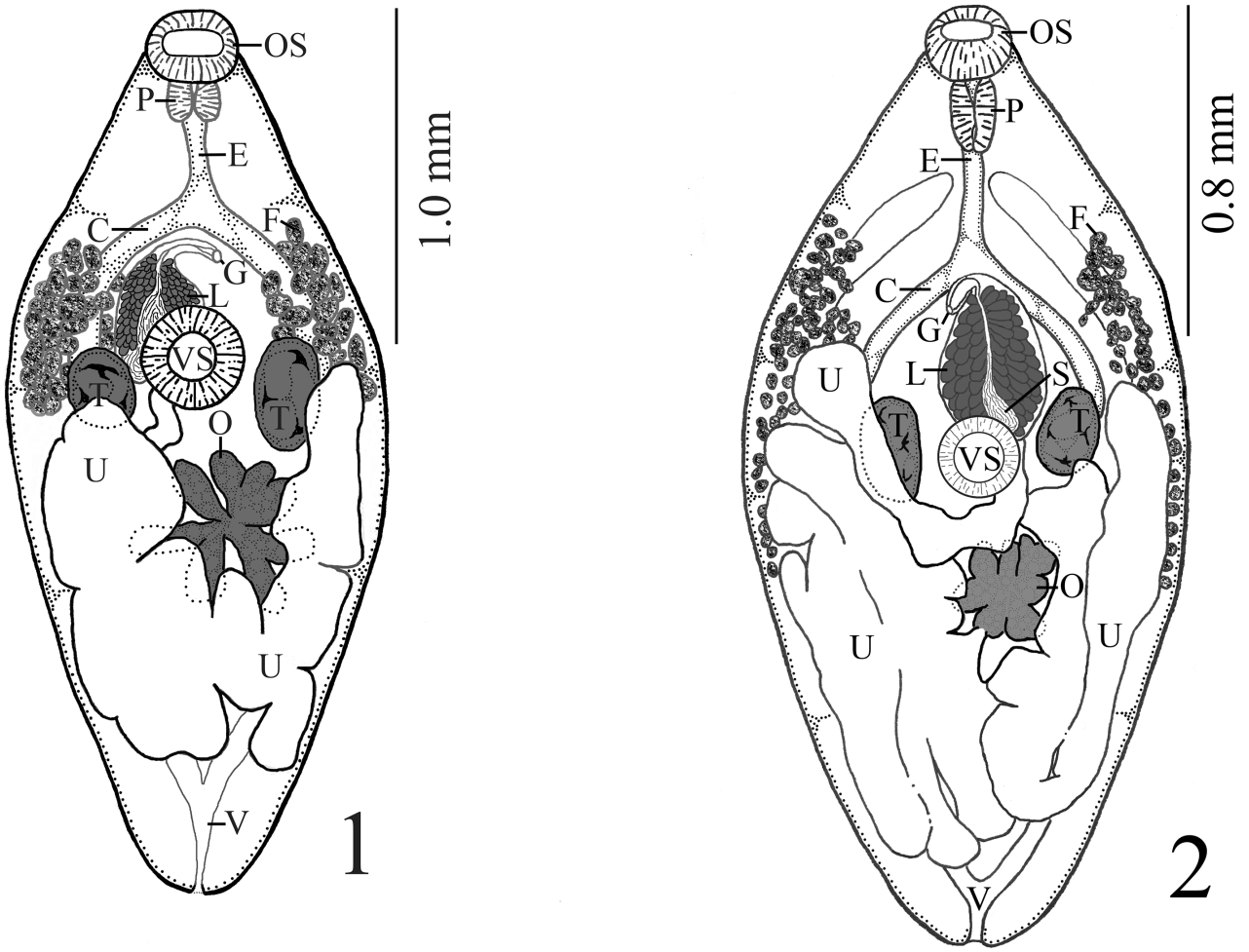
***Faustula keksooni* (MacCallum, 1918) Poche, 1926 (type species)**

(Syn. *Eurema keksooni* MacCallum, 1918 *nec* Hübner, 1820)

(Fig. 1; forebody of type species reconstructed based on the remaining posterior aspect of the oral sucker, the general appearance of the forebody in the type specimen and to some extent the basic morphology of known species of *Faustula*).

Type host: Gills of a small unspotted ray, most likely *Potamotrygon motoro* (Müller & Henle) (Potamotrygonidae).

Type locality: Off Singapore.



FIGURES 1–2. Diagrammatic illustrations of faustulids (ventral views): 1. *Faustula keksooni* (MacCallum, 1918) Poche, 1926 largely based on Price (1938); type species of *Faustula* Poche, 1926. **2.** *Faustula basiri* Hafeezullah & Siddiqi, 1970 based on Hafeezullah & Siddiqi (1970).

Abbreviations: C, cecum; E, esophagus; F, vitelline follicles; G, genital pore; L, large glandular cells in cirrus sac; O, ovary; OS, oral sucker; P, pharynx; S, seminal vesicle; T, testes; U, uterus; V, excretory vesicle; VS, ventral sucker.

Remarks: *Faustula keksooni* differs from all other described species in the genus by having a larger body (2,800 × 1,200), a larger ventral sucker (285; 10% of body length), a longer cirrus sac (640; 23%), a wider ovary (380), wider testes (mean width 255), a longer postovarian space (1,000; 36%) and the uterus ends well short of the posterior extremity. Given the larger body size of the type specimen, some measurements relative to body length show similar morphometric percentages and sometimes there are similarities in morphometric ratios (see Table 1). The combination of a median or nearly median, postbifurcal genital pore and a cirrus sac that surpasses the ventral sucker posteriorly to some extent is shared only with *F. gangetica*. *Faustula gangetica* differs from *F. keksooni* by having a broadly oval body *vs* a more lingulate body; more extensive vitelline fields (vitelline follicles distributed from the level of the posterior end of the esophagus to about the midlevel of ovary *vs* being distributed from just

posterior to the level of the intestinal bifurcation to about the midlevel of the testes); a shorter esophagus (160–180; 10–12% *vs* 370; 13%) and generally larger eggs (16–25 × 12 *vs* 16–20 × 9–11). MacCallum (1918) noted that *Faustula keksooni* (as *Eurema keksooni* MacCallum, 1918) was from the gills; however, the specimen was found at the bottom of the dissecting dish after the gills of the small ray were washed and it may have come from the gullet or mouth. We believe it was likely contamination from a previous autopsy or an accidental infection.

Faustula basiri **Hafeezullah & Siddiqi, 1970**

(Syns. *Faustula hilsai* Rizvi, 1971; *Faustula rahemii* Al-Daraji, 2004)
(Fig. 2)

Type host: Toli shad, *Tenualosa toli* (Valenciennes) (Clupeidae).

Type locality: Off Veraval, India.

Remarks: *Faustula basiri* differs from *F. keksooni* by having a longer forebody relative to body length (42–49% *vs* about 30%); a somewhat longer esophagus (240–456; 11–18% of the body length) and a somewhat shorter egg (maximum length 18 *vs* 20). *Faustula basiri* somewhat resembles *F. gangetica* by having a terminal oral sucker (as originally described for both species); relatively long ceca that surpass the testes posteriorly, terminating near the level of the ovary; a median genital pore that opens immediately posterior to the intestinal bifurcation and vitelline fields that are extensively distributed in the lateral fields of the body. *Faustula gangetica* differs from *F. basiri* by having a smaller body (1,340–1,650 × 790–970 *vs* 2,140–2,580 × 1,030–1,100); a shorter forebody (410; 30% of body length *vs* 912–1,158; 42–49%); a shorter esophagus (160–180; 10–12% *vs* 240–456; 11–18%); a shorter cirrus sac (360–400; 24–27% *vs* 408–528; 19–21%) that surpasses the ventral sucker posteriorly, extending some distance into the hindbody where it approaches the ovary *vs* being confined to the region from immediately posterior to the intestinal bifurcation to about the anterior margin of the ventral sucker; a shorter postovarian space (355; 26% *vs* 660; 30%) and longer eggs (16–25 *vs* 12–18). In the original description of *F. basiri* the oral sucker is illustrated as being slightly subterminal (see fig. 1 of Hafeezullah & Siddiqi 1970).

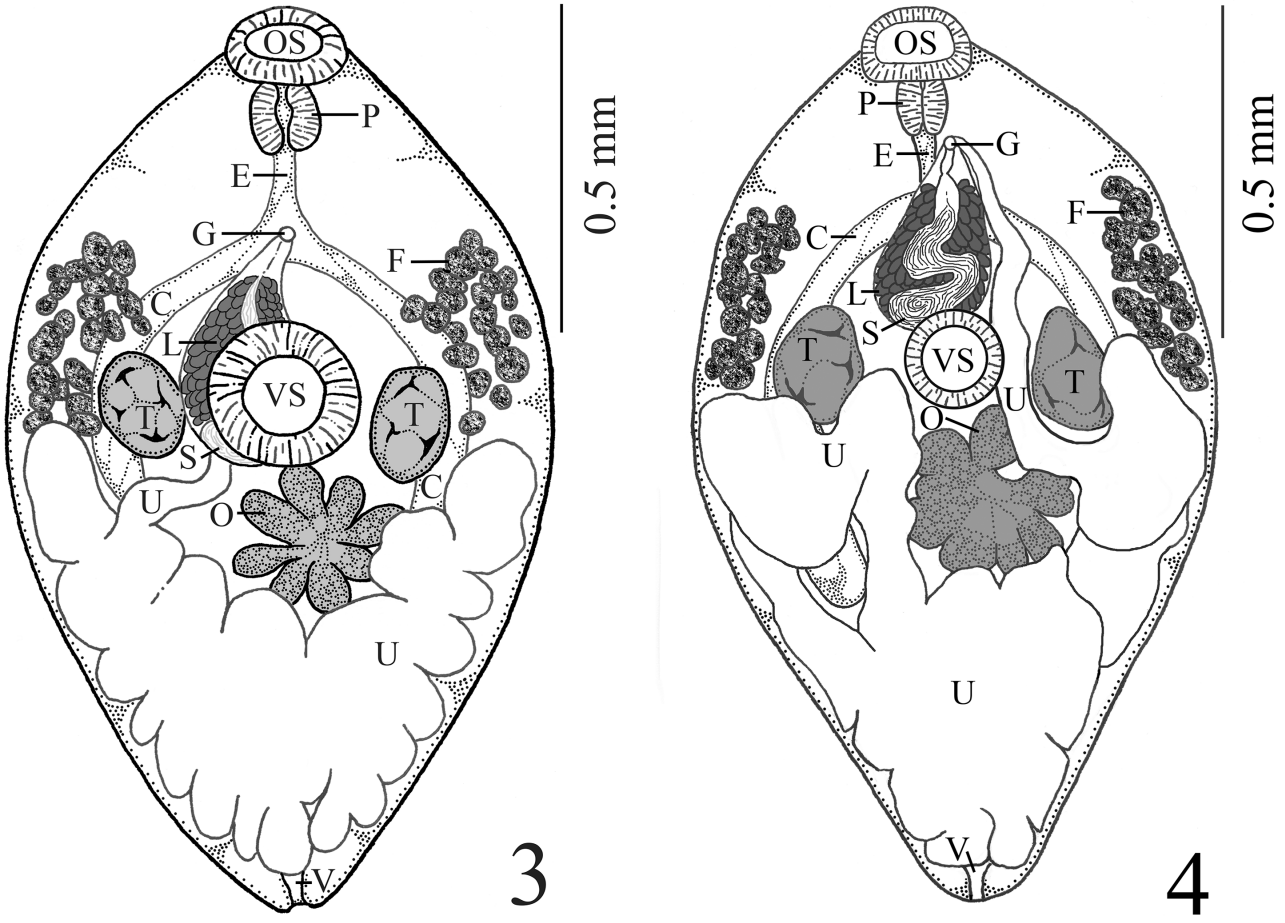
Although there are some 13 species of *Faustula* generally recognized, a little-known potential species, *Faustula rahemii* Al-Daraji, 2004, was described from the intestine of the Hilsa shad, *T. ilisha* (Syn. *C. ilisha*), from the Khor Al-Zubair lagoons by Al-Daraji (2004). Mhaisen *et al*. (2018) included this species in their checklist of parasites from marine fishes from Iraq, but based on the lack of recognition of this species in existing literature and its omission from any records of being synonymized with other species of *Faustula*, these authors suggested that it likely should be considered an invalid species. Our literature search of species of *Faustula* also yielded no published evidence of recognition of this species beyond Mhaisen *et al*. (2018) and the related information provided by these authors. Al-Daraji (2004) separated *F. rahemii* from all other species based on the location of the cirrus sac being preacetabular. However, as Mhaisen *et al*. (2018) pointed out, Al-Daraji (2004) had not compared his species to at least 10 other recognized species. There are 3 similar species like *F. rahemii* by having the cirrus sac anterior to the ventral sucker: *F basiri*; *F. hilsai* as described by Rizvi (1971) and *F. clupeae*. Unlike *F. clupeae*, both *F basiri* and *F. hilsai* are also like *F. rahemii* by having unusually extensive vitelline fields that extend from about the level of the esophagus to near the level of the ovary and the ovary positioned some distance posterior to the ventral sucker; *F. hilsai* has been synonymized with *F. basiri* (e.g., see WoRMS 2021a). Al-Daraji (2004) recognized the similarities between *F. basiri* and *F. rahemii* and provided a comparative table for these two species, which like Table 1 herein, does not conclusively distinguish *F. rahemii*. In the comparative table Al-Daraji (2004) further asserts that *F. rahemii* differs from *F. basiri* by having the ventral sucker "equal or larger than oral sucker"; however, the sucker ratios of these 2 species are similar (1: 0.91–1:0.97 *vs* 1:0.87–1:0.90, respectively), and both have the ventral sucker smaller than the oral sucker. The genital pore of *F. rahemii* was illustrated in fig. 1 by Al-Daraji (2004) as being located at the level of the anterior extent of the intestinal bifurcation, which is most similar to *F. clupeae*. The specimens of *F. rahemii* used in this description were fixed between 2 microscope slides and given that species of *Faustula* tend to be somewhat fragile and susceptible to possible fixation-induced alterations of some characteristics, the subtle difference in the position of the genital pore in *F. rahemii* compared to that in *F. basiri* (just posterior to the intestinal bifurcation) may not represent a creditable difference. *Faustula rahemii* is most similar to *F. basiri* and was described from *T. ilisha*, the most common fish wherein species of *Faustula* have been reported from generally the same geographic region, and it is our opinion it should be synonymized with *F. basiri*.

***Faustula brevichrus* (Srivastava, 1935) Yamaguti, 1958**
(Syns. *Orientophorus brevichrus* Srivastava, 1935; *Faustula chauhani* Gupta & Srivastava, 1960)
(Fig. 3)

Type host: Hilsa shad, *Tenualosa ilisha* (Hamilton) (Clupeidae).

Type locality: India (freshwater).

Remarks: *Faustula brevichrus* differs from all other species in the genus by having a bifurcal genital pore. It further differs from *F. keksooni* by having a narrower pharynx (90–110; 6–7% of body length *vs* 132; 5%) and a shorter esophagus (120–200; 9–12%). *Faustula brevichrus* is somewhat similar to *F. gangetica* by having a cirrus sac that surpasses the ventral sucker posteriorly, but *F. brevichrus* has a subterminal oral sucker; much shorter vitelline fields; a narrower pharynx (90–110; 6–7%); a generally smaller oral sucker/pharynx width ratio (maximum of 1:1.8 *vs* 1:2.2); narrower testes (120 *vs* 160); a longer postovarian space (455; 34%) and shorter eggs (maximum length 20 *vs* 25). It is noteworthy that the specimen of *F. brevichrus* shown in fig.1 of Strivastava (1935) (dorsal view) appears to have been overly compressed during fixation, which may have altered the position of some structures to some extent (i.e., the ventral sucker is shifted to the left while the cirrus sac is shifted to the right). We consider the position of the genital pore and the position of the cirrus sac to be representative of this species and sufficiently different to retain *F. brevichrus* in *Faustula*.



FIGURES 3–4. Diagrammatic illustrations of faustulids (ventral views): 3. *Faustula brevichrus* (Srivastava, 1935) Yamaguti, 1958 based on Srivastava (1935). **4.** *Fastula clupeae* (Srivastava, 1935) Yamaguti, 1958 based on Srivastava (1935).

***Faustula clupeae* (Srivastava, 1935) Yamaguti, 1958**
(Syn. *Orientophorus clupii* Srivastava, 1935)
(Fig. 4)

Type host: Hilsa shad, *Tenualosa ilisha* (Hamilton) (Clupeidae).

Type locality: India (freshwater).

Remarks: *Faustula clupeae* differs from all other species in the genus by having a submedian, prebifurcal genital pore that opens immediately posterior to the posterior margin of the pharynx. It is superficially similar to *F. basiri* by having a preacetabular cirrus sac, but *F. basiri* is larger (2,100–2,580 × 1,030–1,100 *vs* 1,300–1,500 × 700–800); the ceca terminate posteriorly short of the posterior extent of the ovary; the oral sucker as originally described as terminal; the forebody is longer (912–1,158; 42–49% *vs* 475; 36%); the oral sucker/pharynx width ratio is larger (1:1.8–1:2.0 *vs* 1:1.4–1:1.6); the ventral/oral sucker width ratio is smaller (1:0.9–1:1.1 *vs* 1:1.1–1:1.3); the genital pore is postbifurcal and the vitelline fields are longer. Although *F. clupeae* is somewhat similar to *F. brevichrus* in basic morphology (see Table 1) and both were described by Srivastava (1935) from the same host species (Hilsa shad) from freshwater in India, *F. clupeae* differs from *F. brevichrus* by having a shorter esophagus (80–100; 6–7% of body length *vs* 120–200; 9–12%); a somewhat smaller oral sucker/pharynx width ratio (1:1.4–1:1.6 *vs* 1:1.6–1:1.8); a submedian genital pore that is distinctly prebifurcal, opening near the level of the posterior end of the pharynx *vs* being median and located at the level of the anterior extent of the intestinal bifurcation; a shorter cirrus sac (about 280; 19% *vs* 310–360; 21–24%); the cirrus sac positioned from near the level of the posterior end of the pharynx to the anterior margin of the ventral sucker or slightly more posteriorly *vs* extending posteriorly from about the level of the intestinal bifurcation to about the level of the posterior margin of the ventral sucker or slightly more posteriorly; the ovary immediately posterior to the ventral sucker *vs* being some distance posterior to it and the ceca in *F. clupeae* are longer terminating posteriorly near the level of the posterior margin of the ovary rather than about the midlevel of the ovary (see figs. 1 & 4 of Srivastava [1935]). As noted earlier, the specimen of *F. brevichrus* shown in fig.1 (dorsal view) appears to have been overly compressed during fixation, which may have altered the position of some structures to some extent (i.e., the ventral sucker is shifted to the left while the cirrus sac is shifted to the right). We consider the combination of the position of the genital pore and the position of the cirrus sac to be representative of these species and sufficiently different amongst them to retain *F. basiri*, *F. brevichrus* and *F. clupeae* as distinct species within *Faustula*.

Faustula gangetica (Srivastava, 1935) Yamaguti, 1958

(Syns. *Faustula ilishii* [Srivastava, 1935] Yamaguti, 1958; *Orientophorus gangeticus* Srivastava, 1935; *Orientophoros ilishii* Srivastava, 1935; *Faustula mandapamensis* Shima, 1974)

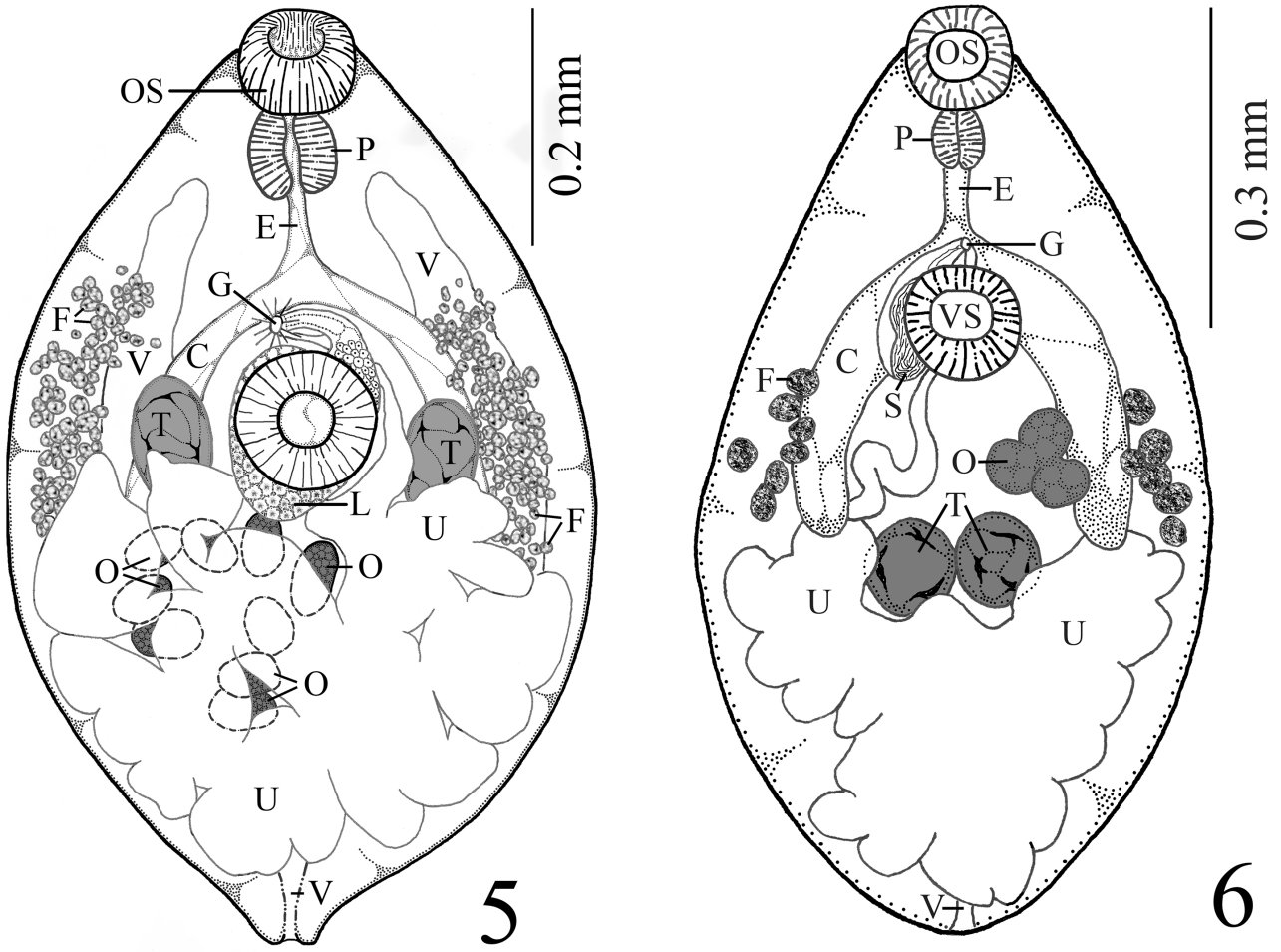
(Fig. 5)

Type host: Hilsa shad, *Tenualosa ilisha* (Hamilton) (Clupeidae).

Type locality: India (freshwater).

Remarks: *Faustula gangetica* is similar to *F. brevichrus* by having a cirrus sac that surpasses the ventral sucker posteriorly, but primarily differs from *F. brevichrus* by having a terminal oral sucker (as originally described); a postbifurcal genital pore and longer vitelline fields. *Faustula gangetica* also is somewhat similar to *F. clupeae*, but it has a longer esophagus (160–180; 11–12%); a somewhat larger oral sucker/pharynx width ratio (1:1.5–1:2.2); a median, distinctly postbifurcal genital pore; a longer cirrus sac (360–400; 24–27%) that surpasses the ventral sucker extending some distance into the intertesticular space of the hindbody to about the level of the anterior extent of the ovary; a shorter postovarian space (about 355; 26% *vs* 475; 35%); larger eggs (16–25 × 12 *vs* 15 × 10); more extensive vitelline fields that extend from the level of the posterior aspect of the esophagus posteriorly to the midlevel of the ovary, terminating at the level of the cecal ends *vs* extending from about the level of the intestinal bifurcation posteriorly to the midlevel of the testes, terminating at the midlevel of the ceca; somewhat shorter ceca that do not extend posteriorly beyond the midlevel of the ovary and *F. gangetica* was described as having a terminal oral sucker. It should be noted that in their redescription of *F. gangetica* Garner *et al*. (2019) considered the oral sucker to be slightly subterminal. For additional details used to distinguish *F. gangetica* from other similar species retained in *Faustula*, see the Remarks sections provided above for *F. basiri* and *F. brevichrus*.

We propose the following key to accommodate those species we feel should be assigned to *Faustula*.



FIGURES 5–6. Diagrammatic illustrations of faustulids (ventral views): 5. *Faustula gangetica* (Srivastava, 1935) Yamaguti, 1958 based on Srivastava (1935). **6.** *Gobiofaustula qikouensis* (Qiu & Li, 1995) **n. comb.** based on Qiu & Li (1995); representative of *Gobiofaustula* **n. gen.**

Key to the species of *Faustula* Poche, 1926 (*senso stricto*)

1a. Genital pore postbifurcal 2
1b. Genital pore bifurcal or prebifurcal 4
2a. Cirrus sac almost entirely in forebody, may slightly overlap anterior margin of ventral sucker . . . . . .*F. basiri* Hafeezullah & Siddiqi, 1970 (Syns. *Faustula hilsai* Rizvi, 1971; *Faustula rahemii* Al-Daraji, 2004) (Fig. 2)
2b. Cirrus sac surpassing acetabular region, may surpass ventral sucker some distance into hindbody 3
3a. Cirrus sac extends posteriorly well into hindbody, approaching anterior extent of ovary; vitelline fields extensively distributed in lateral fields from midlevel of esophagus posteriorly to midlevel of ovary . . . . . *F. gangetica* (Srivastava, 1935) Yamaguti, 1958 (Syns. *Faustula ilishii* [Srivastava, 1935] Yamaguti, 1958; *Orientophorus gangeticus* Srivastava, 1935; *Orientophorus ilishii* Srivastava, 1935; *Faustula mandapamensis* Shima, 1974) (Fig. 5)
3b. Cirrus sac extends posteriorly to about level of posterior margin of ventral sucker or slightly more posterior, does not approach ovary; vitelline fields not extensive, do not surpass level of posterior margin of ventral sucker posteriorly . . . . . *F. keksooni* (MacCallum, 1918) Poche 1926 (Syn. *Eurema keksooni* MacCallum, 1918 *nec* Hübner, 1820) (Fig. 1)
4a. Genital pore prebifurcal, opens immediately posterior to level of posterior margin of pharynx; ventral sucker immediately anterior to ovary . . . . . *F. clupeae* (Srivastava, 1935) Yamaguti, 1958 (Syn. *Orientophorus clupii* Srivastava, 1935) (Fig. 4)
4b. Genital pore bifurcal, opening about level of anterior extent of intestinal bifurcation; ventral sucker removed from ovary . . . . . *F. brevichrus* (Srivastava, 1935) Yamaguti, 1958 (Syns. *Orientophorus brevichrus* Srivastava, 1935; *Faustula chauhani* Gupta & Srivastava, 1960) (Fig. 3)

Proposed new genera based on existing species of *Faustula* (*senso lato*)

Of the 13 species normally recognized in *Faustula* (WoRMS 2021b), there are 2 species other than the type species, *F. keksooni* that was described from a ray collected off Singapore, that have been described from non-clupeiform fish whose hosts were collected from regions relatively far removed from India or the general area of the Indian Ocean that appear to represent undescribed genera: *Gobifaustula* **n. gen.** and *Schellitrema* **n. gen.**

***Gobifaustula* n. gen.**
(Fig. 6)

Type species: *Gobifaustula qikouensis* (Qiu & Li in Shen & Qiu, 1995) **n. comb.** Type and only species.
(Syn. *Faustula qikouensis* Qiu & Li in Shen & Qiu, 1995)

Diagnosis: Body small, somewhat pyriform (see fig. 26 of Qiu & Li 1995 in Shen & Qiu 1995); tegument aspinose. Forebody occupies less than one-half of body length. Oral sucker subterminal, muscular, nearly circular, somewhat globular. Ventral sucker muscular, larger than oral sucker, located well anterior to midlevel of body. Prepharynx short to absent. Pharynx small, oval, muscular. Esophagus, simple, relatively long. Intestinal bifurcation largely in forebody immediately anterior to ventral sucker which may overlap posterior aspect of bifurcation and located well anterior to midlevel of body. Ceca relatively short, terminate about midlevel of body. Testes 2, spherical, entire, symmetrical, contiguous on midline of body, located near midlevel of hindbody. Cirrus sac claviform, surpasses ventral sucker posteriorly by short distance; seminal vesicle originally described as saccular but may be bipartite (see fig. 26 of original description by Qiu & Li 1995), occupies slightly more than one-half of cirrus sac; details of cirrus, ejaculatory duct, pars prostatica unknown. Genital pore median or nearly so, immediately anterior to ventral sucker at juncture of esophagus and intestinal bifurcation. Genital atrium unknown. Ovary pretesticular, intercecal, trilobed in form of triangle, located immediately right of and contiguous with left cecum, occupies area from about midlevel of cecum posteriorly to short distance anterior to level of cecal ends. Laurer's canal unknown. Seminal receptacle contiguous with posterior end of and nestled between posterior 2 lobes of ovary. Vitelline follicles distributed in 2 clusters, 1 on each side of body from about midlevel of ceca or anterior margin of ovary to cecal ends. Uterus occupying bulk of posttesticular space, extends from level of testes to near posterior extremity. Eggs numerous, small, operculate. Excretory vesicle and extent of excretory arms unknown; excretory pore terminal to somewhat dorsally located. Reported as intestinal parasites of gobiid fishes in freshwater tributaries entering the Yellow Sea.

Etymology: The genus is named based on the type of fish (goby; Latin *gobio*) infected by *Gobifaustula qikouensis* and its similarities to members of the Faustulidae (*Faustula*).

Remarks: *Faustula qikouensis* (= *G. qikouensis*) was described from the Asian freshwater goby, *S. ommaturus* (Perciformes: Gobiidae), from near the mouth of a river that opens into the Bo-Hai Sea (considered to be the more inland portions of the Yellow Sea of China). It is similar to species of *Faustula* by having relatively small suckers where the ventral sucker is slightly larger than the oral sucker; gonads that are in the hindbody; a uterus that reaches posterior beyond the testes, mainly concentrated in the hindbody; a median to slightly submedian genital pore; a cirrus sac that overreaches the ventral sucker, surpassing it by a short distance posteriorly and a ventral sucker that is not close to the posterior extremity (located near the posterior aspect of the anterior one-third of body). It differs from species of *Faustula* by having a somewhat pyriform, aspinose body that is markedly tapered anteriorly and broadly rounded posteriorly; a ventral sucker that overlaps the intestinal bifurcation anteriorly; a relatively long hindbody (approximately 60% of the body length); side by side, contiguous testes that are located near the midlevel of the hindbody well posterior to the ventral sucker; a genital pore opening anterior to the intestinal bifurcation near the posterior end of the esophagus; a cirrus sac that encloses a bipartite seminal vesicle; vitelline fields that are in 2 clusters composed of relatively few follicles (6–7/side) that are confined to the middle one-third on each side of the body and a pretesticular, trilobed ovary. Bray (2008b) suggested that this species does not belong in *Faustula* and probably should be transferred to *Bacciger* Nicoll, 1914; however, only species of *Allofellodistomum* Yamaguti, 1971; *Baccigeroides* Dutta, 1995; *Echinobreviceca* Dronen, Blend & McEachran, 1994; *Paradiscogaster* Yamaguti, 1934; *Triganocryptus* Martin, 1958; and *Yamagutia* Srivistava, 1937 have a pretesticular ovary, but none of these genera contain species where the ovary is lobed. Based largely on the combination of the above characteristics,

especially the definitely trilobed, pretesticular ovary and a bipartite seminal vesicle, we feel that *F. qikouensis* is most similar to species of *Baccigeroides.* Since no species assigned to *Baccigeroides* as currently diagnosed has a lobed pretesticular ovary, we propose the erection of *Gobifaustula* to support *Gobifaustula qikouensis* (Syn. *F. qikouensis*) (see fig. 26 of Qiu & Li 1995 in Shen & Qiu 1995).

***Schellitrema* n. gen.**
(Fig. 7)

Type species: *Schellitrema gasterostei* (Schell, 1973) **n. comb.** Type and only species.
(Syn. *Faustula gasterostei* Schell, 1973)

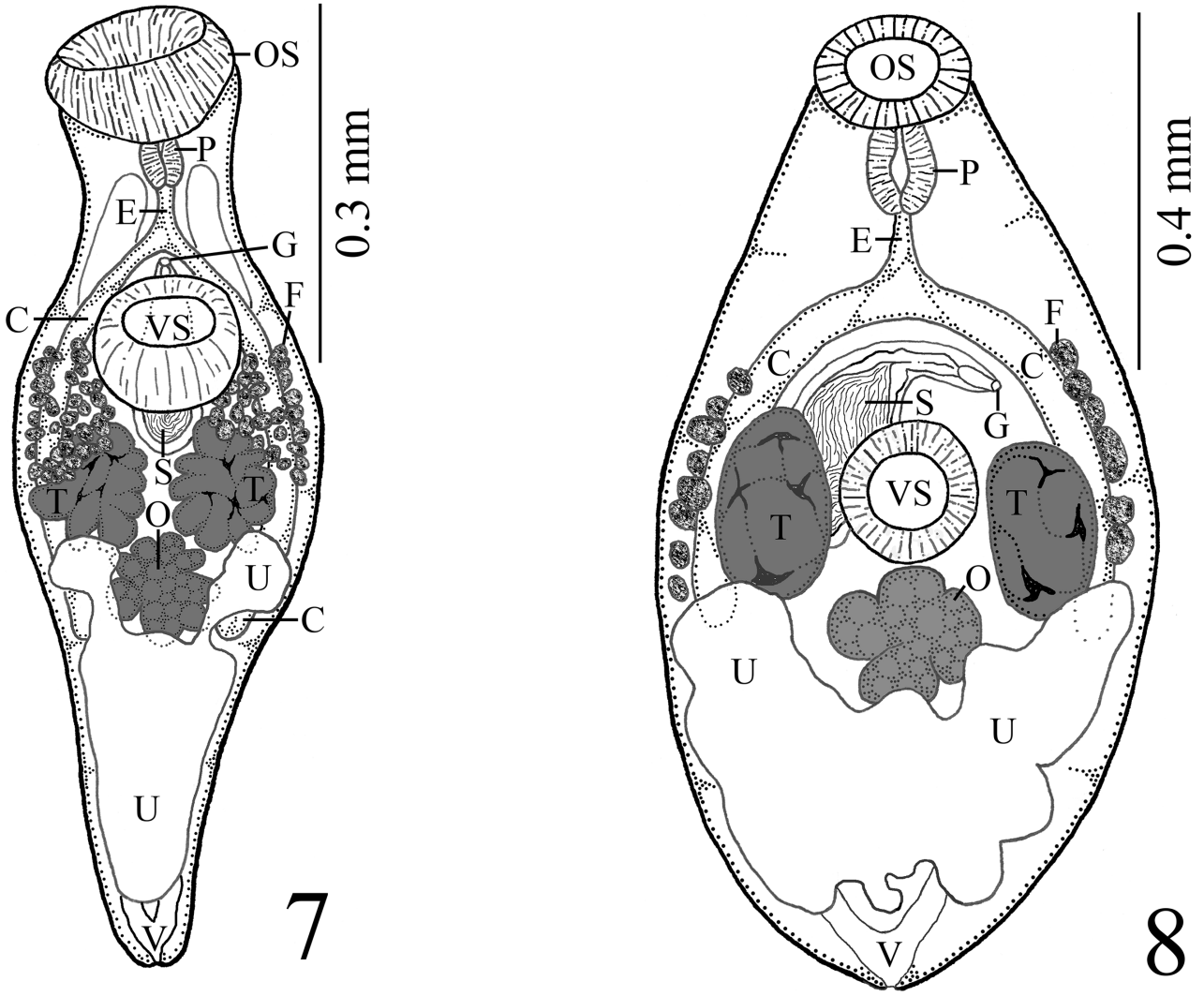
Museum specimens: Holotype USNM 1368020.

Diagnosis: Body relatively small, somewhat biconic-shaped; anterior extremity broadly rounded, followed by short, narrower isthmus-like neck region; maximum width near midlevel of body; posterior end of body relatively extensive, gradually tapers to relatively rounded point; tegument aspinose. Forebody occupies less than one-half of body length, no obvious concentric rings present on ventral surface. Oral sucker terminal, bowl-shaped. Ventral sucker pre-equatorial, muscular, somewhat smaller than oral sucker, slightly wider than long. Prepharynx absent. Pharynx elliptical, muscular. Esophagus relatively short. Intestinal bifurcation short distance anterior to ventral sucker. Ceca relatively long, terminate about two-thirds of distance down body from anterior end. Testes 2, multilobed, symmetrical, mainly intercecal, at midlevel of body short distance posterior to ventral sucker. Cirrus sac clavate, median, overlaps ventral sucker dorsally, surpasses it posteriorly by short distance; sac encloses cirrus, moderately long ejaculatory duct with few prostatic glands, short pars prostatica and relatively long, tubular to nearly saccate, unipartite seminal vesicle. Genital pore postbifurcal, immediately anterior to ventral sucker on midline of body. Ovary multilobed, immediately posttesticular on midline of body. Vitellarium in 2 compact clusters, 1 on each side, posterolateral to ventral sucker. Uterus largely posterior to testes, fills most of posttesticular space. Metraterm weakly developed. Excretory vesicle V-shaped, excretory arms extend to level of pharynx. Intestinal parasite of marine teleosts (three-spine stickleback, *G. aculeatus* Linnaeus [Gasterosteidae]; only reported host) off west coast of USA.

Etymology: The genus is named in honor of the late Dr. Stuart Schell (*Schelli*) in recognition of his many contributions to the study of parasitic helminths and his original description of *F. gasterostei* (= *Schellitrema gasterostei*) within the faustulid-like trematodes (*trema*).

Remarks: *Schellitrema gasterostei* has a median genital pore, located immediately anterior to the ventral sucker; a cirrus sac; the ovary immediately posterior to the testes in the hindbody; an unarmed ejaculatory duct and metraterm; testes located immediately posterior to the ventral sucker in the hindbody; and this species is parasitic in fish suggesting placement in the Faustulidae. It is similar to species of *Faustula* by having a ventral sucker that is near the anterior one-third of body; a median genital pore that opens immediately anterior to the ventral sucker and just posterior to the intestinal bifurcation; a cirrus sac that dorsally overreaches the ventral sucker along the midline of the body and surpasses the ventral sucker posteriorly by a short distance; a posttesticular, distinctly multilobed ovary (composed of some 8 lobes); and a uterus that is posttesticular and largely in the hindbody. *Schellitrema gasterostei* (Syn. *F. gasterostei*) was described from the three-spined stickleback, *G. aculeatus* (Gasterosteidae), from Puget Sound, Washington, USA. Unlike species of *Faustula*, this species has a distinctive, irregularly elliptical, aspinose body with a large terminal oral sucker; a narrower isthmus-like forebody; a broad midlevel region; a tapering, relatively long hindbody (approximately 60% of the body length); a ventral sucker that is smaller than the oral sucker (111–135 *vs* 149–180); a relatively narrow, clavate cirrus sac; multilobed testes that are in the hindbody and vitelline fields that are in 2 small compact groups, composed of relatively few follicles and mostly mid- to post-acetabular being confined to the midlevel of the body or slightly more anteriorly. We agree with Bray (2008) that this species should not be assigned to *Faustula*. Bray (2008) suggested the possible assignment of this species to *Pronoprymna* Poche, 1926; however, *S. gasterostei* has an extensively mutilobed ovary rather than the more typical trilobed ovary as described for species of *Pronoprymna* and the stickleback is an unusual fish host as members of the genus are generally intestinal parasites of clupeiforms. Although it is entirely possible this species does not belong in the Faustulidae, based on the information available we propose *Schellitrema* to accommodate this unusual species, *Schellitrema gasterostei* (Schell, 1973) (see type species description of *F. gasterostei* [= *S. gasterostei*] and fig. 4 of Schell 1973).

Of the 13 previous recognized species assigned to *Faustula* (WoRMS 2021a), there are 3 species described in clupeiform fishes from the Ganges River (River Ganga), India that appear to represent undescribed genera: *Gangafaustula makundai* **n. gen.**, **n. comb.**, *Lingulitrema hilsai* **n. gen., n. comb.** and *Varanasifaustula indica* **n. gen.**, **n. comb.** There are a number of characteristics that indicate that these 3 species represent separate genera and should not be retained in *Faustula*. The most obvious difference is that species of *Faustula* have a distinctive cirrus apparatus wherein there is a short, usually thick-walled cirrus; a relatively short tubular to chamber-like pars prostatica and a seminal vesicle composed of an elongate, upper narrow canal spiraling throughout the middle one-third of the cirrus sac usually containing minimal amounts of sperm terminating in a wider, more oval, chamber-like sac at the posterior extreme of the cirrus sac containing the bulk of the sperm (see the redescription of *F. gangetica* by Garner *et al*. 2019; fig. 3).



FIGURES 7–8. Diagrammatic illustrations of faustulids (ventral views): 7. *Schellitrema gasterostei* (Schell, 1973) **n. comb.** based on Schell (1973); *representative of Schellitrema* **n. gen. 8.** *Gangifaustula makundai* (Agarwal & Verma, 1981) **n. comb.** based on Agarwal & Verma (1981); representative of *Gangafaustula* **n. gen.**

***Gangafaustula* n. gen.**
(Fig. 8)

Type species: *Gangafaustula makundai* (Agarwal & Verma, 1981) **n. comb.** Type and only species.
(Syn. *Faustula makundai* Agarwal & Verma, 1981)

Diagnosis: Body small, broadly elliptical to somewhat pyriform; anterior extremity markedly tapered to form

relatively narrow end; posterior extremity more broadly tapered to form a bluntly pointed end; tegument aspinose. Forebody occupies less than one-half of body length. Oral sucker muscular, globose, somewhat subterminal. Ventral sucker muscular, globose, near midlevel of body, slightly smaller than oral sucker. Prepharynx absent. Pharynx elliptical (elongate-spherical), muscular. Esophagus relatively short. Intestinal bifurcation about midway between suckers. Ceca short, terminate posterior to midlevel of body. Testes 2, entire, symmetrical, near midlevel of body; anterior extent may overlap midlevel of anterior aspect of ventral sucker. Cirrus sac claviform to retort-shaped, anterior one-third proceeds across body from about level of anterior one-third of left cecum to about midline of body, curves posteriorly and slightly overlaps right margin of ventral sucker, terminates about level of posterior margin of ventral sucker or slightly more posteriorly; sac encloses short, narrow ejaculatory duct, modest tubular pars prostatica and relatively large, saccate, naked (not surrounded by glandular cells) seminal vesicle; no large glandular cells apparent around pars prostatica or upper aspect of seminal vesicle. Genital pore immediately postbifurcal, distinctly submedian, sinistral, opens just short of midway between midline of body and body wall. Ovary with 4 lobes, median, anterior one-half occupies about posterior one-third of intertesticular space. Seminal receptacle immediately posterolateral of ovary. Uterus largely posterior to gonads, filling most of posttesticular space. Vitellarium composed of few (approximately 6–10), relatively large follicles linearly organized near lateral margins of body from about level of posterior margin of intestinal bifurcation nearly to posterior margin of testes. Eggs small, operculated. Excretory vesicle V-shaped, extent of excretory arms unknown; excretory pore nearly terminal. Reported as intestinal parasite of species of clupeid fishes in the Ganges River (River Ganga), India.

Etymology: The genus is named after the river in India where the type species was originally collected ("*Ganga*") and its probable assignment within the faustulid trematodes (*Faustula*).

Remarks: *Gangafaustula makundai* is similar to species of *Faustula* by having ceca that are relatively short, terminating at about the level of the posterior margin of the testes or slightly more posterior; a submedian, claviform cirrus sac that lies along the left margin of the ventral sucker, sometimes overlapping it to some extent dorsally and terminating at about the level of the posterior margin of the sucker; symmetrical testes that overlap the posterior end of the ventral sucker laterally to some extent; a median or nearly so, lobed ovary that is primarily posttesticular, but that may extend anteriorly into the posterior aspect of the intertesticular space to some extent and a uterus that is largely posttesticular and mainly in the hindbody. *Gangafaustula makundai* differs from species of *Faustula* by having the ventral sucker somewhat smaller than the oral sucker and more posteriorly positioned about the midlevel of the body; a simple saccate seminal vesicle where large glandular cells are not apparent in the cirrus sac *vs* a winding tubular seminal vesicle that is at least partially embedded in large glandular cells; a distinctly submedian genital pore; few (6–10/ side), large vitelline follicles that are linearly arranged in the lateral fields, 1 line on each side of the body and restricted to the region from the level of the posterior margin of the intestinal bifurcation to near the level of the posterior margin of the testes *vs* follicles being relatively small, more numerous and arranged in compact masses where their anterior extent surpasses the intestinal bifurcation anteriorly being distributed from about the midlevel of the esophagus to the anterior aspect of the posttesticular space of the hindbody or more posteriorly; gonads that are located posterior to the midlevel of the body and an ovary with 4 lobes *vs* 8 or more lobes as seen in species in the genus (e.g., *F. basiri*, *F. brevichrus*, *F. keksooni*).

Lingulitrema n. gen.

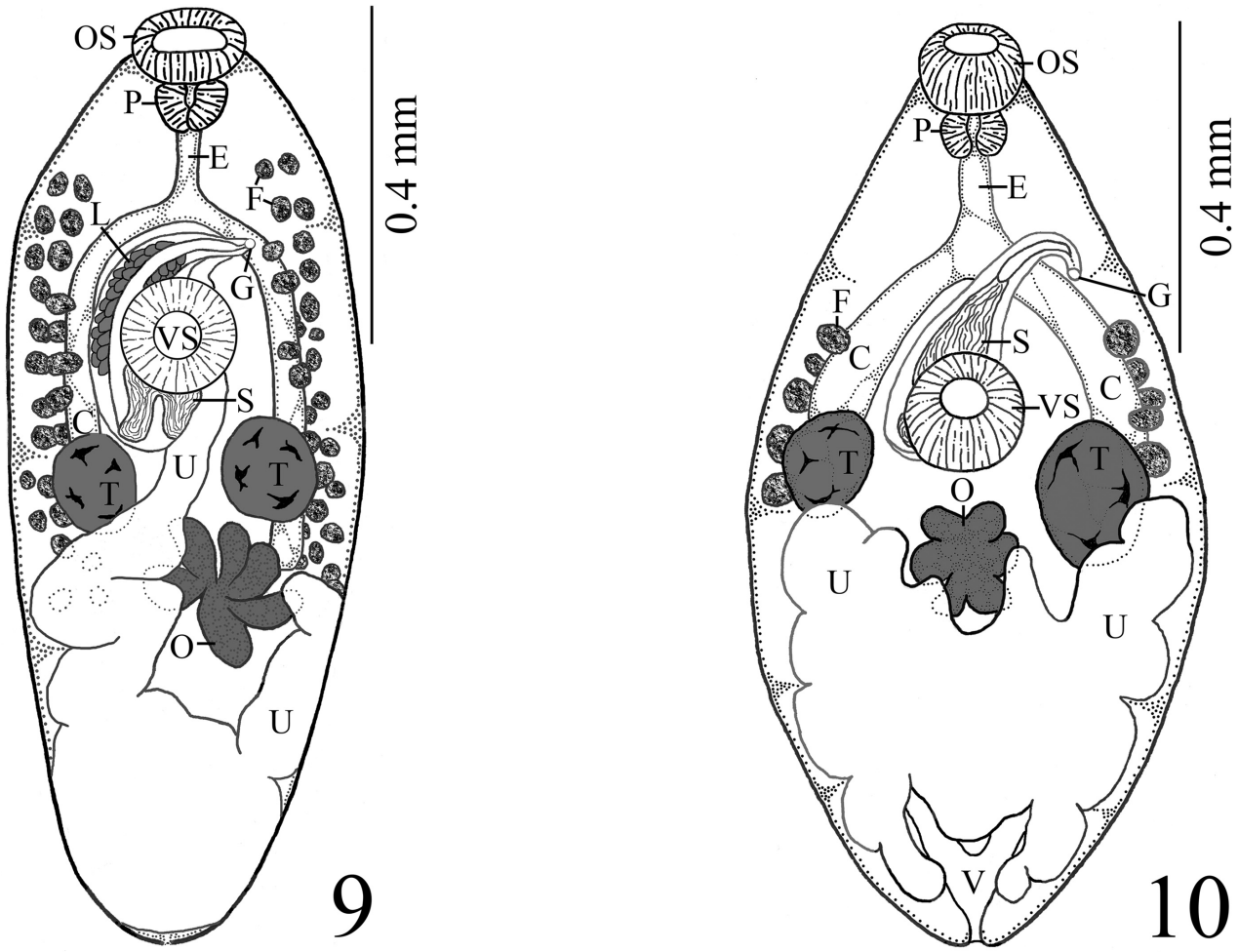
(Fig. 9)

Type species: *Lingulitrema hilsai* (Kumar & Agarwal, 1984) **n. comb.** Type and only species.
(Syn. *Faustula hilsai* Kumar & Agarwal, 1984)

Diagnosis: Body lingulate, anterior extremity broadens posteriorly, widest at one-quarter of distance from anterior end, gradually narrows posterior to midlevel of body to form rounded posterior end; tegument aspinose. Forebody occupies less than one-half of body length. Oral sucker described as terminal; shown as subterminal in fig. 2A of Kumar & Agarwal (1984). Ventral sucker muscular, spherical to round, anterior to midlevel of body, noticeably larger than oral sucker. Prepharynx absent. Pharynx muscular, elliptical to round. Esophagus relatively short to moderately long. Intestinal bifurcation about midway between pharynx and ventral sucker. Ceca relatively long, surpass midlevel of body posteriorly. Testes 2, entire, symmetrical, near midlevel of body. Cirrus sac claviform, lies lateral to right margin of ventral sucker, terminates some distance posterior to it; sac encloses a relatively long, tubular pars prostatica surrounded by numerous prostatic cells and somewhat saccate, laterally-placed S-

shaped seminal vesicle. Genital pore postbifurcal, median to submedian (shown as distinctly submedian, near left cecum in figs. 2A & B of Kumar and Agarwal 1984), sinistral. Ovary posttesticular, slightly sinistral, 5–6 ovarian lobes. Laurer's canal not observed. Seminal receptacle unknown. Uterus largely posterior to gonads, fills most of posttesticular space; metraterm present. Vitellarium, 1 field per side, composed of numerous follicles extensively distributed in lateral fields between midlevel of esophagus and posterior margin of ovary. Eggs small, operculate. Excretory vesicle Y-shaped, extent of excretory arms unknown; excretory pore terminal.

Etymology: The genus is named based on the tongue-shaped body of the type species (*Linguli*; Latin for tongue) within the faustulid trematodes (*trema*).



FIGURES 9–10. Diagrammatic illustrations of faustulids (ventral views): 9. *Lingulitrema hilsai* (Kumar & Agarwal, 1984) **n. comb.** based on Kumar & Agarwal (1984); representative of *Lingulitrema* **n. gen. 10.** *Varanasifaustula indica* (Agarwal & Verma, 1981) **n. comb.** based on Agarwal & Verma (1981); representative of *Varanasifaustula* **n**. **gen.**

Remarks: Apparently unaware of the description of the original *F. hilsai* by Rizvi (1971; see fig. 3), Kumar & Agarwal (1984) described a second species which they also named *F. hilsai* (see figs. 2A, B, C of Kumar & Agarwal 1984). WoRMS (2021a) considers *F. hilsai* Kumar & Agarwal, 1984 a synonym of *F. hilsai* Rizvi, 1971 (both described from *T. ilisha* [Syn. *Hilsa ilisha*] collected from Uttar Pradesh, India); however, although both *F. hilsai* Rizvi, 1971 and *F. hilsai* Kumar & Agarwal, 1984 are about the same size (1,450–1,850 *vs* 1,300–1,500 long), *F. hilsai* Kumar & Agarwal, 1984 differs from *F. hilsai* Rizvi, 1971 by having a shorter forebody (approximately 430, 29% *vs* 740–910, 49–51% of body length); the testes positioned posterior to the ventral sucker *vs* flanking the ventral sucker; a longer cirrus sac (340–360, 24–27% *vs* 190–250, 13–14%); a median ovary with 5–6 ovarian lobes *vs* a distinctly submedian ovary with 8 or more ovarian lobes; a somewhat larger postovarian space relative to body length (440, 32% *vs* 435, 24%); larger eggs (30–50 × 20–30 *vs* 20 × 12) and *F. hilsai* Kumar & Agarwal, 1984 has more extensive vitelline fields (ranging from the midlevel of the esophagus and surpassing the testes posteriorly, reaching to the level of the posterior aspect of the ovary *vs* ranging from about the level of the intestinal

bifurcation to near the level of the posterior aspect of the testes, but not approaching the level of the ovary). We therefore consider *F. hilsai* Kumar & Agarwal, 1984 to be distinct from *F. hilsai* as originally described by Rizvi (1971). *Faustula hilsai* Rizvi, 1971 shares a striking similarity to *F. basiri*. Both have a similar body form; a long esophagus; a ventral sucker that is at the midlevel of the body providing for an unusually long forebody; a large rounded to somewhat pyriform cirrus sac lying immediately anterior to the ventral sucker, enclosing a somewhat *Faustula*-like cirrus apparatus with a tubular pars prostatica and convoluted seminal vesicle both surrounded by numerous large glandular cells; a similar vitellarium pattern; testes that are anterolateral to the ventral sucker; a multilobed ovary (8 or more lobes) that is a short distance posterior to the ventral sucker and slightly sinistral to the midline of the body; and both have basically equivalent measurements, morphometric ratios and morphometric percentages (see Table 1). In our opinion, *F. hilsai* as originally described by Rizvi (1971) should be synonymized with *F. basiri*. Additionally, as *F. hilsai* Kumar & Agarwal, 1984 is established as a species distinct from *F. hilsai* Rizvi, 1971, we propose *Lingulitrema* to accommodate *F. hilsai* Kumar & Agarwal, 1984 as *Lingulitrema hilsai*. *Lingulitrema hilsai* differs from species of *Faustula* by having an extensively elongate, lingulate body form; an oral sucker described as terminal (appears to be slightly subterminal in fig. 2A of Kumar & Agarwal 1984); testes that are located posterior to the ventral sucker near the midlevel of the body or a little more posterior; a distinctly submedian genital pore; a relatively long, tubular pars prostatica surrounded by numerous prostatic cells and a distinctive laterally-placed, S-shaped seminal vesicle *vs* a short pars prostatica with few prostatic cells and a long tubular seminal vesicle that spirals through the posterior two-thirds of the cirrus sac and is at least partially embedded in numerous large glandular cells; an ovary with 5–6 lobes *vs* 8 or more lobes generally seen in species of *Faustula* and *F. hilsai* Kumar & Agarwal, 1984 was originally described as having a smooth (aspinose) body. It should be noted that it has been our experience that species of *Faustula* tend to be somewhat fragile and that the tegumental spines are easily dislodged during routine handling and/or fixation; therefore, the presence or absence of body spines may not be a reliable characteristic in some cases in this genus. It also should be noted that we cannot be completely sure that the lateral placement of the seminal vesicle is not fixation-induced.

***Varanasifaustula* n. gen.**
(Fig. 10)

Type species: *Varanasifaustula indica* (Agarwal & Verma, 1981) **n. comb.** Type and only species.
(Syn. *Faustula indica* Agarwal & Verma, 1981)

Diagnosis: Body small, somewhat elliptical, extremities tapered to form bluntly pointed ends; tegumental spines not reported. Oral sucker, globose, slightly subterminal. Ventral sucker muscular, globose, anterior to midlevel of body, larger than oral sucker. Prepharynx absent. Pharynx oval, nearly circular, muscular. Esophagus relatively short. Intestinal bifurcation about half way between suckers. Ceca relatively short, terminate slightly anterior to midlevel of body. Testes 2, entire, symmetrical, near midlevel of body; anterior extent may overlap posterior margin of ventral sucker dorsally almost to its midlevel. Cirrus sac clavate, overlaps ventral sucker dorsally, may surpass it posteriorly by short distance; sac encloses cirrus, narrow ejaculatory duct, short tubular pars prostatica, relatively long, saccate, naked seminal vesicle. Genital pore at about level of posterior margin of intestinal bifurcation, distinctly submedian, extracecal, immediately left of left cecum. Ovary with 6 lobes, immediately posttesticular or slightly more anterior, near midline of body to slightly submedian. Seminal receptacle described as absent. Uterus largely posterior to gonads, filling most of posttesticular space. Vitellarium composed of few, relatively large follicles (approximately 5–7/side); follicles linearly organized near lateral margins of body from about midlevel of ceca to level of posterior margin of testes or slightly more posterior. Eggs small, operculate. Excretory vesicle V-shaped, extent of excretory arms unknown; excretory pore slightly subterminal. Reported as intestinal parasite of species of clupeid fishes in the Ganges River, India.

Etymology: The genus is named from the location where the type species was collected in India (*Varanasi*) and its probable assignment within the faustulid trematodes (*Faustula*).

Remarks: *Varanasifaustula indica* (Syn. *F. indica*) differs from species of *Faustula* by having a simple cirrus; a narrow ejaculatory duct; a tubular pars prostatica and a simple, saccate, unipartite, naked seminal vesicle *vs* a winding tubular seminal vesicle that is at least partially embedded in large glandular cells; a distinctly submedian, extracecal genital pore; few (5–7/side), relatively large vitelline follicles somewhat longitudinally arranged along

the lateral fields of the body from about the midlevel of the ceca to the level of the posterior margin of the testes *vs* smaller more numerous follicles that range from some distance posterior to the level of the intestinal bifurcation, posteriorly to about the level of the ovary or slightly more anterior; the gonads located near the midlevel of the body and a median ovary with 6 lobes *vs* 8 or more lobes as seen in species in *Faustula*. Note the illustration representing *F. indica* (= *V. indica*) in the original description by Agarwal & Verma (1981) (see fig. 2) is identified as a ventral view, but the location of the cirrus sac and vitelline follicles relative to the ceca, and the ventral sucker relative to the testes and cirrus sac suggest it is a dorsal view. It appears that the specimen illustrated in fig. 2 was rolled so that the structures more closely associated with the dorsal aspect of the body (e.g., posterior aspect of the cirrus sac, gonads) were displaced to the right while structures more closely associated with the ventral surface (e.g., ventral sucker, genital pore) may have been displaced to the left. It is our opinion that the cirrus sac in this species likely more extensively overlaps the ventral sucker, but that the position of the genital pore was not appreciably altered. *Varanasifaustul*a *indica* (Syn. *F. indica*) is somewhat similar to *L. hilsai* discussed above, most notably by having 6 ovarian lobes *vs* 5–6 ovarian lobes in *L. hilsai* (see description and Fig. 2A of Kumar & Agarwal 1984). *Lingulitrema hilsai* also differs from *V. indica* by having longer ceca that surpass the testes for some distance posteriorly, reaching about the midlevel of the ovary; an S-shaped seminal vesicle that lacks large glandular cells; a distinctly submedian genital pore that approaches the cecum and small, more numerous vitelline follicles forming more extensive vitelline fields that extend from the midlevel of the esophagus posteriorly to about the level of the ovary.

The following key to genera within the Faustulidae was developed to accomomodate both previous genera and the 5 new genera proposed herein.

Key to the genera of the Faustulidae modified from Bray (2008)

1a. Cirrus sac absent. . . . . *Pseudobacciger* Nahhas & Cable, 1964[1]
1b. Cirrus sac present 2
2a. Genital pore marginal or nearly so . . . . . *Yamagutia* Srivastava, 1937
2b. Genital pore median to submedian 3
3a. Body conical, with lateral margins folded ventrally and truncate posterior margin . . . . . *Trigonocryptus* Martin, 1958
3b. Body shaped otherwise, lacking folded lateral margins and truncated posterior margin 4
4a. Body somewhat biconic with large terminal oral sucker, narrower isthmus-like forebody, broad ventral sucker region, and relatively long tapering posterior end . . . . . *Schellitrema* **n. gen.**[2] (Fig. 7)
4b. Body oval to elliptical (elongate-oval) with subterminal ovary, sometimes lingulate, usually with broadly tapering extremities 5
5a. Testes and/or ovary in forebody 6
5b. Gonads in hindbody or somewhat overlapping ventral sucker 7
6a. Testes mainly in hindbody; ovary in forebody; ceca long, reach close to posterior extremity *Allofellodistomum* Yamaguti, 1971
6b. Testes in forebody; ovary in posterior forebody, dorsal to ventral sucker or occasionally in anterior hindbody; ceca short, saccate, divergent . . . . . *Antorchis* Linton, 1911 (Syns. *Jonesiella* Hafeezullah & Siddiqi, 1970 *nec* Brady, 1980; *Mesorchis* Linton, 1910 *nec* Dietz, 1909; *Neoparantorchis* Hafeezullah & Siddiqi, 1971; *Parantorchis* Yamaguti, 1934)
7a. Testes near posterior extremity; uterus largely pretesticular, may slightly overlap anterior aspect of testes. 8
7b. Testes some distance from posterior extremity, usually near midlevel of body; uterus largely posttesticular. 10
8a. Ceca relatively long, terminating well posterior of midlevel of body; vitelline follicles relatively large, linear, centered around midlevel of body along lateral margins . . . . . *Pseudofellodistomum* Wang, 1989
8b. Ceca relatively short, not surpassing midlevel of body posteriorly; vitelline follicles relatively small, arranged in clusters, 1 on each side in forebody 9
9a. Ventral sucker relatively large, located at midlevel of body; ovary immediately anterior to testes. . . . . *Echinobreviceca* Dronen, Blend & McEachran, 1994
9b. Ventral sucker relatively small, located near posterior extremity; ovary intertesticular . . . . . *Parayamagutia* Machida, 1971
10a. Ovary pretesticular, may slightly overlap level of anterior aspect of testes. 11
10b. Ovary intertesticular, or posttesticular, may partially extend anteriorly into posterior aspect of intertesticular space 13
11a. Ventral sucker distinctly larger than oral sucker; may be replaced by a non-acetabulate, pad-like structure with muscular ridges or lobes in some species . . . . . *Paradiscogaster* Yamaguti, 1934 (Syns. *Discogaster* Yamaguti, 1934 *nec* Burmeister, 1835; *Discogastroides* Strand, 1934; *Odontocotyle* Hafeezullah & Siddiqi, 1971; *Odontotrema* Hafeezullah & Siddiqi, 1970 *nec* Lindholm, 1927; *Pseudodiscogasteroides* Gupta, 1953; *Neobenthotrema* Wang, 1991)
11b. Normal acetabulate ventral sucker present, not greatly larger than oral sucker, may be somewhat smaller 12
12a. Ovary distinctly trilobed; testes contiguous or nearly so . . . . . *Gobifaustula* **n. gen.** (Fig. 6)
12b. Ovary entire; testes not overly close together . . . . . *Baccigeroides* Dutta, 1995 (Syn. *Baccigeroides* Manna & Datta, 1996)
13a. Ovary entire, may be somewhat irregular, no distinct lobes present *Bacciger* Nicoll, 1914 (Syn. *Ovotrema* Pigulewsky, 1938)[3]

13b. Ovary distinctly lobed 14
14a. Ovary multilobed, with 8 or more ovarian lobes . . *Faustula* Poche, 1926 (Syns. *Eurema* MacCallum, 1918 *nec* Hubner, 1920; *Orientophorus* Srivastava, 1935)
14b. Ovary with less than 8 (6 or fewer) ovarian lobes 15
15a. Ovary with 5–6 ovarian lobes. 16
15b. Ovary with 4 or less ovarian lobes 17
16a. Genital pore extracecal; ceca terminating at level of testes; seminal vesicle long, saccate, naked (not surrounded by glandular cells) . . . . . *Varanasifaustula* **n. gen.** (Fig. 10)
16b. Genital pore distinctly submedian, but not extracecal; ceca surpassing testes posteriorly; seminal vesicle somewhat tubular and S-shaped . . . . . *Lingulitrema* **n. gen.** (Fig. 9)
17a Ovary with 4 ovarian lobes; seminal vesicle saccate, naked and unipartite. . . . . .*Gangafaustula* **n. gen.** (Fig. 8)
17b. Ovary with 3 ovarian lobes; seminal vesicle bipartite . . .*Pronoprymna* Poche, 1926 (Syns. *Pentagramma* Chulkova, 1939 *nec* Van Duzee, 1897; *Pseodopentagramma* Yamaguti, 1971)

[1]Members of this genus lack a cirrus sac. *Pseudosellacotyla* Yamaguti, 1953 is a similar genus wherein species also lack a cirrus sac and it was until recently assigned to the Faustulidae; however, this genus was reassigned to the Cryptogonimidae by Pantoja *et al*. (2018) based largely on molecular evidence. In our opinion, *Pseudobacciger* should not be assigned to the Faustulidae and that future molecular studies will likely show a close relationship of this genus to the Cryptogonimidae.
[2]*Schellitrema* is an unusual genus and in our view likely does not belong in the Faustulidae. Attempts to determine which family this genus might be placed based on morphology were unsuccessful, suggesting it may represent a yet undescribed family. Until we have a better understanding of *S. gasterostei* we have tentatively retained it in the Faustulidae.
[3]*Bacciger* is exceptionally diverse and likely does not represent a unified genus. *Bacciger amblygastris* Machida & Kuramochi 2003 (see fig. 1 of Machida & Kuramochi 2003) has a trilobed ovary and this species does not belong in *Bacciger*. It may possibly belong in *Pronoprymna*. Some descriptions of *Bacciger israelensis* Fischthal, 1980 suggest the presence of a tri-lobed ovary (see fig. 1 of Fischthal 1980); however, the existing descriptions of this species may represent more than 1 species and the presence of a lobed ovary would suggest reassignment of those specimens where that is the case.

Additional taxonomic considerations

Pronoprymna sayori (Yamaguti, 1942) n. comb.

Faustula sayori (Syn. *Orientophorus sayori*) described from the Japanese halfbeak, *H. sajori*, from Tutiura, Japan is similar to species of *Faustula* by having suckers that are about the same size; a cirrus sac that dorsally overreaches the ventral sucker and may surpass it posteriorly by a short distance; a posttesticular ovary and a uterus that is largely posttesticular filling most of the hindbody (see fig. 19 of Yamaguti 1942). However, this species is unlike species of *Faustula* by having a stout body form with a more broadly rounded posterior end; similar-sized, large suckers; a terminal, cup-shaped oral sucker; a cirrus sac that extensively overreaches the ventral sucker posteriorly, invading the intertesticular space to terminate near the level of the posterior margin of the testes; a bipartite seminal vesicle; symmetrical, postacetabular testes located near the midlevel of the body; an ovary that is trilobed; and vitelline fields that are condensed into 2 compact groups and confined to the lateral fields of the second one-fourth of the body. Based on these differences, especially the posttesticular trilobed ovary, the postacetabular placement of the side by side testes, the bipartite *vs* tubular seminal vesicle and the vitelline follicles being condensed into 2 compact groups that are posterolateral to the ventral sucker, we agree with Bray (2008) and more recently WoRMS (2021a) that *F. sayori* does not represent a species of *Faustula*. Bray and Gibson (1980) recommend that *F. sayori* be reassigned to *Pronoprymna* and synonymized it with *P. petrowi* (Layman, 1930) Bray & Gibson, 1980 (Syn. *Monorcheides petrowi* Layman, 1930). However, *P. petrowi* as originally described by Layman (1930) (see fig. 35 of Layman 1930) displays a number of characteristics, including the testes being located more posteriorly *vs* well anterior to the midlevel of the body; the presence of an entire *vs* a trilobed ovary; the cirrus sac terminating a short distance posterior to the ventral sucker *vs* extending posteriorly in to the intertesticular space to near the posterior margins of the testes; vitelline fields that are confined from the midlevel of the ventral sucker to the level of the anterior margin of the testes *vs* terminating more posteriorly about the midlevel of the testes and the presence of a unipartite saccate *vs* bipartite seminal vesicle that distinguish it from *F. sayori* (Syn. *O. sayori*) as described by Yamaguti (1942, 1958). We therefore recommend that *F. sayori* be considered a separate species from *P. petrowi* and be assigned to *Pronoprymna* as *Pronoprymna sayori* (Yamaguti, 1942) **n. comb.** In addition, *Pronoprymna petrowi*

(Syn. *Pentagramma petrowi* [Layman 1930] Margolis & Ching, 1964) as described by Margolis & Ching (1964) and *Pronoprymna petrowi* as described by Shimazu (2018), for the present, should be maintained in *Pronoprymna* as *P. sayori*. However, based on the smaller size of the ventral sucker relative to the oral sucker it is likely that *P. petrowi* as described by Shimazu (2018) is a separate species from *P. sayori*. Until additional specimens and information are available concerning these 2 species, we have elected to support their synonymies with *P. sayori*.

***Pronoprymna pyriformis* (Kumar & Agarwal, 1984) n. comb.**

Faustula pyriformis (see figs. 1A, B, C of Kumar & Agarwal 1984) is similar to species in the genus by having a generally elliptical (elongate-oval), spinose body form with tapering extremities forming bluntly pointed ends; symmetrical (side by side) testes located about the level of the ventral sucker, immediately anterior to and overlapping the level of the anterior aspect of it; a somewhat retort-shaped cirrus sac; a submedian genital pore; a posttesticular, submedian ovary; and a uterus that is largely posttesticular and mainly in the hindbody. *Faustula pyriformis* differs from species of *Faustula* by having the oral sucker notably smaller than the ventral sucker (120–140 wide *vs* 180–190 wide); a trilobed ovary and vitelline follicles that are condensed into small compact groups composed of few follicles (5–8/side), which justifies placement of this species in *Pronoprymna* as *Pronoprymna pyriformis* (Kumar & Agarwal, 1984) **n. comb.** (Syn. *F. pyriformis*). We have noted in specimens of *Faustula* what we feel are subtle fixation-induced changes in the position of structures like the posterior extent of the cirrus sac relative to the ventral sucker and the placement of the ventral sucker relative to the intestinal bifurcation. In our opinion these potential fixation-induced anomalies may account for the unusual anterior (preacetabular) placement of the cirrus sac and the posterior placement of the ventral sucker described for *P. pyriformis*.

***Bacciger varanasiensis* (Agarwal & Kumar 1977) n. comb.**

Faustula varanasiensis (see fig. 1 of Agarwal & Kumar 1977) was described by Agarwal & Kumar (1977) in *T. ilisha* from the Ganges River, Varanasi, India. It resembles species of *Faustula* by having a median to slightly submedian, genital pore located immediately posterior to the intestinal bifurcation; gonads that overlap the ventral sucker to some extent; a coiled seminal vesicle; vitelline fields that range from the level of the esophagus to the level of the posterior margins of the testes or more posteriorly and a uterus that reaches posterior beyond the testes, distributed mainly in the hindbody. However, this species differs from species of *Faustula* by having an oval body form with broadly truncated extremities *vs* the more typical elliptical body form that is more indicative of species of *Faustula*; testes located at the midlevel of the body and a submedian cirrus sac that extensively overlaps the level of the ventral sucker extending about the length of it into the intertesticular space and reaching the anterior margin of the ovary. It should be noted that this species is most similar to species of *Bacciger* and we propose this species be assigned to *Bacciger* as *Bacciger varanasiensis* (Agarwal & Kumar 1977) **n. comb.** However, the combination of characteristics displayed by this species, especially the unusually extensive posterior extent of the cirrus sac (extending well posterior to the ventral sucker), suggests that it may represent an undescribed genus.

Discussion

Specimens of *Faustula* collected for use in the current study tended to be relatively small, exceptionally delicate, and difficult to fix without damage and/or contraction whether using minimal coverslip pressure or without a coverslip. Our observations of specimens of other fauatulids and illustrations from the original descriptions of species currently assigned to the genus suggest that this is likely true for other species in the genus. It is our opinion that the delicate nature of members of the genus often may be reflected in fixation-induced variation in body shape (ovoid [lemon-shaped] to elliptical [elongate-oval]), the position of structures (e.g., genital pore, ventral sucker, cirrus sac) and the size and/or shape of structures (e.g., prepharynx, esophagus, testes) in some described species where damage, morphological disfigurement or contraction occurred, and these induced differences may have led to a proliferation of species descriptions in the genus. We cannot be certain that contraction-induced anomalies fully account for the unusual expressions of characteristics we encountered, but given the delicate nature of species of *Faustula,* such

alterations may at least account for apparent subtle shifts in the locations of some structures during fixation. It is also likely that this proliferation of species in this genus was amplified by many species being described on the basis of few specimens precluding consideration of natural variability and potential collection/fixation-induced anomalies, as was the case for *F. keksooni*, the type species of the genus (n=1; badly damaged specimen with the oral sucker torn off). This possible proliferation of species is further supported by the fact that 9 of the 13 species previously assigned to the genus have been described from the same host (*T. ilisha*), generally from the rivers of India or less frequently from the Indian Ocean, and commonly from the same locality (Varanasi, Ganges River, India).

The location of the testes relative to the ventral sucker; the position of the ovary relative to the testes; the location of the genital pore relative to the intestinal bifurcation; the basic morphology within the cirrus sac and its location; the location of the ventral sucker in the body; the number of ovarian lobes; and the configuration, extent and location of the vitellarium in the body have been considered to be relatively consistent and reliable characteristics for discriminating genera within the Faustulidae and to some extent distinguishing species within genera, and thus, these features commonly have been used in keys. The species currently assigned to *Faustula* vary from having an entire ovary (no lobes as in *F. varanasiensis* [now *Bacciger varanasiensis*]) to being multilobed (i.e. 3 lobes in *F. sayori* [now *Pronoprymna sayori*], 4 in *F. makundai* [now *Gangafaustula makundai*], 6 in *F. indica* [now *Varanasifaustula indica*], 8 or possibly more in *F. brevichrus*). Based on our results, we currently propose the following 5 species be retained in *Faustula*: *F. basiri*, *F. brevichrus*, *F. clupeae*, *F. gangetica* and *F. keksooni*. The number of ovarian lobes appear to us to represent a reasonably consistent feature in distinguishing species in *Faustula* and genera within the Faustulidae as long as specimens are carefully relaxed and appropriately heat fixed.

Bray (2008) considered *Pseudofellodistomum plagiorchis* Wang, 1989 to represent a genus *incertae sedis* largely based on posteriorly situated testes and the lack of information on the cirrus sac contents, proximal female reproductive system, metraterm and excretory system. However, members of this genus appear to fit within the currently broad diagnosis of the Faustulidae by having a generally elliptical (sometimes described as fusiform) body; a spinose tegument; a subterminal oral sucker; a ventral sucker that is somewhat anterior to the midlevel of the body; a short to absent prepharynx; a generally elliptical pharynx; a distinct esophagus; the intestinal bifurcation in the forebody between the suckers; the cirrus sac located in the region between the intestinal bifurcation and the ventral sucker; a median or nearly median genital pore located between the intestinal bifurcation and the ventral sucker; an entire, pretesticular ovary; large vitelline follicles linearly arranged in the lateral fields from about the level of the ventral sucker to the testes and an extensive uterus that is pretesticular. Based on this we agree with WoRMS (2021b) that *Pseudofellodistomum* represents a valid genus. There are only 4 genera (*Echinobreviceca*, *Parayamagutia*, *Triganocryptus* and *Yamagutia*) currently assigned to the Faustulidae that contain species where the testes are positioned somewhere close to the posterior extremity; however, only *Yamagutia* has distinctly diagonal testes. Representatives of *Yamagutia* differ from *P. plagiorchis* by having a shorter, broader body (length/width ratio1:2.5) *vs* being much longer than wide (1:4.4); an elliptical shape; short ceca; an ovary that is relatively close to the testes *vs* being some distance anterior to the testes; a bipartite *vs* a saccate seminal vesicle; numerous relatively small vitelline follicles distributed in clusters (1 on each side of the body) *vs* having few, large vitelline follicles linearly distributed along the lateral margins of both sides of the body and the genital pore is nearly marginal in species of *Yamagutia*. Only *G. makundai* and *V. indica* have large vitelline follicles linearly distributed along the lateral margins of both sides of the body; however, both of these species differ from *P. plagiorchis* by having a posttesticular, lobed ovary and symmetrical testes located at the midlevel of the body.

Assignment of species to genera can be challenging in the Fautulidae, especially with the previously broad diagnoses of some genera (e.g., *Bacciger*, *Faustula*, *Pronoprymna*) and the family itself. In *Faustula* this is further complicated by the delicate nature of these small-bodied species where body shape and often placement of structures may be altered during collection and fixation of specimens, and species often may have overlapping measurements and other similar characteristics. This, along with a lack of data concerning the intraspecific variability of most existing species descriptions in *Faustula* may interfere with the accurate determinations of species and in many cases their placement in an appropriate genus. Currently, there are no DNA sequences listed in GenBank for *Faustula* or *Pronoprymna* and only 9 for species of *Bacciger*. In our opinion, molecular analyses in conjunction with morphological evaluations of additional specimens likely will help researchers to more adequately sort out the phylogenies in this family and assist researchers in more correctly assigning species to genera. Given the difficulties in sorting out species within the Faustulidae and placing them in the correct genus in this family, it will be critical to

ensure that the identifications of the species being sequenced are based on a logical taxonomic framework. We offer this reconsideration of the species of *Faustula* and the genera within the family to assist in these future efforts.

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