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Synopsis of the pterelectrine goby genus *Nematelectris*, with description of a new species from the western and central Pacific Ocean (Teleostei: Gobiidae)

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Abstract. *Nemateleotris lavandula*, new species, is described on the basis of the holotype from Augulupelu Reef, Palau, and twelve paratypes from across the western and central Pacific Ocean, including Fiji, Guam, Japan, and the Marshall Islands. The new species was previously confused with *Nemateleotris helfrichi*, but molecular analysis of mitochondrial COI reveals a difference of 1% in sequence data between both species, in addition to differences in morphometric measurements, live, and preserved colouration details. Both species are allopatric and do not overlap in distribution. The new species is readily separated from all congeners based on the following combination of characters: body lavender to lilac in life; maxilla unmarked, bright yellow in life; caudal fin truncate to weakly emarginate, unmarked, pale yellowish green in life; and snout, lower jaw, preopercle, and postorbital region bright yellow in life. We comment on the relationships among species of *Nemateleotris*, the taxonomic status of *N. exquisita*, and the doubtful identity of *Zagadkogobius ourlazon*. A revised key to species of *Nemateleotris* is provided.

Key words. dartfish, mesophotic, gobioid, Ptereleotrinae, Microdesminae

INTRODUCTION

Fowler (1938) erected the genus *Nemateleotris* for a single specimen of an 'exquisite little eleotrid' fish collected from the *Albatross* expeditions in 1907–1910 to the Philippines and Indonesia. Though unaware of its colouration in life, he was sufficiently impressed by it that he named the specimen *N. magnifica*. The prefix of his new genus is appropriate, and is from the Greek 'nemat', meaning thread, in reference to the long filamentous first dorsal fin of the species. The suffix is not, as the fish is not an eleotrid, but rather a gobiid. The suffix was given presumably because of the unfused pelvic fins in *Nemateleotris*, an unusual condition among Gobiidae but normal for Eleotridae.

Familial classification of *Nemateleotris* and allied dartfish genera has been contentious. The dartfishes, which include the genera *Aioliops*, *Navigobius*, *Nemateleotris*, *Oxymetopon*, *Parioglossus*, *Pterocerdale*, and *Ptereleotris*, were united under the subfamily Ptereleotrinae (sensu Hoese & Motomura, 2009; considered by some authors to be the

family Ptereleotridae [Thacker, 2000; Kuiter & Tonozuka, 2004; Fricke et al., 2011a; Allen & Erdmann, 2012]). This subfamily was one of two, the other being the Microdesminae (the wormfishes), that in older classifications composed the family Microdesmidae (Hoese, 1984). Prokofiev (2017) described his new genus and species *Zagadkogobius ourlazon* on the basis of a single specimen from the South China Sea, which he placed in the subfamily Ptereleotrinae. His new genus, however, possesses several characters that are unusual amongst the ptereleotrines, including differences in squamation and dorsal-fin formula. We believe that Prokofiev's subfamilial allocation of *Z. ourlazon* is doubtful and in need of critical re-evaluation, which we discuss below.

Support for the recognition of Microdesmidae or Ptereleotridae as distinct families has eroded in recent years (but see Kuiter & Tonozuka, 2004; Hoese & Motomura, 2009; Fricke et al., 2011b; Allen & Erdmann, 2012; Randall & Connell, 2013), with growing evidence from both molecular and morphological studies demonstrating the nesting of both groups as a lineage within the Gobiidae sensu Gill & Mooi (2012) at the exclusion of all other gobiids (Gill & Mooi, 2010; 2012; Thacker & Roje, 2011; Tornabene et al., 2013). However, due to the rarity of several taxa (such as the enigmatic Pterocerdale), taxonomic representation of the ptereleotrines and microdesmines has been inadequate, at least in molecular phylogenetic studies. As such, pterelectrine and microdesmine relationships have not been well interrogated, particularly concerning their reciprocal monophyly, their relationships to each other, and their relationships with other gobioid taxa (Thacker & Roje, 2011; Agorreta & Rüber, 2012; Tornabene et al., 2013). Until these relationships are

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resolved, we provisionally recognise the ptereleotrines as an informal grouping within the Gobiidae.

Three additional species of Nemateleotris have been recognised since Fowler's (1938) description of *N. magnifica*. Randall & Allen (1973) revised the genus, describing two species as new — N. helfrichi (Randall & Allen, 1973) from Palau, Guam, and other islands of Micronesia and French Polynesia (type locality, Tahiti), and N. decora from Palau (type locality), Papua New Guinea, the Solomon Islands, and the Coral Sea. The latter species has since been reported widely across the Indo-Pacific, including the Red Sea. Randall & Connell (2013) recognised the Indian Ocean and Red Sea population of *N. decora* as distinct, which they named *N*. exquisita — the justification for which was based on apparent differences in morphometric and live colouration details. From our examination of type specimens of *N. exquisita*, as well as of additional specimens of N. decora (including a paratype), we find these differences uncompelling and here regard N. exquisita as a synonym of N. decora (discussed below).

The scrutiny of *N. decora* and its status as a single widespread species provided the impetus for this study. Examination of the type series of *N. helfrichi* revealed the presence of two strikingly different fishes in both live and preserved colouration details. The taxonomy of *N. helfrichi* is here revised, and in doing so, we recognise two allopatric species — *N. helfrichi* sensu stricto from French Polynesia and surrounding islands in the south-eastern Pacific Ocean, and *N. lavandula*, new species, from the western and central Pacific Ocean. The former species is here rediagnosed, and we comment on the relationships of *Nemateleotris* on the basis of molecular sequence data. A revised key to species of *Nemateleotris* is provided.

MATERIAL AND METHODS

Meristics, morphometrics, and specimen deposition. Measurements were made with digital callipers, recorded

to the nearest 0.1 mm. All measurements to the snout tip were made to the mid-anterior tip of the upper lip. Standard length (SL) was measured from the snout tip to the posterior end of the hypural plate. Predorsal, preanal and prepelvic lengths were measured from the snout tip to the base of the anteriormost spine of the relevant fin. Head length (HL) was measured from the snout tip to the upper attachment of the opercular membrane. Body depth was the vertical distance between origin of first dorsal fin and pelvic fins. Body width was measured at the pectoral-fin bases. Snout length was measured from the snout tip to the anterior orbital rim. Orbit diameter was the horizontal width of the eyeball. Postorbital length was measured from the posteriormost edge of the eyeball to the upper attachment of the opercular membrane. Bony interorbital width was the least measurement. Caudal-peduncle length was measured from the base of the posteriormost anal-fin ray to the ventral edge of the caudal peduncle at the vertical through the posterior edge of the hypural plate. Caudal-peduncle depth was the least depth. Pectoral-fin length was the length of the longest ray. Other measurements are self-explanatory. Morphometric values for the new species are presented in Table 1, expressed as percentage of standard length.

The last ray in the anal and second-dorsal fins is divided at its base and was counted as a single ray. Scales in lateral series were counted from the upper edge of the pectoral-fin base along the mid-side of the body to the posterior edge of the hypural plate. Gill-raker counts include all elements on the outer face of the first arch; the angle raker was included in the second count. Where counts were recorded bilaterally, both counts are given and separated from each other by a slash; the first count presented in the left count. Specimens were temporarily stained with Cyanine Blue 5R to facilitate examination of small structures (Akihito et al., 1993; Saruwatari et al., 1997). Terminology for cephalic pores follow Akihito (1984). Osteological details were determined from radiographs and examination of cleared and stained specimens. The pattern of interdigitation of first-dorsal-fin proximal pterygiophores between neural spines is given as a dorsal-fin pterygiophore formula following Birdsong et al. (1988). In the description of the new species and diagnosis of N. helfrichi, data are given first for the holotype, followed where different by data for the paratypes in parentheses.

Type specimens of the new species are deposited in the Australian Museum, Sydney (AMS), the Bernice Pauahi Bishop Museum, Honolulu (BPBM), the California Academy of Sciences (CAS), the Kanagawa Prefectural Museum of Natural History, Yokohama (KPM-NI), the National Museum of Natural History, Smithsonian Institution (USNM), and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum at the National University of Singapore (ZRC). Type specimens of N. helfrichi s.s. were examined from specimens deposited at BPBM. Type specimens of N. exquisita were examined from specimens deposited at BPBM, CAS, and the South African Institute for Aquatic Biodiversity (SAIAB). One paratype of N. decora was examined from the specimen deposited at AMS. We made use of photographs from the Image Database of Fishes housed at KPM-NI, which are assigned unique numbers with the prefix KPM-NR. Institutional codes follow Sabaj (2020).

Taxon sampling, sequencing, and phylogenetic analysis.

Tissue samples of the new species were obtained from the right pectoral fin of two paratypes (ZRC 62990, 2, 29.8–36.1 mm SL), preserved in 100% ethanol, and stored at -20°C prior to extraction. DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer's protocol. Mitochondrial cytochrome c oxidase subunit I (COI) was amplified from extracted gDNA using the polymerase chain reaction (PCR). Primer sets and PCR conditions follow Chang et al. (2017). Sanger sequencing was outsourced to the Australian Genome Research Facility (Canberra, Australia). Forward and reverse contigs were aligned and trimmed separately using GENEIOUS Prime 2019.1.1 (Biomatters). Successful amplification of COI barcodes for the new species was achieved only for the larger 36.1 mm SL specimen. The COI sequence of the new species was then combined with

Table 1. Morphometric values for Nemateleotris lavandula, new species, expressed as percent SL.

	Holotype						Paratypes	sec					
	AMS 1.16876- 001	AMS I.18411-017 (previously AMS I.18411-010)	BPBM 9527	BPBM 10153	BPBM 12661	12661	BPBM 19974	BPBM 40810	CAS- ICH 27591	KPM- NI 10136	ZRC 62290	62290	USNM 209306
Standard Length	45.6	46.9	25.0	30.9	33.5	35.5	45.4	38.5	35.5	39.0	36.1	29.8	51.5
Greatest body depth	17.1	16.6	18.0	18.1	18.8	19.7	14.1	16.9	18.9	17.2	18.3	16.1	16.5
Greatest body width	10.5	9.0	8.4	6.5	7.2	8.9	6.6	9.4	6.6	9.5	6.7	10.1	9.1
Head length	22.4	22.2	24.4	22.7	23.0	21.4	21.1	26.5	23.1	24.6	24.1	23.5	21.0
Snout length	8.8	4.3	4.8	3.9	8.4	4.2	4.6	3.4	3.9	3.3	4.4	3.7	3.1
Upper jaw	9.9	7.5	7.2	6.1	7.2	5.6	7.0	6.2	8.9	7.2	6.9	7.4	6.4
Orbit diameter	9.4	8.5	9.2	7.6	7.8	8.2	7.3	9.8	8.2	7.4	8.9	9.1	9.7
Postorbital length of head	11.2	11.1	12.4	11.3	11.0	11.3	10.1	12.5	11.0	10.0	12.2	11.1	9.7
Interorbital width	5.7	5.1	4.8	6.5	8.8	5.1	5.5	6.5	5.4	5.4	5.5	0.9	5.0
Caudal peduncle depth	12.3	10.0	13.6	11.7	11.6	11.8	6.6	11.2	6.6	11.0	12.7	11.1	10.9
Caudal peduncle length	4.4	4.7	0.9	5.5	6.9	5.1	6.4	5.5	5.1	5.1	5.0	5.7	5.4
Predorsal length	27.4	25.6	30.0	31.7	29.9	29.0	27.5	28.6	27.9	27.4	29.1	30.2	26.0
Preanal length	57.9	56.1	9.69	57.0	52.8	56.3	9.09	6.95	55.2	55.1	57.3	57.7	56.9
Prepelvic length	24.6	25.2	28.0	25.9	25.4	23.4	25.3	24.9	26.2	24.4	25.2	26.5	23.9
Dorsal-fin base	64.9	68.4	62.8	2.99	0.99	64.7	65.4	65.5	65.4	2.99	8.99	65.4	64.7
Anal-fin base	38.9	40.9	38.0	40.5	36.1	40.0	39.4	36.6	42.3	37.4	38.8	38.6	37.0
Pectoral fin length	21.5	19.0	21.6	16.5	17.3	17.5	17.6	16.4	20.0	17.7	20.0	20.1	16.9
Pelvic fin length	15.8	17.1	18.4	16.5	16.4	13.5	17.0	19.5	17.2	19.2	17.2	14.4	15.0
1st dorsal-fin spine	27.2	33.3	broken	26.5	26.9	30.4	28.4	26.0	31.5	28.7	27.7	33.2	28.9
5th dorsal-fin spine	11.0	9.6	9.6	7.8	6.9	7.0	0.6	7.8	8.2	8.5	7.6	10.4	7.2
6th dorsal-fin spine	7.0	0.9	8.4	6.1	9.9	8.9	7.9	8.9	7.3	7.4	8.0	7.7	5.0
Spine of second dorsal fin	6.1	7.0	6.4	8.9	7.2	7.9	8.4	6.5	6.5	5.9	9.9	8.4	5.2
Penultimate 2nd dorsal-fin ray	17.1	13.2	broken	10.0	broken	15.5	12.1	6.6	broken	13.1	12.5	broken	11.3
Penultimate anal-fin ray	14.9	11.7	13.6	9.4	0.6	8.5	6.6	8.3	broken	12.8	10.8	9.4	11.7
Caudal-fin length	22.1	22.0	22.0	19.7	20.0	19.4	21.4	23.1	21.4	22.3	22.7	20.8	21.9

those of other *Nemateleotris* species available from GenBank and aligned using the MUSCLE v3.8.31 algorithm (Edgar, 2004). To account for possible cryptic diversity in the wideranging *N. decora* and *N. magnifica*, we include 12 and 13 sequences of both species respectively, from specimens sampled across their geographic ranges. *Navigobius vittatus* was used as the outgroup. The final sequence alignment consisted of 651 base pairs. Accession numbers for the new species and comparative sequences of other *Nemateleotris* and *Navigobius* are presented in the Appendix.

We analysed the molecular data set using maximum likelihood in IQ-TREE v2.1.3 (Nguyen et al., 2015). Branch support was assessed using ultrafast bootstrapping (UFBS) approximation with 1,000 replicates (Hoang et al., 2017) and the Shimodaira-Hasegawa-like approximate likelihood-ratio test (SH-aLRT; Guindon et al., 2010) with 1,000 replicates. Node values were taken as robust if they were recovered with support values of UFBS \geq 95 and SH-aLRT \geq 80 (Guindon et al., 2010; Bui et al., 2013). Substitution models were selected using the Bayesian information criterion implemented in ModelFinder (Kalyaanamoorthy et al., 2017). Uncorrected p-distance was calculated for the new species and *N. helfrichi* s.s. using GENEIOUS Prime.

TAXONOMY

Infraclass Teleostei

Order Gobiiformes

Family Gobiidae

Genus Nemateleotris Fowler, 1938

Nemateleotris Fowler, 1938: 131 (type species Nemateleotris magnifica Fowler, by original designation).

Diagnosis. *Nemateleotris* is readily distinguished from all other gobioid genera in having the following combination of characters: dorsal-fin rays VI, I,27–33; first three dorsal-fin spines elongate and pennant like, filamentous in one species, first spine longest, 1.4–3.9 in SL; anal-fin rays I,25–32; pectoral-fin rays 18–21 (usually 20); pelvic-fin rays I,5; pelvic fins separate, not connected to each other by frenum or to body by membrane; total caudal-fin rays 37–45; scales in longitudinal series 110–190; no visible lateral line; total gill rakers 19–25; branchiostegal rays 5.

Description. Dorsal-fin rays VI, I,27–33, all segmented rays unbranched; anal-fin rays I,25–32, all segmented rays unbranched; pectoral-fin rays 18–21, upper and lowermost 3–4 unbranched, all other rays usually branched (sometimes all rays unbranched); pelvic-fin rays I,5; segmented caudal-fin rays 17; upper procurrent caudal-fin rays 9–14; lower procurrent caudal-fin rays 10–14; total gill rakers = 19–25.

Mouth strongly oblique, forming an angle of about 50° to horizontal axis of body; maxilla reaching a vertical through

centre of eye; upper jaw with an outer row of four to six, widely spaced, moderately large, incurved canines on each side, and a medial band of small villiform teeth that narrows posteriorly; lower jaw slightly protruding when mouth closed, with two to four enlarged recurved canines at corner of each side of jaw, the more posterior tooth largest, a middle band composed of two to four rows of low villiform teeth narrowing to a single row posteriorly, and an inner pair of enlarged recurved canines at front corner of each side; no teeth on vomer or palatines; tongue truncate, set far back in mouth.

A low median fleshy ridge on top of head from interorbital space to origin of first dorsal fin; no opercular or preopercular spines; preopercular margin free only ventrally; upper end of gill opening at or slightly dorsal to level of middle of eye, the ventral end extending to below posterior margin of preopercle; anterior and posterior nasal pores separated by a distance about equal to half the pupil diameter; anterior nasal pore small, rounded and terminating in a short fleshy tube; posterior nasal pore larger, rounded, with little or no rim.

No visible lateral line on body; pores of cephalic lateral line system in two main series, a preopercular canal of three large pores on upper margin of preopercle, the uppermost pair at approximately level of lower edge of pupil, the lowermost slightly below level of lower edge of eye, and an anterior oculoscapular canal of five large pores, the anteriormost immediately above nostril, the second above centre of eye or slightly ahead of this point, the third slightly above eye and slightly anterior to a vertical at posterior edge of eye, the fourth slightly behind eye on a horizontal with about middle of pupil or slightly above, and the last slightly higher than the fourth and nearly in line with a projection from the two preopercular pores; a single median pore of moderate size situated at about mid-interorbital, connected to the left and right oculoscapular canals by a coronal commissure (see N. magnifica in Akihito [1984: fig. 62] and N. helfrichi [Fig. 1]).

Scales very small, non-imbricate, numbering 110–190 in longitudinal series; scales on body ctenoid dorsoposteriorly to about posterior third of dorsal fin, cycloid elsewhere, those anteriorly frequently embedded; no scales on head; no median predorsal scales, but embedded scales extend anteriorly on side of nape to level of gill opening or slightly beyond; prepelvic area of thorax with embedded scales; anterior portion of isthmus naked; no scales on fins except for approximately basal half of caudal fin.

First dorsal fin elevated anteriorly, the first three spines elongate and pennant like, filamentous in one species, the first spine longest, 1.4–3.9 in SL; the second and third spines only slightly shorter, the fourth, fifth, and sixth shorter than second; caudal fin truncate or weakly emarginate, round in one species; pectoral fins moderately pointed, pattern of branching variable, usually the upper and lowermost 3–4 rays unbranched (sometimes all rays unbranched), the middle rays longest, 4.7–6.1 in SL; pelvic fins separate, not connected to each other by frenum, not connected to body by membrane, their origin directly below pectoral-fin base, 3.6–7.4 in SL.

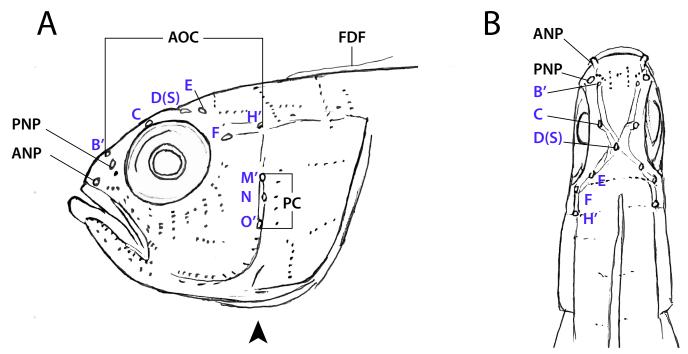


Fig. 1. Laterosensory pores and neuromasts based on holotype of *Nemateleotris helfrichi* (BPBM 11595). A, lateral view; B, dorsal view. Letter codes (in blue) for laterosensory pores follow Akihito et al. (1984). ANP, anterior nasal pore; PNP, posterior nasal pore; AOC, anterior oculoscapular canal; PC, preopercular canal; FDF, first dorsal fin. Arrowhead indicates position where gill membranes are attached to the isthmus.

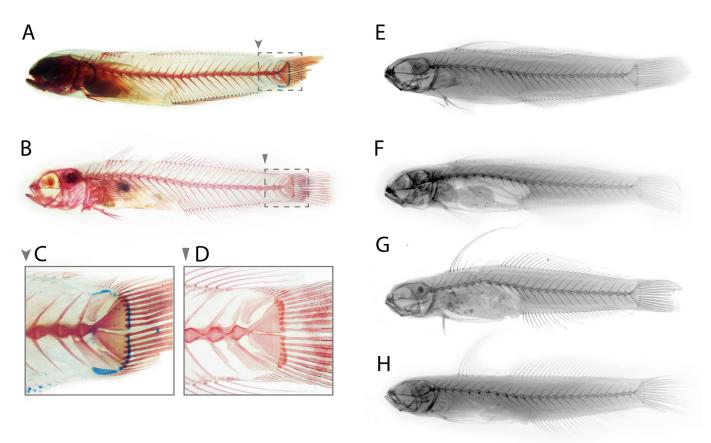


Fig. 2. Cleared and stained images and radiographs of select specimens of *Nemateleotris*. A, *Nemateleotris magnifica*, AMS I.45300-327, 40.5 mm SL, specimen from the aquarium trade; B, *Nemateleotris decora*, AMS I.45300-166, 33.5 mm SL, specimen from the aquarium trade; C–D, close up of caudal skeletons of A and B respectively; E, *Nemateleotris magnifica*, AMS I.25110-035, 46.9 mm SL, Osprey Reef, Coral Sea; F, *Nemateleotris decora*, AMS I.16877-007, paratype, 37.1 mm SL, Osprey Reef, Coral Sea; G, *Nemateleotris helfrichi*, BPBM 11595, holotype, 43.3 mm SL, Tahiti, Society Islands; H, *Nemateleotris lavandula*, new species, KPM-NI 10136, paratype, 39.0 mm SL, Ototo-jima, Chichijima, Ogasawara Islands.

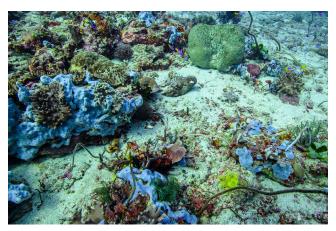


Fig. 3. A pair of *Nemateleotris magnifica* (middle) in habitat typical of the genus, consisting of sand channels and loose coral rubble. Note the presence of other fishes frequenting this habitat, including *Pomacentrus auriventris* and *Meiacanthus grammistes*. Underwater photograph from 15 m, central Sulawesi. Photograph by: V. Chalias.

Osteology. Vertebral column with 10 precaudal and 16 caudal vertebrae (Fig. 2); all vertebrae, except compound ural centrum, with neural spines; neural spines 1 through 20-21 with one or two foramina; epineurals on vertebrae 1 through 15–16, the posteriormost 3–4 sometimes weakly ossified; ribs present on precaudal vertebrae 3 through 10; vertebrae 24 (=PU3) and 25 (=PU2) with modified haemal and neural spines. Neural and haemal spine of PU3 only slightly broader than those of preceding. Haemal spine of PU2 broad proximally, blade-like distally, its flat anterior margin distally articulating with ventral procurrent cartilage, its cylindrical posterior margin articulating with two segmented caudal rays. Terminal vertebral (compound ural) centrum and hypurals 3–4 not differentiated; hypural 5 slender, about half the length of hypurals 1+2, well separated from ural centrum. Hypurals 1+2 undifferentiated and platelike with anteroventral flange. Parhypural autogenous, truncated proximally, with anterior flange, inserting distally in groove on anteroventral flange of hypurals 1+2. Anterior to hypural 5 a single, large epural with a cylindrical core near posterior margin, its flat anterior margin distally articulating with dorsal procurrent cartilage.

Typically, 9–14 unsegmented procurrent rays articulating with each dorsal and ventral procurrent cartilage; total number of segmented caudal-fin rays 17; one segmented ray articulating with epural and hypural 5, respectively; seven branched rays articulating with hypurals 3+4; six branched rays articulating with hypurals 1+2, the ventralmost sometimes displaced slightly below plate; one segmented ray articulating with parhypural and haemal spine of PU2 respectively.

First dorsal fin with six spines. No supraneurals. Two pterygiophores between neural spines 3 and 4, two between neural spines 4 and 5, one between neural spines 5 and 6, one between neural spines 6 and 7, followed by vacant interneural space (interneural gap) between neural spines 7 and 8 (formula 3-22110); proximal and medial radial of first two pterygiophores of second dorsal fin undifferentiated;

remaining pterygiophores of second dorsal fin with autogenous middle and proximal radials. First anal-fin pterygiophore bearing one supernumerary spine and one serial ray, inserting anterior to first hemal arch; subsequent anal-fin pterygiophores each bearing one serially associated segmented ray; proximal tips of all pterygiophores of medial fins cartilaginous.

Etymology. Combination of the Greek *nemat* meaning thread, and the eleotrid genus *Eleotris*. Genus is feminine. Species of *Nemateleotris* are known by a variety of common names, including firefish, firegoby, and dartfish. To maintain consistent terminology with other members of the ptereleotrinae, we use dartfish as the preferred common name, but provide alternative names wherever appropriate.

Habitat and biology. Small (rarely exceeding 70 mm total length), elongate and moderately compressed fishes frequently found hovering close to the substrate near or in coral reefs at depths between 6–100 m, especially in areas replete with sand channels and loose coral rubble (Fig. 3). Diet primarily plankton and other small invertebrates which they pick out of the water column. All species brightly coloured (see key below) and with an elongate pennant-like first dorsal fin which they flick back and forth repeatedly, often in synchrony with their pelvic fins. Most frequently observed singly or in pairs, juveniles sometimes in small groups, often mixed with other plankton feeders. When startled they quickly dart into small holes or crevices in the substrate, emerging a few minutes later when the threat has passed.

Key to the species of Nemateleotris

- Median fins translucent, pale greenish yellow in life; distalmost edge of second dorsal and anal fin lined with yellow spots, one in each interradial membrane space, spots sometimes coalescing; caudal fin unmarked; elevated portion of first dorsal fin in life blue on anterior edge; body in life lavender to lilac, purplish

Nemateleotris magnifica Fowler, 1938

Magnificent Dartfish

Other names: Fire Dartfish; Magnificent Firefish; Red Firegoby

(Figs. 2A, C, E, 3, 8D, 9D, 10A1-A2, 11; Table 2)

Nemateleotris magnificus Fowler, 1938: 131 (holotype USNM 99044, Buka Buka Island, Gulf of Tomini, Sulawesi); Whitley, 1964: 194 (New Caledonia).

Nemateleotris magnifica – Randall & Allen, 1973: 350, figs. 1–3 (redescription); Fourmanoir & Laboute, 1976: 142 (checklist; New Caledonia); Masuda et al., 1984: 245, fig. 62 (checklist, Japanese archipelago); Myers, 1988 (checklist; Marianas Islands); Myers, 1989: pl. 118G (field guide, aquarium photograph of specimen from Micronesia); Kuiter & Debelius, 1994: 266 (field guide, underwater photograph from Southeast Asia); Randall et al., 1997: 415 (field guide, Great Barrier Reef & Coral Sea); Myers, 1999: pl. 164H (field guide, underwater photograph from Micronesia); Allen et al., 2003: 282 (field guide; underwater photograph); Randall, 2005: 564 (field guide, underwater photograph from Sulawesi); Kuiter & Debelius, 2006: 666 (underwater photograph from Malaysia); Allen et al., 2007: 222 (underwater photograph from Christmas Island); Fricke et al., 2011b (checklist; Vanuatu); Fricke et al., 2011a (checklist; New Caledonia); Allen & Erdmann, 2012: vol. 3, 994 (underwater photograph from Papua New Guinea); Randall & Connell, 2013: fig. 4 (underwater photograph from Kwajalein Atoll, Marshall Islands); Allen et al., 2015: 286 (field guide, underwater photograph); Rosenstein, 2019: 272 (field guide; underwater photograph from Fiji).

Diagnosis. Dorsal-fin rays VI, I,28–32; anal-fin rays I,27–30; pectoral-fin rays 19–20; pelvic-fin rays I,5; segmented caudal-fin rays 17; upper procurrent caudal-fin rays 10-12; lower procurrent caudal-fin rays 10-12; total caudal-fin rays 37-41; gill rakers 5-6+17-19=22-25; elevated portion of first dorsal fin very elongate and filamentous (up to 1.4 in SL); caudal fin round; pelvic fins white; anterior body pale pink to white, dusky red posteriorly.

Remarks. Nemateleotris magnifica is widely distributed across the Indo-Pacific, occurring throughout the Indian Ocean (excluding the Red Sea), east to the French Polynesian Islands of the south-eastern Pacific Ocean. It is the only member of the genus to be found in the Hawaiian Islands, where it is rare. It occurs at depths between 6 to 70 m but is rarely observed in depths greater than 28 m, preferring shallower reefs instead.

Etymology. Named after its splendid appearance in life.

Nemateleotris decora Randall & Allen, 1973

Decorated Dartfish

Other names: Elegant Firefish; Purple Firefish; Purple Firegoby

(Figs. 2B, D, F, 8E, F, 9C, 10B1-B2, 11; Table 2)

Nemateleotris decora Randall & Allen, 1973: 361, fig. 5 (holotype BPBM 9533, Augulupelu Reef, Palau); Fourmanoir & Laboute, 1976: 142 (checklist; New Caledonia); Masuda et al., 1984: 245 (checklist; Japanese archipelago); Myers, 1988 (checklist; Marianas Islands); Myers, 1989: pl. 118B (field guide, aquarium photograph of specimen from Micronesia); Kuiter & Debelius, 1994: 267 (field guide, underwater photograph from Southeast Asia). Randall et al., 1997: 415 (field guide, Great Barrier Reef & Coral Sea); Myers, 1999: pl. 164F (field guide, underwater photograph from Micronesia); Allen et al., 2003: 282 (field guide; underwater photograph); Randall, 2005: 564 (field guide, underwater photograph from Halmahera); Randall et al., 2005 (checklist; Marshall Islands); Allen et al., 2007: 222 (underwater photograph from Christmas Island); Fricke et al., 2009 (checklist; Réunion Island); Fricke et al., 2011b: fig. 463 (checklist; Vanuatu); Fricke et al., 2011a (checklist; New Caledonia); Allen & Erdmann, 2012: vol. 3, 993 (underwater photographs from Papua New Guinea and Andaman Islands); Randall & Connell, 2013: fig. 4 (underwater photograph from Kwajalein Atoll, Marshall Islands); Randall & Connell, 2013: figs. 5–8 (photograph of holotype and underwater photographs from Halmahera, Raja Ampat, and Bali); Allen et al., 2015: 286 (field guide, underwater photograph); Rosenstein, 2019: 271 (field guide; underwater photograph from Fiji).

Nemateleotris exquisita Randall & Connell, 2013: 25 (type locality: Mauritius); Tea et al., 2020a (checklist; Réunion Island).

Diagnosis. Dorsal-fin rays VI, I,27–33; anal-fin rays I,28–32; pectoral-fin rays 19–21; pelvic-fin rays I,5; segmented caudal-fin rays 17; upper procurrent caudal-fin rays 10–13; lower procurrent caudal-fin rays 10–12; total caudal-fin rays 37–42; gill rakers 5–6 + 14–18 = 19–24; caudal fin weakly emarginate, tips of upper and lower lobes sometimes pronounced; pelvic fins red-tipped in life; anterior body pale grey to yellowish in life, dusky purple posteriorly.

Remarks. Nemateleotris decora occurs throughout the Indian Ocean, including the Red Sea. In the western Pacific it occurs from the Ryukyu Islands south to the Great Barrier Reef, New Caledonia, and Melanesia. It also occurs in Palau (type locality) east to the Caroline Islands and the Marshall Islands (Randall et al., 2005). The Indian Ocean and Red Sea population was previously regarded as a separate species, *N. exquisita*. The synonymy and relationship of *N. exquisita* and *N. decora* is discussed below.

Etymology. From the Latin meaning elegant and beautiful.

Nemateleotris helfrichi Randall & Allen, 1973

Helfrich's Dartfish

Other names: Helfrich's Firefish

(Figs. 1, 2G, 4A-C, 5, 8A, C, 9A, 10C1-C2, 11; Table 2)

Nemateleotris helfrichi Randall & Allen, 1973: 355, fig. 4 (holotype BPBM 11595, Papeete Harbour, Tahiti, Society Islands [reproduced here in Fig. 4A]; paratypes from Takaroa, Tuamotu Archipelago, and Avera, Rurutu, Austral Islands, but

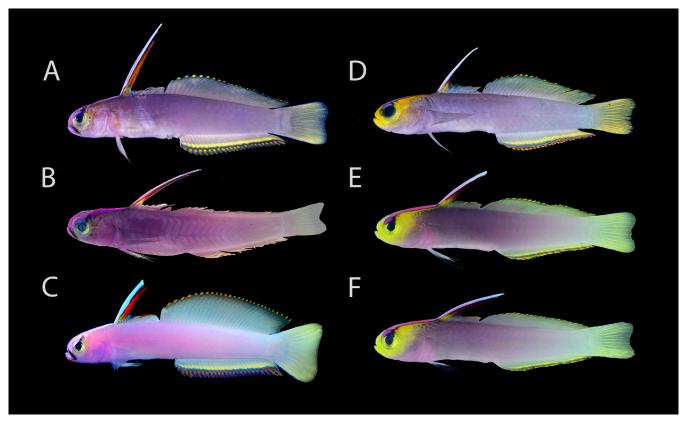


Fig. 4. A–C, *Nemateleotris helfrichi*; D–F, *N. lavandula*, new species. A, BPBM 11595, holotype, 43.3 mm SL, Tahiti, Society Islands; B, USNM 410981, 35.6 mm SL, Moorea, Society Islands, French Polynesia; C, ZRC 61811, 62.4 mm SL, aquarium specimen from the Cook Islands; D, BPBM 10153, paratype (also paratype of *N. helfrichi*), 30.9 mm SL, Rigili Islet, Enewetak Atoll, Marshall Islands; E–F, ZRC 62990, paratypes, 36.1 mm SL and 29.8 mm SL respectively, aquarium specimens from Kwajalein Atoll, Marshall Islands, Micronesia. Photographs by: A, C, D, J.E. Randall; B, J.T. Williams; E, F, H.H. Tan.

not those from Palau, Guam, or the Marshall Islands); Randall & Connell, 2013: fig. 3 (image of holotype, BPBM 11595).

Diagnosis. Dorsal-fin rays VI, I,30 (I,29–30); anal-fin rays I,26 (I,25–27); pectoral-fin rays 20 (20–21); pelvic-fin rays I,5; segmented caudal-fin rays 17; upper procurrent caudal-fin rays 9 (9–14); lower procurrent caudal-fin rays 12 (11–12); total caudal-fin rays 37–43; gill rakers 6 (5–7) + 17 (17–18) = 23 (22–24); elevated portion of first dorsal fin blue on anterior edge; median fins pale yellowish green, caudal fin without any markings, outermost edge of second dorsal and anal fin tipped with a yellow or orange spot, one in each interradial membrane space, spots sometimes coalescing; body lavender to lilac in life; pelvic fins black-tipped; dorsal edge of iris with a black mark at 1 o'clock position, sometimes continuing onto interorbital space as a short streak; maxilla black (in life and preservation); snout bright pink in life.

Remarks. Nemateleotris helfrichi is known from deep reefs in the south-eastern Pacific Ocean. In French Polynesia, it is reported from Tahiti (type location; Fig. 4A) and Moorea (USNM 410981; Fig. 4B) in the Society Islands, Takaroa in the Tuamotu Archipelago (paratype, BPBM 13326), Rurutu in the Austral Islands (paratype, BPBM 13095), Mohotane Island in the Marquesas Islands (USNM 439150), and the Gambier Islands. It is also reported from Rarotonga in the Cook Islands (Fig. 4C). It frequents seaward sand channels

and rubble pans in deep mesophotic reefs at depths between 25–100 m, where it occurs either singly or in pairs.

Etymology. The species is named after Dr Philip Helfrich, Associate Director of the Hawaii Institute of Marine Biology of the University of Hawaii and Director of the Enewetak Marine Biological Laboratory. He was among those who collected the first specimen of this species (Randall & Allen, 1973).

Nemateleotris lavandula, new species

Lavender-blushed Dartfish

(Figs. 2H, 4D–F, 5, 6, 7, 8B, C, 9B, 10E1–E2, 11; Tables 1, 2)

Nemateleotris helfrichi (in part, non Randall & Allen, 1973): Randall & Allen, 1973: 356, fig. 5 (part of description of N. helfrichi; underwater photograph from Palau); Myers, 1988 (checklist; Marianas Islands); Myers, 1989: pl. 118D (field guide, aquarium photograph of specimen from Micronesia); Rivaton et al., 1990: 41 (distribution record from New Caledonia); Myers, 1999: pl. 164G (field guide, underwater photograph from Micronesia); Rivaton & Bourret, 1999: 172 (checklist; New Caledonia); Laboute & Grandperrin, 2002: 420 (field guide, underwater photograph from New Caledonia); Larson, 2001: 3608 (identification guide to species of Microdesmidae); Allen et al., 2003: 282 (field guide, underwater photograph); Randall, 2005: 564 (field guide, underwater photograph from Marshall Islands); Kuiter & Debelius, 2006: 666 (underwater

photograph from Micronesia); Fricke et al., 2011b (checklist; Vanuatu); Fricke et al., 2011a (checklist; New Caledonia); Allen & Erdmann, 2012: vol. 3, 994 (underwater photograph from Fiji); Randall & Connell, 2013: fig. 4 (underwater photograph from Kwajalein Atoll, Marshall Islands); Allen et al., 2015: 286 (field guide, underwater photograph); Koeda et al., 2016: fig. 452 (checklist; underwater photograph from Yonaguni Island, Japan); Motomura & Harazaki, 2017: pl. 10G (checklist; Yakushima Island, southern Japan); Coleman et al., 2018 (checklist; Pohnpei, Federated States of Micronesia); Nakae et al., 2018 (checklist; Amami-oshima Island, Ryukyu Islands, Japan); Rosenstein, 2019: 272 (field guide; underwater photograph from Fiji).

Holotype. AMS I.16876-001 (also paratype of *N. helfrichi*), 45.6 mm SL, Augulupelu Reef, Palau Islands, 28 m, multiprong spear, W.A. Starck II, 4 March 1972.

Paratypes (n=12). AMS I.18411-017 (previously AMS I.18411-010), 46.9 mm SL, Suva Harbour, Fiji, 30–37 m, B. Carlson, B. Goldman, & P. Colin, 16 February 1974; BPBM 9527 (also paratype of N. helfrichi), 25.0 mm SL, Cocos Island, Guam, Mariana Islands, 27.5 m, rotenone, J.E. Randall, P. Helfrich, R.S. Jones, & H. Kami, 28 May 1968; BPBM 10153 (also paratype of N. helfrichi), 30.9 mm SL, outer reef slope of Rigili Islet, Eniwetok Atoll, Marshall Islands, 34 m, quinaldine, G.R. Allen, 30 August 1970 (Fig. 4D); BPBM 12661 (also paratype of *N. helfrichi*), 2, 33.5–35.5 mm SL, outer reef slope of Rigili Islet, Eniwetok Atoll, Marshall Islands, 43 m, rotenone, J.E. Randall, 7 April 1972; BPBM 19974, 45.4 mm SL, outer reef slope of Kwajalein Atoll, Marshall Islands, 50 m, rotenone, J.E. Randall, N.A. Bartlett, R. Hergenrother, & K. Burnett, 8 April 1976; BPBM 40810, 38.5 mm SL, Alet Islet, Puluwat Atoll, Caroline Islands, 10-25 m, quinaldine, R.L. Pyle & B.D. Greene, 11 April 2007; CAS-ICH 27591 (also paratype of N. helfrichi), 35.5 mm SL, Augulupelu Reef, Palau Islands, 28-61 m, rotenone, G.R. Allen & W.A. Starck II, 1 March 1972; KPM-NI 10136, 39.0 mm SL, Ototo-jima, Chichijima, Ogasawara Islands, Japan, 45 m, dip net, O. Morishita & Ehara, 28 August 1995; USNM 209306 (also paratype of *N*. helfrichi), 51.5 mm SL, Augulupelu Reef, Palau Islands, 37 m, multi-prong spear, W.A. Starck II, 10 January 1972; ZRC 62990, 2, 29.8–36.1 mm SL, aquarium specimens collected from Kwajalein Atoll, Marshall Islands (Fig. 4E-F).

Diagnosis. Nemateleotris lavandula is most similar to N. helfrichi, sharing with it the following combination of characters and live colouration details to the exclusion of all other Nemateleotris: caudal fin truncate to weakly emarginate; dorsoposterior ctenoid scales with fewer than 10 ctenii; elevated portion of first dorsal fin blue on anterior edge; median fins pale yellowish green, caudal fin without any markings, outermost edge of second dorsal and anal fin tipped with a yellow or orange spot, one in each interradial membrane space; body lavender to lilac in life; pelvic fins black-tipped; dorsal edge of iris with a black mark at 1 o'clock position, sometimes continuing onto interorbital space as a short streak. It is readily separated from N. helfrichi and all other congeners based on the following: maxilla unmarked (bright yellow in life, pale tan in preservation);

and snout, lower jaw, preopercle, and postorbital region bright yellow in life.

Description. Dorsal-fin rays VI–I,30 (I,29–30), all segmented rays unbranched; anal-fin rays I,27 (I,26–I,28), all segmented rays unbranched; pectoral-fin rays 20/19 (18-20), upper and lowermost 3-4 unbranched, all other rays branched (all pectoral-fin rays unbranched in BPBM 10153; BPBM 12661 [33.5 mm SL specimen]; and ZRC 62290 [29.8 mm SL specimen]); pelvic-fin rays I,5; segmented caudal-fin rays 17; upper procurrent caudal-fin rays 10 (10-14); lower procurrent caudal-fin rays 10 (10–14); total caudal-fin rays 37-45; no visible lateral line; longitudinal scale series 125 (125-140); gill rakers 6 + 17(17-18) = 23(23-24). Body elongate and compressed, depth 5.8 (5.0-6.2) in SL, width 1.6 (1.6–2.9) in depth; head 4.5 (3.8–5.1) in SL; snout 4.6 (4.6-7.8) in head; orbit diameter 2.4 (2.3-3.1) in head; bony interorbital space flat, least width 3.9 (3.5-5.1) in head; caudal peduncle short, deeper than long, least depth 1.8 (1.8–2.5) in head.

Mouth strongly oblique, forming at angle of about 50° to horizontal axis of body; maxilla reaching a vertical through centre of eye, upper jaw 3.4 (2.7–4.3) in head; upper jaw with an outer row of four to six, widely spaced, moderately large, incurved canines on each side, and a medial band of small villiform teeth that narrows posteriorly; lower jaw slightly protruding when mouth closed, with three enlarged recurved canines at corner of each side of jaw, more posterior tooth largest, a middle band composed of two to four rows of low villiform teeth narrowing to a single row posteriorly, and an inner pair of enlarged recurved canines at front corner of each side; no teeth on vomer or palatines; tongue truncate, set far back in mouth.

A low median fleshy ridge on top of head from interorbital space to origin of first dorsal fin; no opercular or preopercular spines; preopercular margin free only ventrally; upper end of gill opening at or slightly dorsal to level of middle of eye, the ventral end extending to below posterior margin of preopercle; anterior and posterior nasal pore separated by a distance about equal to half the pupil diameter; anterior nasal pore small, rounded and terminating in a short fleshy tube; posterior nasal pore larger, rounded, with little or no rim.

No visible lateral line on body; pores of cephalic lateral line system as described above in generic diagnosis; scales small, ctenoid posteriorly on body to about posterior third of dorsal fin, cycloid elsewhere, those anteriorly frequently embedded; no scales on head; no median predorsal scales, but embedded scales extend anteriorly on side nape to level of gill opening or slightly beyond; prepelvic area of thorax with embedded scales; anterior portion of isthmus naked; no scales on fins except for approximately basal half of caudal fin.

First dorsal fin elevated anteriorly, first spine longest, 3.6 (3.0–3.9) in SL, second and third spines only slightly shorter; fifth spine 2.0 (2.0–3.5) in head; sixth spine 3.2 (2.6–3.9) in head; spine of second dorsal fin 3.6 (2.7–4.0) in head;

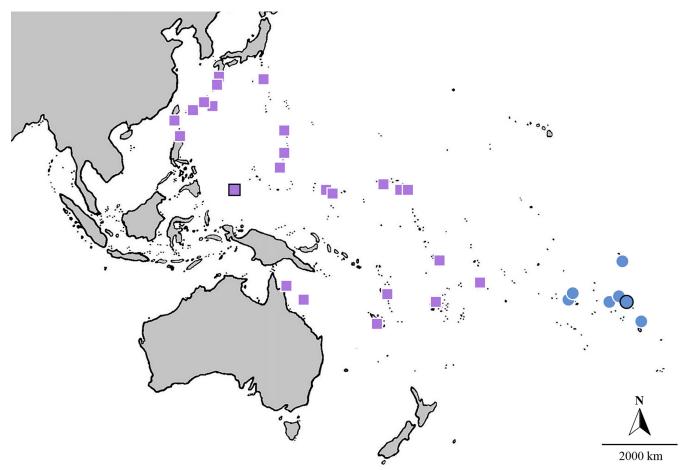


Fig. 5. Distribution records for selected species of *Nemateleotris* based on examined specimens and literature records: lavender squares, *Nemateleotris lavandula*, new species; blue circles, *Nemateleotris helfrichi*. Type localities represented by outlined symbols.



Fig. 6. Nemateleotris lavandula, new species, underwater photograph from Ogasawara, Japan, 35 m. Note juvenile *Cirrhilabrus lunatus* (left) and *Pycnochromis alleni* (above left in background). Photograph by: S. Kobayashi.

penultimate dorsal-fin ray usually longest, 1.3 (1.3–2.7) in head; caudal fin truncate or weakly emarginate, lobe tips rounded, fin length 4.5 (4.3–5.1) in SL; pectoral fins moderately pointed, middle rays longest, 4.7 (4.5–6.1) in SL; pelvic fins separate, their origin directly below pectoral-fin base, length 6.3 (5.1–7.4) in SL.

Colour in life. Based on colour photographs of specimens when freshly dead, and live individuals in the field and aquaria (Figs. 4D–F, 6, 7, 8B, C, 9B, 10E1, 11): snout,



Fig. 7. Nemateleotris lavandula, new species, underwater photograph from Siaes Tunnel, Palau. Photograph by: R. Spangler.

jaws, cheeks, preopercle, and postorbital region bright yellow, remainder of head lavender to lilac; body lavender to lilac, becoming increasingly pale posteriorly toward caudal peduncle; postorbital yellow marking continuing to anterior first dorsal fin as a sharp streak, becoming increasingly anastomosed and suffused away from the head; iris bright yellow, dorsal edge sharply capped in metallic purple with a black mark at 1 o'clock position, sometimes continuing onto interorbital space as a short streak; interorbital region with bright metallic pink triangle, its base originating from

Table 2. Summary of live colouration characters for species of Nemateleotris.

	Nemateleotris decora	Nemateleotris helfrichi	Nemateleotris lavandula, new species	Nemateleotris magnifica
Snout	Purple	Bright pink	Bright yellow	Pale yellow
Maxilla	Purple, lower corner with red or black mark	Marked with black colouration	Unmarked, bright yellow	Unmarked, pale yellow
Predorsal region	Purple triangle of colour, from interorbital space to base of first dorsal fin, coloured region indistinct from purple snout	Bright pink triangle of colour, from interorbital space to base of first dorsal fin, coloured region indistinct from bright pink snout	Bright pink triangle of colour, from interorbital space to base of first dorsal fin, coloured region distinct from bright yellow snout	Thin light blue stripe on predorsal ridge
Body colouration	Pale grey to yellowish anteriorly, becoming increasingly dusky purple posteriorly	Lavender to lilac, lightening posteriorly towards caudal fin	Lavender to lilac, lightening posteriorly towards caudal fin	Pale pink to white anteriorly, grading through bright orange red, becoming increasingly dusky red posteriorly
Pelvic fins	Red-tipped	Black-tipped	Black-tipped	Unmarked, white
First dorsal fin	Elevated portion red, enclosed by purple on all edges	Elevated portion bicoloured, blue on anterior edge, adjacent portion red to dusky red	Elevated portion bicoloured, blue on anterior edge, adjacent portion red to dusky red	Elevated portion white to pale yellow, red margin on anterior edge
Second dorsal and anal fins	Red, outer margin purple edged	Pale greenish yellow, outer margin with yellow spots, one in each interradial membrane space, spots sometimes coalescing	Pale greenish yellow, outer margin with yellow spots, one in each interradial membrane space, spots sometimes coalescing	Orange red, second dorsal fin with a green medial stripe, anal fin with green medial stripe on posterior third
Caudal fin	Truncate to weakly emarginate, purple centrally, upper and lower lobes red	Truncate to weakly emarginate, unmarked, pale greenish yellow	Truncate to weakly emarginate, unmarked, pale greenish yellow	Round, dusky orange red with a pair of oblique green stripes forming a chevron

middle of interorbital space, narrowing along entire length of predorsal space before terminating at origin of first dorsal fin; first two interspinous membrane spaces on elevated portion of first dorsal fin blue; adjacent interspinous membrane space between 2nd and 3rd first dorsal-fin spines red, sometimes dusky red; remaining portion of first dorsal fin translucent lavender, often edged in yellow or orange; second dorsal fin pale yellowish green, distalmost edge with a series of bright yellow or orange spots, one in each interradial membrane space, spots sometimes coalescing; anal fin similar to second dorsal fin, except edged submarginally in bright yellow and bright blue; distalmost edge of anal fin with a series of bright yellow or orange spots, one in each interradial membrane space, spots sometimes coalescing; caudal fin pale yellowish green, slightly translucent on outer edge; pelvic fins pale blue to white, black tipped distally; pectoral fins transparent.

Colour in preservation. (Fig. 10E2): similar to colour in life, except body now purplish grey (fading to tan over time); head and snout now pale tan; interorbital and predorsal triangle of colour now pale grey, bordered in black; first two interspinous membrane spaces on elevated portion of

first dorsal fin now white to pale grey; all black markings remain; median fins translucent hyaline.

Habitat and distribution. Nemateleotris lavandula is widespread across much of the western and central Pacific Ocean (Fig. 5). Its distribution follows the northwestern contours of the Pacific Plate, from Yakushima Island in southern Japan, throughout the Ryukyu and the Ogasawara Islands, and south to Taiwan and the northern Philippines, extending east across Micronesia, including the Caroline Islands, the Marshall Islands, and the Mariana Islands. In Melanesia, the species has been reported from Fiji, Vanuatu, and New Caledonia. It has also been reported from Samoa, American Samoa, Tonga, the Coral Sea, and Hicks Reef on the Great Barrier Reef. It frequents seaward sand channels and rubble pans adjacent to coral reefs at depths between 25–100 m.

Etymology. The species is named *lavandula*, after the genus of flowering plants which includes the ornamental herb lavender, in reference to its beautiful colouration in life. To be treated as a noun in apposition.



Fig. 8. Species of *Nemateleotris* and their putative hybrids. A, *N. helfrichi*, underwater photograph from Rarotonga, Cook Islands; B, *N. lavandula*, new species, underwater photograph from Siaes Tunnel, Palau; C, head profiles of *N. helfrichi* (left) and *N. lavandula*, new species, (right) showing difference in colouration of the head and maxilla; D, *N. magnifica*, underwater photograph from Bali; E–F, *N. decora*, showing variability in colouration of the anterior body, underwater photograph from Fiji and the Maldives (the latter = *N. exquisita* sensu Randall & Connell, 2013) respectively; G, putative *N. magnifica* × *N. decora*, underwater photograph from Izu Peninsula, Japan; H, putative *N. magnifica* × *N. lavandula*, new species, underwater photograph from Okinoerabu Island, Japan. Photographs by: A, P.Jaletzky; B, R. Spangler; C, Y.K. Tea; D, V. Chalias; E, J. Heard; F, M. Harada; G, Y. Yamada; H, K. Uehara.



Fig. 9. Frontal head profiles of selected species of *Nemateleotris*. A, *N. helfrichi*, aquarium specimen from Cook Islands; B, *N. lavandula*, new species, ZRC 62990, paratype in life, specimen from Kwajalein Atoll, Marshall Islands, Micronesia; C, *N. decora*, underwater photograph from Bali, Indonesia; D, *N. magnifica*, underwater photograph from Bali, Indonesia. Photographs by: A, B-box Aquarium, Japan; B, H.H. Tan; C–D, V. Chalias.

Comparisons. Nemateleotris lavandula most closely resembles N. helfrichi, sharing similarities in meristics, morphometrics, and live colouration. Molecular analysis of mitochondrial COI reveals a difference of 1% between both species (uncorrected pairwise distance). This value is lower than the usual threshold of 2-6% between congeneric sister species of coral reef fishes, but higher than most intraspecific variation within species (Steinke et al., 2009). In any case, it is not uncommon for many groups of coral reef fishes to exhibit little or no mitochondrial differentiation, particularly in recently diverged groups where incomplete lineage sorting has occurred, or between groups that have undergone recent introgression. Both species are united in having the following combination of live colouration details not found in other species of Nemateleotris: elevated portion of first dorsal fin blue on anterior edge; median fins pale yellowish green, caudal fin without any markings, outermost edge of second dorsal and anal fin tipped with a yellow or orange spot, one in each interradial membrane space, spots sometimes coalescing; body lavender to lilac in life; pelvic fins black-tipped; and dorsal edge of iris with a black mark at 1 o'clock position, sometimes continuing onto interorbital space as a short streak.

Nemateleotris lavandula differs from N. helfrichi primarily in lacking a black mark on its maxilla (in life and preservation; Fig. 8C) and in having a bright yellow head and snout (vs pink snout and head only weakly suffused with yellow in N. helfrichi; Fig. 9A–B). It further differs from N. helfrichi in having a wider interorbital width (5.1–6.0% SL vs 2.2–3.4% SL) and a larger orbit (8.2–9.4% SL vs 6.6–7.9% SL). It differs from N. decora in having fewer anal-fin rays (26–28 vs 28–32) and in having the posterior most dorsal- and anal-fin rays usually unbranched (versus usually branched in N. decora), and from N. magnifica in having a shorter first dorsal-fin spine (more than 2.5 in SL and non-filamentous vs up to 1.4 in SL and filamentous), a different caudal fin shape (truncate to weakly emarginate vs round), and in

having smaller ctenoid scales on the dorsoposterior body with fewer ctenii (10 or less vs more than 15). Differences in live colouration for all species of *Nemateleotris* are summarised in Figs. 8, 9, 10, and Table 2.

Status of Nemateleotris exquisita. Randall & Connell (2013) described N. exquisita on the basis of 12 specimens (erroneously listed as nine and eleven specimens on separate occasions in the same publication) collected from various localities in the Indian Ocean, including Mauritius (type locality), South Africa, and the Red Sea. They distinguished their new species from N. decora in having: a more slender body (body depth 5.7-6.3 in SL vs 4.9-5.7 in SL); a longer snout (4.0-4.7 in head vs 5.0-7.5 in head); an apparently smaller eye (proportional measurements not given); an apparently shorter first-dorsal fin spine (proportional measurements not given); and a greater maximum size (66.0 mm SL vs 52.5 mm SL; the latter based on examination of 15 specimens of N. decora). They also distinguish N. exquisita from N. decora in having the body more yellow anteriorly (yellow extending beyond the anal-fin origin vs body whitish pale grey anteriorly to not beyond anal-fin). Their comparative data for *N. decora* used in the description of N. exquisita were taken from the original description, based on eleven specimens in the type series.

We examined seven paratypes of *N. exquisita* from the western Indian Ocean, as well as an additional five specimens and one paratype of *N. decora* from the Pacific Ocean. Based on revised comparative data collected, we find overlapping morphometric values for the following characters used in distinguishing *N. exquisita* from *N. decora*: body depth (5.1–6.3 in SL vs 5.7–6.1 in SL); and snout length (3.7–5.4 in head vs 4.0–7.5 in head). One of our specimens of *N. decora* (AMS I.17500-017) had a standard length of 57.4 mm. Additionally, we note that both *N. decora* and *N. exquisita* typically display a wide range of variation in their anterior body colouration, with *N. decora* sometimes appearing

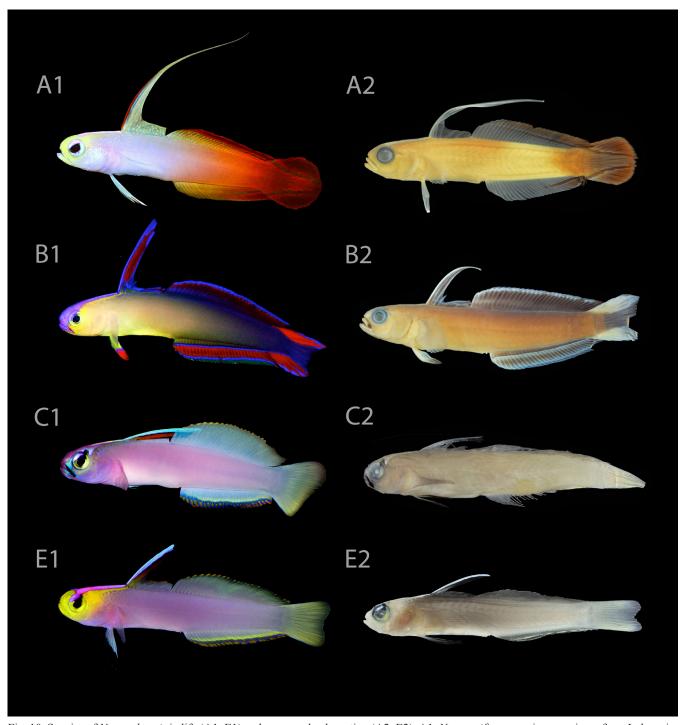


Fig. 10. Species of *Nemateleotris* in life (A1–E1) and preserved colouration (A2–E2). A1, *N. magnifica*, aquarium specimen from Indonesia, specimen not retained; A2, *N. magnifica*, ZRC 47157, 36.6 mm SL, Bali, Indonesia; B1, *N. decora*, aquarium specimen from Indonesia, specimen not retained; B2, *N. decora*, ZRC 47158, 51.3 mm SL, Bali, Indonesia; C1, *N. helfrichi*, aquarium specimen from the Cook Islands, specimen not retained; C2, *N. helfrichi*, ZRC 61811, 62.4 mm SL, Cook Islands; E1–E2, *N. lavandula*, new species, ZRC 62990, paratype, 38.9 mm SL, aquarium specimen from Kwajalein Atoll, Marshall Islands, Micronesia. Photographs by: A1–B1, E2, Y.K. Tea, C1, S.W. Michael; E1, H.H. Tan; A2–C2, K. Lim.

exquisita-like in having a yellower anterior body, (see Fig. 10B1; KPM-NR 49173; Fricke et al., 2011b: fig. 463), and *N. exquisita* sometimes appearing *decora*-like with reduced yellow pigmentation (see Tea et al., 2020a: fig. 20).

The exact distribution of *N. exquisita* and *N. decora* appears to be contentious. In the description of *N. exquisita*, the authors report its occurrence in the Indian Ocean, from South

Africa, Mauritius, the Red Sea, and east to the Andaman Islands. However, they commented on the possibility of a putative specimen of N. $exquisita \times N$. decora photographed in the Maldives (based on a paler intermediate anterior body colouration), stating: "...N. decora presently known westward only to Sulawesi and Bali, and N. exquisita east to the Thai coast of the Andaman Sea, one might expect hybridisation could occur at some intermediate sites such as

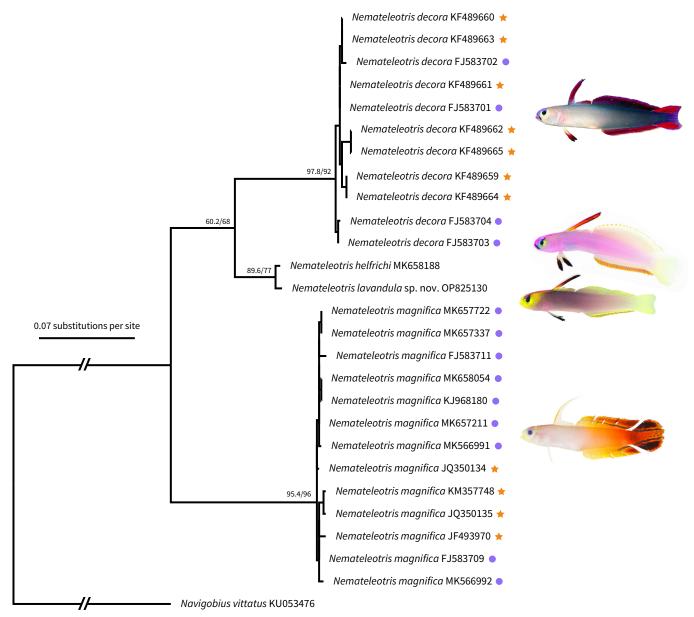


Fig. 11. Maximum-likelihood phylogenetic relationships of *Nemateleotris* inferred using mitochondrial COI. Support values at nodes correspond to SH-aLRT and UFBS support values respectively. Purple circles = Pacific Ocean; orange stars = Indian Ocean. See Appendix for detailed localities. Photographs from top to bottom by: T. Suzuki, Y.K. Tea, H.H. Tan, and J.T. Williams, respectively.

Sumatra. Because of its deep-reef habitat and being difficult to collect, we do not know the definitive distribution of *N. exquisita*. It might range to Sri Lanka like such species as *Chaetodon andamanensis* and *Halichoeres timorensis* and stray to the Maldives." The last two sentences appear to be erroneous, and presumably the authors meant the Pacific Ocean *N. decora* as potentially straying as far west as Sri Lanka and the Maldives (not the Indian Ocean *N. exquisita*) where it may hybridise with *N. exquisita* (*N. decora* has been reported and photographed in Bali, Sumatra, and Christmas Island, these presumably representing the westernmost limit of its Pacific distribution).

Lastly, the authors compared mitochondrial COI barcodes for *N. exquisita* and *N. decora*, finding no differences in sequence data. They alluded to the possibility of incomplete lineage sorting or introgression being a possible explanation for the lack of sequence variability. While this phenomenon

is indeed common for various groups of coral reef fishes (Victor & Randall, 2014; Tea et al., 2016; Victor, 2016; Tea et al., 2020b), the lack of at least one unequivocally robust line of evidence justifying the distinction of *N. exquisita* and *N. decora* is concerning. Until shown otherwise, we recognise *N. exquisita* as a synonym of *N. decora*.

Biogeography and phylogenetic relationships. The biogeography of *Nemateleotris* is rather unusual, comprising only four species, but with three that are widely distributed and one endemic to several island groups. Springer (1982) made note of this in his contributions to Pacific Plate biogeography, further adding that while it was not possible to determine the relationships among *Nemateleotris*, *N. decora* and *N. helfrichi* sensu lato (= *N. helfrichi* + *N. lavandula*) showed greater morphological similarities to each other than either does to *N. magnifica*. While the evidence was slight, he proposed the possibility of an Indo-West Pacific

species, in this case *N. decora*, being sister to the Pacific Plate endemic *N. helfrichi* s.l., with both species having undergone slight dispersal since their divergence leading to sympatry of both species.

Indeed, sympatry for at least three species of *Nemateleotris*, namely *N. decora*, *N. lavandula*, and *N. magnifica*, occurs in several parts of the western Pacific, particularly along the western margins of the Pacific Plate. Except for *N. magnifica*, which occurs from depths between 6–70 m (but not usually below 28 m), the remaining species of *Nemateleotris* primarily occur in mesophotic coral reefs at depths between 25–100 m, with *N. helfrichi* and *N. lavandula* rarely straying above 30 m. Putative hybrids identified based on intermediate colouration have been reported between *N. magnifica* and *N. decora* (Fig. 8G), and between *N. magnifica* and *N. lavandula* (Fig. 8H), although to the best of our knowledge no specimens have been made available for study. No hybrids have been reported for *N. helfrichi*, which shares its distribution range with *N. magnifica*.

Results from our molecular phylogenetic analyses support Springer's proposed relationships, with *N. decora* recovered as sister to a lineage comprising N. helfrichi and N. lavandula (= N. helfrichi s.l. in Springer, 1982) (Fig. 11). We note, however, that both UFBS and SH-aLRT support values at this node were relatively low, and owing to the scarcity of N. helfrichi and N. lavandula specimens in museum collections, only one of each species were represented in our molecular dataset. Nemateleotris magnifica was recovered as the sister lineage to all other *Nemateleotris*. Despite the large geographical distributions of N. magnifica and N. decora, intraspecific variation for both species were generally lower than 1%, even for populations occurring in separate ocean basins (i.e., Pacific and Indian Ocean populations). While some individuals showed intraspecific variation greater than that between closely related sister species (such as N. helfrichi and N. lavandula), they were not correlated with geographically distinct populations. In particular, N. decora from Pacific and Indian Ocean localities do not reflect reciprocally monophyletic groups, further justifying the synonymy of N. exquisita within N. decora. We however emphasise that the relationships inferred in this study are based only on mitochondrial COI, and a more robust dataset with more markers and increased sampling, especially for N. helfrichi and N. lavandula, is likely necessary to adequately assess the relationships between these widespread populations.

Identity of Zagadkogobius ourlazon Prokofiev. Prokofiev (2017) described Zagadkogobius ourlazon on the basis of the 18 mm SL holotype from south of the Anambas Islands in the Riau Archipelago, South China Sea. The specimen was trawled from a depth of 73 m. He placed his new species within the Ptereleotrinae based on it having a laterally compressed body, a lateral positioning of the eyes, five rays in the first dorsal fin, and unbranched rays in the second dorsal and anal fins. The presence of "five rays" (presumably V spines) in the first dorsal fin is unusual, as all seven of the recognised ptereleotrine genera (and indeed most

gobiids) have six spines in the first dorsal fin. Additionally, Zagadkogobius is diagnosed in having very large scales, numbering 25 in lateral series (cycloid anteriorly, ctenoid midposteriorly), a filamentous first dorsal fin, a lanceolate caudal fin, and a coronal commissure connecting the median interorbital pore to the left and right oculoscapular canals. The holotype also possesses large scale pockets on the cheeks, upper portion of the opercle, and head. While some of these aforementioned characters occur within the pterelectrines, the combination of them, as well as the presence of large scales on the body, cheeks, and head makes its identity as a species of ptereleotrine unlikely. These characters are more suggestive of species of *Tryssogobius* instead, which can appear pterelectrine like due to having laterally compressed bodies, as well as a filamentous first dorsal fin and lanceolate caudal fin in some species. Notably, *Tryssogobius* is distinct among gobiids in having large scales on the cheek, opercle, and head, and in having a lateral series of 24–26 large scales (Larson & Hoese, 2001). One species of Tryssogobius, T. quinquespinus, is known to possess five dorsal-fin spines (Randall, 2006), an unusual condition for gobiids, and here shared with Zagadkogobius. Since we were unable to examine the holotype of Z. ourlazon, it is neither possible to confirm its validity nor placement within the Gobiidae (at the generic or phylogenetic level). We do however consider the exclusion of Zagadkogobius as a member of the Ptereleotrinae justified, at least based on consideration of the aforementioned characters.

Material examined. Nemateleotris decora (n=7): AMS I.16877-007, paratype, 37.1 mm SL, Osprey Reef, Coral Sea; AMS I.17500-017, 57.4 mm SL, Tanavulu Point, Florida Island, Solomon Islands; AMS I.17530-004, 50.9 mm SL, Alite Reef, off Malaita, Solomon Islands; AMS I.17504-007, 45.7 mm SL, Cape Tawui, off Rabaul, New Britain; AMS I.45300-166, 33.5 mm SL, cleared and stained specimen from the aquarium trade; CAS-ICH 47426, (specimen almost broken in half, approximately 43.2 mm SL), Tabuaeran Atoll, Line Islands, Kiribati; ZRC 47158, 51.3 mm SL, Bali, Indonesia; Nemateleotris exquisita (n=7): BPBM 21528, paratype, 50.6 mm SL, Ras Muhammed, Red Sea; BPBM 22544, paratype, 61.3 mm SL, west coast off Flic en Flac, Mauritius; CAS-ICH 234071, paratype, 53.0 mm SL, off Flic en Flac, Mauritius; SAIAB 185925, paratype, 46.5 mm SL, Sodwana Bay, Kwazulu-Natal, South Africa; SAIAB 186384, 3, paratypes, 55.0-63.1 mm SL, Sodwana Bay, Kwazulu-Natal, South Africa; Nemateleotris helfrichi (n=5): BPBM 11595, holotype, 43.3 mm SL, Tahiti, Society Islands; BPBM 11598, paratype, 49 mm SL, same data as holotype; BPBM 13095, paratype, 32.9 mm SL, Rurutu, Austral Islands; BPBM 13326, paratype, 40.8 mm SL, Takaroa, Taumotu Archipelago; ZRC 61811, 62.4 mm SL, Cook Islands; Nemateleotris magnifica (n=8): AMS I.22583-035, 28.9 mm SL, Escape Reef, Australia; AMS I.25110-035, 46.9 mm SL, Osprey Reef, Coral Sea; AMS I.25112-048, 2, 38.2–40.3 mm SL, Osprey Reef, Coral Sea; AMS I.39012-014, 35.6 mm SL, Santa Cruz Island, Solomon Islands; AMS I.46486-050, 35.0 mm SL, Morane, Tuamotu Archipelago, French Polynesia; AMS I.45300-327, 40.5 mm SL, cleared and stained specimen from the aquarium trade;

ZRC 47157, 36.6 mm SL, Bali, Indonesia.

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APPENDIX

GenBank accession numbers and locality records for *Navigobius* and *Nemateleotris* used in maximum-likelihood phylogenetic analyses of mitochondrial COI.

Species	Location	Accession number
Navigobius vittatus	Brunei	KU053476
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489663
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489661
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489662
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489665
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489659
Nemateleotris decora	Sodwana Bay, Kwazulu-Natal, South Africa	KF489664
Nemateleotris decora	Manila, Philippines	FJ583702
Nemateleotris decora	Manila, Philippines	FJ583701
Nemateleotris decora	Manila, Philippines	FJ583704
Nemateleotris decora	Manila, Philippines	FJ583703
Nemateleotris helfrichi	Moorea, French Polynesia	MK658188
Nemateleotris lavandula	Kwajalein Atoll, Marshall Islands	OP825130
Nemateleotris magnifica	Gambier Islands, Tuamotu Archipelago, French Polynesia	MK657722
Nemateleotris magnifica	Austral Islands, French Polynesia	MK657337
Nemateleotris magnifica	Marquesas	MK566991
Nemateleotris magnifica	Marquesas	MK657211
Nemateleotris magnifica	Marquesas	MK658054
Nemateleotris magnifica	Moorea	KJ968180
Nemateleotris magnifica	Marquesas	MK566992
Nemateleotris magnifica	Mozambique	JF493970
Nemateleotris magnifica	Manila, Philippines	FJ583711
Nemateleotris magnifica	Réunion Island	JQ350134
Nemateleotris magnifica	Andaman Sea	KM357748
Nemateleotris magnifica	Nosy Be, Madagascar	JQ350135
Nemateleotris magnifica	Vietnam	FJ83709