# Evaluating the phylogenetic position of the goby genus *Kelloggella* (Teleostei: Gobiidae), with notes on osteology of the genus and description of a new species from Niue in the South Central Pacific Ocean

LUKE TORNABENE[1,2*], BRIAN DEIS[3] and MARK V. ERDMANN[4,5]

[1]*School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boast Street, Seattle, WA 98105, USA*

[2]*Burke Museum of Natural History and Culture, University of Washington, 1413 NE 45th Street, Seattle, WA, USA*

[3]*Department of Biology, University of Hawaii at Manoa, 2538 McCarthy Mall, Edmondson Hall 216, Honolulu, HI 96822, USA*

[4]*Conservation International Indonesia Marine Program, Jl. Muwardi No. 17, Renon, Denpasar, Bali 80235, Indonesia*

[5]*California Academy of Sciences, 55 Music Concourse Drive, Golden State Park, San Francisco, CA 94118, USA*

*Kelloggella* is a widely distributed but poorly studied genus of goby (family Gobiidae) that occurs in tide pool and reef flat habitats across the tropical Indo-Pacific region. The phylogenetic position of this genus has never been formally investigated, and its osteology has not been described in detail. The discovery of a new species of *Kelloggella* from the island of Nuie, coupled with the recent availability of fresh specimens, tissues and photographs of *Kelloggella* spp. from Hawaii and Easter Island, has led to the current study. Here, we describe the new species as ***Kelloggella avaiki* sp. nov.** and investigate the phylogenetic position of *Kelloggella* within Gobiidae. Molecular phylogenetic data from nuclear and mitochondrial genes suggest a close relationship between *Kelloggella* and *Gobiodon*, *Eviota* and *Bryaninops*, and possibly *Kraemeria*. A comparative osteological investigation identified few potentially informative characters, including a reduced ventral branch of the posttemporal, epioccipitals meeting along the dorsal midline posterior to the supraoccipital, hypurals 1–2 fused to hypurals 3–4 and the urostyle and the presence of tricuspid teeth. However, these characters occur elsewhere across gobies, and at best only offer weak support for the relationships hypothesized by the molecular tree. Lastly, we provide colour photographs of five species of *Kelloggella* and discuss some of the challenges in delimiting species.

ADDITIONAL KEYWORDS: *Eviota* – Gobiinae –*Gobiodon* – Gobioidei – *Kraemeria* – molecular phylogeny – morphology – systematics.

## INTRODUCTION

The goby genus *Kelloggella* Jordan & Seale, 1905 previously contained five species: *K. cardinalis* Jordan & Seale, 1906, *K. disalvoi* Randall, 2009, *K. oligolepis* (Jenkins, 1903), *K. quindecimfasciata* (Fowler, 1946) and *K. tricuspidata* (Herre, 1935). Hoese (1975) described *K. centralis*, which was later synonymized with *K. quindecimfasciata* by Winterbottom and Emery (1986). Hoese (1975) also considered *K. quindecimfasciata* to be a synonym of *K. oligolepis*, but Sawada (1977) subsequently considered both to be valid species. All species of *Kelloggella* are small, even among gobies (typically <30 mm total length), and occur exclusively

*Corresponding author: E-mail: Luke.Tornabene@gmail.com

in tide pools and high-energy exposed reef flats that are rarely sampled. These factors, coupled with their cryptic behaviour, contribute to specimens being rare in collections. The genus is widely distributed from the Chagos Archipelago in the west to Easter Island in the east, although records are sporadic throughout this range. Larson (1983) studied the ecology and behaviour of *K. cardinalis* in Guam and noted that even in suitable habitat, the species was not common and had a patchy distribution around the island. Similar to many other tide pool inhabitants, *K. cardinalis* can tolerate extreme fluctuations in salinity and temperature. In Guam, individuals were found in pools with salinities as low as 1.1 ppt and as high as 42 ppt, and with temperatures reaching 39 °C (Larson, 1983).

The phylogenetic position of *Kelloggella* within Gobiidae is unclear. Both Gosline (1955) and Hoese (1975) studied the osteology of *Kelloggella* but neither made specific hypotheses regarding phylogenetic affinities. In a survey of gobioid vertebral osteology, Birdsong, Murdy & Pezold (1988) placed *Kelloggella* in a group by itself based on the unique vertebral count of 11 precaudal and 15 caudal vertebrae, coupled with relatively uncommon presence of a single anal-fin pterygiophore (vs. two or more) inserted before the caudal vertebrae. Thacker & Roje (2011) analysed phylogenetic relationships with Gobiidae using sequence data from mitochondrial and nuclear genes, but their analysis did not include *Kelloggella*. Nonetheless, in an attempt to provisionally classify all genera in Gobiidae, they tentatively placed *Kelloggella* in the 'coral goby' group, which was represented by *Eviota*, *Gobiodon* and *Bryaninops* in their molecular tree (Thacker & Roje, 2011). That provisional decision was based on the diminutive size of *Kelloggella* and an alleged superficial similarity to *Eviota*, although no specifics were given regarding the morphological similarities. The monophyly of the 'coral goby' group of Thacker & Roje (2011) has been supported by three subsequent molecular phylogenies (Agorreta & Rüber, 2012; Agorreta *et al*., 2013; Tornabene, Chen & Pezold, 2013), but all studies to date have had very limited taxon sampling within the 'coral goby' group and none included *Kelloggella*.

Comprehensive and detailed taxonomic descriptions often provide information that is invaluable for future comparative morphological/phylogenetic studies, as well as those on the ecology, biogeography and macroevolution. Recently, material has become available that facilitates such a study on *Kelloggella*. During a recent trip to island nation of Nuie in the Central Pacific Ocean, a series of specimens and live photographs of an undescribed species of *Kelloggella* were obtained while sampling tidepools in search of specimens of *Eviota*. In addition, we obtained tissue samples from a new series of specimens of *K. oligolepis* from Hawaii, and from a series *K. disalvoi* from Easter Island, which now enable us to infer the phylogenetic position of the genus using molecular data. Collectively, we take advantage of these new sources of material to provide a detailed description of the new species, *Kelloggella avaiki* sp. nov. We expand on the published information on the osteology of *Kelloggella* through observations of cleared and stained specimens of *K. oligolepis* and the new species and briefly compare their morphology with other gobiids including those hypothesized to be close relatives based on the molecular phylogeny.

## MATERIAL AND METHODS

Measurements were taken with digital callipers to the nearest 0.1 mm. All proportional lengths are given in per cent standard length (SL) unless otherwise noted. The cleared and stained specimens were prepared using the protocol from Dingerkus & Uhler (1977). Dorsal pterygiophore formula follows terminology of Birdsong *et al*. (1988). We use roman numerals to distinguish the unsegmented spines of the dorsal, anal and pelvic fins, from the segmented soft rays, which are represented by Arabic numerals. Counts are given for the holotype first, followed by the range for the paratypes in parentheses if different. Measurements are given for the holotype first, followed by the range of the entire type series in parentheses. Head pore terminology follows Akihito *et al*. 1988. Institutional acronyms were as follows: USNM: National Museum of Natural History, Smithsonian Institution; UW: University of Washington Fish Collection.

We successfully sequenced four of the five genes from Agorreta *et al*. (2013) (*cytb*, *sreb2*, *zic1* and *rag1*) for a specimen of *K. oligolepis* from Hawaii (USNM 440506) and three genes (*sreb2*, *zic1* and *rag1*) for a specimen of *K. disalvoi* from Easter Island (UW 157113). Primers and PCR conditions are identical to those from Agorreta *et al*. (2013). We attempted to sequence these genes from a tissue sample of the new species but were unsuccessful. In addition to our newly generated sequences, we also incorporated *rag1*, *sreb2* and *zic1* sequences for *Kraemeria bryani*, which were downloaded from GenBank (sequences generated by Thacker & Roje, 2011). We aligned these sequences with the total five-gene data set from Agorreta *et al*. (2013) and analysed them using Bayesian phylogenetic inference in the program Mr. Bayes ver. 3.2 (Ronquist *et al*., 2012). Partitioning scheme and substitution model choice followed that of Agorreta *et al*. (2013). The analysis consisted of two parallel Markov Chain Monte Carlo runs, each with four chains, run for 20 000 000 generations. Convergence of parallel runs was assessed by comparing plots of log-likelihood vs. generation in Tracer ver. 1.5 (Rambaut & Drummond, 2007), evaluating the standard deviation of split frequency statistic and the Potential

Scale Reduction Factor statistic in MrBayes, and by visually inspecting the resulting topologies of maximum clade credibility (MCC) trees from each run. We also verified that estimated sample sizes (ESS) for each parameter from each run were greater than 200 using Tracer.

We ran the molecular analysis with four different taxon sets. The first analysis was our full data set, 225 taxa, including those from Agorreta *et al.* (2013), the two species of *Kelloggella* and the additional *Kraemeria* species (*Kr. bryani*). The second analysis excluded both species of *Kraemeria* (*Kr. bryani* and *Kr. cunicularia*), as this genus was reported to be a 'rogue taxon' that decreased support values across the entire phylogeny whenever it was included (Agorreta *et al.*, 2013). The third analysis included the full data set with the exception of two species of *Schindleria*, as this genus is also on the list of potential 'rogue taxon' from Agorreta *et al.* (2013), and their phylogenetic position has proven to be difficult to resolve using molecular data (Thacker, 2003, 2009; Agorreta *et al.*, 2013). The final analysis excluded both *Kraemeria* and *Schindleria*. See Agorreta *et al.* (2013) for details on the deposition of voucher specimens from that study, and Thacker & Roje (2011) for details on the voucher of *Kr. bryani*.

The terminology for gobioid classification used in comparative osteology section largely follows that of Thacker *et al.* (2015), that is, we recognize Oxudercidae (*sensu* Nelson, Grande & Wilson, 2016) and Gobiidae as distinct families. Note that Oxudercidae *sensu* Nelson *et al.* (2016) is equivalent to Gobionellidae of Thacker *et al.* (2009) and subsequent references to that family thereafter (e.g. Thacker & Roje, 2011; Thacker, 2013; Thacker *et al.*, 2015). Nelson *et al.* (2016) recognized that Gobionellidae was a junior synonym of the older Oxudercidae, and this classification has subsequently been adopted by several authors (Betancur *et al.*, 2017; Gierl & Reichenbacher, 2017; Reichenbacher *et al.*, 2017).

# RESULTS

SYSTEMATICS

### *KELLOGGELLA AVAIKI* SP. NOV.

(FIGS 1–6, 9, 10, 12A, 14, 15A)

*Common name:* Star-spangled Goby.

## Type material

*Holotype:* USNM 440501, 20 mm SL, female, Niue, tidepools near Avaiki Hotel, S 18° 59.853′, W 169° 54.630′, MVE-15-036, 25 August 2016, Mark V. Erdmann.

*Paratypes:* All collected with holotype: USNM 440502, 19–20 mm SL, one female and one male, cleared and stained; USNM 440503, 19 mm SL, male, fixed in 95% ethanol; USNM 440504, 15–21 mm SL, six specimens; UW 156489, 19 mm SL, male.

## Generic placement

The following characters, many of which were listed by Hoese (1975), are shared by all species of *Kelloggella* including the new species: tricuspid teeth present in both jaws, the outer row of teeth enlarged in both jaws with lateral cusps reduced, inner row of teeth with three relatively even cusps; body elongate and laterally compressed (body depth five to seven times in SL); head strongly compressed, interorbital region positioned above laterally placed eyes; anterior slope of head distinctly convex, snout profile evenly rounded in lateral view; scales absent; head pores either absent or present only as small pits or as highly reduced pores barely visible in soft flesh of head; first dorsal VI; second dorsal I, 9–12; anal fin I, 7–8 (rarely 9); first dorsal fin low, spines equal to or only slightly longer than rays of second dorsal; anal spine positioned below third or fourth ray of second dorsal; 26 vertebrae (11 precaudal + 15 caudal); first dorsal pterygiophore insertion pattern 3-22110; a single anal-fin pterygiophore inserted anterior to first haemal spine; pectoral rays 12–15; gill opening narrow (ending just below pectoral fin base); mouth slightly oblique, extending posteriorly to beneath middle of eye, anteriorly to directly under anterior tip of snout; pelvic disc short, not extending beyond one-half distance to anus; pelvic I, 5, rays fused into a cup-shaped disc with well-developed anterior fraenum uniting spines; sensory papillae system poorly developed, a few widely spaced papillae around dorsal, posterior and ventral margin of eye, one row of widely spaced papillae extending from posterior of eye to posterior margin of operculum; nares with raised rim, anterior nare longer, sometimes as a tube.

## Diagnosis

Body lacking vertical bars; in life, body and fins with small bright iridescent blue spots and speckles on a dark greyish-blue to black background (Fig. 1); jaws and tip of snout light yellow; second dorsal-fin rays I, 11–13; anal-fin rays typically I, 8; pectoral-fin rays 14.

## Description

Body elongate and strongly laterally compressed; profile of snout and front of head strongly convex, with a distinct layer of soft, squishy and gelatinous tissue over front of head (Fig. 2); anterior nare, an elongate tube positioned immediately above upper jaw, posterior nare with a raised rim, positioned near anterior margin of orbit; first dorsal fin VI, no filamentous

**Figure 1.** *Kelloggella avaiki* **sp. nov.**, live, photo by Mark V. Erdmann.



2 mm
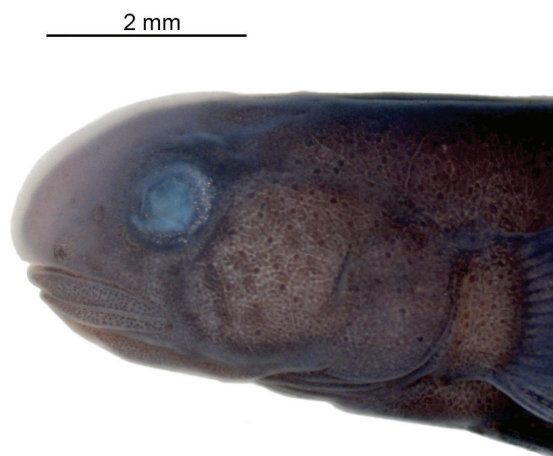
**Figure 2.** *Kelloggella avaiki* **sp. nov.**, dorsal profile of head showing layer of gelatinous tissue. USNM 440504, male (one of the six specimens), 19.8 mm SL.

spines, first two spines longest, subsequent spines consecutively shorter; second dorsal fin I, 12 (11–13); anal fin I, 8 (8–9); all dorsal and anal soft rays branched, the last to base; pectoral-fin rays 14, all branched, except uppermost and or lowermost which are sometimes unbranched; pectoral fin short, extending posteriorly to beneath posterior margin of first dorsal fin; pelvic-fin rays I, 5, fins completely united to form a round disc with a well-developed anterior fraenum, rays extending posteriorly to approximately half the distance to origin of anal fin; segmented caudal rays 16 (15–17); branched caudal rays 12 (12–14); caudal fin broadly rounded; upper and lower procurrent caudal rays 6 plus a rudiment (counted from cleared and stained specimens); gill opening directly preceding and equal in length to pectoral-fin base; gill rakers 1 + 4 (count from largest cleared and stained paratype). Scales absent.

*Morphometrics:* Head length 21% SL (21.0–23.3); eye diameter 5.0% SL (5.0–7.0); snout length 4.0% SL (4.0–5.6); upper jaw length 6.0% SL (6.0–8.1); postorbital length 10.5% SL (10.5–13.1); origin of first dorsal fin 30.5% SL (28.5–32.8); origin of anal fin 63.0% SL (60.1–65.5); body depth at origin of first dorsal 16.0% SL (15.0–16.9); body depth at origin of anal fin 13.0% SL (12.5–15.6); caudal peduncle length 19.0% SL (18.3–20.0); caudal peduncle depth 9.5% SL (9.5–11.7); pectoral fin length 20.0% SL (18.5–22.0); pelvic fin length 16.0% SL (15.0–17.7).

*Colour in life* (Fig. 1): Body uniformly dark greyish-blue to black with small bright iridescent blue spots and speckles; head grey, slightly lighter than body, with two short, dark, broken vertical bars extending ventrally from eye; side of head and operculum with a very light dusting of iridescent blue iridophores; jaws and tip of snout light yellow; first and second dorsal fin dark grey to blank with a lighter distal margin, and with scattered iridescent blue spots; caudal, anal and pelvic fins dark grey to black, caudal and anal with iridescent blue spots; pectoral fins light grey to translucent.

*Colour in preservation* (Fig. 3): Body uniformly dark brown to dark grey, with faint indications of pale spots (blue in life) in females, spots considerably more distinct in preserved males; head slightly lighter than body, with two short, dark, broken vertical bars extending ventrally from eye; first and second dorsal fins, caudal fin, anal fin dark brown to black; caudal fin of females with a distinct pale distal margin.

*Sensory papillae and head pores and canals*: Sensory papillae are poorly developed and present only as individual widely dispersed papillae. Overall, the sensory papillae and head pore pattern generally follow the illustration of Sawada (1977: fig. 2) for *K. centralis*

(=*K. quindecimfasciata*). However, several of the 'pits' in the 'pit lines' illustrated by Sawada (1977) are present as distinct pores in *K. avaiki*. Specifically, most specimens possess pores B′, C, D, E, F′, all paired (Fig. 4). One specimen appears to also possess terminal pore G′. Pores are small and difficult to see in the soft fleshy tissue of the head and are best observed when the specimen is submerged in ethanol under indirect illumination from the side.

*Urogenital papillae* (Fig. 5): Male urogenital papilla, an elongate and conical tube, heavily pigmented with melanophores except around the opening; female urogenital papilla, a short stout tube with two four fleshy folds (two lateral, one anterior, one posterior), papilla with scattered melanophores.

### Osteology

The osteology of *K. oligolepis* was studied by Gosline (1955) in a broad comparison of other gobioids, with special emphasis on *Awaous*, *Eleotris*, *Eviota*, *Gobiodon*, *Kraemeria*, *Microdesmus* and *Ptereleotris*.



**Figure 3.** *Kelloggella avaiki* **sp. nov.**, preserved. A, USNM 440501, holotype, 20 mm SL, female. B, USNM 440504, male (one of the six specimens), 19.8 mm SL.
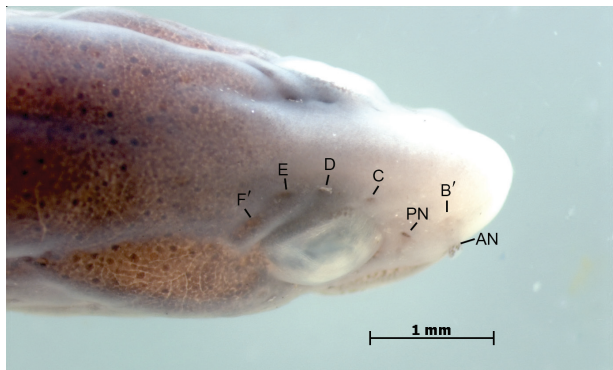


**Figure 4.** *Kelloggella avaiki* **sp. nov.**, arrangement of head pores. USNM 440504, male (one of the six specimens), 19.8 mm SL. AN, anterior nare; PN, posterior nare.

Only a few features were specifically noted or illustrated for *Kelloggella* in that study. Figures 8–17 show the main osteological features of *Kelloggella* based on cleared and stained specimens of *K. oligolepis* (UNSM 440505) and ***K. avaiki* sp. nov.** (USNM 440502). Two of the four specimens of *K. oligolepis* and one of the two specimens of *K. avaiki* did not uptake any alcian blue stain in their cartilage or failed to absorb alizarin red stain in their fins and other bones close to the exterior of the body, and thus most observations are from the three remaining specimens that stained well for both bone and cartilage stains. The following is a brief summary of the main features of the *Kelloggella*, for the purposes of comparison to other gobiid genera that are putatively close relatives to the genus.

*Cranium* (Fig. 6): The roof of the cranium of *Kelloggella* is composed primarily of the frontals anteriorly and relatively large supraoccipital posteriorly. There is no dorsal crest on the frontals or supraoccipital. The epioccipitals meet along the dorsal midline, posterior to the supraoccipital. The posterior end of the narrow sphenotic joins the anterolateral corner of the supraoccipital, runs anteriorly along the lateral edge of the frontal and terminates as the posterolateral edge of the orbit.

*Dentition* (Figs 7, 8): Dentition is generally similar in *K. oligolepis* and *K. avaiki*. There are broadly four different tooth morphologies that are arranged similarly
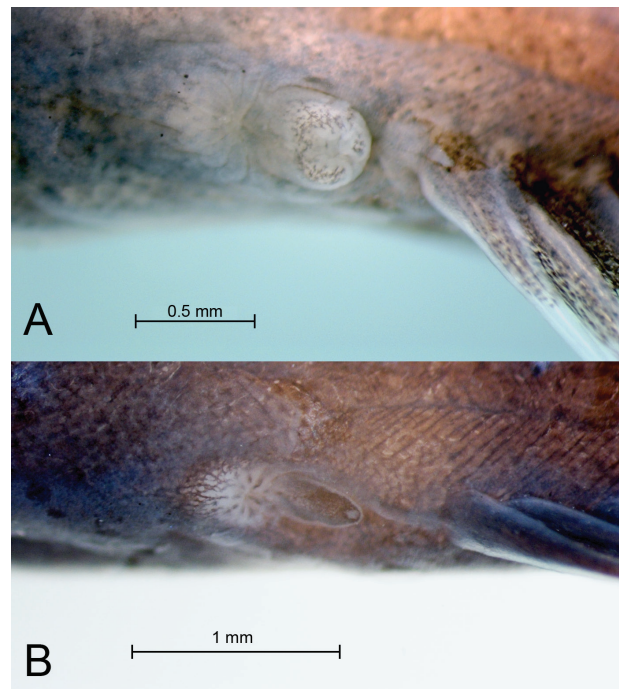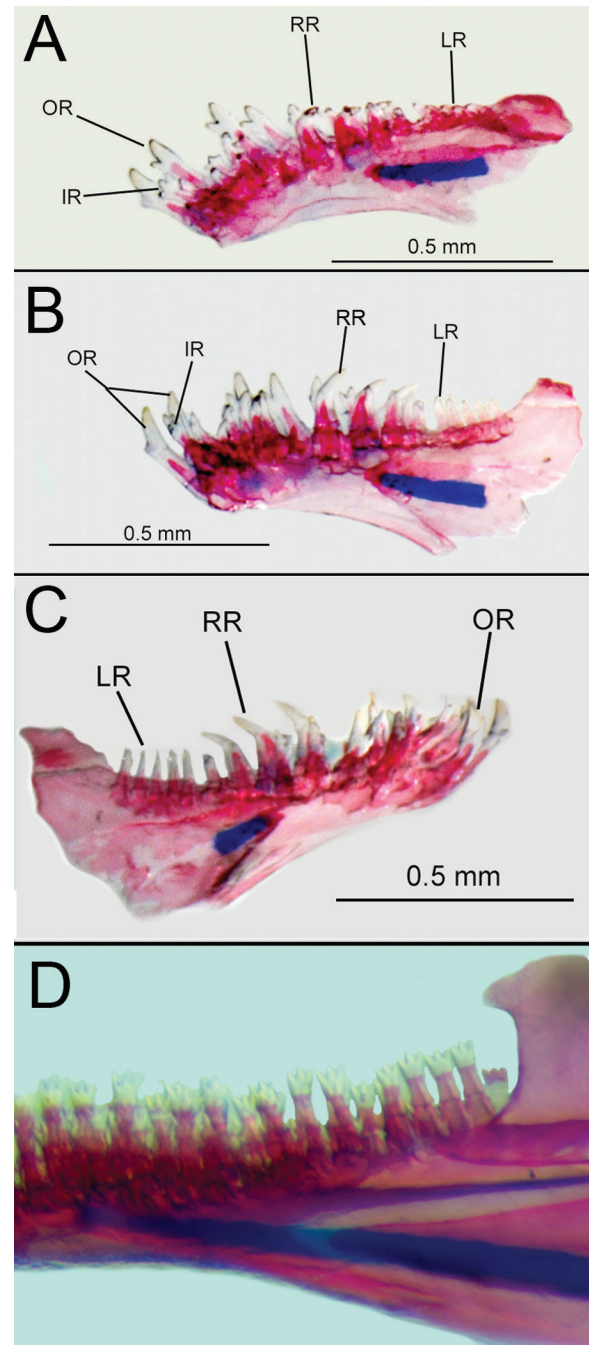


**Figure 5.** *Kelloggella avaiki* **sp. nov.**, urogenital papillae. A, female. B, male.
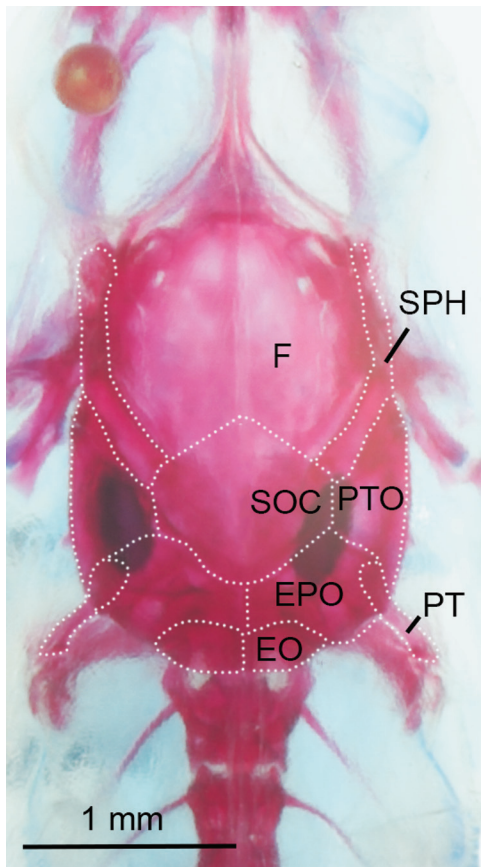
**Figure 6.** *Kelloggella avaiki* **sp. nov.**, cranial bones, USNM 440502. EO, exoccipital; EPO, epiotic; F, frontal; PT, posttemporal; PTO, pterotic; SOC, supraoccipital; SPH, sphenotic.



**Figure 7.** A–C, dentary of *Kelloggella oligolepis*, USNM 440505. A, dorsomedial view. B, medial view. C, lateral view. D, dentary of *Eviota* sp. UW 157173, lateral view. IR, inner row; LR, lateral row; OR, outer row; RR, recurved row.

in both jaws. Anteriorly, there is an outer row of enlarged, anteriorly angled tricuspid teeth ('outer row' or OR in Figs 7, 8). The middle cusp is the largest, and the lateral cusps are often worn completely, giving the appearance of only two asymmetrical cusps. Behind this row is series of about two to four rows of smaller, more evenly spaced tricuspid teeth ('inner row' or IR in Figs 7, 8), with the cusps being of equal length. Along the middle of the jaws is a row of two to five enlarged, distinctly recurved teeth ('recurved row' or RR in Figs 7, 8), with these teeth being smaller and less curved in females. Lastly, along the posterior end of both jaws, there is a row of four to seven short, thin conical or slightly recurved teeth, evenly spaced and of equal height ('lateral row' or LR in Figs 7, 8).

*Suspensorium* (Fig. 9): The arrangement of the suspensorium in *Kelloggella* does not differ substantially from the typical arrangement of gobies from the family Gobiidae (*sensu* Thacker, 2009). In general, the arrangement is similar to that of *Microgobius*, a
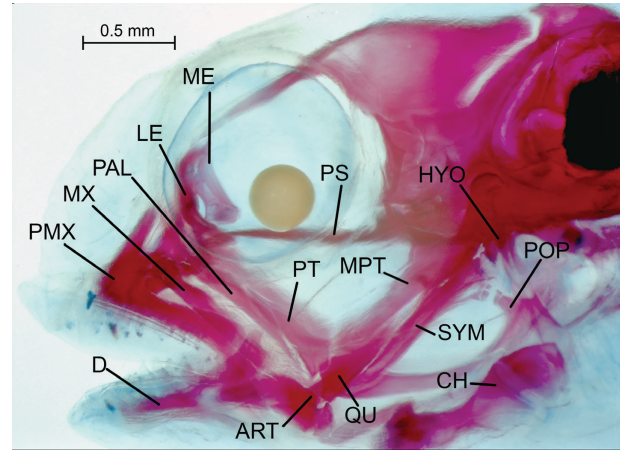
rather generalized gobiid genus whose suspensorium has been figured several times in literature (e.g. fig 2A of Thacker, 2013; figs 1, 7 of Birdsong, 1975). There is no endopterygoid (mesopterygoid). The metapterygoid connects broadly with the anteroventral surface of the hyomandibular, extends anteroventrally where it lies
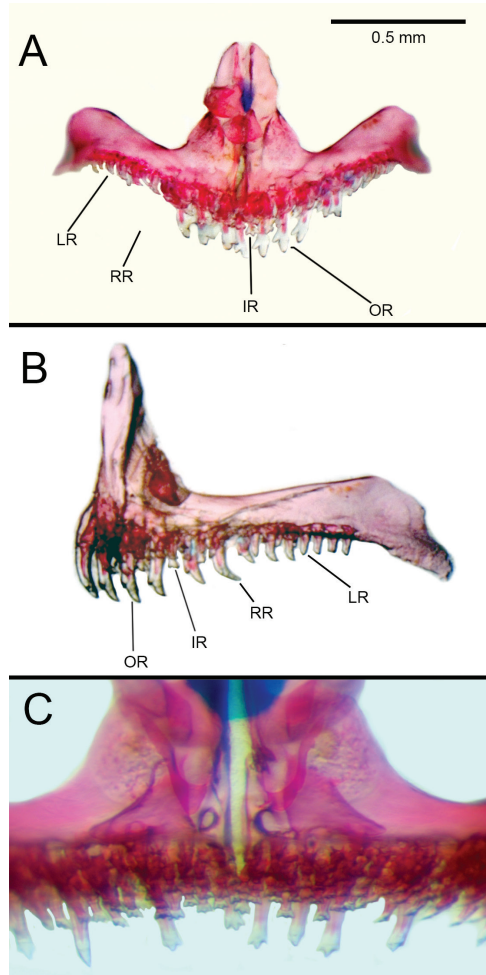
**Figure 8.** A, B, premaxilla of *Kelloggella oligolepis*, USNM 440505. A, posterior view. B, medial view. C, premaxilla of *Eviota* sp. UW 157173, posterior view. IR, inner row; LR, lateral row; OR, outer row; RR, recurved row.



**Figure 9.** Suspensorium of *Kelloggella avaiki* sp. nov., USNM 440502. ART, articular; CH, ceratohyal; D, dentary; HYO, hyomandibular; LE, lateral ethmoid; ME, median ethmoid; MPT, metapterygoid; MX, maxilla; PAL, palatine; PMX, premaxilla; POP, preopercle; PT, ectopterygoid; QU, quadrate; SYM, symplectic.

in opposition with the anterodorsal surface of the symplectic and ultimately articulates with the quadrate in a shallow cup-like groove. In *K. avaiki*, the metapterygoid is slightly elongate and more narrow and slender than that in *K. oligolepis*, in which the metapterygoid is wider with the anterior portion being expanded dorsally. Birdsong (1975) and Larson (2001) report sexual dimorphism in the extent of anterior development of the metapterygoid in *Microgobius signatus* and in some species of *Mugilogobius*, but this does not seem to explain the interspecific variation seen here, as male and female specimens of both species possess similarly shaped metapterygoids, and similarly sized jaws overall. The anterodorsal surface of the quadrate broadly connects to the ectopterygoid, which opposes the palatine along 3/4 of its posterior surface. The posterodorsal and posteroventral surfaces of the symplectic connect

via cartilage to the hyomandibular and preopercle, respectively (the cartilage is poorly stained in Fig. 9).

*Pectoral and pelvic girdle* (Figs 10–12): Unlike the vast majority of gobiids where the posttemporal is forked anteriorly into two long, well-developed ossified anterior arms, the posttemporal in *Kelloggella* possesses a well-developed upper arm but the lower arm is reduced to a very short ossified anterior process (Figs 10, 11D, 12A). The upper arm connects directly to the cranium, whereas the stubby projection representing the lower arm connects via a long ligament. Hoese (1975) reports the ventral arm of the posttemporal as being absent in *Kelloggella*, and Gosline (1955) also described the lower arm as being present only as a ligament; neither study made mention of the short bony strut representing the lower arm. The posterior surface of the posttemporal joints the lateral surface of the anterior half of the supracleithrum, which in turn is bound ligamentously to the dorsolateral surface of the cleithrum. The cleithrum, which does not differ from the typical gobiid form, has a deeply forked dorsal head and a broad anterior flange for attachment of the adductor muscle of the pectoral fin. The pectoral fin possesses four radials, the dorsalmost of which is the smallest and is triangular in shape; the ventral three are larger and rectangular to dumbbell shaped. All radials are weakly ossified in most specimens. Ventrally, the cleithrum forms two processes; the anterior process is stout and connects ventrally to the corresponding process on the cleithrum of the opposing side, and the posterior process connects to the pelvic bone. The pelvic
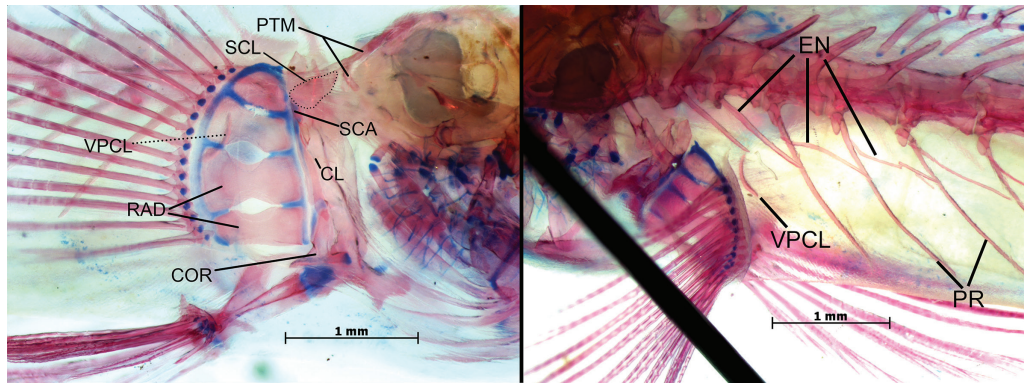
**Figure 10.** Pectoral girdle of ***Kelloggella avaiki* sp. nov.**, USNM 440502. CL, cleithrum; COR, coracoid; EN, epineural; PR, pleural rib; PTM, posttemporal; RAD, radial; SCA, scapula; SCL, supracleithrum; VPCL, ventral postcleithrum. Dotted lines are added to highlight the position of the SCL. Note that the VPCL is visible behind the pectoral fin radials in the left frame.
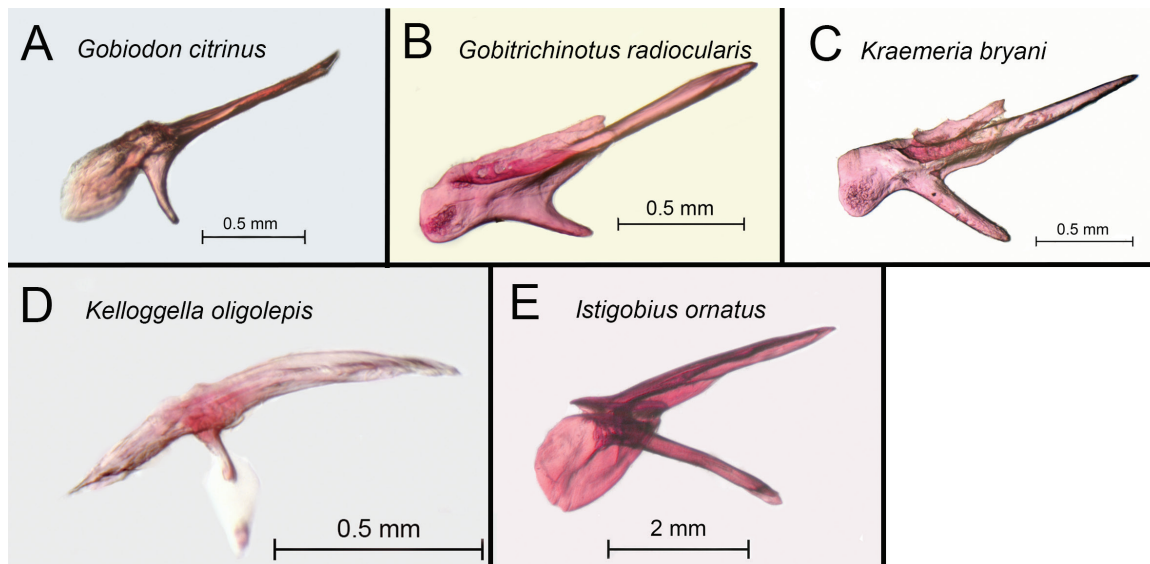


**Figure 11.** Posttemporals, dissected. A, *Gobiodon citrinus*, USNM 306266. B, *Gobitrichinotus radiocularis*, USNM 435309. C, *Kraemeria bryani*, USNM 143153. D, *Kelloggella oligolepis*, USNM 440505. E, typical gobiid morphotype, *Istigobius ornatus*, USNM 287161.

intercleithral cartilage separating the cleithra from the pelvic bone is well developed, whereas the ventral intercleithral cartilage between ventral tips of the opposing cleithra is absent or reduced such that it is unstained in our specimens. Note that Gosline (1955), who at the time was not working with trypsin cleared and double stained specimens, reports that he could not find a coracoid or an ossified scapula in *Kelloggella*. We note that the scapula is cartilaginous in *Kelloggella*; however, a well-developed coracoid is present in both species examined here (Fig. 10). Gosline (1955) also made no note of a dorsal or ventral postcleithrum. Dorsal postcleithra are known only from 'basal' gobioids (e.g. Eleotridae, Butidae, Odontobutidae). Akihito

(1969) observed ventral postcleithra in 74 of 106 gobioid species examined, including many gobiids. Both species of *Kelloggella* examined here have a ventral postcleithrum present as a thin bone suspended in connective tissue ventral to the second vertebrae (Fig. 10). As in other gobioids, it is well separated from the pectoral girdle, and superficially resembles an autogenous detached pleural rib, which are lacking on vertebrae 1 and 2 in *Kelloggella*.

*Gill and hyoid arches* (Fig. 13): The dorsal gill arches (Fig. 13A) possess four epibranchials. The dorsal head of epibranchial one is deeply forked, with the posterior fork connecting to the anterior surface of
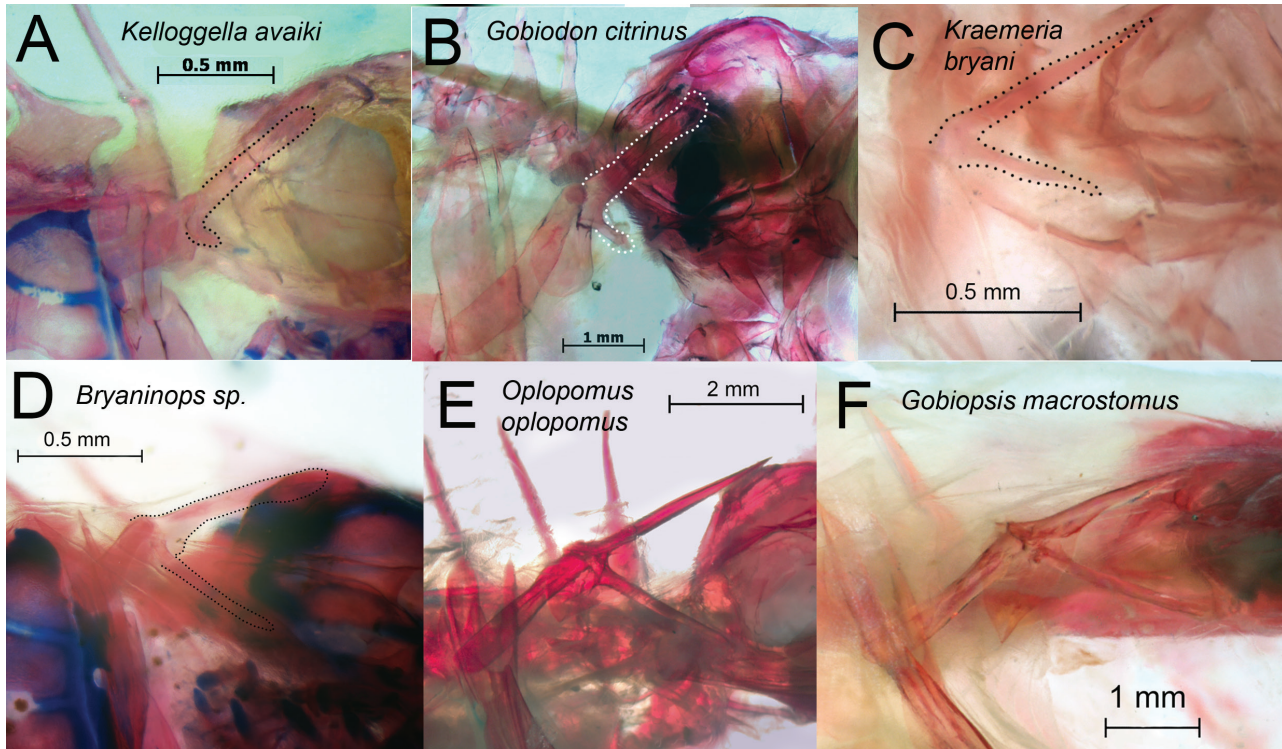
**Figure 12.** Posttemporals, *in situ*. A, ***Kelloggella avaiki* sp. nov.**, USNM 440502. B, *Gobiodon citrinus*, USNM 306266. C, *Kraemeria bryani*, USNM 143153. D, *Bryaninops* sp., USNM 435307. E, *Oplopomus oplopomus*, USNM 287159. F, *Gobiopsis macrostomus*, USNM 216191. Morphotypes D–F are the typical gobiid form.
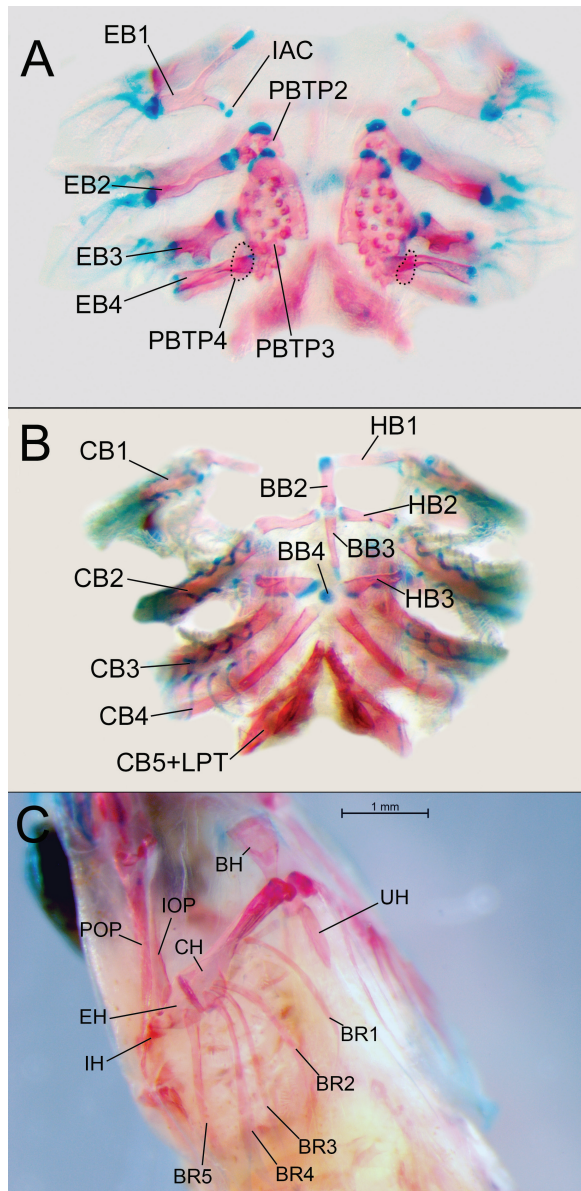
pharyngobranchial toothplate 2 via the interarcual cartilage. Epibranchial 2 connects dorsally to the lateral surface of pharyngobranchial toothplate 2, which itself is bound cartilaginously to the large pharyngobranchial toothplate 3. Epibranchials 3 and 4 articulate directly with pharyngobranchial toothplate 3, with pharyngobranchial toothplate 4 being small and located ventral to epibranchial four. Ventral gill arches (Fig. 13B) possess five ceratobranchials. The first three connect to hypobranchials 1–3, respectively, whereas ceratobranchial 4 connects directly to a cartilaginous basibranchial 4. Ceratobranchial 5 bears the lower pharyngeal toothplate, which is connected to the opposing ceratobranchial only at its anterior tip. The basihyal is broadly spatulate or fan-shaped (Fig. 13C). There are five branchiostegals, the first of which originates on the anterior arm of the ceratohyal, the next three clustered on the posterior half of the ceratohyal, and the fifth on the epihyal.

*Vertebral column and median fins* (Figs 10, 14): Vertebral column with 11 precaudal vertebrae and 15 caudal vertebrae. Vertebrae 1 through 11 possess thin but distinctly ossified epineurals. The first dorsal-fin pterygiophore insertion pattern is 3-22110, which is the most common pattern among gobiids.

The second dorsal-fin pterygiophores are inserted into interneural spaces in approximately a 1:1 manner, except that the pterygiophores of the $11^{th}$ and $12^{th}$ rays of the second dorsal fin are inserted in a single interneural space. There is one anal-fin pterygiophore inserted anterior to the first caudal vertebrae, and the subsequent interhaemal spaces each possess one, two, one, one and two anal-fin pterygiophores, respectively.
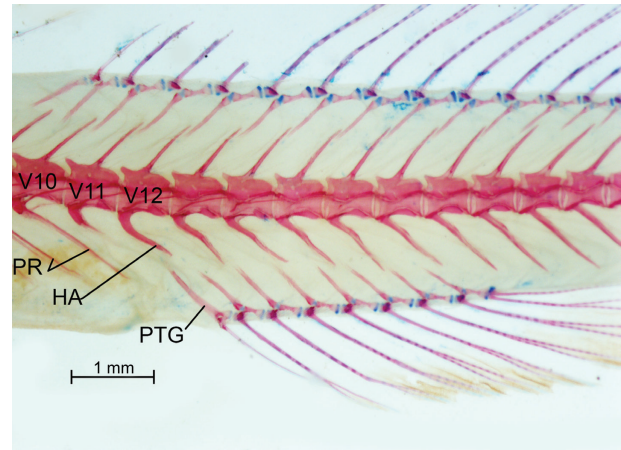
*Caudal skeleton* (Fig. 15): In the caudal skeleton, there is both a single epural and parahypural. Hypurals 1–2 and 3–4 are fused to the terminal caudal element and are partially fused to one another along approximately 1/3 to 1/2 of their length. Aside from this feature, the remaining aspects of the caudal skeleton of *Kelloggella* are typical of most gobiids. The small $5^{th}$ hypural is in close contact with hypural 3–4 along approximately 1/2 of its dorsal surface. Both the dorsal and ventral procurrent cartilages each support six unsegmented caudal rays. The remaining caudal rays are supported by the neural spine (one unsegmented ray), the parahypural (two segmented rays, one branched), hypural 1–2 (five segmented rays, all branched), hypural 3–4 (six segmented rays, all branched rays), hypural 5 (two

**Figure 14.** Vertebral column of ***Kelloggella avaiki* sp. nov.**, USNM 440502. HA, haemal arch; PR, pleural rib; PTG, pterygiophore; V, vertebra.

*Etymology*

The specific epithet *avaiki* is a noun in apposition. In Polynesian, the word 'Avaiki' commonly refers to the scared homeland of ancestors. Specifically, in Nuie, 'Avaiki' refers to an area of tidepools and coastal caverns near the type locality of this species that are revered as the sacred bathing pools of kings. The common name refers to the bright spots on the dark background of the body, which resemble stars in the night sky.
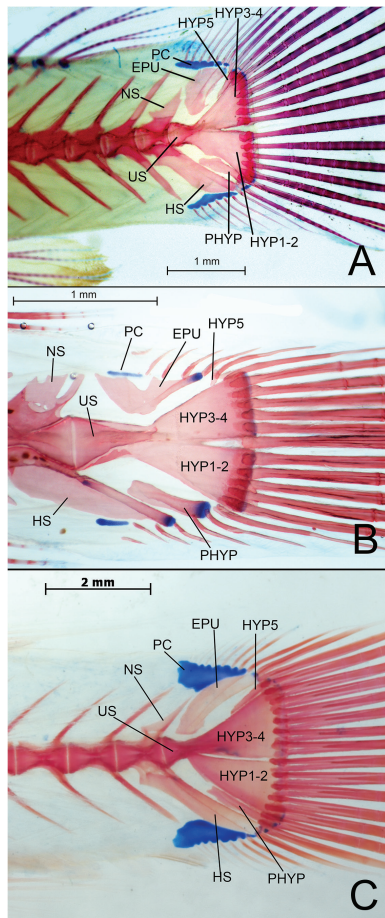
*Habitat and distribution*

The new species is currently known only from Niue in the South Central Pacific. It was collected from the lower intertidal zone on a narrow reef flat exposed to strong wave energy and was found living in small water-filled crevices in the reef pavement. It was fairly abundant on the reef flat where it was collected, with an estimated five to 10 individuals per m$^2$ in the lower intertidal zone.

*Molecular phylogenetics*

Analysis of the most complete data set, which includes the entire Agorreta *et al*. (2013) data set plus *K. oligolepis*, *K. disalvoi* and a second species of *Kraemeria* (*Kr. bryani*), shows *Kelloggella* sister to *Kraemeria* with moderate support (0.76 posterior probability, Figs 16, 17). This clade is part of larger, less resolved clade (0.51 posterior probability) that included *Schindleria* and the three genera of the 'coral gobies' *sensu* Thacker & Roje (2011), also referred to as the '*Gobiodon*-lineage' in Agorreta *et al*. (2013): *Gobiodon*, *Bryaninops* and *Eviota*. The relationships between the 'coral gobies', *Schindleria* and *Kraemeria* + *Kelloggella* are unresolved and depicted as a trichotomy (<0.50 posterior probability).



**Figure 13.** Gill arch and hyoid arch bones of *Kelloggella*. A, dorsal gill arches, dorsal view, *K. oligolepis*, USNM 440505. B, ventral gill arches, ventral view, *K. oligolepis*, USNM 440505. C, ventral view of branchial bones and hyoid arch *in situ*, *K. oligolepis*, USNM 440505. BB, basibranchial; BH, basihyal; BR, branchiostegals rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; IAC, interarcual cartilage; IH, interhyal; IOP, interopercle; LPT, lower pharyngeal tooth plate; PBTP, pharyngobranchial tooth plate; POP, preopercle; UH, urohyal.

segmented rays, one branched) and the epural (one segmented ray).

**Figure 15.** Caudal skeletons. A, ***Kelloggella avaiki* sp. nov.**, USNM 440502. B, *Kraemeria samoensis*, USNM 439365. C, typical gobiid form, *Oplopomus oplopomus*, USNM 287159. EPU, epural; HS, haemal spine; HYP, hypural; PC, procurrent cartilage; PHYP, parahypural; NS, neural spine; US, urostyle.

Removing *Schindleria* from the analysis (Fig. 17B) increased the support value for the clade containing *Kelloggella*, *Kraemeria* and the 'coral gobies' from 0.51 to 0.76, with the support value for the sister relationship between *Kraemeria* and *Kelloggella* being nearly identical to the results from the full data set analysis. Removing *Kraemeria* from the full data set increased the support for the clade containing the 'coral gobies' and *Kelloggella* from 0.51 to 0.96 and resulted in *Schindleria* being resolved in a well-supported (0.96 posterior probability) clade referred to as the '*Gunnellichthys*-lineage' (Agorreta *et al.*, 2013) or the worm gobies and dartfishes (includes the former families/subfamilies Ptereleotridae and Microdesmidae) (Fig. 17C). Removing both *Schindleria* and *Kraemeria* resulted in the same topology for the 'coral gobies' and *Kelloggella* as the analysis that removed only *Kraemeria* (Fig. 17D).

## DISCUSSION

### PHYLOGENETIC POSITION OF *KELLOGGELLA* WITHIN GOBIIDAE

Our molecular phylogenetic hypotheses (Figs 16, 17) show support for a close relationship between *Kelloggella* and several members of the 'coral gobies' group as delineated by Thacker & Roje (2011), also known as the '*Gobiodon*-lineage' *sensu* Agorreta *et al.* (2013). When *Kraemeria* was included in our analyses, it was consistently resolved as being sister to *Kelloggella*, but with low support (0.76–0.77 posterior probability). *Kelloggella* has not been included in any molecular phylogenetic analysis of gobies to date, so a close relationship to *Kraemeria* cannot be evaluated against past studies; however, a close relationship between *Kraemeria* and the 'coral gobies' has not been suggested by any other analysis to date. Thacker & Roje's (2011) analysis based on three nuclear genes and three mitochondrial genes showed a moderately well-supported topology (bootstrap value of 81) depicting *Kraemeria* sister to a large group of Indo-Pacific gobies referred to as the 'lagoon gobies' and the 'silt shrimp gobies', which did not include the 'coral gobies' *Bryaninops*, *Gobiodon* or *Eviota*. An earlier study using only mitochondrial loci instead showed *Kraemeria* in a well-supported (96 bootstrap value) clade with *Coryphopterus*, *Lophogobius* and *Fusigobius* (Thacker, 2009). In an earlier study with more limited sampling of mitochondrial genes and taxa (Thacker, 2003), *Kraemeria* was recovered in the clade now recognized as the Oxudercidae. Finally, Agorreta *et al.* (2013) failed to recover the position of *Kraemeria* and classified them as a 'rogue taxon' – removing them from the analysis increased support values across the tree. Interestingly, the level of support for the large clade containing *Kraemeria*, *Kelloggella* and the 'coral gobies' changed depending on whether *Schindleria* was in the analysis. When both *Schindleria* and *Kraemeria* were included, there was little support (0.51 posterior probability) for this large clade; however, removing *Schindleria* increased this support to 0.76. It should be noted that no study to date has suggested a relationship between the genera making up the 'coral gobies' and *Schindleria*. Instead, morphological and molecular data (Johnson & Brothers, 1993; Thacker, 2000; Hoese & Motomura, 2009; Gill & Mooi, 2010; Agorreta *et al.*, 2013) have historically shown *Schindleria* to be more closely related to the worm gobies (subfamily Microdesminae), and together these groups collectively may be specialized members of the dartfishes (former family Ptereleotridae). When *Kraemeria* is removed from the analysis, not only does the support for the relationship between the 'coral gobies' and *Kelloggella* improve substantially (from 0.76 to 0.94–0.96), but *Schindleria* is once again resolved with the worm gobies and dartfishes (Fig. 17D). The
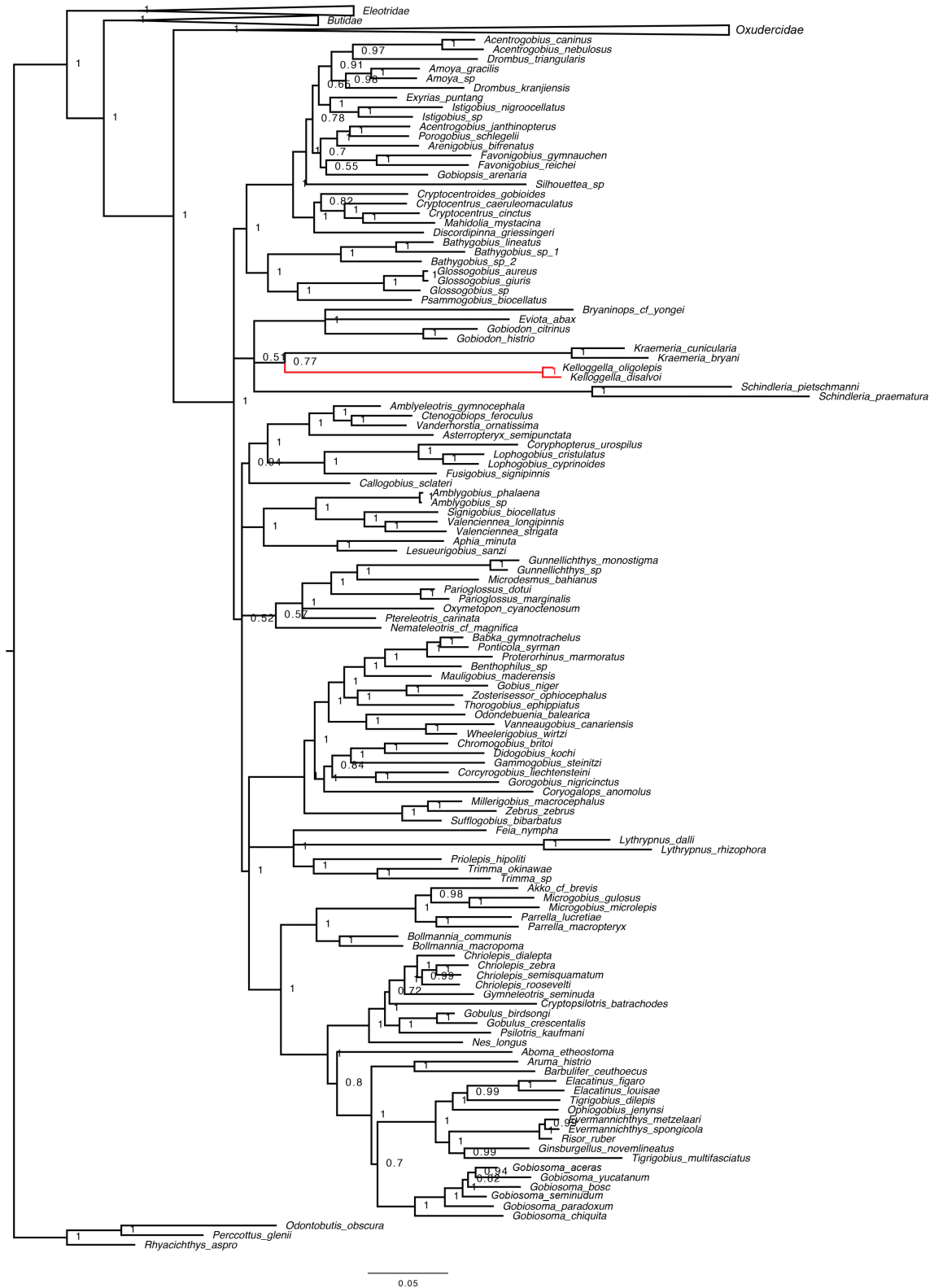
**Figure 16.** Molecular phylogenetic hypothesis of Gobioidei based on five gene segments from the full data set, including 222 species from Agorreta *et al.* (2013), plus two species of *Kelloggella* and *Kraemeria bryani*. Support values are Bayesian posterior probabilities. Relationships with support less than 0.50 are shown as polytomies.
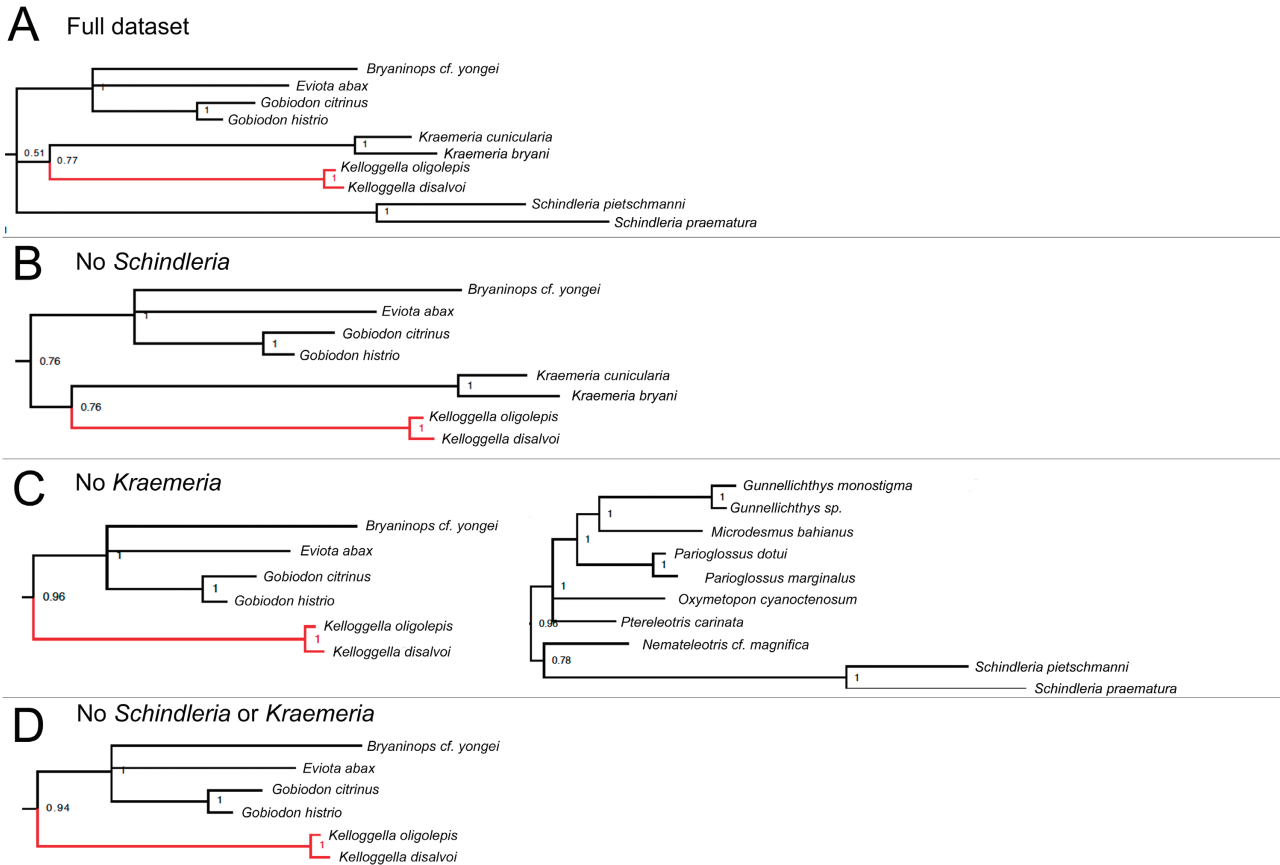
**Figure 17.** Comparison of phylogenetic hypothesis for *Kelloggella* based on the different data sets used in this study. Support values are Bayesian posterior probabilities. Relationships with support less than 0.50 are shown as polytomies. Full trees for B, C and D are available as Supporting Information (Figs S1–S3).

three branches leading to *Kraemeria*, *Kelloggella* and *Schindleria* are among the longest on the phylogeny, indicating high rates of molecular evolution in these groups, coupled with a lack of extant (or sampled) closely related taxa along these long branches. Thus, it is quite possible that the grouping together of these long branches is an artefact of long-branch attraction.

We re-examined several osteological features of *Kelloggella* in attempt to find characters indicating a potential gobiid sister group, with emphasis on putative relatives from the molecular analysis. To this end, we were largely unsuccessful. Most of the osteological features observed in *Kelloggella* were broadly plesiomorphic across Gobiidae. A head with thick, bulbous and gelatinous covering appears to be unique to *Kelloggella*. Also unique to *Kelloggella* is the combination of an 11 + 15 vertebral count coupled with one anal pterygiophore inserted anterior to the first haemal arch. Several groups of gobioids possess a single anal pterygiophore inserted anterior to the haemal arch, including the Thalasseleotridae, most genera included in the former subfamilies Ptereleotrinae

(Gobiidae) and Oxudercinae (Oxudercidae), and in some species of the *Nes* subgroup of the Gobiosomatini (Gobiidae) (Hoese, 1984; Birdsong *et al.*, 1988; Hoese & Gill, 1993; Tornabene *et al.*, 2016b). However, none of these groups possesses an 11 + 15 vertebral count, which is rare among gobies. In a survey of vertebral column osteology by Birdsong *et al.* (1988), only the oxudercid genera *Stigmatogobius*, *Tridentiger* and *Redigobius* were found to regularly possess an 11 + 15 count. There are several characters that are shared between *Kelloggella* and other genera that, if truly homologous, could provide additional support for the relationships suggested by our molecular phylogeny: (1) a reduced ventral arm of the posttemporal; (2) partial fusion of hypurals 1–2 to hypurals 2–3 and the urostyle; (3) the joining of the epioccipitals along the dorsal midline of the skull, posterior to supraoccipital and (4) tricuspid teeth in both jaws. However, these characters are present in several other distantly related gobiids (discussed below), and their phylogenetic signal is questionable at best.

Gosline (1955) noted that the posttemporal was reduced in *Kraemeria samoensis*, with the lower arm being present only as a bony strut. We examined the posttemporal of three kraemeriines: *Kr. samoensis*, *Kr. bryani* and *Gobitrichinotus radiocularis* (Figs 11, 12). Our specimen of *Kr. bryani* is in poor condition; the position of the skull is badly distorted, relative to the pectoral girdle and vertebral column, and elements of each were beginning to disarticulate, ultimately obscuring the anterior points of articulation of the posttemporal. Nevertheless, the specimen did appear to possess a posttemporal with a well-developed ventral anterior arm (Fig. 11C), which was somewhat shorter than the typical gobiid form (Figs 11E, 12D–F), but not as reduced as in *Kelloggella*. However, both *Kr. samoensis* and *Gobitrichinotus radiocularis* possess a significantly reduced ventral arm (Fig. 11B), and *Kr. sexradiata* apparently lacks a ventral arm entirely (Matsubara & Iwai, 1959). Thus, if symmetrical arms on the posttemporal are the plesiomorphic condition for gobioids, and a reduced ventral arm of the posttemporal was a synapomorphy character uniting *Kelloggella* and *Kraemeria*, it would require a subsequent reversal, that is, the re-elongation of this arm in *Kr. bryani*, or some degree of phenotypic plasticity. Among other gobioids, the lower arm of the posttemporal is also reduced in *Xenisthmus* and absent in *Tyson* (Springer, 1983), both species belonging to the eleotrid subfamily Xenisthminae and not Gobiidae (Thacker, 2009). *Schindleria*, a gobiid, also lacks a ventral arm of the posttemporal, but this trait, along with many other features that are lost or reduced in *Schindleria*, is probably due to the extreme developmental truncation observed in this group (Johnson & Brothers, 1993). Other species from the literature that possess ventral arms of the posttemporal that are reduced in length include *Silhouettea evanida* (Larson & Miller, 1986), *Lebetus orca* (only partially reduced and not reduced in *Lebetus guilleti*; Miller, 1963; Herler & Kovačić, 2002), *Egglestonichthys patriciae* (only partially reduced; Miller & Wongrat, 1979) and *Callogobius* cf. *hasseltii* (only partially reduced and not reduced in some other species *Callogobius*; Miller & Wongrat, 1979; Naomi Delventhal, Royal Ontario Museum, personal communication). None of these genera appear closely related to *Kelloggella*; *Lebetus* belongs to the Oxudercidae (Agorreta *et al*., 2013; Thacker, 2013), *Silhouettea* is nested deep within a distantly related clade of gobiids (Fig. 16) and *Egglestonichthys*, while never formally included in a phylogenetic analysis, is likely to be closely related to *Priolepis* (Winterbottom & Burridge, 1992). The only other genus of Gobiidae recovered near *Kelloggella* in our tree where we observed highly asymmetrical arms of the posttemporal was *Gobiodon* (*G. citrinus*;

Figs 11A, 12B). Both *Gobiodon* and *Kelloggella* have heads and bodies that are strongly laterally compressed, and because of this the angle at which the upper and lower arms of the posttemporal attach to the skull arranged in a way such that the point of attachment of the upper arm of the posttemporal is more dorsal than in other gobiids. This could result in a very long upper arm, with a comparatively shorter lower arm, especially in *Gobiodon*, which has a very deep head and body. Therefore, even in these two putatively closely related taxa, it is possible that the shared asymmetry in the lengths of the arms of the posttemporal in these two genera are due this convergence in overall head and body shape associated with being laterally compressed (possibly due to living in narrow spaces, between branches of coral for *Gobiodon*, cracks in tide pools for *Kelloggella*), rather than being due to shared common ancestry. By contrast, some other gobiids that are more dorsoventrally compressed often have very elongate, symmetrical arms of the posttemporal, such as *Afurcagobius* (Gill, 1993), *Platygobiopsis* (Okiyama, 2008) and *Gobiopsis macrostomus* (Fig. 12F). Other members of the 'coral goby' group examined (*Eviota*, *Bryaninops*, *Pleurosicya*, *Paragobiodon*) have the typical gobiid posttemporal morphology. Overall, the phylogenetic significance of a reduced ventral arm of the posttemporal is questionable at best, and it alone does not offer convincing support for a close relationship between the kraemeriines and *Kelloggella*, or the affinity of either of these genera to *Gobiodon* or other 'coral goby' genera.

The second character shared between *Kelloggella* and *Kraemeria* is the fusion of hypurals 1–2 with hypurals 3–4 and the urostyle (Fig 15A, B). In *Kelloggella*, the upper and lower portions of the hypural plate are fused along 1/3 to 1/2 of their bases, and in *Kraemeria*, they are fused along at least 1/2 of their bases. However, fusion of hypurals is not unique to *Kelloggella* and *Kraemeria*, but is also found in other gobiids including the *Gobiosoma* group of the Gobiosomatini (Birdsong, 1975; Birdsong *et al*., 1988), *Schindleria* (Johnson & Brothers, 1993), some species of *Trimmatom* (Winterbottom & Emery, 1981), *Coryogalops*, *Anatirostrum* (Ahnelt *et al*., 2000) and *Chromogobius* (Van Tassell, 2001). Fused hypurals are variably present in *Eviota*, and in other 'coral goby' genera examined (*Gobiodon*, *Paragobiodon*, *Bryaninops*, *Pleurosicya*), the upper and lower hypural plates are not fused.

Gosline (1955) also noted that *Kelloggella*, *Kraemeria* and *Microdesmus* were unique among the taxa he examined in that they possess epioccipitals that are connected along the dorsal midline of the skull posterior to the supraoccipital, rather than being separated along the dorsal midline by a posterior extension of

the supraoccipital (Fig. 6). We concur that the latter arrangement is the most common on gobiids and that connection of epioccipitals along the midline is not typical, but several other gobiid and oxudercid species possess epioccipitals that join along the midline, including *Akko* (Birdsong & Robins, 1995), *Silhouettea* (Larson & Miller, 1986), *Cerdale* (Thacker, 2000) and *Sicydium* (Thacker, 2000), and in small individuals of some *Eviota* species. In most groups where the epioccipitals are not connected along the midline, it is typically only a thin elevated posterodorsal crest of the supraoccipital that separates the epioccipitals, rather than the main anterior portion of the supraoccipital that forms part of the roof of the cranium. Thus, merely a simple reduction in the supraoccipital crest (a character that is highly variable in gobies) can result in the epioccipitals being joined medially. Epioccipitals are separated in all of the 'coral goby' genera examined here.

One final character of interest is the presence of tricuspid teeth in *Kelloggella*. Dentition has not been extensively surveyed across the tremendous diversity of gobies, but to our knowledge, tricuspid teeth have so far only been reported in two groups that belong to the Oxudercidae, *Tridentiger* and the subfamily Sicydiinae. For the first time, we also report tricuspid teeth in an undescribed species of *Eviota* from Pohnpei (Figs 6D, 7C). Both jaws in this species contain multiple rows of tricuspid teeth, the outer row being the longest and with the lateral cusps being slightly worn, similar to that observed in *Kelloggella*. Dentition has not been widely surveyed in *Eviota* – a genus that contains well over 100 species. In the few instances where dention was mentioned, teeth in *Eviota* have been described as being conical (e.g. Matsuura & Senou, 2006), recurved canines (e.g. Suzuki & Greenfield, 2014) or villiform (e.g. Lachner & Karnella, 1978). However, all species are incredibly small and cusps may be impossible to see in specimens that are not cleared and stained. If the phylogeny shown here (Figs 16, 17) are accurate, and tricuspid teeth are homologous for *Kelloggella* and *Eviota*, this would require a loss of tricuspids in the other 'coral goby' genera. Teeth in *Bryaninops* and *Pleurosicya* are conical or canine, and *Gobiodon* teeth are highly variable, with species possessing distinct recurved canines, conical pointed teeth and or patches of villiform teeth (Harold & Winterbottom, 1999; Riedlecker & Herler, 2008; Herler, Bogorodsky & Suzuki, 2013).

Collectively, morphological support for a relationship between *Kelloggella*, *Kraemeria* and the 'coral gobies' is weak at best, hinging largely on characters that are not limited to these groups. We conclude that *Kelloggella* and *Kraemeria* are not likely each other's closest relatives based on (1) the lack of a single unambiguous morphological synapomorphy uniting the two genera, (2) the low support for this relationship in the molecular data, (3) the fact that removing *Kraemeria* increases support values for the relationship between *Kelloggella* and 'coral gobies' (Figs 16, 17) and across the entire tree (Agorreta *et al*., 2013) and (4) *Kraemeria* has variously been placed among different gobiid clades in previous molecular studies, sometimes with stronger support than the relationship shown here (Thacker, 2009; Thacker & Roje, 2011). Morphological support for monophyly of the 'coral gobies' *sensu* Thacker & Roje (2011), with or without the inclusion of *Kelloggella*, is currently lacking.

Using morphological characters alone to determine intergeneric relationships of gobies has long been recognized as a challenging endeavour, largely due to repeated trends towards miniaturization (leading to morphological reduction and loss), coupled with a rapid period of evolution and morphological specializations associated with adaption to specific microhabitats, the latter of which obscure the signal of potentially informative characters. The 'coral gobies' appear to be a prime example of this. If the genera *Gobiodon*, *Eviota*, *Bryaninops* and *Kelloggella* do indeed form a monophyletic assemblage (with or without the inclusion *Kraemeria* and other putative allied genera), as genetic data have shown repeatedly, then this group not only lacks a single known morphological synapomorphy but also displays a remarkable mosaic of variation in the characters that goby morphologists have long used to diagnose genera and groups of genera. For example, in the known genera of 'coral gobies', we see substantial variation in head pores, scales, pelvic fin morphology, dentition, caudal-fin osteology, body shape, suspensoria morphology, posttemporal shape, vertebral counts, pterygiophore insertion pattern and many other characters. Some of these are undoubtedly associated with adaptations for life on specific microhabitats (hard or soft corals, tidepools, sponges, sand and rubble substrates). Understanding the phylogenetic information in these characters requires careful investigation of the distribution of these characters not only within the group of interest (perhaps as many of 200 species in the case of 'coral gobies') but also across Gobiidae (at least 174 genera and more than 1700 species) to gain a better understanding of character polarity. Recent studies on groups of gobies that have fewer species but similar morphological diversity have demonstrated the feasibility of this approach, particularly when combined with multilocus molecular phylogenetic data, for example, Tornabene *et al*. (2016b). The latter study examined the distribution of morphological characters across a subset of Gobiosomatini and demonstrated that, while no morphological characters examined were entirely free from homoplasy across the entire group, many still possessed significant phylogenetic signal and were useful for diagnosing genera when used in combination.

COMPARISONS WITHIN *KELLOGGELLA*

*Kelloggella avaiki* can easily be distinguished from all other species by the presence of bright blue spots on the body and fins, with a dark grey, dark blue or black background. *Kelloggella cardinalis* is uniformly green to light greenish-grey, with red-orange fins (Fig. 18; also see photos in Allen, Steen & Orchard, 2007 and Allen & Erdmann, 2012). All other species of *Kelloggella* possess distinct vertical bars (or in females of some species, vertically paired spots or blotches) down the side of the body (Fig. 19).

Five species of *Kelloggella* have been described that possess distinct vertical bars in males, including *K. oligolepis* (type locality Hawaii), *K. quindecimfasciata* (type locality Ryukyu Islands, Japan), *K. centralis* (type locality Rarotonga, Cook Islands), *K. tricuspidata* (type locality Hiva Oa, Marquesas) and *K. disalvoi* (type locality Easter Island) (Fig. 19). Female coloration is either similar to the males or consists of paired spots or vertically oriented blotches instead of vertical bars. There has been confusion regarding which of these species are valid, with *K. centralis* being synonymized with *K. quindecimfasciata* (Sawada, 1977) and *K. quindecimfasciata* being considered as synonym of *K. oligolepis* (Hoese, 1975; the latter two are both currently considered valid; Eschmeyer, Fricke & van der Laan, 2017). Among these five nominal species with vertical bands, *K. tricuspidata* (Fig. 19I) is perhaps the most distinct and is distinguished from the others in having fewer dark vertical bars (7 vs. 9–11), which are distinctly narrower (white interspaces equal to or wider than dark bars vs. being notably narrower than dark bars), and in possessing six or seven inner rows of tricuspid teeth in each jaw (vs. two to four inner rows). The other four nominal species have been distinguished from each other by authors by a combination of characters including modal differences in the number of bars on the body of males (i.e. 9 vs. 10 vs. 11); the presence or absence of sexual dichromatism; differences in the thickness of vertical bars on body; dentition; modal differences in number of branched caudal rays (15 vs. 16); modal differences in the number of pectoral rays (12 vs. 13 vs. 14); modal differences in the number of anal rays (I, 7 vs. I, 8) and modal differences in second dorsal rays (I, 10 vs. I, 11 vs. I, 12). In examining both *K. oligolepis* and *K. disalvoi* from their respective type localities, there is considerable variation in the number and width of the bands on the body, both between individuals of a population, and also before and after preservation within a single individual (e.g. Fig. 19A–F). In addition, sexual dichromatism has been variously reported for *K. oligolepis*. Hoese (1975) noted that *K. oligolepis* lacked pronounced sexual dichromatism. At the time, he was basing this on his observations of individuals from both Hawaii and Easter Island (=*K. disalvoi*). Greenfield & Randall (2004) and Randall (2009) noted that *K. oligolepis* in Hawaii were sexually dichromatic
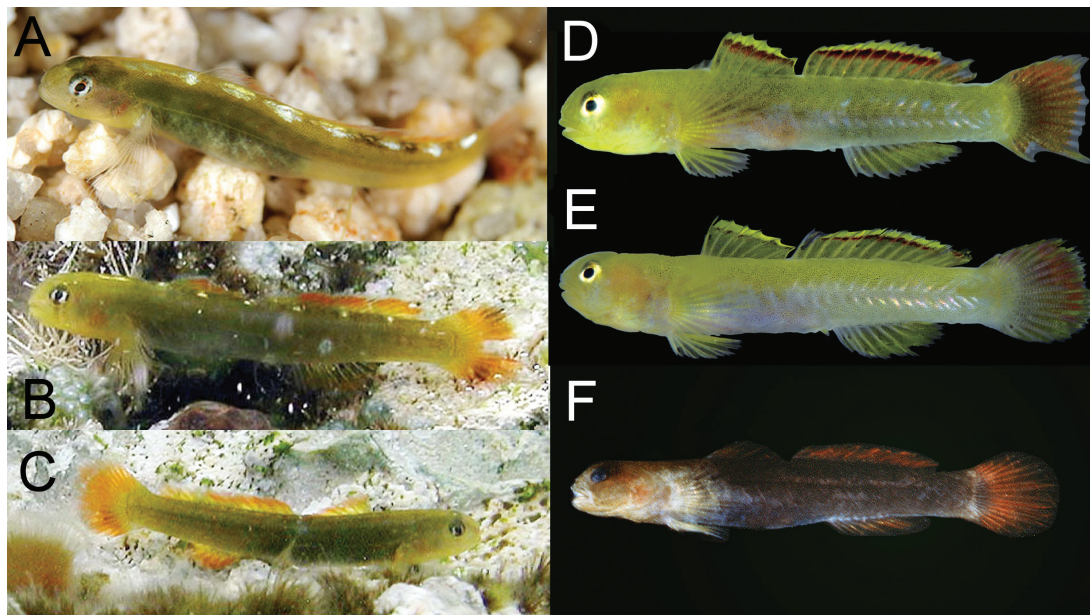


**Figure 18.** *Kelloggella cardinalis* from different localities. A, Ishigaki-Jima, Yaeyama Island, Japan, photo by Takeshi Uchida, © Kanagawa Prefectural Museum of Natural History, KPM-NR 73787. B, C, Saipan, Northern Mariana Islands, photo by Katsuya Kosaki, © Kanagawa Prefectural Museum of Natural History, KPM-NR 80338, 80350. D, E, Chabana, Yoronjima Island, Japan, photos provided by the Kagoshima University Museum. F, Papua New Guinea, photo by John E. Randall.

**Figure 19.** *Kelloggella* spp. with vertical stripes. A–F, *K. disalvoi*, UW 157114, alternating fresh vs. ethanol-fixed specimens, photos by Mauricio Landaeta. G, a collection of *K. disalvoi* (plus one non-Gobiidae), Easter Island, photo by Mauricio Landaeta. H, *K. disalvoi*, Easter Island, photo by John E. Randall. I, *K. quindecimfasciata*, Nuku Hiva, Marquesas, photo by John E. Randall. J, *K.* cf. *quindecimfasciata*, ROM 37091, Chagos Archipelago, photo by Richard Winterbottom. K, L, *K. oligolepis*, Hawaii, photos by Keoki Stendor.

(Fig. 19K, L), and Randall noted the *K. disalvoi* were not. On the contrary, recent collections of *K. disalvoi* indeed showed variation in colour pattern with sex, and to a lesser extent, with size (Fig. 19A–G). Given the overlap among some of the aforementioned characters (e.g. number of vertical bars), intraspecific variation in others (e.g. width of vertical bars and female colour patterns), the difficulty in accurately observing dentition from specimens that are not cleared and stained and the fact that some characters have been incorrectly reported in past studies (e.g. branched caudal-ray counts; see Winterbottom & Emery, 1986 for details), we are hesitant to take a strong stand regarding which species are valid. Therefore, we unfortunately refrain from including a key for the genus at this time. Additional geographic sampling is needed to sort out the validity

of this species group, ideally in concert with an integrative taxonomic approach that includes data from DNA sequences, morphology and live/fresh coloration of both sexes. This approach has recently proved useful, if not essential, in clarifying the taxonomy of other diminutive, morphologically similar groups of gobies from the ultra-diverse tropical Indo-Pacific region (e.g. Winterbottom *et al*., 2014; Greenfield & Tornabene, 2015; Tornabene *et al*., 2015, 2016a).

*Comparative cleared and stained material examined:* USNM 440505, *Kelloggella oligolepis*; USNM 253375, *Eviota* sp.; USNM 225183, *Eviota* sp.; USNM 221756, *Eviota* sp.; USNM 230083, *Eviota* sp.; USNM 71405, *Eviota abax*; USNM 216580, *Eviota distigma*; USNM 223063, *Eviota* sp.; USNM 287162, *Acentrogobius*

*madraspatensis*;USNM30626,*Lythrypnusdalli*;FMNH 121346, *Lythrypnus dalli*; USNM 216191, *Gobiopsis macrostomus*; USNM 147966, *Coryogalops ocheticus*; USNM 306266, *Gobiodon citrinus*; USNM 287159, *Oplopomus oplopomus*; USNM 244143, *Amblygobius decussatus*; USNM 236664, *Parioglossus raoi*; USNM 287163, *Bathygobius* cf. soporator; USNM 287161, *Istigobius ornatus*; uncataloged, *Nes longus*; USNM 435307, *Bryaninops* sp.; USNM 435308, *Cryptocentrus strigilliceps*; USNM 435309, *Gobitrichinotus radiocularis*; USNM 439365, *Kraemeria samoensis*; USNM 143153, *Kraemeria bryani*. UW 157173, *Eviota* sp. nov.*;* UW 157174 *Pleurosicya mossambica*; UW 19036, *Ptereleotris microlepis*; UW 11991, *Paragobiodon echinocephalus*; FMNH 107439, *Paratrimma nigramenta*.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Molecular phylogenetic hypothesis based on the full data with *Schindleria* removed. Support values are Bayesian posterior probabilities. Relationships with support less than 0.50 are shown as polytomies.
**Figure S2.** Molecular phylogenetic hypothesis based on the full data with *Kraemeria* removed. Support values are Bayesian posterior probabilities. Relationships with support less than 0.50 are shown as polytomies.
**Figure S3.** Molecular phylogenetic hypothesis based on the full data with both *Schindleria* and *Kraemeria* removed. Support values are Bayesian posterior probabilities. Relationships with support less than 0.50 are shown as polytomies.